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Review Paper

Deliberate introduction of invisible invaders: A critical appraisal of the impact of microbial inoculants on soil microbial communities

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ABSTRACT

Non-target effects of deliberately released organisms into a new environment are of great concern due to their potential impact on the biodiversity and functioning of ecosystems. Whereas these studies often focus on invasive species of macro-organisms, the use of microbial inoculants is often expected to have specific effects on particular functions but negligible overall effects on resident microbial communities. Here, we posit that such introductions often impact native microbial communities, which might influence ecosystem processes. Focusing on soil communities, we used a literature search to examine the impact of microbial inoculation (often the release of beneficial microorganisms in agricultural systems) on resident microbial communities. Of 108 studies analyzed, 86% showed that inoculants modify soil microbial communities in the short or long term. In addition, for studies analyzing the consequences of microbial inoculants in the longer term, 80% did not observe the resilience (return to the initial state) of the resident community following inoculation. Through the knowledge gathered from each study, we propose a synthetic and mechanistic framework explaining how inoculants may alter resident microbial communities. We also identify challenges as well as future approaches to shed more light on this unseen reality.

1. Microbial invasions

Fortuitous and deliberate introduction of non-native organisms across biogeographic barriers by human activities can perturb and subsequently alter biological diversity over space and time (Vitousek et al., 1997; Gaston et al., 2003; Hulme, 2009). Ecologists have shown that the invasion of habitats by exotic macro-organisms poses a significant threat, not only to the extinctions of resident species but also to ecosystem functioning in various environments (Roy et al., 2019). Human-mediated invasion (HMI) can decrease native species richness and evenness (Blackburn et al., 2004) as well as change the composition (Shiganova et al., 2001) and genetic diversity of resident communities (Kreiser et al., 2000; Kawamura et al., 2006; Roman and Darling, 2007). Many studies have focused on the impacts of introducing particular species on resident plant or animal communities (Pyšek et al., 2012; Falcão et al., 2017; Wainwright et al., 2017). Well-known examples are the effects of introducing predatory species to regulate prey populations on islands, potentially leading to undesired impacts on the native communities (Kenis et al., 2009; Bahlai et al., 2015). Aside from such negative consequences, invasion could also render positive outcomes and be perceived as beneficial. In particular, HMI can increase the abundance of some taxa and promote key ecosystem services (Simberloff et al., 2013).

Contrary to large organisms, studies on the impact of microbial invasions are less frequent (Litchman, 2010), despite the fact that microbes have been intentionally released into open environments for a long time. Some microorganisms are naturally released to the atmosphere (Morris et al., 2014), aquatic (Amalfitano et al., 2015), and terrestrial ecosystems (Weil et al., 2017), but for deliberate invasion, it is mostly the case in the environmental/agricultural sector, where introduced microorganisms are used for soil bioremediation, biocontrol, and biofertilization purposes (Vejan et al., 2016; Ahmad, 2017). In addition,

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microbial releases into soil are emerging as an approach for the conservation or restoration of biodiversity (Harris, 2009; Sutherland et al., 2019). Soil microbial introductions thus aim at regulating or improving ecosystem processes and services such as the promotion of plant yield, litter decomposition, nutrient cycling and the maintenance of soil fertility (Ouahmane et al., 2007; Bounaffaa et al., 2018; Rodríguez-Caballero et al., 2018; Tamayo-Vélez and Osorio, 2018). However, the effects sometimes deviate from the intended purposes. For instance, the introduction of *Fusarium* and *Rhizoctonia* strains to control invasive weeds can lead to a decline in the weed population and suppress the native plant species, through synergistic interactions with root-disrupting insects and other potentially growth-suppressive microbes (Kremer et al., 2006). Even though the soil microbial community might have the ability to reorganize and return to the original state (resilience) after the disturbance induced by inoculation, this result highlights the potential ecological and evolutionary impacts of microbial inoculation to soil resident communities, which remain largely unknown. Understanding the effect of microbial inoculation on soil microbial communities may be hampered by the overwhelming diversity of the latter and by hurdles in the methods used to characterize this diversity (Allison and Martiny, 2008; Le Roux et al., 2011; Jurburg and Salles, 2015). Moreover, the assumed ubiquity of microbial species, their rapid growth, and high level of functional redundancy (Wertz et al., 2007) may also explain why inoculant-induced changes in the composition of soil microbial communities were either assumed to be insignificant or just overlooked. However, as the use of microbial inoculants increases with the deployment of sustainable agricultural practices (Verma et al., 2019), research needs to better evaluate to what extent such introductions, successful or not, impact the resident microbial communities. Recently, Trabelsi and Mhamdi (2013) evaluated 15 studies addressing the impact of inoculation on those soil microbial communities they considered mostly significant. Clearly, several of these studies revealed substantial impacts of the inoculants on soil microbiomes. In addition, Ambrosini et al. (2016) presented an overview of plant-inoculant interactions and their impacts on microbial communities, indicating that these interactions might promote positive effects on soil fertility. Given the relevance of the topic, we present here the results of a systematic literature review on the extent to which soil communities are influenced by microbial releases, whether the soil microbiome is capable of returning to the original state after disturbance (resilient) as well as the mechanisms driving these potential inoculation-induced changes in soil microbial community.

