

# Environmental drivers of ant species richness and composition across the Argentine Pampas grassland

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**Abstract** Understanding the underlying mechanisms causing diversity patterns is a fundamental objective in ecology and science-based conservation biology. Energy and environmental-heterogeneity hypotheses have been suggested to explain spatial changes in ant diversity. However, the relative roles of each one in determining alpha and beta diversity patterns remain elusive. We investigated the main factors driving spatial changes in ant (Hymenoptera, Formicidae) species richness and composition (including turnover and nestedness components) along a 500 km longitudinal gradient in the Pampean region of Argentina. Ants were sampled using pitfall traps in 12 sample sites during the summer. We performed a model selection approach to analyse responses of ant richness and composition dissimilarity to environmental factors. Then, we computed a dissimilarity partitioning of the contributions of spatial turnover and nestedness to total composition dissimilarity. Temporal habitat heterogeneity and temperature were the primary factors explaining spatial patterns of epigeal ant species richness across the Pampas. The distance decay in species composition similarity was best accounted by temperature dissimilarity, and turnover had the greatest contribution to the observed beta diversity pattern. Our findings suggest that both energy and environmental-heterogeneity-related variables are key factors shaping richness patterns of ants and niche-based processes instead of neutral processes appear to be regulating species composition of ant assemblages. The major contribution of turnover to the beta diversity pattern indicated that lands for potential reconversion to grassland should represent the complete environmental gradient of the Pampean region, instead of prioritizing a single site with high species richness.

**Key words:** diversity patterns, energy, environmental heterogeneity, nestedness, turnover.

## INTRODUCTION

Understanding the underlying mechanisms causing diversity patterns is a central topic in ecology and a key issue in science-based conservation biology (Gaston 2000; Leather *et al.* 2008; Brown 2014; Tittensor & Worm 2016). A variety of hypotheses have been suggested to explain spatial patterns of species richness (Willig *et al.* 2003; Stein *et al.* 2014). Many of these can be grouped in energy-related hypotheses or habitat heterogeneity-related hypotheses. However, those hypotheses were rarely tested together and the relative roles of energy and habitat heterogeneity in determining spatial patterns of species richness were overlooked.

Energy-related hypotheses propose that temperature is limiting richness (the species-temperature hypothesis) through physiological constraints (Currie 1991; Kaspari *et al.* 2000b; Sanders *et al.* 2007) or

by driving speciation rates (Rohde 1992). Alternatively, temperature and rainfall determine resource availability (the species-productivity hypothesis); an increase in resources may promote large population sizes and reduce the probability of local extinctions, thus increasing species richness (Kaspari *et al.* 2000b, 2004). Across different environmental gradients, energy-related variables are the main drivers of ant diversity (Kaspari *et al.* 2004; Sanders *et al.* 2007; Dunn *et al.* 2009), and particularly in South America, the species-productivity hypothesis has gathered most evidence to explain latitudinal patterns of species richness of a wide range of taxonomic groups (Hawkins *et al.* 2003). The species-heterogeneity hypothesis is based on the existence of more opportunities to fit a variety of species niches in complex environments. Stein *et al.* (2014) found support to this hypothesis across global to local extents for a wide range of taxa. Moreover, at the regional or smaller scales, habitat heterogeneity showed to be a key factor in determining species richness of insects including ants (Davidowitz & Rosenzweig 1998;

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Pacheco & Vasconcelos 2012). Here, we examine the energy and habitat heterogeneity hypotheses in a common analytical framework.

Composition dissimilarity between communities, or beta diversity, is a major component of biodiversity. Spatial changes in species composition occur because of differences in species ecological niches in relation to environmental conditions in the process of environmental filtering (Soininen *et al.* 2007). Alternatively, assemblage formation might be primarily driven by spatial processes such as dispersal limitations (Hubbell 2001). Thus, along environmental gradients, the composition of two spatially close communities is expected to be more similar than two communities far apart (this is, the distance decay in similarity *sensu* Nekola and White (1999) and Soininen *et al.* (2007)) due to greater environmental similarity between nearby sites or due to dispersal processes. The evidence so far indicates that energy-related variables are the major driver of ant beta diversity at the regional and larger geographical scales (Paknia & Pfeiffer 2014; Wepfer *et al.* 2016).

Two phenomena may be reflected in the patterns of beta diversity: species turnover and nestedness of assemblages (Baselga & Orme 2012; Legendre 2014). Species turnover is the replacement of species caused by gaining and losing species along environmental gradients. Nestedness occurs when assemblages in species-poor sites are subsets of species of successively richer sites, and it is caused by non-random extinction or colonization. Identifying the primary component of beta diversity has implications for conservation. For example, if turnover is the dominant component of beta diversity, approaches for conservation planning should be taken from a regional perspective to cover different sites; but if nestedness is dominant, high-diversity sites could be prioritized (Angeler 2013). Most previous studies on beta diversity patterns (e.g. Qian *et al.* 2009), including ants (e.g. Pacheco & Vasconcelos 2012), did not distinguish between the components of beta diversity or only measured turnover (Paknia & Pfeiffer 2011; Wepfer *et al.* 2016; but see Bishop *et al.* 2015).

Insects are major biotic components in most terrestrial ecosystems and the most species-rich group representing approximately 60% of all the known global species (Stork 1988; Colwell & Jonathan 1994). However, and despite many efforts, there is a gap of knowledge on insect diversity patterns (Clark & May 2002; Dunn *et al.* 2010; Szweczyk & McCain 2016). Furthermore, evidence showed that alpha diversity patterns of different insect families may be incongruent (Paknia & Pfeiffer 2011). Particularly, ants are taxonomically and functionally rich playing a variety of key roles in many terrestrial ecosystems (Folgarait 1998) and are known to respond to environmental

changes (Kaspari *et al.* 2003; Sanders *et al.* 2007; Kone *et al.* 2014).

In South America, the Pampean region was originally temperate grasslands crossed by ravines. Like other grasslands of the world, the Pampas has a history of anthropogenic use. After the European settlement in the 16th century, lands were first used for extensive ranching followed by agriculture increasing in intensity during the 20th century. Currently, lands are almost completely converted into agriculture and livestock (Bilenca & Miñarro 2004). Rangelands represent the closest situation to the original vegetation, both in structure and floristic composition, but they are managed intensively (Baldi *et al.* 2006). Highly degraded grasslands such as the Pampean region need urgent programs to encourage reconversion of selected agricultural lands, and ants have been suggested as grassland recovery indicator (Campbell & Crist 2017). We ask whether ant diversity spatial pattern at the regional scale is mainly determined by temperature, productivity or environmental heterogeneity. By considering all environmental factors in a common analytical framework, we attempt to give light on the relative roles of energy and heterogeneity variables as drivers of the spatial patterns of ant diversity. Furthermore, here we explore for the first time the underlying mechanisms causing spatial patterns of species richness and beta diversity (both the turnover and nestedness components) of ants across the Pampean region of Argentina. We sampled epigeal ants and estimated energy-related variables and environmental heterogeneity variables along a longitudinal gradient covering 500 km, identify the main factors that explain diversity patterns, and discuss the mechanisms causing those patterns.

