

Chapter 10

Mudflat Ecosystem Engineers and Services



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Abstract Ecosystem engineers play a fundamental role in the creation, maintenance and transformation of habitats in tidal flats. Highly diverse in terms of size, phylogeny, and effect on their environment, they can facilitate or hinder a number of organisms, but generally have a positive influence on both the abundance and the

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diversity of mudflat organisms. The magnitude of the engineering effect is, however, largely dependent on the biotic and abiotic environment of the engineer. In particular, stressful habitats such as mudflats host a large number of ecosystem engineers; understanding interactions between them, and how they vary with abiotic variables, is therefore of crucial importance, to evaluate how ecosystem engineers affect benthic communities and ecosystem functioning. Such understanding will also help human populations which benefit from mudflat organisms and/or functioning (i.e. which derive ecosystem services from them), to maintain and manage the sustainability of tidal flats, in a way which maintains human health and well-being.

1 Introduction

Despite being stressful environments, with little apparent complexity, tidal flats host a large diversity of organisms, in the sediment, on the sediment and above the sediment. Along with morphological, physiological, and behavioural adaptations necessary to survive in such systems, numerous organisms benefit from facilitative interactions with other organisms. These non-trophic interactions promote the settlement or development of at least one species, without negatively affecting the other; for instance, through modification of habitat or reduction of an environmental stress. Facilitation is being increasingly recognised as an important mechanism that explains assemblage formation and composition and ecosystem functioning, especially in stressful habitats such as the intertidal. (Bertness and Leonard 1997).

Research on facilitation by habitat modification was stimulated in 1994, when Jones and colleagues proposed the concept of ecosystem engineering to describe the creation, maintenance and transformation of habitat by organisms (Jones et al. 1994). This concept has received considerable attention since then, with more than 2600 papers citing this founding article, 1100 of them published in the last 4 years (Web of Science 2017). Research has focussed on the identification of ecosystem engineers and the characterisation of their effects, the modelling of engineering effects, the interactions of engineers with their biotic and abiotic environment, or between several engineers, as well as the implications of engineering effects in terms of ecosystem functioning, goods, services, and management.

Sediment reworking organisms were suggested to be a good example of ecosystem engineers, due to their strong impact on sediment properties, and therefore on associated communities and ecosystem functioning (Jones et al. 1994). In intertidal flats, the exclusion of one bioturbator species such as the lugworm *A. marina* has indeed been shown to have diverse sediment-mediated effects on benthic communities (Volkenborn et al. 2009). Coastal systems host a striking diversity of ecosystem engineers (see e.g. Passarelli et al. 2014), most of them affecting the sediment (Reise 2002), either directly (e.g. construction and maintenance of burrows by *Hediste diversicolor*) or indirectly (e.g. modification of hydrodynamics by surface-

protruding tubes built by the sandmason worm *Lanice conchilega*). In addition to their effects on sediments, ecosystem engineers of tidal flats also constitute a major source of hard substrate, necessary for the recruitment of several species (such as algae, Thomsen et al. 2010), and as the main provider of habitat complexity (Zühlke et al. 1998; Bouma et al. 2009). Therefore, ecosystem engineers are key drivers of the diversity and functioning of mudflats.

Human populations derive numerous benefits from tidal flats, some quite obvious, such as the provision of fish and shellfish, and some less known, such as nutrient recycling. However, these services may be altered when the biotic and/or abiotic environment of ecosystem engineers change, leaving the system in a different functioning state that it used to be. Understanding how ecosystem engineers modify biodiversity and ecosystem functioning, how they interact with their environment, and what are the consequences of such interactions on mudflats, is thus essential in order to maintain the provision of ecosystem services to human populations.

In this review, we will first analyse how the diverse ecosystem engineers that inhabit mudflats influence their diversity and functioning, at different time and space scales. We will then assess how the biotic and abiotic environment of ecosystem engineers alter their abundance and effects on ecosystems, with a special focus on interactions between ecosystem engineers. Finally, we will review the variety of ecosystem services provided by mudflats and their ecosystem engineers, and discuss consequences for coastal management.

2 Diversity of Ecosystem Engineers in Mudflats

2.1 *Engineers vs. Non-engineers*

Ecosystem engineering may have a longer history than many other ecological interactions, such as predation or competition. The early and abiotic conditions on the newly formed planet Earth did not last for long and in geological terms life evolved very rapidly (Dodd et al. 2017) with the first evidence of life almost 4 billion years before present, not long, geologically speaking, after the formation of the planet (4.6 billion years). Life immediately began to have an effect on the new planet, and while it took some time for the complete change in atmospheric conditions (from anoxic to oxic) as a result of microbial metabolism (Catling and Claire 2005), much earlier indications of life are present. Early microbes created structures, laminations in sediments, akin to modern day biofilms, and those laminations were preserved in the fossil record as stromatolites (Krumbein et al. 2003, see Chap. 8). This may be the first organismal engineering activity (Paterson et al. 2008) that we can recognise.

This example highlights two issues: (1) ecosystem engineering is not new; and (2) an organism does not have to be large and charismatic to influence the environment; a large number of small ones may be equally, or more, important (Boogert et al. 2006). However, that is not to say that a single isolated bacterium does not influence its surroundings, but is this ecosystem engineering? This is a

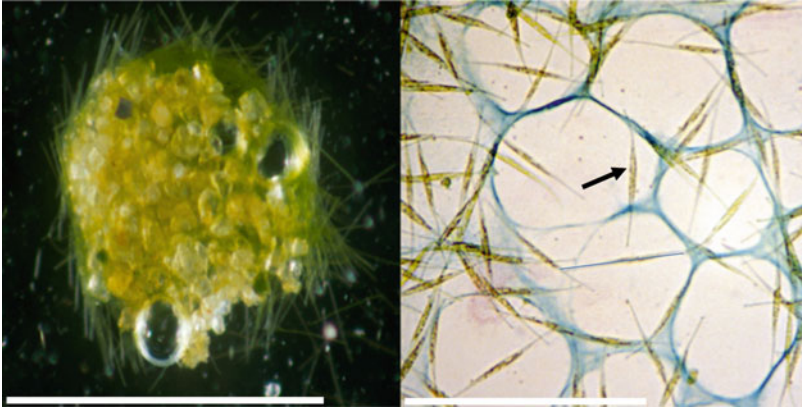


Fig. 10.1 Small-scale ecosystem engineering by cyanobacteria *Oscillatoria* spp. (left) and the polymers produced by diatoms *Cylindrotheca gracilis* (right, black arrow to diatom, polymers stained with Alcian blue; from culture: f/2 Guillard in artificial seawater at 25 PSU). Scale bars: 100 μ m.

question of scale and so it is to some extent arbitrary to decide “how much effect must be created before the effect is recognised as ecosystem engineering”, which may be very much a question of context and perspective. A relevant example is the secretion of extracellular polymeric substances (EPS) from bacteria and microphytobenthos. A microbial mat is easily recognised as having an engineering impact whereas a single diatom cell may not, but the single cells still secrete polymer and will stick local grains together, albeit the effect is on a very small scale (Fig. 10.1). However, since the effect is measurable, is it ecosystem engineering? The reality is that all living organisms alter their environment to some extent; it would be incredible if they did not, but there is a wide variety of impact ranging from almost quiescent “deep bacteria” (Whitman et al. 1998) with extremely slow metabolism, to the obvious and rapid activity of bowerbirds. We apply the term ecosystem engineering to those cases where the effect is deemed significant from a human perspective. This may recognise very large-scale effects more easily, beaver dams and coral reefs, but may miss less obvious examples such as biogeochemical pathways supplying nutrients. All organisms are capable of ecosystem engineering; the recognition of the process is a function of scale, knowledge and perceived importance.

