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Lichen-biocrust diversity in a fragmented dryland: Fine scale factors are better predictors than landscape structure

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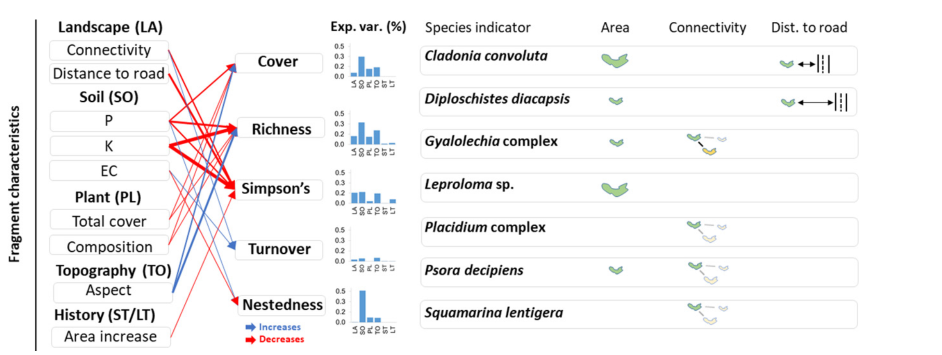
HIGHLIGHTS

- Biocrust cover, richness and composition were mostly unresponsive to changes in landscape structure.
- Soil properties better explained the variation in biocrust cover and diversity.
- Species composition in biocrust and vascular plant communities were coupled.
- Some biocrust species can act as indicators of fragment area, connectivity and distance to road.
- Landscape structure and habitat quality need to be evaluated jointly to assess fragmentation impacts on biocrusts.

GRAPHICAL ABSTRACT



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ABSTRACT

Biological soil crusts (or biocrusts) are widespread, diverse and important components of drylands sometimes threatened by global change drivers. However, their response to fragmentation processes is poorly known. The aim of this study was to assess the effects of changing landscape structure, given by land use change and the presence of linear infrastructure (e.g., roads), on the cover and diversity of lichen-biocrusts. We also evaluated the influence of several subrogates of fragment quality, such as soil properties, vascular plant community structure and topography. Biocrust cover and diversity were measured in 50 remnants of a Mediterranean shrubland. The fragments varied in size, connectivity and distance to a road, but also in plant and soil attributes, topography and fragment history. We applied general linear and mixed models to assess the effects of environmental variables on biocrust communities. Biocrust cover, richness and species composition were mostly unresponsive to changes in landscape structure, while connectivity and distance to the road decreased species diversity. Soil properties better explained the variation in biocrust cover and diversity. Changes in plant community and biocrust community composition were coupled. We also identified several biocrust species with strong capacity to reflect landscape structure. Our findings suggest that landscape structure needs to be evaluated jointly with other environmental factors to fully understand the consequences of fragmentation processes on biocrust communities and the subsequent implications for their functional role in drylands.

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1. Introduction

Fragmentation of habitats is one of the most pervasive drivers of global change (Pimm and Raven, 2000; Saunders et al., 1991). The reduction and isolation of habitat remnants has ecological and evolutive consequences catalysed by changes in microclimatic conditions such as radiation balance, wind regime and hydrological processes together with alterations in the habitat continuity (Saunders et al., 1991).

Responses to habitat shrinkage and loss of connectivity are found at different organizational levels. For instance, effects of fragmentation at the species level are a function of the dispersion and colonization capacity, longevity and resistance to the new biotic and abiotic conditions imposed by this global change driver (Damschen et al., 2008; Hanski, 1999; Dupré and Ehrlén, 2002; Wilson and MacArthur, 1967). At the community level, habitat loss and isolation usually exerts negative effects on species richness and abundance. Fragmentation also induces spatial variation in species composition within natural remnants as a consequence of species gains/losses due to changes in environmental conditions and new species interaction over time (Conradi et al., 2017; Henle et al., 2004). Also, in advance diversity patterns and shifts in composition among fragments mirror landscape configuration in the past (Ellis and Coppins, 2007; Lindborg and Eriksson, 2004).

Traditionally, the replacement of natural vegetation by agricultural lands has been the major cause of landscape fragmentation; i.e., reducing and isolating habitat remnants (Saunders et al., 1991). More recently, linear infrastructure, such as roads, has been gaining importance as a determinant of landscape structure (Forman and Alexander, 1998). On one hand, the construction of roads also implies the elimination of natural habitat, the reduction of remnant connectivity and, additionally, the alteration of microclimate, chemical composition and dust input on the surrounding landscape (i.e., disturbance effect). On the other hand, road margins can provide new habitat and benefit the movement and dispersion of certain species along the road (Coffin, 2007). Thus, linear infrastructure can either limit the dispersion of species from one side to the other of the landscape (i.e., barrier effect) or favour particular ecological fluxes (i.e., corridor effect) (see Arenas et al., 2017).

