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The effects of biome and spatial scale on the Co-occurrence patterns of a group of Namibian beetles

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ABSTRACT

Co-occurrence patterns (studied by C-score, number of checkerboard units, number of species combinations, and V-ratio, and by an empirical Bayes approach developed by Gotelli and Ulrich, 2010) are crucial elements in order to understand assembly rules in ecological communities at both local and spatial scales. In order to explore general assembly rules and the effects of biome and spatial scale on such rules, here we studied a group of beetles (Coleoptera, Meloidae), using Namibia as a case of study. Data were gathered from 186 sampling sites, which allowed collection of 74 different species. We analyzed data at the level of (i) all sampled sites, (ii) all sites stratified by biome (Savannah, Succulent Karoo, Nama Karoo, Desert), and (iii) three randomly selected nested areas with three spatial scales each. Three competing algorithms were used for all analyses: (i) Fixed-Equiprobable, (ii) Fixed-Fixed, and (iii) Fixed-Proportional. In most of the null models we created, co-occurrence indicators revealed a non-random structure in meloid beetle assemblages at the global scale and at the scale of biomes, with species aggregation being much more important than species segregation in determining this non-randomness. At the level of biome, the same non-random organization was uncovered in assemblages from Savannah (where the aggregation pattern was particularly strong) and Succulent Karoo, but not in Desert and Nama Karoo. We conclude that species facilitation and similar niche in endemic species pairs may be particularly important as community drivers in our case of study. This pattern is also consistent with the evidence of a higher species diversity (normalized according to biome surface area) in the two former biomes. Historical patterns were perhaps also important for Succulent Karoo assemblages. Spatial scale had a reduced effect on patterning our data. This is consistent with the general homogeneity of environmental conditions over wide areas in Namibia.

1. Introduction

Distribution of living organisms is a very intricate coincidence of causes. It depends on a combination of large scale biogeographical patterns, local interactions (both autoecological and synecological) in a short time scale, influenced by demographic stochasticity and chance (Brown and Lomolino, 1998). Always keeping in mind the complexity of the assemblage of a natural community, in the present study we target our analyses on the intra- and interspecific relations. Diamond (1975) focused the importance of community assembly on species competitive interactions to generate predictable patterns of co-occurrence. In addition, coexistence patterns are often complicated in natural communities, and aggregation patterns can be as common as segregation patterns (e.g., Gotelli and Ulrich, 2010). Whilst segregation patterns are generally due to interspecific competition for limited resources (e.g., Gotelli and Graves, 1996), aggregation patterns may be due to divergent reasons, including niche similarity among species inhabiting given sites with abundant re source availability, or niche facilitation. Although statistical tools aiming at disentangling whether a given community is non-randomly assembled via species' segregation or species aggregation have been recently formulated (Gotelli and

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Ulrich, 2010), these two alternative scenarios have been poorly explored with field data, and to our knowledge, this has never been done previously in any taxonomical group of Afro-tropical invertebrates. Especially could be possible that, from a regional pool of species, some combination will never be found in nature because of interspecific interactions; and that in a community, particular pairs of species may never co-occur.

Broad synecological patterns can be explored with various statistical tools, which aim at uncovering eventual non-random community structure (Gotelli and Graves, 1996). Among these tools, co-occurrence analysis, based on indicators (e.g., C-score and number of checkerboard units) evaluated on a binary presence/absence matrix, are particularly suitable (Stone and Roberts, 1990; Gotelli and Graves, 1996). Despite co-occurrence analyses, accomplished with appropriate Monte Carlo methods, have widely been used in recent years with land vertebrates (e.g., Gotelli et al., 1997; Gotelli, 2000; and also in the Afrotropical Region, see Hofer et al., 2003; Luiselli et al., 2007), up to now these types of analyses have rarely been performed for determining community structure in floricolous insects of arid tropical environment, with very few community studies (e.g., Cambefort, 1991; Cambefort and Walter, 1991). In this regard, studies of insect community structure may be particularly interesting in arid environments of southern Africa, such as in Namibia, where a great proportion of the taxa is endemic (thus making the community structure very unusual compared to other generalized communities of the same organisms from elsewhere) and whose current distribution is not only the result of the long history of isolation experienced by these species, but concurrently also due to the extreme ecological pressures which are typical of deserts and semi-deserts (Jarvis and Robertson, 1997; Barnard, 1998; Maggs et al., 1998; Simmons et al., 1998).

