

A microbial perspective on biological invasions in aquatic ecosystems

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Abstract Microorganisms are essential components of all aquatic ecosystems and are primarily responsible for biogeochemical cycles and key environmental processes. Despite their potential to influence the ecological functioning of biological communities and ecosystems at a global scale, the mechanisms of microbial invasions still lack specific and generalizable theories. Here, we review some of the ecological mechanisms, among those relevant under the global change scenario, which may facilitate the spread of microbial invaders, with a specific focus on aquatic prokaryotes (i.e. Bacteria). We summarize a selection of ecological features of vulnerable microbial communities (functional and structural stability, diversity, invasibility, and invasiveness) and environmental

stressors for invasions (temperature increase, pollution, nutrients and resources fluctuations, and food web alterations). Owing to the rapid microbial adaptation to laboratory conditions, straightforward experimental approaches appear as suitable and informative tools to explore the invasion mechanisms in artificially assembled communities. We conclude by delineating future research steps required for a better understanding of the potential consequences of microbial invasions in the aquatic environment.

Keywords Microbial community · Bacteria · Pathogens · Invasibility · Invasiveness

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Introduction

Biological invasions, defined as the entry, establishment, and spread of non-native species into a new region, unquestionably constitute a global and major threat to biodiversity, strongly affecting the ecosystem functioning and determining serious ecological, economic, and social consequences (Vitousek et al., 1996; Pimentel et al., 2000). They are considered the second leading cause in the loss of biodiversity at a global scale, only preceded by habitat destruction (Perrings et al., 2005). Traditionally, ecologists have focused their interests on the “visible”, macroscopic components within ecosystems (Lodge, 1993). The database DAISIE (Delivering Alien Invasive Species

Inventories for Europe) shows the updated list of invasive animals and plants among the most harmful to aquatic and terrestrial ecosystems (Hulme et al., 2010). There are numerous examples of biological invasions in aquatic ecosystems (Meinesz et al., 1993; Bollens et al., 2002; Gherardi, 2006), and the alien species listing is constantly updated (McGeoch et al., 2012). Molnar et al. (2008) estimated that only 16% of the marine eco-regions could be considered free from invasive species, by reviewing over 300 cases around the globe.

When it comes to the ecology of aquatic microorganisms, distinguishing invasive species might be questionable owing to a number of microbial peculiarities. On the one hand, it is difficult to understand whether a species' successful dominance is caused by introductions, since microbes are believed to show cosmopolitan distribution (Taylor & Bothwell, 2014), although this issue is still debated in literature. Global diversity patterns and dispersal limitations have been reported (Ladau et al., 2013), but the geographic distance between habitats is considered irrelevant to microbial community assembly (Barberan et al., 2014). On the other hand, environmental changes may promote invasive characteristics of native or newly introduced species, thus suggesting that species' impact could be more important than its origin (Simberloff et al., 2012). Microbial dispersal, colonization, and invasion mechanisms have consequences not only for individual fitness, but also for population dynamics and species distribution.

Studies exploring the invasions by human- and plant-associated microbes and the ecological factors driving pathogens diversity and distribution have so far shaped researches on microbial invasions, with important results on limiting the spread of a number of diseases (van der Putten et al., 2007; Randolph & Rogers, 2010; Gatto et al., 2013). When enlarging our perspective to non-pathogenic bacteria, a reduced number of studies on natural and artificially designed microbial systems demonstrated how the spread of non-native microbes within established communities has the potential to influence the composition of the microbial community (e.g. the maritime traffic and the transport of ship's ballast waters; Drake et al., 2007) by impacting on its ecological functions (Hornak & Corno, 2012). However, the system complexity and the lack of generalizable theories make it difficult to predict the potential impacts of microbial invaders and

to identify basic ecological processes that may promote invasibility of a natural community in aquatic ecosystems.

