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MINI-REVIEW

Integrating microbial ecology in bioprocess understanding: the case of gas biofiltration

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Abstract Biofilters are packed-bed bioreactors where contaminants, once transferred from the gas phase to the biofilm, are oxidized by diverse and complex communities of attached microorganisms. Over the last decade, more and more studies aimed at opening the back box of biofiltration by unraveling the biodiversity-ecosystem function relationship. In this review, we report the insights provided by the microbial ecology approach in biofilters and we emphasize the parallels existing with other engineered ecosystems used for wastewater treatment, as they all constitute relevant model ecosystems to explore ecological issues. We considered three characteristic ecological indicators: the density, the diversity, and the structure of the microbial community. Special attention was paid to the temporal and spatial dynamics of each indicator, insofar as it can disclose the potential relationship, or absence of relation, with any operating or functional parameter. We also focused on the impact of disturbance regime on the microbial community structure, in terms of resistance, resilience, and memory. This literature review led to mitigated conclusions in terms of biodiversity–ecosystem function relationship. Depending on the environmental system itself and the way it is investigated, the spatial and temporal dynamics of the microbial community can be either correlated (e.g., spatial stratification) or uncoupled (e.g., temporal instability) to the ecosystem function. This lack of generality shows the limits of current 16S approach in complex ecosystems, where a functional approach may be more suitable.

Keywords Microbial ecology · Biofiltration · Diversity · Community structure · Resilience · Stability

Introduction

Engineered ecosystems are characterized by two components: a biotic component (communities) and a process component (matter and energy flows). Even though they are the key actors of the biological processes, little is known about the microbial communities involved in bioprocesses: how are they influenced by the environmental conditions, and how do they drive the ecosystem function? Unraveling the biotic/abiotic interactions is one of the most challenging issues for ecologists (Briones and Raskin 2003). In addition to a fundamental purpose, this better understanding can provide control, diagnostic and prevision tools for process monitoring.

The biotic component has been more and more investigated during the last decades, thanks to the rapid development of molecular tools (Talbot et al. 2008). Even though not exempted from potential bias (Cabrol et al. 2010; Von Wintzingerode et al. 1997), they provide a more representative image of the community, without restricting to cultivable cells. The latter only represent 4% to 30% of the total biomass in gas biofilters (Khammar et al. 2005; Tresse et al. 2003), and less than 15% in activated sludge (Amann et al. 1995).

Biofilters are packed-bed reactors used for biological purification of waste gases containing inorganic contaminants (e.g., ammonia, hydrogen sulphide) and volatile organic

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compounds (VOCs) such as ketones, volatile fatty acids, sulphur, and aromatic compounds. Biofiltration combines physicochemical mass transfer and microbial oxidation within the biofilm which develops at the outer surface of the packing material (Devinny et al. 1999). As model ecosystems where inputs and outputs are controlled and monitored, biofilters constitute relevant tools to explore ecological concerns such as the biodiversity-ecosystem function (BEF) relationship. However, the investigation of microbial communities in biofilters is still relatively scarce, compared to other engineered ecosystems such as bioreactors for wastewater treatment. Hence, rather than limiting the literature review to the field of gas biofiltration, we will emphasize the parallels between biofiltration and bioprocesses for wastewater treatment, both involving the same kind of biodegradation mechanisms and addressing similar ecological questions.

In this review, we will consider the density, the diversity, and the structure of the microbial community as the three main characteristic community indicators. We will pay special attention to the temporal and spatial dynamics of each indicator. Indeed, the investigation of potential relationships between the microbial dynamics and operating and/or functional parameters can reveal the coupling or uncoupling between macroscopic and community components (Fig. 1). Besides the intrinsic community dynamics under stationary conditions, we will report some works that stress the importance to assess how the microbial community structure is impacted by transient environmental disturbances, and how it influences, in return, the macroscopic function of the ecosystem under perturbed conditions. Considering the limited number of studies in the field of biofiltration, and the contrasted conclusions depending on experimental conditions, the difficulty of giving an overview of the topic should be noted. However, keeping in mind the specificity of each system, we report here the observation of and the rationale for the major trends of the BEF relationship in engineered ecosystems. It should be added that we will focus on the microbial community structure globally (distribution of species abundance and its evolution), rather than listing an inventory of species identification in specific (biofiltration) environments.

