

INVITED REVIEW: PART OF A SPECIAL ISSUE ON ROOT BIOLOGY

Interactions between exotic invasive plants and soil microbes in the rhizosphere suggest that ‘everything is *not* everywhere’

Marnie E. Rout^{1,2,*} and Ragan M. Callaway²

¹USDA-ARS Fort Keogh Livestock Range & Research Laboratory, 243 Fort Keogh Rd., Miles City, MT 59301, USA and

²Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA

*For correspondence. E-mail marnie.rout@ars.usda.gov

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• **Background** The study of soil biota in the context of exotic plant invasions has led to an explosion in our understanding of the ecological roles of many different groups of microbes that function in roots or at the root–soil interface. Part of this progress has been the emergence of two biogeographic patterns involving invasive plants and soil microbes. First, in their non-native ranges invasive plants commonly interact differently with the same soil microbes than native plants. Second, in their native ranges, plants that are invasive elsewhere commonly interact *functionally* with soil microbes differently in their home ranges than they do in their non-native ranges. These studies pose a challenge to a long-held paradigm about microbial biogeography – the idea that microbes are not limited by dispersal and are thus free from the basic taxonomic, biogeographical and evolutionary framework that characterizes all other life on Earth. As an analogy, the global distribution of animals that function as carnivores does not negate the fascinating evolutionary biogeographic patterns of carnivores. Other challenges to this notion come from new measurements of genetic differences among microbes across geographic boundaries, which also suggest that meaningful biogeographic patterns exist for microorganisms.

• **Scope and Conclusions** We expand this discussion of whether or not ‘everything is everywhere’ by using the inherently biogeographic context of plant invasions by reviewing the literature on interactions among invasive plants and the microorganisms in the rhizosphere. We find that these interactions can be delineated at multiple scales: from individual plants to continents. Thus the microbes that regulate major aspects of plant biology do not appear to be exempt from the fundamental evolutionary processes of geographical isolation and natural selection. At the important scales of taxonomy, ecotype and ecosystem functions, the fundamental ecology of invaders and soil microbes indicates that everything might *not* be everywhere.

Key words: Biogeography, plant invasions, microbial distributions, nutrient cycling, plant–microbe interactions.

BACKGROUND AND AIMS

Exotic plant species commonly escape regulation by natural microbial enemies residing in roots and at the interface between roots and soils (Kulmatiski *et al.*, 2008), yet they also often benefit substantially from mutualisms with soil biota in introduced ranges (Marler *et al.*, 1999; Richardson *et al.*, 2000a; Reinhart and Callaway, 2006). The effects of these inhibitory and beneficial symbiotic microbes on plant invasions can occur through the direct effects of diminished pathogenic and/or enhanced mutualistic interactions, and indirect effects manifest through alterations of ecological and ecosystem processes (Wardle *et al.*, 2011). For example, indirect effects can occur through changes in nutrient cycling, all of which are functions of soil microbial communities, which tilt competitive outcomes in favour of invaders and against natives (Hawkes *et al.*, 2005). Soil microbes inhabiting the roots or at the root–soil interface have been implicated in several classes of hypotheses for invasive plant success, primarily enemy release, empty niches, novel biochemical interactions, and adaptation to particular conditions associated with human culture (reviewed by Mitchell *et al.*, 2006). In many of these cases clear biogeographic patterns involving invasive plants and soil microbes have been demonstrated

(Reinhart *et al.*, 2003; Reinhart and Callaway, 2004, 2006; Hawkes *et al.*, 2005; Callaway *et al.*, 2011).

Biogeographic patterns in the abundance and unusually strong impact and dominance of some exotic plants have been posed as ‘paradoxes’ because they are inconsistent with the overriding importance of local adaptation – how can species without the opportunity to locally adapt exclude those that have co-existed (Sax and Brown, 2000)? These authors ultimately concluded that pre-adaptations for human-altered environments, release from enemies, regional species pools, and the historical contingency of evolution of invasion rendered the paradox an ‘expectation’. Whether the profound ecological transformations associated with invaders are a paradox or an expectation, we strongly agree that a full understanding of the biogeographic nature of intricate webs of biological interactions among species has the potential to unlock the mysteries underlying exotic invasions. Conversely, exploring the apparently paradoxical biogeographic patterns of invaders has the potential to reveal mechanisms underlying general ecological questions. Despite commonly reported observations of higher abundances or greater impacts of some exotic species in their introduced ranges compared

with their native home ranges (Darwin, 1859; Elton, 1958), this pattern has been empirically demonstrated by a number of studies (Woodburn and Sheppard, 1996; Grigulis *et al.*, 2001; deWalt, *et al.*, 2004; Jakobs *et al.*, 2004; Hierro *et al.*, 2005; Beckmann *et al.*, 2009; Williams *et al.*, 2010; Inderjit *et al.*, 2011; Callaway *et al.*, 2012). Certainly not all exotics become invasive, and Firm *et al.* (2011) compared the abundances of a large number of exotic plant species between native ranges and found that 14 of 26 species demonstrated greater ‘localized dominance’ in their non-native range than in their native range, but that 11 species showed the opposite pattern.