This gap of knowledge can be explained either by the chronic methodological constraints and the inability to cultivate most of aquatic microbes, which have hampered the exploration of the microbial world and its immense biodiversity, or by the lack of adequate information on the biogeography of microbes (Gilbert et al., 2010). Nowadays, deep sequencing techniques and novel molecular approaches allow a better tracking of microbial species, thus helping to address whether microbial invaders do exist at either the global or local scale. However, differentiating between true absence and inadequate sampling can be still problematic, and there is a need to develop population genetic approaches to "source track" movement of specific microbial variants.

A number of studies have focused on the impact of dispersal on the stability and diversity of microbial communities (Lindstrom & Ostman, 2011; Severin et al., 2013), but only recently distinguishing between microbial dispersal and invasion mechanisms can be highlighted from an ecological perspective (van der Putten et al., 2007). The role of "micro-invaders" as a useful model for larger organisms and "macro-invaders" was hitherto encouraged (Litchman, 2010).

Here, we provide a synthetic outlook on the importance and potential impact of invasive microbes in aquatic ecosystems, and on some of those environmental stressors and ecological mechanisms that may facilitate their spread (including those relevant under the global change scenario). Different from previous publications, we will specifically focus on microbial invasions by aquatic prokaryotes (mainly Bacteria, given the current lack of information about the role of Archaea as invaders). We recall that microbial eukaryotes (e.g. fungi, microalgae) and viruses, which are however not the subject of this paper, can act as potential invaders in aquatic environments (Lawrence, 2008; Taylor & Bothwell, 2014).

The importance of microbial invasions in aquatic ecosystems

Microorganisms in marine and freshwater ecosystems include by far the largest portion, mostly unexplored, of the biodiversity on the planet (Pedros-Alio, 2006;

Zinger et al., 2012). Since microbial community changes can directly affect food webs and ecosystem stability, a thorough understanding of microbial dynamics is necessary to determine, predict, and manage ecosystem functioning, especially in the light of global anthropogenic changes caused by anthropogenic forces (Nogales et al., 2011).

The classical ecological theory of invasions relates community stability and diversity to the occupancy of the ecological niches, and then implemented at the microbial level with system productivity (Loreau & Mouquet, 1999; Chave et al., 2002). Accordingly, microbial communities are considered highly stable and relatively resistant to environmental changes and invasions. However, the neutral theories of biodiversity offered new perspectives on the stability of natural systems, underlining that the abundance of individual taxa within communities could be largely governed by random events under changing environmental conditions (e.g. speciation, extinction, dispersal, and ecological drift) (Rosindell et al., 2011; Barberan et al., 2014). Dispersal limitation and stochasticity play major roles in the assembly of natural communities, and this has been supported by the experimental evidence that coexisting populations in microbial multi-species systems can have chaotic behaviors (Becks et al., 2005). The distribution of prokaryotic species is not uniform at the local, regional, and global scales, and some emerging evidences suggest that aquatic microorganisms may exhibit large-scale biogeographical patterns, resembling those of macroorganisms (Amend et al., 2013; Logares et al., 2013; Ladau et al., 2013). Moreover, microbial assemblages are typically characterized by a relatively small number of occasionally dominant species and a very large number of species at very low abundance, the so-called “rare” biosphere (Pedros-Alio, 2012; Zinger et al., 2012).

By investigating whether bacterial taxa demonstrate endemism in aquatic environments, some authors reported evidences of a persistent and unexplored microbial seed bank, with changes in community composition reflecting the shifts in the relative abundance of taxa, rather than their presence or absence (Gibbons et al., 2013). The differences in community composition across space and time may be the consequence of the “opening” and “closing” of ecological niches, or the dispersal and growth of rare *versus* dormant taxa from the seed bank (Fazi et al.,

2008; Lennon and Jones, 2011; Gibbons et al., 2013). The change from the view of a stable community resistant to immigration to a community with dynamic ecological niche alternations in which rare local species and non-native strains periodically can encounter a time frame with ideal conditions for a bloom, may have thus strong implications in addressing future research lines on the ecology of aquatic microbial communities.

