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RESEARCH PAPER

Facilitation allows plant coexistence in Cuban serpentine soils

R. Oviedo[1], M. Faife-Cabrera[2,3], A. Noa-Monzón[2], J. Arroyo[4], A. Valiente-Banuet[5,6] & M. Verdú[7]

1 Instituto de Ecología y Sistemática de La Habana, La Habana, Cuba
2 Jardín Botánico de Villa Clara, Facultad de Ciencias Agropecuarias, Universidad Central 'Marta Abreu' de Las Villas, Santa Clara, Cuba
3 Department of Plant Biology and Soil Sciences, Faculty of Science, University of Vigo, Vigo, Spain
4 Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Sevilla, Spain
5 Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, México, México
6 Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de México, México, México
7 Centro de Investigaciones sobre Desertificación (CIDE, CSIC-UV-GV), Moncada, Valencia, Spain

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Correspondence
M. Verdú, Centro de Investigaciones sobre Desertificación (CIDE, CSIC-UV-GV), Apartado Oficial. 46113 Moncada, Valencia, Spain.
E-mail: Miguel.Verdu@uv.es

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ABSTRACT

Serpentine soils represent stressful habitats where plants have to cope with heavy metals, moisture limitation and low nutrient availability. We propose that facilitation is an important mechanism structuring plant communities under such stressful conditions. Facilitation has been shown to generate the spatial association of species, forming discrete vegetation patches of phylogenetically distant species. We measured these spatial and phylogenetic signatures left by facilitation in a serpentine plant community of central Cuba. Our results show that seedlings preferentially grow under plants of different species, and that adults are significantly aggregated into vegetation patches. In these patches, adults tend to co-occur with distant relatives, ultimately forming phylogenetically diverse neighbourhoods. We discuss possible mechanisms explaining how species adapted to serpentine areas may be acting as nurses, reducing the stressful conditions for the establishment of other species.

INTRODUCTION

Serpentine soils are formed by the weathering of ultramafic rocks, representing stressful habitats for plants because of high concentrations of toxic heavy metals such as iron, nickel, chromium and cobalt. Moreover, because serpentine soils are usually rocky, resulting in shallow soils with high rates of watershed run-off, plants must also cope with moisture limitation and depressed nutrient levels. Plants inhabiting these environments often tolerate both chemical and drought stresses, as well as high soil temperatures because of the sparse plant cover in the community (Brady *et al.* 2005). These stressful conditions can be alleviated under the canopy of established plants, where irradiation and temperature are reduced and water and nutrient availability are increased (Callaway 2007). Species adapted to live under stressful conditions may modify the environment and facilitate the establishment of other species. There is worldwide evidence that stress produces a change in plant interactions towards facilitation in terms of survival, or towards a reduction in competition in terms of growth and reproduction (He *et al.* 2013). Facilitation has repeatedly been shown to be an important mechanism structuring plant communities under stressful conditions, such as those arising in serpentine soils (Tirado & Pugnaire 2005; Verdú & Valiente-Banuet 2008). However, most efforts aiming to explain plant community structure in serpentine soils have focused on competitive interactions, especially between non-serpentine and serpentine species or ecotypes (Kazakou *et al.* 2008; Going *et al.* 2009; Moore & Elmendorf 2011), although evidence exists that facilitation may also be operating (Espeland & Rice 2007; Leger & Espeland 2010). A spatial signature of facilitation is the aggregation of species in such a way that the plants co-occur, thus forming discrete vegetation patches (Eccles *et al.* 1999; Kéfi *et al.* 2007; Scanlon *et al.* 2007). In contrast, communities shaped by competition tend to show spatial segregation of species (Maestre *et al.* 2009).