## METHODS

### Study area

The study was conducted in the Central-South section of the Pampean grassland ecoregion of Argentina, in the sub-region known as flooded Pampa (Soriano 1992) (Fig. 1). The climate in the region is temperate warm with a mean annual temperature of 16°C and mean annual precipitation decreasing from 1100 mm in the Northeast to 600 mm in the Southwest (Cabrera 1976). The natural vegetation is a graminaceous steppe dominated by grasses such as *Stipa*, *Piptochaetium*, *Aristida*, *Melica*, *Briza*, *Bromus*, *Eragrostis* and *Poa* (Cabrera 1976). However, during the 20th century the native vegetation has been altered almost completely as a result of the progressive development of agriculture and advance of the agricultural frontier (León *et al.* 1984; Viglizzo *et al.* 2001). Currently, main annual crops in the region are soybean, corn, sunflower, wheat and oat (Baldi *et al.* 2006). The geomorphology of the ecoregion determines a gradient of land use, from almost 100% croplands in the North through mixed-farming to a pastoral-farming

scenario in the South (Filloy & Bellocq 2007). In the Central-South section of the ecoregion, where this study was conducted, the shallow soil, salinity, poor drainage and floods make the land less valuable for agriculture; thus, free-range livestock is the primary human activity that result in lands covered mainly by either spontaneous vegetation or cultivated pastures (Viglizzo *et al.* 2003). In recent years, cattle raising was intensified with the use of perennial legume-based pastures, indicating a simultaneous intensification of both agriculture and livestock farming (Viglizzo *et al.* 2003).

### Study design and ant sampling

Using thematic maps and satellite images, we identified a longitudinal climatic gradient covering 500 km from 58.1°W to 63.8°W, at relatively constant latitude (between 36.5 and 37.5°S) and altitude (90–150 m.a.s.l.). We located 12 sampling sites every 30–40 km along the gradient (Fig. 1). Each sampling site consisted in a linear track, located on a secondary unpaved road with N-S direction, where ants were sampled and environmental variables were measured. At each sampling site, epigeal ants were sampled by using six trap sets (pairs of pitfall traps, 50-m apart) separated by 1-km (Dormann *et al.* 2007). Traps were located

in the cropfield or cattle pasture next to the road and under the wire fence to prevent damage from cattle. Each trap consisted of a plastic container (500 mL volume, 85 mm diameter) with 150 mL of a propylene glycol and water (1:2) solution (Andersen 1991). Traps operated during two periods of 21 and 28 consecutive days during the summer (January–March). During each sampling period, traps were visited regularly every 10 days when samples were collected and traps refilled. Samples were preserved in 80% alcohol for later identification. Pitfall trapping is widely used to sample epigeal arthropods (Delsinne *et al.* 2010; Szweczyk & McCain 2016; Campbell & Crist 2017), and provides a good representation of ant communities in open grassland ecosystems (Andersen 1991; Melbourne 1999).

Ants were sorted to species level using available taxonomic keys, revisions of groups or dissertations as detailed below: *Acromyrmex* (A. F. Sánchez-Restrepo, pers. comm.), *Brachymyrmex* (Kusnezov 1978; Ortiz 2012), *Crematogaster* (pers. coll), *Dorymyrmex* (Kusnezov 1978), *Gnamptogenys* (Arias-Penna 2008), *Hypoponera* (Dash 2011), *Linepithema* (Wild 2007b), *Pheidole* (Wilson 2003), *Neivamyrmex* (Watkins 1976), *Pogonomyrmex* (Johnson 2015), *Solenopsis* (Pitts 2002; Pacheco & Mackay 2013; pers. coll), *Trachymyrmex* (Mayhé-Nunes & Brandão 2005; Brandão & Mayhé-Nunes 2007) and *Wasmannia* (Longino & Fernández 2007). Following comparable studies, individuals from taxonomically

