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Organisms as cooperative ecosystem engineers in intertidal flats

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ABSTRACT

The importance of facilitative interactions and organismal ecosystem engineering for establishing the structure of communities is increasingly being recognised for many different ecosystems. For example, soft-bottom tidal flats host a wide range of ecosystem engineers, probably because the harsh physico-chemical environmental conditions render these species of particular importance for community structure and function. These environments are therefore interesting when focusing on how ecosystem engineers interact and the consequences of these interactions on community dynamics. In this review, we initially detail the influence on benthic systems of two kinds of ecosystem engineers that are particularly common in tidal flats. Firstly, we examine species providing biogenic structures, which are often the only source of habitat complexity in these environments. Secondly, we focus on species whose activities alter sediment stability, which is a crucial feature structuring the dynamics of communities in tidal flats. The impacts of these engineers on both environment and communities were assessed but in addition the interaction between ecosystem engineers was examined. Habitat cascades occur when one engineer favours the development of another, which in turn creates or modifies and improves habitat for other species. Non-hierarchical interactions have often been shown to display non-additive effects, so that the effects of the association cannot be predicted from the effects of individual organisms. Here we propose the term of "cooperative ecosystem engineering" when two species interact in a way which enhances habitat suitability as a result of a combined engineering effect. Finally, we conclude by describing the potential threats for ecosystem engineers in intertidal areas, potential effects on their interactions and their influence on communities and ecosystem function.

Contents

1. Introduction

Interspecific competition has long been considered as the main process in structuring communities. Yet, in the last decades, the potential role of positive interactions between species has been increasingly recognised. Positive interactions involve at least two organisms, and benefit one or more organisms without negatively affecting any other organism (Bertness and Leonard, 1997). Positive interactions can be direct or indirect, obligatory or facultative and may be trophic or not. Among them, facilitative interactions describe non-trophic interactions where organisms promote, through their presence or activity, the settlement or development of other species. Facilitation and competition often occur simultaneously in communities, and the nature of the interaction between two individuals can even change according to growth stage or environmental conditions (Callaway and Walker, 1997). Also,

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indirect facilitation of a species by another can offset the negative effects of competition between these organisms.

In this context, species contributing to the creation, modification or maintenance of habitats, and therefore having a crucial effect on other species, have been defined as ecosystem engineers by Jones et al. (1994). Ecosystem engineers can be found in terrestrial and aquatic ecosystems: for instance, earthworms that alter the composition of soils, beavers that create dams and seagrasses that modify local hydrodynamics (Fonseca et al., 1982), stabilise sediment (Gacia and Duarte, 2001), and provide a substratum for epibionts, are often referred to as ecosystem engineers. These can either transform living or non-living material in the environment from one physical state to another, or modify, through their physical presence and activity, the access to resources for other organisms. For instance, benthic macrofauna change the physical, chemical and biological properties of sediment through bioturbation (Braeckman et al., 2010), and thus are defined as allogenic ecosystem engineers. In contrast, submerged macrophytes, through their own structure, attenuate the light available for benthic organisms (Lee et al., 2001) and are therefore defined as autogenic ecosystem engineers.

The engineering effect may vary according to the considered species, and is therefore not always positive for the community in terms of diversity or abundance. For example, the exclusion of the lugworm *Arenicola marina* from intertidal sediment facilitates the development of tube-building worms, but hinders the settlement and growth of subsurface deposit feeders (Volkenborn and Reise, 2007). However, at large spatial and temporal scales, the overall impact of ecosystem engineers on ecosystems is generally positive (Jones et al., 1997). The global effect of an ecosystem engineer will mainly depend on 6 factors: the spatial distribution of its population; its density; the time period over which a population has been present at a site; the durability of impacts in the absence of the original engineer; the per capita activity of individual organisms and its lifetime; and, finally, the number and type of resources modulated by the engineer, and the number of species depending on these flows (Jones et al., 1994, 1997). Most engineers modify their environment with small-scale processes, which ultimately affect ecosystem functioning; yet, there are still questions about the links between effects at small or large spatial scales.