It was interesting to have an overview of the insights provided by microbial ecology exploration in gas biofilters, about 10 years after the first publication on this subject. However, when reviewing the bibliographic data, the conclusions appeared to be extremely variable depending upon the experimental conditions applied, as well as the methodological approach employed to study the diversity. The same kind of discrepancies (high/low diversity, dynamic/stable communities…) was observed in other ecosystems. But this variability does not mean that nothing can be learnt from these studies. On the contrary, in each individual study, the microbial ecology approach reveals important and interesting information which must be cautiously interpreted according to the specific context in which it was obtained, before comparing it to other studies. We think that, unless great information loss, such a review should not ignore the specificities of each system and look for generality at all costs, but rather emphasize the different forms of the tenuous and intricate biodiversity ecosystem function relationship in different ecosystems.

It was part of the aim of this review to show these discrepancies. Furthermore, the absence of clear conclusion for the BEF relationship was particularly observed when the total bacterial community was targeted, through unspecific 16S rDNA targeting. This observation led to another

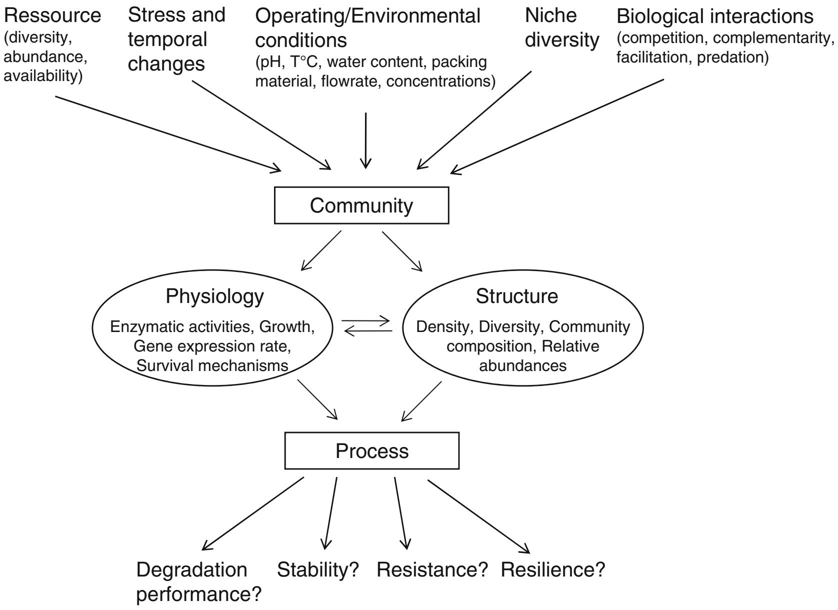

Fig. 1 Links between environmental drivers, community response (at physiological and structural levels) and ecosystem process, modified from Lynch et al. 2004 and Schimel et al. 2007

important point we wanted to highlight, i.e., the need for a more specific approach, permitting to overstep the shortcomings of current methods, by targeting active and functional members of the community, effectively involved in contaminant degradation.

Bacterial density

The first attempt to characterize a microbial community relies on the estimation of its density. As assessed by direct microscopic counts after DAPI staining, cell densities in gas biofilters typically range from 10^9 to 10^{10} cells per gram of dry material, for organic carriers such as wood chips, roots, or peat (Friedrich et al. 2003; Khammar et al. 2005; Von Keitz et al. 1999).

From a temporal point of view, cell density is usually stable over months in wastewater and waste gas bioreactors (Carvalho et al. 2006; Song and Kinney 2000; Van der Gast et al. 2008). Most of the time, despite some fluctuations, density cannot be consistently linked with any environmental or functional parameter (Khammar et al. 2005; Gentile et al. 2007; Widenfalk et al. 2008).

From a spatial point of view, if a vertical stratification of cell densities is reported in the bioreactor, it mostly follows the concentration gradient (Carvalho et al. 2006; Kim and Jaffé 2007; Kim and Sorial 2007), but it can also be reversed (Khammar et al. 2005). In the case of easily degradable compounds, the high contaminant concentration favors the growth of copiotrophic organisms (Borin et al. 2006; Hekmat et al. 2004) resulting in higher cell density in the inlet section (Pineda et al. 2004; Sundh et al. 2003), while the progressive substrate and/or nutrient limitation leads to a decrease of cell density along the biofilter height (Acuña et al. 1999; Kim and Sorial 2007). On the contrary, for recalcitrant compounds, the lower biomass density at the inlet may be attributed to more drastic conditions in terms of moisture content and contaminant toxicity (García-Peña et al. 2005; Khammar et al. 2005; Song and Kinney 2005). On a long term, despite an initial stratification, the density of bacterial colonization tends to homogenize along the biofilter height (Grove et al. 2004; Juteau et al. 1999).

Eventually, as it is hardly correlated to functional parameters, in terms of both temporal and spatial variability, the total bacterial density is not a sufficient indicator to reveal the potential links between microbial and functional components.

