Niche-based processes and temporal variation of environment drive beta diversity of ants (Hymenoptera: Formicidae) in dryland ecosystems of Iran[*]

Omid PAKNIA & Martin PFEIFFER

Abstract

Clarifying the mechanisms that determine diversity in communities is a key task in biodiversity conservation. Niche differentiation, dispersal limitation, and stochastic processes are possible causes of variation in community composition, or beta diversity. In this study we quantified variation in ant assemblages related to environmental and spatial factors. We used pitfall traps to sample ant assemblages across a ca. 1200 km transect through arid and semi-arid heterogeneous environments of Iran. We then applied these data to canonical analysis to disentangle the relative importance of environmental and spatial processes. A total of 69 species / morphospecies were collected along the North-South transect. *Cataglyphis* was the most speciose genus with 12 species, followed by *Messor* and *Monomorium* with ten and seven species, respectively. Our parsimonious environmental and spatial models jointly explained 62% of the variation in community composition of ants. Community composition was primarily controlled by environmental factors (45%). Variation in ant species composition was driven by the amount of precipitation and also by its occurrence patterns. A large number of species were highly localized to a certain habitat. The overall findings suggest that mechanisms linked to environmental filtering and niche-based processes may be regulating beta diversity on ants in the Persian semi-deserts and deserts. Environmental factors appear also to control ant dispersal. Future conservation studies on insects should carefully take the temporal pattern of precipitation into account.

Key words: Beta diversity, contemporary climate, dispersal, Iran, PCNM analysis, variation partitioning.

Omid Paknia (contact author), University of Ulm, Institute for Experimental Ecology, Albert Einstein Allee 11, D-89069 Ulm, Germany; present address: Institute of Animal Ecology and Cell Biology, TiHo Hannover, D-30559 Hannover, Germany. E-mail: omid.paknia@ecolevol.de; omid.paknia@gmail.com

Martin Pfeiffer University of Ulm, Institute for Experimental Ecology, Albert Einstein Allee 11, D-89069 Ulm, Germany; present address: National University of Mongolia, Department of Ecology, Baga toiruu 47, Ulaanbaatar 210646, Mongolia.

Introduction

Ant community ecologists have historically focused much of their efforts on studying factors and mechanisms related to variation in alpha diversity (e.g., SANDERS & al. 2003, DUNN & al. 2009, RYDER WILKIE & al. 2009). As a result, we have a better knowledge about the drivers of alpha diversity than we do about beta diversity. Beta diversity in this context means variation in species composition among sites (ANDERSON & al. 2011). Beta diversity and the factors that contribute to its variation have foundational roles in general ecological theory (e.g., RICKLEFS 1987) and key implications for effective conservation management (e.g., JOST & al. 2010, PAKNIA & PFEIFFER 2011a). A large body of studies, conducted on other organisms, has demonstrated that beta diversity is a niche-based process (e.g., BRAY & CURTIS 1957, JANKOWSKI & al. 2009). More specifically, beta diversity is simultaneously regulated by extrinsic factors related to environmental conditions and geography such as climate variables and geographical position and by intrinsic features related to species' traits such as body size (see SOININEN & al. 2007 for a review). An alternative theory proposes that beta diversity is the result of spatial processes. The neutral view of community composition postulates that all species in local communities are effectively equivalent. Regarding the changes in community composition, this latter view grants primacy to spatial factors, namely dispersal limitation (HUBBELL 2001). Limited dispersal among local communities will tend to cause community similarity to be inversely associated with spatial distance. Consequently, one major prediction of this theory is a smooth decay in community similarity with distance due to dispersal limitation of species.

It is unlikely that ecological communities are strictly niche-based or strictly dispersal-based. Aspects of both processes likely operate simultaneously (see SIEPIELSKI & al. 2010). The important question is how the relative weights of these two processes differ in their contribution to community assembly. Regarding the ants, quantifying the relative contributions of environmental conditions and spatial factors to species composition can help to improve our understanding of the drivers of ant beta diversity.

