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Scattered far and wide: A broadly distributed temperate dune grass finds familiar fungal root associates in its invasive range



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ABSTRACT

Deterministic and stochastic factors interact to generate biogeographic patterns in fungal communities, challenging efforts to predict which fungal assemblages will develop in association with introduced plants. The coastal dune grass Ammophila arenaria has been moved around the world. We sampled A. arenaria roots in its native range in the United Kingdom, and in Australia and New Zealand where it is invasive. The co-occurring native dune grass Leymus arenarius was also sampled in the United Kingdom, and the native dune grass Spinifex sericeus was sampled in Australia and New Zealand. A. arenaria associates with root fungal communities in its invasive range that are richer than those in the United Kingdom, and richer than those in co-occurring native grasses, demonstrating that exotic plants are not necessarily depauperate in fungal associates. Most of the dominant OTUs associating with A. arenaria were shared among all three geographic regions. However, community composition varied among regions, with differences in temperature, nitrogen and pH correlating with community change. Within regions, community composition varied among dunes, although the majority of sequences obtained were in OTUs that were detected in multiple dunes. Host plant species identity influenced fungal community composition, although the majority of the data were in OTUs that were shared between hosts. While the roots sampled appeared healthy, many of the dominant fungi recovered are potentially pathogenic. This study demonstrates that many fungi are widely dispersed, and that introduced plants are likely to associate with functionally diverse fungal communities that include species from their native ranges. However root-associated fungal community composition is variable, even at regional and local scales in a common plant in a common environment.

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1. Introduction

Root-associated fungi have fundamental impacts on plant health, and consequently can influence plant community structure (Aguilar-Trigueros and Rillig, 2016; Dostalek et al., 2013; Rillig et al., 2014; Shi et al., 2016). Fungal associates may, therefore, influence the success of introduced plants (Vestergård et al., 2015). Different root fungal communities could result in differential plant performance in the native versus the introduced range, and even influence whether a plant becomes invasive. For example, depauperate fungal communities can constrain the spread of introduced plants where mutualists are lacking (Nuñez et al., 2009; Pringle et al., 2009; Spence et al., 2011). On the other hand, the Enemy Escape hypothesis suggests that invasive plants flourish when released from pathogens encountered only in their native range (Keane and

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Crawley, 2002). However, introduced plants can quickly acquire fungal associates from a range of functional groups after they arrive in a new location and some might counteract this effect (Day et al., 2015; Majewska et al., 2015). Altogether there is a lack of data comparing entire fungal communities in the roots of plants in their introduced versus their native ranges. High throughput sequencing, which allows the examination of fungal communities to a much greater extent than previous methods, has not yet been extensively adopted by invasive plant ecologists (Coats and Rumpho, 2014).

Differences in fungal communities associating with a plant in its native and introduced range will depend in part on the dispersal abilities of the potential associates. The Baas Becking hypothesis assumes dispersal is unlimited, stating that 'everything is everywhere, but the environment selects'. While this hypothesis influenced expectations regarding fungal dispersal for decades (Baas Becking, 1934; Hazard et al., 2013) in recent years it has been largely abandoned (Bahram et al., 2014). Although molecular studies indicate that some fungal taxa have high dispersal capacity (Fröhlich-Nowoisky et al., 2012; Kivlin et al., 2014) and broad ranges (Bonfim et al., 2016; Cox et al., 2016; Davison et al., 2015; Timling et al., 2014) consistent with Baas Becking, fungi can also be dispersal limited, even at regional and local scales (Beck et al., 2015; David et al., 2016; Talbot et al., 2014).

Following dispersal, abiotic environmental conditions may determine establishment success (Peay et al., 2016). At regional scales, climatic conditions may be an important limiting factor (Glynou et al., 2016; Miyamoto et al., 2015; Tedersoo et al., 2014). At more local scales, soil conditions including levels of nitrogen, phosphorus (Leff et al., 2015), carbon (Wu et al., 2013) and pH (Geml et al., 2014) influence fungal communities.