Here we consider ecological questions involving invasive plants and the below-ground microbes occurring in roots and at the root–soil interface. In this context, the ‘paradox’ of invasion derives from processes mediated by soil microbes; primarily pathogenic and mutualistic processes, and those that may mediate striking increases in net primary productivity (NPP) and increased soil nitrogen pools with invasion (Liao *et al.*, 2008; Rout and Callaway, 2009). Considered together, biogeographic variation in interactions among plants and their associated soil microorganisms, and larger-scale biogeographic changes in ecosystem functions controlled by these microorganisms, brings a new look at a classic paradigm in microbiology.

WHAT IS A MICROBIAL ‘SPECIES’?

‘*Everything is everywhere, but the environment selects*’ as stated by Lourens Baas Becking has provided the context for one of biology’s most intriguing questions (Baas Becking, 1934). Microbial taxa have been thought to be free from geographic boundaries because of their great ancestral age, vast population sizes, environmental hardiness and ability to disperse (O’Malley, 2007; see Box 1 timeline). Thus regional evolutionary trajectories for microbes have been presumed not to exist – until the emergence of molecular techniques. Molecular methods surpassed morphological approaches and redefined microbial phylogenies and biogeography. Initially, these new phylogenies were based on data obtained from the small subunit ribosomal RNA (SSU r-RNA) (Stackebrandt and Goebel, 1994). Phylogenetic trees constructed from these operational taxonomic units (OTUs) were used to assess microbial biogeography (Green *et al.*, 2004; Horner-Devine *et al.*, 2004, 2007; Green and Bohannan, 2006), and the results challenged the idea that everything is everywhere. However, this approach also raised even more questions since contradictory phylogenies can be constructed from functional genes, such as those for RNA polymerase (Hirt *et al.*, 1999). Thus, two prokaryotic microorganisms can have >97 % OTU similarity based upon SSU r-RNA, but possess genes driving dramatically different ecological and biological functions (McInerney *et al.*, 2008; Fraser *et al.*, 2009). Ernst Mayr set the species definition for macro-organisms such as plants (Mayr, 1942), but a similar, unequivocal definition has yet to be fully accepted for microorganisms (particularly prokaryotes), but the currently accepted distinction for two species is at 97 % OTU similarity.

Box 1. Defining a microbial ‘species’: the evolution of the microbial species concept and the ‘everything is everywhere’ debate.

Augustin Pyramus de Candolle (1778–1841)

- Stated ‘lower organized taxa’ were not dispersal limited and were ubiquitous
- Lower taxa included fungi, lichens and algae
- Foundation for the ‘everything is everywhere’ debate

Charles Darwin (1809–1882)

- Supported de Candolle’s assertion in *On the Origin of Species*, ‘...the lower any group of organisms is, the more widely it is apt to range’ (1859)

Ferdinand Cohn (1828–1898)

- Classified bacteria as plants; placed microscopic organisms (**bacteria and fungi**) into the ‘lower organized taxa’ distinction of de Candolle

Robert Koch (1843–1910)

- Developed Koch’s Postulate, which demonstrated consistent effects of microorganisms under identical physiological conditions supporting the uniformity assertion for microbial distributions

Martinus Beijerinck (1851–1931)

- Empirically demonstrated the cosmopolitan nature of microbes, reinforcing the ubiquity of microbial taxa and the role of the environmental filter

Lourens Baas Becking (1895–1963)

- Stated, ‘*Everything is everywhere; but the environment selects*’ in 1934
- This ‘law’ was formulated based on the empirical laboratory work of Beijerinck and observational studies of salt lake microbes (algae and crustaceans)

Bergey’s Manual of Determinative Bacteriology (1st edn 1923 – 8th edn 1994)

- This publication is the primary resource, from the first edition in 1923 to the eighth edition in 1994, for the identification of bacterial species.
- In the initial editions, attempts to classify prokaryotes according to phylogenetics were disregarded in lieu of phenetic taxonomy
- As the definitive guide for bacterial species, the manual influenced the disregard of microbial biogeography until the late 1970s with the emergence of molecular techniques

More detailed sequence-based approaches have been used to assess microbial community function through targeting of *functional* genes (based on DNA and/or RNA). These genes include those that are relevant to the ecology of the organism, multiple housekeeping genes (multilocus sequence analysis), and metagenomic studies (Fraser *et al.*, 2009). The processing of raw RNA-seq data is still rapidly evolving. As entire plant and microbial genomes have been sequenced, it has become clear that microbial evolution not only occurs over short time periods, but also that selection can occur through horizontal gene transfer, accounting for high proportions of bacterial genomes (see Welch *et al.*, 2002). Rapid microbial generation times and the prevalence of horizontal gene transfer provide potential mechanisms for the development of regional genetic differences, or ecotypes, to arise in response to the effects of local plant species and communities. Applying functional gene-based molecular approaches to biogeographical studies can enhance our understanding of microbial ecotypes, which would be defined as ‘.^^. ecological niches characterized by the selective advantages they confer to specific genes’ (Fraser *et al.*, 2009). The advantages of this approach, as well as the main limitation (the lack of longitudinal data from natural microbial populations) are discussed in length by Fraser *et al.* (2009), and are not the main focus of this article.

