

## REVIEW AND SYNTHESIS

# Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems

Elena Litchman\*

*Kellogg Biological Station,  
Michigan State University,  
Hickory Corners, MI 49060, USA*

\*Correspondence: E-mail:  
litchman@msu.edu

### Abstract

Although the number of studies on invasive plants and animals has risen exponentially, little is known about invasive microbes, especially non-pathogenic ones. Microbial invasions by viruses, bacteria, fungi and protists occur worldwide but are much harder to detect than invasions by macroorganisms. Invasive microbes have the potential to significantly alter community structure and ecosystem functioning in diverse terrestrial and aquatic ecosystems. Consequently, increased attention is needed on non-pathogenic invasive microbes, both free-living and symbiotic, and their impacts on communities and ecosystems. Major unknowns include the characteristics that make microbes invasive and properties of the resident communities and the environment that facilitate invasions. A comparison of microbial invasions with invasions of macroorganisms should provide valuable insights into general principles that apply to invasions across all domains of life and to taxon-specific invasion patterns. Invasive microbes appear to possess traits thought to be common in many invasive macroorganisms: high growth rate and resource utilization efficiency, and superior competitive abilities. Invading microorganisms are often similar to native species, but with enhanced performance traits, and tend to spread in lower diversity communities. Global change can exacerbate microbial invasions; therefore, they will likely increase in the future.

### Keywords

Bacteria, dispersal, diversity, free-living, fungi, global change, invasive species, invasiveness, microbial biogeography, protists, symbiotic, traits.

*Ecology Letters* (2010) 13: 1560–1572

## INTRODUCTION

Microbes play key roles in all ecosystems on Earth, contributing almost half of global primary productivity and driving major biogeochemical cycles (Field *et al.* 1998). Understanding microbial community structure and function will help us understand how diverse ecosystems function and might re-organize in the face of global environmental change. The rapidly evolving field of microbial ecology investigates and applies general ecological principles to microbial systems and is a cornerstone for studying microbes in ecosystems. Ecological studies of microbes cover many exciting topics such as the general patterns of microbial diversity and distribution, interactions of microbes with other taxa, such as plant-microbe interactions, microbial competition and coexistence, and the effects of global environmental change on microbial communities. One

aspect of microbial ecology that has not yet received much attention is microbial invasions, especially by non-pathogenic free-living and symbiotic microbes, including bacteria, fungi and protists. Although there are excellent syntheses discussing invasive pathogenic microbes and the effects of plant invasions on microbes (Parker & Gilbert 2004; van der Putten *et al.* 2007; Randolph & Rogers 2010), the general problem of invasive non-pathogenic microbes in both aquatic and terrestrial ecosystems has not been thoroughly addressed, despite an increasing number of reported invasions. In this review, I assess the current knowledge of invasive non-pathogenic, i.e. free-living and symbiotic (mostly mycorrhizal and rhizobial) microbes in freshwater, marine and terrestrial ecosystems, examine published studies to identify general patterns in non-pathogenic microbial invasions and outline major challenges and research directions in the field.

Invasions by organisms from all major microbial domains of life, such as viruses (although it is debated whether viruses are true life forms), bacteria, protists and fungi, have been reported (Briand *et al.* 2004; Reid *et al.* 2007; Allan *et al.* 2009; Pringle *et al.* 2009a). Among the invasive microbes, pathogens of plants, animals and humans are much better studied than the free-living or symbiotic microbial invaders, because they are easier to detect by their impact on macroscopic species and often have more obvious consequences for communities and ecosystems (Desprez-Loustau *et al.* 2007). However, non-pathogenic microbes are also spreading, with significant impacts on communities and ecosystems. Moreover, various genetically engineered microbes are being introduced into the environment for bioremediation, agricultural and other purposes and may have a significant invasive potential (Pieper & Reineke 2000). It may seem a remote possibility now, but invasive microbes may potentially pose a risk not only for the ecosystems on Earth but also for other planets, as humans explore the solar system (Nicholson *et al.* 2009).

Microbial invasions present unique challenges for invasion biology and deserve more attention and research. Given the increase in the spread of invasive microbes, a general framework is required for the emerging field of microbial invasion ecology to help synthesize individual studies on a variety of invasive microorganisms, guide current and future research and advance our understanding of microbial invasions. This emerging field would benefit from defining microbial invasions broadly and, consequently, including invasions by pathogenic, as well as non-pathogenic microbes from diverse taxa.

There are multiple definitions of invasive species and most of them emphasize rapid spread and/or negative impact of introduced species on local ecosystems (Ricciardi & Cohen 2007). Here, I define invasive microbes as microorganisms (viruses, archaea, bacteria, protists and fungi) that proliferate in a new range and impact local communities or ecosystems. The notion of invasive microbial species is complicated because of the difficulties associated with establishing the 'non-nativeness' of microbes and with applying the very concept of 'species' in many microbial taxa (Staley 2006). Too few morphological characteristics, frequent horizontal gene transfer and the dependence of species identification on the methods used often make defining microbial species challenging (Hanage *et al.* 2005; Konstantinidis *et al.* 2006). Shifting species concepts for microbes may also obscure the invasive nature of a species considered (Pringle & Vellinga 2006). Despite these challenges, the number of documented invasions by non-pathogenic free-living or symbiotic microbes is growing. A number of key questions (Box 1) need to be answered to elucidate general patterns and relationships in the current and forthcoming studies of

invasive microbes, if we are to successfully detect, forecast and mitigate past, present and future microbial invasions. Although some of these questions can be addressed using existing data, many remain largely uncharted territory. The goal of this review is to summarize what is currently known about invasive non-pathogenic microbes and to, hopefully, stimulate more research efforts to find answers to these key questions.

#### Box 1 Key questions on microbial invasions

- How can we detect microbial invasions?
- What are the similarities and differences between invasions by microorganisms vs. macroorganisms?
- Are invasion patterns similar among free-living, symbiotic or pathogenic microorganisms, prokaryotes vs. eukaryotes?
- What are key traits associated with high invasive potential? Are these traits universal across microbial taxa or depend on taxonomic affiliation (e.g. eukaryotes vs. prokaryotes or viruses)?
- Are there trade-offs between a microorganism's invasiveness and other life history traits?
- What are community and ecosystem characteristics that facilitate microbial invasions? Are these characteristics universally important across microbial domains and between microbes and macroorganisms?
- How does global environmental change affect microbial invasions?
- How do invasive microbes change resident communities of both micro- and macroorganisms and ecosystem functioning?
- How can microbial invasions be prevented or mitigated?

#### DISPERSAL PATTERNS AND DETECTION CHALLENGES – CAN THERE BE INVASIVE MICROBES?

Baas Becking's view of microbial distributions ('everything is everywhere, but the environment selects'; de Wit & Bouvier 2006) has been an influential paradigm in microbial ecology but does not apply to all microbes (Martiny *et al.* 2006; Pringle *et al.* 2009b). Recent studies have shown that many microbial species exhibit geographic patterns in their distributions at different scales and that many microbes have clearly restricted ranges, similar to macroorganisms (Whitaker *et al.* 2003; Martiny *et al.* 2006; Telford *et al.* 2006). These restricted ranges may result both from environment filtering and dispersal limitation (Martiny *et al.* 2006). Non-cosmopolitan distribution patterns create the

potential for invasive microbes to arise, when non-native microbes invade and spread into new habitats. Understanding what makes certain microbes invasive (i.e. spread and proliferate in a new range), both with respect to the microorganisms' traits and the community and ecosystem properties is a key unanswered question (Box 1).