When considering the importance on these non-trophic interactions, it might be appropriate to replace the well-known food web by a more complete interaction web (Kéfi et al., 2012; Lawton and Jones, 1995). For instance, the influence of bioturbating worms on microphytobenthos cannot be easily predicted without considering non-trophic interactions (Fig. 1, Passarelli et al., 2012a). These authors demonstrated that while worms consume microphytobenthos, they also stimulate microalgal growth through indirect facilitation, including mechanisms such as bioturbation redistributing nutrients.

Habitat creation, modification, and facilitation processes are crucial in some specific ecosystems. Indeed, biogenic habitat alterations can increase local diversity by allowing immigration of less well-adapted species by moderating harsh conditions (Bertness and Leonard, 1997; Hacker and Gaines, 1997). Therefore, ecosystem engineers play critical roles in intertidal areas, where species are subject to a large range of physical stresses: desiccation, variations of salinity and temperature (Little and Kitching, 1996). Also, numerous studies have shown the importance of facilitation and ecosystem engineering in these environments (Bertness and Leonard, 1997). The presence or absence of a single critical species can completely alter the structure of the whole community. For instance, the long-term exclusion of the bioturbating worm, *A. marina*, from a tidal flat modifies sediment properties, microbial and macrofaunal communities, by stimulating the development of sediment-stabilising organisms which are naturally excluded where *A. marina* is dominant (Volkenborn and Reise, 2007; Volkenborn et al., 2007, 2009). Such transitions between two stable ecosystem states are often prompted by positive feedback mechanisms, where organisms belonging to each community stimulate the development of its own community (Wilson and Agnew, 1992). For instance, the development of diatom biofilms on tidal flats will contribute to sediment stabilisation, therefore limiting the erosion of their own habitat, and stimulating their own population growth (van der Heide et al., 2007).

The common occurrence of ecosystem engineers in intertidal flats makes it an interesting system to study such interactions. These species are likely to interact in a manner which makes it difficult to differentiate the overall engineering effect of the association from the contribution of the individual species. This review focuses on soft-bottom intertidal areas in temperate waters, where numerous ecosystem engineers have been studied and described (Table 1). In this short review, we do not try to address every possible example but concentrate on systems that, in our experience, serve to highlight the co-engineering concept. Once introduced, this approach should be relevant to many other systems not considered in detail here, such as coral reef (Bozec et al., 2013), mussel and oyster beds (Grant et al., 2012; Lejart and Hily, 2011) among others. In addition, there is no reason to limit the approach to marine systems and expect terrestrial examples to emerge. Therefore, the role of some biogenic structures, which provide habitat complexity, is described first as spatial complexity that is important in maintaining local diversity (Bouma et al., 2009; Zühlke et al., 1998). The second part of the review will then focus on the ecosystem engineers which promote sediment stabilisation or destabilisation, and affect the settlement and growth of a large range of other species. Finally, the interaction of the engineers

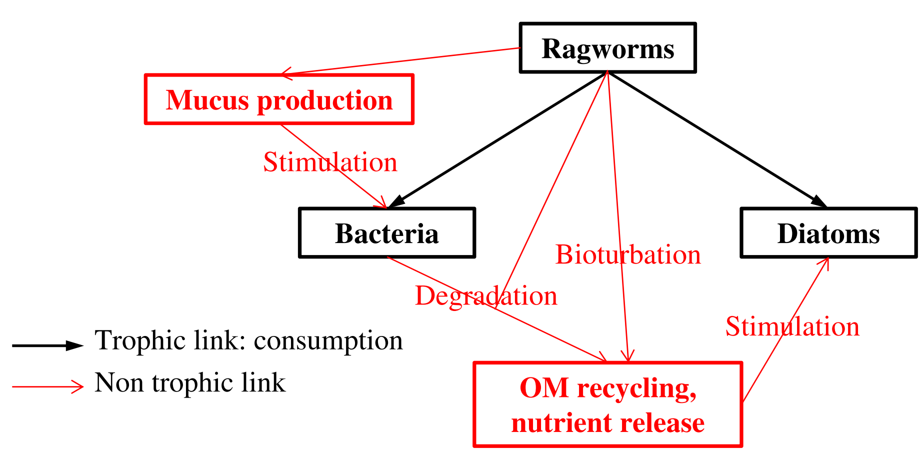

Fig. 1. Trophic web (in black) and interaction web (whole diagram) in a simplified benthic system with ragworms, diatoms and bacteria. Results from Passarelli et al. (2012a).