To some degree, whether or not ‘everything is everywhere’ is a matter of scale. In other words, microbes may disperse everywhere, but if their rate of evolution is faster than their rate of dispersal, then local adaptation will result. Additionally, since horizontal gene transfer can occur within minutes, local adaptation is likely. At some broad taxonomic or functional level everything does appear to be everywhere (Finlay, 2002). Put another way, nitrifiers and decomposers have been found in all biogeographic regions where they have been sought. But such broad functional patterns do not negate regional differences in evolutionary trajectories at smaller taxonomic or functional scales. The global distribution of carnivores does not negate the fascinating evolutionary biogeographic patterns of carnivores. The potential exemption of microbes from biogeography raises profound biological questions. Geographical isolation is a primary mechanism for speciation among higher taxa, so if there has been little or no biogeography in the evolutionary history of microbes, then how did these branches on the tree of life become so extraordinarily genetically and taxonomically diverse? Clearly, the vast ancestral age of microorganisms on the planet, rapid generation times, and horizontal gene transfer all contribute to this diversity. Thus it seems unlikely that biogeographic exemption can be given to microorganisms.

WHAT IS AN ‘INVADER’?

It is important to be clear about how we define ‘invader’ if we are to fully take advantage of these organisms as a global natural experiment. Based on the formal definition presented by Richardson *et al.* (2000b), which states that invaders are: ‘*Naturalized plants* that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants and thus have the potential to spread over a considerable

area’. Of course not all exotics are invasive, and here we refer to invaders as exotic plant species that exhibit greater density, abundance or community dominance in their non-native ranges than in their native ranges (see Hierro *et al.*, 2005). Clearly such species can vary in invasion intensity with some being ‘weak invaders’ and others ‘strong invaders’ (Simberloff, 1981; Ortega and Pearson, 2005). This variation in invasion intensity is likely correlated with the intensity of the mechanisms regulating invasions. For example, Ortega and Pearson (2005) found that weak invaders were positively correlated with native species richness while strong invaders were negatively correlated with native diversity. Importantly, it is the relationships between soil microbes and these ‘strong invaders’, rather than simply species that are exotic, that provide the greatest opportunities to explore the biogeography of microbes.

PLANT INVASIONS AND MICROBIAL BIOGEOGRAPHY

Recent genetic research has shown that microbial community composition changes with geographic distance; the relationship between sampled area and the accumulation of taxa is similar to that for macro-organisms (Green *et al.*, 2004; Horner-Devine *et al.*, 2004, 2007; Green and Bohannan, 2006). Redefining phylogenies through molecular characteristics has also led to the discovery of new locally distributed microbial species, based on 97 % OTU similarity, suggesting the existence of biodiversity-based scaling rules. It is important to remember that the taxonomic scale at which one samples a community defines the range in which the members are phylogenetically identified. For example, Bryant *et al.* (2008) found that increasing the taxonomic scale used to define bacteria (90 %, 94 % and 97 % sequence similarity) decreased the strength of observed diversity patterns with changing elevation. They concluded that biogeographic patterns for microbes occurred, but they were not the same as those of plants, and this general trend was upheld regardless of the taxonomic scale used. Currently, scaling problems make it difficult to compare biogeographic patterns between microbes and plants and future comparisons between these two groups would benefit from comparisons based exclusively on molecular approaches. Even with these limitations, such advances have placed us on ‘the cusp of a complete reversal of opinion’ about the biogeography of microbes (O’Malley, 2007), and have led to a movement to integrate ecological function with genetically based phylogenies in order to unify microbial species definitions (Fraser *et al.*, 2009). It is in this context of ecological function that plant invasions provide the ideal systems in which to search for strong biogeographical patterns for soil microbes. In this review, we maintain that plant invasions demonstrate biogeographic patterns in the ecological functions performed by soil microbes that help to unify biogeographic concepts across all life forms, including soil fungi (Green *et al.*, 2004) and bacteria (Horner-Devine *et al.*, 2004). These patterns correspond well with current knowledge that variation in microbial genomes is great enough (McInerney *et al.*, 2008) to permit strong functional differences in microbe-based processes in soils being invaded. We argue that studies of the

role of soil microbes in plant invasions would benefit from functional gene analyses of plant-associated microbial communities and treating the invasive plant host as a primary bioassay for detecting these events.