Microorganisms, due to their small sizes, fast growth and large populations, are thought to disperse faster and over longer distances than most macroorganisms (Shurin *et al.* 2009); however, direct evidence for this idea is not readily available (Jenkins *et al.* 2007). Although the ease of dispersal can lead to a frequent cosmopolitanism among microbes (Finlay 2002), many microbes remain dispersal-limited (Whitaker *et al.* 2003; Winsborough *et al.* 2009). Breakdown of dispersal barriers can accelerate invasions of new habitats by a wide spectrum of pathogenic as well as free-living and symbiotic microorganisms (Ramette & Tiedje 2007). Many microbial invasions proceed by means of macroscopic vectors, including invasive plants, insects, birds, etc. (Anagnostakis 1987; Vellinga *et al.* 2009). The well-documented existence of invasive microbial pathogens, i.e. pathogens that have not been present or detected at a given location before, supports the notion that dispersal barriers exist for microbes and suggests that microbes may be qualitatively, if not quantitatively, similar to macroorganisms in their dispersal patterns. Similarly, the existence of non-pathogenic endemic microbes may be possible in part because of these dispersal barriers (Winsborough *et al.* 2009). At least eukaryotic microbes, such as protists (e.g. diatoms) and fungi, include endemic species (Taylor *et al.* 2006; Vanormelingen *et al.* 2008; Winsborough *et al.* 2009). Given the diversity of dispersal ranges in prokaryotes, there should also be endemic, cosmopolitan and invasive bacteria and archaea. Some cases have already been documented: several cyanobacteria have invaded lakes across Europe and North America from the tropics (Dyble *et al.* 2002; Wiedner *et al.* 2007) and nitrogen-fixing bradyrhizobia from Australia have been found in Portugal, possibly introduced recently with exotic plants but already associated with native vegetation (Rodriguez-Echeverria 2010).

As mentioned earlier, the relative lack of attention to microbial invasions by non-pathogenic microbes compared with invasions by macroorganisms or pathogenic microbes is, in part, due to the cryptic nature and difficult detection of such invasions (Wyatt & Carlton 2002; Desprez-Loustau *et al.* 2007). Pathogenic invasive microbes often have dramatic and easily observable impacts on macroscopic species. For example, chestnut blight, an invasive parasitic fungus, almost completely decimated the American chestnut, dramatically altering forest ecosystems (Paillet 2002). The spread of West Nile virus in Western Hemisphere is associated with significant bird die-offs and human mortality

(Rappole *et al.* 2000). Currently, there are no published examples of the impacts of non-pathogenic microbes of a similar scale. However, there is growing evidence that the effects could be significant: for instance, invasive mycorrhizal fungi may be replacing native fungal species in several ecosystems (Zachow *et al.* 2009; Wolfe *et al.* 2010).

Determining if a species is invasive requires knowledge of the prior and current community composition, which is challenging for many microbial, especially bacterial, archaeal and viral, communities. Molecular fingerprinting methods, such as DGGE (denaturing gradient gel electrophoresis), T-RFLP (terminal restriction fragment length polymorphisms) and ARISA (automated ribosomal intergenic spacer analysis), enable establishing community profiles, and the phylogenetic affiliations of the detected species can be established in cases where DNA fragments can be sequenced. However, fingerprinting methods capture only a small fraction of all microbial species present in natural environments and most methods are semi-quantitative at best (Ramette 2009). Thus, unless invaders become dominant community members, they can easily go undetected (Bent & Forney 2008), even when samples are repeatedly taken at a given location to account for natural seasonal and longer-term variability in microbial communities. However, to some extent this is also true for macroorganisms, since potentially invasive species present at low densities early in the invasion cannot be reliably detected, which leads to a systematic underestimation of invasion risk (Taylor & Hastings 2005). Real-time quantitative PCR and similar techniques have the potential to overcome the problem of quantification and are just beginning to be applied to highly diverse microbial communities (Rousk *et al.* 2010). The future holds great promise, however, as high-throughput sequencing such as 454 pyrosequencing, Illumina sequencing, and similar techniques are becoming widespread and could overcome many of the problems associated with the classical molecular methods used to describe microbial community composition (Qin *et al.* 2010).

In some instances, indirect methods can be used to determine whether a microbe is invasive. For example, Pringle *et al.* (2009a) inferred the invasive nature of an ectomycorrhizal fungus by analysing its haplotype networks and comparing genetic diversity for several loci in European and North American populations. North American populations had a much lower genetic diversity for all the loci analysed, despite having twice as many individuals sampled. The data also indicate multiple introductions of the fungus to North America (Pringle *et al.* 2009a).

## TRAITS THAT CAN MAKE A MICROBE INVASIVE

Many studies of macroscopic invaders have tried to define traits common to many invasive species in an effort to

assess the likelihood that a given species becomes invasive. Trait-based characterizations of species and communities are becoming widespread (McGill *et al.* 2006), including characterization of traits of invasive species (Funk & Vitousek 2007; van Kleunen *et al.* 2010) and application of trait-based approaches to microbes (Green *et al.* 2008; Litchman & Klausmeier 2008). Identifying the traits of microorganisms affecting their invasive potential should be extremely useful for forecasting and mitigating microbial invasions (Table 1 and Fig. 1).

A recent increase in studies comparing general ecological patterns found in macro- and microorganisms suggest that microbes might be similar to macroorganisms in many respects. For example, microbes show evidence of dispersal limitation (Taylor *et al.* 2006; Martiny *et al.* 2006) and exhibit broad diversity patterns consistent with the trends found for many groups of macroorganisms (Green & Bohannan 2006; Vyverman *et al.* 2007). Given these similarities, one can hypothesize that some invasive characteristics may be similar across multiple domains of life, from archaea and bacteria to micro- and macro-metazoans. Among the traits frequently cited as increasing the probability of invasiveness in macroorganisms are being an *r*-strategist and a generalist, high phenotypic plasticity, having good dispersal capabilities and a high genetic

diversity enabling rapid adaptation to novel environments (Sakai *et al.* 2001). Higher values of traits associated with performance (e.g. growth rate, resource acquisition capability) are also a characteristic of invasive species, at least in plants (van Kleunen *et al.* 2010). Are these traits characteristic of invasive microbes?

Many groups of microbes have high growth rates compared with macroorganisms, because of the allometric scaling of growth rate with body size. However, within microorganisms, there is a wide range of maximum growth rates that may depend not only on cell size but also on phylogenetic position (Šimek *et al.* 2006) and metabolic type as well, with some microorganisms growing exceptionally slow. Results of at least two studies suggest that invasive free-living protists and cyanobacteria have growth rates that are relatively high compared with those of native microorganisms occupying a similar niche (Istvanovics *et al.* 2000; Spaulding & Elwell 2007).

Invasive species establishing in low-resource environments may have a high resource use efficiency or possess traits allowing them to gain access to resources unavailable to other species, such as the capacity to fix molecular nitrogen (Funk & Vitousek 2007). Published studies suggest that these characteristics apply to invasive microbes as well. An invasive protist, the diatom *Didymosphenia geminata*

**Table 1** Traits that might increase invasiveness, hypothesized to be important in macroorganisms, as well as more microbe-specific traits

|  | Evidence available for invasions by various microbial groups   |
|--|--|
| <i>Trait hypothesized to increase invasiveness in macroorganisms</i> |  |
| High growth rate   | Cyanobacteria <sup>1</sup> , protists <sup>2</sup>   |
| High non-assisted dispersal capability                               | Most microbes  |
| Vector-assisted dispersal, including via humans                      | Cyanobacteria <sup>3</sup> , fungi <sup>4</sup> , protists <sup>5</sup>                                      |
| Dormant stages such as spores  | Cyanobacteria <sup>6</sup> , fungi <sup>4</sup> , protists <sup>5, 7</sup>                                   |
| Generalist strategy or low host specificity for symbiotic forms      | Cyanobacteria <sup>6,8</sup> , fungi <sup>9–11</sup>   |
| High competitive ability   | Cyanobacteria <sup>8</sup> , fungi <sup>12,13</sup> , protists <sup>5</sup>                                  |
| High resource use efficiency   | Cyanobacteria <sup>8</sup> , fungi, protists <sup>2</sup>  |
| High or low similarity to native species                             | Cyanobacteria <sup>8</sup> , rhizobial bacteria <sup>14</sup> , fungi <sup>10</sup> (high similarity)        |
| Toxicity (negative allelopathy)                                      | Cyanobacteria <sup>3</sup> , fungi <sup>9</sup> , protists <sup>15</sup> , pathogenic bacteria <sup>16</sup> |
| Phenotypic plasticity  | Fungi <sup>17</sup>  |
| <i>Traits hypothesized specifically for invasive microbes</i>        |  |
| Specific metabolic pathways or modes of nutrition                    | Protists <sup>18</sup>   |
| Large genome size  | Helpful for adapting to new environmental conditions outside the original distribution range                 |
| High genetic diversity   | Fungi <sup>12</sup>  |
| Frequent gene transfer   | Helpful for adapting to new environmental conditions outside the original distribution range                 |

Significance of some of these traits for microbial invasions are supported by existing studies, others are hypothetical and await empirical validation.