Bacterial diversity

Diversity estimators (richness, evenness, or Shannon indices) are computed from multivariate data provided by fingerprinting or clone library sequencing.

Spatial and temporal variability

From a temporal point of view, bacterial diversity is usually stable over time in wastewater and waste gas bioreactors, under constant (Ayarza et al. 2010; Falk et al. 2009; Van der Gast et al. 2008) or disturbed (Nadarajah et al. 2007; Smith et al. 2003) operating conditions. From a spatial point of view, several works highlighted the higher diversity of bacterial communities within the inlet section of the reactors (Calvo-Bado et al. 2003; Roy et al. 2009; Sakano et al. 2002). The development of highly diverse communities seems to be enhanced by high resource availability (Borin et al. 2006), especially for easily biodegradable substrates (Fernandez et al. 2000; Lozada et al. 2006) at non-toxic concentrations (Li et al. 2007; Sei et al. 2004), while recalcitrant and/or toxic compounds induce more specific (less diverse) populations (Bayle et al. 2009; Eichner et al. 1999; Van der Gast et al. 2008).

High diversity in biofilter communities

Insofar as we consider gas biofilters packed with organic material and treating relatively low concentrations of odorous compounds (as it is mostly the case at full scale), the biofiltration communities are usually characterized by high diversity levels (e.g., Friedrich et al. 2003). Apart from the primary degraders, this high diversity may result from the proliferation of microorganisms growing on by-products, as well as saprophytes consuming products from the cell lysis, the extracellular polymeric substances (EPS) matrix, or the packing material (Borin et al. 2006; Stoffels et al. 1998). The active primary degraders can represent as little as 4% of the community (Møller et al. 1996), while saprophytes are dominant (Hekmat et al. 2004; Juteau et al. 1999; Song and Kinney 2000). Moreover, the high diversity can be interpreted as the expression of species coexistence. Coexistence may arise (a) through niche differentiation, especially in biofilm structures characterized by a variety of microhabitats (Fernandez et al. 1999; Massol-Deyá et al. 1997), and (b) from functional complementarity, through resource partitioning or positive interactions among different species (Loreau et al. 2001; Tilman 2000).

Relation between diversity and function

It is now well-established that the bacterial community diversity is influenced by environmental conditions (Fig. 1), principally the contaminant concentration (Briones et al. 2007; Pholchan et al. 2010). The reverse (i.e., to what extent the diversity drives the macroscopic function in terms of biodegradation performance or stability) is still a critical question for ecologists (Fig. 1).

In the context of gas biofiltration, the effect of diversity on removal efficiency has not been explored in a systematic way. High purification performances have been reported in biofilters exhibiting either high (Ding et al. 2008) or low (Steele et al. 2005) microbial diversity. There are still challenges in designing experiments to conclusively discern the contribution of diversity to function, being careful of the meaning given to the overused and confusing word "diversity" (e.g., precising where in the community the diversity happens).

This discrepancy reflects the highly controversial debate on diversity function which arose in other ecosystems. Indeed, since the key works of Naeem (Naeem et al. 1994) and Tilman (Tilman and Downing 1994) on plant communities, the positive effect of diversity on ecosystem function and stability has been evidenced in various environments, at different scales, for widespread or specialized functions: microbial nitrification (Rowan et al. 2003; Wittebolle et al. 2009c), microbial respiration (Bell et al. 2005), mercury reduction (Von Canstein et al. 2002), carbon assimilation (Ptacnik et al. 2008), and decomposition and mineralization of organic matter in soil (Girvan et al. 2005; Griffiths et al. 2000). On the basis of theoretical ecology and modeling, the stabilizing effect of diversity may rely on statistical averaging (known as "portfolio effect"), while the contribution of diversity to improve productivity has been mainly attributed to complementarity between differentiated niches (Lehman and Tilman 2001).

Other community factors driving the ecosystem function

However, high efficiency and stability have been reported independently of the diversity level in wastewater reactors (Cook et al. 2006; Fernandez et al. 2000; Mota et al. 2005), aquatic mesocosms (Engelhardt and Kadlec 2001), and soil (Wertz et al. 2006). Beyond the potential artifacts of the experimental design (sampling effect, hidden treatment) (Huston 1997; Wardle et al. 2000), various authors showed that, rather than by the diversity itself, the ecosystem function was influenced by components of the diversity (Giller et al. 2004; Schläpfer and Schmid 1999). Among these components are the evenness of the species distribution (Hillebrand et al. 2008; Wittebolle et al. 2009b), the species composition with the presence of particular traits (Cook et al. 2006), the positive species interactions, such as synergism, facilitation, and cometabolism (Hooper et al. 2005; Møller et al. 1998; Shim et al. 2006), and the functional redundancy (Loreau et al. 2001). In the latter case, among a large reservoir of organisms conducting the same function, the loss of any species will have little effect on process since other species will fill the gap (this is obviously not valid for specialistic function) (Lynch et al. 2004). Moreover, under environmental changes, the redundant species are no more redundant; their wide range of stress response enhances the chance for a minor but resistant species to emerge, thus increasing the system stability according to the insurance hypothesis (Elmqvist et al. 2003; Franklin and Mills 2006; Loreau et al. 2001).