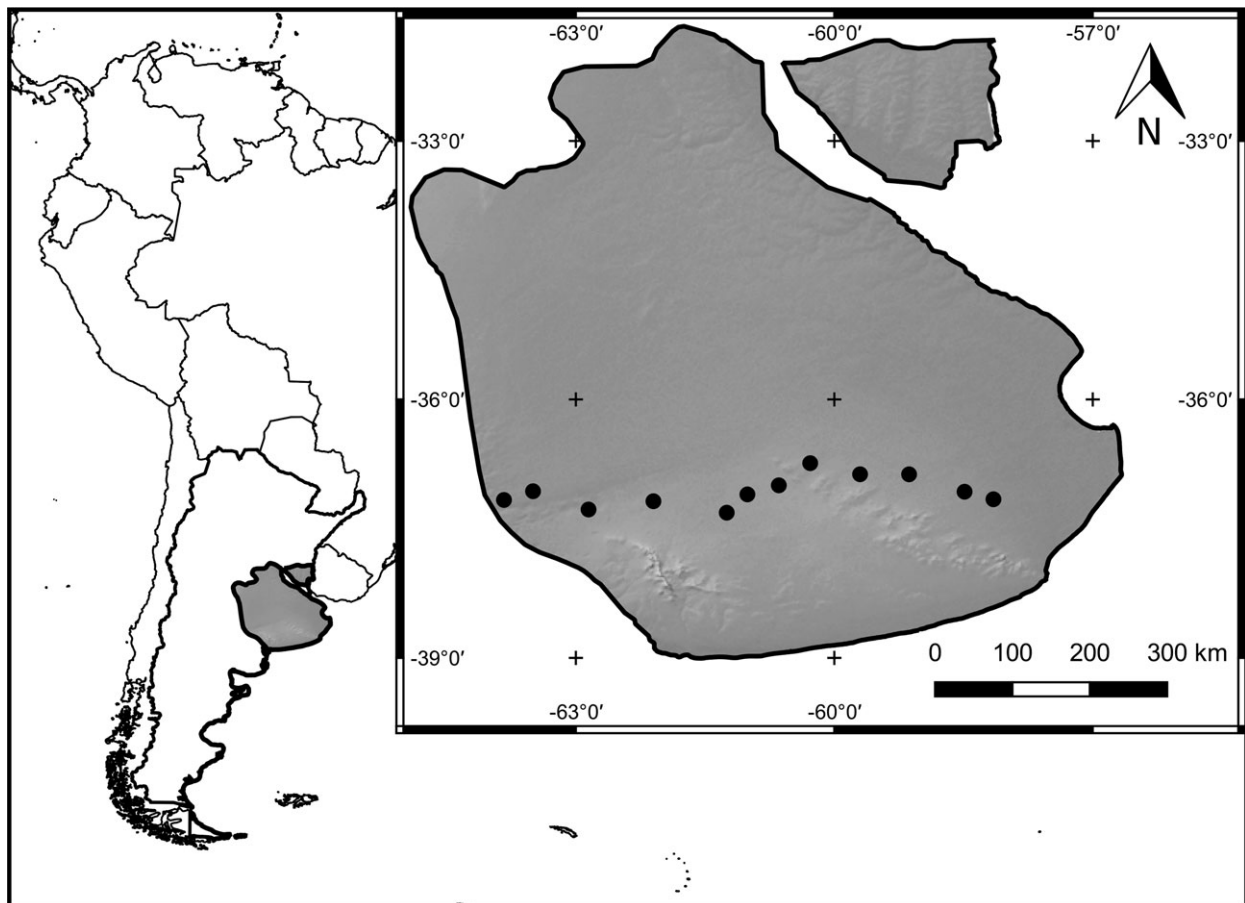


Fig. 1. Location of the 12 sites used to sampling ants in the Pampean region of Argentina.

difficult genera were sorted to morphospecies. This was the case of samples containing only minor workers of *Pheidole* and *Solenopsis* that do not match with any minor worker of the identified species using major workers. For *Crematogaster*, only a few individuals were collected and the identification was done by comparison with personal collection of CIP and posterior checking of species description and status (Mayr 1887; Wild 2007a). Ant web was used as an additional tool for identifications (AntWeb. Available from <http://www.antweb.org>). Voucher specimens of each ant species are held in the Insect Collection of the Community Ecology and Macroecology Laboratory at the Universidad de Buenos Aires.

### Estimation of environmental variables

To characterize the environmental scenario at each sample site, three energy-related variables and two habitat heterogeneity variables were generated (Table 1). To estimate the environmental variables, we located the 12 linear tracks in 5TM LANDSAT satellite images and established a strip area of  $10 \times 1$  km centred in the linear track. The net primary productivity (NPP) is commonly used in studies of species-energy relationships as an estimate of the resource available to high trophic levels (Mittelbach *et al.* 2001). We used the normalized difference vegetation index (NDVI) as a surrogate of the NPP (Hawkins *et al.* 2003; Bonn *et al.* 2004). To estimate the NDVI, we used 93 5TM LANDSAT satellite images from the five summers prior to ant sampling covering the entire gradient. Thus, we calculated NDVI values, in each strip area and we estimated the mean NDVI of the five summers (Apellaniz *et al.* 2012). Values of mean annual temperature and rainfall were obtained from the WorldClim data base for each strip area (Hijmans *et al.* 2005). That global database generated climatic values through interpolation of climate data of 50 years averages from weather stations using a 30' grid (1 km<sup>2</sup> resolution). Environmental heterogeneity may affect local diversity through space or time (Stein *et al.* 2014). Spatial environmental heterogeneity generally accounts for the variety of options to accommodate species based on major niche dimensions (habitat and food availability) (Costanza *et al.* 2011; Keil *et al.* 2012). Temporal environmental heterogeneity accounts for the stability of environmental conditions or resources (Oindo *et al.* 2000). In anthropogenic systems, variables related with the spatial heterogeneity of land cover classes (Kinnunen *et al.* 2001; Atkinson *et al.* 2002) and temporal NPP variability (Oindo *et al.* 2000) have been used to account for spatial and temporal environmental heterogeneity, respectively. Thus, within each strip area, we estimated the percentage of each land use

**Table 1.** Environmental variables considered in the study to explain spatial variation in ants richness and composition

Factor/Hypothesis	Variable
Energy	Normalized difference vegetation index Temperature Precipitation
Habitat heterogeneity	Land cover heterogeneity NDVI heterogeneity

(considering: pastures, oats, alfalfa, barley, sunflower, corn, soybean, sorghum, wheat, stubble) (Fillooy & Bellocq 2007; Apellaniz *et al.* 2012). To estimate land cover heterogeneity, we used the Shannon-Wiener diversity index based on the proportion of land uses recorded in the strip area. Furthermore, to assess the temporal NPP variability for each strip area, we estimated the NDVI heterogeneity by calculating the standard deviation of the mean NDVI (Costanza *et al.* 2011).

### Environmental factors driving spatial patterns of species richness

Species richness for each sample site was calculated as the total number of species captured pooling six traps (one per trap set as some were lost; when both traps remained, we randomly selected one). To assess the effectiveness of our sampling effort, we computed species accumulation curves and estimated the sample coverage estimate (i.e. sample completeness: the proportion of the total number of individuals in a community that belong to the species represented in the sample) (Chao & Jost 2012), using *iNEXT* software (Chao *et al.* 2014; Hsieh *et al.* 2016). Then, the mean sample coverage was calculated by averaging all sample sites. To identify the main environmental variables explaining spatial changes of species richness across the Pampean region, we used a model selection approach (Burnham & Anderson 2002) by performing General Linear Models (GLM). We modelled species richness with a Normal distribution instead of a Poisson distribution (typical of count data such as richness) (Buckley 2015) as giving large counts, the Poisson distribution approximated a Normal distribution (Buckley 2015). We first screened environmental variables for multicollinearity using pairwise correlations among all variables and check that correlation coefficient was less than 0.75 (Badik *et al.* 2015).

We ran all possible models defined by all combinations of variables and ranked them following the Akaike information criterion (AICc, as we used the corrected version for small sample sizes) using the *model.sel* function of the R package *MuMin* (Barton 2016). To account for hump-shaped relationships, we included both linear and quadratic terms of each variable in the predictor set, and the linear terms were always kept in the model when testing the quadratic term. Models with a difference in AICc values lower than two were considered as equivalent to the minimum AICc model (Burnham & Anderson 2002), and hence they were selected as the best set of models. Finally, to verify that the selected models accounted for the spatial structure of ant data, the spatial autocorrelation of residuals was examined using the Moran's Index estimated with the *Moran.I* function of the R package *Ape* (Paradis *et al.* 2004).