(1) Padisak (1997), (2) Spaulding & Elwell (2007), (3) Neilan *et al.* (2003), (4) Schwartz *et al.* (2006), (5) Whitton *et al.* (2009), (6) Wiedner *et al.* (2007), (7) Wyatt & Carlton (2002), (8) Istvanovics *et al.* (2000), (9) Pringle *et al.* (2009a), (10) Pringle *et al.* (2009b), (11) Migheli *et al.* (2009), (12) Murat *et al.* (2008), (13) Zachow *et al.* (2009), (14) Rodriguez-Echeverria (2010), (15) Chambouvet *et al.* (2008), (16) Sekirov & Finlay (2009), (17) Desprez-Loustau *et al.* (2007), (18) Rengefors *et al.* (2008).

(Lyngbye) *M. Schmidt*, spreading in low-nutrient streams worldwide has the ability to efficiently utilize organic phosphorus, giving it a competitive advantage in low-nutrient conditions (Whitton *et al.* 2009). Another invasive freshwater protist, *Gonyostomum semen* (Ehrenberg) Diesing, spreading in Scandinavian lakes, is a superior competitor for nutrients and light, able to assimilate dissolved organic carbon and to access resources both in surface and deep water by migrating vertically in the water column (Salonen & Rosenberg 2000; Rengefors *et al.* 2008). A cyanobacterial invader of temperate lakes, *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya & Subba Raju, can fix atmospheric nitrogen, which allows it to escape N limitation (Briand *et al.* 2004). This species may also utilize other limiting resources, such as phosphorus, more efficiently than resident cyanobacteria (Istvanovics *et al.* 2000) and, thus, be a superior nutrient competitor. An invasive fungus of the genus *Trichoderma* on the island of Tenerife also appears to be a strong competitor compared with the native fungi (Zachow *et al.* 2009). The same genus is invasive on another island (Sardinia) and has displaced native fungi in most environments there; it is hypothesized to have broader niches compared with native fungi (Migheli *et al.* 2009). Taken together, the above examples suggest that invasive microorganisms, although generally similar to resident microorganisms of the same functional group, are more efficient at a given function, may have wider ecological niches and exhibit a generalist strategy (Parker & Gilbert 2004).

As in macroorganisms, the invasive potential of microbes should depend on their abilities to disperse. Microbial species even of similar size can have drastically different dispersal patterns shaping their distribution ranges from endemic to regional to cosmopolitan. Perhaps somewhat differently from macroorganisms, microbes with the highest dispersal capabilities may not have the highest invasive potential as they might already be distributed worldwide, having colonized many ecosystems in the past and, thus, would be less likely to become invasive in the future. Microbes with very low dispersal potential are also unlikely to become invasive, suggesting that microbes with intermediate dispersal capabilities may have the highest invasive potential. Different phylogenetic microbial groups may cluster at different parts of the dispersal capability axis. For example, viruses might have higher average dispersal capabilities than other microbial groups and, consequently, appear to exhibit low global diversity (Breitbart & Rohwer 2005). Among fungi, species with open fruiting bodies (sporocarps) may have a higher dispersal and invasion potential than species with closed sporocarps (Schwartz *et al.* 2006). Vector-assisted dispersal, including human-mediated dispersal, likely alters the hypothesized relationships between dispersal capability and invasive potential,

often increasing microbial invasion probability (Anderson *et al.* 2004; Spaulding & Elwell 2007).

The ability to disperse and successfully establish may be correlated with the type of environment favoured by a microbe and with its metabolic characteristics. If a microbial species occupies a unique environment or has a narrow ecological niche, its establishment probability is expected to be low. For example, archaea occupying hot springs that are interspersed in a drastically different landscape matrix may have a low probability of surviving in the surrounding landscape unless they reach another suitable habitat patch. However, many microbes can survive in hostile environments in inactive states (Ramette & Tiedje 2007) and resume growth once they reach suitable habitats; this ability could potentially increase their invasive potential.

Other life-history characteristics can also influence the rate of spread of invasive microbes. Free-living microbes might be spreading faster than the obligate symbionts or parasites because their spread is not limited by the availability of hosts. For example, an invasive free-living saprotrophic fungus that invaded Europe from Australasia is estimated to spread at least twice as fast as an ectomycorrhizal fungus (obligate symbiont) invading North America from Europe (Pringle *et al.* 2009a).

Certain genetic characteristics of microbes may also increase the potential for being invasive. Horizontal gene transfer is commonplace in prokaryotes, and frequently gives rise to evolutionary innovations that help microbes adapt to novel environments (Ochman *et al.* 2000; Breitbart & Rohwer 2005). Horizontal gene transfer also occurs in eukaryotic microbes (both prokaryote–eukaryote and eukaryote–eukaryote), although perhaps less frequently than in prokaryotes, and may aid adaptation as well (Keeling & Palmer 2008). Frequent gene transfer and high genetic diversity in some microbes might allow colonizing novel habitats more easily (Hunt *et al.* 2008). For example, a more genetically diverse Chinese truffle (symbiotic fungus) may be displacing the native, closely related but less diverse, truffle in Italy (Murat *et al.* 2008). A large genome size tends to enable greater metabolic versatility and, consequently, more efficient exploitation of multiple ecological niches (Konstantinidis *et al.* 2006). Overall, it is plausible that several genetic characteristics (i.e. frequent gene exchange, large genome size and high allelic diversity) increase the invasion probability of introduced microbes and facilitate their adaptation to novel environments.

Some invasive microbes can produce toxins negatively affecting various species, including humans. For example, several species of invasive cyanobacteria spreading into temperate zone in Europe and North America can produce potent hepatotoxins that affect invertebrates, birds and mammals (Fastner *et al.* 2007). Invasive protists, such as marine dinoflagellates, can be toxic as well (Wyatt & Carlton

2002; Chambouvet *et al.* 2008). Invasive symbiotic fungi of the genus *Amanita* invading North America and New Zealand are also poisonous, at least to insects and mammals (Dickie & Johnston 2008; Pringle *et al.* 2009a). Microbial pathogens of plants, animals and humans produce various toxins as well. Investigating whether toxic metabolites aid in invasion success, similar to invasive plants (Callaway & Aschehoug 2000), could help predict invasions by a broad range of toxic microorganisms.

It appears that trait differences play an important role in determining the invasive potential of a microbe and, therefore, neutral framework may not be relevant for microbial invasions. An open question with respect to traits facilitating the invasion of both microbes and macroorganisms is whether trade-offs exist between traits that increase invasiveness and others. Knowledge of such trade-offs might aid control of invasive species.

