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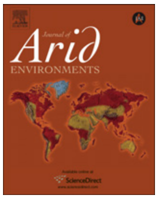

Productivity alone does not explain species richness of ants – An example from Central Persian deserts

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ABSTRACT

The existing literature proposes that productivity is responsible for biodiversity gradients in terrestrial habitats at large extents. At smaller spatial scales, however, other explanatory variables diminish or weaken the effect of the productivity predictor. These ideas have not been tested directly using ant communities. We studied a small extent of the geographical gradient of ant species richness in the Central Persian Desert ecoregion, Iran. We evaluated support for productivity and a series of alternative models with additional variables to examine determinants of ant species richness. Our results supported nine models. The productivity model and the tolerance–productivity model received the highest support. A curvilinear relationship was evident between ant species richness and productivity. In contrast to earlier work, we found that the ant species richness increased with increasing latitude. Our results suggest that in this desert ecosystem, plant productivity is the most important variable that controls ant species richness. Productivity did not completely explain the spatial gradient in ant species richness. At small spatial scales, other variables that co-vary with productivity have significant roles.

1. Introduction

The study of spatial gradients in the number of local coexisting species has long attracted community ecologists. At large spatial scales such as the global or a continental scales, an extensive literature suggests that a water–energy combination, measured indirectly as plant productivity, drives biodiversity gradients in terrestrial habitats (Hawkins et al., 2003). At small spatial scales, however, studies sample only a small range of possible productivity values. Consequently, patterns observed at smaller spatial scales may differ markedly, preventing generalizations. At small spatial scales the effect of the water–energy combination on species richness is weakened by effects of habitat complexity (Jimenez-Valverde and Lobo, 2007), dispersal (Shurin and Allen, 2001) and stress tolerance (Gough et al., 1994).

These scale-dependent differences are also observed in ants. Ants are important herbivores, omnivores or predators in most terrestrial ecosystems, and their richness varies widely among habitats. At global and continental scales ant species richness correlates positively with productivity (Kaspari et al., 2000) and negatively with annual temperature range (Dunn et al., 2009). At smaller scales, however, there is no such generalization. For example, studies in arid or semi-arid lands do not demonstrate a positive correlation between ant species richness and rainfall (but see Davidson, 1977; Marsh, 1988). The diversity of seed harvesting ants in Australia is not positively correlated with rainfall (Morton and Davidson, 1988). Similarly, there is no positive correlation between ants species richness and rainfall in the arid regions of Mongolia (Pfeiffer et al., 2003) and the Paraguayan dry Chaco (Delsinne et al., 2010).

In general, however, deserts and semi-deserts are productivity-controlled ecosystems. Low precipitation, high evapotransporation ratios and high temperature limit primary productivity to very low levels (Noy-Meir, 1973). As a result, productivity is suggested as the main limiting factor for species richness of animals in warm and dry ecosystems (Hawkins et al., 2003). Why does ant species richness fail to follow this expected pattern? The absence of a relationship or a negative relationship between rainfall (as a surrogate of productivity) and ant species richness might arise from the important effects of other environmental variables: edaphic variability (Morton and Davidson, 1988), covariance of productivity with climate factors such as temperature (Pfeiffer et al., 2003), and

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the social behaviour of ant taxa (Delsinne et al., 2010). However, it can also be argued that none of these studies has measured productivity directly. In contrast to rainfall, NDVI, the Normalized Difference Vegetation Index, is a direct measure of productivity (Evans et al., 2005; Kerr and Ostrovsky, 2003), and has successfully been applied as a proxy for habitat heterogeneity in a few studies on ant community ecology (Lassau et al., 2005; Narendra and Ramachandra, 2008).

In the present analysis, we used NDVI to examine the geographical gradient in species richness of ants in the Central Persian desert basins of Iran across a small latitudinal gradient. Our objective was to assess whether or not gradients in ant species richness parallel productivity gradients. We considered five competitive models for explaining the ant species richness gradient in the semi-cold drylands of our study region. These are: 1) the *productivity* model that suggests the geographical variation in ant species richness correlates positively with productivity. In this model, species richness is regulated by taxon density, which in turn responds directly to productivity (Kaspari et al., 2000); 2) the *habitat complexity model*, proposing that higher species richness occurs in an area with greater diversity of habitats because ant species have habitat preferences and structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources (Gibb and Parr, 2010); 3) the *tolerance model*, assuming that species richness in a particular area is limited by the number of species that can tolerate the local conditions, such as temperature (Mezger and Pfeiffer, 2010); 4) the *evolutionary diversification model* that suggests evolutionary rates are faster at higher ambient temperatures due to shorter generation times, higher mutation rates, and faster physiological processes (Allen et al., 2002); 5) The *plant–ant interaction model* suggests that plant species richness directly affects ant species richness. In arid lands plant–ant interactions are either antagonistic, in which plants are food resources for ants (e.g. harvester ants), or mutualistic (Rico-Gray and Oliveira, 2007). In this study we examine the strength of support for these five models (Table 1) and all of their possible combinations (total of 32 models), attempting to determine the relative importance of these model(s) in explaining ant species richness in a dryland ecosystem.

