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Original article

Non-random co-occurrence of native and exotic plant species in Mediterranean grasslands

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ABSTRACT

Invasion by exotic species in Mediterranean grasslands has determined assembly patterns of native and introduced species, knowledge of which provides information on the ecological processes underlying these novel communities. We considered grasslands from Spain and Chile. For each country we considered the whole grassland community and we split species into two subsets: in Chile, species were classified as natives or colonizers (i.e. exotics); in Spain, species were classified as exclusives (present in Spain but not in Chile) or colonizers (Spanish natives and exotics into Chile). We used null models and co-occurrence indices calculated in each country for each one of 15 sites distributed along a precipitation gradient and subjected to similar silvopastoral exploitation. We compared values of species co-occurrence between countries and between species subsets (natives/colonizers in Chile; exclusives/colonizers in Spain) within each country and we characterised them according to climatic variables. We hypothesized that: a) the different coexistence time of the species in both regions should give rise to communities presenting a spatial pattern further from random in Spain than in Chile, b) the co-occurrence patterns in the grasslands are affected by mesoclimatic factors in both regions. The patterns of co-occurrence are similar in Spain and Chile, mostly showing a spatial pattern more segregated than expected by random. The colonizer species are more segregated in Spain than in Chile, possibly determined by the longer residence time of the species in the source area than in the invaded one. The segregation of species in Chile is related to water availability, being species less segregated in habitat with greater water deficit; in Spain no relationship with climatic variables was found. After an invasion process, our results suggest that the possible process of alteration of the original Chilean communities has not prevented the assembly between the native and colonizer species together.

1. Introduction

In ecology, community assembly constitutes a relevant issue from the theoretical and applied points of view (Young et al., 2001; Hillebrand and Matthiessen, 2009; HilleRisLambers et al., 2012; Pyšek and Chytrý, 2014). Most studies on species co-occurrence have focussed upon the importance of different ecological factors acting on the species present in a given region such as dispersal, abiotic filters and biotic interactions (Chase, 2003; Diamond, 1975; Götzenberger et al., 2011; Casado et al., 2015). However, other studies highlighted the importance of evolutionary and biogeographical processes in the configuration and composition of the regional species pool (HilleRisLambers et al., 2012; Ricklefs, 2004), which can be even more influential than local filters (Chase, 2003; Zobel and Partel, 2008). In many cases, the regional species pool comprises a mixture of species from different evolutionary origin, particularly in regions presenting high levels of plant invasion (Harrison and Grace, 2007).

Community assembly is driven by the action of different biotic factors, such as interspecific competition, tolerance, or facilitation

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(Diamond, 1975; Madrigal et al., 2011; Gutiérrez et al., 2014), as well as environmental filters (e.g. climatic or edaphic conditions) and habitat histories (Arianoutsou et al., 2013; Holmgren et al., 2000; Pauchard et al., 2004). Following an invasion process, both biotic and abiotic factors act on a regional species pool that is made up of elements from different biogeographical origin and history of arrival; thus, non-random processes are underlying the assembly of the community (Sanders et al., 2003; Figueroa et al., 2004; Davis et al., 2011; Dostal, 2011; Martin and Wilsey, 2012; Sutherland et al., 2013). The assembly of this pool of species in the invaded range can adjust to different types of spatial patterns: a) a non-random segregated pattern, characteristic of communities in which pairs of species co-occurred less than expected by random as a consequence of competition processes or due to groups of species exhibiting different environmental preferences; b) a non-random aggregated pattern, characteristic of communities in which pairs of species co-occurred more than expected by random as a result of tolerance and facilitation mechanisms rather that competitive ones, or due to groups of species with similar environmental preferences; c) a pattern that does not differ from random, most likely characteristic of communities that are not very conditioned by either biotic or abiotic relationships (Connor and Simberloff, 1979; Diamond, 1975; Gotelli and Graves, 1996; Götzenberger et al., 2011). In the context of plant invasion, comparison of assembly patterns between the region of origin and the invaded ranged of the colonizer species can provide valuable information on the ecological factors underlying the community assembly.

