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

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A B S T R A C T

Non-random patterns in the functional structure of communities are often interpreted as evidence for different forces governing their assembly. However, community assembly processes may act antagonistically, counteracting 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 tracable imprints on the functional structure of communities, some studies have interpreted non-random patterns as evidence of different dominant forces governing their assembly (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; Cornell et al., 2006). Following this rationale, directional changes in community-weighted mean trait values (CWM; Garnier et al., 2004; Vióle 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
dominated by species with stress-tolerance trait values (e.g. low specific leaf area, SLA; Wilson et al., 1999; Damschen et al., 2012; Hubbel 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 understory 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
the Sierra, together with an extensive dolomite outcrop along its western edge (Martin et al., 2008). The climate is predominantly Mediterranean with precipitation concentrated in spring and autumn (mean annual precipitation is ranged between 200 and 900 mm), while the warmest season coincides with effective drought in summer.

2.2. Vegetation survey and data collection

We selected two south-oriented elevation gradients for each of the three main types of bedrocks present in the Sierra Nevada (dolomite, limestone and mica-schist), being separated from one other along the west-to-east axis of the range. Within each elevation gradient, we drew at random three 75-m-long and 1-m-wide transects at three different elevations (~1300, ~1650 and ~1950 m a.s.l.) that passed through dwarf-shrub vegetation (chamaephytes and few nanophanerophytes) on sunny slopes beyond the edge of the tree canopy, when present (see Molina-Venegas et al., 2016 for details). We only were able to sample one transect-site on the dolomites at ~1950 m because there is only one dolomite peak over 1900 m in the Sierra Nevada. Within each transect, we counted the total number of individuals of each population of woody species and subspecies. Given the survey was conducted within a single year, seedlings were excluded because they show a high inter-annual variation in emergence and mortality under Mediterranean conditions (and particularly in the Sierra Nevada, see Mendoza et al., 2009), and may therefore lead to spurious conclusions.

In order to measure microhabitat preferences among plants in the communities, each individual was assigned to one of three exclusive categories (guilds); overstorey, understorey and open-ground. The overstorey guild was constituted by those plants that presented at least one individual of any species growing under their canopy projection. Individuals growing under the shrub canopy (i.e. under overstorey plants) were assigned to the understorey guild, and the remainder plants formed the open-ground guild. Individuals that could not be clearly assigned to any of these categories were excluded (< 5% of sampled individuals). We did not consider one limestone transect-site at ~1950 m because the vegetation of this site was constituted almost exclusively by open-ground individuals, presumably due to recent disturbance. Thus, our final dataset consists in two different matrices of 16 communities (Fig. 2) with 261 populations (community-dataset) and 48 vegetation layers (i.e. guilds) with 261 populations (guild-dataset), respectively. The 261 sampled populations correspond to 74 woody species (see Table S1).

Spatial association of juveniles with larger plants has been considered as observational evidence of facilitative interactions in former studies (Siles et al., 2008; Verdú et al., 2009). However, establishing a criterion to distinguish between adult plants and juveniles in our study system may be tricky, given the small size of the vegetation (dwarf-shrub communities) and the effect of herbivory, which may increase resemblance between adult and juvenile plants. Although we recognize that looking for juvenile recruitment is the optimal approach to detect the signature of facilitation in natural communities, we decided not to distinguish between adult and juvenile plants. Our approach is rather conservative, and prevent us from making systematic errors in life-stage assignments.

We measured the average specific leaf area (SLA) of each population of the species within transects using standardized protocols (Cornelissen et al., 2003). We sampled five healthy individuals (or part of them) per population, taking two fully developed and healthy leaves per individual (see Appendix 2 for details). Importantly, intraspecific trait variation can change the outcome of ecological interactions (Bolnick et al., 2011), and therefore incorporating intraspecific variance in community ecology studies is highly recommended.