A growing body of literature has evaluated the relative importance of these two driving forces by comparing the

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[*] This paper is dedicated to the memory of Elisabeth K.V. Kalko, to honour her dedication as an outstanding scientist and mentor.

variation in species composition explained by niche dimensions (environmental factors) to that explained by dispersal limitation (spatial factors). The existing literature, however, shows a strong bias towards vertebrates and tropical zones. There is a limited number of studies on insects which have considered the impact of spatial structure on beta diversity (BASELGA 2008, DEL TORO 2013), even though spatial structuring has been found to play a fundamental role in many ecosystems (PIRES & al. 2009, SATTLER & al. 2010).

The aim of the present study is to determine the causes of beta diversity in ant assemblages along a latitudinal transect in a dryland ecosystem. Ants are an ideal taxon for evaluating the ecological impact of environmental and spatial factors, as they are common terrestrial insects, especially in arid regions (BESTELMEYER & WIENS 2001, DELSINNE & al. 2010). Ants have all been widely accepted as worthy bioindicators in conservation studies and practices (ANDERSEN & al. 2002, PAKNIA & PFEIFFER 2011a). Patterns of alpha diversity of ant communities have been demonstrated at a wide range of spatial scales (KASPARI & al. 2003, DUNN & al. 2009, PAKNIA & PFEIFFER 2012). Nevertheless, there is a lack of knowledge about the impacts of spatial structure and environment on the beta diversity of ants (PAKNIA 2013). Only a few studies have been carried out in tropical forests (VASCONCELOS & al. 2010, MEZGER & PFEIFFER 2011). By analyzing spatial and environmental variables in the tropical forests of Amazon (VASCONCELOS & al. 2010) and Borneo (MEZGER & PFEIFFER 2011), these studies showed that environmental and spatial factors only weakly explained variation in ant assemblages, suggesting a potential role of neutral processes in the aggregation of ant species assemblages in tropical regions.

In this study, for the first time, we evaluate the influence of environmental and spatial factors on the beta diversity of ant assemblages across a ca. 1200 km transect in arid and semi-arid regions, in Iran. Our approach contained the following steps:

(1) Patterns of decrease in similarity with geographical distance could yield information on the importance of dispersal. The main explanations for a decline in community similarity with distance are either gradual changes in the environment or species' dispersal limitation. As we sampled our assemblages across patchy and heterogeneous habitats, we expected that the associated similarity decay would not be smooth.

(2) Arid and semi-arid areas experience constant fluctuations in climatic factors, e.g., precipitation and temperature. In addition, sampling ant assemblages across a long and heterogeneous environmental gradient increases the influence of possible spatial factors on the variation of the ant assemblages. We expected that both environmental and spatial factors contribute significantly in variation among assemblages.

(3) When environment is heterogeneous, many species will show an association to particular habitats. We expected that a large number of species are associated with particular habitats.

Materials and methods

Study area and sampling design: Ant assemblages were sampled from May to July of 2007 along a North-South transect of ca. 1200 km at 16 sample sites (n = 16), in eight protected areas (each containing two sample sites) in Iran
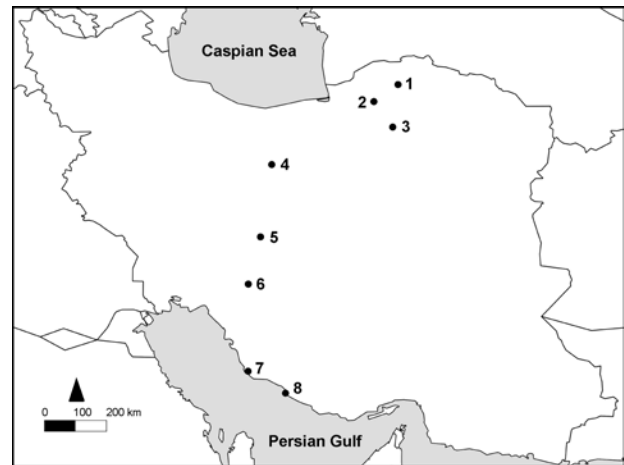

Fig. 1: Map of Iran depicting eight protected areas. The numbers indicate the following protected areas: (1) Mirzabailu, (2) Khoshyelagh, (3) Turan, (4) Kavir, (5) Kolahghazi, (6) Dena, (7) Mond, (8) Naiband.