Some examples of commonly recognised ecosystem engineers in mudflat can be found in Passarelli et al. (2014).

2.2 Classification of Ecosystem Engineers

When Jones and colleagues proposed the concept of ecosystem engineering in 1994, they immediately defined 2 types of ecosystem engineers: on one hand, autogenic engineers that transform the environment through their own physical structure,

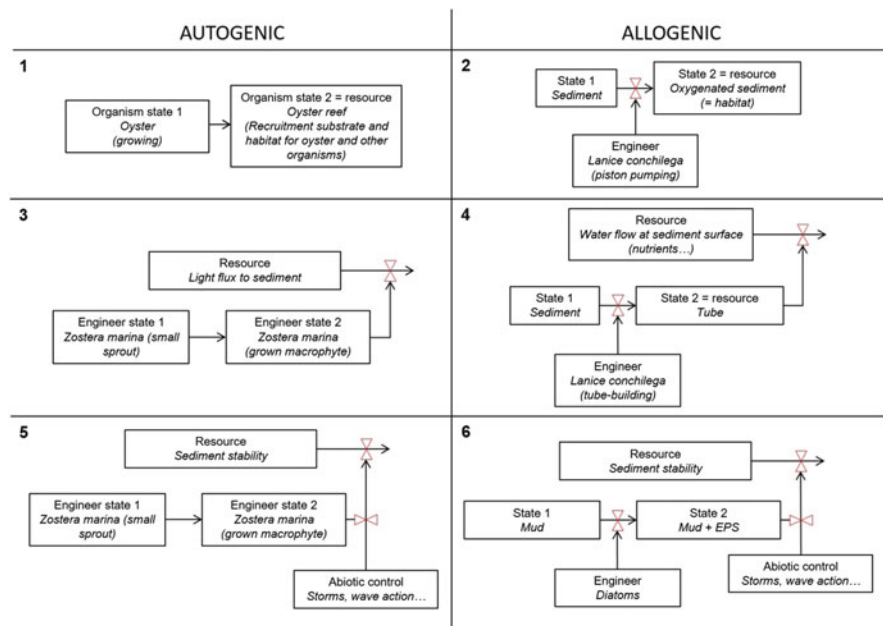


Fig. 10.2 Autogenic and allogenic ecosystem engineering: diverse mechanisms of action. Figure adapted from Jones et al. (1994), with examples from mudflats. The hourglass symbol shows potential point of modulation. Case 1 was initially excluded from ecosystem engineering by Jones et al. (1994), but subsequently proposed to be included (Jones et al. 1997); it is however worth noting that the provision of trophic resource (organism in state 2 as a food source) is not ecosystem engineering.

where the engineer remains part of the engineered environment; e.g. submerged macrophytes, such as *Zostera* species, whose leaves modify hydrodynamics (Fonseca et al. 1982), sedimentation (Ganthly et al. 2013), light (van der Heide et al. 2007), and many other parameters (Lee et al. 2001). On the other hand, allogenic engineers alter their environment by transforming other material from one state to another; e.g. burrowing macrofauna rework sediment (Meadows and Meadows 1991), alter its stability (Meadows et al. 1990), and pump oxygen into the sediment (Forster and Graf 1995).

Jones and colleagues also proposed subcategories, as illustrated in Fig. 10.2 with examples from tidal flats; an ecosystem engineer can alter its environment by different actions and therefore belong to different categories and subcategories. Ecosystem engineers can directly create a habitat for other organisms, either by their own growth (autogenic engineers, case 1) or by transforming a living or non-living material (allogenic engineers, case 2); for instance, the sand mason worm *Lanice conchilega* oxygenates sediments by piston pumping (Forster and Graf 1995). Oxygenated subsurface sediment can thereafter be colonised by diverse organisms (Reise 2002). Another mechanism of action of ecosystem engineers is the modulation of resource flow to other organisms (cases 3 and 4). For instance, tube-

building polychaetes modify, through their tubes, water flow at sediment surface, and therefore access to nutrients for benthic organisms (Luckenbach 1986; Zühlke et al. 1998). Seagrasses, shells, and faecal casts of *Arenicola marina* have similar effects (Friedrichs et al. 2009). Finally, Jones et al. (1994) separate in different categories engineers that modulate the effect of “powerful abiotic control”, such as fires or hurricanes. Organisms which stabilise the sediment either directly or indirectly (case 5 and 6), therefore preventing sediment erosion by storms, can be attributed to these categories.

Beyond their interest to illustrate the diverse possible mechanisms of ecosystem engineering, these categories serve to illustrate general patterns for certain groups of ecosystem engineers. For example, organisms modifying water flow at the sediment surface are highly diverse in terms of phylogeny; examples include tube-building polychaetes (Zühlke et al. 1998) and amphipods (Rigolet et al. 2014), seagrasses (Fonseca et al. 1982), kelps (Eckman et al. 2003), snails and shells, and even faecal casts by the lugworm *Arenicola marina* (Friedrichs et al. 2009). Yet, their actions on sediment have been shown to be primarily dependent on the density of the structures (Friedrichs et al. 2000), with an increase of the flow toward the sediment and sediment destabilisation by the turbulent flow at low density; while a higher density of structures limits water flux into sediment, and therefore increases sediment stability. The size and shape of the structures still influence the exact flow (Friedrichs et al. 2009). Functional classes of ecosystem engineers have been proposed to take these similarities into account (Berke 2010).

The different mechanisms of ecosystem engineering also have consequences on the persistence of the effect after the death of the engineer. For example, following the same case of organisms building biogenic structures, leaves of *Zostera marina* will stop having an effect on water fluxes as soon as the leaves die, are carried away, or eaten. On the other hand, tubes built by polychaetes can survive the worms themselves (Zühlke 2001). On a larger spatial and temporal scale, oyster reefs can become accreted, and deeply modify the assemblages of organisms in the surrounding environment (Lejart and Hily 2011), even after the death of the oysters (Summerhayes et al. 2009). The persistence of the engineering effect after the engineer’s death is dependent upon the persistence of its remains for autogenic engineers; for allogenic engineers, which modify other materials, the effects are more likely to last after the death of the engineer (Hastings et al. 2007). However, because the maintenance of the “engineered” state might require constant action from the engineer, the persistence of the effect might be short-lived (Reise 2002).

