



Microbial associations for bioremediation. What does “microbial consortia” mean?

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Abstract

Microbial associations arise as useful tools in several biotechnological processes. Among them, bioremediation of contaminated environments usually takes advantage of these microbial associations. Despite being frequently used, these associations are indicated using a variety of expressions, showing a lack of consensus by specialists in the field. The main idea of this work is to analyze the variety of microbial associations referred to as “microbial consortia” (MC) in the context of pollutants biodegradation and bioremediation. To do that, we summarize the origin of the term pointing out the features that an MC is expected to meet, according to the opinion of several authors. An analysis of related bibliography was done seeking criteria to rationalize and classify MC in the context of bioremediation. We identify that the microbe’s origin and the level of human intervention are usually considered as a category to classify them as natural microbial consortia (NMC), artificial microbial consortia (AMC), and synthetic microbial consortia (SMC). In this sense, NMC are those associations composed by microorganisms obtained from a single source while AMC members come from different sources. SMC are a class of AMC in which microbial composition is defined to accomplish a certain specific task. We propose that the effective or potential existence of the interaction among MC members in the source material should be considered as a category in the classification as well, in combination with the origin of the source and level of intervention. Cross-kingdom MC and new developments were also considered. Finally, the existence of grey zones in the limits between each proposed microbial consortia category is addressed.

Key points

- *Microbial consortia for bioremediation can be obtained through different methods.*
- *The use of the term “microbial consortia” is unclear in the specialized literature.*
- *We propose a simplified classification for microbial consortia for bioremediation.*

Keywords Microbial consortium · Bioremediation · Environmental biotechnology · Consortia engineering

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Introduction

Bioremediation involves a set of biotechnological processes that take advantage of biological systems, such as enzymes (Zdarta et al. 2022), microorganisms (Ahmad 2021), and plants (Basit et al. 2021) which can be applied to the soil, sediments, and water to remove or stabilize contaminants (Cabral et al. 2022). These strategies are used worldwide due to their relatively low cost, effectiveness, and environmental friendliness (Orellana et al. 2017). Bioremediation could be considered as a simple catabolic process involving a group of pollutants being degraded or removed by a biological system, usually microorganisms. Nevertheless, it is known to be

a dynamic process involving multiscale complexity (de Lorenzo 2008). A recent search for scientific articles conducted on ScienceDirect (November 2021) using “bioremediation” as a keyword delivered a total of 20,935 publications since 1998, being the last years the most prolific: 2020 with a total

of 2034 and 2021 with 2470. These numbers are a clear indication that the field of bioremediation is in full bloom. Fig. 1

Bioremediation is applied for both organic (Perelo 2010; Kang 2014; Madadi and Bester 2021) and inorganic pollutants (Choudhary et al. 2017; Verma and Kuila 2019).

