

Understanding microbiomes through trait-based ecology



Jennifer L Wood

Applied Environmental
Microbiology
Department of Physiology
La Trobe University
Bundoora, Vic. 3086, Australia
Email: Jen.Wiltshire@latrobe.edu.au



Ashley E Franks

Applied Environmental
Microbiology
Department of Physiology
La Trobe University
Bundoora, Vic. 3086, Australia
Email: a.franks@latrobe.edu.au

Ecology is the study of the interactions amongst organisms and their environment¹. In microbial ecology, a major goal is to understand how environmental microbiomes impact ecosystem health and function. This desire to mechanistically link micro and macro processes is increasingly highlighting the importance of functional ecology, which aims to develop an understanding of relationships using functional traits, as opposed to species names. A functional trait may be any morphological or physiological trait that influences the performance or fitness of an individual in a given environment, such as regeneration time, size, antibiotic production or motility². Although it is not possible to measure a given trait for each individual within an environmental microbiome, community-level functional traits can be derived from the community metagenome either directly via shotgun sequencing or predictively (for bacteria) from 16S rRNA profiles³. In understanding environmental microbiomes, functional traits have unique properties that can be utilised to (1) compare microbiomes using an ecological framework, (2) understand processes governing community assembly, and (3) build predictive ecological models.

Functional comparisons of environmental microbiomes

Functional traits are not necessarily conserved across phylogenetically closely-related taxa, but rather are conserved amongst organisms with similar life strategies. As such, trait-based comparisons of environmental microbiomes can be used to elucidate repeated ecological patterns across microbiomes even if they are taxonomically distinct. For example, if one was attempting to understand ecological similarities amongst geographically dispersed

microbiomes from comparable ecosystems (e.g. wetland microbiomes), one may find that the communities contain vastly different suites of species. In this instance species names alone cannot be used to identify ecological trends uniting these microbiomes. However, because the microbiomes are from similar ecosystems, it is likely that within each microbiome different species will employ similar life strategies to survive and thus exhibit similar functional traits. In this way, functional traits can identify meaningful ecological patterns across taxonomically distinct microbiomes.

Linking micro to macro: understanding of processes governing community assembly

The concept that environmental filters act on traits – not species – can be used to interpret how environmental parameters alter microbiomes in an ecologically meaningful way. The twin-filter hypothesis proposes that a two-step filtering process acts on local species pools: a primary ‘ecological filter’ increases the trait similarity within a community by selecting for similar life strategists (i.e. environments characterised by severe nutrient stress will select for traits that produce stress-tolerant life strategists); secondary ‘proximal filters’ then select against traits which affect survival but are not integral to the broad life strategy (e.g. variation in tolerance to environmental toxins or resistance to local pathogens and predators), creating dissimilarity within the local subset of species and generating the final community structure (Figure 1)⁴. By examining which traits are enriched by a given environment, or environmental parameter, we can begin to hypothesise how a community is experiencing that environment and why different communities diverge in their ecology. For example, Wood *et al.*⁵ demonstrated that the community-level changes induced by the

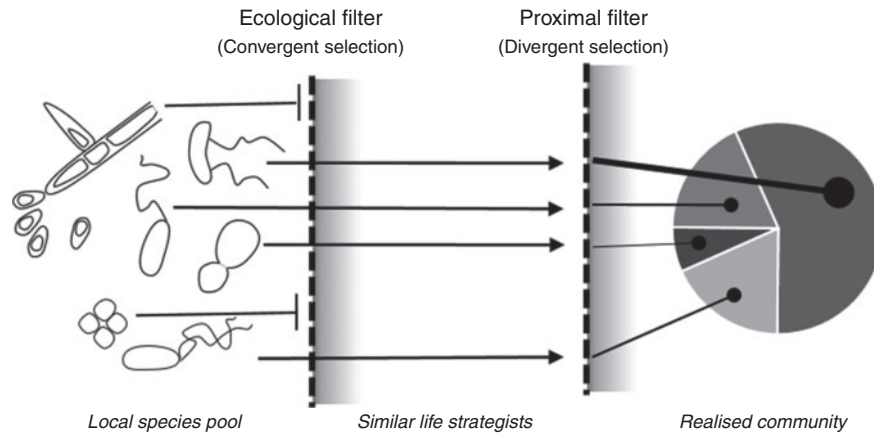


Figure 1. Schematic representation of the twin-filter hypothesis⁴. The local species pool provides a source of species that can potentially enter a community. An ecological filter acts on life-history associated traits, selecting for species that exhibit similar life strategies (e.g. stress tolerators, competitors, colonisers). Secondary ‘proximal filters’ such as toxins, predators or the type of carbon present determine final community composition.