(Fig. 1). Epigaeic ants were captured by pitfall trapping which is the most appropriate method for collecting ants in open areas such as steppe and deserts (AGOSTI & al. 2000). Sample sites were at least 1000 m and at most 2000 m apart. At each site we laid out a 290 m long transect of pitfall traps. Along each transect 30 pitfall traps were placed spaced at 10-m intervals. The minimum 1 km distance between sample sites removed any pseudoreplication of local ant assemblages in our study. The midpoint of each transect was recorded using a Global Position System device (Garmin eTrex®). We left pitfall traps open for three days. Ant species were determined when possible (BOLTON 1994, COLLINGWOOD & AGOSTI 1996, RADCHENKO 1997) or else assigned to morphospecies. Voucher specimens of each ant species are held in the AntBase.Net Collection (ABNC) of the Institute of Experimental Ecology of the University of Ulm (http://www.antbase.net) and in the private ant collection of the corresponding author.

Data analysis: Data analysis includes three main steps: (1) Using mantel correlogram, we investigated the decay of similarity among ant assemblages and also environmental factors across geographical distances; (2) We used a variance partitioning ordination approach to quantify the relative importance of environmental and spatial factors for species turnover among ant assemblages; and (3) We used indicator species analysis to measure the association of species to their habitats.

Mao Tao function of EstimateS 7.5.2 software was used for the calculation of interpolated accumulation curves (COLWELL 2005). This model was adopted to produce sample-based species accumulation curves derived from incidence-based data (COLWELL & al. 2004). These curves were applied for measuring the sampling effort. The Chao2 estimate was used for calculation of species richness for each site assuming that sampling went to completion. The incidence-based non-parametric estimators such as Chao2 are widely used in ant ecology to correct sensitivity of the counts of observed species to total abundance and the number of individuals collected in the samples (GOTELLI & al. 2011).

A species × sample site (presence-absence) matrix was prepared as a community dataset. The resulting assemblage data matrix was Hellinger-transformed to express species occurrences as square-root transformed balanced occurrences in each sampling site (LEGENDRE & GALLAGHER 2001).

To describe the spatial structure of species assemblages in relation to geographical distance, we used the normalized Mantel statistic (correlogram), which determines linear relationships between two sets of distance-based data: the species composition matrix and the geographical distance matrix. A Mantel statistic is another form of distance – decay analysis. It provides, however, a more detailed analysis than an overall distance – decay graph. GPS coordinates of transects were converted to a geographical distance matrix of Euclidean distances (km) by software SAM 3.1 (RANGEL & al. 2006). The R language (R DEVELOPMENT CORE TEAM 2007) function "mantel.correlog" in the vegan package (OKSANEN & al. 2009) was used to compute our multivariate Mantel correlogram with Pearson correlation. We also described spatial structure of environmental factors using the SAM 3.1 package to calculate values of Moran's I and to produce correlograms for the selected environmental variables (see below). For both methods we applied the Sturge equation to estimate distance classes, the Bonferroni progressive correction (α = 0.05), and 999 permutations for significance tests.

We examined the contribution of environmental and spatial factors by partitioning the variation in species composition between these two groups of factors (PERES-NETO & al. 2006). Variation partitioning methods are suitable as explanatory tools to develop hypotheses about contributions of dispersal-based and niche-based processes to community composition (LEGENDRE & al. 2005, GILBERT & BENNETT 2010, PERES-NETO & LEGENDRE 2010, DINIZ-FILHO & al. 2012). To model variation of species composition of ants along our ecological transect, a set of environment variables (see Appendix S1, as digital supplementary material to this article, at the journal's web pages) was used including elevation, habitat heterogeneity, productivity (normalized difference vegetation index) and five climate variables (mean annual temperature, mean diurnal temperature range, mean annual precipitation, mean summer precipitation and relative humidity; see Appendix S2 for more details). In sum, mean annual temperature was from 13 to 26 °C, and mean diurnal temperature range was between 9 and 17 °C. Mean annual precipitation ranged from 121 to 860 mm and mean summer precipitation ranged from 0 to 16 mm. The relative humidity ranged from 38 to 60. The "forward.sel" function of the packfor package (DRAY & al. 2007) of R language (R DEVELOPMENT CORE TEAM 2007) was used to select those environmental variables that contributed significantly to the explanation of ant composition. The advantage of this forward selection function is that two criteria (alpha level and adjusted R^2 of the full model) are used to stop the variable selection procedure. This procedure returns fewer variables than the full model with a smaller value of adjusted R^2. However, these variables are more realistic than the variables of the full model (BLANCHET & al. 2008). Applying redundancy analysis (RDA), we made a global (full model) test of the variables and calculated the adjusted R^2 of the global model, which

was used as the second criterion in forward selection. Forward selection was applied at the α = 0.05 level and an adjusted R^2 of 0.51 (= full environmental model) with 999 random permutations. After variable selection, the co-linearity of the selected environment variables was inspected with the "vif.cca" function of the "vegan" package. We used only the selected variables in subsequent analyses.

