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Can co-occurrence networks predict plant-plant interactions in a semi-arid gypsum community?

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ABSTRACT

Biotic interactions are important drivers shaping communities and their net effect can be difficult to assess when many species are involved or the study system is not well-known. Co-occurrence data are increasingly used to infer biotic interactions, but their accuracy remains poorly studied. We hypothesize that the predictions of biotic interactions based on co-occurrence networks are scale-dependent, being more accurate when co-occurrence is sampled at the spatial scale at which biotic interactions occur. We studied a plant community in a semi-arid gypsum environment, where plant-plant interactions result in a clumped distribution of the vegetation, which allows a straightforward identification of the scale at which interactions occur (i.e. vegetation patches). We used Bayesian network inferences to detect co-occurrence patterns at two spatial scales (patches of about 0.05 m^2 and plots of 2.25 m^2), and measured plant-plant interactions based on the effects of plant species on the establishment and recruitment of their neigbours. The co-occurrence network inferred at the patch scale did not reflect the plant-plant interactions observed, and the networks inferred at two different spatial scales showed contrasted topologies. Negative spatial associations between species predominated in the network inferred at the patch scale, partially due to a low species richness in vegetation patches. Meanwhile, positive relationships predominated at the plot scale. Relationships at the plot scale could reflect the final outcome of multi-specific biotic interactions, but without providing accurate information about pairwise interactions. Our results suggest that co-occurrence networks can be useful to generate hypothesis about the mechanisms structuring communities, but caution is needed in the interpretation of co-occurrence patterns in terms of biotic interactions, even when they are measured at apparently appropriate spatial scales.

1. Introduction

The role of biotic interactions is central in community ecology (Brooker et al., 2007), as they can influence species invasibility (Bulleri et al., 2008), and biodiversity patterns (Valiente-Banuet and Verdú, 2007). Despite their important role as drivers of community structure, biotic interactions might be difficult to assess under certain circumstances. Thus, when species identification is not straightforward and molecular techniques are required to explore community composition, inferences from co-occurrence data are widely used to study patterns of biological interactions and their temporal dynamics (Steele et al., 2011; Eiler et al., 2012; Kara et al., 2013; Wang et al., 2017). However, despite the widespread use of co-occurrence networks in community ecology, their accuracy to predict ecological interactions has been insufficiently validated (Berry and Widder, 2014).

Assessing how accurate is biotic interactions inference from co-occurrence data would benefit from systems where coexistence mechanism are relatively well known, and where biotic interactions can be easily characterized. In arid environments, biotic interactions are likely to influence the spatial distribution of vegetation. The strong effect of water stress in these environments, together with the presence of plants with a short-distant dispersal, leads to a characteristic spatial organization of plant species into vegetation patches surrounded by bare ground (Callaway, 2007; Navarro-Cano et al., 2014). This positive spatial association in vegetation patches has been shown to be correlated with plant facilitative interactions, assessed using experiments of neigbours removal (Tirado and Pugnaire, 2005). Plant-plant positive interactions have a central role shaping the composition of vegetation patches (Callaway, 2007; Drezner, 2006; Pugnaire et al., 1996). However, it is uncertain whether facilitative interactions influence the emergent structure of plant communities at a larger spatial scale. Since the relative importance of different processes varies across different

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spatial scales (HilleRisLambers et al., 2012), it might be misleading trying to infer biotic interactions from data sampled at an unappropriate spatial scale. In semi-arid environments, it is feasible to identify the spatial scale at which biotic interactions occur, as vegetation is organized in vegetation patches. Thus, these environments provide useful systems to assess the accuracy of biotic interactions inference based on co-occurrence information and whether the accuracy is scale-dependent.

A particular type of semi-arid environment is found in gypsum outcrops. Gypsum environments are characterized by a hard physical crust limiting plant establishment, chemical stress, principally due to an excess of calcium, and water stress (Escudero et al., 2015). In facilitative interactions, a facilitated plant gets a benefit from growing associated to another plant (i.e. nurse plant), without reverting in any damage for the latter (Callaway, 2007). Nurse plants in gypsum soils can enhance plant establishment under their canopy by reducing the environmental stress, leading to a predominant spatial distribution of plants in vegetation patches (Navarro-Cano et al., 2014). In a gypsum plant community, we assessed plant-plant interactions using classical studies of distribution patterns (Hutto et al., 1986) and plant fitness measurements (i.e. establishment and recruitment), and we studied co-occurrence patterns at a local (i.e. within vegetation patches) and at a larger spatial scale (2.25 m^2). We hypothesize that co-occurrence networks will capture biotic interactions when they are inferred from co-occurrence data sampled at the spatial scale at which biotic interactions are prone to occur (i.e. the vegetation patch scale). We tested (1) whether plant-plant interactions are accurately inferred from the pattern of species co-occurrence within vegetation patches, and (2) whether the co-occurrence networks inferred depend on the spatial scale at with co-occurrence is assessed (i.e. vegetation patch *vs*. plot).