2.3. Community-weighted mean SLA values and null model testing

We estimated the mean SLA value for each community (n = 16) and guild (n = 48) in the dataset weighted by their respective species abundances (i.e. community-weighted mean, CWM; Garnier et al., 2004; Vioule et al., 2007) as:

$$\text{CWM} = \sum_{i=1}^{S} n_i \cdot t_i$$

where $S$ is the total number of species in a given community or guild, $t_i$ is the SLA value of the corresponding population of the species $i$, and $n_i$ is the relative abundance of the species $i$ in a given community or guild. In order to test for non-random patterns in the observed CWM-SLA values, we used two different null model-based approaches. First, we tested whether the observed CWM-SLA values of the communities departed from random expectation given SLA values across all populations in the dataset (community-scale analyses). To do so, we compared the observed CWM-SLA values of the communities to null distributions generated by randomly shuffling SLA values across all populations in the dataset 9999 times. Second, we tested whether the observed CWM-SLA values of the guilds departed from random expectation given SLA values across populations within their corresponding communities (guild-scale analyses). To do so, we compared the observed CWM-SLA values of the guilds to null distributions generated by randomly shuffling SLA values across populations within each community 9999 times.

Note that unlike the community-scale randomization scheme, the latter was constrained within the communities, which allowed us to estimate whether the observed differences in CWM-SLA between guilds within the communities depart from random expectation given the SLA values observed in the communities.

We calculated an effect size CWM-SLA score (ES-CWM-SLA) for each community and guild based on the probability $P$ for the observed CWM-SLA values to be higher than expected given their corresponding null distributions as:

$$P = \frac{\text{number(null < obs)} + \text{number(null = obs)}}{2^{10000}}$$

This one-side probability was used to calculate ES-CWM-SLA scores by subtracting 0.5 to $P$ and multiplying by 2 (Kelt et al., 1995; Chase et al., 2011; Bernard-Verdier et al., 2012). This non-parametric calculation of effect sizes was preferred to the widely used standardized effect size (SES; e.g. Kembel, 2009; Verdú et al., 2009) due to the asymmetry or otherwise non-normality in many of the null distributions generated in the study. ES scores vary between −1 and 1, with values close to −1 and 1 indicating that the observed values are lower and higher than expected based on the null distributions, respectively.

2.4. Statistical analyses

First, we conducted unpaired Student’s t-tests to evaluate whether lithological origins of soils and elevation explain differences in ES-CWM-SLA scores between the communities (community-scale analyses). The ES-CWM-SLA scores of the communities were used as the dependent variable, whereas bedrock (dolomite, limestone and mica-schist) and elevation (low, medium and high) were used as two different explanatory factors, separately (i.e. three unpaired t-tests per explanatory factor). Second, we conducted paired t-tests to evaluate whether lithological origins of soils and elevation explain differences in ES-CWM-SLA scores between guilds within the communities (guild-scale analyses). To do so, we grouped the communities (n = 48 guilds) in six different ways, according to the different bedrock types and elevational belts; (i) n = 15 guilds in dolomites, (ii) n = 15 in limestones, (iii) n = 18 in mica-schists, (iv) n = 18 at low elevation, (v) n = 18 at medium elevation and (vi) n = 12 at high elevation. Then, we conducted paired t-tests between the levels of the explanatory factor guild (i.e. understorey, overstorey and open-ground) within each group of communities, using the ES-CWM-SLA scores as the dependent variable (i.e. three paired t-tests per group of communities). For all tests, we
considered a nominal $\alpha$ level of 5%. Although our data might not fit the assumptions for parametric statistics (i.e. normality could not be tested due to low sample sizes), the Student's $t$-test is still appropriate when sample size is low (de Winter 2013). All the analyses were conducted in R version 3.2.2 (R Development Core Team, 2015).

3. Results

Our dataset consisted of 11,779 individual plants. Overall, communities on limestones showed higher number of individuals, and so did communities at medium elevation (Table S2). Most individuals were assigned to the open-ground guilds across all substrates and elevations, whilst the overstorey guilds were formed by fewer individuals.

At the community scale, we found significant differences in ES-CWM-SLA between communities growing on different type of bedrocks (Fig. 3a and Table 1). Communities on dolomite habitats showed significantly lower scores than communities on mica-schists ($t = -2.268$, $p < 0.001$; Table 1), the latter showing the highest scores across all the communities. Dolomite communities also showed lower scores than communities on limestones, thought differences were only marginally significant ($t = 2.005$, $p = 0.06$), and the latter showed significantly lower scores than communities on mica-schists ($t = -2.7009$, $p = 0.04$). We found no significant differences between communities growing at different elevations (Fig. 3b).

