



Original article

Effect of livestock grazing in the partitions of a semiarid plant–plant spatial signed network



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ABSTRACT

In recent times, network theory has become a useful tool to study the structure of the interactions in ecological communities. However, typically, these approaches focus on a particular kind of interaction while neglecting other possible interactions present in the ecosystem. Here, we present an ecological network for plant communities that consider simultaneously positive and negative interactions, which were derived from the spatial association and segregation between plant species. We employed this network to study the structure and the association strategies in a semiarid plant community of Cabo de Gata–Níjar Natural Park, SE Spain, and how they changed in 4 sites that differed in stocking rate. Association strategies were obtained from the partitions of the network, built based on a relaxed structural balance criterion. We found that grazing simplified the structure of the plant community. With increasing stocking rate species with no significant associations became dominant and the number of partitions decreased in the plant community. Independently of stocking rate, many species presented an associative strategy in the plant community because they benefit from the association to certain ‘nurse’ plants. These ‘nurses’ together with species that developed a segregating strategy, intervened in most of the interactions in the community. Ecological networks that combine links with different signs provide a new insight to analyze the structure of natural communities and identify the species which play a central role in them.

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1. Introduction

Scientists have employed network theory to study the interactions within real systems for a long time (Boccaletti et al., 2006), including systems from a variety of fields as economics, sociology, physics, biochemistry, and ecology (Bascompte, 2007). In ecology, network analyses have become a powerful tool to study ecosystems as they address simultaneously the structural properties of a system (e.g. ecological community) and the role that its components (e.g. species) play in that structure (Newman, 2003). However, most research in ecological networks has focused in one particular type of interaction, such as trophic (feeding interactions between predator and prey, Dunne et al., 2002) and mutualistic relationships (mutually beneficial interaction between species, Bascompte and Jordano, 2007), while in nature various interactions happen at the same time. Only recently ecologists have started to analyze networks which include different types of interactions

simultaneously, but mostly with theoretical perspective (Fontaine et al., 2011; Kefi et al., 2012; but see Melian et al., 2009). Here we propose an empirical ecological network, which combines positive and negative interactions (competition and facilitation among plants) for the first time.

One particular system of interactions present in nature is the competitive–facilitative interactions that plant species establish among them. Plant species coexist in a particular habitat, where they compete for space and resources with other plants (Fowler, 1986). In addition, some plant species benefit the establishment of other plants because they accumulate nutrients under their canopies or provide protection against environmental factors (Pugnaire et al., 1996). This beneficial effect is called facilitation and has been suggested as a major structural factor influencing the organization of stressed plant communities (Brooker et al., 2008). Interactions between plant species influence the spatial distribution of vegetation, as competitive interactions are related with spatial segregation between plants while positive interactions are related with spatial aggregation (Tirado and Pugnaire, 2005). Although spatial distribution of vegetation depends not only on biotic interactions but on seed dispersal patterns and soil

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heterogeneity (Escudero et al., 2005), it is possible to approximate positive and negative interactions between plant species studying their spatial association and it is a common practice to study plant–plant interactions at community level (Cavieres et al., 2006; Verdu and Valiente-Banuet, 2008; Wiegand and Moloney, 2004).

The study of plant–plant interactions is of particular interest in arid and semiarid ecosystems. In arid ecosystems vegetation is distributed in multi-specific patches within a matrix of bare soil. Typically, patches consist of assemblages of shrubs that act as shelters against harsh environmental conditions ('nurses'), and several other plants that can only survive within these shelters (Armas and Pugnaire, 2005; Sala and Aguiar, 1995). Thus, positive interactions between plant species result in a strong vegetation spatial distribution pattern (Sala and Aguiar, 1995). Spatial association between plant species has been already employed to study the interaction network between plant species in an arid ecosystem, but only considering positive interactions present between 'nurses' and facilitated species (Verdu and Valiente-Banuet, 2008, 2011). We propose to include the negative interactions within the plant community to the network by deriving them from the spatial segregation between species.

In arid and semiarid ecosystems, competition occurs primarily about water, but allelopathy and the exploitation of minerals can be operating as well (Fowler, 1986). These mechanisms mainly act on a local state among neighboring plants and become apparent in reduced size and higher individual plant mortality as compared to plants growing apart. Therefore, competitive interactions drive to spatial segregation of species. It is important to point out that spatial segregation does not only depend on competition but usually is the result of a complex interaction between competition and differences in microhabitat characteristics (Schenk et al., 2003; Schenk and Mahall, 2002). Nevertheless, it has been proposed that resource poor areas such as arid environments express the most intense positive and negative interactions, and consequently, they are the habitats where spatial pattern depends most on biotic interactions (Goldberg et al., 1999).