The divergence of empirical evidence for diversity–function relationship is no longer surprising if we consider that contrasting predictions can play a role in this relation. First, processes carried out by a limited range of microorganisms (e.g., nitrification, methane oxidation), are more sensitive to a loss of diversity than processes sustained by a wide range of microorganisms (respiration, denitrification, and organic matter decomposition) for which there is more functional redundancy (Griffiths et al. 2000). Secondly, according to the driving force of the ecosystem process—selection or complementarity—the productivity will be favored by, respectively, dominance of a particular trait or evenness distribution of a diverse community (Hillebrand et al. 2008). To finish, in a stable environment, the highest process rate is sustained by a particular optimal trait, from which any deviance (by increasing the diversity) will be functionally unfavorable. On the contrary, when the process undergoes environmental fluctuations, its productivity and stability are enhanced by higher trait variance, which provides faster adaptation capacity to new constraints (Hillebrand et al. 2008).

To conclude, even if dominant species are sufficient in mono-contaminant ecosystems, a consensus seems to accept the existence of a positive diversity effect in complex ecosystems—despite unclear mechanisms implying various diversity components. This effect may be stronger in variable than in stable environments (Hillebrand et al. 2008; Loreau et al. 2001) and when the biodegradation involves metabolic pathways scattered across different species (Griffiths et al. 2000).

Microbial community structure

The community structure is an image, at a given time and place, of the assemblage and organization of the community. It represents how the community members are distributed among species of different relative abundance, exhibiting different functional properties and contributions, and able to interact. Investigating the spatial and temporal dynamics of both ecosystem components (microscopic and macroscopic) provides clues to disentangle the potential relationship between ecosystem function and community structure.

Spatial variability

As attached biomass systems, biofilters exhibit physico-chemical gradients through the bed height (decrease of pollutant and increase of by-product concentrations), leading to heterogeneous environmental microhabitats. Most biofiltration studies highlighted a longitudinal distribution of biodegradation activities characterized by higher removal efficiency near the gas inlet (Cabrol et al. 2009). Are these concentration and activity profiles correlated to the microbial distribution?

Stratification

The microbial community composition is generally heterogeneous along the bed height of attached biomass bioreactors, as observed in waste gas (Hayes et al. 2010; Khammar et al. 2005; Li and Moe 2004; Maestre et al. 2010) and wastewater (Roy et al. 2009; Sakano et al. 2002) treatment. The variability of the community structures along the bed height is usually correlated with macroscopic parameters, at two possible levels.

First, the structural stratification can be seen as the result of the physicochemical stratification through the differential selective pressure imposed by distinct concentration levels. Secondly, the structural stratification can in return influence the functions which are realized at the different levels. A first example of this correlation between microbial distribution and functional stratification is the spatial partition of mixed biofilm communities of heterotrophic and nitrifying bacteria in gas biofilter. The restriction of ammonia-oxidizing bacteria to the outlet section of the filter was explained by both outcompetition of heterotrophic bacteria for oxygen consumption and inhibition by HNO_2 (Juhler et al. 2009). Another example of structure/function correlation has been revealed in a plug-flow type anaerobic reactor consisting of eight sequential compartments, where different functions (volatile fatty acids and methane production) were performed by bacterial communities with different structures (Roy et al. 2009).

Not only the concentration, but also the composition of the gas to be treated plays a role in shaping the community structure along the reactor. In biofilters treating a mixture of gaseous compounds, the readily degradable compounds are removed near the gas inlet, while the more recalcitrant ones are degraded in lower sections. This functional stratification is correlated to different community structures along the biofilter depth, suggesting that different populations are involved in different compound removal (Cabrol 2010).

Homogenization

Nevertheless, the spatial change of the community structure is not always correlated with the distribution of the degradation activity (Friedrich et al. 2003). Despite the functional stratification, the microbial community composition sometimes exhibits a surprising longitudinal homogeneity in gas biofilters (Hekmat et al. 2004; Sercu et al. 2006; Tresse et al. 2002) and wastewater bioreactors (Carvalho et al. 2006; Massol-Deyá et al. 1997; McGuinness et al. 2006).