Table 1. CSR theory definitions used to classify traits as competitive, stress-tolerant or ruderal, adapted from Grime and Pierce⁴. Selected macro and microbiological functional traits are given as examples of traits that can be associated with each C, S or R definition.

Trait definition	Macro (plant) example	Micro example
Competitive trait: Traits facilitating the monopolisation of local resources	High chlorophyll concentration Large leaves Large canopy Allelochemical production Large root spread	High membrane transporter density Siderophore production Biofilm formation Production of antimicrobial compounds Filamentous growth
Stress-tolerant trait: Traits facilitating survival in chronically underproductive environments	Slow growth Mechanical defenses (spines) Chemical defenses Detoxification mechanisms Production of free radical scavengers	Slow growth Altered membrane chemistry Melanin/pigment production Increased DNA repair ability Production of free radical scavengers
Ruderal trait: Traits facilitating the rapid re-establishment of a population	Short life cycle High photosynthetic capacity High seed number High seed dispersal ability	Rapid growth Increased capacity for central metabolic flux Overwintering structures (e.g. sclerotia) High spore dispersal ability Motility

presence of a plant rhizosphere were due to the selection of traits linked to microbial competition for resources (i.e. antibiotic production, siderophore production). Similarly, DeLong *et al.*⁶ demonstrated the presence of contrasting ecologies between communities from the phototrophic zone and from near-ocean floor depths, with foraging traits selected for in the phototrophic zone, whilst survival (stress tolerance) traits were characteristic of communities at depth.

Building trait-based predictive models

Functional traits can be incorporated into ecological classification frameworks which aim to predict how environmental microbiomes will change over time. Grime’s CSR theory is an ecological classification framework that groups traits in terms of three broad life strategies: competitive, stress tolerance and ruderal (colonisation) life strategies⁶. Each life strategy group is an umbrella term that

encompasses multiple functional traits which achieve the same outcome (Table 1). For example, stress tolerance traits may be defined as any trait that constitutes an investment in the maintenance of organismal biomass. In plants this may be the production of thorns or chemical compounds to deter herbivory. In an environmental microbiome this may manifest as an increase in the prevalence of DNA repair pathways or genes involved in the production of free radical scavengers.

The CSR theory proposes that organisms face a three-way resource trade-off between the investment in C, S or R life strategies, which is governed by the levels of stress (due to resource availability) and disturbance present in an environment⁴. The theory predicts that when stress and disturbance are minimal, the investment of resources into competitive traits confers a selective advantage that outweighs the loss in fitness due to reduced investment in other adaptive strategies, such as stress-tolerance or colonisation

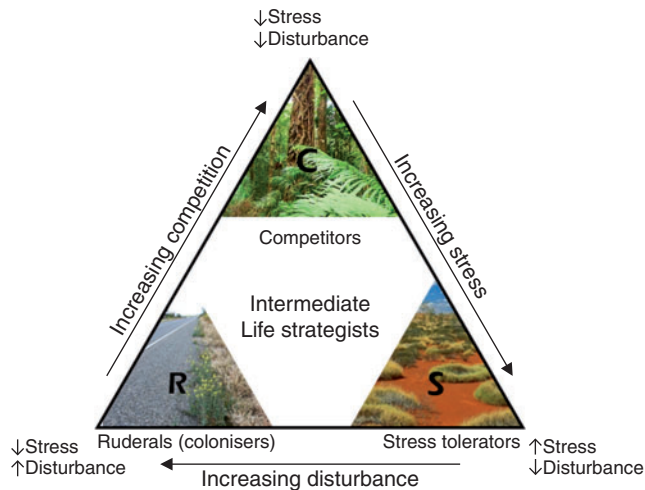


Figure 2. Diagrammatic representation of the CSR theory - Competitive, stress tolerant and ruderal life strategies (and their associated functional traits) form a three-way resource trade-off triangle. The selective advantage of each life strategy – and consequentially the amount of resources allocated to it – are governed by levels of environmental stress and disturbance. Where: **Stress** = external constraints limiting the rates of resource acquisition, growth or reproduction; **Disturbance** = an event causing the partial or complete destruction of cellular material. Images depict plant communities that represent typical examples of C, S or R dominated communities.

potential (Figure 2). In these communities, competitive interactions – and organisms with traits that contribute to a competitive life strategy – will prevail. Conversely, the theory predicts that stress-tolerance traits and life strategies will prevail when stress is high (i.e. resources are limited) but disturbance is low. Stress tolerant life strategists tend to be slow growing and are adapted to retaining resources. Finally, when stress is low but disturbance is high the theory predicts that ruderal traits, which pertain to re-colonisation potential, will confer a selective advantage and ruderal life strategists will prevail.

