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Arbuscular mycorrhizal fungal spore communities of a tropical dry forest ecosystem show resilience to land-use change

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ABSTRACT

We explored the resilience of arbuscular mycorrhizal fungal (AMF) communities of a tropical dry forest ecosystem to land use as pastures. We compared spore community species richness, composition, abundance, and similarity between old-growth forests and active pastures, as a measure of resistance and examined the trajectory of change in successional fields when pasture use stopped to evaluate recovery. Despite a few changes in species richness, community composition and structure were strikingly similar in all sites, including the active pastures. The spore communities were considered resistant to land use as pastures and showed minor changes along succession when management stopped. We found a significant negative relation between the frequency of Diversisporales and Glomerales indicating a selective species turnover driven mainly by the families Gigasporaceae and Glomeraceae. This was, however, unrelated to land use or successional time. These results suggest the AMF communities of this ecosystem seem resilient to management as pastures.

1. Introduction

Tropical dry forests are among the most threatened ecosystems in the world and have lost at least 60% of their original cover as a consequence of conversion to agriculture and pastures (Miles et al., 2006). Conversion and management usually alter soil (García-Oliva et al., 1999, 2002; Cotler and Ortega-Larrocea, 2006; Sandoval-Pérez et al., 2009), vegetation (Mora et al., 2014; Trilleras et al., 2015), and environmental conditions (Lebrija-Trejos et al., 2011; Pinzón-Perez, 2013), at least temporarily. Plant productivity usually starts to decline after some years of management and eventually leads to land abandonment and secondary succession in the abandoned fields (Burgos and Maass, 2004). As a result, the landscape turns into a mosaic of fields containing active agriculture and pastures, secondary vegetation of different ages, and primary vegetation (Gavito et al., 2008).

Resilience is the capacity of an ecosystem, or its components, functions or processes, to withstand disturbance by resisting, reorganizing while undergoing change and recovering, so as to retain essentially the same function, structure, identity, and feedback (Holling, 1973). The components or properties of an ecosystem are resilient when they are resistant to a change in their environment or when they are altered but recover when this change ends. Both, resistance and recovery are complementary measures of resilience that can be assessed with analytical tools (Hodgson et al., 2015). Species richness and composition of some plant and animal communities in tropical dry forest ecosystems were not altered by land conversion and management while others changed but showed a return to pre-conversion levels, usually within a few decades, through natural regeneration in abandoned fields (Lebrija-Trejos et al., 2008; Maza-Villalobos et al., 2011a,b; Villa-Galaviz et al., 2012; Mora et al., 2014; Suazo-Ortuño et al., 2015). Those studies based on land-cover comparisons suggested an overall resilience of different organisms to the changes originated by land-use change and management practices. A recent resilience assessment made for vegetation and soil properties (Ayala-Orozco et al., 2017) showed

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indeed that the majority were resilient to land-use change. The resilience of communities of soil organisms, however, has been poorly studied in this highly dynamic process of continuous environmental transformation (Falconer et al., 2015).

The Glomeromycotina are soil fungi of special interest because of their symbiotic interaction with the majority of plants (Schüßler et al., 2001) and their influence on plant nutrition (Jakobsen, 1998), plant diversity (Van der Heijden, 2002), nutrient cycling and soil structure (Rillig and Mummey, 2006). Arbuscular mycorrhizal fungi (AMF) distribution, development and survival are influenced by environmental factors such as fertility, humidity, compaction, and temperature in soil, as well as topography, altitude and latitude (Camargo-Ricalde, 2002). Additionally, there are also important biotic factors such as host compatibility and dispersal capability (Smith and Read, 2008). AMF community composition is redefined continuously in response to the environment and functional characteristics of the species present (Kivlin et al., 2011).

Land-use change and land management are drivers of environmental changes that may lead to new species arrangements in AMF communities, depending on the type, intensity and duration of the environmental alterations and on the AMF species functional traits (Koide et al., 2013). AMF exhibit functional traits like the proportion of mycelium development inside and outside the roots, or P transfer capacity to plants, which seem to be preserved at the family level (Hart and Reader, 2002). Understanding the changes in community composition may help to predict what species will stay or disappear after an environmental change (Xiang et al., 2014) and the consequences of the departure or arrival of species on the functions AMF perform in ecosystems (Maherali and Klironomos, 2007).

