

## Chapter 4

# Microbial Responses to Pollution— Ecotoxicology: Introducing the Different Biological Levels

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**Abstract** The environmental pollutions generated by human activities are important concerns that environmental risk assessment procedures have the purpose to evaluate and mitigate the effects. Microorganisms are among the first impacted by human generated pollutions. Furthermore, because they are essential actors in ecosystem functioning the evaluation of the pollution effects on microorganisms is of paramount importance. Their response may serve as proxy to report the effects on, and the recovering capacities of, the ecosystem. The behaviour of microorganisms in response to chemical pollution has been largely studied. In this chapter, we introduce the mechanisms underlying the microbial adaptation capacities involved in response to pollutants. We also discuss the basic knowledge inspiring microbial ecotoxicological tools reporting the pollutant effects that have been developed at the different biological organization levels, from genes and cellular processes to population and microbial community responses.

**Keywords** Microbial physiology · Microbial metabolism · Community ecology · Microbial adaptation · Metabolic versatility

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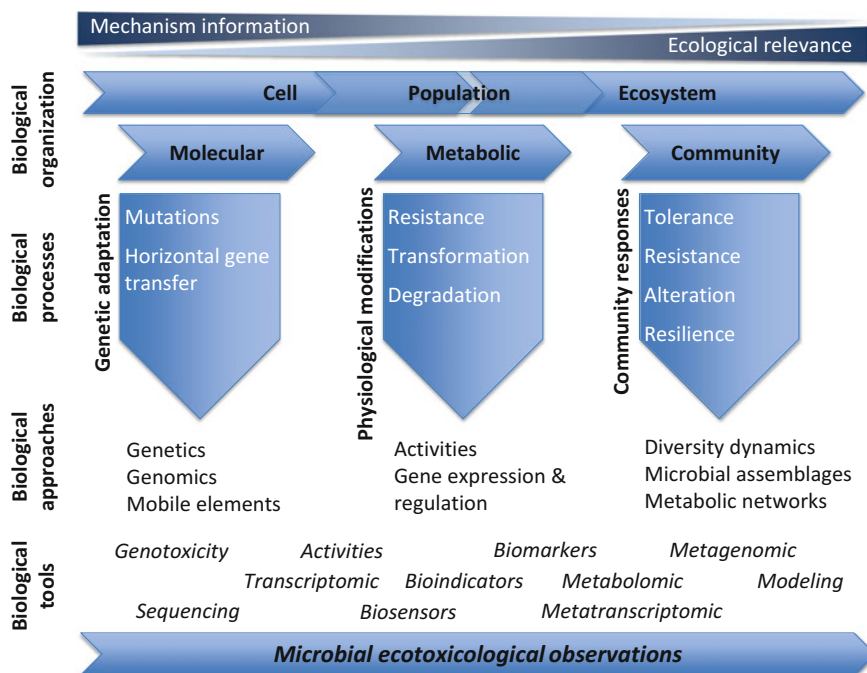
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## 4.1 Introduction

Modifications in microbial community structure and composition have been largely reported after the addition of pollutant, whether organic (Bordenave et al. 2004, 2007; Hjorth et al. 2007; Vercraene-Eairmal et al. 2010; Chronopoulou et al. 2013; Stauffert et al. 2013, 2014, Stauffert et al. 2015a, b; Cravo-Laureau and Duran 2014; Ben Said et al. 2015) or metallic/metalloid (Duran et al. 2003, 2008; Viret et al. 2006; Dominique et al. 2007; Ramond et al. 2009). In agreement with these studies, specific microbial communities have been described in polluted environments according to the nature of the pollutant (Bruneel et al. 2008; Paissé et al. 2008; Volant et al. 2014; Bargiela et al. 2015; Duran et al. 2015; Rodriguez-R et al. 2015; Misson et al. 2016). Such observations made at the microbial community level are of ecological relevance providing information on the behaviour of microbial communities in response to pollutants. The information indicating whether microbial community composition is resistant, resilient, or functionally redundant is of primary importance at the ecotoxicological point of view. It has been proposed to include the modification of microbial community composition into ecosystem process models in order to predict the response of ecosystem to disturbances (Allison and Martiny 2008). Actually, the modification of microbial community structures translates the metabolic versatility of microorganisms that is expressed at the cellular and population levels by the capacities to resist, transform and/or degrade the different classes of pollutants (Parales and Haddock 2004). However, it is noteworthy that the degradation and transformation capacities also depend on the interactions between microorganisms resulting in microbial networks performing complex task as demonstrated for the degradation of hydrocarbon compounds in marine environments (for review, see Head et al. 2006; McGenity et al. 2012). Several studies have demonstrated that assessing microbial activities at work during a pollution event provides relevant knowledge on the metabolic capacities affected by a pollutant and on the potential for ecosystem recovery in presence of metals (Bruins et al. 2000), pharmaceuticals (Barra Caracciolo et al. 2015) and other organic pollutants (Diepens et al. 2014). The metabolic versatility of microorganisms is related to genetic adaptation mechanisms that include mutations and horizontal gene transfer (Pieper et al. 2004; Stokes and Gillings 2011; Guieysse and Wuertz 2012; Puglisi et al. 2012). A large number of genotoxicity tests have been developed using microorganisms (Kokkali and van Delft 2014; Ma et al. 2014) for toxicity evaluation of polluted environmental sites.