Regarding microbial releases in an agricultural context, the European Regulation Number 1107/2009, Article 24, expects firms or practitioners to demonstrate that there are no 'unacceptable effects on the environment', and states that the objective to protect human, animal and environmental health should predominate regarding the objective to increase plant production (Commission, 2009). This is open to interpretation, but lack of inoculant persistence in the environment and of important effects of the inoculant on the soil microbiota are often expected, in addition to a significant effect on the targeted agro-ecosystem function. Actually, microbial releases into soil often result in transient loads of inoculant that quickly fade away with time. For instance, it has been shown that following maize seed inoculation with *Azospirillum lipoferum* CRT1, the inoculant disappeared at the 6-leaves stage (Florio et al., 2017). Given this transitory survival, many practitioners and scientists assumed that microbial releases would have negligible effects on the resident soil microbial communities. However, quick disappearance of a bacterial inoculum in soil does not necessarily imply a lack of lasting legacy on the soil resident community. For example, the introduction of non-pathogenic *Escherichia coli* into soil shifted the niche structure and increased the niche breadth of resident bacterial communities, leading to changes in the relative abundances of important bacterial genera in soil such as *Bacillus*, *Pseudomonas*, *Burkholderia*, and *Bradyrhizobium* (Mallon et al., 2018).

In this review, we posit that the effect of microbial inoculation on soil resident microbial communities is often significant. In the first part, we examine the significance of shifts in resident microbial composition in response to inoculation and their potential to influence soil ecosystem processes. We base our analyses on a systematic literature search and more detailed presentation of selected examples, highlighting that microbial inoculants do not need to be long-lasting in soil to alter resident communities. In the second part, we discuss microbial community resilience and recovery time, i.e. we examine whether the inoculant-induced shifts are transient or persistent. We then present our current understanding of the mechanisms that underly the alteration in resident microbial abundance, structure, and activities. Finally, we describe the current challenges and recommend potential approaches to foster our knowledge in this area.

2. Microbial releases can modify the structure of native soil communities

To evaluate whether microbial inoculants alter soil microbial community composition, we reviewed studies that addressed the impact of microbial inoculation on soil microbial communities. A search in Web of Science on February 27, 2019 using the keywords (''impact'', ''inocul*'' and ''microbial communit*'') or (''effect'', ''inocul*'' and ''microbial communit*'') in their titles, abstract, or subject words generated 855 references. Screening process on their abstracts and titles reduced the 855 hits to 125 relevant articles (Fig. 1a). Studies that were not conducted in soil, did not employ microbial inoculation, and whose impact did not refer to native soil microbial communities, were excluded. The full text of each of these 125 articles was assessed; from these, 17 studies that relied only on plate counts were excluded due to methodological issues associated with cultivation constraints. From the remaining 108 studies, 86 used bacterial inoculants, 22 inoculated fungi, while only 2 used the combination of both. All included proper control samples and when inoculation implied soil disturbance (e.g. sowing with seeds coated with an inoculant in Florio et al., 2017), we verified that the control included the same disturbance (e.g. sowing with non-inoculated seeds). We further grouped the studies into three categories according to the method used to measure the impact on resident soil microbial communities: 26 studies used high throughput sequencing (HTS) (Figs. 1b), 78 used profiling methods including molecular, fatty acid, and physiological profiling (Fig. 1c), and 4 used quantitative PCR targeting particular taxonomic or functional groups (Fig. 1d). Here, we decided to group studies that used profiling methods along with HTS in an HTS method cluster while studies that used sanger sequencing of amplicon clone libraries derived from specific DGGE bands were included in a profiling method cluster.

