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Gigasporaceae versus Glomeraceae (phylum Glomeromycota): A biogeographic tale of dominance in maritime sand dunes

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ABSTRACT

Community composition of arbuscular mycorrhizal fungi (AMF) is influenced by host, soil chemistry, and climatic conditions at the local and regional scale, but little is known about factors shaping community composition on a global scale. In this study, the pattern of dominance by families in Glomeromycota in maritime sand dunes worldwide was examined to test the hypothesis that soil pH is a major factor shaping AMF community structure. We analyzed 38 publications from the literature containing data on soil chemistry and species composition and calculated relative species richness (RSR) for each of the families Gigasporaceae, Glomeraceae, and Acaulosporaceae. Regression and multivariate analyses were performed to determine the relationship and association of RSR of families with soil pH, temperature and precipitation and biogeographical realms. Of the 119 AMF species found in sand dunes, members of Gigasporaceae and Glomeraceae dominated in all studies. In Nearctic dunes, Gigasporaceae and Glomeraceae co-dominated fungal communities while Gigasporaceae dominated in Neotropical dunes and Glomeraceae dominated Palearctic and Oriental/Sino-Japanese realms. Overall, the proportion of species in Gigasporaceae was above 40% in soil pH < 6.5 while the proportion of those in Glomeraceae exceeded 40% in soil pH > 6.5. Soil pH was negatively correlated with RSR of Gigasporaceae but positively correlated with RSR of Glomeraceae. Thirteen species were detected in at least four biogeographical realms and are considered cosmopolitan. Redundancy analysis evidenced soil pH and one Moran's spatial variable as significant predictors of Glomeromycota family composition. Moran's I correlograms showed positive spatial autocorrelation only at distances < 2000 km for soil pH and family composition. We conclude that soil pH was a major factor influencing the dominance of Gigasporaceae and Glomeraceae in sand dunes worldwide, and the proportional dominance of each family was distinct amongst biogeographical realms.

1. Introduction

The phylum Glomeromycota was erected by Schüssler et al. (2001) to group all arbuscular mycorrhizal fungi (AMF) and *Geosiphon pyriformis*, a rare localized endemic fungal species in a symbiosis with the cyanobacterium *Nostoc punctiforme*. AMF are soil fungi that form compatible arbuscular mycorrhizal symbioses with the majority of land plants (Wang and Qiu, 2006). Absence of host specificity and ancient origin contribute to their widespread distribution in terrestrial ecosystems, including maritime sand dunes on different continents (Koske, 1975, 1987; Abe et al., 1994; Stürmer and Bellei, 1994; Koske and Gemma, 1997; Beena et al., 2001; Blaszkowski and Czerniawska, 2011).

Species in Glomeromycota are distributed in four orders, 11 families and 19 genera (Redecker et al., 2013). Gigasporaceae, Glomeraceae, and Acaulosporaceae represent the most speciose families within the phylum, containing 82% of the 288 currently described species. The Glomeraceae was erected by Pirozynski and Dalpé (1989) to accommodate species with spores formed terminally on one or more subtending hyphae, singly or in sporocarps, and having at least one layer of the spore wall continuous with a subtending hypha. It represents the largest family within the phylum and includes the genera *Glomus*, *Funneliformis*, *Rhizophagus*, *Septoglomus*, *Sclerocystis*, *Dominikia*, and *Kamienskia*. Some

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members were moved to a new family (Claroideoglomeraceae) containing the genus *Claroideoglomus* (Schüssler and Walker, 2010). Gigasporaceae and Acaulosporaceae were erected by Morton and Benny (1990). Gigasporaceae consists of the genera *Gigaspora, Racocetra, Dentiscutata, Cetraspora,* and *Scutellospora*, grouping species that form spores borne terminally on a bulbous base and knobby or echinulate auxiliary cells. Acaulosporaceae consists of only one genus, *Acaulospora*, and groups species forming a sporiferous saccule followed by differentiation of spores within or attached to the saccule's subtending hypha.

Gigasporaceae species are considered to be dominant in mycorrhizal communities of sand dunes in the Americas as a result of extensive surveys of maritime dunes along the Atlantic Coast of the United States, North America (Koske, 1981a, 1987; Koske and Halvorson, 1981; Gemma and Koske, 1989; Gemma et al., 1989; Koske and Gemma, 1997) and in the coastal areas of Brazil, South America (Trufem et al., 1989, 1994; Stürmer and Bellei, 1994; Cordoba et al., 2001; Silva et al., 2012; Stürmer et al., 2013). In contrast, Glomeraceae appears to be the dominant family in sand dunes of Europe (Blaszkowski, 1994; Campubri et al., 2010; Blaszkowski and Czerniawska, 2011), Asia (Abe et al., 1994; Beena et al., 1997, 2000a, 2000b) and Hawaiian island (Koske, 1988; Koske and Gemma, 1996). AMF in Acaulosporaceae and other families widely occur in sand dunes, but they are not dominant sporulators within native communities.