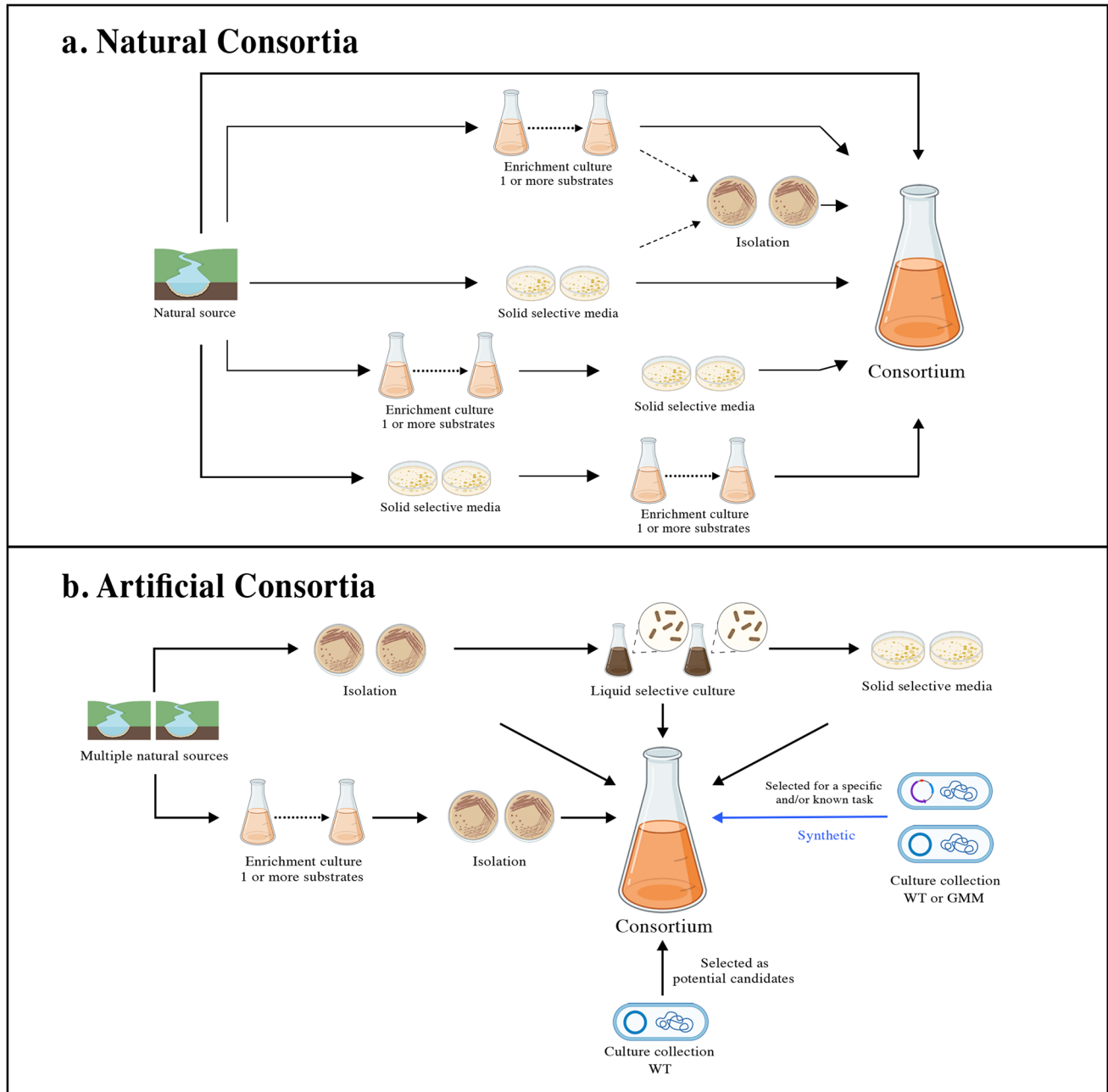


Fig. 1 Categories of microbial consortia based on their origin and the methods used to obtain them; **a** Natural microbial consortia (NMC) come from a single source where microorganisms may interact naturally. They are typically obtained through one or successive (dotted line) enrichment cultures. In some cases, an isolation step is considered directly from the source or after enrichment or solid culture (dashed line). **b** Artificial microbial consortia (AMC) are composed of microorganisms isolated from different sources (including

natural and culture collections) and combined following some criteria. Synthetic microbial consortia (SMC) (blue line) are a type of AMC whose members (WT or GMM) and proportions are carefully designed and chosen to achieve the desired goal. NMC and AMC, including SMC could be composed of members of the same kingdom (single kingdom consortia) or by members belonging to different kingdoms (cross-kingdom consortia). Created in Biorender.com

For organic compounds, there are two main approaches: biostimulation and bioaugmentation (Speight and El-Gendy 2018; Nadhirawaty and Titah 2019; Gutiérrez et al. 2020). The first one is applied when the matrix presents enough catabolic potential for pollutant degradation and consists of adding nutrients and/or oxygen to enhance the metabolism of the indigenous contaminant-degrading microbes and consequently, the biodegradation rate. This is usually achieved by balancing the C:N:P ratio in the polluted soil through the addition of inorganic salts or fertilizers (Júlio et al. 2018; Della-Flora et al. 2022). Owing to its simplicity and effectiveness, its application has been widely reported for a variety of environments (Simpanen et al. 2016; Omokhagbor Adams et al. 2020), including extreme ones (Martínez Álvarez et al. 2017). The second one is applied when the matrix lacks enough catabolic capability to degrade the contaminant and involves inoculation using contaminant-degrading microorganisms or biosurfactant-producing microorganisms (when the pollutant has a high K_{ow}). This strategy arose during the 1980s and the 1990s (Vogel 1996) and was initially carried out using a single microorganism (with a proven degradation capability) as inoculum. Some important setbacks using bioaugmentation, such as predation, grazing, and lack of removal improvement (Bouchez et al. 2000; FU et al. 2009; Radwan et al. 2019), led the research to new developments (Wilderer et al. 1991; Bouchez et al. 2000; Ruberto et al. 2010; Dueholm et al. 2015). One significant change was the change of a single microorganism for microbial associations or the so-called *consortia* as inoculants. This approach was used for bioremediation and other biotechnological applications (Qian et al. 2020; Sgobba and Wendisch 2020; Zhang and Zhang 2022). Time ago, the microbial infallibility principle was proposed by Alexander (1965): “Every biologically synthesized organic molecule doubtlessly will, under some set of circumstances, be destroyed by one or several species”. According to this, due to metabolic versatility and genetic variability, microbial communities would be able to degrade most organic compounds under adequate conditions. In this way, microbial associations could achieve a complex task that is impossible for a single strain alone (Mee et al. 2014). The so-called division of labor is one of the outstanding traits of MC (Tsoi et al. 2018) and the existence of complementary degradation allows microorganisms to follow a syntrophic lifestyle (Zhou et al. 2011). That is how microbial communities can degrade a myriad of compounds (Ramakrishnan 2012), including organic pollutants as hydrocarbons (Varjani 2017), polychlorobiphenyls (Abramowicz 1995; Benitez et al. 2021), and other contaminants such as plastics (Ali et al. 2021).

Pollutant biodegradation depends on several factors, such as molecular structure, solubility, bioavailability, toxicity, and the existence of adequate enzymes, among others (Azubuike et al. 2016; Ławniczak et al. 2020). What

is more, the fact that microorganisms carry the genetic potential to degrade a molecule does not mean that they are capable of performing that task. For instance, the polychlorobiphenyl-degrader *Burkholderia xenovorans* LB400 cannot completely degrade these compounds due to physiological reasons despite containing all the needed genes for PCBs degradation (Pieper et al. 2004; Agulló et al. 2007). As affirmed by (de Lorenzo 2008), bioremediation depends on genetics and enzymology but also on physiological and ecological aspects.

Several ways of obtaining microbial associations for bioremediation are possible, giving the place to a variety of different definitions when referring to the term *microbial consortium*. Again, Alexander (1997), pointed out “Environmental microbiology is blessed, or possibly cursed, with a multitude of terms that are often contradictory, sometimes misused, and frequently misunderstood even by the specialists”. That is how it is possible to find expressions like “unique natural microbial cocktail” (Sorkhoh et al. 1995), “multi-population system” (Smith et al. 2013), or “fungal-bacterial co-cultures for the removal of organic pollutants” (Espinosa-Ortiz et al. 2021) just to mention some of them. The same lack of consensus reaches other fields such as industrial biotechnology (Sabra et al. 2010; Canon et al. 2020).