The complete list of HTS method-based studies with all related information and parameters is displayed in Table 1. The lists of the 78 studies using profiling methods and of the 4 qPCR-based studies can be found in the supplementary document (Tables S1 and S2). The result showed that, in over 96% of the HTS studies, microbial release led to changes in microbial community composition. For studies using profiling methods, 82% showed an impact following inoculation whereas 18% did not report any significant effect. Those corresponded to 14 studies based on molecular profiling such as DGGE and [T]RFLP. Regarding studies using qPCR targeting taxonomic or functional groups, all of them reported a significant impact (Fig. 2). In general, 30% of the studies using DGGE, TGGE, or [T]RFLP did not report any significant effect of inoculation whereas the other methods did, highlighting that the outcome might be associated with the method used to characterize inoculant effect of the soil resident community. Furthermore, studies that used HTS in combination with other methods (11%) indicate that impact was observed for all methods tested. Keeping in mind these methodological limitations, the data presented in the 108 studies allow us to draw a few generalizations.

First, changes in microbial composition in response to microbial release were observed in different conditions and through diverse

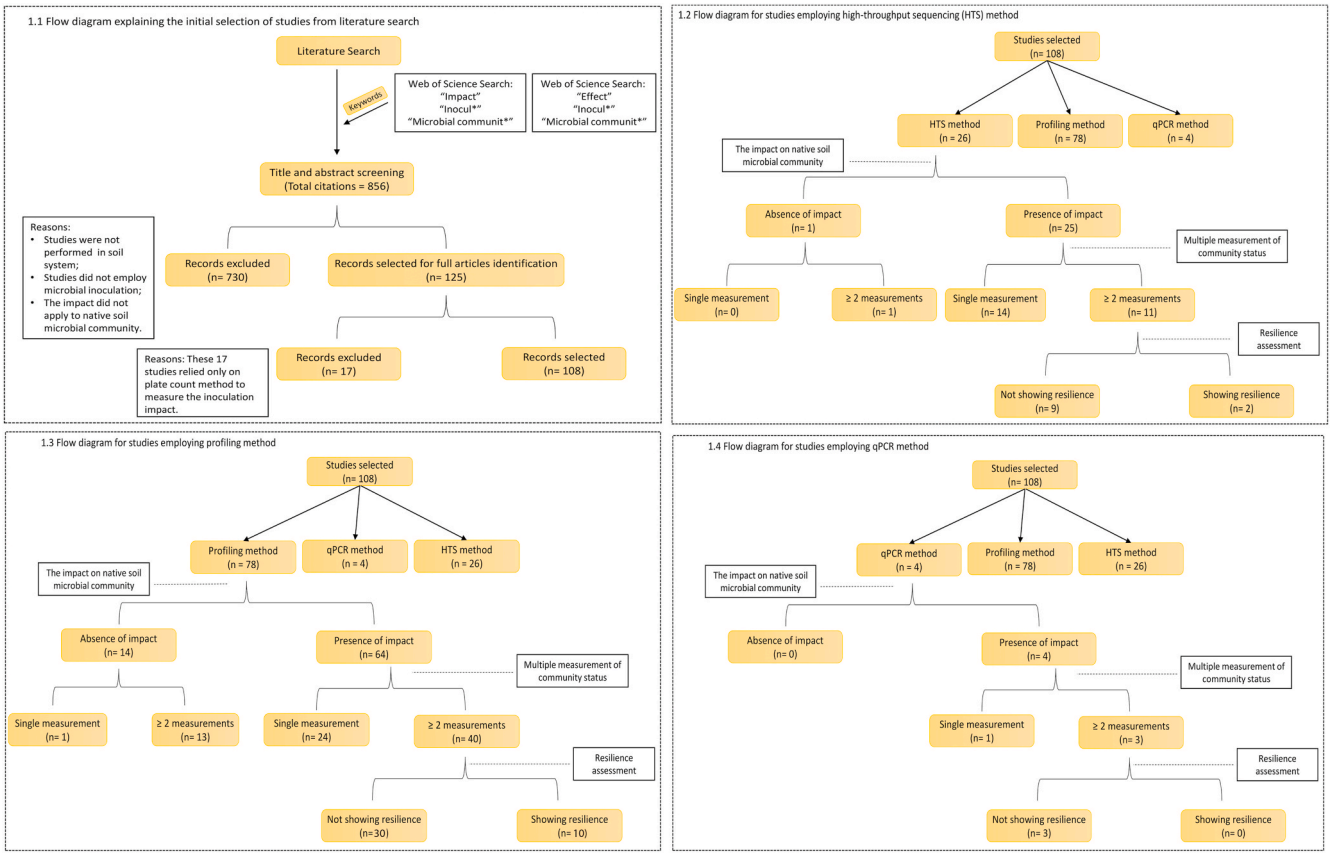


Fig. 1. Flow diagrams describing the process of article selection and screening of selected articles based on the presence/absence of impact, multiple measurement of impact, and evaluation of post-inoculation resilience. Fig. 1a describes the selection process of studies which consist of abstract screening and full text assessment, providing the reasons of possible exclusion of a given study. Fig. 1b describes the identification of studies employing high-throughput sequencing (HTS). Studies that used profiling methods along with HTS were included in HTS method. Fig. 1c describes the identification of studies employing profiling methods, including molecular (i.e. DGGE, TRFLP, ARISA), fatty acid (i.e. FAME, PLFA) and physiological (CLPP) profiling methods. Studies that used Sanger sequencing of amplicon clone libraries derived from specific DGGE bands were included in profiling method. Fig. 1d describes the identification of studies employing qPCR methods.