### Environmental factors driving beta diversity

Similarity in ant species composition between all pairs of sample sites was estimated using the Jaccard similarity index. The environmental dissimilarity was estimated as the Euclidean distance for a total of five environmental

distances representing five dimensions of species ecological niche. Also, geographic distance was estimated based on Euclidean distance, representing dispersal limitations. All variables were standardized.

We modelled the decay of species similarity for each environmental variable and for the geographic distance performing General Linear Models (GLM) (Burnham & Anderson 2002) and, we selected the best model using the Akaike criterion. Finally, we assessed if the decay in species composition similarity was efficiently accounted by the environmental dissimilarity. Thus, we plotted the Pearson residuals of composition similarity, after removing the influence of environmental dissimilarity, as a function of the geographic distance among sites and confirmed the absence of a spatial tendency by obtaining a random pattern.

To quantify both components of beta diversity, we calculated the dissimilarity between all pairwise of sample sites, partitioning the contributions of spatial turnover and nestedness to total beta diversity (Baselga 2010); using the software *Betapart* in R (Baselga & Orme 2012). We modelled total composition dissimilarity, turnover and nestedness as the response variables and the environmental distance involved in the selected best model of the distance decay analysis as the independent variable. We compared the slope and the deviance of the resulting models to establish the role of each component of the beta diversity.

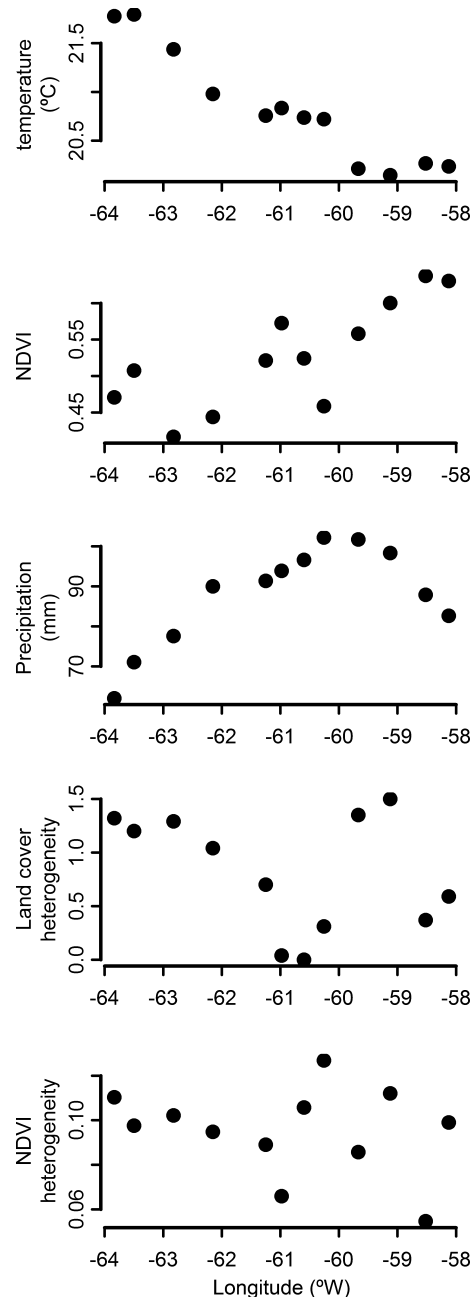
## RESULTS

### Spatial patterns of environmental variables

Energy-related variables but not habitat heterogeneity-related variables changed with a clear pattern along the longitudinal gradient in the Pampean region. Temperature increased from East (20.1°C) to West (21.8°C) whereas the NDVI showed the opposite pattern (from 0.6 in the E to 0.4 in the W) (Fig. 2). Precipitation showed a unimodal pattern with a peak of 102 mm at 60°W, and land cover heterogeneity (range 0–1.35) and NDVI heterogeneity (range 0.05–0.12) showed no clear spatial patterns. Environmental variables did not have strong intercorrelations (Appendix S1); therefore, all variables were included in the modelling process (Table 1).

### Environmental factors driving spatial patterns of species richness

The trapping system collected a total of 13259 individual ants representing six subfamilies, 16 genera and 47 species/morphospecies (Appendix S2). The species accumulation curves showed that our sampling effort captured a high (Mean: 82.3%) and relatively constant (Standard Error: 6.5%) percentage of the species richness estimated for each sample site.



**Fig. 2.** Longitudinal pattern of environmental variables in the Pampean region of Argentina.

The spatial pattern of ant richness showed two peaks at the West and middle areas of the environmental gradient (Appendix S3). Species richness varied from 13 to 24 among sample sites. Workers of *Wasmannia williamsoni* (Kusnezov 1952) were captured the first time in Buenos Aires province (Cuezzo *et al.* 2015).

To identify the main factors explaining for spatial changes in species richness, we evaluated a total of 20 models (Appendix S4). Four of them showed to be plausible explanations of changes observed in ant

species richness ( $\Delta AICc < 2$ ) (Table 2). Three represented straight linear relationships between species richness and NDVI heterogeneity, temperature and NDVI. The remaining model showed a second degree polynomial relationship between richness and NDVI heterogeneity. Models showed that ant richness increased with temperature and temporal NDVI heterogeneity (either linear or from an intermediate NDVI heterogeneity value), and contrary to the predictions it declined with NDVI (Fig. 3). The polynomial relationship with NDVI heterogeneity as the independent variable explained the highest percentage of deviance (DE%) (Table 2). The Moran's index showed no spatial structure on each of the model residuals indicating that all models efficiently accounted for the spatial structure of ant species richness.

### Environmental factors driving beta diversity

The model selection of the distance decay analysis showed that similarity among ant assemblages was best explained by temperature distance among sample sites (Table 3). Thus, the more similar are two sites in temperature values, the more similar are in ants assemblage composition. Furthermore, geographic distance model was less supported than the temperature model ( $2 < \Delta AICc < 10$ ) and there was no support for the models between assemblage similarity and NDVI, NDVI heterogeneity or land cover heterogeneity distances along the studied gradient ( $\Delta AICc > 10$ ) (Burnham & Anderson 2002).

Total species composition dissimilarity increased with temperature dissimilarity (DE% = 39.5, slope = 0.078) (Fig. 4). The turnover component of beta diversity showed a similar pattern of spatial variation to the total species dissimilarity; thus, species replacement accounted for a higher proportion of the

total dissimilarity than the nestedness component at all distances (turnover: DE% = 29.1, slope = 0.099; nestedness: DE% = 3.4, slope = -0.017).