### COMMUNITY AND ENVIRONMENTAL CHARACTERISTICS THAT COULD FACILITATE MICROBIAL INVASIONS

The other half of the equation determining invasion success is the community and environmental characteristics enabling establishment and invasive spread. What makes a particular community and ecosystem more susceptible to invasions? A common property of communities hypothesized to increase their susceptibility to invasions is low species or functional-group diversity, with the extreme examples of low-diversity islands lacking whole functional groups or guilds and plagued by invasive species (Dukes 2002). Low-diversity ecosystems are more likely to have

ecological niches that can be occupied by invaders (Fridley *et al.* 2007), although this explanation is somewhat controversial. Little is known on whether invasive microbes spread preferentially in low diversity microbial communities, but published studies appear to support this hypothesis (Table 2). An invasive toxic cyanobacterium, *C. raciborskii*, tends to invade lakes with very high nutrient concentrations (Padisak 1997), which often have low phytoplankton diversity. Similarly, the invasive protist *D. geminata* spreads in low-nutrient streams that might also have a reduced diversity (Spaulding & Elwell 2007). In humans, lowered diversity of gut microbes can increase susceptibility to microbial pathogens because distinct functional types of resident microbiota are responsible for different aspects of immunity (Sekirov & Finlay 2009). In contrast to the microbial examples above, there is also evidence from some plant communities that more diverse vegetation can be more frequently invaded than low-diversity communities (Levine & D'Antonio 1999). The patterns may be scale-dependent, with a negative relationship between diversity and invasibility at fine scales and a positive relationship at larger scales (Fridley *et al.* 2007). It may be that microbial invaders are successful in both low- and high-diversity communities and that invasion success is primarily dependent on factors other than diversity *per se*.

An important question is whether it is the diversity of a microbial community versus the macroorganism community that has a stronger effect on microbial invasiveness. For symbiotic microbes, similar to pathogenic ones, the diversity of host communities is likely a key determinant of invasion success. For specialist symbionts, low host diversity may correspond to a high density of the host species and, thus,

**Table 2** Community and environmental characteristics with potential to facilitate microbial invasions

|  | Evidence available for invasions by various microbial groups                       |
|--|--|
| <i>Community or environment characteristic hypothesized to facilitate invasions by macroorganism</i> |  |
| Low diversity (taxonomic, functional, genetic)   | Cyanobacteria <sup>1</sup> , pathogenic bacteria <sup>2</sup> , fungi <sup>3</sup> |
| High isolation (island ecosystems)   | Fungi <sup>4</sup>   |
| High disturbance level   | Protists <sup>5</sup> , bacteria <sup>6</sup>                                      |
| High or fluctuating resource supply  | Cyanobacteria <sup>7</sup>   |
| High anthropogenic impact  | Cyanobacteria <sup>1</sup> , protists <sup>5</sup>                                 |
| High host density (for symbiotic or pathogenic forms)  | Mycorrhizal fungi <sup>8</sup> , bacteria <sup>9</sup>                             |
| Absence of predators and pathogens ('enemy release' hypothesis)                                      | Protists <sup>10</sup>   |
| Presence of other invasive species ('invasion meltdown')   | Rhizobial bacteria <sup>9</sup>  |
| <i>Characteristics specific to microbial invasions</i>   |  |
| Low metabolic diversity of resident microbial community  | Unknown  |
| Resource forms not fully or less efficiently utilized by resident community                          | Nitrogen-fixing cyanobacteria <sup>11</sup> , protists <sup>12</sup>               |

(1) Padisak (1997), (2) Sekirov & Finlay (2009), (3) Murat *et al.* (2008), (4) Dickie & Johnston (2008), (5) Spaulding & Elwell (2007), (6) Andrew *et al.* (2000), (7) Wiedner *et al.* (2007), (8) Pringle *et al.* (2009b), (9) Rodriguez-Echeverria (2010), (10) Chambouvet *et al.* (2008), (11) Briand *et al.* (2004), (12) Rengefors *et al.* (2008).

may aid transmission and establishment (Allan *et al.* 2009). Another aspect of diversity that could be important for the establishment and spread of invasive microbes is the diversity of metabolic types in a resident microbial community, with low metabolic diversity possibly encouraging invasions. It may be that microbial species possessing metabolic pathways not represented in the resident community are more likely to invade where the corresponding resources are not fully utilized or less efficiently utilized.

The structure and dynamics of biotic interactions in a newly invaded range may be an important determinant of the success of exotic species (Mitchell *et al.* 2006). For example, the absence of pathogens in a recently invaded range was shown to contribute to the invasive success of many plants (Mitchell *et al.* 2006). Subsequently, invasive species may acquire more pathogens and parasites in the invaded range that can control their densities (Mitchell *et al.* 2006). The 'enemy release' mechanisms and the changes in other biotic interactions may also play a role in the spread and subsequent control of invasive microorganisms. For example, when a toxic protist, dinoflagellate *Alexandrium minutum* Halim, invaded the Atlantic coastal waters off France, it developed excessive blooms; two decades later, it became effectively controlled by a parasitic dinoflagellate and the blooms disappeared (Chambouvet *et al.* 2008).

Frequently, plant invasions are associated with disturbed ecosystems (D'Antonio *et al.* 1999). Evidence that microbial invasions can also be favoured by disturbances are found in invasions by human pathogens: microbial gut flora resists invasions by pathogenic microorganisms, but when natural gut communities are disturbed, for example, by antibiotics, pathogen invasions are more likely (Andrew *et al.* 2000). Non-pathogenic microbes may also be aided by disturbances, as suggested by the finding that changes in flow regimes corresponded with the invasive spread of a freshwater diatom in streams (Kirkwood *et al.* 2007).

Highly variable environment may increase chances of invasive species establishment, with invasions more likely when resource levels are high (Davis *et al.* 2000). Fluctuations in environmental factors may also create windows of opportunity for the establishment of invasive microorganisms. For instance, extreme weather fluctuations could stimulate the spread of emerging plant pathogens (Anderson *et al.* 2004).

The type of environment or region might also influence the success of microbial invasions. Island communities with a high proportion of endemic species have been shown to be particularly vulnerable to invasions by macroorganisms (Berglund *et al.* 2009), and this principle may apply to microbes as well. There are several reports of islands (e.g. New Zealand and islands in the Mediterranean Sea) being invaded by numerous exotic microorganisms, including

fungi and protists (Spaulding & Elwell 2007; Dickie & Johnston 2008; Migheli *et al.* 2009; Zachow *et al.* 2009).

## GLOBAL CHANGE EFFECTS ON MICROBIAL INVASIONS

Global climate change and other anthropogenic stressors, such as increased nutrient inputs and land-use changes, could act synergistically to promote microbial invasions, similar to invasions by macroorganisms (Walther *et al.* 2009). Because of the fewer dispersal barriers for microbes, compared with macroorganisms, environmental change might play a disproportionately large role in allowing microbial spread. Global warming could stimulate invasions by tropical and subtropical microbes into temperate latitudes. Increasing air temperatures have been implicated in the spread of malaria and other pathogenic microbes into higher altitudes and latitudes on several continents (Pascual *et al.* 2006). Free-living tropical toxic cyanobacteria are currently spreading into temperate latitudes where water temperatures are rising; heat waves appear to stimulate their emergence from dormant cysts and, consequently, may facilitate invasion (Wiedner *et al.* 2007). Predicted increases in frequency of extreme events such as heat waves (Walther *et al.* 2009) may thus promote microbial invasions.

