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## Communities of fungal endophytes in tropical forest grasses: highly diverse host- and habitat generalists characterized by strong spatial structure



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#### ABSTRACT

Plant-symbiotic fungi influence the structure and function of all terrestrial ecosystems, but factors shaping their distributions in time and space are rarely well understood. Grasses (Poaceae), which first arose and diversified in tropical forests, harbor diverse but little-studied endophytes in the lowland forests of Panama. We used sequence data for 402 isolates from two sampling years, 11 host species, and 55 microsites at Barro Colorado Island, Panama to investigate the influence of host and habitat (soil type, forest age) in shaping endophyte diversity and composition. In contrast to previous studies, we found no evidence for host- or habitat specificity. Instead, endophytes demonstrated strong spatial structure consistent with dispersal limitation, with community similarity decaying markedly over a scale of hundreds of meters. Spatial structure that is independent of host species and habitat reveals remarkable heterogeneity of endophyte—host associations at small geographic scales and adds an important spatial component to extrapolative estimates of fungal diversity.

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#### Introduction

A fundamental goal of ecology is to understand the factors that determine the distributions of species. All macroscopic species engage in close biotic interactions with microbes, and the outcomes of such interactions can differ under particular environmental conditions or as a function of the local pool of interacting species and genotypes (Thompson, 2005; Gallery et al., 2007; Pan et al., 2008; Peay et al., 2010). Therefore, it is important to diagnose not only the geographic distributions of microbial symbionts, but also the underlying abiotic and biotic constraints that shape their ecological associations at

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multiple spatial scales. Plant—microbe symbioses are among the most important biotic forces shaping the structure and function of terrestrial plant communities (e.g., Read et al., 2004), but in contrast to knowledge regarding the distributions of host plants, relatively little is known regarding the forces that delineate distributions of microbial partners in time and space (Martiny et al., 2006; Fierer, 2008).

One of earth's most common plant-microbe symbioses is that of endophytic fungi (Arnold, 2007). Fungal endophytes defined functionally as fungi that occur within healthy plant tissues without causing overt harm (Petrini, 1991) - are known from every major lineage of plants, and from all terrestrial biomes. These primarily ascomycetous fungi include one especially species-rich and ubiquitous functional group, the Class 3 endophytes (sensu Rodriguez et al., 2009). Class 3 endophytes (hereafter, endophytes) typically are horizontally transmitted, form numerous, independent, and highly localized infections in healthy above-ground tissues of plants, and have been recorded from every plant species examined to date (Rodriguez et al., 2009). In lowland moist forests in the Neotropics, these endophytes are especially diverse: a mature, asymptomatic leaf of a dicotyledonous tree usually hosts more than a dozen cultivable species, with turnover in species composition among leaves, individual plants, and geographically distant sites (e.g., Lodge et al., 1996; Saikkonen et al., 1998; Arnold et al., 2003; Arnold and Herre, 2003; Arnold and Lutzoni, 2007; Arnold et al., 2009). Their ecological roles have not been studied in most cases, in part because of the complexity of assessing the roles of individual strains in the context of assemblages that can comprise hundreds of endophyte species for a single host plant. However, recent work has begun to reveal important interactions between tropical endophytes and their hosts, including defense against pathogens and herbivores, alteration of photosynthetic efficiency, and changes in water relations (e.g., Pinto et al., 2000; Arnold et al., 2003; Arnold and Engelbrecht, 2007; Van Bael et al., 2009a, 2009b).

In general, very little is known regarding the factors that shape the distributions of endophytes at local or regional scales. Significant turnover among biomes can be ascribed to differences in plant communities, abiotic factors such as seasonality, and underlying biogeographic history for both plant and fungal partners (Arnold and Lutzoni, 2007; Arnold et al., 2009; U'Ren et al., 2012). However, relatively little research has been done at a scale appropriate to determine the relative importance of host- and habitat features in shaping local distributions. For tropical endophytes, a growing body of literature indicates that abiotic factors such as relative humidity, exposure to ultraviolet radiation and desiccation, and the density of leaf litter can shape the abundance and composition of inocula at small spatial scales, yielding at least short-term effects on the number of endophyte infections per leaf, their diversity, and their composition (Rodrigues and Samuels, 1990; Rodrigues, 1994; Lodge et al., 1996; Rodrigues and Dias, 1996; Bayman et al., 1998; Fröhlich and Hyde, 1999; Arnold et al., 2000, 2001; Guo et al., 2001; Kelemu et al., 2001; Gamboa and Bayman, 2001; Cannon and Simmons, 2002; Suryanarayanan et al., 2002; Arnold and Herre, 2003; Arnold and Lutzoni, 2007). However, factors shaping endophyte communities in sites with relatively uniform abiotic and biotic conditions, such as the understory of intact tropical forests, are not known. Spatial heterogeneity has been detected in several studies within individual forests (e.g., Arnold et al., 2000), but because such studies typically focus on only a small number of sites, the spatial scale of turnover in endophyte communities within forests has not been determined. Similarly, the interplay of distance and microhabitat conditions such as soil type or land-use history, important in shaping some plant-fungal associations (e.g., Dumbrell et al., 2010), has not been evaluated. In turn, strict-sense host specificity of tropical endophytes appears to be rare (Cannon and Simmons, 2002; Suryanarayanan et al., 2002; Pandey et al., 2003; Murali et al., 2007; Arnold and Lutzoni, 2007), although conclusions are somewhat uncertain because signatures of host preference have been reported in some communities (e.g., Suryanarayanan et al., 2000).

We examined the relative importance of hosts and habitat characteristics in structuring endophyte communities in a lowland tropical forest. We focused on grasses (Poaceae), which first arose and diversified in the shaded margins of tropical forests (Kellogg, 2001). In a companion paper (Higgins et al., 2011), we showed that grasses in the forest understory harbor highly diverse Class 3 endophytes, rather than the well-studied clavicipitaceous endophytes that characterize many pasture, woodland, and domesticated forage grasses (i.e., Class 1 endophytes, sensu Rodriguez et al., 2009). Our finding of host generalism among fungal communities as a whole, and in more detailed analyses of two common genera, Colletrotrichum and Anthostomella (Higgins et al., 2011), prompted us to explore other ecological factors that might influence endophyte assemblages. Here, we use sequence data from cultivable fungi obtained from two sampling years and 55 geographically proximate sites to investigate soil type and forest age as factors that may structure endophyte communities.

#### Materials and methods

This study was conducted at Barro Colorado Island, Panama (BCI;  $\sim 9^{\circ}9'$  N,  $79^{\circ}51'$ W), a former hilltop isolated from mainland forests by the creation of Gatun Lake in 1914. The island is composed of mature forest (>400 yr old) and secondary forest in areas cleared approximately 100 yr ago. It has been protected as a research reserve since 1923 and maintained by the Smithsonian Institution since 1946. For a full site description see Leigh et al. (1996).

As detailed in Higgins et al. (2011), we focused on 11 locally common species representing six subfamilies of Poaceae (sensu Barker et al., 2001) (Table 1). All are perennial and occur frequently in the understory of primary and secondary forest at BCI (Croat, 1978). In addition to representing a phylogenetically diverse array of species, focal hosts represented subfamilies that arose and persisted in forest environments (Anomochlooideae, Pharoideae, Bambusoideae, Ehrhartoideae), and subfamilies that ancestrally transitioned to open environments (Centothecoideae, Panicoideae) (Kellogg, 2001).

Fifty-five study sites were selected to maximize coverage of the 1400 ha island (Supplementary Appendix 1, Fig 1). For each site we collected information on soil type (Fig 1) and forest age Download English Version:

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