The study of microbial invasions in aquatic ecosystems can be of tremendous importance also for human and environmental health perspectives, with respect to invasions by opportunistic pathogenic microbes (Gatto et al., 2013). Recent outbreaks of water-borne diseases have emphasized the close relationship between the spread and evolution of pathogenic bacteria in the environment, and the evolution of virulent and antibiotic-resistant genotypes (Walther & Ewald, 2004). *Vibrio cholerae* represents so far the best example of an environmental emerging water-borne pathogen (Vezzulli et al., 2013). Blokesch & Schoolnik (2007) reported that the acquisition of a specific gene cluster generated a new invasive serogroup within a community of bacteria associated to chitin-containing shells of small crustaceans. The aquatic environment may act as a reservoir for pathogenic bacteria (including faecal bacteria), which may acquire, during their stay in the secondary habitat, new determinants of virulence or resistance as a consequence of the myriad of interactions (e.g. gene transfer mechanisms) with the resident microbial communities (Luna et al., 2010).

Stability, diversity, and invasibility of aquatic microbial communities

The mechanisms affecting the invasion by non-native species depend on: (i) the community invasibility, defined as the susceptibility to the invasion by non-native species and (ii) the species invasiveness, based on the biological characteristics of the invader and the number of “propagules” which are able to reach the new environment (Levine, 2000; Colautti et al., 2006). The success of exotic species is determined by the reduced ability of the ecosystems to resist to the invasion itself, while the invading aptitude is likely related to the absence of natural enemies (natural enemy hypothesis) or to the ability to cope successfully

with the natural enemies and spread uncontrollably (Keane & Crawley, 2002; Shade et al., 2012).

The so-called invasion paradox describes that native–exotic richness relationships will depend on spatial scaling and focal taxa, because species richness responds differently to the underlying environmental heterogeneity (Fridley et al., 2007). The general theory predicts the existence of a positive relationship between diversity and resistance to invasions at a fine spatial scale, but it can be negative at a broad scale. Some evidence suggests that aquatic ecosystems with higher diversity are less susceptible to invasion (Hooper et al., 2005). The more diverse communities may use the resources in a more efficient way (Levine, 2000; Tilman, 1999), but the relationship between ecosystem functioning and biodiversity in aquatic ecosystems is currently among the most debated topics (Hooper et al., 2012). The most species-rich communities show fewer ecological empty niches, because the resources are used more efficiently, thus reducing the likelihood of success by the invaders. This mechanism is based on the complementary use of the space and resources by native species (Ricciardi et al., 2013). Moreover, a higher biodiversity increases the probability that a particular community is represented by one or more species capable of limiting the invasive species (Tilman, 1999; Fargione & Tilman 2005). In microbial ecology, a number of studies have so far reached different conclusions, suggesting that the relation between diversity and resistance of the community to the invasion is not always positive (Jousset et al., 2011b; Eisenhauer et al., 2013).

The resistance of a microbial community to invasion and the ecological success of a non-native species is related to the overall stability of the system. For communities of larger organisms, ecosystem stability acts against the success of an invasion by reducing the number of available niches (Tilman, 1999), thus relating to the number of ecological niches, the complexity and originality of existing interactions, the productivity, the efficiency, and the biodiversity of resident communities (Shade et al., 2012).

Eisenhauer et al. (2013) tested the effect of diversity on the invasibility of *Pseudomonas fluorescens* communities in microcosms differing in resource richness, and found that the invader success was negatively correlated with the diversity of the resident community, but the functional dissimilarity had greater significance than taxonomic richness.

