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Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment

Yudi M. Lozano [a, *], Sara Hortal [a, b], Cristina Armas [a, c, d], Francisco I. Pugnaire [a]

[a] Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Carretera de Sacramento s/n, E-04120, La Cañada de San Urbano, Almería, Spain
[b] University of Western Sydney, Hawkesbury Institute for the Environment, Hawkesbury Campus, Locked Bag 1797, Penrith NSW 2751, Australia
[c] Institute of Ecology and Biodiversity, Casilla 653, Santiago, Chile
[d] Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena, Chile

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ABSTRACT

Secondary succession studies have mainly focused on plants, but little is known about the fate of soil microbial communities and their relationship with plant succession after disturbance, particularly in dry ecosystems. We examined changes in soil properties and of plant and soil microbial communities across a chronosequence of abandoned arable fields that included five successional stages according to time of abandonment stretching near a century. We hypothesized the existence of a parallel secondary succession above- and below-ground and explored the possible linkages between plant and microbial communities as well as the role of changes in soil properties over the successional gradient. Soil microbial communities were characterized by PLFAs analysis, enzymatic activities, and pyrosequencing of the 16S rDNA. We found clear patterns of plant and microbial secondary succession characterized by an increase in organic C, NH_4^+, and silt content as well as in soil microbial biomass and activity along the successional stages, linked to an increase in plant productivity and diversity. Plant and microbial composition were significantly different among successional stages, although no distinct microbial communities were observed in the two initial stages, suggesting that microbial succession may lag behind plant succession. However, the degree of change in the composition of soil microbial communities and plant communities across our chronosequence evidenced that above- and below-ground secondary succession developed with similar patterns and correlated with changes in multiple ecosystem functions such as increases in above-and below-ground productivity, diversity and nutrient accumulation as plant and microbial succession progressed.

1. Introduction

Plant secondary succession has been considered as a process of little applicability in arid environments (Cramer and Hobbs, 2007) or even non-occurring (Rowlands, 1980). Several reports have shown that plant secondary succession does actually occur in these extreme habitats (e.g., Bonet, 2004; Scott and Morgan, 2012) but our knowledge on secondary processes in arid environments is still poor, especially in comparison to more temperate regions (Abella, 2010) where plant succession often shows a relatively rapid and predictable trajectory in species diversity and composition (e.g., Foster and Tilman, 2000).

Soil microbial communities also change over time as it has been shown in different environments, from soils deglaciated only 20 years ago (Nemergut et al., 2007), to of *ca.* 77,000 years old inland dunes (Tarlera et al., 2008). Changes in microbial community composition with time are influenced by factors such as carbon inputs, plant–microbial interactions (Tarlera et al., 2008) competition (Nemergut et al., 2007), soil variables such as pH, C, N and P concentrations (Banning et al., 2011) or land use history (Jangid et al., 2011). It has been suggested that plant community composition and soil chemistry explain different parts of the variation in soil microbial communities (Mitchell et al., 2012), but still little is known about the links between below-ground and above-ground succession processes.

The few existing studies on secondary succession in arid ecosystems have almost exclusively focused on the dynamics of plant communities, with little attention to soil microorganisms.

* Corresponding author. Tel.: +34 950281045; fax: +34 950277100.
E-mail addresses: ym.lozano@eeza.csic.es, lozano.ym@gmail.com (Y.M. Lozano).

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However, interactions between plants and soil microorganisms may have important consequences for plant community dynamics, becoming key factors for community assemblage and ecosystem functioning (Kardol et al., 2013). We know that soil organisms influence plant community composition (Van der Putten et al., 2013), affecting plant performance either positively (Bever, 2003; Rodríguez-Echeverría et al., 2013) or negatively (Klironomos, 2002); and that plants in turn influence microbial communities and drive changes in physico-chemical soil properties (Van der Putten et al., 2013). Published reports on soil microbial changes with time concerned temperate ecosystems but never, to our knowledge, dry environments. Such reports, however, lacked enough information (e.g., microbial biomass, activity and composition) to help explain such variations.

Here we address changes with time in soil properties and in plant and soil microbial community structure in abandoned arable fields in a dry environment. We established a chronosequence of abandoned agricultural fields in SE Spain spanning ca. one century. Our specific aims were (i) to characterize changes in plant communities, soil properties and soil microbial communities at different times after agricultural abandonment, and evaluate whether changes follow a successional pattern; (ii) to elucidate whether changes in plant and microbial community mirrored each other; and (iii) to explore linkages among soil properties and plant and microbial communities along the chronosequence. In this dry environment we expected to find a process of succession in belowground soil communities intimately linked to above-ground plant succession in plants.

