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Soil conditions drive changes in a key leaf functional trait through environmental filtering and facilitative interactions

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ABSTRACT

Non-random patterns in the functional structure of communities are often interpreted as evidence for different forces governing their assemblage. However, community assembly processes may act antagonistically, countering each other's signatures on the functional structure of communities, which may lead to spurious inferences on the underlying mechanisms. To illustrate this issue, we assessed the joint effects of environmental filtering and facilitative interactions on a key leaf functional trait (i.e. specific leaf area, SLA) in Mediterranean dwarf-shrub communities, using a two-scale sampling approach. Specifically, we analyzed differences in community-weighted mean SLA values (CWM-SLA) between communities (community-scale) and between guilds within communities (guild-scale, i.e. individuals sampled in understorey, overstorey and open-ground conditions) across contrasted soil environments and elevational gradients. We found that communities on harsh edaphic conditions (i.e. dolomite habitats) showed significantly lower CWM-SLA values than communities on more fertile habitats. In contrast, elevation was a poor predictor of differences in CWM-SLA between the communities. This suggests that environmental filtering may influence leaf trait variation along soil gradients irrespective of elevation. On the other hand, communities on dolomite habitats showed strong differences in CWM-SLA between understorey (higher CWM-SLA) and either open-ground and overstorey guilds (lower CWM-SLA), whereas communities on more fertile soils showed no differences between the guilds. The strong differences in CWM-SLA between understorey and non-understorey guilds in dolomite communities suggest that facilitative interactions may be particularly at stake under stressful edaphic conditions, thus partially mitigating the effect of environmental filtering (i.e. low SLA values) on communities growing in harsh soils.

1. Introduction

Community assembly theory is complex and comprises multifold neutral and niche-based processes (Weiher et al., 2011). Based on the widespread idea that these processes leave tractable imprints on the functional structure of communities, some studies have interpreted non-random patterns as evidence of different dominant forces governing their assemblage (Götzenberger et al., 2012; Kraft et al., 2015; Funk et al., 2017). Environmental filtering and historical contingency may determine the species in the regional pool that can thrive in a given community, according to their suitability to local conditions (Diamond, 1975; Keddy, 1992; Cornwell et al., 2006). Following this rationale, directional changes in community-weighted mean trait values (CWM; Garnier et al., 2004; Violle et al., 2007) along environmental gradients have been interpreted as evidence of habitat filtering processes (Cornwell and Ackerly, 2009; Lebrija-Trejos et al., 2010). However, once species have passed through the environmental filter, biotic interactions might also shape the functional structure of communities (de Bello et al., 2012). For example, community traits may converge towards certain values if highly competitive species tend to displace weak competitors (Mayfield and Levine, 2010). On the other hand, functional diversity may increase if limiting similarity is the dominant process (Stubbs and Wilson, 2004). Therefore, communities are expected to be shaped by the joint effects of abiotic filtering and biotic interactions (Cavieres et al., 2014; Michalet et al., 2015a).

Although competitive interactions have long been the dominant biotic factor in conceptual models of community assembly (see Webb et al., 2002; Mayfield and Levine, 2010), facilitative interactions have recently gained prominence in the literature (e.g. Valiente-Banuet and Verdú, 2013; McIntire and Fajardo, 2014; Soliveres et al., 2015). Facilitation among species is highly dependent on the abiotic environment (Bertness and Callaway, 1994; Callaway, 2007), and is thought to be particularly relevant under harsh environmental conditions (Xiao et al., 2013; Bulleri et al., 2016). Communities in stressful habitats are usually

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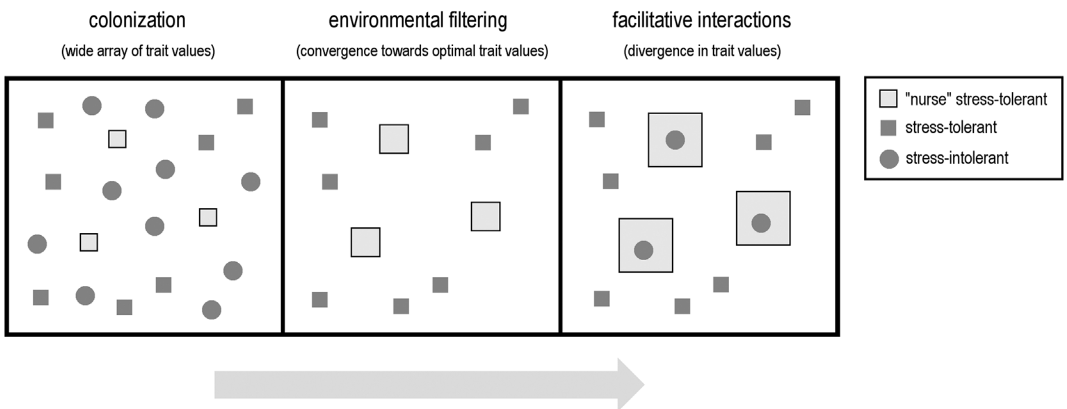