The decline in N : P ratios in lakes (Weyhenmeyer *et al.* 2007), caused by anthropogenic P loading, might also contribute to the invasion success of invasive N-fixing cyanobacteria. Furthermore, anthropogenic changes in both concentrations and ratios of elements could create niches suitable for microbes with metabolic pathways not previously present in a given ecosystem. For example, a recent increase in conductivity in the Laurentian Great Lakes may have allowed the invasion by a brackish diatom, *Pleurosira laevis* (Ehrenberg) Compère, which is now the largest diatom in these lakes (R. Lowe, pers. comm.). Likewise, a recent invasion of the Baltic Sea by a toxic dinoflagellate, *Prorocentrum minimum* (Pavillard) Schiller, has been attributed to increased nitrogen inputs and decreasing Si : N ratios (Pertola *et al.* 2005). Climate-driven changes in ocean circulation might have enabled a marine diatom, *Coscinodiscus wailesii* Gran & Angst, from the Pacific Ocean to invade European shelf seas in the late 20th century (Edwards *et al.* 2001).

Land-use changes and changes in farming techniques, in particular, are one of the important drivers behind the spread of fungal and bacterial plant pathogens (Anderson *et al.* 2004) and are likely to promote non-pathogenic microbial invasions as well. Human-driven alterations in resident plant or animal community structure may also stimulate microbial spread. Anthropogenic decrease in bird diversity appears to have a positive feedback on the

prevalence of West Nile virus (Allan *et al.* 2009). Current agricultural practices focusing on growing monocultures often lead to a rapid spread of novel microbial plant pathogens (Anderson *et al.* 2004) and could also promote invasions by symbiotic microbes with high host specificity.

Human-assisted breakdown of dispersal barriers is a major cause of invasive species spread. Inadvertent or deliberate species introductions by humans are still on the rise, including potential microbial introductions. For example, programmes to transport mycorrhizal fungal species globally for agricultural purposes are likely to lead to further spread of invasive fungi and other associated microbes (Schwartz *et al.* 2006; Dickie & Johnston 2008). Recreational fishing may have promoted the spread of an invasive diatom, *D. geminata*, in pristine streams in New Zealand and North America (Spaulding & Elwell 2007), and an invasive toxic cyanobacterium, *C. raciborskii* may have spread from Australia to Europe through a transfer of scientific samples (Neilan *et al.* 2003). Several marine diatoms and dinoflagellates were introduced into European coastal waters most likely via ship traffic (Wyatt & Carlton 2002).

#### ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF MICROBIAL INVASIONS

Similar to invasive macroorganisms, invasive microbes likely have a number of significant ecological and evolutionary impacts on resident communities and ecosystems. These effects can be both short term and long term, with both microbial and macroorganism resident communities affected. One of the most conspicuous effects of invasive microbes is the decline or elimination of native species by exotic plant and animal pathogens (Anagnostakis 1987). The alterations of species abundances can profoundly change both community composition and, directly or indirectly, ecosystem functioning. Effects are not restricted to pathogens. Non-pathogenic microbes can also cause shifts in community composition and alter various aspects of ecosystem functioning. A freshwater invasive protist, *D. geminata*, for example, has been shown to significantly alter the benthic macroinvertebrate community, possibly by growing extensively on substrates occupied by macroinvertebrates (Gillis & Chalifour 2010). Once established, invasive microbes may impact resident community dynamics and succession. Several incidences have been documented. An exotic endophytic fungus associated with an invasive grass, tall fescue, deters herbivores and redirects herbivore pressure on woody plants, thus slowing a successional transition from grassland to forest (Rudgers *et al.* 2007). An invasive mycorrhizal fungus originating in the western USA has become a novel symbiont of endemic plants in California (Pringle *et al.* 2009a), and this novel association

could affect not only the success of the plant species, but also nutrient cycling and other ecosystem properties (Pringle *et al.* 2009b). Nitrogen-fixing invasive cyanobacteria can significantly alter nitrogen budgets of the aquatic ecosystems they invade. Microbes with metabolic capabilities not previously present in an ecosystem can shift the balance between different forms of elements such as nitrogen, phosphorus and microelements, and thus influence major biogeochemical cycles.

Successful microbial invasions may pave the way for invasive macroorganisms associated with these microbes. For example, invasions by ectomycorrhizal fungi may help invasions by plants relying on such mutualists (Collier & Bidartondo 2009), thus contributing to the invasional meltdown, i.e. when earlier invasions facilitate the subsequent invasions. Exotic nitrogen-fixing rhizobia from Australia were shown to facilitate invasion by a non-native legume in Portugal (Rodriguez-Echeverria 2010). Invasive microbes also have the potential to facilitate future invasions by other microbes, similar to macroorganisms (Mitchell *et al.* 2006). It is also possible that not only single species, but also whole microbial consortia may invade new environments. Given their potential for rapid adaptation, microorganisms might be successful invaders not only in regions with environmental conditions similar to those in their native distribution range, but also in environments with different characteristics, both in their native and new geographic ranges.

Invasive species also have numerous direct and indirect evolutionary impacts on native communities (Mooney & Cleland 2001). Evolutionary processes involving invasive species not only change the native communities but can also aid in invasive spread. Hybridization of exotic species with native relatives has been shown to increase the invasive potential (Lambrinos 2004). Interspecific hybridization was also shown to cause rapid evolution of introduced fungal pathogens on plants and increase their invasiveness, with a possibility of a 'superpathogen' evolving (Brasier 2001). It is quite likely that hybridization encourages invasions by non-pathogenic microbes as well. Invasive microbes may also provide new genes for resident microbial communities through horizontal gene transfer, thus potentially increasing the resident community's genetic diversity.

#### DISCUSSION

Based on the extensive literature search conducted for this review, only a few free-living and symbiotic microbial invaders have been studied so far. Inevitably, the number of known invasive microbes will increase and we need to consider invasive microbes within the discipline of invasion biology to tackle microbial invasions more effectively (Box 2). We can use already known invasive microbes as

model organisms to seek generalities in microbial invasions and their community and ecosystem impacts, and develop new ways of control. For example, it appears that invasive non-pathogenic microbes may share many traits of invasive macroorganisms. They often have high growth rates, superior competitive abilities and adaptations to utilize unique resources (Table 1). Moreover, as in invasive plants and animals, enemy release may play a role in the successful spread of invasive non-pathogenic microbes; subsequent acquisition of parasites and pathogens may then control them at a later stage (Table 2). Low-diversity communities and island ecosystems may be highly susceptible to invasions by microorganisms. Further synthesizing studies on various invasive microbes and comparing them with patterns observed in macroorganisms should help advance not only the emerging field of microbial invasion ecology but also the invasion biology in general.

#### Box 2 Next steps in research on invasive microbes

- Formulate general questions on the detection, ecology and spread of invasive microbes, and seek answers by both theoretical and empirical approaches.
- Use known microbial invaders (pathogenic, free-living and symbiotic) as model organisms to address key questions.
- Adapt existing and develop new molecular and statistical methods to detect microbial invasions.
- Develop models with enough realism to successfully assess and predict the dynamics of microbial invasions.
- Develop databases of microbial invasions. For some microbes, such as plant pathogens and ectomycorrhizae, such databases are already being assembled (Anderson *et al.* 2004; Vellinga *et al.* 2009).
- Devise ways to prevent and mitigate the proliferation of invasive microbes that take into account patterns of spread.