## DISCUSSION

Our findings indicate that both energy and habitat heterogeneity are key factors in shaping spatial patterns of alpha (i.e. species richness) and beta diversity (i.e. changes in species composition) of ants at the regional scale. Across Argentine Pampas, changes in ant species richness were explained by temporal habitat heterogeneity and temperature whereas changes in species composition were best explained by temperature dissimilarity. Also, we found that turnover was the major component of beta diversity along the environmental gradient. Those responses of community attributes suggest that ant diversity is mainly directed by environmental conditions, which may be acting as filters determining the variations in species richness and composition of ant assemblages across the Pampas. Species ecological niches are likely involved in the process of assemblage formation at the local scale, giving shape to the spatial diversity patterns within the region.

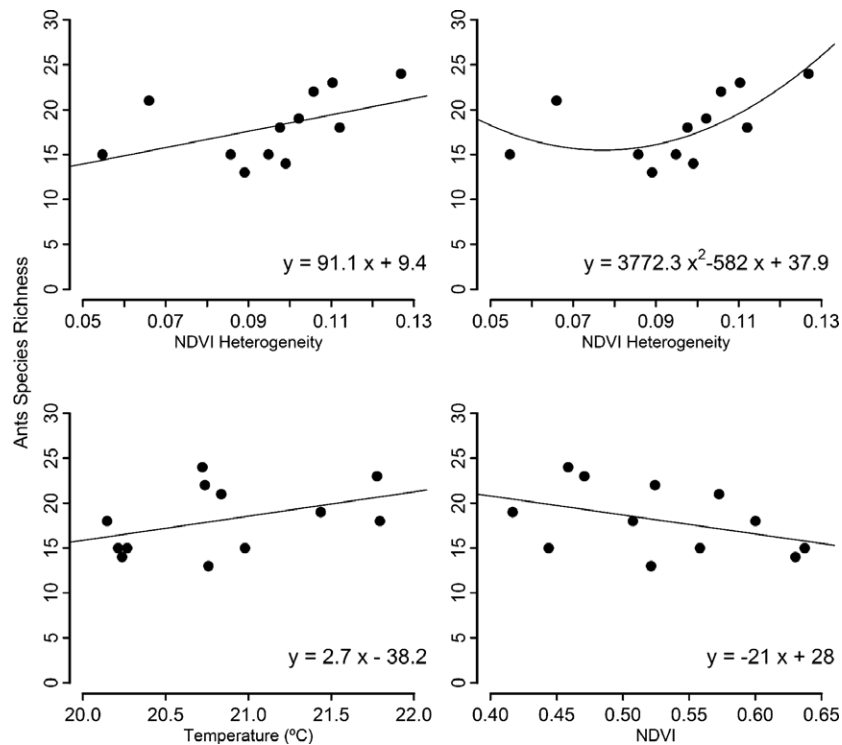
### Environmental factors driving spatial patterns of species richness

Spatial patterns of epigeal ant species richness were similarly explained by NDVI heterogeneity, temperature and NDVI, as indicated by the Akaike criterion. Among them, the model including NDVI heterogeneity as the independent variable showed the most predictive power for ant species richness as indicated by the explained deviance. Samples sites with high NDVI heterogeneity (i.e. high standard deviations of NDVI values) are probably sites where crop rotation practices were implemented over the 5-year-period when that variable was estimated. As previously found, temporal changes in environmental conditions can change the competitive dominance among species allowing for more species to coexistence (Cerda *et al.* 1997). Moreover, according to Andersen (2008), ant species coexistence is also determined by processes acting at the time of colony establishment. Once established, when conditions turn adverse, colonies reduce their sizes instead of disappearing. Thus, in the Pampean region temporal habitat heterogeneity due to seasonal land use rotation may likely encourage the establishment of different ant species at different times, helping to avoid competitive exclusion. Our result highlights the importance of taking into account temporal patterns of habitat heterogeneity in ant diversity studies.

**Table 2.** Results of ant richness models with equivalent Akaike's Information Criterion corrected for small sample size ( $\Delta AICc < 2$ )

Models	AICc	$\Delta AICc$	DE (%)	Moran's I
H_NDVI	70.59	0	23.14	-0.04
H_NDVI + H_NDVI <sup>2</sup>	71.21	0.62	45.33	0.02
T	71.40	0.81	17.74	-0.07
NDVI	71.53	0.94	16.87	-0.11

Model rankings were based on AICc values. H\_NDVI, Variables are: Normalized Difference Vegetation Index heterogeneity; T, Temperature; and NDVI, Normalized Difference Vegetation Index. DE: Deviance explained by the model where  $DE_i = (D_{null} - D_i) / D_{null} \times 100$ . Moran's I: Moran's Index.



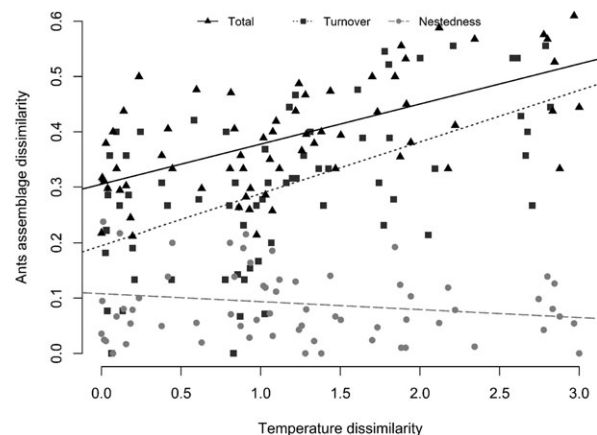
**Fig. 3.** The best-fitted models ( $\Delta\text{AICc} < 2$ ) selected from the relationships between ant species richness and the environmental variable.

**Table 3.** Model selection for the distance decay in similarity of ant assemblage composition along a longitudinal gradient in the Argentine Pampas

Model/variable distance	Slope	AICc	$\Delta\text{AICc}$
Temperature	-0.078	-137.76	0
Geographic distance	-0.081	-134.66	3.10
Precipitation	-0.065	-126.80	10.97
Normalized difference vegetation index	-0.033	-110.10	27.66
Land cover heterogeneity	-0.019	-107.44	30.32
NDVI heterogeneity	0.004	-106.21	31.55

Model rankings were based on AICc values.

Energy-related hypotheses were also supported by the species-temperature hypothesis. Ant species richness responded positively to temperature, although such response was weaker than to NDVI heterogeneity, as showed by the low explained deviance. The species-temperature hypothesis is well documented for ant species richness, especially at regional to continental spatial scales (e.g. Kaspari *et al.* 2003; Bishop *et al.* 2014 for regional scale; Dunn *et al.* 2009 for continental scale). In temperate climates, as where our study area located, ants showed to be warming tolerants (Diamond *et al.* 2012); moreover, ants are known to improve their reproductive performance at relatively high temperatures (Hölldobler & Wilson 1990; Andersen 1992; Dunn *et al.* 2009).