Until recently, most studies of microbial involvement in invasions have focused on the microbial ecology of escaping above-ground pathogens (Anderson *et al.*, 1986), attack by invasive above-ground pathogens (Kennedy and Weste, 1986; Brown and Hovmøller, 2002; Torchin and Mitchell, 2004), and above-ground pathogens as biological control agents of exotic invaders (Charudattan, 2001). This suite of above-ground interactions among invasive plants and pathogens demonstrate clear biogeographic and evolutionary patterns. Yet *below-ground* interactions among invasive plants and the broad functional roles of harmful and beneficial microbes at the root–shoot interface and in nutrient cycling have only recently been addressed (see Liao *et al.*, 2008; Rout and Callaway, 2009). Also until recently, the nutrient-cycling perspective on invasions and soil microbes fitted quite well into the ‘everything is everywhere’ paradigm. Microbes driving nutrient cycling appear to function quite similarly, at least in our current understanding, and drive the same basic cycles everywhere on the planet. Yet we now know that many invasive plants often *interact* differently with these broad functional groups of microbes in roots and at the root–soil interface in invaded ranges than they do with the same functional groups in native ranges. Invaders can alter the functions of these microbial communities, leading to plant–microbe feedbacks that alter the microbial community composition favouring positive feedbacks for the invader (Klironomos, 2002; Hawkes *et al.*, 2005). These biogeographic differences in interactions cause substantial shifts in the ecological nature of microbial mutualistic relationships (Parker *et al.*, 2006; Callaway *et al.*, 2008, 2011), escape from fungal pathogens (Reinhart *et al.*, 2005), functional changes in soil bacterial communities measured in terms of microbial biomass (Liao *et al.*, 2008), plant–soil feedbacks (Reinhart *et al.*, 2003; Kulmatiski *et al.*, 2008), and nutrient cycling dynamics (Rout and Chrzanowski, 2009). If plant–microbe interactions are substantially altered in the plant invasion process, either relative to interactions in the invader’s home range, or relative to general plant–microbe interactions among native species, the ‘everything is everywhere’ paradigm is suspect. Importantly, the ‘environment selects’ component of the paradigm is emphasized by evidence from exotic invasions, but with a crucial divergence from the original idea. The environment appears to *naturally* select in an *evolutionary* context, rather simply through a filtering of the global species pool. We use the word *naturally* here, but it is important to understand that invasions are highly correlated with human-induced disturbances, particularly agriculture, forestry and urban development (Pyšek *et al.*, 2010). Our understanding of the impacts of these anthropogenic disturbances on soil microbial community structure is still limited, but evidence from studies of plant invasions discussed here suggests that the functions performed by soil microbial communities are commonly altered (Liao *et al.*, 2008).

The first clue from plant invasions for microbial biogeographic patterns is that exotic invasions commonly disrupt

processes mediated by soil bacteria. Plant invasions typically reduce local plant species richness; and local richness has been repeatedly shown to increase ecosystem NPP (Tilman *et al.*, 2001). Paradoxically, many plant invasions, despite dramatic decreases in local diversity, appear to increase local soil nitrogen pools and total ecosystem nitrogen stocks (Liao *et al.*, 2008; Rout and Callaway, 2009). These are processes completely regulated by soil-dwelling and/or symbiotically mutualistic microbes. Increases in ecosystem NPP (Liao *et al.*, 2008) combined with *increased* soil nitrogen pools and total ecosystem nitrogen stocks (Liao *et al.*, 2008; Rodgers *et al.*, 2008; Rout and Chrzanowski, 2009) suggest we should investigate more deeply biogeographically based shifts in the microbial roles in the plant-invasion process, specifically at the plant–soil root-zone interface. Dramatic increases in soil nutrient concentrations have been widely reported in many plant-invaded communities (Dassonville *et al.*, 2008; Gomez-Aparicio and Canham, 2008; Liao *et al.*, 2008; Rodgers *et al.*, 2008; Rout and Chrzanowski, 2009); importantly, these are processes mediated by bacteria residing at the plant–soil interface. This combination of changes is odd. Such changes may be correlated with anthropogenic disturbances that often facilitate invasions (Pyšek *et al.*, 2010), especially ones that increase nitrogen deposition thus creating a positive feedback for plants capable of accessing these inputs quickly, attaining high biomass, and /or those containing high leaf-nitrogen concentrations. Such changes might also occur when native species replace other natives, but a fundamental ecological paradigm is that short-term increases in NPP deplete soil resources. The effects of invaders on these processes in their home ranges are not known, and when biogeographic differences in abundances are minimal (see Firn *et al.*, 2011) impact may also be minimal. However, for the many invasive species that are far less abundant in their home ranges we would expect much weaker ecosystem effects. The dramatic and consistent alterations of soil nutrient cycles associated with invaders in introduced ranges (Heneghan *et al.*, 2006; Dassonville *et al.*, 2008; Gomez-Aparicio and Canham, 2008; Liao *et al.*, 2008; Rodgers *et al.*, 2008; Rout and Chrzanowski, 2009) suggests that invasive species can exert novel effects, relative to the effects of native plants, on soil microbes. If invaders affect microbially mediated soil processes in predictably different ways than natives, two equally interesting hypotheses exist. Either plants with ‘invasive’ traits (see Baker, 1965), as a general group, also happen to affect soil microbes differently than plants without such invasive traits – but somehow do not display these traits in their native range – or microbes in various parts of the world are functionally similar (e.g. there are nitrifiers everywhere), but subtly different with respect to the way they interact with plants that share a long-term evolutionary history.

Morphological and physiological traits of invasive plants are highly likely to alter nutrient cycles, but these changes cannot occur without concomitant responses by microbial, specifically bacterial, communities that reside in the rhizosphere. For example, invasive grasses in California double gross nitrification rates, relative to natives, by increasing the abundance and changing the composition of ammonia-oxidizing bacterial communities in comparison to

native grass communities (Hawkes *et al.*, 2005). In other cases the apparently unique biochemistry of invaders affects microbial decomposers (Aerts, 1997), in turn altering nutrient mineralization rates. However, to our knowledge there has been only one explicitly biogeographic study comparing invader effects on ecosystem processes in home and away ranges, and thus this remains a major knowledge gap in ecology. Thorpe *et al.* (2011) found that in a non-native range of *Centaurea stoebe* (spotted knapweed), soils experimentally treated with *C. stoebe* plants and catechin, a component of the invader's root exudates, significantly reduced resin-extractable nitrate, nitrification rate and gross nitrification in soils. These effects of *C. stoebe* and catechin on nitrogen-related processes were different in Romanian grasslands, where *C. stoebe* is native. In Romanian soil, *C. stoebe* had no effect (compared with other native plant species) on plant-available forms of nitrogen, nitrification rate or gross nitrification. These results suggest biogeographic differences in the way an invasive plant species alters nitrogen cycling through the direct effects of root exudates. Despite the minimal evidence for such mechanistic effects, the consistent trend in the effects of invaders on microbially mediated soil ecosystem processes suggests the possibility of regional evolutionary trajectories (e.g. Thompson, 2005) for soil microbes.