The spatial factors of ant samples was determined and modeled by using principle coordinates of neighbor matrices (PCNM). This method is used to model spatial structure as predictor variables of variation in ecological assemblages in applications of multiple regression or canonical ordination (BORCARD & LEGENDRE 2002). We computed PCNM variables by the "quickPCNM" function of the *PCNM* package (LEGENDRE & al. 2009) of R language from the species composition matrix and the GPS coordinates of the transects and used the "forward.sel" of packfor package, double stopping criterion (α = 0.05, adjusted R^2 of 0.34) and 999 random permutations to select the best PCNM eigenfunctions by forward selection. The selected PCNMs eigenfunctions were used as spatial explanatory variables in the variation partitioning of the ant species composition data.

RDA was used to partition the proportion of the variation in species composition of ants explained by environmental and spatial variables. Using the "varpart" function of the vegan package of R language, the following fractions of total variation of ant composition were calculated: total explained variation [E + b + S], environmental variation [E], spatial variation [S], the common variation shared by environment and space [b], and unexplained variation [d]. Furthermore, we calculated the fraction of variation in ant composition that can be explained by purely environmental variables [E | S] and the fraction of variation that can be explained purely by spatial variables [S | E]. We used adjusted R^2 statistics for variation partitioning as recommended by PERES-NETO & al. (2006). The significances of testable fractions, [E], [S], [E + b + S], [E | S], and [S | E], were tested by means of 999 permutations by the "rda" and "anova.cca" functions in the vegan package.

RDA was used for the fraction [E] to examine the relationship between ant assemblages and environmental variables. The fitted scores of the first two canonical axes were extracted and mapped in a biplot to visualize the pattern of the species composition in each of these fractions. The extracted fitted scores were also used to run multiple regression analyses, which selected those environmental and spatial parameters that were used as explanatory variables to check which parameters contributed most to the site scores of these fractions, as judged from their partial coefficients. RDA was computed by using the vegan package. Multiple regression analyses were performed with STATISTICA 8.0 (STATSOFT 2007).

To determine characteristic species of the various sites, we used "indicator species analysis" (DUFRÊNE & LEGENDRE 1997) with PC-ORD 5.17 (MCCUNE & MEFFORD 2006). This analysis calculates indicator values for each species by combining the relative abundance of a certain species with its relative frequency of occurrence in the various transects. The estimated values were tested for statistical significance by randomization tests (Monte Carlo, 1000 permutations).
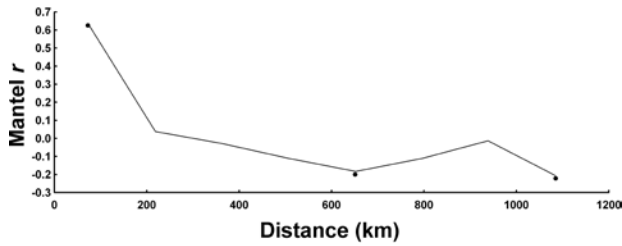
Fig. 2: Mantel correlogram showing spatial correlation (Mantel *r*) for the ant assemblages. Black circles indicate significant spatial autocorrelation after progressive Bonferroni corrections (α = 0.05, 999 permutations).

Results

A total of 69 species / morphospecies along the North-South transect were collected (for further details, see PAKNIA & PFEIFFER 2011b: tab. S1). *Cataglyphis* was the most speciose genus with 12 species, followed by *Messor* and *Monomorium* with ten and seven species, respectively. By contrast, we found only one species per genus for *Aphaenogaster*, *Lasius*, *Paratrechina*, *Pachycondyla*, and *Proformica*. The most common species were *Monomorium indicum kusnezovi* SANTSCHI, 1928 and *Cataglyphis nigra* (ANDRÉ, 1881), which occurred in 30% and 23% of all pitfall traps, respectively. In contrast, five species *Aphaenogaster gibbosa* (LATREILLE, 1798), *Lasius* cf. *alienus* (FOERSTER, 1850), *Messor* cf. *striaticeps* (ANDRÉ, 1883), *Paratrechina* cf. *longicornis* (LATREILLE, 1802), and *Crematogaster* sp. 5 were unique and occurred only in one pitfall trap. *Lepisiota semenovi* (RUZSKY, 1905) and *Monomorium indicum kusnezovi* had the widest distribution and occurred at seven out of 16 sites.