**Fig. 4.** Variations in ant assemblage dissimilarity, turnover and nestedness with temperature dissimilarity.

Thus, mechanisms involving physiological limitations may be acting along our longitudinal gradient. Alternatively but not exclusively, higher temperatures may promote a major forager abundance (Stuble *et al.* 2013) and longer foraging time allowing the access of more individuals to food resources, thus reducing extinction risk (Kaspari *et al.* 2000b, 2004; Sanders *et al.* 2007). Even though the model including NDVI was one of the best models, we found a negative relationship between ant richness and the NDVI.

Although productivity is often positively related to species richness, negative relationships were previously described for ants. Crist and Wiens (1994) and Kaspari and Weiser (1999) was argued that the high vegetation coverage, associated with high NDVI, may interfere with ant movements or with the detection of chemical signals. Furthermore, some highly productive sites may hold few plant species resulting in low ant diversity (Kaspari *et al.* 2000a); that may be the case of landscapes dominated by monocultures such as the Pampean region. Furthermore, ant species richness showed no relationship with rainfall across the Argentine Pampas, and similar results were found along a 400-km transect on a rainfall gradient from 460 to 887 mm year<sup>-1</sup> in the Paraguayan dry Chaco (Delsinne *et al.* 2010). Therefore, evaluating energy and heterogeneity hypothesis in a common framework showed that both are likely maintaining ant richness pattern at a regional scale.

### Environmental factors driving beta diversity

Ant community composition appears to be controlled by niche-based processes in relation to environmental filtering rather than by dispersal limitations across the Pampean region. Our results indicate that temperature would be acting as a filter for some species, likely driving spatial changes in ant species composition. As changes in species composition were weakly associated with the geographical distance between sites, dispersion limitation dilutes as a strong explanation for those changes. Other studies also suggest that environmental conditions (i.e. niche-based processes), rather than a neutral stochastic process (i.e. dispersion), may be the main driver of spatial patterns of ant beta diversity. Ant turnover seems to be primarily driven by environmental factors in arid lands (Paknia & Pfeiffer 2014), in the tropical forests (Vasconcelos *et al.* 2010) and in warm temperate grasslands (this study). We found that dissimilitude in temperature explained best the variation in beta diversity of ants. In arid areas of Iran temperature range and precipitation explained most of the variation in ant species composition (Paknia & Pfeiffer 2014), but precipitation was the most relevant factor in the floodplain forests of the Brazilian Amazon (Vasconcelos *et al.* 2010).

The partitioning of beta diversity indicated that differences in assemblage composition were due to species turnover and nestedness accounted for a small proportion of beta diversity. Therefore, along the longitudinal gradient in the Pampean region, ant beta diversity was mainly driven by the replacement of species. The few studies disentangling the response of both components of ant beta diversity found contrasting results. Bishop *et al.* (2015) found that beta

diversity occurred mainly by turnover along a mountain gradient. In contrast, Ślipiński *et al.* (2012) found that nestedness was the primary component of beta diversity along increasing levels of urbanization. Thus, turnover seems to be the relevant component accounting for beta diversity changes along environmental gradients at broad scales by covering the different optimal conditions for different species promoting species replacement along space. At small spatial scales, nestedness is likely the key component of beta diversity changes when the environment suffers drastic modification and only a subset of tolerant species remain composing the ant assemblages.

The Pampean region of Argentina is highly degraded due to land conversion to agriculture and livestock, and the reconversion of marginal agricultural lands should be undertaken urgently. Species turnover was responsible for changes in beta diversity across the region, and it may presumably be for many other arthropod groups (Andersen 1991). In landscapes where turnover is the major component of beta diversity, protected area selection may be done along the complete gradient (Socolar *et al.* 2016). Therefore, from an applied perspective, our results indicate that the Pampean region requires that lands for potential reconversion to native grassland should be selected including the complete environmental gradient, rather than prioritizing a single site with high species richness.

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### REFERENCES

- Andersen A. N. (2008) Not enough niches: non-equilibrium processes promoting species coexistence in diverse ant communities. *Austral Ecol.* **33**, 211–20.
- Andersen A. N. (1991) Sampling communities of ground foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Aust. J. Ecol.* **16**, 273–9.
- Andersen A. N. (1992) Regulation of momentary diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *Am. Nat.* **140**, 401–20.