Facilitation-driven co-occurrence, as in many other ecological interactions, is not randomly produced but follows a phylogenetic pattern that tends to be conserved through the evolutionary history of lineages (Valiente-Banuet & Verdú 2007; Gómez *et al.* 2010). Thus, the phylogenetic relatedness among species, a metric that collects the evolutionary history of lineages, may successfully predict the coexistence of species (Ackerly 2003; Wiens & Graham 2005). As a general rule, species tend to spatially aggregate with distant relatives because of enhanced facilitation and/or reduced competition (Valiente-Banuet & Verdú 2008). More specifically, facilitation tends to join distant relatives, because they have complementary regeneration niches. Furthermore, competitive exclusion is not produced between these distant relatives because they have differentiated niches (Valiente-Banuet & Verdú 2008). Plant coexistence in multi-species vegetation patches shaped by facilitation thus follows a complex mixture of phylogenetically determined positive and negative interactions that vary over time (Castillo *et al.* 2010). The final outcome of all these processes is that plant coexistence in multi-species vegetation patches tends to be maximised under phylogenetically diverse neighbourhoods.

Living in multi-species patches necessarily allows indirect interactions to emerge. Indirect interactions through a third plant species usually alleviate the pair-wise competition (Callaway 2007). In addition, indirect interactions through other beneficial organisms, *e.g.* mycorrhizal fungi, have been linked to facilitation in general (Van Der Putten 2009; Montesinos-Navarro *et al.* 2012) and with serpentine soils in particular (Maas & Stuntz 1969; Branco & Ree 2010). Together, these observations suggest that vegetation patches are formed through the addition of species arranged in a phylogenetically diverse neighbourhood, where indirect interactions benefit them.

Serpentine outcrops are widespread on the island of Cuba, forming a kind of edaphic archipelago surrounded by other non-stressful soils, mostly derived from limestones. These serpentine outcrops harbour a rich list of very narrow endemic species in an otherwise high endemism region (Borhidi 1996). Despite good floristic knowledge, how these plant communities are assembled and spatially organised is poorly understood. Here, we propose that facilitation-driven co-occurrence is a mechanism allowing coexistence of plants in the extreme environment imposed by serpentine soils in central Cuba. We test whether the spatial and phylogenetic signals left by plant facilitation occur in serpentine soils; more specifically we test whether (i) there is an aggregated spatial co-occurrence pattern between distantly related species, and (ii) the phylogenetic diversity of the vegetation patches increases with the number of species.

MATERIAL AND METHODS

Study site

The study area was located in the Motembo serpentine area in the northwest of the province of Villa Clara, central Cuba (Fig. 1A). This area is an ultramafic massif of over 40 km^2 composed of intensely tectonised dunite and harzburgite clasts (Franco 2001). Soils are very shallow (20 cm), typical reddish-brown fersialitic, with mean pH of ~6, 1.13 ml 100 g^{-1} P_2O_5, 32.77 ml 100 g^{-1} K_2O, 0.64 % and 0.19 % Na (Rojo & Herrera 1986). These soils have strong deficiencies of Ca and Mo, and high concentrations (toxic to most plants) of Mg, Fe, Ni and other heavy metals (Borhidi 1996, 1999). The terrain is hilly, with gentle slopes and hypsometry between 60 and 100 m, promoting surface drainage of rainwater through streams and creeks that flow into the La Palma River (ICGC 1985). The climate is typically tropical, dry seasonal, with a mean annual temperature of 25 °C (Lapinef Pedroso 1990), annual average precipitation of 1200 mm (Gagua *et al.* 1990) and mean annual evapotranspiration of 2100 mm (Díaz Cisnero 1990). The rainy season is from May to October (Vidallet Rodríguez 1990).

The vegetation is characterised by xeromorphic thorny scrubland containing around 233 species and subspecies of vascular plants, grouped in 168 genera and 66 families (Capote & Berazain 1984; Franco Flores *et al.* 2004). The level of endemism is high (49.4%), including not only Cuban endemics but also local endemics (*Byrsonima motembensis* Britton & Small, *Paspalum edmondii* León, *P. motemboense* León, *Cheilophyllum sphaerocarpum* Urb. and *Scleria motemboensis* Britton). The most frequent species are *Phyllanthus orbicularis* Kunth, *Neobracea valenzuelana* Urb, *Tabebuia lepidota* Britton, *Piscidia cubensis* Urb, *Acacia daemon* Ekman & Urb, *Bourreria microphylla* Griseb, *Buxus flaviramea* (Britton) Mathou, *Chamaechrista lineata* (Sw.) Greene and *Bonania emarginata* Wright ex Griseb.