As outlined in Fig. 4.1, the microbial processes involved in the response to pollutants provide the opportunity to develop microbial ecotoxicological tools at the different biological organization levels from gene to ecosystem, which at the academic point of view are relevant to assess microbial mechanisms and address ecological considerations respectively. In this chapter we summarize the microbial responses at different biological levels, which provide the basic knowledge of tools now available allowing ecotoxicological observations from genotoxicity tests to the development of ecosystem process models.



**Fig. 4.1** Microbial ecotoxicological observations and biological organisation levels. The microbial ecotoxicological tools are based on microbial processes including genetic adaptation, physiological modifications and community responses that translate mechanisms operating at cell, population and ecosystem levels respectively

## 4.2 Microbial Physiology and Metabolism

The physiological responses of microorganisms to pollutants have been initially mainly addressed using culture-based approaches. Many pollutants could be degraded or transformed by microbial action, microorganisms being adapted and selected to xenobiotic compounds introduced into the environment. In most cases, biodegradation capacities or metabolic pathways have been described in model strains. Thereby, physiological, morphological, taxonomic, and metabolic characteristics have been studied to better understand potential capacities and behaviour of microorganisms face to pollutants.

Microbial pathways involved in the degradation of organic pollutants have been intensively studied for decades. Microorganisms have developed diverse strategies to degrade organic pollutants in presence and in absence of molecular oxygen. Under aerobic conditions the oxygen could be not only the final electron acceptor but also a co-substrate for some catabolic processes, as described for some aromatic compounds (Fuchs et al. 2011; Diaz et al. 2013). For example, bacteria have the capacity to use polycyclic aromatic hydrocarbons (PAHs) as carbon and energy

sources (see Chap. 7). These bacteria possess dioxygenases (RHD) which introduce hydroxyl groups into the aromatic nucleus allowing to open the cycle, and then complete mineralization of the compound is carried out via the tricarboxylic acid cycle (Cerniglia 1992). In contrast, eukaryotic microorganisms possess cytochrome P450 monooxygenases involved in detoxification pathways rather than in assimilation processes of PAHs (Cerniglia 1992; Doyle et al. 2008). Under anaerobic conditions, microorganisms have developed a wide range of catabolic strategies (Zhang and Bennett 2005). Two mechanisms have been described for PAHs activation, including direct carboxylation or methylation followed by addition to fumarate, then the degradation pathway further proceeds via  $\beta$ -oxidation after activation with coenzyme (Co)A (Heider and Schühle 2013; Meckenstock et al. 2016; Rabus et al. 2016). Further examples of microbial adaptation to organic pollutants are provided by the degradation capacities for polychlorinated biphenyls (PCBs) and pesticides. PCBs degradation includes anaerobic reductive dechlorination, an energy-yielding process where PCBs serve as electron acceptor, and aerobic breakdown of the biphenyl structure through an oxidation reaction (Field and Sierra-Alvarez 2008; Sowers and May 2013; Passatore et al. 2014). Regarding pesticides, microbial metabolic transformation could be classified as a catabolic response where pesticides serve as energy sources, as a detoxification metabolism or as incidental metabolism when pesticides do not serve as energy sources (Matsumura 1989).