- Angeler D. G. (2013) Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. *Divers. Distrib.* **19**, 772–81.
- Apellaniz M., Bellocq M. I. & Filloy J. (2012) Bird diversity patterns in Neotropical temperate farmlands: the role of environmental factors and trophic groups in the spring and autumn. *Austral. Ecol.* **37**, 547–55.
- Arias-Penna T. M. (2008) Subfamilia ectatominae. In: *Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia* (eds E. Jiménez, F. Fernández, T. M. Arias & F. H. Lozano-Zambrano) pp. 53–100. Instituto de Investigaciones de Recursos Biológicos, Alexander von Humboldt, Bogotá, Colombia.
- Atkinson P. W., Fuller R. J. & Vickery J. A. (2002) Large-scale patterns of summer and winter bird distribution in relation to farmland type in England and Wales. *Ecography*. Munksgaard International Publishers. **25**, 466–80.
- Badik K. J., Shapiro A. M., Bonilla M. M., Jahner J. P., Harrison J. G. & Forister M. L. (2015) Beyond annual and seasonal averages: using temporal patterns of precipitation to predict butterfly richness across an elevational gradient. *Ecol. Entomol.* **40**, 585–95.
- Baldi G., Guerschman J. P. & Paruelo J. M. (2006) Characterizing fragmentation in temperate South America grasslands. *Agr. Ecosyst. Environ.* **116**, 197–208.
- Barton K. (2016) *MuMIn: Multi-Model Inference. R Package Version 1.15.6*. [Cited 2 December 2017.] Available from URL: <https://CRAN.R-project.org/package=MuMIn>
- Baselga A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–43.
- Baselga A. & Orme C. D. L. (2012) Betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–12.
- Bilenca D. & Miñarro F. (2004) *Identificación de áreas valiosas de pastizal en las pampas y campos de Argentina, Uruguay y sur de Brasil*. Fundación Vida Silvestre Argentina, Buenos Aires.
- Bishop T. R., Robertson M. P., van Rensburg B. J. & Parr C. L. (2014) Elevation-diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *J. Biogeogr.* **41**, 2256–68.
- Bishop T. R., Robertson M. P., van Rensburg B. J. & Parr C. L. (2015) Contrasting species and functional beta diversity in montane ant assemblages. *J. Biogeogr.* **42**, 1776–86.
- Bonn A., Storch D. & Gaston K. J. (2004) Structure of the species-energy relationship. *Proc. R. Soc. B: Biol. Sci.* **271**, 1685–91.
- Brandão C. R. F. & Mayhé-Nunes A. J. (2007) A phylogenetic hypothesis for the Trachymyrmex species groups, and the transition from fungus-growing to leaf-cutting in the Attini. In: *Advances In Ant Systematics (Hymenoptera: Formicidae): Homage To E. O. Wilson – 50 Years Of Contributions*, (eds R. R. Snelling, B. L. Fisher & P. S. Ward) pp. 72–88. Memoirs of the American Entomological Institute, Gainesville.
- Brown J. H. (2014) Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22.
- Buckley Y. M. (2015) Generalized linear models. In: *Ecological Statistics: Contemporary Theory and Application*, (eds G. A. Fox, S. Negrete-Yankelevich & V. J. Sosa) pp. 131–47. First, Oxford University Press Inc., Oxford.
- Burnham K. P., Anderson D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York, NY.
- Cabrera A. L. (1976) Fitogeografía de la República Argentina. In: *Enciclopedia Argentina de Agricultura y Jardinería* (ed W. F. Kugler) pp. 1–85. ACME, Buenos Aires.
- Campbell K. U. & Crist T. O. (2017) Ant species assembly in constructed grasslands is structured at patch and landscape levels. *Insect Conserv. Divers.* **10**, 180–91.
- Cerda X., Retana J. & Cros S. (1997) Thermal disruption of transitive hierarchies in mediterranean ant communities. *J. Anim. Ecol.* **66**, 363–74.
- Chao A. & Jost L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–47.
- Chao A., Gotelli N. J., Hsieh T. C. *et al.* (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* **84**, 45–67.
- Clark J. A. & May R. M. (2002) Taxonomic bias in conservation research. *Science* **297**, 191–2.
- Colwell R. K. & Jonathan C. A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. Biol. Sci.* **345**, 101–18.
- Costanza J. K., Moody A. & Peet R. K. (2011) Multi-scale environmental heterogeneity as a predictor of plant species richness. *Landscape Ecol.* **26**, 851–64.
- Crist T. O. & Wiens J. A. (1994) Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos* **69**, 37.
- Cuezzo F., Calcaterra L. A., Chifflet L. & Follett P. (2015) Wasmannia Forel (Hymenoptera: Formicidae: Myrmicinae) in Argentina: systematics and Distribution. *Sociobiology* **62**, 246–65.
- Currie D. J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* The University of Chicago Press. **137**, 27–49.
- Dash S. T. (2011) *A Taxonomic Revision of the New World Hypoponera Santschi, 1938 (Hymenoptera:Formicidae)*. The University of Texas at El Paso, El Paso.
- Davidowitz G. & Rosenzweig M. L. (1998) The latitudinal gradient of species diversity among North American grasshoppers (Acrididae) within a single habitat: a test of the spatial heterogeneity hypothesis. *J. Biogeogr.* **20**, 553–60.
- Delsinne T., Roisin Y., Herbauts J. & Leponce M. (2010) Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco. *J. Arid Environ.* Elsevier Ltd. **74**, 1149–55.
- Diamond S. E., Sorger D. M., Hulcr J. *et al.* (2012) Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Glob. Change Biol.* **18**, 448–56.
- Dormann C. F., Schweiger O., Augenstein I. *et al.* (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Glob. Ecol. Biogeogr.* **16**, 774–87.
- Dunn R. R., Agosti D., Andersen A. N. *et al.* (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol. Lett.* **12**, 324–33.
- Dunn R. R., Gue B., Weiser M. D. & Sanders N. J. (2010) Geographic gradients. In: *Ant Ecology*, (eds L. Lach, C. Parr & K. L. Abbott) pp. 38–58. Oxford University Press Inc., New York.
- Filloy J. & Bellocq M. (2007) Respuesta de las aves rapaces al uso de la tierra: un enfoque regional. *Hornero* **22**, 131–40.
- Folgarait P. J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.* **7**, 1221–44.