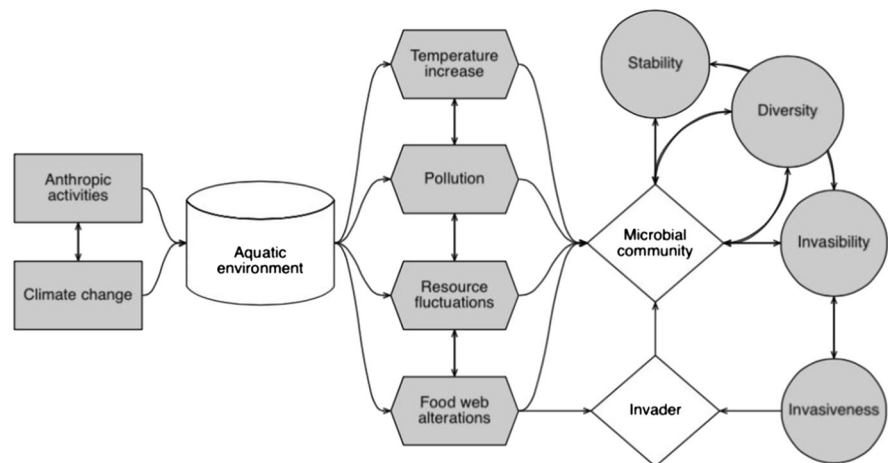
Recently, an inverse relationship between soil microbial diversity and the survival of the invading enterohemorrhagic species *Escherichia coli* O157:H7 was reported, suggesting that soil microbial diversity is a key factor controlling the extent to which bacterial invaders can establish (van Elsas et al., 2012). In other studies, the stability of a microbial community is related to the complexity of the established inter- and intra-species interactions (Morin, 1999; Price & Morin, 2004).

Thus, we can assume that more stable (and ecologically complex, often but not always, more diverse) communities are also more efficient in the substrate utilization, and thus may leave less space for the establishment of non-native species. Recent experimental evidences demonstrated that the establishment of complex bacterial interactions (e.g. cooperation) result in shorter generation times and enhanced efficiency of the system (Corno et al., 2013; Jousset et al., 2013). The validity of this theoretical framework, although tested successfully for plants (Dukes, 2001; Eisenhauer et al., 2008), has not been evaluated for aquatic microbes. The few studies conducted with microbial communities have used bacteria colonizing the rhizosphere (Hodgson et al., 2002) or simplified aquatic communities composed by protists and rotifers (Jiang & Morin, 2004). Thus, a comprehensive reinterpretation of the general theories would be necessary, by either considering the complexity of the interactions among the aquatic microbes, or incorporating the concepts of diversity, invasibility, and invasiveness in microbial ecology.

Environmental stressors and microbial invasions

Natural microbial communities are currently subjected to a wide range of environmental and anthropogenic stressors (Nogales et al., 2011). These stressors have the potential to affect the microbial invasion processes in the aquatic ecosystems (Fig. 1). Among the many factors analyzed in literature, here we will discuss some of those being particularly relevant within the global change scenario: (i) climate change and global temperature increase, (ii) pollution by anthropogenic contaminants, (iii) resource fluctuations and nutrient availability, and (iv) food web alterations.

Fig. 1 Schematic diagram synthesizing the global mechanisms (*rectangles*) which are impacting the aquatic compartment, together with some of the major environmental stressors (*hexagons*) and ecological features (*circles*) which drive the interconnected invasion dynamics between the microbial community and potential invaders (*diamonds*)



Climate change and global temperature increase

According to projected climate trends of global warming, ecological responses to recent climate change appear unequivocal (Walther et al., 2002). There are several documented examples of animal and plant species becoming invasive by migrating to higher latitudes or higher elevations where temperatures are more favorable to their survival. Accordingly, temperature increase is retained as one of the key factor driving microbial invasion by warm-water species and vector-associated parasites at a global scale (Capdevila-Arguelles & Zillett, 2010; Vezzulli et al., 2012). In particular, the increase of sea surface temperature was related to the spread of vibrios in coastal and brackish waters, which might be the cause of globally increasing trend in their associated diseases (Vezzulli et al., 2013).

In this respect, disentangling microbial biogeographical patterns become essential for applied issues of major concern to humankind, such as the control of diseases and their vectors and the likely effects of global climate change on the maintenance of microbial diversity.