Fig. 1. Conceptual model to explain the antagonistic effect of habitat filtering and facilitative interactions on community structure under harsh environmental conditions. At the pioneer stage (left-panel), propagules of species with different stress tolerances (i.e. wide array of trait values) arrive into the community. Then, harsh environmental conditions filter out stress-intolerant species from the community, which converges towards optimal trait values (central-panel). Finally, "nurse" species reach a minimum size to provide effective microclimatic amelioration to stress-intolerant species, which are then able to locally increase their abundance and persist under the shrub canopy (right-panel). Thus, facilitative interactions between "nurse" and stress-intolerant species lead to strong differences in trait values between understorey and non-understorey individuals. The arrow represents the temporal dimension.

dominated by species with stress-tolerance trait values (e.g. low specific leaf area, SLA; Wilson et al., 1999; Damschen et al., 2012; Hulshof et al., 2013). However, overstorey "nurse" plants are known to provide microclimatic amelioration in relation to surrounding areas, which may help species with less stress-tolerant trait values (e.g. high SLA) to locally increase their abundances and persist (Bruno et al., 2003; Michalet et al., 2006). Therefore, although harsh environmental conditions are expected to filter communities towards optimal CWM trait values (Mason et al., 2010; Laughlin et al., 2011), facilitative interactions occurring under the same environmental conditions may lead to different CWM values between species that exhibit contrasting niche requirements within the communities (i.e. between understorey and non-understorey species, see Fig. 1), thus mitigating the effect of environmental filtering on the functional structure of communities (Soliveres et al., 2012). Therefore, environmental filtering and facilitative interactions could act antagonistically, and may counter each other's signatures on the functional structure of communities.

Facilitative interactions are particularly relevant in structuring Mediterranean woody plant communities (Verdú et al., 2009; Rey et al., 2016). Although water availability is the most obvious factor influencing positive interactions among Mediterranean plants (Armas et al., 2011; Pugnaire et al., 2011; Gross et al., 2013), other sources of stress may also be at stake. Mediterranean landscapes show a high incidence of stressful substrates which support highly peculiar and specific plant communities, such as those growing on serpentines (Kruckeberg, 1986; Anacker, 2011), gypsum (Escudero et al., 2015), sandstones (Arroyo and Marañón, 1990) and dolomites (Mota et al., 1993). Among these, dolomite communities have received considerably less attention (but see Pignatti and Pignatti, 2014). Dolomite is a sedimentary rock in which a good deal of calcium has been replaced by magnesium (Jones, 1950), and may impose a severe restriction for plant growth and establishment (Mota et al., 2008). In addition, dolomite soils are sandy and gravelly, prone to drain rapidly and provoke water stress (Michalet et al., 2002). Besides, other less stressful substrates are also common in the Mediterranean, such as those derived from limestones and mica-schists. Thus, a directional change in the CWM of a trait related to stress-tolerance (e.g. SLA; Wilson et al., 1999) from communities that grow on harsh dolomite habitats to communities that thrive on less stressful soils (i.e. from low to high CWM-SLA values) may indicate that soil conditions act as an environmental filter influencing community functional structure (Spasojevic and Suding, 2012). On the other hand, facilitative interactions are expected to be particularly at stake in communities on harsh dolomite habitats (Bertness and Callaway, 1994; Callaway, 2007), which may lead to functional divergence between understorey and non-understorey species (Soliveres et al., 2012).

Elevation gradients are also known to be an important factor in structuring Mediterranean plant communities (Loidi et al., 2015; Molina-Venegas et al., 2016). Many components of regional climate and local environment vary in a non-random fashion along elevation gradients (Lomolino, 2001), and thus the intensity of biotic interactions may be affected accordingly (Callaway et al., 2002; Cavieres et al., 2016). In the context of Mediterranean-type ecosystems, facilitative interactions seem more relevant at low elevation, likely due to a stronger severity of summer drought in comparison to Mediterranean alpine habitats (Cavieres et al., 2006). Therefore, it is reasonable to think that both soil conditions and elevation may drive the functional structure of communities.

In this study, we assessed the joint effects of environmental filtering and facilitative interactions on a stress-related functional trait (i.e. SLA) in Mediterranean dwarf-shrub communities, using a two-scale sampling approach. Specifically, we analyzed differences in community-weighted mean SLA values (CWM-SLA) across communities (community-scale) and between guilds within communities (guild-scale, i.e. individuals sampled in understorey, overstorey and open-ground conditions) along contrasted soil environments and elevational gradients. We hypothesized that communities growing on stressful dolomite habitats would show low CWM-SLA values (i.e. higher water-use efficiency and a conservative resource-use strategy), though they would exhibit strong differences in CWM-SLA values between understorey and non-understorey guilds if facilitative interactions are also at stake (Soliveres et al., 2012; see Fig. 1). In contrast, communities growing under more benign conditions (i.e. limestones and particularly mica-schists) would show higher CWM-SLA values, as well as little or no differences between understorey and non-understorey guilds. We also hypothesized a greater effect of environmental filtering and facilitative interactions at low elevation (i.e. low CWM-SLA values and strong differences between understorey and non-understorey guilds) due to a stronger severity of summer drought in comparison to higher elevations (i.e. high CWM-SLA values and no differences between guilds).

2. Materials and methods

2.1. Study area

The Sierra Nevada is a core range of the Baetic-Rifan complex in southern Iberian Peninsula. Its rugged topography (up to 3482 m a.s.l.) harbours a heterogeneous lithology, with a broad central mica-schist core that extends linearly from west-southwest to east-northeast for about 100 km. This siliceous central core is surrounded by a discontinuous limestone border that forms the middle and lower slopes of