INVASIVE SOIL MICROORGANISMS

There are many examples of invasive microbes involved in plant diseases, and these invasions demonstrate quite clearly both the geographic limits of the microbial disease agents and the impact of anthropogenic dispersal beyond these limits (Archie *et al.*, 2008). Many of these are fungal pathogens that reside in the rhizosphere for at least part of their life-cycle (Loo, 2009). In contrast, there are very few studies that convincingly demonstrate similar patterns for invasive soil microbes that drive biogeochemical cycles (van der Putten *et al.*, 2007), which are primarily bacterial species. The literature on invasive microbes involved in plant diseases has been thoroughly reviewed elsewhere (Narayanasamy, 2010), and here we simply mention several dramatic cases that provide excellent examples of a biogeographic framework for these soil–plant-related microorganisms.

Cryphonectria parasitica was introduced to North America from Eurasia, and this fungal pathogen has for all practical purposes driven the North American chestnut (*Castanea dentata*) to extinction (Anagnostakis, 1987). The effects of this fungal pathogen are minor on *Castanea* hosts in its native range. Perhaps one of the world's more terrible invaders is *Phytophthora cinnamomi*. Native to south-east Asia (Bergot *et al.*, 2004), this soil-borne pathogen has been introduced throughout the world where it causes root rot and rapid mortality for many woody species (Moreira and Martins, 2005; Garbelotto *et al.*, 2006).

Other evidence for geographic isolation, evolutionary divergence, and thus important biogeographic patterns with fungi involve hybridization among once isolated taxa that have been brought together by recent human dispersal and subsequent invasion. For example, at least one hybrid

invasive soil fungal pathogen appears to have arisen from the introduction of biological control agents used to suppress the invasive forb, *Euphorbia esula/virgata* (leafy spurge) (Kremer *et al.*, 2006). The impacts of these introduced pathogens can be exceptionally strong when they hybridize with local pathogens (reviewed by van der Putten *et al.*, 2007). While local hybridization between introduced fungal biocontrols and resident pathogens has only been speculated on, there is strong evidence that hybridization among fungal pathogens from different biogeographical regions has caused several disease outbreaks in plants. Hybridization among once-isolated fungal species within the genus *Phytophthora* is credited for the evolution of new pathogenic isolates that cause sudden oak death (Arnold, 2004), a recent fungal infection affecting alder trees in Europe (Brasier *et al.*, 1999) and potato blight (Grünwald and Flier, 2005). Brasier *et al.* (1999) noted that natural interspecific hybridization among fungi is very rare, but that accelerated pathogen evolution may be occurring through genetic exchange between introduced, or introduced and resident, fungal pathogens. They found morphological and genetic evidence for a new, highly aggressive *Phytophthora* pathogen of alder trees in Europe was composed of a suite of interspecific hybrids from non-native species and argued that the genetic profiles indicate a recent origin and rapid continuing evolution. Later evidence indicated that pathogenic *Phytophthora* isolates contained hybrid genotypes from non-pathogenic strains (Arnold, 2004), supporting the hypothesis of accelerated pathogen evolution due to genetic exchange with resident fungi. Similarly, in Mexico and South America, co-evolution among *Phytophthora infestans*, other *Phytophthora* pathogens and *Solanum* (the genus of potatoes) species native to Mexico provide a source of resistance genes (R-genes) utilized by several *Phytophthora* species (Grünwald and Flier, 2005). Thus, the native range of potatoes is in fact the centre of origin not only of the potato blight pathogen *P. infestans*, but also of several related pathogenic *Phytophthora* species.

Such well-known patterns of fungal pathogen invasion, in particular pathogens that operate in the rhizosphere, and hybridization among previously isolated taxa are strikingly inconsistent with the idea that everything is everywhere for microbial taxa.

BACTERIA: EVIDENCE OF BIOGEOGRAPHIC PATTERNS

Initially, broad ranges of microbial taxa were included in the concept that everything is everywhere (de Candolle and Sprengel, 1821; Cohn, 1867), which was later credited to and since associated with Baas Becking (1934), but the modern focus has been primarily on bacteria (see Box 1 timeline). Fundamental taxonomic and functional groups of bacteria and, in particular soil bacteria, were once thought to be highly genetically homogeneous around the globe. This perspective is due in part to the strong morphological similarities within taxa, and this has hindered examination of bacterial variation because these organisms with virtually identical morphologies can vary substantially in their functional responses to different plant species. For sexually

reproductive species, specifically macro-organisms and to a large degree fungi, centuries of collection and identification across the world has allowed us to determine what is native where; yet, these historical collections do not exist for bacteria. Only recently through advances in molecular techniques have we been able to investigate taxonomic detail for bacteria beyond morphology.

