



A native and an invasive dune grass share similar, patchily distributed, root-associated fungal communities



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ABSTRACT

Fungi are ubiquitous occupiers of plant roots, yet the impact of host identity on fungal community composition is not well understood. Invasive plants may benefit from reduced pathogen impact when competing with native plants, but suffer if mutualists are unavailable. Root samples of the invasive dune grass *Ammophila arenaria* and the native dune grass *Leymus mollis* were collected from a Californian foredune. We utilised the Illumina MiSeq platform to sequence the ITS and LSU gene regions, with the SSU region used to target arbuscular mycorrhizal fungi (AMF). The two plant species largely share a fungal community, which is dominated by widespread generalists. Fungi detected on only one species were rare, accounting for a small proportion of the data. The SSU region recovered AMF from more samples and from more Glomeromycota lineages than ITS or LSU. A high degree of turnover among samples was observed, but there was no evidence for strong distance-decay.

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1. Introduction

Many different fungi associate with plant roots, including mycorrhizal fungi, endophytes and pathogens. Their co-occurrence in root systems has been demonstrated by laboratory experiments (Lace et al., 2014; Sun et al., 2014), greenhouse investigations (Zhou et al., 2016) and field surveys (Muller and Hilger, 2015; Vandegrift et al., 2015). Arbuscular mycorrhizal fungi (AMF) are relatively well characterised. Their position on the mutualism – parasitism continuum can shift with the environment (Johnson and Graham, 2013). Potential benefits that AMF confer to the host plant include the provision of nutrients (Smith et al., 2011; Thirkell et al.,

2016) and protection from abiotic stresses such as drought (Boyer et al., 2015) or high salinity (Estrada et al., 2013). Endophytes, typically defined as non-mycorrhizal plant occupants causing no visible disease (Schulz and Boyle, 2005), are less well studied (Mandyam and Jumpponen, 2014) but can also benefit their host (Rodriguez et al., 2008; Hubbard et al., 2014; Murphy et al., 2015). Endophytes can be extremely flexible in their environmental niche and function. The capacity of some endophytes to occupy both roots and insects was recently reviewed by Barelli et al. (2016) and there is evidence that horticultural pathogens can live as benign endophytes in other crops or in natural ecosystems (Malcolm et al., 2013; Martin and Dombrowski, 2015). However, many fungal plant root occupants remain poorly understood (Sieber and Grunig, 2013), despite their probable importance for plant community composition (Dostalek et al., 2013; Rillig et al., 2014; Shi et al.,

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2016).

The role of host identity in structuring root fungal communities is unclear (Dickie et al., 2015). Field investigations suggest the effect of host species is context-specific for fungal communities, with this found to be an important control in some cases (Becklin et al., 2012; Hazard et al., 2013; Tejesvi et al., 2013; Vályi et al., 2014; Kernaghan and Patriquin, 2015), but not in others (Saks et al., 2013; Porrás-Alfaro et al., 2014; Glynou et al., 2016; Li et al., 2015). The phylogenetic relationships of the hosts being compared may be important, with root fungal community similarity increasing with host relatedness in grasslands (Wehner et al., 2014). This trend has also been shown for plant pathogens in general (Gilbert and Webb, 2007; Barrett et al., 2009). Closely related plants may tend to share fungal communities because the host traits that influence interactions with fungi tend to be phylogenetically conserved (Wehner et al., 2014) with plant functional group and plant life form known to be potentially important for AMF community composition (Chagnon et al., 2015; Varela-Cervero et al., 2015). But even here, the evidence is contradictory, with other studies reporting increasing differences between AMF communities as host relatedness increases in some environments (Reinhart and Anacker, 2014; Veresoglou and Rillig, 2014) and host species differences being detected even at the level of cultivar in agricultural systems (Corredor et al., 2014; Mao et al., 2014).