Hirsch et al. (1984) suggested that microorganisms must be associated through a physical attachment in a specific spatial arrangement, typically found in biofilms, to be considered a consortium. A clear example of that was provided by Nielsen et al. (2000) working with a two-members bacterial consortium (*Burkholderia* sp. and *Pseudomonas* sp). The consortium was able to concomitantly metabolize chlorobiphenyl (CBP) since *Pseudomonas* sp. Degraded chlorobenzoate produced from CBP by *Burkholderia* sp. The most astonishing finding was that these bacteria only grew as mixed microcolonies when fed with CBP while showing separately growth when citrate was used as substrate (completely metabolizable by both). Caldwell et al. (1997) applied the term consortium to describe the mixtures of organisms present in (and resulting from) degradative enrichment cultures using contaminated matrixes as a source of microorganisms. Brenner et al. (2008) affirm that a consortium is composed of multiple interacting microbial populations. This idea takes into consideration the requirements of a variety of members and demands that they must interact. The mere presence of more than one microbial population in a certain spatial compartment is not enough. In the same way, McCarty and Ledesma-Amaro (2019) defined MC as a group of microorganisms (from different species or at least different strains) that show interactions such as cross-feeding or engineered behaviors. These authors use the terms “microbial consortia” and “microbial community” in the same sense, although the latter is usually applied to

describe the whole microbial population which naturally inhabits each corner of the environment (Schröer et al. 2020; Tarquinio et al. 2021). However, to contribute with the lack of consensus analyzed here, a MC can be considered a microbial community obtained through a certain isolation method (Wright et al. 2019). What is more, nowadays the idea of “microbiome” providing a more complex concept related to microbial community description. A deeper analysis of this topic was commented by Berg et al. (2020). In this review the term “consortium” will refer to a group of microorganisms obtained through human intervention, while “community” will refer to a group of microorganisms that inhabit a certain environment.

There seem to be few agreements among definitions of what a microbial consortium is: (i) they are composed of, at least, two different microbial populations, and (ii) the combination or association of microorganisms results in different, usually more powerful, metabolic capabilities than those of single strains. In light of that, in this work, we discuss the several ways to achieve, name, and classify functional MC, considering the different scopes and limitations that were given to them in the field of environmental microbiology.

Microbial consortia classification

Working with microbial associations allows a huge number of variants. From a general biotechnological perspective, Bernstein and Carlson (2012) proposed to classify MC into four categories. According to them, NMC are those derived from environmental samples through successive selection aiming for a certain activity (e.g., hydrocarbon degradation). AMC are those composed of different wild-type microorganisms that do not interact in nature. SMC are those exclusively composed of metabolically engineered microorganisms (by genetic or regulatory modifications) to optimize a certain functionality (e.g., sequential biocatalysis) and if members are a mixture of both wild-type and engineered cells, they consider the consortium as semi-synthetic. This classification fits in only partially with some of the multiple terms used to characterize consortia in the bioremediation field. For these reasons, we consider that further analysis of the classification criteria is desirable to unify the use of language related to MC applied to bioremediation.

The classification of consortia as natural, artificial, and synthetic is based on the origin of microbial members (single source or multiple sources), the pre-existence of the microbial interaction in the source material, the level of human intervention on their composition (including genetic modifications), and the method used to obtain them. The quality of the microbe’s source (pristine or polluted, natural or synthetic material) is not considered here as a classification

criterion. To follow these ideas from a simplified point of view, it is possible to classify bioremediation-related MC considering some basal features that are described in the following sections.

For the development of engineered MC as bioremediation tools, it is important to consider that the existence of potential previous interaction among consortia members defines to a large degree their features and could be considered as the first level of classification: natural and artificial. The conservation or loss of these interactions depends largely on the method applied for consortium obtention and is a key issue to take into consideration (Table 1).

Natural microbial consortia

Microbial associations in which members were not deliberately chosen by humans could be considered as natural consortia. They occur (or may occur) in nature, come from a single source (e.g., a single soil), and are relatively simple to obtain through an enrichment method. They were used even without knowing their composition as a black-box approach. This simplicity made natural consortia useful tools for a bounteous number of applications beyond bioremediation (Lorah et al. 2008; Sabra et al. 2010; Marchevsky et al. 2015).

The enrichment procedure favors the development of some members of a whole naturally occurring microbial community. It is widely used for obtaining natural degrading consortia. By using a pollutant as the only carbon and energy source, it is possible to exert selective pressure on a microbial population and consequently obtain an enrichment culture with cells able to cope with the desired condition (Ma et al. 2021). It is also a powerful tool to obtain NMC containing species that would not grow on solid media since it allows contact among cells, favoring the interchange and interactions required to grow (Stewart 2012).

Although enrichment cultures alter the original microbial proportions, the resulting consortium may be considered a naturally occurring association because the interactions among its members might be present and active in the original matrix. It is also possible that the enrichment culture conditions trigger new associations and capabilities, different from those active in the community of origin. As reviewed by Joergensen and Wichern (2018), soil contains dormant microorganisms that do not grow due to C limitation. These microorganisms involve a set of metabolic capabilities that are turned off or functioning at a basal level. The changes in physical or chemical conditions provided by the enrichment culture can activate them, resulting in new interactions and abilities. An interesting analysis, including molecular and microbiological insights, was reported by Spini et al. (2018) for enrichment cultures to isolate