The absence of correlation between the physicochemical and microbial spatial distributions might be linked to experimental biases linked to the lack of sensitivity of the community profiling method or the persistence of dead cell DNA (Lynch et al. 2004). Besides, the longitudinal microbial homogeneity can be explained by the growth of ubiquist and generalist populations (Curtis and Sloan 2004) which are not influenced by the gradient environmental conditions and/or not involved in primary substrate degradation. It can be also due to the environmental standardization along the bed height, arising from (a) the supply of carbon and energy source by the packing material (Friedrich et al. 2003), or (b) the percolation of water and nutrients through the packing material in biofilters, a fortiori in biotrickling filters (Tresse et al. 2002) and wastewater bioreactors.

Temporal variability

Acclimatization phase

The biofilter start-up is generally the most structurally dynamic period (Sercu et al. 2005a; Stoffels et al. 1998, as also reported for wastewater treatment bioreactors (Ayala-del-Río et al. 2004; Miura et al. 2007; Wittebolle et al. 2009a). When the system has been inoculated—as frequently done—by sludge from full-scale WWTP, the structure of the microbial community which develops after the acclimatization is dramatically divergent from the inoculum one (Steele et al. 2005), even if the inoculum had been previously adapted to the contaminants (Falk et al. 2009). This divergence is mostly attributed to drastic changes between full-scale and pilot-scale environment (Eichner et al. 1999; Kaewpipat and Grady 2002), mainly in terms of growth conditions (attached biofilm vs planktonic biomass) and substrate availability (food to microorganism ratio) (Miura et al. 2007; Tresse et al. 2002). In the case of organic packing material (i.e., already colonized by an endogenous microflora), both the inoculation and the operating conditions are sufficient to induce substantial modifications of the endogenous community structure (Ding et al. 2008), even despite the absence of contaminants (Pineda et al. 2004; Sei et al. 2004).

The acclimatization period is generally characterized by a significant decrease of the tremendous inoculum diversity in biological filters for waste gas treatment (Ding et al. 2008; Maestre et al. 2010; Stoffels et al. 1998) and wastewater treatment reactors (Sakano et al. 2002). The diversity loss can be interpreted as community specialization, through various mechanisms: selection of the fittest species (Eichner et al. 1999; Sakano and Kerkhof 1998); competitive exclusion (Steele et al. 2005); toxic effect of the contaminants; and reduction of resource variety (Konopka et al. 2007). More globally, the enrichment and dominance of a specific population, favored by specific operating conditions, is due to its competitive advantages in terms of growth and substrate affinity, as highlighted by kinetic studies (Baptista et al. 2008; Massol-Deyá et al. 1997).

Several works revealed the emergence of species which were not detected in the inoculum (Sakano et al. 2002). They proceed from (a) the inoculum wherein their abundance was below the detection limit of the analytical method, (b) the endogenous diversity reservoir constituted by the packing material itself, and (c) the polluted gaseous effluent or aerosols through immigration mechanisms (Ho et al. 2008).

Temporal stability at steady state

In biofilters run under constant operating conditions, the structure of the total bacterial community can maintain a high degree of temporal stability (Sercu et al. 2005b; Tresse et al. 2002), as also observed for various macroscopic functions in wastewater treatment reactors: anaerobic digestion (Dollhopf et al. 2001), nitrification (Wittebolle et al. 2009a), denitrification (Gentile et al. 2006), biodegradation of organic contaminants (Falk et al. 2009; Konopka et al. 2007; LaPara et al. 2002), and aromatic hydrocarbons (Massol-Deyá et al. 1997). The temporal stability of the community composition has even been reported despite changing operating conditions (Carvalho et al. 2006; Smith et al. 2003).

It has been suggested that the constancy of the community structure would be due to the low diversity of the community (Curtis and Sloan 2004), when for example all of the enzymes needed for the function of interest can be packaged within one organism (Gentile et al. 2006) and when the capacity to carry out the considered function is not easily transferred to other microorganisms (Carvalho et al. 2006).

However, significant correlation could not be pointed out between the size and/or the function of the targeted population and its dynamics. On the contrary, it is reasonable to assume that the constancy of the community is rather connected with (a) the protective and constant environment provided by the biofilm EPS matrix (Ayala-del-Río et al. 2004; Massol-Deyá et al. 1997) and (b) the strong selective pressure imposed by the environment (Carvalho et al. 2006; Massol-Deyá et al. 1997), especially by the presence of contaminant (Lozada et al. 2007). The temporal variability of the community is reduced by the strengthening of the environmental stringency, such as periodical substrate feed (Carrero-Colón et al. 2006), addition of toxic pollutant (Ayala-del-Río et al. 2004), or increase of contaminant concentration in an industrial effluent (Van der Gast et al. 2008). It should be noted that when the analytical tools are not sensitive enough to assess the community profile, the stability of the dominant species may hide the instability of minor species.