2. Methods

2.1. Study area

The field site was located at Llanos de Rueda (37.05° N, 2.22° W, 503 m altitude) a flat piedmont of approximately 120 ha in the Tabernas Basin, Almería, Spain. The climate is semiarid with a mean annual precipitation of 235 mm, mild winter temperatures (mean minimum temperature of 4.1 °C) and hot summers (average maximum temperature of 34.7 °C) (Lázaro et al., 2001). Extreme air temperatures above 45 °C and below freezing temperatures are not uncommon in the hottest and coldest months, respectively (Spanish National Meteorological Institute, 2012). Soil parent material is a gypsum siltstone. Soils are orthic solonchacks with inclusions of calcic regosols, characterized by very low water holding capacity, low organic matter content, moderately alkaline pH (8.5) and low electrical conductivity (Pérez Pujalte et al., 1987).

The plant community is a sparse and short shrubland with low cover dominated by shrubs like *Artemisia barrelieri* (Besser), *Hammada articulata* (Moq.) O. Bolòs & Vigo, *Helianthemun almeriense* (Pau), *Salsola oppositifolia* (Desf.), *Thymelaea hirsuta* (L.) Endl, and perennial grasses as *Stipa tenacissima* (L.) and *Lygeum spartum* (L.) Kunth (Peinado et al., 1992).

2.2. Chronosequence selection

To define the chronosequence we used information from three different sources, (i) land use maps of the study area from 1928 (scale 1:25,000) and 1949 (scale 1:5000) (Geographic and Cadastral Institute of Spain); (ii) orthophotos from 1956, 2000 and 2009, registered in the Environmental Information Network of Andalucía (REDIAM) with spatial reference ETRS89_30 and a geometric resolution of 1.0 m (years 1956 and 2009) or 0.5 m (year 2000) (Fig. S1); and (iii) direct field assessment performed in 2012.

Both land use maps and orthophotos were digitized with ArcGIS 10.0 (ESRI, Redlands, California, USA) using clustering analysis to group objects with similar features. Objects were attributed to land uses taking into account shadow tone, color, shape, texture features and geometric resolution (Mitchell, 1999). Attributed land uses were checked by field assessment, available information in the literature, historical records from the Almería Historic Archive, and confirmed by interviews with people with first-hand knowledge of the area.

All digitized maps were overlapped in order to identify changes in land use. We recorded areas used as croplands anytime in the past and recorded their dates of abandonment (Fig. S1). Each of the identified areas was assigned into one of the following five categories according to the date of abandonment, i.e. the last 3, 12, 56, 63 years and >84 years or native grasslands. The most recently abandoned fields were marginally cultivated to sustain game bird populations, while traditional agricultural use consisted on non-irrigated crops for human subsistence. We considered native grasslands as the endpoint of succession, and grouped in this category any areas not cultivated after 1928 (i.e. areas abandoned more than 84 years ago).

Five 30 m^2 plots were randomly selected in each identified stage, giving a total of 25 plots. All plots were located as close as possible (maximum distance of 1 Km), and shared similar soil, climatic conditions and topographic position.

2.3. Plant community composition and soil sampling

We surveyed plant communities in May 2012 using transects. In each of the 25 plots we randomly placed five transects 25 m in length. We identified species found along transects and measured the length of intercepted segments (*i.e.* the transect length occupied by a given species). For each perennial species we calculated the percent cover by transect and then the average percent cover by plot. We also recorded the number of individuals for each perennial species in each plot as the sum of individuals recorded in the five transects per plot, and assessed plant diversity using the Shannon's diversity index. All taxa were identified to species level.

Seven soil cores, 4.5 cm in diameter and 10 cm deep, were collected at regular distances along each transect, combined, homogenized and sieved through 2 mm mesh to form one composite soil sample per plot. Each of the 25 composite soil samples collected was divided in two subsamples, one (approximately 100 g) was stored at −20 °C for soil microbial molecular analyses following Hortal et al. (2013); and Tscherko et al. (2005), and the other (approximately 400 g) was kept at 4 °C for physical and chemical analyses. Samples were processed within four weeks after collection.

2.4. Soil analyses

Soil electrical conductivity (EC) and pH were measured in each soil sample using a 1:10 (w:v weight:volume) aqueous solution with a conductivity- and pH-meters (Crison, BA, Spain), respectively. Total soil carbon (C), organic C after removal of inorganic carbon with HCL 2N (Schumacher, 2002), and total nitrogen (N) content were determined using a C/N analyzer (LECO Truspec, MI, USA). Anion phosphate (PO_4^{3-}), nitrate (NO_3^-), and sulfate (SO_4^{2-}) concentrations in water extract (1:10 soil:water) were analized by HPLC (Metrohm, HE, Switzerland). Soil ammonium content (NH_4^+) was calculated from the urease activity (below). Percentage of clay, sand and silt were measured by granulometry.

2.5. Bacterial composition: pyrosequencing

DNA was extracted from 0.25 g of homogenized soil from each of the 25 soil samples using the PowerSoil® DNA Isolation Kit (MO BIO