The species richness per site ranged from 8 - 14, and the Chao2 estimates of site species richness varied from 8 - 15. In 12 of the 16 sites, the rarefaction curves of the samples leveled off, indicating that further sampling with the pitfall trap method would probably have not added new species. The other four curves showed high degrees of asymptotic behaviour (Appendix S3).

Species composition did not decay smoothly with distance. Instead, it exhibited significant positive spatial autocorrelation over short distances and then steep decrease and significant negative spatial autocorrelations over long distances (Fig. 2), indicating that the ant assemblages were more similar than they would be by chance at the shortest distance and were more dissimilar than expected by chance at the farther distances. Environmental parameters also exhibited positive spatial autocorrelation over short distances and negative spatial autocorrelation over long distances (Fig. 3).

The forward selection retained three significant environmental variables for the modeling of species composition: annual precipitation ($F = 3.15$, $P < 0.001$), summer precipitation ($F = 3.67$, $P < 0.001$), and mean diurnal temperature range ($F = 3.75$, $P < 0.001$). The cumulative adjusted R^2 of this selected model was 0.39. PCNM generation over 16 sites produced nine positive PCNM eigenvalues. Forward selection procedure retained three significant PCNMs out of nine positive PCNM vectors: PCNM 3 ($P = 0.005$), PCNM 5 ($P = 0.001$), and PCNM 6 ($P = 0.029$). Adjusted R^2 of the selected model was 0.32.
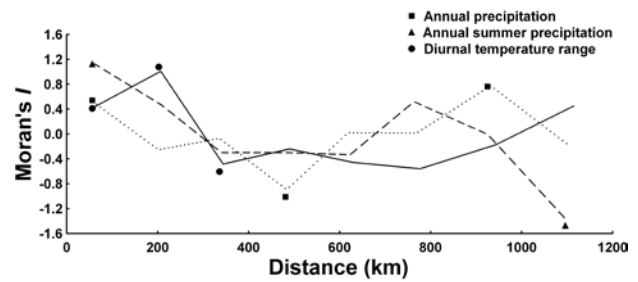

Fig. 3: Correlogram showing spatial correlation (Moran's *I*) for three environmental variables entered in the variation partitioning model: annual precipitation, annual summer precipitation, and mean diurnal temperature range. Black circles, black triangles and black quadrates indicate significant spatial autocorrelation after progressive Bonferroni corrections (α = 0.05, 999 permutations).

Tab. 1: Variation partitioning of the ant community composition by using two subsets of data: spatial (PCNMs) and environmental variables. E = environmental, S = spatial, E | S = purely environmental, S | E = purely spatial, b = the common fraction of variation shared by space and environment, and d = undetermined.

Fraction	d.f.	R^2	Adjusted R^2	*P* value
E	3	0.51	0.39	0.001
S	3	0.33	0.17	0.003
E + b + S	6	0.77	0.62	0.001
E	S	3	0.66	0.45	0.001
b	0	–	-0.06	Untestable
S	E	3	0.53	0.23	0.001
d	–	–	0.38	Untestable

Variation partitioning of ant species composition included three environmental and three spatial (PCNM) explanatory variables. In total, both the spatial and the environmental variables explained 62% of the species composition variation and left 38% unexplained (Tab. 1). Spatially dependent environmental variables explained 39% of the variation in species composition. Partialling out the negative spatial structure of environmental variables, purely environmental factors explained a larger amount of variation, equal to 45% of species composition (Tab. 1). Selected PCNM variables, explained 17% of total variation of species composition. Purely spatial variables explained 23% of the total variation. All testable fractions were significant (all $P < 0.003$).