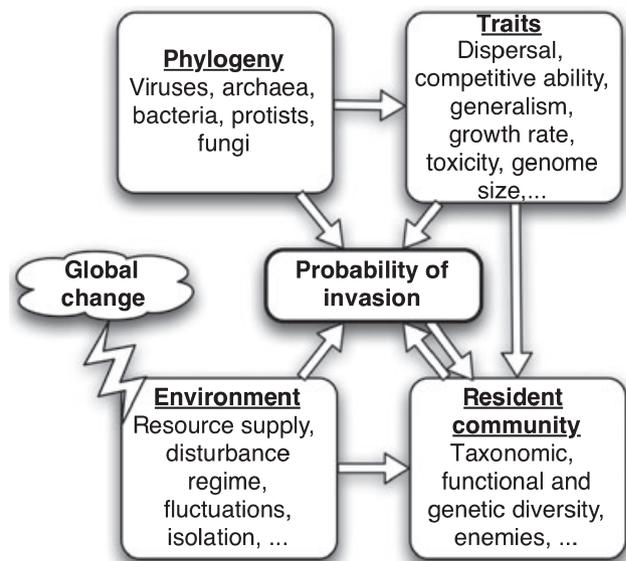
#### Links with other disciplines

Microbial invasion ecology needs to encompass physiological, population and community ecology as well as ecosystem science, because microbes connect multiple levels of biological organization, from cellular to ecosystem level. Microbial biogeography should form a cornerstone of microbial invasion ecology. Currently studies of microbial biogeography are on the rise (Martiny *et al.* 2006;

Horner-Devine *et al.* 2007; Caron 2009), partly because powerful methods for characterizing microbial distributions have become available (Ramette & Tiedje 2007). A natural next step is to go beyond documenting distributional patterns of microbial communities and to focus on the appearance of microorganisms in communities where they were previously not detected. For some microbial taxa with distinct morphological characteristics (e.g. some cyanobacteria, protists or fungi), the identification of invasive species may be easier than for others, and that explains, in part why most known invasive microbes belong to these taxa. In the future, however, with further development of tools to characterize microbial communities and extensive sampling, distinguishing between native and invasive microbes should become increasingly feasible even for the most challenging groups.

#### Dispersal studies

Microbial biogeography would benefit from more studies on microbial dispersal, both in terrestrial and aquatic environments. Different microbes, either within or across taxonomic groups, have vastly different rates and ranges of dispersal that would influence their likelihood of becoming invasive. Developing a quantitative theoretical framework, including models of invasive spread, would aid in predicting the invasive potential of a given microbe. Can invasive microbial spread be modelled using approaches developed for macroorganisms? Models with competition and diffusion-advection in heterogeneous environments have been used to predict the spread of genetically engineered microbes (Kareiva *et al.* 1996; Lewis *et al.* 1996). Although invasive



**Figure 1** Conceptual diagram showing the influence of multiple factors determining invasion probability for microbes.

microbes might spread faster than macroorganisms, the qualitative patterns appear to be similar. Pringle *et al.* (2009a), using a model of spread for invasive macroorganisms, estimated the rate of spread of a fungus invading the West Coast of North America and found it to be up to fivefold faster than the rate of spread of some invasive plants.

Because of the cryptic nature of invasive microbes, patterns of spread are harder to describe, even qualitatively, than those of macroorganisms. Therefore, both reliable molecular and statistical methods need to be adapted and developed to detect the spread of microbial invaders, and mathematical models of spread are needed that include relevant microbial biology such as information on ecological strategies and metabolism types.

### Connections with medical research

Applying ecological principles to studying microbial invasions and drawing parallels from invasion biology of macroorganisms may also be helpful to medical researchers for understanding the dynamics of human infectious diseases. Principles developed for microbes invading terrestrial and aquatic ecosystems can be applicable to the microbial communities associated with humans, i.e. human microbiomes (Hattori & Taylor 2009). Ecological understanding of both the characteristics of microbial species that make these species invasive and the properties of the resident communities may help develop new methods for preventing and treating infectious diseases (Kuehl *et al.* 2005). Conversely, placing studies on invasions of humans by microbial pathogens in a general ecological context might yield novel insights into invasions by non-pathogenic microbes in terrestrial and aquatic ecosystems. Thus, there is potential for synergy in studying microbial invasions by ecologists and medical researchers.

### Control measures

Preventing moving plants or animals across regions and applying quarantine measures might be effective in reducing the spread of some microbial taxa, such as agricultural pathogens (Palm 2001). Treating ship ballast water can prevent not only the spread of alien macroorganisms but also the spread of microbes as well (Drake *et al.* 2007). However, many microbes, especially free-living forms, have a multitude of dispersal pathways that are poorly known and, therefore, virtually impossible to control at present (Vellinga *et al.* 2009). However, as we learn more about ecological traits and the patterns of spread of invasive microbes, new approaches for controlling the proliferation of invasive microbes will likely be developed. In addition, microbial invaders already known can be used as models to devise and test control measures.

In conclusion, invasions by non-pathogenic free-living and symbiotic microbes have been documented for diverse aquatic and terrestrial ecosystems. These invasions may significantly alter resident microbial and macroorganismal community structure and ecosystem functioning and may be accelerated by global environmental change. An increased attention to microbial invasions and developing the field of microbial invasion ecology should help address numerous challenges associated with such invasions. New studies should be based on the knowledge acquired in microbial ecology, biogeography and general invasion biology. A combined effort from a broad range of microbial ecologists, invasion biologists and, possibly, medical researchers will help move this emerging field forward.

### ACKNOWLEDGEMENTS

This work was in part supported by the NSF Grants DEB-0610531, DEB-0845932 and OCE-0928819 to E.L. I thank M. Fujimoto, J. Mellard, E. Grman, J. Lau, three anonymous referees and, especially, C. Klausmeier and M. Gessner for insightful comments that improved the manuscript. C.K. also helped with Fig. 1. This is Kellogg Biological Station contribution no. 1576.

### REFERENCES

- Allan, B.F., Langerhans, R.B., Ryberg, W.A., Landesman, W.J., Griffin, N.W., Katz, R.S. *et al.* (2009). Ecological correlates of risk and incidence of West Nile virus in the United States. *Oecologia*, 158, 699–708.
- Anagnostakis, S.L. (1987). Chestnut blight – the classical problem of an introduced pathogen. *Mycologia*, 79, 23–37.
- Anderson, P.K., Cunningham, A.A., Patel, N.G., Morales, F.J., Epstein, P.R. & Daszak, P. (2004). Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends Ecol. Evol.*, 19, 535–544.
- Andrew, P.W., Oyston, P., Smith, G.L. & Stewart-Tull, D.E. (eds.) (2000). *Fighting Infection in the 21st Century*. Wiley-Blackwell, Hoboken.
- Bent, S.J. & Forney, L.J. (2008). The tragedy of the uncommon: understanding limitations in the analysis of microbial diversity. *ISME J.*, 2, 689–695.
- Berglund, H., Järemo, J. & Bengtsson, G. (2009). Endemism predicts intrinsic vulnerability to non-indigenous species on islands. *Am. Nat.*, 174, 94–101.
- Brasier, C.M. (2001). Rapid evolution of introduced plant pathogens via interspecific hybridization. *Bioscience*, 51, 123–133.
- Breitbart, M. & Rohwer, F. (2005). Here a virus, there a virus, everywhere the same virus? *Trends Microbiol.*, 13, 278–284.
- Briand, J.F., Lebourlanger, C., Humbert, J.F., Bernard, C. & Dufour, P. (2004). *Cylindrospermopsis raciborskii* (Cyanobacteria) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming? *J. Phycol.*, 40, 231–238.

