# Ecological understanding of root-infecting fungi using trait-based approaches

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**Classification schemes have been popular to tame the diversity of root-infecting fungi. However, the usefulness of these schemes is limited to descriptive purposes. We propose that a shift to a multidimensional trait-based approach to disentangle the saprotrophic–symbiotic continuum will provide a better framework to understand fungal evolutionary ecology. Trait information reflecting the separation of root-infecting fungi from free-living soil relatives will help to understand the evolutionary process of symbiosis, the role that species interactions play in maintaining their large diversity in soil and *in planta*, and their contributions at the ecosystem level. Methodological advances in several areas such as microscopy, plant immunology, and metatranscriptomics represent emerging opportunities to populate trait databases.**

## Limitations of categorical approaches to study plant–soil fungal interactions

Understanding the effects of plant–soil fungal interactions in natural communities has become a major research area in plant science [1]. Interest in these interactions stem from increasing awareness that soil biota play an important role in plant performance, plant community assembly, and ecosystem functioning [2].

However, the complexity of soil fungal communities challenges our ability to understand the effects of such interactions on plant performance and on ecosystems processes. Recent surveys show that roots interact with phylogenetically diverse groups of fungi [3]. Moreover, the effects of particular plant–fungal combinations depend on environmental conditions and on the host and fungal genotypes [4]. In diverse communities and variable environments, net responses may be due to complex indirect interactions among co-occurring fungi and plants [5].

Given these complex associations, researchers regularly classify fungal taxa into broad categories according to particular criteria. These criteria may be based on nutritional mode (e.g., 'biotroph', 'necrotroph', or 'saprotroph' [6]; see Glossary), presence of hyphal melanization and formation of septa (e.g., 'dark septate endophytes' [7]), or on a mix of taxonomic, morphological, and physiological characteristics (e.g., 'arbuscular mycorrhizal' or 'ectomycorrhizal' [8]). These classificatory approaches have been important for distilling broad generalities from the rich brew of fungal–plant interactions such as the recognition of contrasting plant defense mechanisms against infecting fungi with different nutritional modes [9].

However, assignment of root-infecting fungi into fixed categories is problematic for species labeled as 'endophytes'. For example, some of the criteria used in delineating endophyte classes [10] are quantitative (number of potential hosts, number of co-infections within a host, or degree of tissue colonization), but their delineation is imprecise (narrow vs broad host range; low vs high *in planta* diversity; extensive vs limited *in planta* colonization). Similarly, a suggestion that 'endophytic functional groups' should be based on their effects on host fitness resulted in the rather unsatisfying conclusion that 'some

### Glossary

**Biotroph:** nutritional mode in which a fungal symbiont exclusively relies on living host cells as a source of nutrients.
**Functional trait:** species traits directly linked with a particular ecosystem process. Different species sharing similar functional traits are pooled into functional groups.
**Life history trait:** traits reflecting allocation of resources of an individual into different fitness components.
**Necrotroph:** nutritional mode in which a fungal symbiont causes host cell death in order to acquire nutrients.
**Saprotroph:** nutritional mode in which a free-living fungus obtains nutrients from decaying organic matter, without inducing the death of the tissue.
**Symbiosis:** a physiological or structurally intimate interaction between phylogenetically unrelated organisms, without implying a specific effect of fitness on either organisms.
**Trait:** any morphological, physiological, or phenological character of an organism.

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endophytes may be latent pathogens, some may be derived from pathogens, and others may be latent saprotrophs, but many are neither' [11]. Such classification schemes can provide a useful initial framework to understand poorly studied plant–fungal interactions, but the resulting generalizations often include the listing of so many exceptions to the proposed scheme that the framework is not useful operationally.

We argue that a shift in focus from classification schemes to a multidimensional trait-based approach reflecting the biology of the fungi is necessary for a better understanding of the ecology and evolution of root-infecting fungi. These approaches consider species as a conglomerate of unique combinations of multiple traits, which could be depicted as species being points defined by multiple traits represented as dimensions (Figure 1). This view directly links particular ecological and evolutionary questions with trait information. The proposed multidimensional trait-based program presented here is focused on the traits that allocate 'endophytic' or 'pathogenic' root fungi to a symbiotic lifestyle and separate them from free-living saprotrophic relatives. We explain how trait information can be used to address three essential questions: What are the mechanisms behind the evolution of root endophytic or pathogenic lifestyles from free-living fungi and vice versa? What is the importance of trait similarity in explaining the co-occurrence patterns of fungal genotypes or species *in planta* and in the soil? And, which traits might be used to understand the functional diversity of soil fungi? This is illustrated conceptually in Figure 1.

## A fungal-trait approach: understanding the saprotrophic–symbiotic continuum

Trait-based approaches rely on measurements of phenotypic characters or traits to guide inferences about particular ecological or evolutionary processes (Box 1). For example, plant scientists have successfully used such approaches to understand how fire has influenced the evolution within the Pinaceae by combining trait information with phylogenetic reconstructions [12], to measure the relative importance of abiotic factors and biotic interactions in shaping community assembly of tropical trees by measuring trait overdispersion in local communities [13], or to understand how plant diversity influences the variability of decomposition rates within climate regions by combining decomposition data with leaf traits from databases [14].