2. Materials and methods

2.1. Study area

We conducted the study in the Central Persian Desert Basins ecoregion, in Iran. This ecoregion covers approximately 600,000 square kilometres of arid steppes and desert in central Iran, flowing over into Afghanistan. Dominated by large areas of salt deserts, sabkhas and salt marshes, the region hosts a great variety, in weather conditions, soil composition, and topography. Annual precipitation varies between 50 mm and 500 mm. The average annual temperature fluctuates between 15 °C and 24 °C and temperature range varies between 10 °C and 17 °C. The region's elevation varies between 1000 m and 1900 m. This habitat can be regarded as a transitional zone between the hot deserts of Arabian Peninsula and the cold deserts of Central Asia. The local flora includes halophytic species *Acanthophyllum* spp., *Astragalus* spp. and *Euphorbia* spp. in the form of herbs and small shrubs.

2.2. Data collection

We sampled ant assemblages at 32 separate sites within eight protected areas (Fig. 1) between 28 April to 30 May 2008. This period is the end of the wet season, and is the yearly peak in ant activity. The study was conducted across three latitudinal degrees, with the maximum distance between sites being 546 km. Within each protected area we chose four sampling sites, which were separated on average by 1108 m (±696 m SD). This distance between sample sites removed any pseudoreplication of ant assemblages in our study. At each study site, a series of 20 pitfall traps were laid out in a 5 × 4 patterns, with traps spaced at 10 m intervals. The traps were constructed of cylindrical plastic cups 65 mm in diameter and 100 mm in depth. The cups were filled two-thirds with a 1:1 mixture of propylene glycol and water to preserve captured ants. All pitfall traps were left open for a period of four days. In lab, we identified ants to species where possible or assigned them to morphospecies (Table S1). Voucher specimens of each species collected are held in the AntBase.Net Collection (ABNC) at the Institute for Environmental Sciences of the University of Koblenz-Landau (http://www.antbase.net) and in the private ant collection of the corresponding author.

We measured or extracted five environmental variables, which were related to the tested models (Table 1). Climate variables (temperature range and annual mean temperature) were extracted from the Worldclim database at ~1 km spatial resolution data layer (Hijmans et al., 2005). We used the NDVI data layer obtained from the NASA MODIS algorithm (MOD13Q1) at 250 m spatial resolution and 16 days temporal resolution for a period of May 2007–May 2008 as surrogate of Net Primary Productivity (NPP) (Kerr and Ostrovsky, 2003). The number of plant species was counted along two 40 m transects within each pitfall sampling grid. The mean number of these two transects was considered as plant species number in each grid. Habitat complexity was measured by determining foliage height and density by following method. A 1 m^2 plastic quadrat was placed over each pitfall trap, in total 20 quadrats for each pitfall grid. At each of the four corners of the quadrat a 160 cm rod was placed vertically through the vegetation, and the number of contacts with the foliage was recorded. The total number of contacts within each sampling plot was calculated as a measure of habitat complexity.

Table 1
The five candidate models (predictors) used in analysis and their correlation (Spearman correlation) with the ant estimated species richness. See text for details of the explanatory variables and explanation of the models.

Model	Explanatory variables	Hypotheses	Correlation (*r*)	*P* value
Productivity	NDVI	Available energy in the environment directly affects ant species richness	0.72	0.009
Complexity	Habitat complexity	Complexity of habitat facilitates the coexistence of a greater number of species	0.49	0.06
Tolerance	Temperature range	Ant species richness is limited to those species that can tolerate the local condition	−0.55	0.05
Biotic interaction	Plant species richness	Plant species richness in the environment directly affects ant species richness	0.45	0.03
Ambient energy	Mean annual temperature	Evolutionary rates are faster at higher ambient temperatures	−0.44	0.09