Understanding host-specific relationships in fungi is particularly important in the context of invasive plant ecology. Invasive and co-occurring native plants can share fungal communities (Knapp et al., 2012) and both may benefit from fungal root occupants (Molina-Montenegro et al., 2015). However invasive plants can also impact fungal communities to the detriment of native plants (Callaway et al., 2008; Ruckli et al., 2014; Yang et al., 2014). The 'enemy release hypothesis' suggests that invasive plants flourish because, for a time at least, local pathogens do not occupy them or have a minimal impact relative to pathogens in the host's native range and/or to impacts on co-occurring native competitors (Keane and Crawley, 2002). This hypothesis is supported by evidence for decreased fungal pathogen loads on plants introduced to North America compared to those in the species' native ranges in Europe (Mitchell et al., 2010). *Pinus contorta* seedlings grew better in soils from Sweden, where the plant has been introduced, than in soils from *P. contorta*'s native range in Canada, due to differing biotic interactions (Gundale et al., 2014). However, common garden experiments in California found no evidence that native clover species suffered greater negative impacts from fungal pathogens than do co-occurring exotic clover species (Parker and Gilbert, 2007). The invasive plant *Vincetoxicum rossicum* associates with many potentially pathogenic fungal root occupants in Canada. Roots of plants sampled from sites invaded less than 12 years previously had fungal communities as rich as those from sites invaded around 100 years ago, suggesting pathogens can accumulate quickly on non-native plants (Day et al., 2015). Focusing instead on fungi that can associate with new arrivals, the 'enhanced mutualism hypothesis' points to occasions where invasive plants appear to receive support from beneficial microbes (Sun and He, 2010; Baynes et al., 2012). The forb *Solidago canadensis*, which is invasive in China, benefitted more from soil micro-organisms in greenhouse experiments than the native grass *Stipa bungeana* (Sun and He, 2010) and *Triadica sebifera* seedlings had higher levels of AMF colonisation in their introduced range in the United States than in their native range in China (Yang et al., 2015). However a meta-analysis by Bunn et al. (2015) found that, in general, invasive plants do not experience greater benefits from mutualists than native plants.

Ammophila arenaria (L.) Link is an important sand dune stabiliser in its native Europe (Huiskes, 1979), and was moved to the United States for erosion control more than a century ago (Lamson-

Scribner, 1895). The species has been established in Humboldt Bay, Northern California, where it has become invasive, since at least 1901 (Buell et al., 1995). Here, it co-occurs with the grass *Leymus mollis* (Trin.) Pilg., which is native to Asia and North America (Barkworth et al., 2007). *L. mollis* is well adapted to coastal dunes being tolerant of burial, salt spray and high substrate salinity (Gagné and Houle, 2002) but has been widely displaced by *A. arenaria* on the west coast of the United States (Pickart and Sawyer, 1998). Soil feedback experiments in the greenhouse suggest that *A. arenaria* has not benefitted from release from soil enemies in this region (Beckstead and Parker, 2003). Seedling growth was lower in non-sterilised than in sterilised soil, and multiple potential pathogens were isolated from them. Recent efforts using culturing indicate that *A. arenaria* shares a common root endophyte community with co-occurring dune grasses (David et al., 2016). However there are no studies examining the whole fungal community associated with *A. arenaria* roots and co-occurring dune plants. There are few studies of endophytes in non-agricultural herbaceous plants (Sieber and Grunig, 2013) and little work to date using next generation sequencing to study the mycobiota of invasive plants (Coats and Rumpho, 2014).

Next generation sequencing is becoming a vital tool in microbial community profiling, rapidly revealing the complexity of plant microbiomes (Schlaeppi and Bulgarelli, 2015). It enables detection of non-culturable fungi and permits the simultaneous screening of large numbers of samples (Lindahl et al., 2013). The phylogenetic groups detected will, to some extent, be influenced by the gene region that is amplified (Tederloo et al., 2015). Long favoured for its relatively accurate taxonomic resolution to species level, the internal transcribed spacer (ITS) is the official barcode region for fungi (Schoch et al., 2012) and the best represented in public databases (Brown et al., 2014). The large subunit (LSU) region, however, is useful for resolving deeper taxonomic relationships (Porter and Golding, 2012), may detect a wider range of taxa, and can also be easier to amplify (Bonito et al., 2014, first author, pers. obs.). The small subunit (SSU) region is commonly used for AMF, and the majority of AMF sequences in public databases are generated with SSU primers (Öpik et al., 2014). Sequencing multiple gene regions may provide a more complete community picture than one region alone.

Here we use Illumina MiSeq next generation sequencing of the ITS, LSU and SSU rDNA genes to examine the fungal communities in the roots of *A. arenaria* and *L. mollis* where the plants co-occur in an extensive foredune at Humboldt Bay, northern California. In addition to comparing the fungal communities in these two plant species and the performance of the alternative gene regions, this study examines distance-decay effects in compositional turnover across the site. Measurements of pH were also taken at each sample point as pH has previously been found to co-vary with fungal communities in dunes (Geml et al., 2014; David et al., 2016).

2. Materials and methods

2.1. Study site

Root samples were collected from an established foredune section immediately north of the Lanphere Dunes in the Humboldt Bay National Wildlife Refuge, California, during June 2013. While dune restoration activities have been carried out in adjacent areas since the 1980s, the section sampled had not been subject to such management. The seaward face of the foredune was dominated by *A. arenaria*, but also included *L. mollis*. The native grass occurred in patches of 'Leymus mollis Herbaceous Alliance' (for a description of this vegetation type see California Native Plant Society, 2015), scattered among large blocks of dense *A. arenaria*, and with

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