Pollution by anthropogenic contaminants

The global environmental spread of contaminants and xenobiotic products may potentially reduce the resistance of natural communities to biological invasions. The presence of toxic molecules (e.g. hydrocarbons, pesticides, pharmaceuticals, and antibiotics) can increase the local availability of resources (Zoppini

et al., 2014), either directly (as most of those molecules are large organic compounds of weak composition, readily available for the resistant microbes) or indirectly by damaging local communities and therefore their ability to compete effectively. Competition is an important limiting factor of microbial food webs in aquatic ecosystems (Thingstad, 2000), and its modifications may have drastic consequences on the microbial community (Hanson et al., 2012), especially in environments where chemical pollutants and drugs can be released in large quantities as a consequence of a variety of human and veterinary purposes (Kuemmerer, 2009).

For example, it is reasonable to imagine a negative effect on the fitness of the microbial species directly affected by antibiotics, which should facilitate those species not directly targeted by the molecules, or those less competitive from an ecological perspective which, however, could even use antibiotics as a growth substrate (Blom & Pernthaler, 2010). Thus, antibiotics are able to directly modify the composition and function of microbial communities (Proia et al., 2013) and even to select for super-invasive multiresistant species (Fischbach & Walsh, 2009), as in the case of pathogenic bacterial serotypes (e.g. *Salmonella* spp.) that may invade the human gut microbiota (Crowell et al., 2009). Furthermore, the antibiotic resistance genes associated with mobile genetic elements (e.g. blaTEM or blaCTX, and vanA) might be considered as novel emerging threats due to the interactions between resident species and antibiotic resistant, non-native bacteria, owing to long-lasting transformation, survival, and proliferation processes,

with serious implications for the human health (Stoll et al., 2012).

Resource fluctuations and nutrient availability

Resource fluctuations depend on the extent of allochthonous nutrient inputs and the metabolic performances of native communities. Nutrient limitation leads to the exclusion of less-competitive species for resource exploitation (Yang et al., 2008). Moreover, stress factors and environmental disturbances may limit the ability of native communities to compete with potential invaders. This reflects the reduction of the overall fitness of the microbial community, with a strong simplification of the morphological distribution (e.g. cells size) and the selection of species that are less demanding in terms of nutrient availability.

By using insights from both experiments and long-term monitoring studies, the fluctuation of resources was identified as one of the most important ecological factors in determining the community invasibility (Davis et al., 2000; Li & Stevens, 2012). Briefly, an invasive species must have access to a range of resources (e.g. light, water, nutrients in mineral form, and organic carbon for heterotrophs) to spread. Consequently, the potential success of invasive species is enhanced when limiting resources are more accessible. In presence of interspecific competition, the resource availability is reduced and, assuming the intensity of competition as inversely correlated with the amount of unused resources, it seems logical to identify factors that reduce competition as those that may indirectly encourage biological invasions (Diehl & Feissel, 2001; Chakraborty & Li, 2010).

Therefore, the invasibility of a community is not a static feature, but rather a dynamic characteristic of ecosystems depending on fluctuating resources over time (Davis and Pelsor, 2001; Li & Stevens, 2012).

Food web alterations

A further consideration linked to aquatic ecosystems is based on the evidence that microbial communities are fundamental components of the aquatic food web. Thus, the inter- and cross-kingdom microbial interactions affect the overall ecosystem productivity, and invasive microbes have the potential to alter significantly the functioning of the invaded system (Morin, 1999; Fazi et al., 2008; Friman et al., 2014). Microbial

invasions can indeed affect microbial community structure and functioning, but at the same time can have a limited impact on species diversity and in some cases even preserve diversity (Jousset et al. 2011a; Hornak & Corno, 2012). Together with abiotic factors, some biotic factors represent major causes of death of microorganisms in aquatic environments, among which predation (mostly by protozoan nanoflagellates and ciliates) and viral lysis are the most important (Torsvik et al., 2002; Callieri et al., 2006; Corno, 2006). These factors are controlled and counterbalanced by the intrinsic capacity of the systems and the diversity of resident populations (Eisenhauer et al., 2012). Thus, the study of these controlling factors should be incorporated in the investigation of the possible effects of invasive species on the trophic web structure.