- Callaway, R.M. & Aschehoug, E.T. (2000). Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, 290, 521–523.
- Caron, D.A. (2009). Past President's Address: protistan biogeography: why all the fuss? *J. Eukaryot. Microbiol.*, 56, 105–112.
- Chambouvet, A., Morin, P., Marie, D. & Guillou, L. (2008). Control of toxic marine dinoflagellate blooms by serial parasitic killers. *Science*, 322, 1254–1257.
- Collier, F.A. & Bidartondo, M.I. (2009). Waiting for fungi: the ectomycorrhizal invasion of lowland heathlands. *J. Ecol.*, 97, 950–963.
- D'Antonio, C.M., Dudley, T.L. & Mack, M. (1999). Disturbance and biological invasions: direct effects and feedbacks. In: *Ecosystems of Disturbed Ground* (ed. Walker, L.R.). Elsevier Amsterdam, pp. 413–452.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Desprez-Loustau, M.L., Robin, C., Buee, M., Courtecuisse, R., Garbaye, J., Suffert, F. *et al.* (2007). The fungal dimension of biological invasions. *Trends Ecol. Evol.*, 22, 472–480.
- Dickie, I.A. & Johnston, P. (2008). *Invasive Fungi Research Priorities, with a Focus on Amanita muscaria*. Landcare Research Lincoln, New Zealand.
- Drake, L.A., Doblin, M.A. & Dobbs, F.C. (2007). Potential microbial bioinvasions via ships' ballast water, sediment, and biofilm. *Mar. Pollut. Bull.*, 55, 333–341.
- Dukes, J.S. (2002). Species composition and diversity affect grassland susceptibility and response to invasion. *Ecol. Appl.*, 12, 602–617.
- Dyble, J., Paerl, H.W. & Neilan, B.A. (2002). Genetic characterization of *Cylindrospermopsis raciborskii* (Cyanobacteria) isolates from diverse geographic origins based on nifH and cpcBA-IGS nucleotide sequence analysis. *Appl. Environ. Microbiol.*, 68, 2567–2571.
- Edwards, M., John, A.W.G., Johns, D.G. & Reid, P.C. (2001). Case history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic. *J. Mar. Biol. Assoc. U.K.*, 81, 207–211.
- Fastner, J., Rucker, J., Stuken, A., Preussel, K., Nixdorf, B., Chorus, I. *et al.* (2007). Occurrence of the cyanobacterial toxin cylindrospermopsin in northeast Germany. *Environ. Toxicol.*, 22, 26–32.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. & Falkowski, P.G. (1998). Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Finlay, B.J. (2002). Global dispersal of free-living microbial eukaryote species. *Science*, 296, 1061–1063.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D. *et al.* (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, 88, 3–17.
- Funk, J.L. & Vitousek, P.M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446, 1079–1081.
- Gillis, C.A. & Chalifour, M. (2010). Changes in the macrobenthic community structure following the introduction of the invasive algae *Didymosphenia geminata* in the Matapedia River (Quebec, Canada). *Hydrobiologia*, 647, 63–70.
- Green, J. & Bohannan, B.J.M. (2006). Spatial scaling of microbial biodiversity. *Trends Ecol. Evol.*, 21, 501–507.
- Green, J.L., Bohannan, B.J.M. & Whitaker, R.J. (2008). Microbial biogeography: from taxonomy to traits. *Science*, 320, 1039–1043.
- Hanage, W.P., Fraser, C. & Spratt, B.G. (2005). Fuzzy species among recombinogenic bacteria. *BMC Biol.*, 3, 6.
- Hattori, M. & Taylor, T.D. (2009). The human intestinal microbiome: a new frontier of human biology. *DNA Res.*, 16, 1–12.
- Horner-Devine, M.C., Silver, J.M., Leibold, M.A., Bohannan, B.J.M., Colwell, R.K., Fuhrman, J.A. *et al.* (2007). A comparison of taxon co-occurrence patterns for macro- and microorganisms. *Ecology*, 88, 1345–1353.
- Hunt, D.E., David, L.A., Gevers, D., Preheim, S.P., Alm, E.J. & Polz, M.F. (2008). Resource partitioning and sympatric differentiation among closely related bacterioplankton. *Science*, 320, 1081–1085.
- Istvanovics, V., Shafik, H.M., Presing, M. & Juhos, S. (2000). Growth and phosphate uptake kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in throughflow cultures. *Freshw. Biol.*, 43, 257–275.
- Jenkins, D.G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R. *et al.* (2007). Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.*, 16, 415–425.
- Kareiva, P., Parker, I.M. & Pascual, M. (1996). Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? *Ecology*, 77, 1670–1675.
- Keeling, P.J. & Palmer, J.D. (2008). Horizontal gene transfer in eukaryotic evolution. *Nat. Rev. Gen.*, 9, 605–618.
- Kirkwood, A.E., Shea, T., Jackson, L. & McCauley, E. (2007). *Didymosphenia geminata* in two Alberta headwater rivers: an emerging invasive species that challenges conventional views on algal bloom development. *Can. J. Fish. Aquat. Sci.*, 64, 1703–1709.
- van Kleunen, M., Weber, E. & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.*, 13, 235–245.
- Konstantinidis, K.T., Ramette, A. & Tiedje, J.M. (2006). The bacterial species definition in the genomic era. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 361, 1929–1940.
- Kuehl, C.J., Wood, H.D., Marsh, T.L., Schmidt, T.M. & Young, V.B. (2005). Colonization of the cecal mucosa by *Helicobacter hepaticus* impacts the diversity of the indigenous microbiota. *Infect. Immun.*, 73, 6952–6961.
- Lambrinos, J.G. (2004). How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, 85, 2061–2070.
- Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.
- Lewis, M.A., Schmitz, G., Kareiva, P. & Trevors, J.T. (1996). Models to examine containment and spread of genetically engineered microbes. *Mol. Ecol.*, 5, 165–175.
- Litchman, E. & Klausmeier, C.A. (2008). Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.*, 39, 615–639.
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L. *et al.* (2006). Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.*, 4, 102–112.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