Despite the importance of AMF for ecosystem functioning (Johnson et al., 2006), the resilience of AMF communities to recurrent and long-term disturbance pressure, such as land-use change, is still unknown. Several studies have documented changes in AMF communities under various land covers resulting from land-use change in temperate (Lumini et al., 2010; Oehl et al., 2010; Cortés-González et al., 2012) and tropical (Gavito et al., 2008; Stürmer and Siqueira, 2011; Pereira et al., 2014) ecosystems. Although comparison of land cover may give some indications of resilience, no study to our knowledge has explicitly explored the resilience of AMF communities to land-use change and pasture management in tropical dry forests.

This study evaluated the resilience of AMF spore communities to land-use change by examining the resistance of undisturbed tropical dry forest communities to pasture management and their recovery through successional time after management stopped. We: (1) characterized the structure and composition of AMF in a group of sites including active pastures, successional fields of different ages and old-growth forests; (2) compared AMF spore community species richness, composition, abundance, and similarity between old-growth forests and active pastures, as a measure of resistance to land conversion and pasture management, and examined the trajectory of change in successional fields to evaluate recovery after pasture management; and (3) explored if differences in soil and environmental properties were associated with differences in AMF community composition in the land covers examined. We hypothesized that AMF communities of this ecosystem would be resilient to land-use change mainly due to a rapid recovery after management ceased. We expected that, given the significant alterations in plant communities during pasture management, AMF communities would not be resistant to this land-use change but would recover rapidly as has been shown for soil properties and plant and animal communities of this tropical dry forest ecosystem when management stops.

2. Materials and methods

The study area is located on the Pacific coast (Fig. 1) in the state of Jalisco, in Mexico (19°29′ N, 105°01′ W). This is a tropical dry forest ecosystem with a mean annual temperature of 25 °C and mean annual rainfall of 746 mm concentrated between June and October (García-Oliva et al., 2002). Soils of the region are usually Regosols and characterized as poorly developed and shallow (Cotler et al., 2002).

We used a group of sites that included two active pastures with more than 15 y under this land use, six sites with secondary vegetation of different successional age ranging from 6 to 34 yr, and two old-growth forests (OGFs) to analyze AMF community changes. In the absence of data documenting the dynamic changes of AMF composition in fields undergoing the entire process: primary forest → land conversion → pasture management → land abandonment → succession, we used a space-for-time approach (Quesada et al., 2009). This allowed us to compare the changes sequentially in time using fields that at the time of measurement were in different stages of the process. OGFs were located within the Chamela-Cuixmala Biosphere Reserve and pastures and successional plots outside the reserve. OGFs were well preserved in this region until they were converted to agriculture and pasture use in the 1970s and 1980s as a result of a governmental program of land distribution. For this reason, all pasture and successional sites have management histories shorter than 40 yr (Table 1). Pastures are under low-input management, with no tillage, herbicides, or fertilizers, but with intense grazing and frequent burning to control invasion of other plants and boost grass development. When productivity decays and pastures are abandoned, disturbance is more infrequent, usually as coppicing and occasional grazing (Trilleras et al., 2015). We gathered the most homogeneous set of sites as possible considering that both the landscape and the management histories are highly diverse.

All sites were located on independent hillsides (Fig. 1). Only two sites, the OGFs, are 300 m apart; the rest of the sites are separated by at least 1 km to reduce spatial confounding effects. Soil samples were taken in November 2011, 1 month after the last rain of that year, in 15 × 10 m plots marked along the slope. The beginning of the dry season is a good time for sampling because AMF sporulation peaks and spores have not undergone severe desiccation or attack by other organisms (Gavito *pers. comm.*). The plots were divided in three 5 × 10 m sections (top, middle and low) and five sampling points were marked with a minimum of 1.5 m spacing, within each section. Soil was sampled from 0 to 10 cm depth of the mineral soil, by inserting a shovel as uniformly as possible considering the abundance of rocks and pebbles and soil compaction in most sites. At the same time we measured soil temperature at 10-cm depth besides each sampling point by inserting the metal probe of an oven thermometer. The five samples of approximately 500 g from each section were kept separate (15 samples per site) and sealed in plastic bags until processing. In the lab a subsample of each soil sample was weighed fresh as soon as possible and moisture content was determined by weight difference after oven-drying to constant weight. The rest of the soil sample was refrigerated at 4 °C and processed for AMF spore extraction and identification within 8 months.

Soil properties were measured in a separate study performed 1 yr before our sampling in the same plots and with the same sampling strategy. Soil properties were measured from one composite sample for each section obtained by mixing thoroughly a subsample from the five samples collected. Bulk density samples were taken from one random sampling point in each section of the slope using intact cores taken with a 6-cm diameter PVC cylinder. The core was stored in a sealed plastic bag until processing in the