Recently, tremendous progress has been made towards identifying very strong biogeographic patterns within bacterial functional groups – at the level of the genus. Bahl *et al.* (2010) found that the hypolithic cyanobacteria in the genus *Chroococcidiopsis* are phylogenetically variable in deserts around the world. However, multilocus phylogenetic associations were highly correlated with current distributions. Parallel pyrosequencing confirmed that *Chroococcidiopsis* variants were specific to either hot or cold deserts and there was no evidence of recent inter-regional gene flow. Therefore, the common ancestry of these congeneric populations predates the formation of the modern continents. While not in the context of invasions and the rhizosphere, their results indicate that global distribution of desert cyanobacteria has not resulted from widespread contemporary dispersal but from ancient evolutionary legacies. In similar fashion, Papke *et al.* (2003) studied island-like cyanobacterial communities residing in hot springs in North America, Japan, New Zealand and Italy. The genetic diversity of cyanobacteria indigenous to the hot-springs from the respective regions was surveyed using molecular techniques (16S rRNA and 16S – 23S internal transcribed spacer regions combined with lineage-specific oligonucleotide probing). They confirmed that geographical isolation had occurred at global and local spatial scales, and there was variation among different cyanobacterial lineages with regard to their distributions. Since there was no correlation between these distributions and the chemical characteristics of these hot-springs (20 chemical parameters assayed), these results indicate the biogeographical distribution of these thermophilic cyanobacteria is not driven by available niches. Instead, geographical isolation is at least partially responsible for these biogeographic patterns.

We are beginning to understand how such biogeographic and even local functional diversity occurs. Bacteria can acquire novel genes through horizontal gene transfer within and among broad taxonomical prokaryotic groups (Welch *et al.*, 2002). This is not trivial because it drives rapid evolution of antibiotic resistance (Recchia and Hall, 1997), transfer of the *Rhizobium* nodulation plasmid (Freiberg *et al.*, 1997) and accounts for 18–60% of the *Escherichia coli* genome (Lawrence and Ochman, 1998; Welch *et al.*, 2002). Exotic plant invasions add to this growing body of science that points to biogeographic differentiation among bacteria.

BACTERIA: EVIDENCE OF BIOGEOGRAPHIC PATTERNS INVOLVING INVASIVE PLANTS

We also find biogeographical patterns by comparing basic ecological processes involving interacting plant species and bacteria between the home and invaded ranges of the plant (see above; Thorpe *et al.*, 2011). Some of the best examples

of biogeographic patterns come from studies of rhizobia, endophytic nitrogen-fixing (N_2 -fixing) bacteria that form nodules in legumes and, thus, a complex mutualism with plants; and many of these nodule-forming plant species are prominent invaders. Leguminous invaders must either bring their specific symbionts with them, or possess the ability to form mutualisms with a wide range of bacterial taxa. Interestingly, both patterns exist. Several exotic, but *non*-invasive legumes, were unable to nodulate when first introduced to a new geographical region, even though native legumes and their symbionts were present (reviewed by Parker *et al.*, 2006), suggesting strong biogeographic differences for these root-dwelling bacteria. *Robinia pseudoacacia* (black locust) is a leguminous tree native to North America, but globally invasive. Interestingly, *R. pseudoacacia* functions well with many different genotypes of N_2 -fixing bacteria within a number of genera including *Rhizobium*, *Bradyrhizobium* and *Mesorhizobium* (Ulrich and Zaspel, 2000). Callaway *et al.* (2011) compared mutualistic and antagonistic biota in soils collected in the native, expanded and invasive ranges of *R. pseudoacacia* and found that the invader formed nodules in all soils with a broad phylogenetic range of N_2 -fixing bacteria, and leaf nitrogen concentrations remained consistent, regardless of the soil in which the plant was grown. This suggests that the global expansion of *R. pseudoacacia* was not limited by the lack of appropriate mutualistic N_2 -fixing bacteria, and thus limited biogeographic patterns. Yet, even for this highly promiscuous legume, there is some evidence for biogeographic differences in the functions performed by these bacteria. For example, a strain of *Rhizobium* isolated from invasive *R. pseudoacacia* in Argentina was a superior symbiont to the ‘native soil-borne *Rhizobium*’ (Ferrari and Wall, 2007).

Cytisus scoparius (scotch broom) is another root-nodulating legume that has become a major invader throughout the world. Seedlings of *C. scoparius* experimentally transplanted into sites in the invasive range in North America, either with or without inoculum from other *C. scoparius* plants, demonstrated far less nodulation and biomass without inoculum (Parker *et al.*, 2006). This study suggests successful invasions of *C. scoparius* rely upon these microbial mutualists, and that these nodule-inducing symbionts express functional biogeographic patterns. The genetic diversity of *Bradyrhizobia* associated with the invasive leguminous tree, *Acacia longifolia*, was compared between Australian sites that varied in the time since invasion (Parker *et al.*, 2002; Rodriguez-Echeverria *et al.*, 2007). Long-invaded sites had higher genetic diversity of *A. longifolia*-associated rhizobia than sites currently undergoing invasion. Additionally, some phylogenetically related isolates showed overall low levels of genetic similarity, indicating rapid and divergent evolutionary trajectories were occurring for these microbial symbionts even across a temporal invasion gradient. *Acacia longifolia* invasions support the idea that geographic barriers exist for micro-organisms, and that invasion gradients provide unique opportunities to study factors that influence microbial biogeographic patterns. The effects of invasive leguminous plants and their associated N_2 -fixing symbionts can have impacts that reach beyond the plant hosts, causing ecosystem-level perturbations (discussed above with regard to nutrient cycling).