For example, the top-down control exerted within the trophic web strongly influences and shapes the morphological and genotypic composition of microbial communities (Pernthaler, 2005). It could lead to changes in the composition toward species of larger size and/or those able to produce filaments or aggregates (Corno et al., 2008). However, the impact on the overall microbial diversity is still uncertain and unpredicted. A stronger impact of predation may produce a marked selection toward those microbial species possessing a wide morphological plasticity. On the other hand, with a reduced impact of predation, the diversity of the community could be stable or even increase through the issuance of additional nutrient substrates (as wastes from predation) or removal of more competitive species, according to the well-known ecological mechanism of “killing the winner” (Winter et al., 2010).

Laboratory-based microbial model systems

Besides the analyses of the native communities in their natural environments and in times of rapid advancement of experimental methods (Naeem, 2008), the mechanisms of microbial invasions can also be explored in artificially assembled communities. The relative simplicity of microbial model systems render them powerful tools for the study of biological invasions (Jessup et al., 2005). Microbial communities rapidly adapt to laboratory conditions in chemostats, batch cultures or microcosms (van Elsas et al., 2012).

Therefore, these systems represent ideal experimental models to test microbial invasions, by considering (i) the high abundance of individuals, (ii) the fast generation times, (iii) the high reproducibility and the opportunity to set up parallel treatments to test different ecological factors, (iv) the possibility for manipulating diversity and species composition, and (v) the ability to perform robust statistical analyses based on large numbers of data (Bohannan and Lenski, 2000; Corno and Jurgens, 2008). This experimental approach allows the study of microbial communities under controlled and reproducible conditions (e.g. light, UV radiation, temperature, dilution level, and trophic substrate concentration). The community can be directly exposed to selected stressors: (i) introduction of specific or a pool of selected microbial invaders, (ii) fluctuation of available resources (e.g. nutrients and organic carbon), (iii) predation (promoting the selection of resistant species or strains), and (iv) the addition of chemical contaminants. Invasive species can be monitored, following the inoculum, for their abundance and activity by using, if necessary, also mutant or genetically marked strains to facilitate their identification. This approach allows evaluating the effect of microbial diversity on the susceptibility of the microcosms to be invaded by non-resident species. The random assembly is a prerequisite to test the role of microbial diversity and to exclude other factors that may co-vary with diversity (Huston, 1997). The levels of diversity can be constructed and modulated (e.g. dilution-to-extinction) (Peter et al., 2011) by assembling microbial communities with diversity (richness) progressively increasing the number of species (Langenheder et al., 2010).

Overall, any methodological approach that overcomes the limitations of cultivation-based techniques allows a more realistic evaluation of the impact of the reduction of diversity on the functionality of microbial communities (Xu, 2006).

Biological invasions and aquatic microbes: conclusions and open questions

Despite the growing awareness of the importance of biological invasions by both pathogenic and non-pathogenic microbes, the knowledge on the factors and conditions that may favor this phenomenon is still very limited. It is consequently necessary to further

investigate the diversity of native communities in aquatic systems, and those factors potentially able to promote the microbial invasion in aquatic ecosystems. We attempted to identify the next steps in view of a better understanding of microbial invasions and their potential consequences:

- Verify the fundamental ecological assumptions and theories about the response patterns to environmental and anthropogenic stressors.
- Formulate predictive models on the role of natural microbial communities by including the ecological processes harnessing dispersal, colonization, and invasion mechanisms.
- Explore the relationships between the microbial community invasibility and the ecological stability in terms of biodiversity, species diversity, and degree of occupation of niches.
- Define the genotypic and metabolic response (biodiversity and fitness) of natural microbial communities (either mixed or artificial) to natural and anthropogenic stressors.
- Evaluate the effect of different levels of microbial diversity (ecological, morphological, and physiological) on the resistance to invasive species, including pathogenic microbes.
- Define the degree of success by invasive species in terms of abundance, biomass, and metabolic key functions, such as the degradation of substrates for the maintenance of strategic community fitness and stability of food webs.

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