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Total number of authors:
12

Published in:
Microbial ecology and water engineering & biofilms specialist groups (MEWE2016)

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Kinnunen, M., Dechesne, A., Proctor, C., Hammes, F., Johnson, D., Quintela-Baluja, M., Graham, D., Daffonchio, D., Fodelianakis, S., Hahn, N., Boon, N., & Smets, B. F. (2016). A conceptual framework for invasion in microbial communities. In *Microbial ecology and water engineering & biofilms specialist groups (MEWE2016)* (pp. 200-201). IWA.

MICROBIAL ECOLOGY AND WATER ENGINEERING
& BIOFILMS SPECIALIST GROUPS

MEWE2016

Conference September 4th-7th, 2016, Copenhagen, Denmark

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A conceptual framework for invasion in microbial communities

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Keywords: community ecology; community dynamics; alien microbial type; resident community

Studies with a special focus on microbial invasion are gaining momentum. Several papers have tried to describe the determinants of invasion success, such as resident community diversity and richness. While these efforts advance our knowledge on microbial invasion, we find that results from these studies are not often consistent or even contradictory. We suggest that a unanimous set of definitions and a consistent framework is needed to interpret the processes determining invasion success. Hence, we propose a simple definition of invasion in a microbial community as the establishment of an *alien microbial type* in a *resident community* and suggest a community ecology framework as developed by Vellend, (2010) to clarify the potential determinants of invasion (Kinnunen *et al.*, 2016). This framework identifies four fundamental processes that control community dynamics: (1) dispersal, (2) selection, (3) drift and (4) diversification.

First, we define the *resident community* simply as any given community investigated for potential invasion. Here, it is important to realize that absolute proof of the absence of the *alien type* is often impossible to achieve and the spatial limits to the resident community can be arbitrary.

Second, we propose a simple and inclusive definition of an *alien type*: any biological type not currently part of the resident community can be considered a potential invader (Davis *et al.*, 2005; Tilman, 1997).

Then we propose to interpret invasion within the processes of community assembly as follows:

Dispersal: An *alien type* will have more opportunities to immigrate into a community when dispersal to the resident community is strong. Dispersal may be critical to invasion success, especially when considering the relative abundance of the alien type. Low relative abundance reduces the probability of establishment (Blackburn *et al.*, 2015) because a few immigrants are more subject to stochastic events that may lead to their extinction.

Selection: Selection for the alien type can be positive or negative, depending on the resident community's composition, its dynamics, and the environmental conditions. Selection is often conceptualized by considering the potential niche overlap between the *alien type* and the *resident community*. In extreme cases, the alien can fill an empty niche because it possesses metabolic traits absent from the community and can thus easily establish. More commonly however, the alien type is required to outcompete at least one member of the resident community in order to establish itself. Richness of the resident community is often used as a proxy for its ability to compete with the alien type (Dunstan and Johnson, 2004; Jousset *et al.*, 2011), because more diverse communities have higher probability to host resident types that are competitively superior to the alien either as individuals or as interacting types (Figure 1.1A).

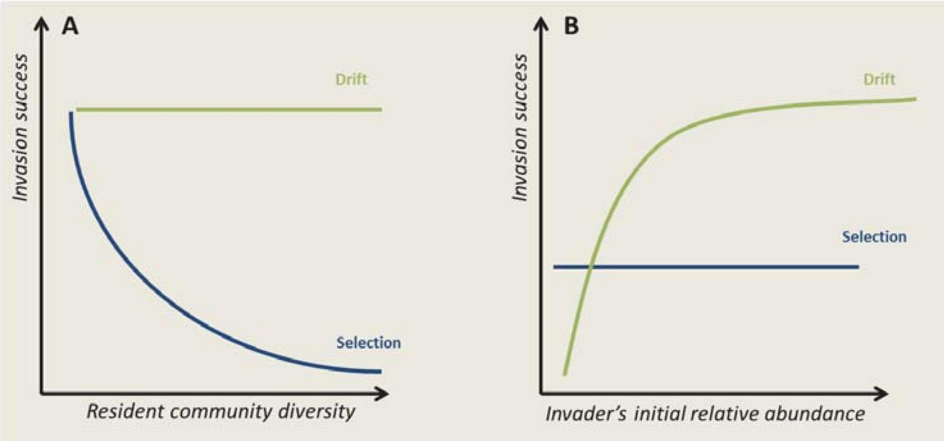

Figure 1.1 Hypothetical relation between average invasion success and (A) resident community diversity and (B) initial relative abundance of the invader, in communities where either competition (selection) or drift govern community assembly.

Drift: If all community members have equal fitness, then drift is important: the establishment of the alien type is then a random process, depending mainly on its relative and absolute abundance (Figure 1.1B). Although it cannot be easily quantified, drift is always present in biological communities but this process is especially important in communities of low abundance, because discrete division/death events have stronger consequences.

Diversification: Diversififcation can occur in the invader population or in the resident community and is thought to be positively related to population size. Diversification can increase the chances for an *alien type* to establish if some of the mutations are adaptive (Tayeh *et al.*, 2015). Conversely, diversification of the resident community members might produce insurance effects and increase community resistance to invasion.

By presenting invasion research in a community ecology framework, it is apparent that some processes have received more attention than others. Selection-focused studies have overwhelmed invasion research, while other processes shaping community dynamics are rarely considered. Therefore, the impact of the dynamics, and not only composition, of the resident community on invasion is neglected. Thus, we suggest to design and conduct experiments focusing on the role of dispersal, drift, and diversification, because these processes have received less attention. In this way, a complete picture of invasion as a community process can be obtained.

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