2. Material and methods

2.1. Study site and field data

We studied a gypsum outcrop of 2.5 ha located in Petrer (Alicante), Spain (coordinates: 38°29′N, 0°44′O; elevation: 568 m). The climate is semi-arid, with an annual mean rainfall of 414 mm, and a variation of 55 mm between the driest and the wettest months. Mean daily maximum and minimum temperatures are 3.3 °C and 13.3 °C in January, and 18.4 °C and 30.6 °C in August. The plant community is dominated by chamaephytes, and the most abundant species are *Helianthemum squamatum (L.) Dum. Cours.*, *Teucrium libanitis Schreb.* and *Helianthemum syriacum (Jacq.) Dum.Cours*. Plants are often clustered forming vegetation patches surrounded by bare ground (Fig. 1). This vegetation distribution is characteristic of stressful semi-arid environments where adult plants can reduce the abiotic stress facilitating the establishment of other plants (Callaway, 2007; Navarro-Cano et al., 2014).

We randomly sampled 111 plots of 1.5 m of side, distributed at least 10 m apart from the closest plot. All plants within the plot, either in vegetation patches or isolated were identified and registered. We considered a vegetation patch when more than one plant were growing associated, and thus had the potential to interact. We considered that plants were associated to the same patch when their canopies overlapped, or when leave litter showed a previous overlapping of their canopies. When a patch was partially included within the plot, we only considered the portion of patch area and plants that were within the plot, in order to assess spatial associations. However, we also recorded species composition of the whole patch to infer co-occurrence at the patch level.

Nurse plants are defined as plant species that can establish on the bare ground, and whose establishment can enhance that of other plant species later on (Callaway, 2007). Therefore, in shrub land communities were many species share a similar physiognomy and growth rate, the largest plants within a vegetation patch are likely to be those that firstly established. Thus, we identified the tallest plant of a patch as the nurse plant (or dominant species), and when more than one plant was the tallest (i.e had similar sizes), all were considered as nurse plants of that patch. The height of the plants is highly correlated with their biomass, estimated by approximating the volume to: maximum diameter x minimum diameter x height ($N = 240$, $r = 0.73$, p-value < 0.001). Thus plant height was used to identify the largest species in each patch. The rest of individuals in the patch were considered as facilitated plants. We measured the maximal and minimal diameters of the patches, and approximated their areas to ellipses. We also identified and estimated the canopy area of plants growing on the bare ground. We recorded all plant species in each plot, but only shrubs and chamaephytes were abundant enough to be considered in further analyses. For each species we distinguish two contrasted age-classes (juvenile and adult). For chamaephytes species, we considered plants without lignification as juveniles. In the case of shrubs, where small individuals can be already lignified, we defined the two contrasting age-classes as follows: we calculated maximum diameter of the canopy of five large individuals, and we consider juveniles those individuals whose maximum diameter of canopy was inferior to a fifth of the mean of maximum diameter of the large individuals measured. Using a fifth of the size of large individuals is an arbitrary criterion, but suits our purpose of defining two contrasting age-classes, one of them being five times larger than the other. An enhancement of the survival within vegetation patches at any developmental stage will provide evidence for the benefits of growing associated to other plants. Thus, any threshold to define age-classes will be equally informative to assess differences in survival.

2.2. Distribution and fitness based characterization of the interactions in the community

The spatial association of different life stages to vegetation patches allows assessing whether the survival from one life-stage to the next (transition from seeds to juveniles (juveniles' establishment), and from juveniles to adults (ratio: adults/juveniles)) are enhanced or reduced when plants are associated to other plants, compared to when they grow solitary on the bare ground.

First, we assessed whether plants tend to be spatially associated in vegetation patches by determining the numbers of juvenile and adults of each species growing on bare ground and in vegetation patches, regardless of the nurse species in each patch. For each plant species, this distribution was compared to the number of plants expected to be found in patches *vs* bare ground, based on the total sampled area occupied by patches (Hutto et al., 1986). For instance, if patches occupy 20% of the total area sampled, and thus bare soil occupies 80%, the expected number of individuals on the bare soil is 80% of the total of individuals sampled. Binomial tests were performed to compare the distribution observed and expected, for juveniles and adults of each species.

Second, to detect plant-plant specific interactions, we studied the distribution of the plants under vegetation patches dominated by a given nurse species, and under other patches, regardless of which is the dominant species. To do so, we excluded the plants on bare ground from the analysis, we identified the nurses of each patch, and attributed the area of the patch to each of them. We first studied plant establishment, i.e. the transition from a seed to a juvenile plant, which encompassed dispersal and survival of early life-stages. To test for the preferential establishment of species B under species A, we recorded the distribution of the juveniles of B in patches dominated by A, and in other patches regardless of the dominant species. We used exact binomial tests to compare this distribution with that expected based on the proportion of the area covered by patches, and by patches dominated by species A. In patches where there was more than one nurse, the area of the vegetation patch was attributed to each nurse successively in each test.

We then assessed whether recruitment (i.e. the transition from a juvenile to an adult plant) was enhanced or reduced in vegetation