We explain how application of such trait-based approaches may be valuable at a conceptual level in understanding the saprotrophic–symbiotic continuum in root-infecting fungi. This continuum is pertinent to this set of

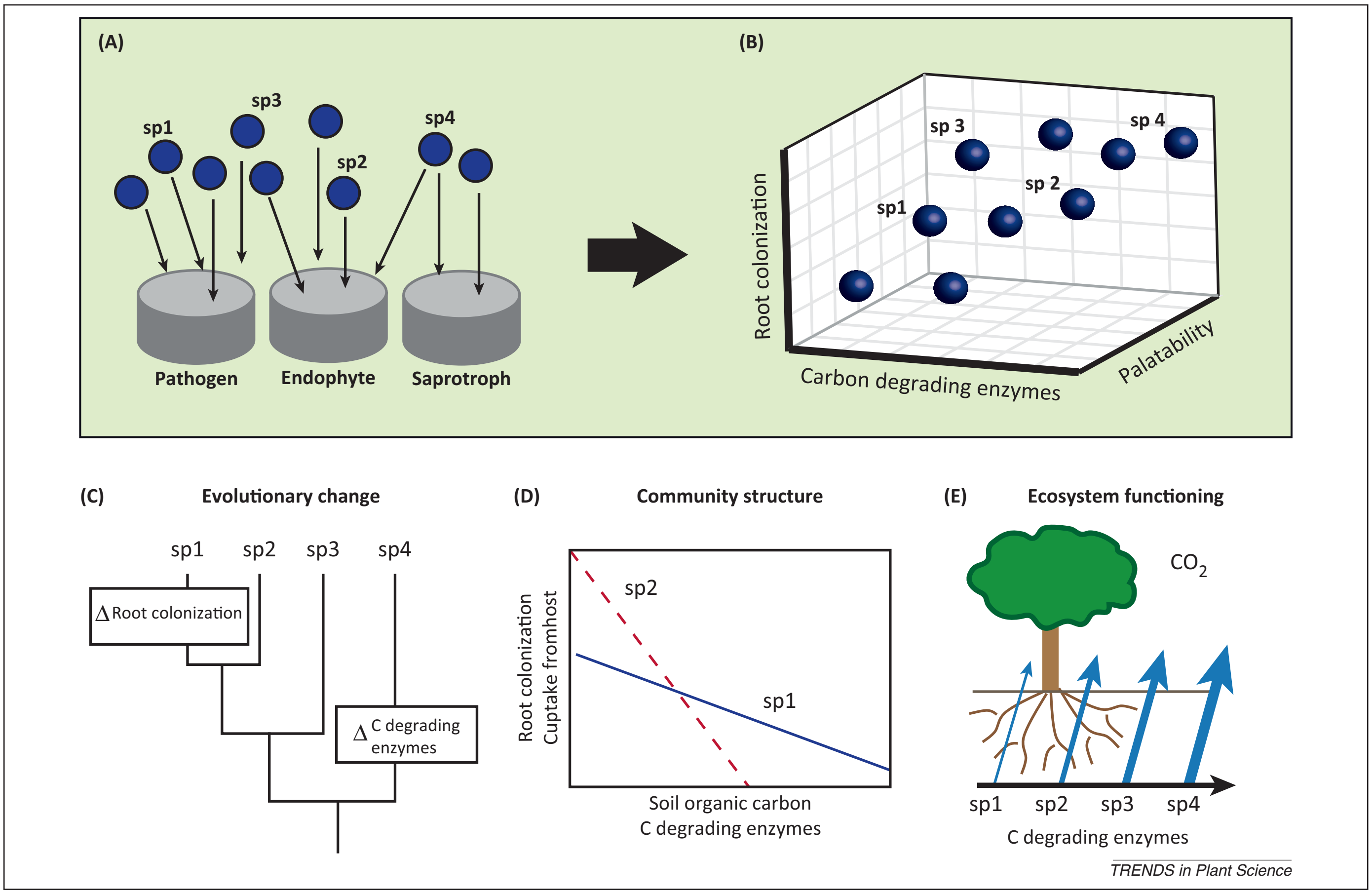

**Figure 1**. From categorization to trait analysis for root-infecting fungi. Schematic representation of a trait-based approach to understanding the ecology and evolution of root-infecting fungi. Instead of placing species into fixed categories **(A)** such as pathogen, endophyte, or saprotroph, trait-based multivariate approaches represent species as particular combinations of traits in various dimensions **(B)**. Such information can be coupled with: **(C)** phylogenetic data to understand evolutionary change; **(D)** their relationships to species performance under different environmental conditions to understand mechanisms of community assembly and species coexistence and; **(E)** with their effects on ecosystem properties to explore their role in these processes. Note: the graphic in (D) represents the lower resource boundaries above which species 1 and 2 can still grow (zero net growth isoclines as in [54]). In this figure, the position of lines depends on the traits the species possess to exploit two resources: carbon from the host or from decaying matter.