The use of ecological theories, such as the CSR hypothesis, presents a clear route towards developing predictive models which could be incorporated into ecosystem-level conservation and management practices. Indeed, even though CSR theory has its roots in plant ecology, the core principals are recognised as being applicable to microbial communities^{7–9}. A current barrier to developing predictive trait-based models is that ecological interpretations of microbial traits often rely on prevalent opinions from the literature, rather than on empirical data. For example, the production of antimicrobial metabolites is generally considered to be a competitive trait¹⁰. However, compounds recognised for their antibiotic activity *in vitro* have been shown to influence biofilm formation in *Bacillus subtilis* suggesting their primary role may be cell–cell communication¹¹.

Future research using controlled microcosms with defined gradients of resource availability (stress) and disturbance are needed to confirm ecological assumptions about functional traits. Trait

screening using controlled conditions can also be used to identify core predictor traits that can routinely and robustly discriminate between environmental microbiomes with contrasting ecologies. Ultimately, the development of broad ecological theories that facilitate the classification and comparison of microbiomes from disparate environments will assist in realising the full potential of large-scale collaborative initiatives, such as the TerraGenome project¹², the Earth Microbiome project (EMP)¹³ and Australia's Biomes of Australian Soil Environments (BASE)¹⁴ project.

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Biographies

Dr Jennifer L Wood is post-doctoral fellow in the Applied and Environmental Microbiology Laboratory at La Trobe University. She has recently completed her doctoral research which investigated the utility of functional approaches in understanding soil microbiomes for which she was awarded the 'Nancy Millis award for theses of exceptional merit'. Her broad research interest is in developing trait-based approaches to interpret and predict how environmental and anthropogenic changes impact microbial community ecology and function. Currently she is working with the

Defence Science Technology Group investigating functional changes associated with microbiologically influenced corrosion in marine environments.

Associate Professor Ashley E Franks is head of the Applied and Environmental Microbiology Laboratory at La Trobe University. He conducted his doctorate research as part of the Centre of Marine Biofouling and Bioinnovation at the University of New South Wales by investigating antifungal compounds produced by marine bacteria in biofilms. During his PhD he spent 4 months at the University of Exeter in the UK on an Adrian Lee Fellowship to develop dual bacterial/yeast biofilm systems. On graduating he

moved to the Biomerit Research Centre in Cork, Ireland to work on bacterial plant interactions as a Government of Ireland Fellow in Science Technology and Engineering. This research looked at how to use bacteria to help plant growth. He then took a position as a Senior Scientist and Research Professor within the Geobacter Project at the University of Massachusetts Amherst in the USA where he worked on microbes that make electricity. He currently serves as the Chair of the Awards Committee for the International Society of Microbial Electrochemical Technology and was previously the Secretary of Synthetic Biology Australasia.

Incorporating fungal community ecology into invasion biology: challenges and opportunities



Eleonora Egidi

Department of Physiology,
Anatomy and Microbiology
La Trobe University
Kingsbury Drive
Bundoora, Vic. 3083, Australia



Ashley E Franks

Applied Environmental
Microbiology
Department of Physiology
La Trobe University
Bundoora, Vic. 3086, Australia
Email: a.franks@latrobe.edu.au

Recently, the role of the plant-associated mycobiome (i.e. the fungal community) in influencing the competitive success of invasive plant species has received increasing attention. Fungi act as primary drivers of the plant invasion process due to their ability to form both beneficial and detrimental relationships with terrestrial plant species. Here we review the role of the plant mycobiome in promoting or inhibiting plant species invasion into foreign ecosystems. Moreover, the potential to exploit these relationships for invasive plant control and restoration of native communities is discussed. Incorporating fungal community ecology into invasion and restoration biology will aid in the management and control of invasive plant species in Australia.

Alien invasive plant species represent an ever-increasing worldwide problem. The expansion of invasive species in non-native ranges can dramatically alter the structure and population dynamics of the invaded community, with the negative impact of invasive

plants on ecosystem structure and function resulting in changes to native vegetation composition and productivity, nutrient cycling, soil characteristics, and even human well-being¹.

Many factors regulate exotic species naturalisation and invasion success, including the ability to rapidly access resources, allelopathy, and the modification of ecosystem processes (reviewed in Levine *et al.*²). However, an increasing body of evidence suggests a pivotal role for the plant-associated mycobiome (i.e. the fungal community) in influencing the competitive success of invasive species³⁻⁶. Fungi are important terrestrial ecosystem components, acting as mutualists, pathogens, decomposers, and food sources. Because of their primary role as drivers of many ecosystem functions and their ability to establish intimate relationships with terrestrial plant species (e.g. mycorrhizal fungi or leaf endophytes) (Figure 1), fungal communities can critically influence plant fitness and survival and, hence, their colonisation and invasion patterns^{5,7}.