



Research article

Patterns of species relatedness created by competitive exclusion depend on species niche differences: Evidence from Iberian Atlantic grasslands



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ABSTRACT

It is commonly assumed that closely related species share more similar niches than do distantly related species, thus limiting their ability to coexist and leading to patterns of phylogenetic over-dispersion. On the contrary, recent theoretical developments argue that competitive exclusion may lead to patterns of either over-dispersion, clustering or randomness, depending on the relative importance of niche differences and interspecific competitive ability differences. In this study, we utilized semi-natural grassland communities to test the hypothesis that the pattern of species relatedness generated by competitive exclusion depends on species niche differences. Instead of inferring processes from observed patterns, we experimentally manipulated grassland plots to test the effects of competitive exclusion. We compared grazed plots (in which grazing functioned as an equalizing mechanism and suppressed aboveground competition) with neighbouring plots experimentally excluded from grazing over the course of nine years (in which aboveground competition was not prevented). Weak niche differences between species allowed competitive exclusion to generate phylogenetic clustering, because phylogenetically structured plant canopy height and capacity for lateral spread conferred superior competitive ability to grasses that outcompeted species in all dicot branches. By contrast, moderate niche differences allowed competitive exclusion to result in a *random* pattern of phylogenetic species assembly, because species niche differences partially counterbalanced competitive exclusion by superior competitors in the grass family. We conclude that patterns of species relatedness created by competitive exclusion in Iberian Atlantic grasslands depend on species niche differences. Competitive exclusion may cause differential patterns of phylogenetic assembly.

1. Introduction

Among the ecological processes implicated in the question of how species assemble and coexist (Götzenberger et al., 2012), competitive interactions and their potential stabilization by niches (Chesson, 2000) are perhaps the most important processes occurring at local (fine-grain) spatial scales (HilleRisLambers et al., 2012). To understand the effect of competitive interactions on species assembly, the so-called competition-relatedness hypothesis (CRH) (Cahill et al., 2008) has often been proposed and tested (Cavender-Bares et al., 2009; Dayan and Simberloff, 2005; Webb et al., 2002). CRH proposes that closely related taxa likely share more similar niches compared to distantly related counterparts, limiting their ability to coexist (HilleRisLambers et al., 2012). Additionally, it has often been suggested that under the CRH, and in the presence of phylogenetic niche conservatism, competitive

exclusion would create patterns of phylogenetic over-dispersion (or repulsion) in local communities (Cavender-Bares et al., 2009; Swenson et al., 2006; Webb et al., 2002). Thus, if the observed species have important differences in their traits relevant for niche preferences, and these traits are phylogenetically conserved, competitive interactions and environmental filtering should lead to contrasting phylogenetic patterns. Specifically, i) strong interspecific competition should lead to patterns in which closely related species coexist less often than expected by chance (phylogenetic over-dispersion); by contrast, ii) dominant processes of environmental filtering would create phylogenetic under-dispersion or clustering, because closely related species would share the necessary traits to simultaneously exist in a given environment.

However, as shown by Mayfield and Levine (2010), the empirical evidence supporting the CRH and its supposedly subsequent patterns in

Abbreviations: CGO, Clonal Growth Organs; CRH, Competition-Relatedness Hypothesis; E, Exclusion plot; G, Grazing plot; H, Canopy Height; LS, Lateral Spread; MWC, Mean Soil Water Content

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plant ecosystems is not consistent. Therefore, Mayfield and Levine (2010), and later HilleRisLambers et al. (2012), used Chesson's (2000) coexistence theory to propose an updated theoretical framework to predict the effects of competitive exclusion on phylogenetic community patterns. In particular, Mayfield and Levine (2010) (Fig. 4), and HilleRisLambers et al. (2012) (Figs. 3–4) argued that it is both the importance of niche differences and the existence of interspecific competitive ability differences (as measured by relevant traits) what determine the impact of competitive exclusion on phylogenetic patterns. Essential differences in plant niches, if positively correlated with phylogenetic distance, would cause indeed phylogenetic over-dispersion (as predicted by CRH). However, essential differences in competitive ability, if positively correlated with phylogenetic distance, would cause closely related species (which share traits that confer competitive ability) to coexist more often than expected by chance, thereby creating patterns of phylogenetic clustering (Mayfield and Levine, 2010). Therefore, in the presence of important and phylogenetically conserved differences in competitive ability, the expected pattern of species relatedness would be either: i) clustered (if weak differences in species niche preferences are prevalent), ii) over-dispersed (if species niche differences exceed competitive ability differences), or iii) random (if species niche differences match competitive ability differences) (Mayfield and Levine, 2010).

Mayfield and Levine's (2010) theoretical framework has been previously used in community assembly studies (Bennett et al., 2013; Godoy et al., 2014; Herben and Goldberg, 2014; Muscarella et al., 2016). In particular, Bennett et al. (2013) and Godoy et al. (2014) used experimental approaches to test the effect of phylogenetic relatedness on species assembly patterns resulting from competitive exclusion. They showed that strong competition did not always lead to patterns of phylogenetic over-dispersion (Bennett et al., 2013) and that differences in competitive ability can be phylogenetically structured (Godoy et al., 2014). However, within the above framework, the potential effects of plant niche differences on competitive exclusion, and the corresponding associated patterns, appear to remain unexplored.