Temporal dynamics at steady state

Conversely, numerous works attested that stable function could be sustained by highly dynamic communities in ammonia and VOCs biofilters (Friedrich et al. 2003; Sakano and Kerkhof 1998; Von Keitz et al. 1999) and in bioreactors performing various functions, such as anaerobic digestion (Fernandez et al. 1999), nitrification (Graham et al. 2007; Wittebolle et al. 2008), organic contaminant removal (Ayarza et al. 2010; Miura et al. 2007), and aromatic hydrocarbon degradation (Baptista et al. 2008). In these reactors, the temporal dynamics is defined by (a) short-term changes of bacterial composition, (b) no persistence of particular OTU, (c) no convergence to the same climax community (Fernandez et al. 1999), and (d) no correlation between the structural variability and any operating parameter (Nadarajah et al. 2007).

These works suggest that a constant microbial community is not essential to sustain high functional performance and stability of the process (Wittebolle et al. 2008). Rather than the persistence of a specific population, a given arrangement among populations seems more important to achieve process stability (Fernandez et al. 1999).

At first, structural oscillations can be explained by uncontrolled and unnoticed fluctuations of operating conditions which influence the community composition (Miura et al. 2007). Moreover, a major source of variability lies in the complex network of microbial interactions (Graham et al. 2007), creating condition for non-equilibrium dynamics. The maintenance of functional stability despite continuous shifts of microbial population is an indication of functional redundancy, which is ensured by the presence of a reservoir of species able to perform the same ecological function (Briones and Raskin 2003; Franklin and Mills 2006). Beyond these deterministic approaches, microbial community dynamics could be attributed to stochastic mutations according to the neutral theory (Curtis and Sloan 2004).

Inter-replicate variability

Apart from the spatial and temporal variability of the community, it is interesting to address the question of inter-replicate variability. Despite their difficulty to implement in practice, running parallel bioreactor replicates provides key information about the deterministic or stochastic forces driving the ecosystem community. The reproducibility of the community structure (in terms of species composition, spatialization and temporal patterns of species succession) has been frequently reported in wastewater treatment systems (Ayarza et al. 2010; Wittebolle et al. 2009a), suggesting that the microbial community is driven by deterministic mechanisms (Loreau et al. 2001). On the contrary, highly divergent communities encountered in replicate systems (Carrero-Colón et al. 2006; Konopka et al. 2007) would indicate neutral mechanisms governed by stochastic events (Curtis and Sloan 2004). The inter-replicate variability is mainly due to minor species while the distribution of more abundant taxa is more reproducible (McGuinness et al. 2006). As stated by others, we infer that the validation of reproducibility is essential for the use of model ecosystems in microbial ecology studies (Roeselers et al. 2006).

Microbial ecology under transient regimes

As a result of fluctuating industrial activity, full-scale biofilters are usually operated under changing conditions in terms of gas stream composition, concentration, and flow rate, which can impair their functional performance (Kraakman 2003). It is thus of prime importance to identify the factors and magnitude of changing conditions that can alter the functioning and biological composition of the biofilters.

Substrate pulses as a transient regime

Apart from perturbations of operating parameters (e.g., moisture, temperature), different kinds of load perturbations have been applied at lab-scale to study the biofilter transient response, such as starvation and step increase of contaminant load. However, we believe that abrupt and transient increases of load during short periods (“shock loads”) are more likely to mimic the feed fluctuations observed at industrial facilities.

As ephemeral events of resource superabundance (Holt 2008), resource pulses induce microbial responses in terms of growth and decay rates or enzymatic activity (Carrero-Colón et al. 2006; Ergon et al. 2001), leading to potential shifts in biofilter microbial community structure (Yang et al. 2008). However, whether the responses of the biological component to resource pulses reflect genetic or physiologic adaptation is still unclear (Carrero-Colón et al. 2006; Holt 2008). The physiological effects may regulate the short-term stress response, whereas shifts in community composition are more likely to regulate the response over longer periods (Schimel et al. 2007).

From an ecological perspective, we report here the response of biofiltration communities undergoing a disturbance regime according to an integrated three-level framework, in terms of resistance, resilience, and memory.

