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Short communication

Unpredictable assembly of arbuscular mycorrhizal fungal communities

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ABSTRACT

In their analysis of arbuscular mycorrhizal fungal communities sampled from roots collected around the globe, Davison et al. (2015, Science 349: 970) demonstrated that these fungi exhibit low endemism and suggested that their biogeography is largely determined by local environmental conditions. Here, we show that, within similar environments, these communities are largely unpredictable based on environmental conditions and exhibit patterns that are either consistent with neutral models of community assembly or are more stochastic than what models based on environmental filtering, nichebased assembly, or neutrality would predict. We also show that the degree of unpredictability is related to geography and the characteristics of the host plant, suggesting opportunities for future research to understand assembly processes in mycorrhizal fungal communities.

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A primary goal of microbial ecology is to understand the drivers controlling the diversity and distribution of microorganisms (Martiny et al., 2006; Powell et al., 2015; Tedersoo et al., 2014). Mycorrhizal fungi have been a significant focus for this research given their intimate relationship with their hosts and their functional importance (Antoninka et al., 2015; Lekberg et al., 2007; Tedersoo et al., 2014). In their global survey of rootassociated arbuscular mycorrhizal (AM) fungal communities, Davison et al. (2015) demonstrated that local climatic and edaphic properties, as well as the spatial distribution of the local communities, could explain species turnover among samples (as well as diversity within samples). Their main conclusion was that the biogeographic and phylogenetic patterns observed are consistent with low endemism, and they go on to suggest that AM fungal biogeography is largely determined by local environmental conditions. This is an important advance with functional consequences evident for natural and managed systems.

However, looking at Fig. 3F in their publication, betadiversity (Sørensen dissimilarity, indicative of species turnover) is very high among communities within each sampled plot, with most observations falling far to the upper end of the distribution. This pattern is counter-intuitive since, under similar environmental conditions and through interactions with the same regional species pool, local communities should converge upon a common, predictable composition and betadiversity should be low. The

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E-mail addresses: Jeff.Powell@westernsydney.edu.au (J.R. Powell), Alison.Bennett@hutton.ac.uk (A.E. Bennett). pattern in their Fig. 3F suggests that, locally, community assembly processes lead to substantial divergence and result in outcomes that are largely unpredictable based on environmental conditions in each plot. This could be due to extensive local environmental variability, a deterministic view that is unlikely given that site selection involved an assessment of the similarity of habitat conditions. Alternatively, complex outcomes of interspecific interactions (e.g., priority effects; Lin et al., 2015; Werner and Kiers, 2015) or neutral interactions associated with random mortality and immigration events (Caruso et al., 2011; Lekberg et al., 2007) could lead to stochastic assembly processes.

To test this, we used a null model approach that is based on the assumption that species-environment matching is unimportant in determining the outcome of community assembly (Etienne, 2007; Hubbell, 2001). The model is used to estimate parameters associated with diversity within the fungal metacommunity and the degree of immigration into each local community (Etienne, 2009). Communities are then simulated based on model estimates (Etienne, 2007); attributes of these 'neutral' scenarios are then compared to the observed distribution of pairwise dissimilarities (Beck et al., 2015; Powell et al., 2015). Further details on these methods can be found in Powell et al. (2015). Using the data from Davison et al. (2015), this process was performed on 66 OTUsample matrices representing all samples collected from a unique host plant species within a single plot; only those species-plot combinations that included at least four independent samples within the plot for the plant species under consideration were included in the analysis. We report the results of analyses on the OTU-sample matrices that were generated by the authors assigning sequences to 'virtual taxa' (VTX). However, analyses of



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Fig. 1. Effect sizes based on median compositional (Sørensen) dissimilarity, relative to predictions of the neutral model, in AM fungal communities associated with roots sampled from multiple individuals of one plant species in individual $30 \text{ m} \times 30 \text{ m}$ plots. Responses are ranked in order from most convergent to most divergent relative to the neutral model prediction. Circles represent the median dissimilarity of the observed distribution relative to the average of the median across 100 simulated distributions; lines indicate the 95% confidence interval of this effect size. The average (±standard error) of the response for each major plant group are presented at the bottom (P_{group} =0.015 using a linear mixed effects model including plant species as a random term).

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