Sampling

We recorded the vegetation in six parallel transects of 100 × 10 m each. Vegetation patches were clearly delimited in space (Fig. 1B) and we could assign each recorded plant to a single patch. Seedlings (*i.e.* non-reproductive individuals <20-cm high) in transects were also recorded. Plant cover was estimated using the line intercept method.

Statistical analysis

We assessed inter-specific co-occurrence patterns using the C-score algorithm and the fixed rows–equiprobable columns null model to check whether species tend to aggregate or segregate, suggesting facilitation or competition, respectively, as the main assembly mechanism in our study community (Maestre *et al.* 2009). A C-score smaller than the expected value under the null model is indicative of facilitation, while a higher value is indicative of competition. The observed C-score was compared against those derived from 5000 randomly assembled matrices in Ecosim version 7.0 (Gotelli & Entsminger 2001).

The phylogenetic signature of co-occurrence patterns was established through the correlation between C-scores and phylogenetic distances between species. The phylogenetic distances between species were computed from a phylogenetic supertree assembled with the help of the program Phylomatic, as implemented in Phylocom version 4.2 (Webb *et al.* 2008). The tree topology of our community tree was obtained after matching the family names in our study site with those included in the angiosperm megatree used in Phylomatic (R20120829.new), based on work of the Angiosperm Phylogeny Group (Stevens 2001). Then, we dated the tree with family age estimates from Wikström *et al.* (2001) and the Bladj algorithm, which distributes undated nodes evenly between nodes of known ages (Webb *et al.* 2008).

The C-score is zero when two species co-occur in the same places (*i.e.* aggregation) and 1 when species never co-occur (*i.e.* segregation). A positive correlation between C-score and phylogenetic distance is indicative of co-occurrence of closely related species, while a negative correlation indicates co-occurrence of distantly related species. The correlation index was compared against a null model randomising 1000 times abundances within species. The analysis was done with the Picante package for R (Kembel *et al.* 2010).

To check whether phylogenetic diversity of the patch increased with species richness, we correlated the mean phylogenetic distance (MPD) of the patch to the number of species inhabiting that patch.

RESULTS

We recorded 2017 individuals belonging to 109 species (Fig. 2). Most individuals (88.4%) lived spatially aggregated with other