In the specific case of mudflats and coastal sediment, Bouma et al. (2009) proposed that autogenic and allogenic ecosystem engineers have inverse effects on epibenthic (which live on the mud or near the mud surface) and endobenthic communities (which live in the mud; e.g. *A. marina*). Autogenic, principally epibenthic ecosystem engineers, such as *Spartina anglica*, create a complex epibenthic habitat, increasing the density of organisms in this habitat at the expense of endobenthic organisms. On the other hand, the numerous allogenic engineers that rework the sediment (see e.g. Meadows et al. 2012), creating burrows and oxygenating

otherwise anoxic habitats, facilitate other infauna, and therefore increase the diversity of endobenthic organisms.

The diversity and composition of infaunal assemblages are largely controlled by the sediment stability, itself being strongly dependent of biofilm-forming microorganisms (see Chap. 8).

2.3 Case Study: Biofilms and Sediment Stabilisation

A careful review of the literature would unearth a number of relevant studies that expand knowledge on the effects of biofilms on sediment behaviour, but the general realisation that biological mediation must be considered when working with, or predicting or modelling natural sediment behaviour (Black et al. 2002; Murray et al. 2002), has been slow to take hold. This might seem surprising, since the early studies of biogenic stabilisation were often quite clear and convincing (Manzenrieder 1983; Paterson and Black 1999). Perhaps the real problem was how to communicate this research in a way that was meaningful to different interest groups. For example, a physical modeller might ask for the erosion threshold of an intertidal flat, in order to prepare a suitable model. The standard way of deriving this would be to measure grain size and then predict an erosion threshold from a known relationship developed in the laboratory (e.g. Shields criterion, Shields 1936, and see Chap. 8). This is almost always wrong; even ignoring the sedimentological context of the natural spatial variability of sediment distribution and particle mixing, the biology is missing. Using hydrodynamics and sediment geotechnics in an ecological context can create inroads to further development between the two disciplines.

An early study by Dade et al. (1990) was prescient. These workers incubated bacteria on sand, and measured their effect on the erosion threshold; in addition, they also extracted the polymer they considered to be the “active” agent of the biological stabilisation, from a similar culture of bacteria, and tested the effect of this polymer on sand behaviour. The results were informative. The bacteria stabilised the bed more effectively than the polymer on its own but both tests were more stable than the control sand (Fig. 10.3). From this, we might expect that it would be possible to incorporate in the model a “proxy” for biological stabilisation, perhaps by determining the concentration of extracellular polymeric substances (EPS); however, this has proven difficult.

Dade’s early results may also help explain why this is the case. The natural population of bacteria is more effective than the polymer on its own. There may be several reasons for this. The extracted polymer is no longer in the same molecular conformation as the EPS mixture formed under natural conditions. In addition, the bacteria may secrete some polymers randomly, but also some in a much more targeted manner, such as attached to surfaces, essentially creating networks of polymer strands and bridges, which are unlike the extracted material being added uniformly to a clean substratum. It is therefore unsurprising that the growth of a

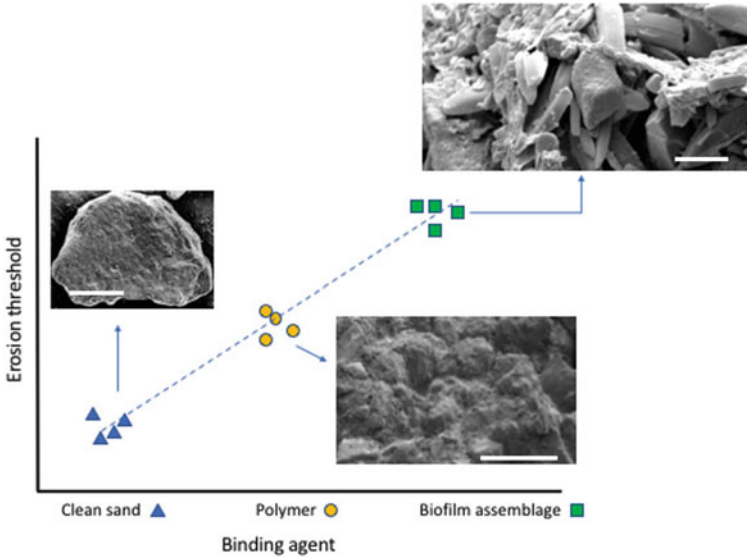


Fig. 10.3 Schematic representation of the effect of clean sand, extracted polymer, and biofilm development on sediment erosion threshold (after Dade et al. 1990). Scale bars: clean sand 50 μm ; others 100 μm .

biofilm imparts more structure and is more effective at binding material. Even if this were not a limitation, biogenic effects would still be subject to the natural variability of biological systems; moreover, the spatial patchiness and variability of biofilm formation is well-known, and also applies to other EPS producers such as diatoms (Jesus et al. 2005). Defew et al. (2003) showed that a multivariate and often site-specific approach would be required to predict the influence of biogenic effects of sediment stability, and while developments in spatial analysis, molecular tools and advances in remote sensing may all offer new opportunities, there is still a void in terms of communication and research using natural systems to address this shortcoming. This requires an interdisciplinary approach (Malarkey et al. 2015), to better integrate increasing knowledge of biogenic stabilisation with modelling platforms capable of incorporating biogenic effects.

2.4 Influence of Ecosystem Engineers on Biodiversity and Ecosystem Functioning

Ecosystem engineers influence both the abundance, and, because their effects are species-specific, the composition of surrounding assemblages. For example, species which stabilise sediment tend to facilitate the recruitment and growth of organisms that rely on sediment stability, while they exclude organisms having a contrary effect

(Woodin and Jackson 1979). Also, a single ecosystem engineer species can affect assemblages of organisms of very different sizes and habitats; for instance in mudflats, *Lanice conchilega* influences the recruitment and development of micro-organisms, meiofauna, and macrofauna (Passarelli et al. 2012b), as well as associated epibenthic and fish populations (Rabaut 2009).

A good example of an effect at multiple levels comes from the experiments of Volkenborn and colleagues, who excluded the lugworm *Arenicola marina* from 400 m² plots during 3 years. This exclusion led to the accumulation of fine particles and organic matter in the sediment, eventually modifying its chemical and physical properties, and also altering the growth of microphytobenthos, as measured by chlorophyll concentrations (Volkenborn et al. 2007). Exclusion also increased the abundance of ragworms *Hediste diversicolor*, which benefited from reduced competition, while *Scoloplos armiger* were negatively affected by the change of sediment chemistry (Volkenborn and Reise 2006). Exclusion of *A. marina* also benefitted other macrofaunal species such as clams and tube-building polychaetes, as well as some algal species who settled on the tubes (Volkenborn and Reise 2007; Volkenborn et al. 2009). These authors pointed out that such engineering effects were highly dependent on time, space, and on the recruitment success of *A. marina* (Volkenborn and Reise 2007).