RDA of fraction environment retained three axes (axis 1: $R^2 = 0.22$, axis 2: $R^2 = 0.17$, and axis 3: $R^2 = 0.12$; all $P < 0.001$). The first two axes discriminated ant species composition in four groups (Fig. 4). Summer precipitation had the largest partial contribution to axis 1 ($R = -0.97$, $P < 0.0001$), and annual precipitation the largest partial contribution to axis 2 ($R = -0.98$, $P < 0.0001$). Axis 1, which can be interpreted as a summer precipitation gradient, discriminated the four northern steppe sites from other sites (Fig. 4). The second axis, which was strongly correlated with annual precipitation, split ant species composition into three assemblages. The first group contained the two western

Tab. 2: Indicator ant species with their indicator values and statistical significance. Only the four species with the highest indicator values for each habitat have been listed. The means and standard deviations are given together with *P* values for the null-hypothesis of no difference between sites (MCCUNE & MEFFORD 2006).

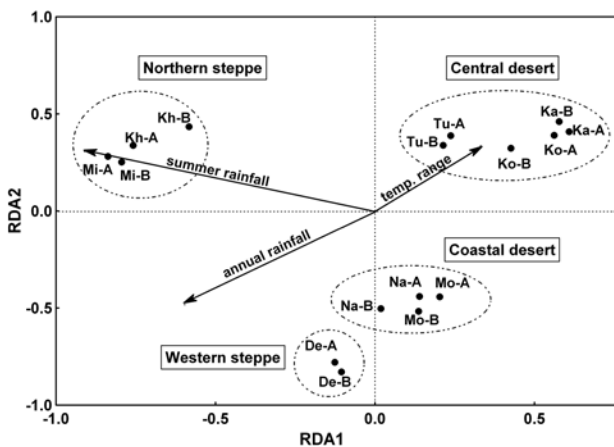| Species	Habitat	Indicator value (IV)	IV from randomized groups		*P* value
			Mean	Standard Deviation	
Tetramorium schneideri EMERY, 1898	Northern steppe	56.8	2.5	0.94	0.0002
Camponotus fedchenkoi MAYR, 1877	Northern steppe	56.7	2.2	0.94	0.0002
Messor denticulatus SANTSCHI, 1927	Northern steppe	51.1	2.7	0.91	0.0002
Crematogaster sp. 2	Northern steppe	44.9	2.1	0.98	0.0002
Cataglyphis cf. *foreli* (RUZSKY, 1903)	Central desert	87.1	2.4	0.98	0.0002
Cataglyphis cinnamomea (KARAVAIEV, 1910)	Central desert	43.6	3.0	0.91	0.0002
Cataglyphis emeryi KARAVAIEV, 1911	Central desert	41.7	2.8	0.89	0.0002
Cataglyphis noda BRULLE, 1833	Central desert	40.6	3.1	0.91	0.0002
Cataglyphis frigida persica (EMERY, 1906)	Western steppe	60.0	2.1	0.99	0.0002
Cataglyphis kurdistanica PISARSKI, 1965	Western steppe	50.8	3.0	0.93	0.0002
Camponotus gestroi EMERY, 1878	Western steppe	40.2	2.0	1.00	0.0002
Camponotus aethiops (LATREILLE, 1798)	Western steppe	38.5	2.3	0.95	0.0002
Monomorium dentigerum (ROGER, 1862)	Coastal desert	60.9	2.8	0.93	0.0001
Monomorium sp.	Coastal desert	60.4	2.7	0.91	0.0002
Cataglyphis rubra (FOREL, 1903)	Coastal desert	45.0	2.9	0.94	0.0002
Messor caducus (VICTOR, 1839)	Coastal desert	43.3	2.0	1.02	0.0002

Fig. 4: Redundancy analysis biplots of the first two axes corresponding to environmental variation [E]. Abbreviations indicate De: Dena, Ka: Kavir, Kh: Khoshyelagh, Ko: Kolahghazi, Mi: Mirzabailu, Mo: Mond, Na: Naiband and Tu: Turan. The two transects within each region are shown as A and B.

steppe sites, which received the highest amount of annual precipitation, 862 mm year^{-1}. The second group contained the four coastal desert sites, receiving more than 235 mm annual precipitation (Fig. 4). The third group contained the remaining sites, including the northern steppe and the central desert regions, both with lower than 185 mm annual precipitation (Fig. 4). RDA of the purely environmental fraction retained also three significant axes. The first two axes of this analysis separated ant compositions almost similar to the former RDA analysis, so we do not show the associated biplot. The indicator analysis determined a large number of species as indicators (56 out of 69 species, all *P* < 0.01), suggesting strong associations of ants to their habitats (Tab. 2; see Appendix S4 for a list of 56 ant species with significant indicator values).