Factors known to affect AMF species distribution and abundance include soil depth, season, soil properties and vegetation (see works cited in Abbott and Robson, 1991). Among edaphic factors, soil pH has been hypothesized to affect distribution of AMF species (Porter et al., 1987; Sieverding, 1991), and frequency of their occurrence (Siqueira et al., 1989). Soil pH has been shown experimentally to directly influence spore germination (Giovannetti, 1983; Hepper, 1984; Siqueira et al., 1984). Using a three-dimensional non-metric multidimensional scaling (NMDS) ordination, Fitzsimons et al. (2008) determined that soil pH and nitrate levels, together with timing of any disturbance, were good predictors of changes in AMF community. Among climatic factors, temperature often is hypothesized to be an important variable impacting on fungal occurrence and distribution (Pirozynski, 1968; Koske, 1987; Widden, 1987). At the continental scale in Europe, soil pH, soil organic C, and land use influenced AMF community composition over natural and managed ecosystems (Bouffaud et al., 2016). At the global scale, assessment of AMF fungal diversity using DNA-based method evidenced that soil pH, soil organic C, temperature and precipitation were the main factors influencing variation in AMF community richness across forest, grasslands, semi-desert, and successional ecosystems (Davison et al., 2015). However, none of the studies at the continental and global scale included maritime sand dunes as an ecosystem.

Studies of AMF community composition in sand dunes published until now provide the stage to compile information on AMF species richness and to elucidate which factors influence AMF distribution in this ecosystem worldwide. Investigation of AMF community structure at a global scale is important to understand the geographical distribution of these soil fungi (Bouffaud et al., 2016). The aims of this paper were to survey global patterns of dominance by Gigasporaceae, Glomeraceae, and Acaulosporaceae in maritime sand dunes around the world, and to determine factors that influence glomeromycotan family composition in this ecosystem. As a corollary of previous works, we tested the hypothesis that soil pH predicts AMF family composition in sand dunes worldwide.

2. Material and methods

A literature search of publications reporting composition and distribution of AMF species in sand dunes was conducted using the ISI Web of Science® database with the combination of the strings "mycorrhiz*" and "sand dunes", covering a period from 1970 to 2016. The search resulted in 234 publications that were scanned to determine: (a) identity and sporulation data on AMF species found in sand dunes, (b) soil pH, and (c) phosphorus levels. Of these publications, 37 were found to report AMF species diversity although not all of them included information on soil pH and P levels (Supplementary Table S1). All publications were treated as one survey, except studies of Koske (1987) and Stürmer et al. (2013) that were carried out in a regional level whose data for each zone sampled were treated separately, and Silva et al. (2015) that sampled two areas with very distinct soil pH. Nomenclature for families and genera proposed by Redecker et al. (2013) was followed in this paper.

The number of species in Gigasporaceae, Glomeraceae, Acaulosporaceae, and other glomeromycotan families was obtained from each study, after which relative AMF species richness (RSR) in each family was calculated as: $\mathrm{RSR} = [\mathrm{SR}i/\mathrm{SR}total] * 100$, where $\mathrm{SR}i$ = number of species per family i and $\mathrm{SR}total$ = total number of species per study. Data from seasons were combined when a published survey reported species richness from two or more seasons. Based on Holt et al. (2013), biogeographical realms were designated as Neotropical, Panamanian, Nearctic, Palearctic, Saharo-Arabian, Afrotropical, Madagascan, Sino-Japanese, Oriental, Oceanian, and Australian.

Mean annual precipitation and temperature for each survey were obtained from WorldClim – Global Climate Data (Hijmans et al., 2005) while soil pH and phosphorus levels were obtained from that reported for each survey. Latitude and longitude were obtained using Google Earth when not informed in the publication.

2.1. Statistical analysis

The Pearson's r coefficient was computed to examine the relationship between RSR of Glomeraceae and Gigasporaceae in relation to soil pH using JMP® statistical software.

The role of environmental and spatial variables in explaining the variation of the RSR of families Glomeraceae, Gigasporaceae, and Acaulosporaceae among surveys was assessed through a procedure using the redundancy analysis (RDA) and the variance partition method (Peres-Neto and Legendre, 2010). The latter procedure permits the partition of the explained variance by the predictor variables into the following three components: [a] the 'pure' environmental variables, [b] the spatially structured environmental variables, and [c] the 'pure' spatial structure (Peres-Neto and Legendre, 2010).

Based on the geographical coordinates (latitude and longitude) of each survey, 29 spatial variables named Moran's Eigenvector Maps (MEM) (Dray et al., 2006) were created by means of a connectivity matrix obtained by the Delaunay triangulation (Borcard et al., 2011). This step was conducted using the package 'spacemakeR' in R, following the suggestions of Borcard et al. (2011). The MEM were regressed to the family composition matrix through a RDA model. The composition matrix consisted of the RSR of each family recorded in each study site The selection of significant MEM in the model was done using the package 'packfor' in R, via the 'forward' procedure, as presented by Blanchet et al. (2008).

The environmental variables - namely soil pH, soil phosphorus