In this paper, we investigated the co-occurrence patterns of Namibian Meloidae communities. More specifically, we aimed at uncovering eventual non-random competitive structures linking the various species within- and among communities.

In particular, we will answer to the following key questions:

(1) Are there general non-random patterns in co-occurrence of Namibian meloid beetles? We expect that a non-random structure will be absent in these beetles assemblages during our surveys because we did not sample the various beetle assemblages in each site of study during phases of population outbreaks. Indeed, it has been demonstrated that in phytophagous insects, intensive competition for the access to available resources may occur only during phases of insect outbreaks (Jermy, 1985). Lack of interspecific competition in phytophagous adult insects is attributed to the striking interspecific diversity which characterizes this insect category, meaning that plant communities provide an enormous amount of potential niches for them (Jermy, 1985).

(2) Is there any effect of the south-western African biome types on the random versus non-random structure of blister beetle assemblages? In this regard, it has been shown that, with regard to a group of ectothermic vertebrates, species richness at a given site was positively correlated to likelihood of uncovering a non-random structure (Luiselli, 2008). It is still unknown whether this pattern is general among animal communities. However, if this pattern is general, then we would expect to find a deterministic structure in the Savannah and Succulent Karoo biomes, because these two vegetation zones are characterized by a considerable Meloidae species diversity (number of species normalized by total surface) of a magnitude degree higher than Desert and Nama Karoo (values: 0.0184 in Succulent Karoo; 0.0218 in Savannah; 0.00397 in Desert; 0.00416 in Nama Karoo), as it has been demonstrated in recent studies (Pitzalis et al., 2014, 2016; Bologna et al. in press).

(3) Is there an effect of the spatial scale on the random versus non-random structure of blister beetle assemblages? We expect that, given the extension of southern African biomes and the relative homogeneity of them all throughout the southern portion of the continent, the scale effect should be small. Other studies found hierarchic effects of scale, with co-occurrence patterns of all species, species with larger abundances, and species with larger sizes being significantly higher than expected by chance at smaller scales, whereas at larger scales no significant differences compared to randomized matrices were usually observed, although with some exceptions in very heterogeneous habitats (e.g., Ulrich and Gotelli, 2007; Zhang et al., 2009).

2. Materials and methods

2.1. Study area

Field researches were conducted throughout almost the whole territory of Namibia, with a total of 186 sampling sites (Fig. 1). The climate of Namibia is primarily xeric, except in the north-eastern Caprivi strip, with rain being concentrated from January to April in most of the country, but in Winter (August–October) in south-western and southern central portion of the country (Tyson, 1986). Sampling sites occurred in all biomes of Namibia. These were (White, 1983):

1) Desert, characterized by extreme aridity, with primary therophytic plant dominance with chamaephytes being still important; temperatures may range 3–40 °C; mean rainfall around 20 mm per year, with an irregular distribution throughout the year.
2) Nama Karoo, characterized by bushlands with or without small trees (dominant plants: chamaephytes and hemicryptophytes), with non-succulent dwarf bushes and succulent plants; mean temperature is 3–26 °C; mean rainfall is 40–240 mm per year (Irish, 1994), and has a stochastic distribution throughout the year.
3) Succulent Karoo, characterized by succulent plant bushland (dominant plants: chamaephytes), with sandy and stony soils of Western Namaqualand in South-western Africa; mean temperature is 1–19 °C; mean rainfall is less than 200 mm per year, and occurs only in winter (July–August).
4) Savannah, characterized by grassy and bushy vegetation with co-dominance of phanerophytes and hemicryptophytes; mean temperature is variable by geographic zone, whereas mean rainfall is about 230 mm.

The number of sampling sites per biome was higher in tree and shrub savannah and in Nama Karoo, whereas it was much lower in the Namib Desert because of logistic constraints and the well known scarcity of Meloidae species in extremely arid environments.

Each sampling site was assigned to a given biome based on as referred in biomes map of Irish (1994), and (2) its values of temperature and rainfall recorded as follows (Table 1): we collected the mean of minimum and maximum temperature, and the mean of minimum and maximum rainfall of our sampling months.

2.2. Taxonomic model

Meloidae is a family of phytophagous beetles, of about 3000