Discussion

In this study, we found that the major part of variation (62%) among ant species composition in Iranian arid and semi-arid regions is interpretable by environmental and spatial variables. This result is in contrast to two comparable studies on tropical forests ants (VASCONCELOS & al. 2010, MEZGER & PFEIFFER 2011), which detected little evidence for the influence of spatial and environmental parameters on the species composition of ants. MEZGER & PFEIFFER (2011) found that environmental and spatial parameters influence ant species richness (47.7%), but not species composition (16.2%), and concluded that other factors like competition and neutral processes drive ant species composition in Bornean rainforest. Similarly, environmental and spatial factors explained 24.5% of variation in ant species richness and 31.2% of variation in ant species composition in Amazonian forests (VASCONCELOS & al. 2010). These findings suggest that in tropical forests species composition of ant communities may be determined in large measure by stochastic processes. Although different sampling methods were used in these studies, the high sampling effort in all studies reduces the possibility that these differences may simply be an artifact of different methodologies.

In our parsimonious model, three spatially structured climate variables, mean diurnal temperature range, annual precipitation, and summer precipitation, explained 39% of beta diversity. This suggests that mechanisms linked to environmental filtering and niche-based processes may be regulating beta diversity on ants in the Persian semi-deserts and deserts. In arid and semi-arid areas precipitation is well known for having a strong influence on many biological processes, such as primary production (considered usually as the surrogate of primary production in the community ecology analyses). Precipitation in these areas is, moreover, often sporadic and unpredictable (NOY-MEIR 1973). Here we demonstrate that the amount of yearly precipitation and the pattern of its occurrence explain a significant component of variation in ant species composition across arid areas of Iran (Fig. 4a). The RDA ordination discriminated the western steppe assemblage from the remaining sites by its high amount of annual precipitation. The western steppe region is characterized by sparse oak forests that contrast starkly with other regions where the dominant vegetation is decidedly scrub-like. This remarkable difference of vegetation diversity and structure appears to support groups of ants, which are dependent on high diversity and density of vegetation as either food / nest sources or niche for foraging. As a consequence, two out of four main indicator species in this region are the arboreal foraging species *Camponotus gestroi* EMERY, 1878 and *Camponotus aethiops* (LATREILLE, 1798).

In the same line, summer precipitation, which has crucial impact on flowering and biomass of plants, appears to support a different assemblage of ants, remarkably granivorous ants, which are in close symbiotic (however antagonistic) relation with plants. In their long-term experiment in a North American arid grassland, KASPARI & VALONE (2002) found that the abundance of granivorous ants was positively influenced by seed production following summer precipitation. This is a potential explanation for the discrimination of the ant assemblage of the northern steppe, where a notable number of indicator species are granivorous, such as *Messor denticulatus* SANTSCHI, 1927, and *Tetramorium schneideri* EMERY, 1898 (Tab. 2).

Regarding two western and northern steppe regions, it is tempting to put forward a parsimonious mechanism for generating variations in community composition by suggesting primary productivity and its temporal availability as key driver of beta diversity. However, it remains unanswered why precipitation and not NDVI as a better surrogate of primary productivity has been entered in the final model. We are not able to explicitly answer this question, but we predict that quite likely precipitation also has indirect influence on variations in ant community composition. For example, a combination of soil type and moisture availability can have remarkable impact on the colonization of ants, preventing some species and instead supporting other species (HILL & al. 2008).

Similar as in Mongolian drylands (PFEIFFER & al. 2003), our findings show that mean diurnal temperature range can explain significant variation in ant beta diversity. Sites within the central desert region of Iran were separated from other sites by their larger diurnal temperature ranges. The central desert region has an extreme continental climate with large diurnal and annual temperature fluctuations and cold winters with 30 - 90 days below freezing per year

(BRECKLE 2002). The wide fluctuations in temperature almost surely prevent the colonization of certain regions by many ant species lacking physiological or behavioral adaptations to large temperature fluctuations and very low minimum temperatures. The Iranian central desert region receives a lower amount of annual precipitation than other sites (Fig. 4). As a result, ant species in this region have to cope with low primary productivity in addition to temperature fluctuations. Interestingly, the indicator species in this habitat, such as *Lepisiota semenovi* (RUZSKY, 1905) and six *Cataglyphis* species, are omnivores and scavengers, which are common diet strategies in desert ecosystems with low primary productivity (see ROJAS & FRAGOSO 2000).