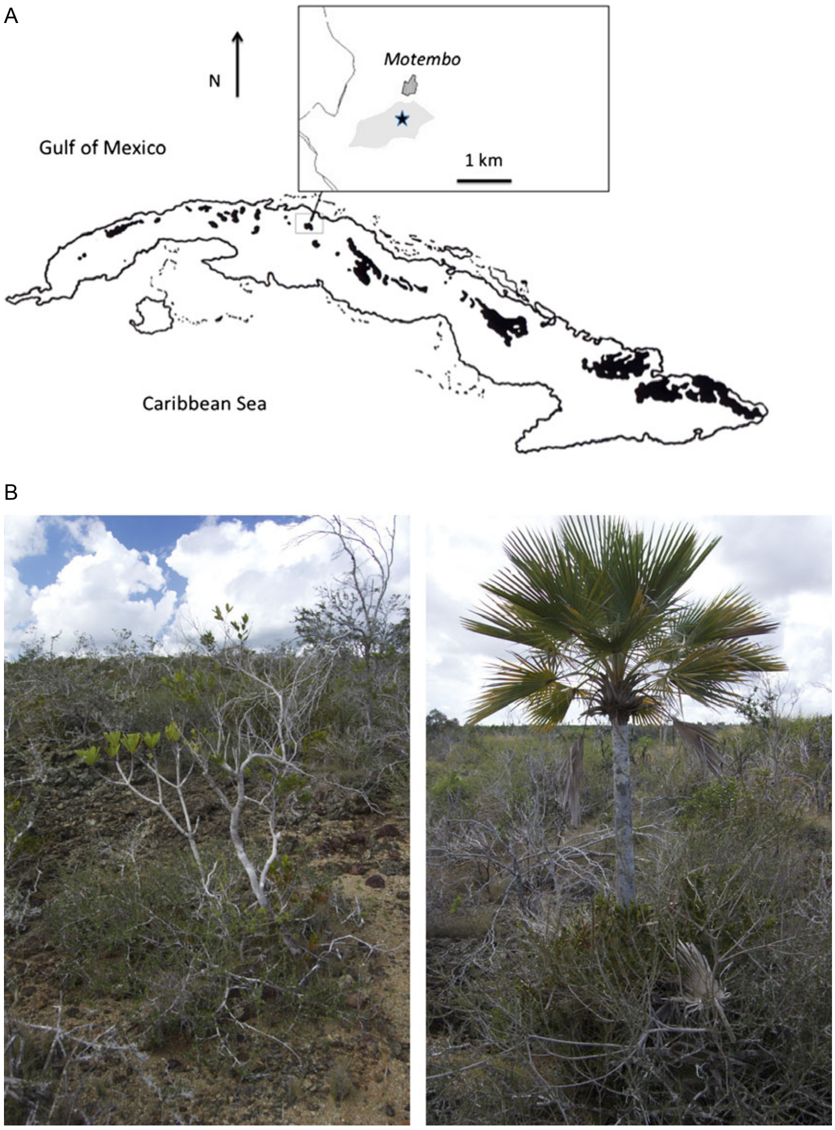

Fig. 1. (A) Map of Cuba showing the serpentine outcrops along the island. The star in the insert shows the study site. (B) Vegetation patches in the serpentine soils.

species, which was significantly higher than the null expectation for vegetation cover in the area (58.21%: $\chi^2_1 = 1801$, $P \ll 0.001$). Spatially aggregated plants formed 156 multi-species patches, with the number of species ranging from two to15, with an average of 5.5 species. We recorded 67 seedlings, 64 of which were recruited within patches while only three were recruited on open ground, strongly suggesting that recruitment is not random as expected from the vegetation cover, but follows a pattern of facilitation ($\chi^2_1 = 79.5$, $P \ll 0.001$).

In our study, community species tend to be significantly aggregated because the observed C-score (72.73) was significantly smaller than the expected C-score (81.3 ± 0.14; mean ± variance of 5000 simulated indices; $P < 0.001$) under the null model. The co-occurrence patterns followed a phylogenetic pattern in which species co-occurring in the same patches were distantly related ($r = -0.003$, $P \leq 0.001$). The mean phylogenetic distance between coexisting species increased logarithmically with the number of species coexisting in the vegetation patch ($R^2 = 0.33$, $t = 8.74$, $df = 154$, $P < 0.0001$; Fig. 3).

DISCUSSION

Our results show all the spatial and phylogenetic signatures of facilitation as a mechanism structuring ecological communities: (i) seedlings preferentially growing under other plants, (ii) spatial aggregation of adult species, (iii) co-occurrence of distantly related species and (iv) plant coexistence in phylogenetically diverse neighbourhoods. The finding that facilitation rather than competition is the main driver of community assembly in our study site is consistent with the classical consideration of low-fertility soils as refuges from competition, because slow-growing, stress-tolerant soil endemics are unable to compete with faster-growing species (Anacker & Harrison 2012). This is because the physiological trade-offs imposed by serpentine soils may prevent a single species from being both