- Migheli, Q., Balmas, V., Komon-Zelazowska, M., Scherm, B., Fiori, S., Kopchinskiy, A.G. *et al.* (2009). Soils of a Mediterranean hot spot of biodiversity and endemism (Sardinia, Tyrrhenian Islands) are inhabited by pan-European, invasive species of *Hypocrea*/Trichoderma. *Environ. Microbiol.*, 11, 35–46.
- Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N. *et al.* (2006). Biotic interactions and plant invasions. *Ecol. Lett.*, 9, 726–740.
- Mooney, H.A. & Cleland, E.E. (2001). The evolutionary impact of invasive species. *Proc. Natl Acad. Sci. U.S.A.*, 98, 5446–5451.
- Murat, C., Zampieri, E., Vizzini, A. & Bonfante, P. (2008). Is the Perigord black truffle threatened by an invasive species? We dreaded it and it has happened! *New Phytol.*, 178, 699–702.
- Neilan, B.A., Saker, M.L., Fastner, J., Torokne, A. & Burns, B.P. (2003). Phylogeography of the invasive cyanobacterium *Cylindrospermopsis raciborskii*. *Mol. Ecol.*, 12, 133–140.
- Nicholson, W.L., Schuergel, A.C. & Race, M.S. (2009). Migrating microbes and planetary protection. *Trends Microbiol.*, 17, 389–392.
- Ochman, H., Lawrence, J.G. & Groisman, E.A. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature*, 405, 299–304.
- Padisak, J. (1997). *Cylindrospermopsis raciborskii* (Woloszyn'ska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Arch. Hydrobiol. Suppl.*, 107, 563–593.
- Paillet, F.L. (2002). Chestnut: history and ecology of a transformed species. *J. Biogeogr.*, 29, 1517–1530.
- Palm, M.E. (2001). Systematics and the impact of invasive fungi on agriculture in the United States. *Bioscience*, 51, 141–147.
- Parker, I.M. & Gilbert, G.S. (2004). The evolutionary ecology of novel plant-pathogen interactions. *Annu. Rev. Ecol. Evol. Syst.*, 35, 675–700.
- Pascual, M., Ahumada, J.A., Chaves, L.F., Rodo, X. & Bouma, M. (2006). Malaria resurgence in the East African highlands: temperature trends revisited. *Proc. Natl Acad. Sci. U.S.A.*, 103, 5829–5834.
- Pertola, S., Kuosa, H. & Olsonen, R. (2005). Is the invasion of *Prorocentrum minimum* (Dinophyceae) related to the nitrogen enrichment of the Baltic Sea? *Harmful Algae*, 4, 481–492.
- Pieper, D.H. & Reineke, W. (2000). Engineering bacteria for bioremediation. *Curr. Opin. Biotechnol.*, 11, 262–270.
- Pringle, A. & Vellinga, E.C. (2006). Last chance to know? Using literature to explore the biogeography and invasion biology of the death cap mushroom *Amanita phalloides* (Vaill. Ex fr.: Fr.) Link. *Biol. Invasions*, 8, 1131–1144.
- Pringle, A., Adams, R.I., Cross, H.B. & Bruns, T.D. (2009a). The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. *Mol. Ecol.*, 18, 817–833.
- Pringle, A., Bever, J.D., Gardes, M., Parrent, J.L., Rillig, M.C. & Klironomos, J.N. (2009b). Mycorrhizal symbioses and plant invasions. *Annu. Rev. Ecol. Evol. Syst.*, 40, 699–715.
- van der Putten, W.H., Klironomos, J.N. & Wardle, D.A. (2007). Microbial ecology of biological invasions. *ISME J.*, 1, 28–37.
- Qin, J.J., Li, R.Q., Raes, J., Arumugam, M., Burgdorf, K.S., Manichanh, C. *et al.* (2010). A human gut microbial gene catalogue established by metagenomic sequencing. *Nature*, 464, 59–70.
- Ramette, A. (2009). Quantitative community fingerprinting methods for estimating the abundance of operational taxonomic units in natural microbial communities. *Appl. Environ. Microbiol.*, 75, 2495–2505.
- Ramette, A. & Tiedje, J.M. (2007). Biogeography: an emerging cornerstone for understanding prokaryotic diversity, ecology, and evolution. *Microb. Ecol.*, 53, 197–207.
- Randolph, S.E. & Rogers, D.J. (2010). The arrival, establishment and spread of exotic diseases: patterns and predictions. *Nat. Rev. Microbiol.*, 8, 361–371.
- Rappole, J.H., Derrickson, S.R. & Hubalek, Z. (2000). Migratory birds and spread of West Nile Virus in the Western Hemisphere. *Emerg. Infect. Dis.*, 6, 319–328.
- Reid, P.C., Johns, D.G., Edwards, M., Starr, M., Poulin, M. & Snoeijs, P. (2007). A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminiae* in the North Atlantic for the first time in 800,000 years. *Global Change Biol.*, 13, 1910–1921.
- Rengefors, K., Palsom, C., Hansson, L.A. & Heiberg, L. (2008). Cell lysis of competitors and osmotrophy enhance growth of the bloom-forming alga *Gonyostomum semen*. *Aquat. Microb. Ecol.*, 51, 87–96.
- Ricciardi, A. & Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biol. Invasions*, 9, 309–315.
- Rodriguez-Echeverria, S. (2010). Rhizobial hitchhikers from Down Under: invasional meltdown in a plant-bacteria mutualism? *J. Biogeogr.*, 37, 1611–1622.
- Rousk, J., Baath, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G. *et al.* (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J.*, 4, 1340–1351.
- Rudgers, J.A., Holah, J., Orr, S.P. & Clay, K. (2007). Forest succession suppressed by an introduced plant-fungal symbiosis. *Ecology*, 88, 18–25.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A. *et al.* (2001). The population biology of invasive species. *Annu. Rev. Ecol. Syst.*, 32, 305–332.
- Salonen, K. & Rosenberg, M. (2000). Advantages from diel vertical migration can explain the dominance of *Gonyostomum semen* (Raphidophyceae) in a small, steeply-stratified humic lake. *J. Plankton Res.*, 22, 1841–1853.
- Schwartz, M.W., Hoeksema, J.D., Gehring, C.A., Johnson, N.C., Klironomos, J.N., Abbott, L.K. *et al.* (2006). The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecol. Lett.*, 9, 501–515.
- Sekirov, I. & Finlay, B.B. (2009). The role of the intestinal microbiota in enteric infection. *J. Physiol. (Lond.)*, 587, 4159–4167.
- Shurin, J.B., Cottenie, K. & Hillebrand, H. (2009). Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia*, 159, 151–159.
- Šimek, K., Horňák, K., Jezbera, J., Nedoma, J., Vrba, J., Straškrábová, V. *et al.* (2006). Maximum growth rates and possible life strategies of different bacterioplankton groups in relation to phosphorus availability in a freshwater reservoir. *Environ. Microbiol.*, 8, 1613–1624.
- Spaulding, S. & Elwell, L. (2007). *Increase in Nuisance Blooms and Geographic Expansion of the Freshwater Diatom *Didymosphenia geminata**. U.S. Geological Survey Report, 2007–1425, 38 pp.
- Staley, J.T. (2006). The bacterial species dilemma and the genomic-phylogenetic species concept. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 361, 1899–1909.

- Taylor, C.M. & Hastings, A. (2005). Allee effects in biological invasions. *Ecol. Lett.*, 8, 895–908.
- Taylor, J.W., Turner, E., Townsend, J.P., Dettman, J.R. & Jacobson, D. (2006). Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 361, 1947–1963.
- Telford, R.J., Vandvik, V. & Birks, H.J.B. (2006). Dispersal limitations matter for microbial morphospecies. *Science*, 312, 1015.
- Vanormelingen, P., Verleyen, E. & Vyverman, W. (2008). The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. *Biodivers. Conserv.*, 17, 393–405.
- Vellinga, E.C., Wolfe, B.E. & Pringle, A. (2009). Global patterns of ectomycorrhizal introductions. *New Phytol.*, 181, 960–973.
- Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D.A. *et al.* (2007). Historical processes constrain patterns in global diatom diversity. *Ecology*, 88, 1924–1931.
- Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kuhn, I. *et al.* (2009). Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.*, 24, 686–693.
- Weyhenmeyer, G.A., Jeppesen, E., Adrian, R., Arvola, L., Blenckner, T., Jankowski, T. *et al.* (2007). Nitrate-depleted conditions on the increase in shallow northern European lakes. *Limnol. Oceanogr.*, 52, 1346–1353.
- Whitaker, R.J., Grogan, D.W. & Taylor, J.W. (2003). Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science*, 301, 976–978.
- Whitton, B.A., Ellwood, N.T.W. & Kawecka, B. (2009). Biology of the freshwater diatom *Didymosphenia*: a review. *Hydrobiologia*, 630, 1–37.
- Wiedner, C., Rucker, J., Brüggemann, R. & Nixdorf, B. (2007). Climate change affects timing and size of populations of invasive cyanobacterium in temperate regions. *Oecologia*, 152, 473–484.
- Winsborough, B.M., Theriot, E. & Czarnecki, D.B. (2009). Diatoms on a continental “island”: Lazarus species, marine disjuncts and other endemic diatoms of the Cuatro Ciénegas basin, Coahuila, Mexico. *Nova Hedvigia*, Suppl. 135, 257–274.
- de Wit, R. & Bouvier, T. (2006). ‘Everything is everywhere, but, the environment selects’; what did Baas Becking and Beijerinck really say? *Environ. Microbiol.*, 8, 755–758.
- Wolfe, B.E., Richard, F., Cross, H.B. & Pringle, A. (2010). Distribution and abundance of the introduced ectomycorrhizal fungus *Amanita phalloides* in North America. *New Phytol.*, 185, 803–816.
- Wyatt, T. & Carlton, J.T. (2002). Phytoplankton introductions in European coastal waters: why are so few invasions reported? In: *Alien Marine Organisms Introduced by Ships in the Mediterranean and Black Seas* (ed. Briand, F.). Commission Internationale pour l’Exploration Scientifique de la Mer Méditerranée, 20, 41–46.
- Zachow, C., Berg, C., Mueller, H., Meincke, R., Komon-Zelazowska, M., Druzhinina, I.S. *et al.* (2009). Fungal diversity in the rhizosphere of endemic plant species of Tenerife (Canary Islands): relationship to vegetation zones and environmental factors. *ISME J.*, 3, 79–92.

Editor, Mark Gessner

Manuscript received 15 June 2010

First decision made 23 July 2010

Second decision made 6 September 2010

Manuscript accepted 26 September 2010