The biotic soil environment is also important (Nemergut et al., 2013). The fungal communities associating with the roots of cooccurring established plants are likely to be a major source of fungal inoculum available to introduced plants. However, it is difficult to predict whether an identical or alternative community will develop in a new arrival to a plant community. Plant host species identity has been shown to impact fungal community composition in some studies (Barrett et al., 2009; Becklin et al., 2012; Kernaghan and Patriquin, 2015; Tedersoo et al., 2010; Tejesvi et al., 2013; Vályi et al., 2014), but in other cases, host plant identity has had limited or no influence on root endophytes (David et al., 2016; Glynou et al., 2016; Knapp et al., 2012) and communities of arbuscular mycorrhizal fungi (Davison et al., 2015; Li et al., 2015; Saks et al., 2013). The degree of relatedness between resident and introduced plant host species may impact the degree to which they share available fungal lineages (Bufford et al., 2016; Wehner et al., 2014). As well, both facilitation and competition among fungi render arrival order important in determining fungal community composition (Fukami et al., 2010; Werner and Kiers, 2015). Stochastic factors further impact the assembly of fungal communities, compounding variation at small spatial scales and complicating efforts to predict fungal community composition at any given location (Beck et al., 2015; Powell et al., 2015).

Ammophila arenaria (L.) Link is a coastal dune grass native to Europe that was transported around the world for erosion control in the latter part of the 19th century (Bell, 1987; Dixon et al., 2004; Wiedemann and Pickart, 1996). It is known to share many fungi with native dune grasses in the United States (David et al., 2016; Johansen et al., 2015), but a direct comparison of fungal communities in its native and introduced ranges has not previously been undertaken. There have also not been previous efforts to examine fungal communities in co-occurring native grasses outside of the United States.

In this study, we used next generation sequencing to characterize the fungal communities associated with *A. arenaria* roots in

three regions – its native range in the United Kingdom, and in Australia and New Zealand where the plant has been introduced. In addition, spatially explicit sampling allowed us to characterize heterogeneity in the fungal communities within regions and within dunes. Although a common biome was sampled, the regions encompassed were separated by vast distances across which abiotic factors differed, and we predicted that the fungal community richness would be similar but composition would differ among regions. Within regions, where dispersal limitation is likely to be less important and environmental conditions less variable, we predicted that fungal community richness and composition would be similar among dunes. Given the frequently disturbed nature of the dune environment, we hypothesised that there would be high spatial turnover in fungal community composition within dunes and this would be related to distance between samples. We also examined the fungal communities in the roots of co-occurring native dune grasses in each of the three regions. These grasses provide baseline community composition data, and also enable us to examine whether host plant identity impacts fungal community composition in the dune environment. However, given the level of relatedness between the two grasses in each location, and the results from our previous study of the fungal communities in a dune in the United States (Johansen et al., 2015), we hypothesised that host plant identity impacts would not be significant. Finally, we examined the general community profile of fungi occupying the roots of dune grasses.

2. Materials and methods

2.1. Sample collection

We collected *Ammophila arenaria* samples from three regions the United Kingdom (UK, two sites in England, five sites in Wales), Australia (four sites) and New Zealand (four sites) (Fig. 1). Root samples of the native dune grass Spinifex sericeus were collected from one of the Australian (Lakes Entrance) and one of the New Zealand (Waikawa Beach) sites. Root samples of the native grass Leymus arenarius were collected from one site (Newborough Warren) in England. A. arenaria was highly dominant at each of the sites where only this species was collected. At Lakes Entrance in Australia, Spinifex sericeus was slightly more prevalent than A. arenaria. At the other sites in the other regions where alternative grasses were collected, they were co-dominant with A. arenaria. All samples were collected during summer; UK samples were collected during June 2014, New Zealand samples during January 2015 and Australian samples during February 2015. Site location details, soil properties and climate data are provided in Table S1 (supplementary data). At each site, 24 root samples of A. arenaria were collected from the foredune face. Usually this was in a 100 m \times 12 m belt transect, with the shorter side placed between the dune toe and first ridge, but at one site in Australia (Seven Mile) the belt transect was reduced to 100 m \times 9.5 m to keep the transect within the foredune face. At the sites in England and Australia where two plant species were sampled, the species intermingled on the dune, and roots were collected from each where they grew within 1 m of each other. These transects were expanded to 150 m, and 200 m, respectively. At the New Zealand site, the two species typically grew in monocultural blocks. Therefore 12 samples of each were collected in pairs along a transect where two such blocks were adjacent, and the other 12 were collected from 50 m \times 12 m quadrats on either side. Sampling points were selected via randomstratification, with the dunes divided vertically into thirds (lower, middle and upper dune sections), and eight sample points were taken in each. Roots were collected from the depth at which they first appeared, with the minimum depth sampled being

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