Coping with organic compounds involves a metabolic response, connecting the specific catabolic pathway with the energetic/biosynthetic metabolism of the cell, and a stress response for protection from the toxic effect of organic pollutants and adaptation to suboptimal growth conditions. Although extended research has been carried out focusing on degradation, other physiological responses may constitute important events preceding catabolism of organic pollutants, as bioavailability, chemotaxis, intracellular accumulation, tolerance mediated by physical and biochemical barriers (Sardessai and Bhosle 2002; Jain et al. 2005; Zhang and Bennett 2005; Chavez et al. 2006; Murinova and Dercova 2014; Parales et al. 2015; Duran and Cravo-Laureau 2016). Knowledge on metabolism of organic pollutants is still rather fragmentary and the diversity of bacterial strategies is highly underestimated.

Regarding metals, transformations could be related to energetic metabolisms, when used as electron donor or acceptor. Resistance and detoxification mechanisms have been also developed by microorganisms to cope with toxic metals. In some cases, oxidases or reductases are synthesized transforming metals into a volatile compound (e.g. mercury, Barkay and Wagner-Dobler 2005) or in less toxic compounds (e.g. arsenic, Cervantes et al. 1994). Incidental or indirect mechanisms (biomethylation, indirect reduction), as well as the presence of metal carriers, or even the formation of structures able to immobilize toxic compounds have been described (Prabhakaran et al. 2016). Research on the fate and ecological effects of some *emerging* pollutants, as nanoparticles, has become a focus of attention only recently (Concha-Guerrero et al. 2014; Cervantes-Avilés et al. 2016; Simonin et al. 2017). The interaction of nanoparticles with microorganisms is addressed in Chap. 5.

The impact of pollutants and degradation capacities reported in laboratory studies reflect only potential degradation that may occur in the natural environment. Environmental parameters, as temperature, salinity and pH, physical-chemical properties of pollutants, their concentration, as well as concentration and diversity of microorganisms, are all factors that play an important role in the biodegradation process (Pieper 2005; Shahgholi and Gholamalizadeh Ahangar 2014; Duran and Cravo-Laureau 2016). Therefore it is essential to consider all these parameters to characterize in-depth physiological and metabolic response of microorganisms to pollutants. Nowadays the integration of all these parameters via in situ studies is still difficult. Thus, experimental ecology approaches have been developed; mimicking as close as possible the environmental conditions. These approaches combine the advantages of lab-controlled systems with the possibility of extrapolation to the real situation found in complex ecosystems (Cravo-Laureau and Duran 2014).

The physiological and metabolic versatility of microorganisms is a key advantage in the response and in the adaptation to pollutants. Although culture-dependent methods generally recover a small portion of the diversity from environments, they are still a critical component of research and bioremediation development (Watanabe 2001). However, proteogenomic, metabolomic, transcriptomic and metagenomic studies revealed novel degradation pathways, allowing to consider metabolism of viable but non-cultivable microorganisms. The use of integrative culture-dependant and culture-independent methods, including *omics* approaches, has enabled an unprecedented view of metabolic pathways and clues to the evolution of degradation pathways and physiological and metabolic adaptation strategies to changing environmental conditions (Cravo-Laureau and Duran 2014; Ufarte et al. 2015).

### 4.3 Microbial Community Responses

Recent cultivation-independent genome approaches and sampling of previously unexamined environments have revealed the unsuspected huge diversity of microorganisms, both eukaryotic and prokaryotic (Hug et al. 2016; Lennon and Locey 2016). This considerable taxonomic diversity strongly echoes their capabilities to thrive in a large range compartments on earth where they ensure through their activities the sustainability and functioning of the ecosystems (Azam 1998; Field et al. 1998; Guerrero and Berlanga 2006; Pomeroy et al. 2007; Falkowski et al. 2008; Van Der Heijden et al. 2008; Bardgett and Van Der Putten 2014). In the environment microorganisms are assembled in communities of various degrees of complexity. These assemblages result of complex interactions that maintain the cohesion of the communities. Interactions are of two orders:

- biotic interactions, either trophic or non-trophic, among microorganisms of the community and among microorganisms and surrounding or host macroorganisms: plants and animals.
- abiotic interactions defined by physical-chemical conditions relevant to the environment in which the communities thrive.