For individual species, the effect of ecosystem engineers can be either positive or negative, so there is no reason to assume that the net effect of an engineer on biodiversity will always be positive at a patch scale (Jones et al. 1997). However, ecosystem engineers who increase the complexity of a habitat tend to have a positive effect on the diversity, while those who render the habitat more homogenous decrease it (Crooks 2002; Cruz Sueiro et al. 2011). This is because transforming simple habitats into complex ones creates additional niches (Bell 1985), and can also provide refuge from predators (Woodin 1978; Bouma et al. 2009).

Given that engineering effects are highly dependent on time and space, non-engineered habitats, engineered habitats and previously engineered habitat will coexist at a larger temporal and spatial scale. By increasing the patchiness of habitats, the engineer will generally increase diversity at a landscape scale (Jones et al. 1997; Volkenborn and Reise 2007). This is especially true since the effect of engineers on associated assemblages can change after their death and during the degradation of their structures (Summerhayes et al. 2009).

Ecosystem engineers usually facilitate their own recruitment, especially beyond a given threshold (Bouma et al. 2009). When settled, organisms then modify their environment, which attracts new species. Mudflats are highly dynamic systems, and as such they are stressful for many organisms. Ecosystem engineers can reduce the magnitude of variations of physical and chemical parameters, facilitating the settlement and growth of other species, therefore acting as foundation species (Altieri et al. 2007). The creation of this new habitat, however, can be made at the expense of another (Bertness 1984).

Indeed, the combination of thresholds and positive feedback mechanisms make possible the coexistence of several stable states (Wilson and Agnew 1992; van der Heide et al. 2007; Bouma et al. 2009). This can be illustrated by the seagrass *Zostera*

marina, which reduces nutrient concentration in the water column, and softens the current and wave action. Both mechanisms decrease turbidity, which facilitates the development of the seagrass, and its associated assemblages. If the population of *Z. marina* decreases, e.g. following a disease, the turbidity will remain high; this will hinder the development of the seagrass. The threshold for the survival of a population seems to be around 1000 shoots per square meter (van der Heide et al. 2007).

Any biotic or abiotic variable able to modify the abundance of an ecosystem engineer is therefore likely to have a large influence on the abundance, composition and diversity of the communities.

2.5 Evolutionary Perspective of Ecosystem Engineering

Since Charles Darwin first presented the theory of evolution to the world (Darwin 1859) evolutionary science has itself evolved considerably (Laland et al. 2014). The mechanisms of evolution are under increasing scrutiny as the science of molecular genetics increases in sophistication, allowing the interrogation of genes and genomes at a speed and resolution that was until recently unthinkable (Hall 2007). There are also many discussions in terms of evolutionary theory trying to explain how the pressures that lead to evolutionary change can be classified and modelled. Ecosystem engineering is a relevant example. It is understood that the activity of ecosystem engineers alters the environment, and one school of evolutionary thought, presented under the “Extended Evolutionary Synthesis” (EES) theory (Extended Evolutionary Synthesis 2016), suggests that the activity of the engineer in changing the environment should in itself be recognised as a distinct evolutionary pressure. EES proposes that engineering activity significantly alters the evolutionary trajectory of organisms exposed to the effect (Fig. 10.4). A classic example would be bacteria evolving in a soil that has been bioturbated by earthworms, but there are many other examples. This hypothesis is described under the theory of “niche construction” (Odling-Smee et al. 2003), an evolutionary partner to ecosystem engineering.

Even greater complexity can be imagined when aspects such as “cooperative ecosystem engineering” as proposed by Passarelli et al. (2014) are considered. There is no restriction on this activity that suggests cohorts of organisms may provide similar pressures or effects. In addition, species may also interfere with one another diluting selective pressures. As noted earlier, the first evidence of life on earth are laminated structures preserved in rock arising from the activity of bacterial biofilm assemblages. This early ecosystem engineering creates more stable sedimentary gradients, potentially driving evolutionary change (Paterson et al. 2017). Although this hypothesis is contested by many evolutionary biologists (Laland et al. 2014), it is clear that ecosystem engineering does have a significant impact on the local environment of both the engineers and of cohabiting species, and the theory of

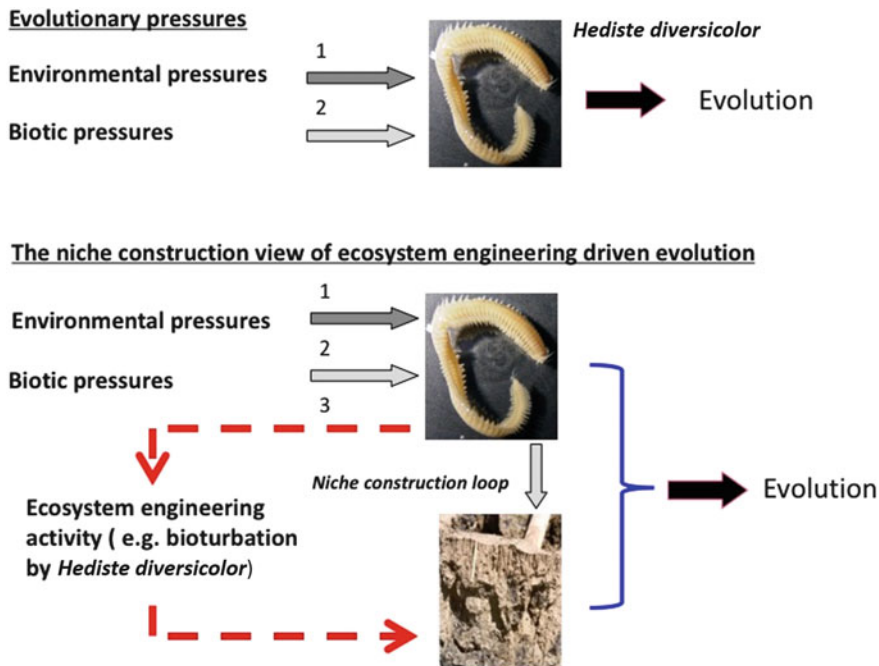


Fig. 10.4 Simplified schematic representation of the niche construction theory. 1: environmental pressures. 2: biotic pressures. 3: alteration of local environment by ecosystem engineering. Engineering activity (e.g. bioturbation by *Hediste diversicolor*) alters the local environment for other organisms, altering their evolutionary trajectory.

niche construction is worthy of consideration, emphasising the evolutionary importance of ecosystem engineering.