Grasslands in different Mediterranean climate regions share a large amount of species, most of which are natives from the Mediterranean Basin, but exotics elsewhere (Arianoutsou et al., 2013). These regions maintain herbaceous communities presenting high values of plant richness (Cowling et al., 1999; Máltez-Mouro et al., 2010; Ovalle et al., 2006; Pineda and Montalvo, 1995). In the present paper we analysed the spatial patterns of herbaceous species co-occurrence in grasslands in two Mediterranean regions (Spain and central Chile) subjected to similar environmental conditions and cultural regimes within a silvopastoral system. The Spanish Mediterranean grasslands are seminatural communities dominated by annual species, almost all of them native. In Chile, the invasion process is associated with the introduction of European agriculture in the XVI century (Arroyo et al., 1995; Groves and di Castri, 1991). Over 500 species of exotic plants, most of these from the Mediterranean Basin, have been reported for central Chile (Figueroa et al., 2011; Martín-Forés et al., 2012), and represent 18% of the flora in this region. If only Chilean seminatural grasslands are considered, this percentage surpasses 40% (Martín-Forés et al., 2012). The time of residence of herbaceous species introduced into Chile varies greatly (Castro et al., 2005) and their early distribution possibly followed a pattern associated with anthropogenic activities such as agriculture and grazing, instead of being determined by environmental factors (Figueroa et al., 2004; Fuentes et al., 2013; Groves and di Castri, 1991; Wilson et al., 2009).

The present study aimed to identify interregional differences in the spatial pattern (i.e. species co-occurrence) of grassland communities in Spain and Chile. We studied fifteen sites in each country distributed along a precipitation gradient and sampled during two consecutive years. We assessed the co-occurrence patterns in both regions by comparing observed patterns in plant communities with null models simulating random patterns of species assembly. We analysed the co-occurrence patterns of the grasslands of both regions, considering all the species they comprise, and their classification attending to their distribution: native and colonizer (i.e. exotics) species in Chile and exclusive (those species present in Spain but not in Chile) and colonizer species (species that have become naturalized in Chile) in Spain. Although community assembly occurs with the set of the whole pool of species, this classification enables us to identify the different spatial distribution between native and colonizer species in Chile, as well as to make comparisons for colonizer species between both countries.

Other studies have used null models to detect patterns of plant species assembly in invasion processes, particularly comparing between invaded and uninvaded areas along environmental gradients (Cornwell and Ackerly, 2009; Jansen et al., 2011; Santoro et al., 2012; Horn et al., 2015). However, as far as we know, no previous research has focused on the spatial patterns of a whole community of plant species that undertook transcontinental naturalization by comparing species assembly between the source area and the invaded region. We hypothesized that: a) spatial patterns of Spanish grassland communities will be further from random (either more segregated or more aggregated) than in Chile due to the greater time of coexistence among the species in the area of origin than in the invaded range. These spatial patterns appear to be the consequence of the effects of competition and progressive niche differentiation of species over time (i.e. species segregation) or due to tolerance, facilitation processes and niche complementarity (i.e. species aggregation) (Silvertown, 2004); b) due to the similar environmental and cultural context existing in both countries, the variation of the species co-occurrence among sites will respond with the same trend to mesoclimatic variations within each region (supported by Reitalu et al., 2008).

2. Material and methods

2.1. Study area

The study was conducted in the Spanish *dehesa* and the Chilean *espinal*, two silvopastoral systems used for extensive livestock grazing in Mediterranean grassland areas. Both ecosystems are very similar in terms of physiognomy, livestock, management technology and the associated cultures (Marañón, 1988; Ovalle et al., 1996). They differ with regard to their woody vegetation but are very similar in the structure of the herbaceous vegetation. The *dehesa* contains scattered trees of holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) or cork oak (*Quercus suber* L.) within a herbaceous matrix mainly comprising winter annuals (Joffre et al., 1999; Marañón et al., 2009). Its origin dates back several centuries or millennia, when human intervention in woodlands transformed the landscape into a pseudosavannah (Le Houérou, 1981; López et al., 2007). On the other hand, the *espinal* represents a recent and largely anthropogenic formation (Ovalle et al., 1999) associated with a transformation of the landscape following the Spanish colonization in the 16th century (Arroyo et al., 2000; Figueroa et al., 2004). It is covered with dispersed trees of *Acacia caven* Mol. (known as *espino*) within a herbaceous matrix mainly comprising annual plants, native and exotic species from the Mediterranean Basin (Del Pozo et al., 2006; Ovalle et al., 1996, 2006). The *dehesa* represents the source area for almost all of the Chilean exotic species of the *espinal*, and therefore constitutes an excellent scenario for studying the processes of colonization and naturalization of exotic species (Jiménez et al., 2008; Martín-Forés et al., 2012; Pauchard et al., 2004).

In Spain the investigation was conducted in the centre-west of the Iberian Peninsula, from 40°13′ N to 37°51′ N and from 4°23′ W to 7°02′ W (Fig. 1). In Chile we selected an area comprising 600 km from 32°35′ to 37°00′ S and from 70°46′ to 72°35′ W. The two study areas covered a wide range of climate conditions in which *dehesas* and *espinales* are distributed. Mean annual temperature ranged from 14.5 to 16.9 °C and from 13.1 to 17.0 °C in Spain and Chile, respectively, whereas annual precipitation varied from 468 to 1030 mm and from 303 to 1168 mm, respectively (Table 1). Soils in