Determining and predicting the effect of contaminants in natural environments, that are the ultimate goals of ecotoxicology, involves to address complex biological organization, communities, ecosystems, or landscapes and necessitate to cover large spatial scales (Beketov and Liess 2012; Newman 2015). Also a critical issue in ecotoxicology studies consists in disentangling the part of the response that is due to the contaminant (either chemical or physical properties), that can be termed as a direct effect, from that due to biological interactions among organisms, thus an indirect effect (see Chap. 14 for more development). Investigating the impact of pollutants on microbial communities are often addressed by two main approaches, namely *in situ* studies where polluted sites are compared to reference sites or investigated along gradients of contamination (Païssé et al. 2008; Volant et al. 2014), and microcosm or mesocosm studies that aimed at approaching environmental conditions similar to those of natural ecosystems while keeping under control their fluctuations (Vercreaene-Eairmal et al. 2010; Paule et al. 2013; Stauffert et al. 2013; Bour et al. 2015).

Although microorganisms have developed tremendous ranges of metabolic capacities and stress-related pathways and strategies (see previous section and Chap. 5), environmental pollutants such as toxic metals and hazardous organic compounds constitute nevertheless important environmental pressures that may have adverse effects on the metabolism and the survival of several taxa. Indeed taxon owns only a limited fraction of whole microorganism metabolic repertoire even though some taxa may exhibit larger metabolic capacities. In this case such ecological versatility frequently allows the strains to cope with several pollutants and face large ranges of environmental conditions (Brazilian National Genome Project Consortium 2003; Nelson and Fraser 2004; Mongodin et al. 2006). Impact of pollutants on microbial communities depends greatly on their chemical properties, bioavailability and persistence (Calvet 1989; Bonnet et al. 2007; Spagnuolo et al. 2010; Xiao et al. 2013), as well as their physical properties that, in turn, can modify the properties of the milieu (e.g. crude oil pollution, Dachs et al. 2000).

On the other side physical and chemical properties of the milieu influence also the time of residence and the bioavailability of the pollutant in the environment (Barriuso et al. 1996), for instance several authors demonstrated a clear relationship between organic matter content in soils and the sequestration of pesticides (Chung and Alexander 2002; Bogan and Sullivan 2003; Moreno-Jiménez et al. 2013; Woignier et al. 2013). Pollution history at site is also determinant because microbial community previously exposed to pollutant may be promptly mobilised in subsequent exposure, and, when effective, biodegradation of the pollutant can be enhanced and can occur faster compared to an environment exposed for the first time (Walker 1987; Head et al. 2006; Baxter and Cummings 2008; Lauga et al. 2013).

This memory effect may result of an increased tolerance of the community to the pollutant as a consequence of physiological adaptations or community shifts (Widenfalk et al. 2008; Azarbad et al. 2015; Mauffret et al. 2017). As a consequence of differences in pollutants sensitivity among microbial species disruption on microbial communities was evidenced. Studies conducted to investigate the impact of pollutants on microbial communities demonstrated that both diversity (richness and evenness) and function structures host by microorganisms might be impaired under pollutants pressure. Several studies have reported shifts in the community structure, decrease of richness or changes in abundance of some taxa either at environmentally relevant or high concentrations of pollutants (Li et al. 2006; Foley et al. 2007; Johnston and Roberts 2009; Lubarsky et al. 2012; Pascual et al. 2014; Ibekwe et al. 2016; Jiao et al. 2016; Misson et al. 2016; Mustafa et al. 2016; Wang et al. 2016). Interestingly in a study that aimed at investigate the impact of diuron (an herbicide) on river epilithic biofilms, (Vercraene-Eairmal et al. 2010) demonstrated that bacterial communities at the most contaminated site were less affected under realistic exposure to diuron than communities developing under lower exposure in their native site. This result suggests that adaptation and resistance may have emerged in the former community under selection pressure and then spread in the communities or, alternatively, that the community was shaped and stabilized in such contamination background allowing for resistance to subsequent exposure. Cases of resistance and adaptation at the community level have also been reported in different studies among which Acosta-González and Marqués (2016) in oil-polluted marine coastal sediments or Mukherjee et al. (2014) in a creosote-contaminated site. Resistance and adaptation may operate through over-expression or higher frequency of genes conferring pollutant tolerance, by selective growth of metal-tolerant microorganisms or via acquisition of new genetic tolerance-related capabilities through mutation or horizontal gene transfer, this latter aspect is presented in the following section and Chap. 6. In contrast some authors did not observe any or poor impact on community structure. Albeit such result could indeed correspond to a real situation revealing non-toxic effect of the pollutant on microbial communities, it can also indicate the onset of resistance phenomenon at the whole community level that may have occurred in the past. Additionally it cannot be exclude that methods of investigation or data analysis may have fail to detect a marginal effect of the pollutant (Wu et al. 2016).