methodological approaches. For example, using amplified ribosomal RNA gene restriction analysis (ARDRA) and 16S rRNA gene amplicon sequencing, the release of *Sinorhizobium meliloti* L33 was found to reduce the diversity of beneficial *Pseudomonas* spp, including *Pseudomonas putida* in the rhizosphere (Schwieger and Tebbe, 2000). Furthermore, the release of biofertilizer containing *B. amyloliquefaciens* W19 and *Trichoderma guizhounse* NJAU 4742 enhanced the abundance of taxa with potentially antagonistic effect towards plant pathogens (*Lysobacter* spp, Gp4 and Gp6 of the *Acidobacteria*, *Bacillus*, as well as *Nitrospira* spp), as determined by amplicon sequencing of the 16S rRNA gene (Xiong et al., 2017). This result might be caused by a synergism effect or the ability of inoculants to recruit microbes with such traits (for detail of mechanisms, see next section). In this sense, the release of an inoculant can potentially affect the structure of the resident soil communities. Microbial invasion might also impact the genetic diversity of indigenous resident communities through interactions and horizontal gene transfers (HGT) favoring genetic changes. Transfer of a mobilizable plasmid was found in the wheat rhizosphere in the field, from Pseudomonas fluorescens to Gram-negative bacteria with dominance of Enterobacter spp (Van Elsas et al., 1998). HGT has also been observed in Brazil, where massive inoculation of soybean specific *Bradyrhizobium* strains takes place every cropping season (Araujo et al., 2012; Hungria and Mendes, 2015). For instance, Barcellos et al. (2007) and Silva Batista et al. (2007) observed high rates of horizontal transfer of symbiotic genes from the inoculants *Bradyrhizobium japonicum* and *Bradyrhizobium elkanii* to indigenous rhizobia in the Cerrado. In India, Satya Prakash and Annapurna (2006) and Ansari et al. (2014) reported an increase in the genetic diversity of indigenous soil Rhizobia following massive inoculation of *Bradyrhizobium* commercial strains.

Second, inoculation-induced changes in abundance and structure of soil microbiomes might lead to shifts in the functioning of the latter. For instance, the overrepresentation of microbes having antagonistic effects on plant pathogens can induce suppressiveness in conducive soil (Shen et al., 2015; Xiong et al., 2017). Moreover, the abundance of bacteria known to cause N losses and induce plant diseases such as *Rhodanobacter* spp and *Mycobacterium* spp, respectively, decreased upon the introduction of *Paenibacillus mucilaginosus* 3016, whereas the abundance of beneficial bacteria such as *Bradyrhizobum* spp and *Pseudomonas* spp increased. Importantly, these changes were related to modified enzymatic activity levels in the soil (Ma et al., 2018). Actually, several studies showed that the introduced microbial inoculants could change soil phosphatase, sulfatase, chitinase, esterase, urease, and other enzyme activities, thus impacting nutrient cycling, fertilization, decomposition and biocontrol activities (Mar Vázquez et al., 2000; Nassal et al., 2018; Wu et al., 2018).