3 Mudflat Ecosystem Engineers in Their Biotic and Abiotic Environment

3.1 *Ecosystem Engineers and Interaction Webs: Example of Sediment Stabilisation by Biofilms*

Shortly after proposing the concept of ecosystem engineers, Lawton and Jones (1995) suggested that engineering effects have their place in larger interaction webs, which would combine both trophic and non-trophic interactions. Engineers are indeed themselves organisms which undergo variations of their biotic and abiotic environment, which can influence their abundance and densities, and thus their engineering effect. More recently, Hastings et al. (2007) proposed that integrating non-trophic, engineering interactions into food webs was especially important when

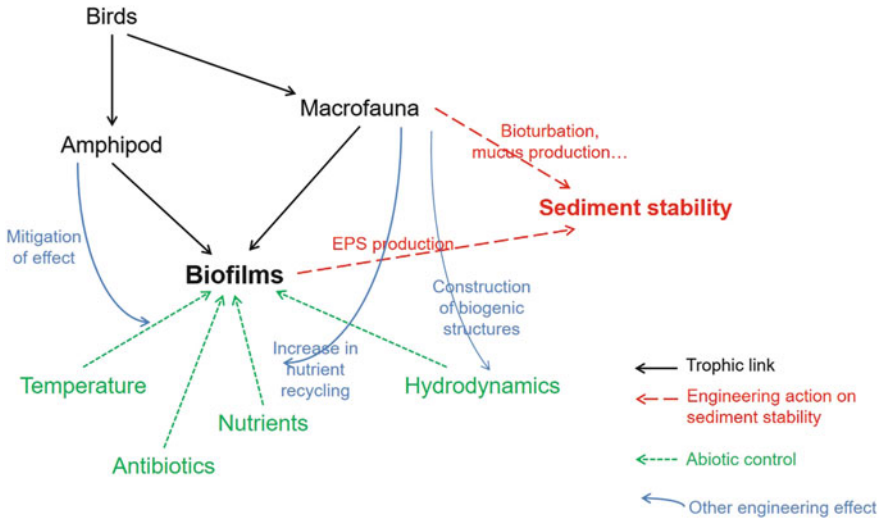


Fig. 10.5 Interaction networks around biofilms and sediment stability, detailing trophic (black arrows) and non-trophic (through action on abiotic factors) interactions in the examples discussed in Sect. 3.1.

the time and spatial scale at which these interactions occur is very different from the scale at which trophic interactions occur. Our previous example of biofilms and sediment stabilisation, illustrates the need to build interaction webs when trying to assess the magnitude or dynamics of an engineering effect (Fig. 10.5).

A first point is that biofilms are a trophic resource for consumers, such as the amphipod *Corophium volutator* (Daborn et al. 1993; Hagerthey et al. 2002) and the common mud snail *Hydrobia ulvae* (Andersen et al. 2002; Hagerthey et al. 2002). The selective-feeding *C. volutator* has a strong influence on biofilms, both reducing biomass and altering the composition of the microphytobenthic assemblage; on the other hand, the unselective grazer *H. ulvae* reduces microphytobenthic biomass but does not affect the composition of the assemblage (Hagerthey et al. 2002). These consumers are therefore likely to have contrasting effects on the biofilm's engineering capacity (Andersen et al. 2002). Also, Daborn et al. (1993) demonstrated that, when *C. volutator* is consumed by migratory birds, an "ecological cascade" takes place where birds, by feeding on the amphipods, decrease the consumption of biofilms and therefore increase sediment stabilisation. The development of biofilms is also controlled by various abiotic parameters, such as nutrients or light. A good example is the bioadvective gardening by the lugworm *A. marina*, i. e. the transport of nutrients from depth to surface, where they become available for microphytobenthos (Chennu et al. 2015).

To complicate the picture even more, diverse types of interactions can take place between the same two engineers. For example, *C. volutator* feeds on biofilms, but

also mitigates the effect of temperature on biofilm development (Hagerthey et al. 2002). The ragworm *Hediste diversicolor* feeds on biofilms as well, but this worm also reworks sediment and potentially increases the recycling of nutrients, therefore stimulating the growth of biofilm (Passarelli et al. 2012a). Therefore, considering the trophic links alone might lead to conclude that *H. diversicolor* will have a negative impact on sediment stabilisation by biofilms (Passarelli et al. 2014), while in fact the worms can stimulate biofilm growth and the engineering effect (Passarelli et al. 2012a). With that in mind, it seems necessary to understand the various trophic and non-trophic interactions on ecosystem engineers with their environment if we are to estimate the magnitude of engineering effects and their variability in space and time.

3.2 Effects of Abiotic Parameters on Ecosystem Engineers, and Consequences for Mudflats

Numerous environmental variables alter the development of ecosystem engineers, and through them their associated communities. This can be a seasonal effect in the case of *Lanice conchilega*, as these sand-mason worms can suffer massive mortalities in winter, causing a change in sediment properties (Alves et al. 2017). Bateman and Bishop (2017) used a meta-analysis to decipher the factors contributing to the variations of the engineering effects of bivalves on the assemblages of epifauna and infauna. They conclude that even if some engineers, such as oysters, generally had a large effect compared to others, the magnitude of the engineering effect was very variable, and also deeply affected by environmental context. Human actions can also modify habitat, and through them the development of engineers. For example, recreational clam-digging activities deeply alter the distribution of the lugworm *Arenicola marina* (Boldina and Beninger 2014), an ecosystem engineer known to have major effect on sediment properties and macrofaunal communities (Volkenborn and Reise 2006; Volkenborn et al. 2009). Global changes in temperature will also affect the biogeographic range of engineers (Wetthey et al. 2011) and therefore the functioning of ecosystem. Finally, massive pollution events can have in-depth consequence for the composition and functioning of coastal systems: for example, the *Deepwater Horizon* oil spill in US led to large loss of oysters *Crassostrea virginica*, which in turn led to the destruction of fish habitat, reduced nutrient recycling and increased sediment erosion (Powers et al. 2017).

Ecosystem engineers modify the abiotic parameters of the habitat in which they live, therefore potentially facilitating their own development (positive feedback; Bruno et al. 2003). These mechanisms will influence the population dynamics of the engineers, either keeping the population below a certain density in the case of negative feedbacks, or increasing densities above a certain threshold, which then facilitates the survival of the population. These feedbacks also mean that “switches” between two alternative states can happen, following a perturbation (Wilson and Agnew 1992). For example, diatom biofilm development on mudflats enhances the

accumulation of silt, which stabilises the sediment and further stimulates diatom development (Van De Koppel et al. 2001). If the biofilm is disturbed by an external perturbation, the sediment might be eroded, which will further reduce diatom development. Such switches have been demonstrated with *Zostera marina*, whose recovery after a disease was hindered by the increase of turbidity prompted by their own death (van der Heide et al. 2007).