Table 1 Consortium types and main characteristics

Consortium Type	Main Characteristic	Important Traits	Useful Examples in This Review
Natural microbial consortium (NMC)	Previous interactions between the microbial members that comprise it can be assumed	<ul style="list-style-type: none"> • Microorganisms come from the same sample unit. • Low human intervention. • Characterized by its function rather than its members. • May include tedious/unculturable microorganisms 	Ambujom (2001); Milicic-Terzic et al. (2001); Ruberto et al. (2006); Lorah et al. (2008); Villaverde et al. (2018)
Artificial microbial consortium (AMC)	No previous interaction among members that comprise it	<ul style="list-style-type: none"> • Microorganisms come from different sources. • High human intervention. • Characterized by its members rather than its function. • Microorganisms are previously isolated 	Villaverde et al. (2012); Shahbaz Anwar et al. (2013); Shankar et al. (2014); Mnif et al. (2015); Patowary et al. (2016)
Synthetic microbial consortium (SMC)	A particular case of AMC, where microbial members are selected considering a defined task or function, usually complementary to those of other members	<ul style="list-style-type: none"> • Microorganisms come from different sources. • The highest human intervention. • May include -but not necessarily- GMMs. • The summum of consortium engineering 	Gilbert et al. (2003); Alnahhas et al. (2020)
Cross-kingdom consortium	A consortium consisting of at least, 2 microbial members from different kingdom	<ul style="list-style-type: none"> • Microorganisms may come from the same or from a different origin 	Ficker et al. (1999); Ellegaard-Jensen et al. (2014); Lee et al. (2018); Yuan et al. (2018)

oil-degrading microorganisms from soils. These authors found that soil depth as well as the number of enrichment steps did not significantly affect the composition of the microbial community obtained after enrichment. According to that, the resulting community after enrichments is shaped by the compound used as substrate and the microbes present in the source material (e.g., contaminated soil).

Examples of NMC for bioremediation are abundant. For instance, Ambujom (2001) studied a phenol-degrading bacterial consortium obtained after a 4 years-long continuous enrichment culture using sewage from a pumping station as a microorganisms source. Eight out of its ten members were able to degrade phenol. This consortium proved to be a stable composition and kept the ability to degrade phenol under different incubation conditions.

A natural PAH-degrading consortium from Antarctic soils was reported by our research group (Ruberto et al. 2006). Consortium M10 was obtained through four successive enrichment cultures using a mixture of phenanthrene, anthracene, fluorene, and benzo-a-pyrene as carbon and energy source. A deep analysis of its composition using a polyphasic approach combining culture-independent and culture-dependent methods evidenced the consortium was mainly composed of 17 different bacterial populations belonging to the *Pseudomonas*, *Sthenotrophomonas*, *Sphingomonas*, and *Brevibacterium/Pedobacter* genera (Ruberto et al. 2009; Vázquez et al. 2013).

Natural microbial consortia were also used for anaerobic bioremediation. In this sense, Lorah et al. (2008) reported the development and use of anaerobic NMC for the bioremediation of chlorinated volatile organic compounds. They collected microorganisms from sediment samples (Maryland, USA) and built two consortia (WBC1 and WBC2) based exclusively on liquid enrichment cultures using different substrates and subculture periods. WBC1 was obtained after a shorter enrichment time and WBC2 after 11 months. Both consortia were dominated by Clostridiales, 20% in WBC1 and 63% in WBC2. Interestingly, only a small fraction of bacteria present in those consortia (5%) were related to previously reported dechlorinating bacteria (e.g., *Dehalococcoides*) suggesting the presence of several unidentified microorganisms. WBC2 showed lower biodiversity than WBC1 but also a wider range of metabolic activities including fermentation, chemoautotrophy, homoacetogenesis, methanogenesis, and sulfur-cycling, probably due to complementary functions.

All the previous examples took advantage of the potential of (different) enrichment cultures in which the microbial community originally present in the sample evolved due to selection pressure. The result was an NMC whose composition and proportions were only conditioned by the original microbial community, the culture conditions, and time. From the microbial point of view, a single soil portion can

be perceived as a galaxy of countless microhabitats inhabited by different microbial populations (Vos et al. 2013). Naturally-occurring microbial interactions befall in these microhabitats that are much smaller than the sample (Bach et al. 2018). An enrichment culture takes a homogenized soil sample including a bazillion of microhabitats that are put together under the same conditions, resembling the Mos Eisley cantina at Tatooine (<https://www.starwars.com/databank/mos-eisley-cantina>).

Milcic-Terzic et al. (2001) developed a different method for the obtention of a natural degrading microbial consortium. The first step implied the culture of soil suspensions on agarized media with naphthalene, gasoil, and toluene as the sole carbon and energy source. The authors applied the term consortium to the whole biomass developed on the agar surface. After that, they harvested all the colonies and transferred them to a flask containing a liquid saline media with hydrocarbons as substrates. Similarly, Villaverde et al. (2018) built five NMC from contaminated agricultural soils, using consecutive enrichment cultures with the herbicide Diuron as carbon and energy source and a final cultivation on R2A agar from which consortia were obtained. The Diuron mineralization ability of each consortium was tested, finding that one of them (C1) was able to mineralize 81.6% of the herbicide in 29.7 days. Three bacterial strains were identified in C1: *Pseudoxantomonas indica*, *Bacillus anthracis*, and *Bacillus cereus*.

Solid media cultures modify the richness and evenness of the consortia. They only allow the development of microorganisms able to thrive in specific conditions and could distort proportions, considering the cell number present in colonies on agarized media differs significantly from that on liquid media. The resulting consortium composition, in this case, will be different from the one present in the matrix of origin and biased by the initial microbial isolation on agar plates. However, some of the natural interactions among members originally present in the soil would be partially respected, at least qualitatively. Thus, the resulting consortium involves an intermediate complexity level between the enrichment culture approach and the strain isolation/association approach.

Artificial microbial consortia

As an alternative to natural consortia, several authors reported the use of “handmade” or “artificial” associations for pollutant degradation. In these cases, microorganisms come from different sources and then are combined following some criteria. Consequently, it is possible to assume that AMC do not include preexisting microbial associations.

Artificial consortia are a large group of associations composed of selected strains and proportions. This type of

consortium is a useful tool for applied microbiology. The review published by Qian et al. (2020) summarizes applications of artificial consortia for human health, molecules production, biomass refinery, and bioremediation. Details about AMC used in bioremediation are discussed below.