For example, in areas of Hawaii where the invasive leguminous tree *Falcataria moluccana* had established, litter decomposition rates were dramatically increased (Hughes and Uowolo, 2006). It is important to note that, regardless of whether the litter was from the native plant community or from the invasive *F. moluccana*, decomposition rates increased in invaded areas. This indicates that the invaded ecosystem is functionally different compared with that of the native-dominated ecosystem that is being displaced, and suggests that soil-dwelling microbes responsible for decomposition and nutrient turn-over rates are functionally different.

We caution that the biogeographic origins of N₂-fixing organisms are not precisely known because large numbers of genotypes are introduced with legume seeds (Rodríguez-Echeverría *et al.*, 2007) or through agricultural inoculum (Wang and Chen, 2004), potentially to become invaders themselves. With this caveat, rhizobia might be everywhere, but symbiont limitation for some plant species and biogeographical differences in symbiont functions demonstrate strong biogeographical effects on their current distributions. This suggests that the relative abundances of these microbes might differ enough across locations to result in functional differences between communities.

FUNGI

A number of recent studies of invasive plants have demonstrated geographic boundaries for soil fungi (Callaway *et al.*, 2008; Shipunov *et al.*, 2008; Newcombe *et al.*, 2009). For example, Reinhart *et al.* (2003) found that a relatively uncommon North American tree, *Prunus serotina* (black cherry), attained far higher densities when introduced to northern Europe and that these differences in densities corresponded with much stronger negative whole-soil feedbacks in the native range than in the non-native range. Following this, they found that fungal pathogens (specifically oomycetes) from North American soils inhibited the growth of *P. serotina* but pathogens from European soils did not (Reinhart *et al.*, 2005). Soil pathogens, including oomycetes, existed in European soils, but did not inhibit *P. serotina*, suggesting strong biogeographical differences, derived from evolution occurring at the local or regional scale, in the ecological function of this most important soil taxonomic group. Striking biogeographical differences were also demonstrated for the effects of European native *Alliaria petiolata* (garlic mustard), a North American invader, on arbuscular mycorrhizal fungi (AMF; Callaway *et al.*, 2008). Although not mycorrhizal, *A. petiolata* (live plants and biochemical extracts) suppressed AMF in North American soils. However, the effect of the plant and its chemical constituents were far weaker on AMF in soils collected near natural populations of European *A. petiolata*. In soils where the plant was experimentally grown, North American AMF-dependent species were much smaller than when grown in control soils; whereas European AMF-dependent species were unaffected. Interestingly, *A. petiolata* had no effect on non-AMF-dependent species from either range. Biogeographical patterns of AMF have also been assessed in the context of range expansion of *Artemisia tridentata* (big sagebrush). Weinbaum *et al.* (1996) conducted a reciprocal transplant experiment between native

ranges and expanded ranges within North America. When planted with big sagebrush at the introduced sites, AMF performed poorly, indicating that, even with the same host, genotypic adaptation was restricted to the site where these AMF fungi originated and with the sagebrush ecotype at particular local places.

Fungal endophytes are often found in the above-ground parts of plants but can reside in roots and soils. Fungal endophytes can have striking effects on plant growth, defence and competitive ability, and recently biogeographic patterns related to plant invasion have been shown. Genetic analysis of endophytic fungi found in *Centaurea stoebe* in both its native and invaded ranges showed that 85% occurred in only one of the two ranges (Shipunov *et al.*, 2008). In Europe, the native range, the most common endophyte was a haplotype of *Alternaria alternata*. In the invaded range, no haplotype was dominant and many were novel. Some fungal endophytes appear to have been introduced with *C. stoebe*, but the invader also acquired new endophytes after introduction (Shipunov *et al.*, 2008). Similarly, some fungal endophytes isolated from *C. stoebe* seeds caused significant declines in germination of *Festuca idahoensis*, a North American grass competitor (Newcombe *et al.*, 2009). Aschehoug *et al.* (2012) found that *C. stoebe* was a better competitor against North American grass species than native grasses from its European home range in the absence of endophytes; however, one endophyte both increased the biomass of *C. stoebe* and reduced the competitive effect of North American grasses on the invader. The competitive effects of *C. stoebe* on grass species native to North America were enhanced by both fungal endophytes, but not for native European grasses. This body of work indicates strong biogeographic patterns in the taxonomy and ecological functions of fungal endophytes.

Such biogeographical differences in plant pathogenic and mutualistic interactions indicate that meaningful evolutionary relationships occur for microbes within biogeographic boundaries that are similar to the boundaries observed for other evolved interactions (Thompson, 2005). Such subtle differences in ecotypes are likely to be due to the effects of biotic interactions among species on natural selection, discernable through the disruptions of evolutionary trajectories caused by plant invasions.