Several studies indicated that the incidence of the pollutant on the microbial community may be transient, i.e. that once the contaminant was removed, the recovery of at least functional or even taxonomic diversity was observed (Tobor-Kapłon et al. 2005; Boivin et al. 2006; Bordenave et al. 2007; Mertens et al. 2007; Ma et al. 2015). This resilience may be explain by manifold reasons among which microorganism colonization from undisturbed site arising from the vicinity, population dormancy, growth rate ( $r$  vs  $K$  strategies), short time of exposure and functional redundancy.

As a consequence of shift in microbial diversity, it is important to research impact of pollutants on functional traits in the microbial community since their alteration may also seriously jeopardize ecosystem functioning or because they

sustain community resistance, tolerance or resilience when traits are related to biodegradation. Hence several authors showed that pollutants might impair biomass, carbon mineralization, microbial respiration, nitrification and denitrification (Monard et al. 2011; Kumar et al. 2012; Singh et al. 2014; Delgado-Baquerizo et al. 2016; Simonin et al. 2016; Wu et al. 2016) or biodegradation (Caliz et al. 2011; Delgado-Baquerizo et al. 2016). However shifts in community structure could also be neutral on ecosystems functioning demonstrating that functional redundancy hold true in certain situation. This is conceivable if the loss of functionality bear by sensitive microorganisms does not affect trophic structure and is compensated by the functions of tolerant microorganisms still present in the community (Widenfalk et al. 2008; Azarbad et al. 2015). As suggested under the insurance hypothesis, this scheme is all the more likely if diversity is high in the ecosystem (Yachi and Loreau 1999).

The rise of high-throughput sequencing techniques contributes nowadays to uncover the huge diversity of the microbial realm. Our knowledge on bacterial community composition, functions and dynamics know since a decade unprecedented advances. Given this new development alongside other analytical tool important research topics are open. Hence, in 2006, this technologies had shed light on vast pool of low-abundance populations, the rare biosphere, that account for most of the observed phylogenetic diversity in every environment (Sogin et al. 2006). Importantly, microorganisms that constitute this pool, although still neglected in our investigation, may harbour ecologically critical functions in the ecosystem as demonstrated by Pester et al. (2010). Also in the context of future development in microbial ecotoxicology it would be worth asking what could be the role of this rare populations in microbial communities that had to face toxic agents. Additionally it seems necessary to develop new bioinformatics and statistical tools to extract meaningful information and decipher the ecologically relevant information from high-throughput sequencing data and more generally 'omics' technologies. Alongside to data collected at site, integrated approaches should allow to gain important knowledge on ecosystem functioning and has to ultimately lead to a better risk assessment and management of pollution at local but also importantly global scales.

#### 4.4 Microbial Genetic Adaptation

At genome scale, the adaptation is the consequence of genetic variability and evolvability. Indeed, except the core genome involved in essential functions, a part of the genome is suitable to strong variations (Baquero 2009). Three major ways generate genome variations (Arber 2000). First, spontaneous mutations occur in a regular manner at each generation allowing local genomic changes (Feldgarden et al. 2003). Second, the rearrangement of segments of genomic sequences can be mediated by mechanisms such as homologous recombination or transposition (Thomas and Smalla 2000; Sota et al. 2006). Third, the fastest and powerful way to



acquire new functions in bacteria and archaea is the acquisition of sequences from other organisms by horizontal gene transfer (HGT) (Garcia-Vallve et al. 2000; Ochman et al. 2000; Springael and Top 2004; Brochier-Armanet et al. 2011). At least a part of the genes acquired by HGT have a role in adaptation (Lawrence 1999; Marri et al. 2006). The mechanisms that allow the entrance and the establishment of foreign DNA in a genome are well-known (see Chap. 6). The establishment of the new genetic material will be possible if it is autonomous for replication in the recipient cell, or if it is capable of insertion in the chromosomal DNA (without major damage for the integrity of the host genome). Then, numerous genetic elements are involved in HGT, most of them are mobile genetic elements (Smalla and Sobecky 2002; Koonin and Wolf 2008; Boyd et al. 2009; Sentchilo et al. 2013; Darmon and Leach 2014). Moreover, mobile genetic elements are often more abundant in bacterial genomes in extreme environments (Bickhart et al. 2009; Lin et al. 2011), suggesting their role in the adaptation to unfavorable habitats. Thus mobile genetic elements play a major role in the spread and even *de novo* construction of new functions (Top and Springael 2003), and are thus central vectors for diversification and adaptation (Frost et al. 2005).