The action of ecosystem engineers on their habitat can also facilitate the recruitment of better competitors, which will then tend to limit the development of these ecosystem engineers (negative feedback; Bruno et al. 2003). This can lead to stable equilibrium between ecosystem engineers and better competitors, which highlights the possible interplay between abiotic and biotic variables in explaining the magnitude of engineering effects.

3.3 *Interactions Between Ecosystem Engineers*

Ecosystem engineers are involved in numerous interactions with other organisms, such as trophic links. Engineering and trophic interactions are starting to be integrated in models (Kéfi et al. 2012; Sanders et al. 2014), showing that the net effect of one engineer species will depend on its direct engineering effects, its direct trophic influence, and any positive or negative feedback on the engineer itself (Sanders et al. 2014). Ecosystem engineers are also involved in other types of interactions such as parasitism and competition (Jones et al. 1997), such as the mutual exclusion of sediment stabilising and sediment destabilising species (Woodin and Jackson 1979). Also, the trophic interactions in which ecosystem engineers are engaged are themselves dependent on abiotic factors; for example, shade alters the predation of the clam *Macomona liliana* by eagle rays, and therefore their engineering effect on the meiofaunal community (Van Colen et al. 2015).

Ecosystem engineers can also interact among themselves, which can deeply modify their effects on communities. Such interactions can happen when ecosystem engineers act as foundation species, creating habitat for other organisms (Altieri et al. 2007), including other ecosystem engineers. Thomsen et al. (2010) proposed the concept of habitat cascade to describe these interactions where a basal habitat former, by its engineering effect, stimulates the development of an intermediate habitat user and former, which in turn engineers habitat for a focal group of organisms. For example, hard substrate for algal settlement is rare in soft-bottom tidal flats; yet, shellfish and tube-forming polychaetes, such as *Diopatra cuprea* (basal habitat formers), provide suitable substrate for the recruitment of seaweeds, such as *Gracilaria* spp. (intermediate habitat former), which will provide habitat to epibionts (Thomsen et al. 2010). Similarly, the modification of the habitat of the clam *Anadara trapezia* by *Caulerpa taxifolia* influences the burial depth of the clam, which increases the substrate available for epibionts, thereby enhancing their diversity (Gribben et al. 2009). Also, tube-building polychaetes can take advantage of the

absence of the bioturbator *A. marina* following an experimental exclusion; their tubes then provide substrate for algae, which in turn increases the settlement of byssus-drifting bivalves (Volkenborn et al. 2009).

Species facilitated by engineers can also associate with them, further modifying the environment (Alvarez et al. 2015). And in non-hierarchical interactions, the net effect of two species of ecosystem engineers might differ from the sum of individual effects. For example, Boyer and Fong (2005) manipulated, in a saltmarsh, the density of the snail *Cerithidea californica*, which tends to increase microalgal cover, and that of the crab *Pachygrapsus crassipes*, which slightly decreases it. When these two engineers were put together, surprisingly, the microalgal cover disappeared. More recently, Eklöf et al. (2011) investigated the counteracting effects of *Zostera noltii*, which stabilises sediment, and the lugworm *Arenicola marina*, which destabilises sediment by bioturbation. They cleared patches of *Z. noltii* and added lugworms to some of the cleared patch, expecting *A. marina* to reduce recolonization by the seagrass. They did not observe such an effect, until an unplanned disturbance (possibly strong hydrodynamics) increased the size of the cleared patches; then, they demonstrated that the presence of the worm decreased the threshold-size of the patch necessary to prevent the recolonization by the seagrass. They concluded that the interaction between counteracting engineers could influence the response of ecosystems to disturbance.

The effect of two ecosystem engineers can also be synergistic, meaning that their combined effect will exceed the sum of their individual effect. For example, we investigated the effect of *Lanice conchilega* and microphytobenthos on sediment stability (Passarelli et al. 2012b). At high tube density, the tube-building polychaete modifies sediment properties (e.g. grain size) by altering water flow at the sediment surface. Microphytobenthos produces extracellular polymeric substances (EPS) that bind and stick the sediment particles together. The resulting effect of both engineers together is a significant increase in sediment surface adhesion, a proxy for sediment stability (Passarelli et al. 2012b). We proposed the term of cooperative ecosystem engineering to describe this synergistic interaction (Passarelli et al. 2014).

Caliman et al. (2011) demonstrated similar synergistic effects of three bioturbators on nutrient fluxes at the sediment/water interface, mainly driven by complementarity between the species (nymphs of *Campsurus melanocephalus*, adults of *Heteromastus similis* and *Heleobia australis*). However, synergistic effects were only apparent when the volume of sediment available for bioturbation was above a certain threshold. This shows that interactions between ecosystem engineers can themselves be dependent on other factors, which makes the picture even more complex. Eklöf et al. (2015) demonstrated that interactions between ecosystem engineers (seagrass and lugworm), in concert with abiotic conditions, dictate the distribution of engineers and associated communities.

Understanding these interactions is of crucial importance if we are to understand how ecosystem engineers will influence their environment in the future, and what the consequences for human populations are.

4 Importance of Mudflats Ecosystem Engineers for Human Populations: Ecosystem Services

4.1 Definition and Examples of Ecosystem Services

The most commonly-accepted definition of ecosystem services (or ecological services) is that of the Millennium Ecosystem Assessment (MEA 2003), which states that it refers to the benefits that humans derive from ecosystems. The idea that notions such as biodiversity and ecosystem services could be assessed in environmental and economic terms emerged in the 1970s–1980s, and was further popularized by the MEA. The main postulate was clearly anthropocentric, as it stated that monetary valuation should help society to familiarise itself with abstract ecological concepts of biodiversity that are mostly regarded as meaningless or non-understandable by the general public. Since then, policy makers have increasingly recognised the role of environmental valuation for environmental management and conservation purposes; and the number of economic studies seeking to value biodiversity has increased simultaneously. Research effort has increased in all fields, including the marine environment; numerous marine habitats, species, or ecosystems services have been studied, and it has been shown that a decline in biodiversity could result in a change in the provision of goods and services by marine ecosystems, including reduced resilience and resistance to environmental change, declining marine environmental health, reduced fisheries potential, and loss of recreational opportunities (Beaumont et al. 2008).

At around the same time period, mudflats were largely regarded as “unvegetated” habitats, and therefore considered non-productive, compared with vegetated mudflats, such as salt marshes or seagrass beds. It is likely that this restrictive view contributed to diverting the attention of numerous scientists and economists toward apparently more diverse and/or endangered habitats/species, until the profile of its “secret garden” (i.e. microphytobenthos) was raised (MacIntyre et al. 1996; Miller et al. 1996). In addition, the relationship between diversity of microphytobenthos and ecosystem function was recognised only relatively recently (Forster et al. 2006).