The degradation of PVC was studied by Shahbaz Anwar et al. (2013). They combined equal proportions of strains isolated from different plastic waste disposal sites in India based on their degradation capacity, selecting a 4-bacterial strains consortium. Members were identified as *Pseudomonas otitides*, *Bacillus aerius*, *Acanthopleuribacter pedis*, and *Bacillus cereus*. Shankar et al. (2014) designed artificial hydrocarbon-degrading consortia by evaluating the isolates’ hydrocarbon-degrading ability using a basal medium with hydrocarbons (petroleum, diesel, and engine-oil) as substrate. *Bacillus* spp. and *Pseudomonas* spp. were selected and then four consortia were set. In biodegradation experiments, the consortium with the largest number of strains showed the highest rate of removal. Similar results, were previously observed by Ghazali et al. (2004), who built two hydrocarbon-degrading consortia by mixing equal proportions of each member. The first was a 3-member consortium composed of 2 strains of *Pseudomonas aeruginosa* and 1 strain of *Bacillus* sp. The second was a 6-member consortium composed of 2 *Pseudomonas aeruginosa* strains, 3 *Bacillus* spp. strains, and 1 *Micrococcus* sp. strain. Pesticide diuron degradation was studied by Villaverde et al. (2012). They focus the consortium design based on previously reported degrading strains, provided from two culture collections: *Arthrobacter sulfonivorans* and *Variovorax soli*. Lee et al. (2018) selected 6 bacteria strains and 1 yeast among 18 potential candidates based on their hydrocarbon degradation capacity as well as their hydrophobicity/emulsifying activity. Microbial strains were taken from different terrestrial environments in South Korea. This report constitutes an example of a cross-kingdom artificial consortium.

Patowary et al. (2016) took a different approach while looking for a robust bacterial consortium for crude oil degradation. They designed 14 hydrocarbon-degrading bacterial consortia combining 5 bacterial isolates (selected among 23 strains and based on their crude oil degradation ability) obtained from enrichment cultures from 3 different contaminated soil sites. The association of biosurfactant-producer and non-producer bacteria was tested. They obtained 84% TPH removal after 5 weeks of incubation using a consortium composed of two *Bacillus* strains: *Bacillus pumilus* and *Bacillus cereus*, both of which were biosurfactant-producers isolated from soils from different locations. The intentional inclusion of surfactant-producing bacteria provides a higher level of design complexity, making the consortium development more rational.

Similar criteria were considered by Mnif et al. (2015) for diesel biodegradation. Several AMC were developed

using strains isolated from hydrocarbon-contaminated soils in Tunisia. After testing different combinations, they found that a co-culture of an artificial consortium composed of three hydrocarbon-degrading bacteria and two surfactant-producing bacteria was the most efficient one. This association was able to remove 48.8% of the initial pollutant amount. Interestingly, these authors made a distinction between consortium and co-culture. They built an artificial consortium combining three strains of hydrocarbon-degrading bacteria (*Lysinibacillus bronitolerans*, *Bacillus thuringiensis*, and *Bacillus weihenstephanensis*) and considered the biosurfactant producing bacteria *Acinetobacter radioresistens* and *Bacillus subtilis* as co-inoculants and not as consortium members. This distinction seems to be founded on functionality.

Synthetic consortia: going to the next level of rational design

Among the variety of combinations that result in AMC arises a particular group designated as SMC. These are sophisticated versions of artificial consortia which require the inclusion of members considering a specific, known, and defined task or function, usually complementary to those of other members (Kim et al. 2011). This consortium classification may include — but not necessarily — those in which the genetic information of its members is modified to achieve tasks or cooperate in processes in a more efficient way than their wild-type counterparts (Mao et al. 2017). A clear example of such sophistication for SMC is provided by Alnahhas et al. (2020) who designed a consortium that autoregulates its members' proportions as a response to its composition ratio. More examples of these complex composition control mechanisms can be found in the review by Grandel et al. (2021). For Smith et al. (2013), what defines synthetic biology on SMC is the possibility of “predictably engineering novel behaviors in cells.” The idea of functional differentiation and metabolic complementation design in synthetic consortia has been reviewed by McCarty and Ledesma-Amaro (2019) for biotechnological applications and by Che and Men (2019) and Li et al. (2021) for bioremediation. Gilbert et al. (2003) worked with two genetically modified bacterial strains: *Escherichia coli* carrying plasmids encoding genes for a hydrolase and a green fluorescent protein (marker) and *Pseudomonas putida* carrying information for the p-nitrophenol mineralization. Using this consortium that involves a complementary catabolic pipeline, Parathion degradation without accumulation of its toxic metabolite, p-nitrophenol, was achieved.

The adjective “semi-synthetic” was used by Bernstein and Carlson (2012) to refer to consortia composed of wild-type

cells combined with genetically engineered ones. Alternatively, in a review about the use of SMC for biomining and bioremediation, Brune and Bayer (2012) named this kind of association as “hybrid consortia.”

Synthetic consortia are gaining attention in biotechnological fields apart from bioremediation (Zuroff and Curtis 2012; Minty et al. 2013) since through them, it is possible to complement a convenient naturally occurring activity with a tailored designed one, enhancing their potential. Nonetheless, due to environmental concerns about releasing genetically modified microorganisms (GMMs) to natural ecosystems, most microbial consortia for bioremediation are composed of “wild-type” microorganisms.

Cross-kingdom consortia

Both NMC and AMC, including SMC, can be composed of members from the same kingdom (Bacteria, Archaea or Eucarya) resulting in single-kingdom consortia or a mixture of members from different microbial kingdoms, resulting in **cross-kingdom consortia**. As described below, fungal-bacterial and archaeal-bacterial consortia are occasionally used in bioremediation. Additionally, microalgae-bacteria consortia are emerging as a biological tool for the remediation of wastewaters, as was deeply reviewed by Chan et al. (2022). In this work, single-kingdom and cross-kingdom are considered subcategories that come across the main ones (NMC and AMC, including SMC).