Resistance

The resistance capacity is defined as the degree to which the microbial composition remains unchanged in the face of a disturbance (Allison and Martiny 2008). Most studies highlight that the composition of biofiltration communities is sensitive to changes of gas concentration (Borin et al. 2006) or composition (Hayes et al. 2010; Shim et al. 2006). This poor structural resistance capacity in the face of environment disturbance is also reported in wastewater ecosystems (Dollhopf et al. 2001; Nadarajah et al. 2007; Sundh et al. 2003) and soils (Li et al. 2007; Widenfalk et al. 2008).

These composition changes can be interpreted as the differential effects of the disturbance on the different populations within the community. The stress-associated cost falls differently on different organisms, depending on their inherent tolerance and acclimation capacities (Schimel et al. 2007). Indeed, the potential toxic effect of contaminants is species-selective (Song and Kinney 2005; Szabó et al. 2007), while the growth-benefit effect of resource increase during shock loads depends on the species kinetic strategy. It favors the growth of r-strategists at the expense of K-strategists (Chesson et al. 2004).

The lack of ecological resistance is generally not correlated to a poor functional resistance. On the contrary, the composition changes reflect the plasticity and flexibility of the community, i.e., its ability to maintain stable functional traits via rapid adaptations to environmental fluctuations (Fernandez et al. 2000; Loreau et al. 2001). It is well-documented that communities displaying distinct species composition (before and after the disturbance) can yet fulfill the same global macroscopic function, thus supporting the concept of functional redundancy (Botton et al. 2006; Briones and Raskin 2003).

The effect of diversity on resistance is less predictable. The lower the diversity, the more the system resistance will depend on the stress sensitivity or tolerance of the dominant species. (Hillebrand et al. 2008). In other words, the ecosystem function is affected by the extinction order of its species following a disturbance. In absence of compensation, if the most extinction prone species are the most functionally efficient, then the ecosystem function will be disrupted more rapidly than predicted by random species loss (Larsen et al. 2005).

On another hand, communities considered as ecologically resistant (composition-stable) can actually respond to substrate pulses by physiological modifications implying variations of enzymatic activity (Carreiro et al. 2000) or gene expression rate (Callister et al. 2009; Gunsch et al.

2007). The physiological response to stress infers a change of resource allocation from growth to survival pathways (Schimel et al. 2007).

Resilience

The engineering resilience is the rate at which a system returns to its original state after being disturbed (Holling 1973).

From a functional point of view, gas biofilters usually show high resilience capacity, as they are able to recover high and stable removal performance after-shocks (e.g. Cabrol 2010). However, from an ecological point of view, there is no study of structural resilience in gas biofilters to date.

After stress-induced structural changes, the microbial community can either (a) continue changing if the structural breakdown was irreversible (Nadarajah et al. 2007), (b) stay in a new equilibrium state, stable but different from the previous disturbance state (Eichner et al. 1999), (c) recover a structural organization similar to the one before the disturbance (Fernandez et al. 2000; Gentile et al. 2006).

The reversibility of the structural changes may be the sign of phenotypic or physiologic changes. Moreover, a high resilience capacity may result from several microbial features contributing to the fast adaptation capacity of the microorganisms, such as their fast growth rate, their metabolic versatility, their physiologic flexibility, and their rapid evolution through mutations or horizontal gene transfer (Allison and Martiny 2008; Loreau et al. 2001). The resilience of the ecosystem function is often reported to occur faster than the resilience of the community structure (Gentile et al. 2006; Sundh et al. 2003), or even without resilience of the microbial composition, which supports the concept of functional redundancy (Girvan et al. 2005). Rather than to a stable and diverse initial community, the resilience capacity seems to be correlated to a flexible community, able to adapt by both metabolic and structural changes, where the minor species play a major importance (Fernandez et al. 2000; Gentile et al. 2006).

Memory

The history of the ecosystem can shape the ecosystem response to environmental changes (Sousa 1980; Strickland et al. 2009). In some rare cases, previous perturbations of the system may alter the system stability face to further perturbations (Tobor-Kapłon et al. 2005). But it is generally accepted that when exposed to a new stress, the resistance and resilience capacity of an ecosystem are enhanced if it has previously experienced recurrent and small magnitude stresses, as observed in soil (Bressan et al. 2008; Ranjard et al. 2008), marine chemostats (Zemb 2007) and anaerobic digesters (McMahon et al. 2004; Zemb 2007). The community composition, density, and function (enzymatic activities) are more sensitive and less stable when the system is exposed to forcing variables outside its "life-history", compared to systems that have regularly experienced environmental variability (Waldrop and Firestone 2006). However, the effect of pre-exposure to stress is complex and may depend on the relatedness of the consecutive stresses. The pre-exposure to metal has been reported to improve the community resilience only when primary and subsequent stresses were of the same nature (Philippot et al. 2008). Apart from toxic and/or environmental stresses (e.g., pH, metals, chemicals), the alternance of feast–famine conditions is also known to increase the resistance of the ecosystem (Irvine and Moe 2001; Song and Kinney 2000; Wright 2005).