In the terrestrial ecosystem, vegetative cover is widely considered to play a key role in regulating and supporting services related to soil retention and prevention of landslides (Millenium Ecosystem Assessment 2003). *De facto*, it is difficult to believe that bare mud contributes to erosion control and therefore coastal protection, even though microphytobenthos is now considered a major biogeomorphological player in mudflats (see Chaps. 2, 4 and 8). Its ability to enhance sediment stability and influence erosion threshold of intertidal sediments, as well as sediment transport, has been studied extensively (Paterson 1989; Black et al. 2002; Tolhurst et al. 2008; Gerbersdorf et al. 2009; Lubarsky et al. 2010), and is well recognised (Stal 2010). Coastal protection is an important ecosystem service, as the cost of coastal erosion is estimated to reach hundreds of millions of dollars each year in the USA alone (Heinz Centre for Science Economics and the Environment 2000).

Table 10.1 Ecosystem services in the mudflat, and links to ecosystem engineers

Type of ES	Ecosystem service (ES)	Example from the mudflat	Example of mudflat ecosystem engineers directly or indirectly involved in ES
Provisioning	Food production	Fishing, seafood gathering by hand, aquaculture (oysters, mussels, shellfish production) See also Chap. 13	Microphytobenthos (Passarelli et al. 2014) directly as a food source or indirectly at the base of the food web
	Genetic resources: Sources of biological material and products	Genetic variability between individuals within a population	All ecosystem engineers
	Biochemicals	Bioactive compounds	Benthic microalgae and bacteria and their EPS (Lubarsky et al. 2010)
Regulating	Climate regulation	Greenhouse gas regulation	All ecosystem engineers, for instance diatoms
	Waste treatments/ water purification; recovery or removal of nutrients	Nitrogen fixation and removal, P, Fe, Sulphate and methane cycle. See also Chap. 4	Bacterial assemblages of the sediment
Cultural	Recreational activities	Eco-tourism, fishing (see Chap. 12), seafood gathering, seabird watching	Emblematic ecosystem engineers. Ex: honeycomb worm
	Cultural	Educational, scientific value	Emblematic ecosystem engineers
Supporting	Erosion control and sediment retention; coastal protection	Biostabilisation of sediments by microbes	Benthic microalgae and bacteria and their EPS (Lubarsky et al. 2010), engineers forming biogenic structures
	Primary production		Benthic microalgae, seaweeds
	Nutrient cycling	See Chap. 4	Examples include sulphate-reducing bacteria, nitrifying/denitrifying bacteria. . .

Based on the framework given by the MEA (Millenium Ecosystem Assessment 2003), we identified the following ecosystem services provided by mudflats (Table 10.1; Costanza et al. 1997; Markov and Nedkov 2016).

4.1.1 Food Production

Food production includes the vast range of food products derived from plants, animals, and microbes, as well as materials derived from mudflats. The trophic

input of mudflat benthic invertebrates (meiofauna, macrofauna) is largely based on microphytobenthic production. The diet of mudflat fishes (including important commercial species) depends on their life cycle. In general, larvae and/or juveniles feed on zooplankton or harpacticoid copepods (Kanou et al. 2004), later switching to other prey items (e.g. gammaridean amphipods, mysids, polychaetes, detritus, bivalves and fishes). In some cases, mudflat fishes' food webs may be supported predominantly via carbon from adjacent habitats (e.g. macroalgae, seagrasses) and not *in situ* meiofauna or MPB (Project 1997; Melville and Connolly 2005). For more detail on food production, see Chaps. 13 and 14.

4.1.2 Genetic Resources

The genetic variability between individuals within a population of a given species, corresponds to the diversity of genetic resources for that species. Alternatively, the genetic variability within a given population in a biological community forms the genetic resources for an ecosystem. Mudflats are tidally-influenced ecosystems, that are naturally characterised by strong physical and geochemical gradients, under varied geomorphological settings, which give rise to a multitude of habitats and niches. Environment fluctuations can indeed have a direct influence on genetic interactions among traits, as well as the genetic variance in traits themselves (Hedrick et al. 1976; Sgrò and Hoffmann 2004). For instance, the diatoms as a group are characterized by a large variety of sizes and shapes among species, which allows them a large spectrum of interactions with the environment and of niche exploitations. Environmental fluctuations in mudflats are thus a potential source of genome variability; however, few studies have dealt with this issue.

4.1.3 Biochemicals, Natural Medicines, and Pharmaceuticals

Many medicines, bioactive molecules for human health and plant health, biocides, food additives such as alginates, and biological materials are derived from marine ecosystems. Marine polysaccharides have been exploited for many years, and are mainly used as texturing agents in the agri-food and cosmetics industries (principally hydrocolloids, which increase viscosity and give a gel-like texture; Agasse et al. 2015). For example, those extracted from macroalgae represent 40% of the global market of hydrocolloids, which is valued at \$4.4 billion. Europe represents 30% of the market (Kraan 2012). The main polysaccharides are alginates, agars and carrageenan. More recently, microalgae, bacteria and cyanobacteria have been considered an interesting source of polysaccharides. Mudflat benthic bacteria and diatoms are potentially an important source of bioactive molecules for the pharmaceutical industry, including anti-cancer molecules, antivirals, or functional foods such as

the polyunsaturated fatty acids of microalgae (eicosapentaenoic acid: EPA, docosahexaenoic acid: DHA), carotenoids, astaxanthin, beta-carotene, and lutein.

4.1.4 Climate Regulation

Estimates of the annual benthic net production rate obtained through *in situ* measurements of carbon dioxide fluxes at the benthic community level, have been proposed for diverse tidal sedimentary systems including mudflats (Migné et al. 2004; Spilmont et al. 2005; Hubas and Davoult 2006; Spilmont et al. 2006; Davoult et al. 2009). Intertidal muddy sediments are characterized by large fluctuations in environmental parameters in response to the superimposition of diurnal and tidal cycles, which induces a variability of both production and respiration processes over a number of time scales (day, tide, season, year). These systems are generally considered heterotrophic (i.e. net CO₂ degassing; Borges 2005; Migné et al. 2009). Ecosystem engineers, and especially microphytobenthos, play a key role in regulating CO₂ fluxes in these ecosystems. Generally speaking, carbon is fixed by microphytobenthos and transferred very quickly to heterotrophic bacteria and higher trophic levels (Middelburg et al. 2000), but there is currently a large gap in knowledge about the relationships between microbial diversity and C fluxes.

4.1.5 Eutrophication Control

Microphytobenthic biofilms drive and modulate fluxes of carbon (C) and nitrogen (N) across the sediment-water interface, thus playing a pivotal role in the coastal filter function, affecting coastal eutrophication and water quality (Hochard et al. 2010).