The strategies that fungi use to thrive in different environments turn them into suitable tools for the remediation of contaminated soils (Bennett et al. 2001). Fungi provide exoenzymes and the ability to rapidly colonize solid contaminated matrixes. Thanks to their filamentous growth, they can reach distant fractions of soil favoring contact with pollutants and other microorganisms. For instance, fungal-hyphae could be a way towards soil colonization by bacteria, a phenomenon named “fungal-highway,” favoring the migration of bacterial strains that are not able to do it alone (Furuno et al. 2010; Warmink et al. 2011). These studies address the basis of positive interaction between bacteria and fungi with high potential use in soil bioremediation.

Diuron degradation was studied on solid media using different microbial consortia by Ellegaard-Jensen et al. (2014). Combinations of previously isolated (multi origin) bacteria (*Sphingomonas* sp., *Variovorax* sp., and *Arthrobacter globiformis*) and fungi (*Mortierella* sp.) were tested. They obtained the highest Diuron mineralization with a three-member consortium composed of *Mortierella* sp., *Arthrobacter* sp., and *Variovorax* sp. The mineralization percentages showed that isolated strains degraded an average of 2.7% of the initial Diuron concentration, while two members consortia mineralized a mean of 4.6%, and

three members consortia 13.9%. Yuan et al. (2018) used an association between an “indigenous bacterial consortium” and a fungus. The bacterial fraction, named by the authors indifferently as consortium, co-culture, and co-culture of the indigenous bacterial consortium, was composed of two strains (*Paraburkholderia* sp. and *Paraburkholderia tropica*) enriched from contaminated soil, isolated on agarized media, combined in equal proportions, and conserved. The fungus was isolated from different oil-polluted soil and identified as *Scedosporium boydii*. Association of different proportions of bacterial and fungal fractions was evaluated, being 3:1 the most efficient for crude-oil degradation. The authors observed that biofilm formation over the fungus was beneficial for crude oil-biodegradation and favored the development of the consortium’s bacterial members.

Even though microbial assemblages containing archaea are abundant in nature, there are few reports about these microorganisms associated with bioremediation. A pioneer work using an anaerobic enrichment culture of creosote and pentachlorophenol-contaminated aquifer solids from Pensacola, Florida (USA), reported the activity of toluene and o-xylene degrading methanogenic consortium (Edwards and Grbic-Galic 1994). Later, the consortium was characterized by a molecular approach (Ficker et al. 1999) evidencing that it was composed of at least two methanogenic-archaea species (*Methanosaeta* sp. and *Methanospirillum* sp.) and two eubacterial species (*Desulfotomaculum* spp. and an unidentified bacteria). The consortium showed to be highly resilient, keeping degradative activity after starvation and even pasteurization.

New developments for the obtention and comprehension of microbial consortia

The enrichment methods for obtaining optimized MC are still under development looking for new strategies. Consortium simplicity and stability seemed to be related. The obtention of consortia with a reduced number of members (Simplified MC) keeping the essential function was explored by Kang et al. (2020). To do that, focusing on keratinolytic degradation, they developed a method based on the obtention of a (complex) MC through enrichment culture followed by dilution to extinction and re-culture, to obtain the simplest consortium retaining the desirable activity.

A different approach, used by Zegeye et al. (2019), seems to be promising for soil consortia developments. These authors used soil itself as culture media for successive enrichments to obtain and study a keratolytic microbial consortium. With this method, they obtained a richer composition than the one resulting from liquid media enrichment.

To rationally design SMC based on the potential interactions among members, a combinational algorithm was

proposed (Julien-Laferriere et al. 2016) and an application was developed (<http://multipus.gforge.inria.fr>). The algorithm is focused on the design and optimization of SMC for the production of molecules. However, it allows new insights into the research for the comprehension and optimization of pollutants degrading MC.

In the same way, Kuyukina et al. (2022) tested several associations of actinobacteria (*Rhodococcus*, *Dietzia*, and *Gordonia*) obtained from a microbial collection aiming to design a hydrocarbon-degrading artificial bacterial consortium. To do that, they selected one of the possible associations based on their resistance to a model oil. After that, the metabolic interactions among consortium members were evaluated using function-interaction modeling software (Nekrasov et al. 2015). They found that in a five-member consortium, the competition was the most frequent interaction. Amensalism, neutralism, and collaboration were found less frequently. The authors suggested that neutral interactions are a desirable feature for a degrading microbial consortium because it could result in a wide range of target molecules due to a narrower specialization of catabolic activities.

Interesting facts about microbial consortia

Going beyond the definition of what a consortium is, the lack of agreement about terminology allows different particular and heterogeneous uses of language to add information seeking for deeper descriptions of MC. An excellent example was provided by Lee et al. (2018) who added the idea of “native” to an artificial consortium built with 7 strains obtained from different soils from South Korea, to refer to the nationality. They call the association a “Korean native microbial consortium.”

The toluene degrading archaeal-bacterial consortium characterized by Ficker et al. (1999) showed to be stable (under the same culturing conditions) for 10 years, being one of the longest periods reported for a microbial consortium.

In a less explored field, Kachieng’A and Momba (2017) studied the efficiency of a protozoa consortium on hydrocarbon bioremediation. The authors selected three protozoa species isolated from petroleum wastewater sources that were known for their ability to remove heavy metals and other organic compounds. Although higher for the consortium than for the isolates, the biodegradation activities were not significantly different. Nevertheless, it is well established that the larger diversity of enzymes and synergistic relationships found in MC make them highly recommendable tools for bioremediation. Additionally, the bioremediation capability of the selected protozoa was better than that of many bacterial consortia frequently used to this end which proves

that beyond prokaryotes and fungi, there is a huge universe of microbes to consider for bioremediation.