The way the historical contingencies drive the ecosystem community and function relies on either physiological or structural adaptation.

Several physiological adaptations probably play a role in the memory effect, such as the increased synthesis rate of exopolysaccharides (Ayala-del-Río et al. 2004) and heat shock proteins, as well as the increased storage capacity of substrates during feast periods, which can be consumed during famine periods (Chesson et al. 2004; Holt 2008; Irvine and Moe 2001). These physiological adaptations appear under unspecific stress conditions. It may explain that physiological-driven memory effect is observed for various kinds of stress, either similar or completely different from the previous ones experienced by the ecosystem (Ayala-del-Río et al. 2004).

The historical contingencies may also have shaped the community structure (Waldrop and Firestone 2006) and involved modifications of the community composition and abundance ratios, with selection of the most fitted species. The density and diversity of microbial communities are influenced by the historical exposure to contamination (Bouskill et al. 2010). According to the intermediate disturbance hypothesis, variable environments enable to maintain a higher diversity level than under stable conditions (Flöder and Sommer 1999; Yamamoto and Hatta 2004). Moreover, the niche variability of fluctuating environments offers axis for differentiation, thus permitting the coexistence of species with differentiated characteristics (Chesson et al. 2004; Stewart and Levin 1973). This higher diversity, acquired through historical stresses, may confer higher functional and stability advantages to the ecosystem in case of subsequent stress.

Conclusion and perspectives

This literature review led to mitigated conclusions in terms of biodiversity–ecosystem function relationship. Depending on the specific case under study (both the environmental system itself and the way it is investigated), the spatial and temporal dynamics of the microbial community (in terms of density, diversity and structure) can be either correlated or uncoupled to the ecosystem function. This antagonism indicates that the conclusions found in literature must be considered with caution as they depend on several criteria: (a) the analytical tool to explore the microbial diversity; (b) the method to calculate diversity, similarity, and stability indices, according to multiple definitions (Grimm and Wissel 1997), (c) the time scale (Grove et al. 2004), and (d) the specific function and population which are targeted (Peterson et al. 1998). Operating conditions such as pH, packing material, temperature, or the applied inlet load (Ding et al. 2008; Egli et al. 2003) can also influence the temporal and spatial variability. These experimental and methodological factors must be accurately defined in further studies, especially when looking for comparisons with other ecosystems.

The concept of stability must be handled cautiously because of its relativity (Carpenter et al. 2001). Indeed resistance and resilience capacities are tightly dependent upon the component considered within the ecosystem (either biological or functional), the variable chosen to describe this component (e.g., biomass density or system productivity), the kind of disturbance applied to the system, and the environmental conditions prevailing before and after the disturbance period (Botton et al. 2006; Hillebrand et al. 2008). According to the observation level (genetic, physiologic, biochemical), the community organisation and dynamics can be coupled or uncoupled to the disturbances (Chaer et al. 2009).

Finally, the lack of correlation between community dynamics and ecosystem function can effectively indicate the structure–function uncoupling, due to, e.g., functional redundancy, stochastic dynamics, or generalist populations. The potential structure–function link is even obscured and more difficult to establish by the possibility of horizontal gene transfer (Lynch et al. 2004). However, it can also disclose the inadequacy between the ecosystem complexity and the resolutive power of the analytical tool used to study it. For example, specific functional populations actually involved in the degradation can be hidden by the high diversity in complex biofiltration systems with high resource availability and low selective pressure, where most of the community is not involved in primary degradation (Møller et al. 1996; Song and Kinney 2000). In such systems, targeting the total bacterial community, with current 16S rDNA-based methods, may not be discriminant enough to reveal the potential link between a specific minor population and a specific function.

In order to point out significant the BEF relationships which can find practical applications for biofilter monitoring, it will be necessary to go beyond the shortcomings of current 16S rDNA approach, from “who is there” to “who does what” concerns. Further research should focus on active (Boon et al. 2003; Roy et al. 2009) and functional populations (Wittebolle et al. 2008; Falk et al. 2009) actually involved in contaminant degradation. To overstep the simplified statement “one gene one protein”, studies should combine functional gene targeting with proteomics approach. Stable isotope-based labelling of contaminant degraders can also provide deep insights for characterization of actively degrading microbial populations (Alexandrino et al. 2001).

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