Overgrazing is one of the most important sources of stress in plant communities. Grazing reduces the abundance of plant species and modifies the composition and structure of plant communities (McNaughton, 1986; Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998). For example, in dry grasslands grazing decreases plant species diversity while in wet environments grazing can promote it (Olff and Ritchie, 1998). In addition, grazing influences the spatial distribution of vegetation. On one hand, associative defense against grazers between grazing-sensitive species and grazing-resistance species may result in an increase of the clustering in the plant community (Baraza et al., 2006; Graff et al., 2007). On the other hand, intensive grazing may result in a random spatial distribution of the plant community with few grazing-resistance species that compete among them (Alados et al., 2004). This change of the spatial distribution may be modulated by grazing intensity, with low intensities related with positive associations and high intensities related with random patterns (Alados et al., 2004). To maintain sustainable grazing practices, it is essential to evaluate the effect of grazers on the entire plant community because this effect is mediated through the single species' tolerance to grazing in a non-additive and very dynamic way (Engel and Weltzin, 2008). The application of network theory aids to translate these species level interactions to the community level.

In this study, we used spatial association networks to investigate the effect of grazing in the structure of the interactions within a semiarid plant community. To our knowledge, this is the first empirical ecological network that employs positive and negative links simultaneously. The combination of different type of interactions allows a more reliable description of the structure of the

system under study. Specifically, we divided the plant community in specific partitions, subsets of the species which share the same sign of interactions to other partitions. Within a partition all species associate in the same way to the rest of species in the network, so we consider that these partitions reflect species' association strategies in the plant community. We hypothesize that grazing modifies community association strategies; particularly a) an increase in grazing intensity results in a more randomized plant community and simplifies the association strategies in the community, and b) strategies that are best adapted to grazing are most important structuring the community. We predict that the number of partitions will decrease and the plant community will become more randomly associated as stocking rate increases. We also predict that spatial associations will concentrate in partitions that include the species that provide refuge from grazers to others ('nurse'), while partitions including other species (e.g. facilitated species) will present few spatial associations.

2. Methods

2.1. Study area

The study was conducted in Cabo de Gata-Níjar Natural Park (hereafter, Cabo de Gata NP), which is in the Mediterranean coast of southeastern Spain (36° 46' N, 2° 09' W). The park covers 37,570-ha, and the highest elevation is 493 m (El Fraile Peak). The climate is semiarid Mediterranean (drought in summer and most rainfall in spring and autumn. Average annual rainfall = 193.9 mm, Average annual temperature = 19.4 °C, Passera, 1999). Historically, the area has been used as an agro-pastoral system, with cereal cropping on floodplains and livestock (sheep and goats) grazing year-round on the slopes. The plant community is characterized by *Chamaerops humilis* L., *Rhamnus lycioides* L., *Pistacia lentiscus* L. and *Periploca laevigata* Aiton (Peinado et al., 1992). Vegetation data were collected from the southern section of the park, where highly stony soils predominate (Oyonarte et al., 1999). In that region, the vegetation is an open shrubland, with shrubs organized in patches embedded within a matrix of a large tussock grass, *Stipa tenacissima* L. *Stipa tenacissima* is a highly competitive species that colonizes the gaps created within patches by livestock and aridity, and can exclude other plant species from the area (Alados et al., 2006, 2003).

Within the study area, four sites with different stocking rate were selected near the El Romeral farm. One week per season in 2000, the movements of sheep and goats were monitored and the effective stocking rate at each site was calculated multiplying the average stocking rate of the farm (0.65 ind ha⁻¹) by a correction factor based on the proportion of time that livestock spent grazing on that site. Then, sites were ranked based on the stocking rate to which they were exposed (G1 = 0 ind/ha; G2 = 0.27 ind/ha; G3 = 0.46 ind/ha; and G4 = 0.65 ind/ha). Grazing carrying capacity of this plant community was 0.39–0.57 ind/ha (Robles and Passera, 1995); therefore, we assumed that G2, G3 and G4 sites had been exposed to low, medium and high grazing intensity, respectively. Furthermore, we confirmed that G1 site had not been grazed for decades.

2.2. Vegetation survey and network construction

In April, 2001, three 500-m-long linear transects were established randomly at each site, and the Point-Intercept Method was used to quantify the vegetation (Goodall, 1952). In each transect one survey point was established every 20 cm, and all species which intercepted a vertical line on each point were recorded (T = total surveyed points per transect = 2501). Only the presence

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