- Gaston K. J. (2000) Global patterns in biodiversity. *Nature*. Nature Publishing Group. **405**, 220–7.
- Hawkins B. A., Field R., Cornell H. V. *et al.* (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–17.
- Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G. & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–78.
- Hölldobler B. & Wilson E. (1990) *The ants Harvard Belknap*. Springer Verlag, Berlin, Heidelberg, London, Paris, Tokyo, Hong Kong.
- Hsieh T. C., Ma K. H., Chao A. & Hsieh M. T. C. (2016) Package “iNEXT” Title Interpolation and Extrapolation for Species Diversity.
- Hubbell S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Johnson R. A. (2015) A taxonomic revision of South American species of the seed-harvester ant genus *Pogonomyrmex* (Hymenoptera: Formicidae) Part I. *Zootaxa* **4029**, 1.
- Kaspari M. & Weiser M. D. (1999) The size-grain hypothesis and interspecific scaling in ants. *Functional Ecol.* Blackwell Science Ltd. **13**, 530–8.
- Kaspari M., Alonso L. & O’Donnell S. (2000a) Three energy variables predict ant abundance at a geographical scale. *Proc. R. Soc. B: Biol. Sci.* **267**, 485–9.
- Kaspari M., O’Donnell S. & Kercher J. R. (2000b) Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *Am. Nat.* **155**, 280–93.
- Kaspari M., Yuan M. & Alonso L. (2003) Spatial grain and the causes of regional diversity gradients in ants. *Am. Nat.* **161**, 459–77.
- Kaspari M., Ward P. S. & Yuan M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia* **140**, 407–13.
- Keil P., Schweiger O., Kühn I. *et al.* (2012) Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales. *J. Biogeogr.*, **39**, 1473–86.
- Kinnunen H., Tiainen J. & Tukia H. (2001) Farmland carabid beetle communities at multiple levels of spatial scale. *Ecography* **24**, 189–97.
- Kone M., Konate S., Yeo K., Kouassi P. K. & Linsenmair K. E. (2014) Effects of management intensity on ant diversity in cocoa plantation (Oume, centre west Côte d’Ivoire) . *J. Insect Conserv.* Springer International Publishing. **18**, 701–12.
- Kusnezov N. (1952) El género *Wasmannia* en la Argentina (Hymenoptera, Formicidae). *Acta Zool. Lilloana* **10**, 173–82.
- Kusnezov N. (1978) *Hormigas Argentinas : clave para su identificación*. Ministerio de Cultura y Educacion, Tucuman Republica Argentina.
- Leather S. R., Basset Y., Hawkins B. A. (2008) Insect conservation: finding the way forward. *Insect Conserv. Divers.* **1**, 67–9.
- Legendre P. (2014) Interpreting the replacement and richness difference components of beta diversity. *Glob. Ecol. Biogeogr.* **23**, 1324–34.
- León R. J. C., Rusch G. M. & Oesterheld M. (1984) Pastizales pampeanos - impacto agropecuario. *Phytocoenologia*. Schweizerbart’sche Verlagsbuchhandlung. **12**, 201–18.
- Longino J. T. & Fernández F. (2007) Taxonomic review of the genus *Wasmannia*. *Mem. Am. Entomol. Inst.* **80**, 271–89.
- Mayhé-Nunes A. J. & Brandão C. R. F. (2005) Revisionary studies on the attine ant genus *Trachymyrmex* forel. Part 2: the Iheringi group (Hymenoptera: Formicidae). *Sociobiology* **45**, 271–305.
- Mayr G. (1887) Südamerikanische Formiciden. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien. **37**, 511–632.
- Melbourne B. A. (1999) Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Aust. J. Ecol.* **24**, 228–39.
- Mittelbach G. G., Steiner C. F., Scheiner S. M. *et al.* (2001) What is the observed relationship between species richness and productivity? *Ecology* **82**, 2381–96.
- Nekola J. C. & White P. S. (1999) The Distance Decay of Similarity in Biogeography and Ecology The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* **26**, 867–78.
- Oindo B. O., de By R. A. & Skidmore A. K. (2000) Interannual variability of NDVI and bird species diversity in Kenya. *Int. J. Appl. Earth Obs. Geoinf.* **2**, 172–80.
- Ortiz C. (2012) *Revisión taxonómica de las hormigas del género Brachymyrmex Mayr (Hymenoptera: Formicidae: Formicinae)*. Universidad Nacional de Colombia, Bogota.
- Pacheco J. & Mackay W. P. (2013) *The Systematics and Biology of the New World Tided Ants of the Genus Solenopsis (Hymenoptera: Formicidae)*. Edwin Mellen Press, New York.
- Pacheco R. & Vasconcelos H. L. (2012) Habitat diversity enhances ant diversity in a naturally heterogeneous Brazilian landscape. *Biodivers. Conserv.* Springer, Netherlands. **21**, 797–809.
- Paknia O. & Pfeiffer M. (2011) Hierarchical partitioning of ant diversity: implications for conservation of biogeographical diversity in arid and semi-arid areas. *Divers. Distrib.* **17**, 122–31.
- Paknia O. & Pfeiffer M. (2014) Niche-based processes and temporal variation of environment drive beta diversity of ants (Hymenoptera: Formicidae) in dryland ecosystems of Iran. *Myrmecol. News.* **20**, 15–23.
- Paradis E., Claude J. & Strimmer K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–90.
- Pitts J. P. (2002) A cladistic analysis of the *Solenopsis saevissima* species-group (Hymenoptera: Formicidae). *J. Clin. Investig.* **111**, 91–8.
- Qian H., Badgley C. & Fox D. L. (2009) The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Glob. Ecol. Biogeogr.* **18**, 111–22.
- Rohde K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514.
- Sanders N. J., Lessard J. P., Fitzpatrick M. C. & Dunn R. R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Glob. Ecol. Biogeogr.* **16**, 640–9.
- Ślipiński P., ZMihorski M. & Czechowski W. (2012) Species diversity and nestedness of ant assemblages in an urban environment. *Eur. J. of Entomol.* **109**, 197–206.
- Socolar J. B., Gilroy J. J., Kunin W. E. & Edwards D. P. (2016) How should beta-diversity inform biodiversity conservation? . *Trends Ecol. Evol.* Elsevier Current Trends. **31**, 67–80.
- Soininen J., McDonald R. & Hillebrand H. (2007) The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

- Soriano A. (1992) Río de la Plata grasslands. *Ecol. Appl.* Elsevier, **8**, 367–407.
- Stein A., Gerstner K. & Kreft H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–80.
- Stork N. E. (1988) Insect diversity: facts, fiction and speculation\*. *Biol. J. Linn. Soc.* **35**, 321–37.
- Stuble K. L., Pelini S. L., Diamond S. E., Fowler D. A., Dunn R. R. & Sanders N. J. (2013) Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecol. Evol.* **3**, 482–91.
- Szewczyk T. & McCain C. M. (2016) A systematic review of global drivers of ant elevational diversity. *PLoS ONE*, **11**, e0155404.
- Tittensor D. P. & Worm B. (2016) A neutral-metabolic theory of latitudinal biodiversity. *Glob. Ecol. Biogeogr.* **25**, 630–41.
- Vasconcelos H. L., Vilhena J. M. S., Facure K. G. & Albernaz A. L. K. M. (2010) Patterns of ant species diversity and turnover across 2000 km of Amazonian floodplain forest. *J. Biogeogr.* **37**, 432–40.
- Viglizzo E. F., Lértora F., Pordomingo A. J., Bernardos J. N., Roberto Z. E. & Del Valle H. (2001) Ecological lessons and applications from one century of low external-input farming in the pampas of Argentina. *Agr. Ecosyst. Environ.* **83**, 65–81.
- Viglizzo E. F., Pordomingo A. J., Castro M. G. & Lertora F. A. (2003) Environmental assessment of agriculture at a regional scale in the Pampas of Argentina. *Environ. Monit. Assess.* **87**, 169–95.
- Watkins J. (1976) *The Identification and Distribution of New World Army Ants (Dorylinae: Formicidae)*. The Markham Press Fund of Baylor University Press, Waco.
- Wepfer P. H., Guénard B. & Economo E. P. (2016) Influences of climate and historical land connectivity on ant beta diversity in East Asia. *J. Biogeogr.* **43**, 2311–21.
- Wild A. (2007a) A catalogue of the ants of Paraguay (Hymenoptera: Formicidae). *Zootaxa* **1622**, 1–55.
- Wild A. (2007b) Taxonomic revision of the ant genus *linepithema* (Hymenoptera: Formicidae). *Uni. Calif. Publ. Entomol.* **126**, 1–151.
- Willig M. R., Kaufman D. M. & Stevens R. D. (2003) Latitudinal gradients of biodiversity: patterns, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309.
- Wilson E. O. (2003) *Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus*. Harvard University Press, Cambridge.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Spearman correlation coefficients between all the environmental variables.

**Appendix S2.** Species list.

**Appendix S3.** Longitudinal pattern of ant species richness in the Pampean region of Argentina.

**Appendix S4.** Ant richness models selection results.