For the above reason, in this study we used a long-term experiment in which large grazers were excluded to test the hypothesis that the pattern of species relatedness generated by competitive exclusion depends on species niche differences, a so far untested central conjecture of Mayfield and Levine (2010). Although herbivory by large mammals affects several ecological processes (Lezama and Paruelo, 2016), it always represents a strong disturbance that removes plant biomass by trampling and defoliation (Olff and Ritchie, 1998). This disturbance (non-selective shoot herbivory) affects plant competition by equalizing species competitive ability differences (Huston, 1979; Wilson, 2011). Moreover, particularly in highly productive grasslands as the ones here studied (Lezama et al., 2014), large-grazers exclusion results in strong aboveground competition for light and loss of plant diversity (Hautier et al., 2009). In the studied grassland sites, patterns consistent with competitive exclusion have been previously observed after grazer exclusion (Odriozola et al., 2017), but in the present study traits relevant for aboveground competition were included to link observed patterns with competitive exclusion. The considered functional traits were canopy height and clonality, which have been proved to be relevant to competition in fertile grasslands (Craine et al., 2001; Dickson et al., 2014; Gough et al., 2012; Grime, 2001).

Our research combines two strategies proposed by HilleRisLambers et al. (2012) for the study of community assembly processes: experimental manipulation of the abiotic or biotic environment and assessment of trait-phylogeny-environment relationships. First, using large-grazers exclusion fences we manipulated the aboveground competition regime at two grassland sites. Exclusion (E) plots (where strong aboveground competition was present) were compared with adjacent Grazing (G) controls (where grazing acted as an equalizing mechanism *sensu* Chesson (2000), preventing aboveground competition) to study the effect of competitive exclusion. Second, using the RLQ ordination

framework, we were able to link phylogenetically structured species traits with subjacent environmental conditions (Pavoine et al., 2011). The study sites differ in the effect of variation in soil properties on fine-grain community structure (Odriozola et al., 2017). Soil environmental variables had only weak effects at one site, whereas they were moderate at the other. These fine-grain (fine-scale) environmental differences acted as stabilizing mechanisms (Chesson, 2000), allowing species segregation into different niche axes. Furthermore, the contrasting relevance of species niche differences between sites (weak differences in one site vs. important in the other) was formally tested in this study, using Pianka's pairwise niche overlap tests (Pianka, 1973) along hydrological and pH gradients. Therefore, comparing both sites allowed us to examine whether the effects of competitive exclusion depended on the relevance of species niche differences. We derived the next predictions: 1) at field site with weak niche differences between species (weak niche stabilization), after grazers exclusion, species belonging in clades with superior competitive abilities will out-compete species in other clades, resulting in a phylogenetically clustered subset of species; and 2) at the site with moderate effect of plant niches (moderate niche stabilization), competitive exclusion by species in competitively superior clades, after grazers exclusion, will be counterbalanced by niche differences, resulting in the presence of a random subset of species.

2. Material and methods

2.1. Study area

Experiments were conducted at two field sites in a semi-natural grassland system located in Aralar Natural Park: Site 1 (Uzkuiti: 43° 0' 50" N, 2° 4' 3" W: 1300-m elevation) and Site 2 (Igaratza: 42° 59' 9.25" N, 2° 2' 9.7" W: 1247-m elevation). Aralar Natural Park is an 11,000-ha protected area located in the Basque Country (Northern Iberian Peninsula), where calcareous substrates are predominant (Gibbons and Moreno 2002). The area has oceanic climate, with mean annual temperature of 7.0 °C and annual precipitation of about 1330 L m⁻². Traditionally, Aralar grasslands have been used by mixed livestock in a moderate/high stocking rate (~3.2 Livestock Unit ha day⁻¹, 13% beef cattle, 52% dairy sheep, and 35% horses (Odriozola et al., 2014)) and occupy approximately 2077-ha (18.9% of the park area); however, its usage varies seasonally (from May until November, coinciding with the vegetative period). The primary vegetation type is a productive (mean aboveground net primary production of 1.97 Tn Dry Mass ha⁻¹ year⁻¹ with standard error of 0.39 (Aldezabal et al., unpublished data)) native grassland (*Jasione laevis-Danthonietum decumbentis* Loidi 1983), with mainly perennial species. This corresponds to the priority habitat code 6230 of the Habitat Directive (92/43/EEC, European Commission, 2013).

2.2. Experimental design

In order to simulate grazing cessation, and thus allow for aboveground competition, a permanent fenced exclusion (E) plot (50 m × 50 m) was established in May 2005 at each of the two field sites. Next to each E plot, we delineated a grazed plot (G), where sheep, cattle, and horses were allowed to graze freely during the vegetative period (May–November). Both sites were located on relatively flat terrain and, when fences were erected (2005), community structure was not significantly different between E and G plots at either field site (Odriozola et al., 2017). Within each G/E plot, 100 sampling units (0.5 × 0.5 m-quadrats) were laid out, so that quadrats were located 2 m apart, thus creating sampling areas of 18 m × 16 m (Fig. A1 in Supplementary material).

2.3. Vegetation and soil sampling

Sampling was conducted during the growing season of 2014, after nine years of grazer exclusion. In each 0.25 m²-quadrat, floristic

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