In this way, going beyond functional complementation, Yeferni et al. (2022) explore the use of cross-kingdom consortia composed by a PAHs-degrading bacteria (*Shewanella oneidensis*) with four taxa of omnivore-carnivore nematodes (*Enoplolaimus longicaudatus*, *Rhabdodemia sp.*, *Mesacanthion monhystera*, *Enoploides spiculohamatus*) on marine sediments from Tunisia. They proposed that some nematode parameters can be used as phenanthrene-impact indicators in association with the degrading bacteria. What is more, the authors suggested that some of the nematodes would collaborate with phenanthrene removal.

As was evidenced in the previous paragraphs, the term consortium was used to describe a plethora of microbial combinations by scientists working on bioremediation. In that context, interactions among members can be demonstrated or can be putative, and the capability of improving pollutant degradation seems to be enough for a microbial association to be considered a consortium. This affirmation is based on the “common use” criterion. Bernstein and Carlson (2012) pointed out that MC engineering is a discipline focused on assembling microbial associations by enabling, encouraging, or enforcing interactions between distinct cell populations and their environment. From this definition, most microbial associations obtained through any method by humans are engineered MC. This criterion allows a differentiation or contrast with naturally occurring consortia, which inhabit ecosystems as members of microbial communities (Hamer 1997). Considering that, all MC referred to in this review, either natural or artificial, are a product of Microbial Consortia Engineering.

The complex network of interactions of natural degrading consortia explains their enhanced ability to cope with the environment and pollutants when compared to single strains. However, conservation, propagation, and stocking of consortia without further manipulation is a challenging task (Stewart 2012). In part due to these limitations, artificial consortia gain attention in bioremediation.

Microbial source for consortia development is a key factor to classify them. It could be a single one (unique origin) or more than one (multiple origins). The single-origin approach considers the possibility of recovering a natural existing interaction. Multiple-origin design is powered by the search of a wider degradative spectrum as well as more robustness to face different environments. This approach involves several potential constraints that are usually not checked. Compatibility among consortium members, which can never be taken for granted, especially when several microbial sources are included, is one of the most relevant limitations. After formulation, artificial consortia are evaluated for their efficiency to degrade

pollutants and the most efficient combination is chosen, leaving disregarded positive or negative interactions.

The obtention methodology also defines to a large degree consortia features. The combination origin/obtention methodology results in the first level of classification: natural and artificial. If members were already associated (in fact or potentially) from the beginning, a consortium could be considered an NMC. This kind of consortia is obtained mainly by enrichment cultures. The selection pressure defines the members' number and their proportions, as well as all possible interactions among them. Liquid enrichment cultures also allow the development of some fastidious microorganisms which get lost when trying cultivation on agarized media. Thus, through them, it is possible to obtain a higher diversity and pollutant removal efficiency than those obtained using strain isolation. In this way, Hamer (1997) proposed that a microbial consortium obtained through enrichment cultures could be constituted by degrading strains whose fastidiousness to growth is diminished by the interaction with other members. The higher ability of natural degrading consortium to cope with the environment and pollutants relies on their complex interactions network. The same network, however, makes conservation, propagation, and stocking of consortia obtained through this method a challenging, and unsolved, task. To sum up, it is possible to propose that an NMC has a single origin and that it is composed exclusively of wild-type microorganisms. During the enrichment procedure, interactions among members are selected and/or activated from the pool of those present (active or potentially possible) in the natural condition.

The size of the microbial source sample used to start an enrichment culture, especially when working with soils, is particularly relevant. In this sense, heterogeneous distribution of cells and substrates, microhabitats, diversity, and dormant microorganisms (Bach et al. 2018; Joergensen and Wichern 2018) should be taken into consideration. Using a larger sample could include a wider variety of microhabitats and thus more diverse microorganisms, which would result in richer interactions and novel consortia.

At this point, a question arises: if manipulation (e.g., culture on agarized media) modifies qualitatively the microbial composition that could have been obtained from the enrichment culture of a single source (e.g., a soil or water sample point), should the consortium be considered an AMC or an NMC? In this review, the criterion of origin and “potential existence of the microbial association in the source material” was taken into account, classifying them as “natural.” However, this issue should give place for further research and discussion. In this sense, the case reported by Milcic-Terzic et al. (2001) represents a particular case of a natural consortium, isolated through selective conditions: the ability to grow and use hydrocarbons on solid media and the ability to grow and use hydrocarbons in liquid media. This approach

allows the obtention of a consortium to be culturable without important differences in solid or liquid media. This feature is not minor, considering that consortia isolated by enrichment on liquid media often show limitations to grow on agarized ones (Stewart 2012) and thus present drawbacks for stocking and propagation. However, the price to pay for growth capability in solid media is represented by the loss of members and interactions, which are only possible when solid media-associated restrictions are not applied.

Both kinds of consortia, natural and artificial, can present a cross-kingdom composition. Bacteria and fungi are the most prevalent microorganisms forming pollutant-degrading consortia. Archaea started being relevant for the design of the bioremediation process, especially for some extreme environments (Krzmarzick et al. 2018). Members of this kingdom have been identified and reported using molecular biology tools as a component of naturally occurring degrading consortia (Zvyagintseva et al. 1995; Wu et al. 2001; Al-Mailem et al. 2012). However, up to date, there are few reports of the intentional use of a biodegradative consortium with archaeal members.

In an excellent review regarding cross-kingdom MC intended for biotechnology, Zhang et al. (2018) included some definitions. The literature analysis made in this work agrees with most of them, with the only exception of those for the engineered consortium. They defined it as those containing GMMs while for other authors, as was stated before, this definition fits better to the idea of hand-made consortia, obtained from the environment or assembled by humans, through different methods (Brenner et al. 2008; Lindemann et al. 2016; Roell et al. 2019).