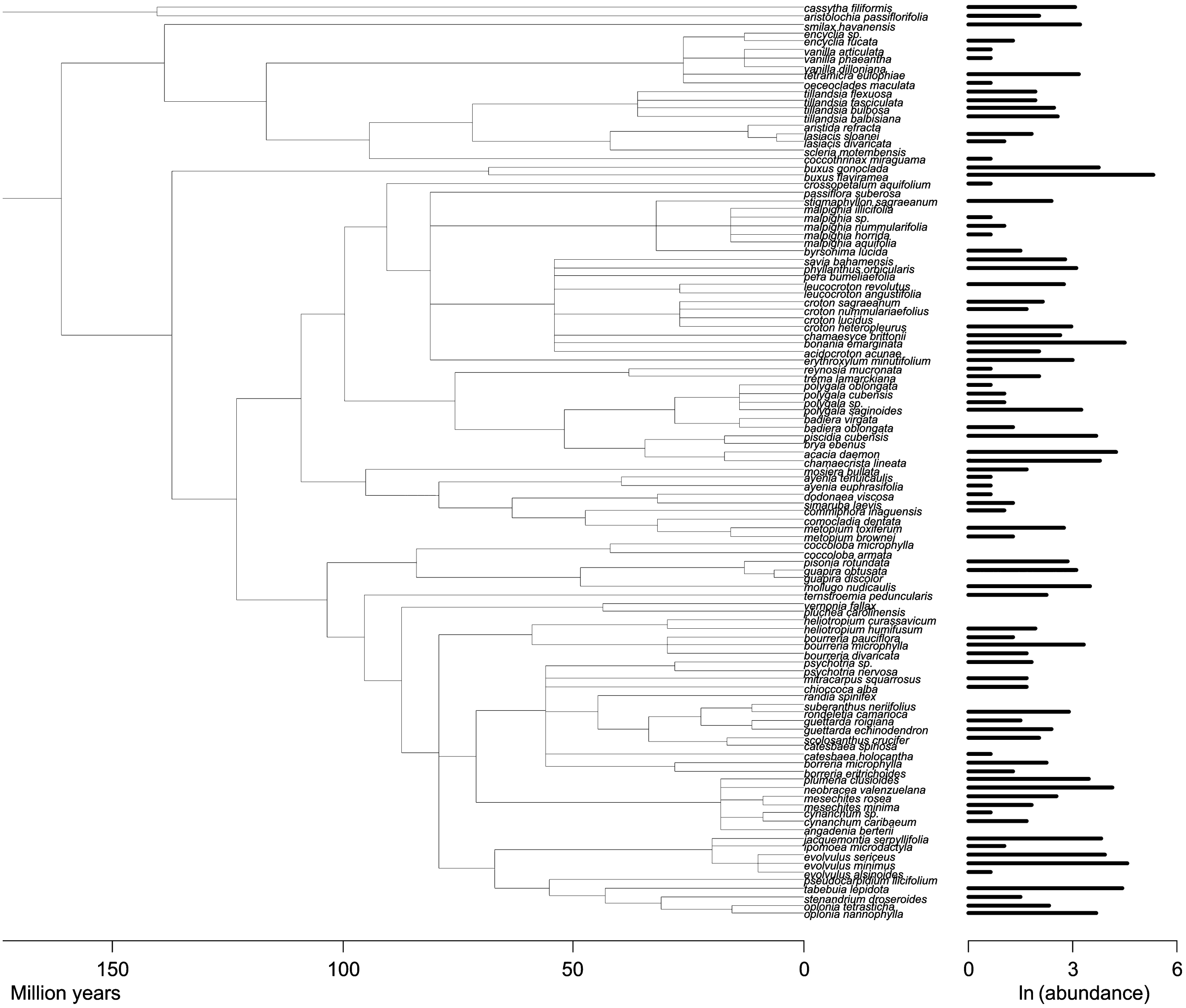

Fig. 2. Phylogenetic tree of the study community showing species abundances. The root of the tree, not appearing in the figure, is dated at 280.5 million years.