At the guild-scale, communities on dolomite habitats showed strong differences in ES-CWM-SLA between the guilds (Fig. 4a and Table 2). Specifically, the understorey guilds showed significantly higher scores than either the open-ground ($t = 6.8459$, $p = 0.002$) and the overstorey guilds ($t = 3.728$, $p = 0.02$). Communities on limestone showed a similar pattern, although differences between the guilds were only marginally significant ($t = 2.6863$, $p = 0.05$ between understorey and open-ground; $t = 2.4024$, $p = 0.07$ between understorey and overstorey). In contrast, communities on mica-schist exhibited no significant differences between the guilds (Table 2). Communities at medium elevation showed significant differences between the understorey and either the open-ground ($t = 4.4472$, $p = 0.007$) and the overstorey guilds ($t = 3.4856$, $p = 0.02$) (Fig. 4b). Finally, high-elevation communities exhibited significant differences between the overstorey and the open-ground guilds ($t = 10.59$, $p = 0.002$).

4. Discussion

There is increasing evidence that facilitative interactions may enhance diversity in species-rich ecosystems (Hacker and Gaines, 1997; Michalet et al., 2006; Allesina and Levine, 2011; McIntire and Fajardo, 2014), and particularly under harsh environmental conditions (Bulleri et al., 2016). However, other community assembly mechanisms such as environmental filtering could act antagonistically and reduce diversity.
(Laliberté et al., 2014), which may erase the signature of facilitation on the functional structure of communities (Soliveres et al., 2012; Gross et al., 2013; Michalet et al., 2015b). In this study, we used a two-scale sampling approach to provide evidence that both mechanisms may jointly shape the functional structure of plant communities, which caution about making inferences of community assembly mechanisms from the sole use of community-level functional patterns.

We found that communities on dolomite habitats showed low CWM-SLA values, suggesting than these communities are rather dominated by slow-growing and stress-tolerant species (Westoby et al., 2002; Wright et al., 2002). In contrast, communities on soils derived from limestones and mica-schists showed intermediate and high CWM-SLA values, respectively (Fig. 3a). This directional change in CWM-SLA suggests that the functional structure of communities may be determined by differential environmental filtering acting along contrasting edaphic conditions (Cornwell and Ackerly, 2009; Lebrija-Trejos et al., 2010; Spasojevic and Suding, 2012). Soils derived from dolomites are nutrient deficient and highly alkaline (Table S3), and show low water-holding capacity (Allison and Stevens, 2001; Michalet et al., 2002).

### Table 1

Results of the unpaired t-tests conducted between communities growing in different bedrock types and elevational belts (differences in ES-CWM-SLA scores). In bold, significant p-values for a nominal α level of 5%.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Comparison</th>
<th>t-statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>bedrock</td>
<td>Dolomites – Limestones</td>
<td>2.2005</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Dolomites – Mica-schists</td>
<td>–2.680</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Limestones – Mica-schists</td>
<td>–2.7099</td>
<td>0.03</td>
</tr>
<tr>
<td>elevation</td>
<td>Low – Medium</td>
<td>–0.9076</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Low – High</td>
<td>–0.2232</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>Medium – High</td>
<td>–1.1612</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Fig. 3. Box-and-whisker plots showing differences in ES-CWM-SLA scores between communities across bedrock types (a) and elevational belts (b). Values close to –1 and 1 indicate that the observed CWM-SLA values are lower and higher than expected for the given null distributions, respectively. Horizontal dotted lines represent visual references at y = 0 (random pattern). The letters indicate pairs of comparisons with significant differences for a nominal α level of 5% (unpaired t-tests).

Fig. 4. Box-and-whisker plots showing differences in ES-CWM-SLA scores between guilds (i.e. understorey, overstorey and open-ground) within communities grouped by bedrock types (a) and elevational belts (b). Values close to –1 and 1 indicate that the observed CWM-SLA values are lower and higher than expected for the given null distributions, respectively. Horizontal dotted lines represent visual references at y = 0 (random pattern). The letters indicate pairs of comparisons with significant differences for a nominal α level of 5% (paired t-tests).
Table 2