Myrmo-ecologists generally focus on factors that represent the total or mean values of climate factors (e.g., SANDERS & al. 2007). In our study, two out of three predictors namely mean diurnal temperature range and summer precipitation represent the variation or temporal pattern of climate factors, suggesting that not only mean values of climate factors but their fluctuation across dial or seasonal cycles are important in determination of the ant beta diversity.

Spatial factors explained significantly 17% of ant beta diversity. This is close to the spatial impact on ant communities in Amazonian forests, which were sampled across a 2000 km transect (VASCONCELOS & al. 2010), while in contrary Bornean ant communities, sampled from a small geographical area, were much less impacted by spatial factors (MEZGER & PFEIFFER 2011). Thus, at large geographical scales ants show a limited dispersal, which cause variance in species composition. These findings suggest that at large extent spatial factors play an important role in the determination of the local composition of species regardless of ecosystem type. The mechanistic basis behind dispersal limitation remains unknown, and might be distinctive among different ecosystems, e.g., controlled by climate variables or ability of species. Dispersal limitation of gynes might be a possible cause for observing similar patterns in widely different ecosystems (PFEIFFER & MEZGER 2012).

At least for our study, it would appear that environmental variables control ant dispersion and limit it to short distances. The result of the Mantel correlogram shows a strong positive spatial autocorrelation at the shortest distance (Fig. 2). Interestingly, this pattern is in concordance with the correlogram of the environmental variables (Fig. 3). We interpret this as indication that dispersal of ants in arid regions is controlled by environmental conditions and not by their dispersal ability. Neutral models, however, which assume that the environment is homogenous, predict that species composition changes across space because of the limited dispersal of species (HUBBELL 2001). The regions studied by us are certainly not homogeneous. This restricts the dispersal processes of many species to a short distance within a homogeneous region (Fig. 2 and 3) and prevents their colonization of habitats with unfavorable conditions.

When no access to relevant and extensive environmental data is available, then the spatial fraction should also be considered as the result of spatially structured yet unmeasured explanatory variables. Because soil texture varied considerably among sites from sandy to clay but was not measured, we predict that soil texture and soil chemistry

are two important components of this fraction as soil texture and chemistry can affect the species composition of ants (HILL & al. 2008, KASPARI & al. 2008).

Of the variation in ant assemblages, 38% remains undetermined. A possible explanation for this fraction is "stochastic processes". In other words, it can be explained as a result of ecological drift, assuming that differences in the species composition of ants result primarily from stochasticity in birth, death, and colonization of species. Again, the relatively smaller value of this fraction in comparison to environmental and spatial fractions, contrasts with the neutral theory, stressing the importance of the niche-based process. Non-spatially structured environmental variables, such as local disturbance (HILL & al. 2008), local mosaic-like environmental variations (PFEIFFER & al. 2003), and biological variables, such as intra- and inter-specific competitive interactions (ANDERSEN 2008, PARR 2008, PFEIFFER & al. 2008), might also be responsible for this fraction.

In conclusion, the significant large impact of the pure environment and spatial fractions and the lack of smooth distance decay both suggest that ant species composition in arid and semi-arid regions of Iran is controlled mainly by niche-based processes. We highlight the importance of environmental factors in the determination of ant beta diversity in arid regions of Iran. One interesting outcome of the study is that the variation in ant species composition is driven not only by the amount of precipitation but also by its occurrence patterns. This finding is even more important when we consider that many future climate scenarios predict substantial changes in temporal patterns of precipitation (VERA & al. 2006, ZAITCHIK & al. 2007). Thus future conservation studies should carefully take the temporal pattern of precipitation into account. In our model, we did not include historical data (phylogeny) and regional species pool, as there is no such a data for the region, but we predict that these factors can play a noteworthy role in structuring of the ant assemblages in our study system.

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