Although there is a complete theoretical framework and evidence of the effects of fragmentation and landscape modification in many biological groups (e.g., birds, mammals, invertebrates and vascular plants; Andrén, 1994; Fahrig, 2003; Fischer and Lindenmayer, 2007; Trombulak and Frissell, 2000), this is not the case for cryptogams and even less for terricolous lichens and mosses, as they are generally less conspicuous. Nevertheless, lichens and mosses composing biological soil crusts or “biocrusts”, along with other organisms, such as cyanobacteria, living in the uppermost soil layers are one of the main ecosystem components in global drylands (Weber et al., 2016).

Biocrusts have critical importance for ecosystem structure and diversity covering almost completely plant interspaces and comprising tens of species at fine scales (e.g., Concostrina-Zubiri et al., 2014). They also contribute to ecosystem services that include fixing carbon and nitrogen (Elbert et al., 2012), stabilizing and protecting soil surface from erosion (Jimenez Aguilar et al., 2009; Zhang et al., 2008), modulating hydrological (Chamizo et al., 2013; Felde et al., 2014) and biogeochemical cycles (Beraldi-Campesi et al., 2009; Concostrina-Zubiri et al., 2013; Delgado-Baquerizo et al., 2015), and structuring biotic interactions (Luzuriaga et al., 2012; Neher et al., 2009). Moreover, lichen-dominated biocrusts are ideal communities for testing predictions related to dryland degradation and fragmentation. First, they comprise species with sexual and vegetative reproduction, with different dispersion and colonization capabilities (Nash, 1996). Second, they are poikilohydric organisms; and thus, very sensitive to changes in environmental conditions such as air humidity (Lange et al., 1994). Finally, they respond greatly to local biotic and abiotic conditions such as vascular plant cover and composition, soil properties, and topography (Weber et al., 2016); which altogether reflects habitat quality.

Still, to our knowledge only a pioneering body of work done in Australia has evaluated the fragmentation effects on biocrusts in drylands (Read et al., 2008, 2014). Cover and richness of biocrust-lichens increased in bigger fragments and foliose lichens were identified as indicators of large (i.e., less degraded) sites in Australian landscapes (Read et al., 2008, 2014). However, little is known for other drylands such as the Mediterranean region, where habitat fragmentation is one of the main drivers of global change (Valladares et al., 2004). Furthermore, to our knowledge there is no previous research on the effects of linear infrastructure on biocrusts communities.

We aimed to understand the effects of fragmentation on biocrust diversity in a fragmented Mediterranean dryland. We focused on lichens, the most conspicuous, rich and common components of biocrusts in Mediterranean grasslands and shrublands (Concostrina-Zubiri et al., 2014; Maestre et al., 2009). This is particularly true in gypsum soils, where stressful conditions for plant growth restrict vascular plant establishment and allow the spread of typically more abundant and diverse lichen-biocrusts (Bowker and Belnap, 2008; Concostrina-Zubiri et al., 2014; Martínez et al., 2006; Martínez-Sánchez et al., 1994).

Here, the two drivers were simultaneously considered: i) land use change; mainly caused by agricultural practices and intensification, and ii) linear infrastructure; as the presence of a busy highway crossing the fragmented landscape. The impact of these two drivers on lichen-biocrusts diversity was measured as changes in the area, shape and connectivity of the remnant fragments, and by the distance from the fragment to the highway. We also took into account several surrogates of fragment quality, such as soil properties, perennial plant community structure and topography, which are well-known determinants of biocrust diversity (Weber et al., 2016). In addition, we included a time-scale integrative variable to represent fragment history; i.e., positive or negative changes in fragment area. In this study, we were mainly interested in the way in which realized assemblages are configured within remnants and the determinants of their variability within and among habitat remnants.

In particular, we tested the following hypotheses: i) biocrust cover and diversity are influenced by fragment area and connectivity, and distance to the highway, ii) biocrust cover and diversity are determined by different aspects of fragment quality; described by vascular plant cover and composition, soil properties and topography, and iii) current biocrust cover and diversity reflect positive changes in fragment area over time. Additionally, we hypothesized that spatial variation in species composition within fragments (i.e., replacement of species and species gains/losses at the local scale) is also driven by: i) fragment area and connectivity, and distance to the road, ii) fragment quality, and iii) changes in fragment area. We also hypothesized that the biocrust composition of realized assemblages responds to landscape factors and fragment quality. Finally, we tested the suitability of biocrust species as indicators of fragmentation, since they have been found to be good indicators of ecosystem disturbance and degradation in other drylands (Read et al., 2008).

2. Materials and methods

2.1. Study area

The study area (ca. 76 km^2) is located in central Spain between the villages Fuentidueña del Tajo (40°7′7.96″N, 3°9′41.96″W, 570 m a.s.l.) and Belinchón (40°2′52.95″N, 3°3′29.68″W, 761 m a.s.l.). The area comprises two adjacent rectangles, each 3 km wide along both sides of a 13 km segment of the A3 national road (Fig. 1). The landscape is characterized by Mediterranean gypsum soil shrubland remnants immersed in an agricultural matrix. The climate is Mediterranean semi-arid, with cold winters and very dry and warm summers. Mean annual precipitation is 443 mm and mean annual temperature is 14 °C with a very intense summer drought (Ninyerola et al., 2005). Soils are predominantly Typic Gypsiorthid (Soil Survey Staff, 1994), with high