<table>
<thead>
<tr>
<th>Environmental axis</th>
<th>Grouping factor</th>
<th>Understorey – Overstorey</th>
<th>Understorey – Open-ground</th>
<th>Overstorey – Open-ground</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t-statistic</td>
<td>p-value</td>
<td>t-statistic</td>
<td>p-value</td>
</tr>
<tr>
<td>Bedrock</td>
<td>Dolomites</td>
<td>3.7280 0.02</td>
<td>6.8459 0.002</td>
<td>−1.7001 0.16</td>
</tr>
<tr>
<td></td>
<td>Limestones</td>
<td>−2.4024 0.07</td>
<td>−0.5267 0.62</td>
<td>0.1413 0.89</td>
</tr>
<tr>
<td></td>
<td>Mica-schists</td>
<td>−0.3406 0.75</td>
<td>−1.8088 0.12</td>
<td>−1.4094 0.22</td>
</tr>
<tr>
<td>Elevation</td>
<td>Low</td>
<td>2.0091 0.10</td>
<td>4.4472 0.007</td>
<td>−2.2753 0.07</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>3.4856 0.02</td>
<td>−1.4949 0.89</td>
<td>10.5860 0.002</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>−1.5168 0.23</td>
<td>−0.1494 0.89</td>
<td>−0.5267 0.62</td>
</tr>
</tbody>
</table>

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dolomite habitats may act as an effective environmental filter selecting slow-growing and stress-tolerant species (or populations) that show low SLA values. In contrast, communities that thrive in more benign soils such as those derived from mica-schists may converge towards high CWM-SLA values, as fast-growing competitive species displace weak competitors and become dominant (Mayfield and Levine, 2010). Further, the lower species richness recorded on mica-schist (n = 12.5 ± 4.09; mean ± SD) in comparison with dolomite habitats (n = 18.8 ± 3.11) supports the competitive exclusion hypothesis (Pausas and Austin, 2001). Finally, soils derived from limestones may occupy an intermediate position between both extremes of the edaphic gradient, allowing species with different resource-uptake strategies to entry the communities. Accordingly, limestone communities sit at the midpoint of the SLA spectrum (Fig. 3a).

Communities on dolomite habitats showed strong differences in SLA between guilds, particularly between the understorey (higher SLA) and either the open-ground and the overstorey guilds (lower SLA). In contrast, communities on mica-schists exhibited no differences between guilds, whilst communities on limestones showed slight (though non-significant) differences (Fig. 4a). These results are much in line with the stress gradient hypothesis (Bertness and Callaway, 1994), which predicts that facilitative interactions would predominate under harsh environments (He et al., 2013; but see Michalet et al., 2006; Holmgren and Scheffer, 2010). Overstorey “nurse” species (or populations) adapted to the harsh edaphic conditions imposed by dolomite habitats (i.e. plants with low SLA values) may provide microclimatic amelioration to less stress-tolerant understorey individuals (i.e. plants with high SLA values), allowing the latter to persist under stressful local edaphic conditions that otherwise would exclude them from the communities (Bruno et al., 2003). As edaphic conditions become more benign (i.e. limestone and mainly mica-schist) the importance of facilitative interactions for recruitment may decrease, and thus differences in CWM-SLA between guilds would narrow. We admit that other processes may alsodicts that facilitative interactions would predominate under harsh environments (Harrison and Rajakaruna, 2011), and they share some similarities with dolomite soils (e.g. nutrient deficiencies and low water-holding capacity; Kruckeberg, 1986). Also, serpentine soils are well-known for their distinctive flora, which consists to a large extent of serpentine habitat specialists (Anacker et al., 2011). Importantly, many species with clear preferences for dolomite outcrops are narrow-endemics (Mota et al., 1993) and share some characteristics with serpentine endemics (e.g. vegetative growth potential, small leaves, sericeous indument; Mota and Valle, 1992; Mota et al., 2011), suggesting an active role of dolomite habitats as drivers for plant adaptation and speciation. Stressful substrates have long attracted the attention of evolutionary ecologists, as they serve as model systems for the study of plant adaptation, speciation, and species interactions (Anacker and Harrison, 2011; Escudero et al., 2015). However, dolomite habitats have passed mostly unnoticed, and future studies should pay particular attention to these characteristic species-rich environments.

Author contributions

RMV, JA conceived the ideas, AA conducted the taxonomical identification, SL collaborated in the writing, RMV conducted the vegetation surveys and data collection, led the statistical analyses and wrote the manuscript.

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