PLANT–SOIL FEEDBACKS

The reciprocal effects of soil biota and plant species on each other in the same soil volume vary over time due to accumulation or attenuation of particular soil taxa in roots or at the root–soil interface that either harm or help the plant species. These changes are called ‘feedbacks’ (Bever, 1994), and disproportional accumulation of pathogenic or parasitic soil taxa leads to negative feedbacks, while the disproportional accumulation of mutualistic taxa leads to positive feedbacks (Klironomos, 2002). Combined, these feedbacks represent a type of legacy that invasive plants are able to transmit through the soil ecosystem, and a legacy that has strong biogeographical context. To our knowledge, few intercontinental comparisons of plant–soil feedbacks have been conducted for invasive species, and all but one showed clear

evidence for stronger negative feedbacks in soil from the native range versus soils from the non-native range (Beckstead and Parker, 2003; Callaway *et al.*, 2004, 2012; Reinhart and Callaway, 2004; Reinhart *et al.*, 2003, 2005; Van Grunsven *et al.*, 2009). In a study attempting to tease apart different components of plant–soil feedbacks for the invasive tree, *Robinia pseudoacacia* (black locust), Callaway *et al.* (2011) found that AMF from the native range stimulated stronger positive feedbacks than AMF from the expanded or invasive ranges, a biogeographic difference not found for invasive plants. *Pythium* pathogens collected from soil in the native range were not more pathogenic than those from other ranges; however, feedbacks produced by the total soil biota were more negative from soils from the native range than from the other ranges, overriding the effects of AMF. Their findings point to important biogeographical evolutionary relationships among plants and soil biota, but those that are not easily explained by studying isolated components of the soil biota, or by looking at individual plant species and their respective soil microbial communities since community-level soil feedbacks are likely to drive plant community-composition patterns (see Klironomos, 2002).

Andonian *et al.* (2011) conducted global-scale analyses of plant–soil feedbacks for a single invasive species, *Centaurea solstitialis* (yellow starthistle), and found that feedbacks with soil microbes indicated pervasive negative effects in both native and non-native regions. In further analyses by Andonian *et al.* (2012) they found that soil microbes had negative effects on *C. solstitialis* plants from all regions, but these negative effects were significantly weaker in soils from non-native ranges in Chile and California than in those from the non-native range in Argentina and the native range in Eurasia. It is important to point out that total soil biota used in some of these studies includes a wide range of taxa and, in some cases might incorporate effects of higher organisms (i.e. soil-dwelling invertebrates) which are taxa that have never been thought free from biogeographical constraints. Differences in plant–soil feedbacks between native and invaded ranges (less negative in the invaded range) strongly suggest that ecological functions of soil microorganisms (as measured by various microbially mediated parameters like nutrient cycling, litter decomposition, etc.) have biogeographic patterns – everything is not everywhere.

In a recent review and meta-analysis, Kulmatiski *et al.* (2008) compared plant–soil feedbacks reported in the literature for native, exotic but non-invasive, and invasive species, and found that invasive plants in soil from non-native ranges experienced significantly weaker soil feedbacks than either native or exotic non-invasive species. Similarly, comparison of plant–soil feedbacks between ten taxonomic pairs of native and introduced old-field plants showed that exotics experienced far weaker negative soil feedbacks than natives (Agrawal *et al.*, 2005). Invasive exotics were not differentiated from non-invasive exotics or resident congeners; however, three of the four species in this study are well-recognized invaders and had the strongest positive feedbacks relative to their congeners. Plant–soil feedbacks suggest that microbial biogeography is both a function of limitations to dispersal and environmental selection on evolutionary trajectories. These factors will remain intertwined until we can improve

our technical abilities to sample at the micro-scale, or until we can identify two habitats that are identical at the micro-scale yet geographically isolated (Fierer, 2008).

CONCLUSIONS

Our understanding of the biogeography of microbes, and microbes in the roots or at the root–soil interface in particular, has been advanced tremendously with modern molecular genetics and through exotic invasions by plants that interact with these microbes. We will soon advance farther through metagenomic and metatranscriptomic analysis of microbes in plant tissues, rhizospheres and root zones and integrate this information with soil biogeochemical data and other ecosystems functions. Holistic approaches to the plant–soil interface in the context of exotic invasions supports recent genetic evidence indicating that biogeographic patterns have evolved for soil microbes that are similar to those that are so easily discerned for macro-organisms. Interestingly, similar metabolic strategies and functional genes appear to have independently evolved in different microbial groups. The now substantial body of literature demonstrating that invasive plants interact with microbes in the root-zone differently in their native and non-native ranges, and in ways that are quantitatively or qualitatively different than those of native plants, is good evidence for microbial biogeography. Perhaps microbial dispersal capabilities are far more limited than previously thought, or rapid evolutionary relationships between soil microbes and plants might be occurring over a short enough time scale such that dispersal cannot disrupt the effects of geographic isolation. Either way, specific geographic patterns in plant–soil–microbial interactions, detectable in part through the ‘natural experiment’ of exotic plant invasions, are revealing a fascinating geographical mosaic (Thompson, 2005) for microbes in which everything is not everywhere. Furthermore, the ‘selection’ component of Baas Beeking’s famous quote appears to need re-interpretation. Selection appears not to be just the environmental filtering of a globally homogeneous species pool, but also *natural* selection on microbes at the local and regional scale.

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