We propose here that the classification made by Bernstein and Carlson (2012) could be enriched considering that NMC include associations of microorganisms that may be interacting in their natural environment but are taken away from it, cultured and re-associated, or re-assembled in a different proportion than those occurring in the environment. As stated in the previous lines, this kind of consortia is one of the most common ones reported for bioremediation. Additionally, we consider the term “semi-synthetic consortium” is redundant, since “synthetic” refers to the design and/or engineering of microbial interactions, beyond the presence or absence of genetic modifications. Nevertheless, as with most classifications, those proposed in this article present gray zones. For example, the inclusion of surfactant-producing bacteria in a hydrocarbon-degrading consortium (Mnif et al. 2015) implies the addition of a member with a defined and known task (biosurfactant production in this case), providing some features of a synthetic consortium. New developments, as well as new uses of known tools or techniques, permanently move limits, demanding flexible classifications and continuous revision of this topic. Consortium stability, or the ability to maintain a stable composition (qualitative

and quantitative), is a desirable feature for a consortium to be used as a technological tool for bioremediation and other applications. Consortia stability can be inferred following the idea of diversity. In this sense, both richness (number of species) and their abundance should be conserved. One of the main objectives of successive enrichment cultures is the obtention of a stable consortium. This goal is challenging when heading the development of a microbial consortium for bioaugmentation, particularly since each re-enrichment culture step represents a new condition and a unique dynamic. It was reported that the bacterial community coming from a single hydrocarbon-contaminated soil through successive enrichment cultures using several n-alkanes (differing in one C atom) as substrate showed a divergent evolution in their composition and no stability was demonstrated after 3 cultivation stages (Kuc et al. 2019). In a different study, where enrichment in soil containing chitin and N-acetylglucosamine was made (Zegeye et al. 2019), relative stabilization of MC was reported after 15 weeks. These reports and the consideration that microbes-pollutant interactions are dynamic raise the question: how stable can MC be? What do we mean when we speak about stability? Is it possible to achieve consortia stability when working with an irregular substrate feed? Is it possible to reach stability in polluted soils, where concentrations are heterogenous and continuously changing? Further research is needed to robustly answer these questions.

Most pollutant-degrading MC are developed to remove contaminants from soil and/or water to return them to the environment after treatment. This fact strongly conditions the use of GMMs members for artificial consortia, as GMMs use is considered risky for environmental health (Gustafsson and Jansson 1993; Velkov 1996; Stemke 2004). For this reason, this option should be set apart for high recalcitrant and toxic pollutants, when no other options are available, or for closed systems designs, without releasing them to the environment.

The idea of consortium is strongly related to cooperation among its members. In their excellent review of social evolution theory for microorganisms, West et al. (2006) define cooperation as “a behavior that increases the fitness of the recipient”, distinguishing between mutually beneficial (win–win) or altruistic (the actor pays a cost) cooperation. This classification involves another question: does cooperation really exist in degradative consortia? Sequential degradation works when the by-product of one actor is used by another actor. If the by-product is produced by member A of the consortium as a pollutant degradation metabolite independently of the presence (and potential benefit) of member B (who can consume it), there would be no cooperation *sensu stricto*. Again, West et al. (2006) define it as a one-way by-product benefit. However, by-product removal by B decreases its concentration, thermodynamically favoring

pollutant degradation by A (Gieg et al. 2014). In that case, a shared interest emerges from A and B selfish behaviors, leading to real cooperation or complementation. Wu et al. (2021), working on the development of bacterial consortia for effective oil degradation, reported a negative interaction between a *Pseudomonas alcaligenes* strain NBRC and a *Microbacterium oxydans* strain CV8.4. While testing several bacterial combinations, these authors observed a significant decrease in oil degradation efficiency when increasing volumes of these strains were added to the mixtures. Based on a partial correlation analysis, they concluded that these strains were mutually antagonistic and should not be combined for oil-degrading consortia design. Islam et al. (2020) reported another example of bacterial antagonism (between *Pseudomonas aeruginosa* and *Bacillus cereus*) during the development of inoculums for a microbial power-generation process. Besides these reports, negative interactions are poorly described for pollutant-degrading consortia. This happens mostly because they are selected based on their removal efficiency, leaving aside ecological interactions. Under this selection criterion, competition for the C source passed unnoticed because, despite being a negative interaction, it results in pollutant removal. Negative interactions in soil microbial communities are hard to study as is reflected by Romdhane et al. (2022). These authors studied the role of negative interactions in soil re-colonization experiments, finding that exclusion competition between certain bacterial families (e.g., Bacillales and Proteobacteriales) is a key factor for microbiome shaping.

Quantitative relationships are rarely considered to design degrading consortia. As a complex mixture of interacting microbial populations, a consortium could lead to the preferential development of one population (due to growth rate) over the other populations. NMC composition results from the interaction of members under certain conditions inherent to their source. In AMC, the initial amount of each member is of utmost importance (Roell et al. 2019).

Conclusion

Microbial consortia used for bioremediation are a heterogeneous group of associations obtained through a wide variety of methods. However, it is possible to rationally classify them facilitating comprehension and comparisons. Applying the “common use” criteria, MC developed for bioremediation could be classified as natural or artificial considering the method applied for their obtention and the source material used. A deeper level of complexity allows us to describe some artificial consortia as “synthetic.” In all cases, cross-kingdom combinations are possible.

Author contribution FM and NB collected and analyzed the data, wrote, drafted, and reviewed the manuscript. LMA and MMM collected data, and WPC wrote and reviewed the manuscript. LR conceptualized the idea, performed experiments, and wrote the manuscript. All authors read and approved the final manuscript.

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Declarations

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

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