4.1.6 Cultural Services: Recreation, Aesthetics, Educational, etc.

As pointed out by Rees et al. (2010), the mudflat recreational industry (e.g. fishing, see Chap. 13 and seabird watching, see Chap. 12) depends directly or indirectly on the presence of natural marine resources. In their study, the marine leisure and recreation industry was valued using both monetary and non-monetary methods (see also Chap. 13). In addition, they showed that the leisure and recreation industry are dependent on biodiversity.

As can be seen from Table 10.1 and from the numerous examples developed here, the links between ecosystem engineers and services are numerous (Fig. 10.6); this is to be expected from the crucial roles of ecosystem engineers in creating and maintaining habitat in stressful systems such as mudflats. Due to the particular population dynamics of ecosystem engineers (see Sect. 3.2), driven by numerous interactions and feedbacks, and to the numerous anthropogenic influences on coasts and mudflats, the management of populations of ecosystem engineers is both a

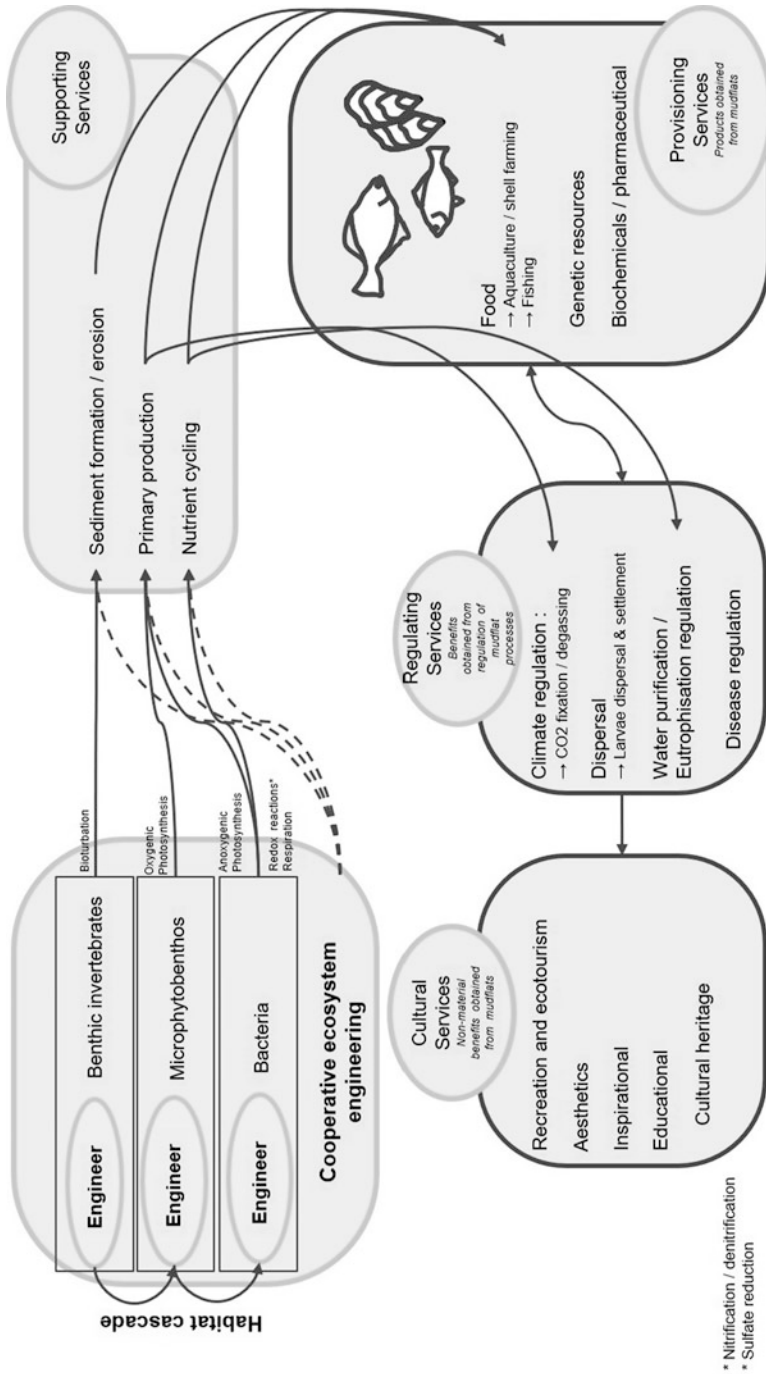


Fig. 10.6 Ecosystem engineers and ecosystem services on the mudflat. See text for details.

challenge and a necessity, if we are to continue to enjoy the services provided by these systems.

4.2 Estimation of Service Value and Implications for Mudflat Management

Decision making, in terms of environmental conservation, becomes political, an often-uncomfortable truth for conservation scientists and ecologists (Borja et al. 2017). The best available scientific knowledge should feed into political decision-making, but the economy is also a powerful force in shaping policy. As described above, one mechanism for realising/emphasising the importance of coastal habitats is to formalise the valuation of the ecosystem services provided. This supports economic valuations becoming more holistic, incorporating both direct and indirect benefits. A detailed review of the methodology is beyond the scope of this chapter (see Hanley and Barbier 2009), but it is important for the next generation of ecological scientists to understand the decision-making processes to help make the best-case possible for management decisions.

Direct economic benefits are relatively straightforward to assess, such as local fisheries and the benefits in terms of direct financial return (see Chap. 13). Others are more complex, and include aspects such as the aesthetic and health benefits of regular outdoor excursions, the denaturing of xenobiotic compounds or the turnover of nutrients. These services are hard to value because there is often no “market” that supports the “trade”; the economic valuation then relies on much more abstract methods such as determining the “willingness to pay” of the relevant human population for particular outcome. A recent example by Pakalniete et al. (2017) considered the willingness of Latvian citizens to “pay” for improving the ecological status of habitats around the Baltic coast. Using highly-structured questionnaires, and a discrete choice (DC) methodology, based on a proposed increase in taxation as the suggested funding mechanism, the sample group was supportive of coastal habitat protection. A similar approach can be applied to less glamorous systems such as mudflats. However, this type of valuation may also have limitations. The level of knowledge of the individual making the assessment may affect the outcome, and charismatic habitats, such as rainforests, may attract higher valuation than less-charismatic systems such as mudflats, despite delivering similar services. Therefore, while methods such as DC are not foolproof, and are widely discussed, they are nevertheless an important step toward promoting the value that society places on ecosystem services. The more information that can be provided about systems such as mudflats, the more likely that evidence in support of good management approaches can be sustained into the future.

5 Conclusion

Mudflats and other coastal systems are largely impacted by human populations, which build on and modify the coastline, release nutrients and pollutants into coastal waters, introduce new species that can become invasive, and collect mudflat organisms for consumption. Because of the crucial roles of ecosystem engineers in controlling diversity and ecosystem functions in mudflats, understanding how mudflat engineers influence and interact with their environment is necessary in order to guide good management practices that will ensure the provision of ecosystem services by mudflats in the future.

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