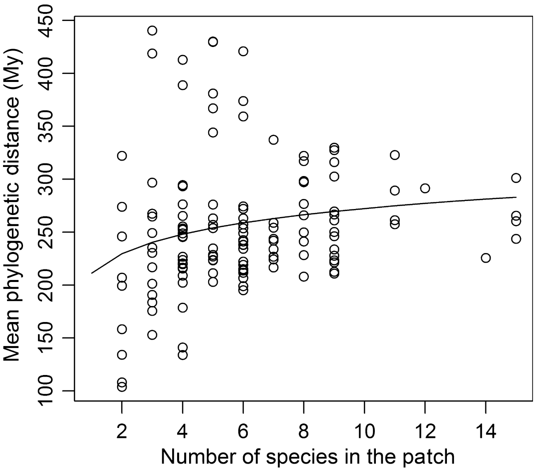

Fig. 3. Mean phylogenetic distance of coexisting species within a vegetation patch in the serpentine soils increases with the richness of the patch.

stress-tolerant and good competitor (Moore & Elmendorf 2011).

Strong adaptations are needed for plants to establish in extreme physicochemical conditions. A crucial characteristic of serpentine plant species is their high tolerance and ability to accumulate metals such as Mg and Ni. Most Ni hyperaccumulators described in Cuba are endemic to the oldest (10–30 My) serpentine soils. In contrast, young (ca. 1 My) serpentine soils, like those of our study site, have fewer endemics and hyperaccumulator species than old serpentines, strongly suggesting a time lag for both speciation and adaptation to serpentines (Reeves *et al.* 1999). In the absence of adaptive traits to cope with new stressful conditions, 'maladapted' species may survive thanks to amelioration of the microhabitat by other species equipped with adaptations to thrive under the new conditions. Thus, higher effects of facilitation should be found in younger than in older stressful environments. Indeed, facilitation has been shown to buffer extinction through the amelioration of stresses such as drought, high temperature and high irradiation or low nutrient availability (Valiente-Banuet *et al.* 2006). As experimental amelioration of serpentine stress through addition of nutrients can reverse species dominance patterns (Moore & Elmendorf 2011), it is tempting to hypothesise that facilitation structures the serpentine plant community by ameliorating the microhabitat. For example, the most abundant species in our study area, *Buxus flaviramea* (Fig. 2), is a strong Ni hyperaccumulator, reaching concentrations above 8300 $\mu g\ g^{-1}$ (Reeves *et al.* 1996). This species is clearly adapted to serpentine soils and may provide suitable microhabitats for the establishment of other species.

The most immediate microhabitat amelioration is related to shade, which reduces irradiance and water loss and buffers extreme temperatures (Callaway 2007), but belowground modifications may also enhance plant coexistence. Facilitation brings together plants that can share resources through mycorrhiza (Van Der Heijden & Horton 2009), by increasing plant nutrient acquisition and tolerance to metals, which are crucial to facilitate plant establishment in stressful environments, including toxic soils (Meharg & Cairney 2000; Sharples *et al.* 2000; Cumming & Nelly 2007). Indeed, most plants tolerant to serpentine soils establish mycorrhizal associations (Branco 2010; Branco & Ree 2010). Other mechanisms linking hyperaccumulation and facilitation through reduced herbivory have recently been investigated (El Mehdawi *et al.* 2011), opening new research avenues to consider positive interactions as powerful drivers of community assembly in serpentine soils.

Besides the economic value, serpentine areas are increasingly considered as having high conservation value, mostly due to the singularity (*i.e.* endemism) of their flora. This is the case in Cuban serpentines, which represent 7% of the land area but harbour 14% of the island endemics (Reeves *et al.* 1999). We suggest that an extra value should be added: that of being representative of ecological and evolutionary processes of community assembly and adaptation driven by extreme environments. Moreover, given the strong differences in age of the serpentine outcrops in Cuba, they offer an opportunity to test the effect of timing of evolutionary adaptations on differentiation and structuring of plant communities. These processes can be studied in detail in the serpentine communities, which might be considered small natural laboratories as islands within the island. Here we provide an example of how evolutionary adaptations of some plant species allow the survival of other species *via* facilitation. Our results are fully consistent with a hypothesis of coexistence determined by facilitation, and mediated by the evolutionary history of the species.

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