It is well known that stress conditions enhance the processes of genetic adaptation (Matic et al. 1995; Beaber et al. 2004; Ubeda et al. 2005; Galhardo et al. 2007; Baquero 2009). Therefore, contamination by xenobiotics is one factor that can stimulate microbial genomic adaptation (Top and Springael 2003; Springael and Top 2004; Marri et al. 2006; Heuer et al. 2008; Monard et al. 2011). Numerous characterized genetic elements, such as plasmids, transposons, genomic islands and integrons, carry adaptive genes involved in the resistance of antibiotics (Stokes and Hall 1991; Hansson et al. 2002; Del Grosso et al. 2007; Barraud et al. 2013; Giakkoupi et al. 2015; Korona-Glowniak et al. 2015), metals (Ji and Silver 1992; Liebert et al. 1999; Tuffin et al. 2005; Novais et al. 2010) and the degradation of organic pollutants (Nakatsu et al. 1991; van der Meer et al. 1991; Romine et al. 1999; Fong et al. 2000; Top and Springael 2003; Chae et al. 2007; Yano et al. 2007; Koenig et al. 2009; Ilori et al. 2015). Even some (e.g. integrons) are also able to exchange these genes in accordance with the contamination pressure imposed in the habitat (Stalder et al. 2012; Abella et al. 2015a). These observations support that all these genetic elements are important actors in adaptive responses to chemical contaminations.

The adaptation acquired by one organism is not only beneficial to the concerned individual, but also advantages the entire community, as for example the acquisition of a degradation function involved in the pollutant removal (Sentchilo et al. 2013). Also, the adaptive function acquired by HGT can be transmitted again to other members of the community. In this way, although the acquisition of new functions can be to the detriment of other functions (Ferenci 2016), it is doubtless an asset for the community. Our current knowledge on the adaptive genetic elements results essentially from analyses of isolated bacterial strains. The analysis of microbial complete-sequenced genomes allowed to estimate the part of sequences acquired by HGT in a given genome (Ochman et al. 2000; Brochier-Armanet et al. 2011). Nevertheless, we know that, within a community, microorganisms are organized in

networks, sometimes showing strong interactions. Then the adaptation must be also studied at the community level. The new techniques of high throughput sequencing should give new information. On one hand, targeting directly the genetic elements involved in HGT (Zaneveld et al. 2008, 2011; Jacquiod et al. 2014), they enable the characterization of new adaptive genes acquired within the community (Huang et al. 2009) as well as the hierarchization of the involvement of the genetic elements in the adaptation mechanisms. On the other hand, metagenomic and metatranscriptomic studies may also contribute to better understand the mechanisms of genetic adaptation within communities in response to chemical pollutants. In particular, the pollution history influences the spread of adaptive genes, which are easily spread within a community subjected to an already experimented pollutant, while it is slower when submitted to a recent pollution or to a new pollutant (Abella et al. 2015a, b; Chessa et al. 2016). Research efforts must be undertaken in this sense in order to complete our knowledge on the genetic mechanisms involved in the adaptation of microbial communities.

#### 4.5 Overview—Concluding Remarks

The metabolic versatility and genetic flexibility, together with community strategies are crucial assets allowing microorganisms to withstand the presence of pollutants. The microbial mechanisms discussed in this chapter provide the basic knowledge for the development of ecotoxicological tools reporting environmental quality. In contrast to chemical analysis methods, microbial ecotoxicological tools enable not only to determine pollutant concentration (biosensors, Chaps. 12 and 13) but also to assess the toxic effect at different biological levels including the genetic/genomic levels (Chaps. 6 and 8), the metabolic level (biomarkers, Chap. 11; bioindicators, Chap. 10) and the community level (Chaps. 8 and 9). Furthermore, microbial ecotoxicological tools allow to determine the microbial capacities to remove pollutants and represent thus useful tools for the implementation and the follow up of bioremediation processes. Because microorganisms are ubiquitous, microbial ecotoxicological tools can be potentially developed and exploited for every ecosystem and for any pollutant. However, the future challenges for the microbial ecotoxicology will be to propose integrated approaches to evaluate the impact of multi-contamination, including emergent contaminants. For this purpose basic knowledge on microbial ecology with a holistic point of view is of paramount importance and therefore such basic research should be encouraged.

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