Third, based on studies presented in the aforementioned tables, even though the abundance of inoculants decreased – sometimes below the detection limit – following inoculation, microbial community composition was still impacted (Kozdrój et al., 2004; Cordier and Alabouvette, 2009; Mallon et al., 2018). In some cases, when invader survivability became low, the impact was found to be transient (Johansen and Olsson, 2005; Baudoin et al., 2009; Yin et al., 2013). However, we advocate that the magnitude of this impact, either long-lasting or transient, might not necessarily relate to the fate of the inoculant populations. As shown in

Table 1
Studies evaluating the impact of microbial inoculation on soil microbial communities based on a High-Throughput Sequencing method.

N°	Introduced microbial species	Inoculant survival monitoring	Inoculation number/ frequency	Microbial community change[a]	Time of measurements of soil community status	Resilience of soil community	Method to characterize the soil community	Authors
1	*Bacillus thuringiensis* strain IAM 12077	N/A	2x	No	at 1 year after inoculation	No	PLFA, *16S and 18S rRNA gene* sequencing	Armada et al. (2018)
2	*Azospirillum* sp. B510	N/A	1x	Yes	at 51 days after transplanting	No	454 pyrosequencing targeting 16S rRNA *gene*	Bao et al. (2013)
3	*Pseudomonas* sp IAC-RBal1, IAC-RBal2, IAC-RBal3, IAC-RBcr2, IAC-RBcr5, IAC-RBmi1, IAC-RBcr1, IAC-RBcr3, IAC-RBcr4, IAC-RBcr6, IAC-RBru1, IAC-RBal4	N/A	2x	Yes	at 4 weeks after planting in the field experiment	No	16S rRNA sequencing	Cipriano et al. (2016)
4	*Pseudomonas* sp. 4311, *Pseudomonas* sp. 4312, *Azospirillum brasilense* Ab-V5, and *Achromobacter* sp. VC36	N/A	1 x	Yes	10 days after plant emergence	No	Ilumina Sequencing targeting 16S rRNA *gene*	da Costa et al. (2018)
5	Biofertilizer containing *Bacillus amyloliquefaciens* NJN-6	Yes, survived and showed relatively stable abundance of vegetative cells between 2.5 and 3.0 log copies/gram soil every year	Continuous	Yes	1,2, and 3 years after inoculation	No	454 Pyrosequencing targeting 16S rRNA *gene* and ITS region	Fu et al. (2017)
6	*Funneliformis mosseae*	N/A	1x	Yes	at 0, 90, 120, 150, and 180 days after planting	No	16S rRNA *gene* sequencing	Gui et al. (2017)
7	*Bacillus aryabhattai* and *Bacillus megaterium*	Yes, but not detected	5x	Yes	at 2, 6, and 8 weeks after inoculation for inoculated soil and at 0 and 8 weeks after inoculation for non-inoculated soil	No	pyrosequencing targeting 16S rRNA *gene*	Jeong et al. (2013)
8	*Rhodopseudomonas palustris*	N/A	4x	Yes	at 122 day after transplanting	No	Ilumina Miseq targeting 16S rRNA *gene*	Jiangbing et al. (2018)
9	*Paenibacillus mucilaginosus* ACCC10013 and *Sinorhizobium meliloti* CCNWSX0020	N/A	1x	Yes	at 90 days after inoculation	No	Ilumina Miseq targeting 16S RNA gene	Ju et al. (2019)
10	*Bacillus amyloliquefaciens* FZB42	N/A	2x	Yes	at 0,2,5 weeks after planting	No	Metagenome sequencing targeting bacterial DNA	Kröber et al. (2014)
11	*Enterobacter ludwigii, Rhodococcus erythropolis, Enterobacter cancerogenus, Cedecea davisae, Arthrobacter sp.,*	N/A	1x	Yes	at 3 months	No	454 pyrosequencing targeting 16S rRNA *gene*	Liu et al. (2015)
12	*Bacillus subtilis* XF-1	N/A	3x	Yes	cotyledon stage, seedling stage, rosette stage, early heading stage, and mature stage	Yes, after seedling stage for fungal community	454 pyrosequencing targeting 16S rRNA *gene* and ITS region	Liu et al. (2018)
13	*Paenibacillus mucilaginosus* 3016	Yes, the number was not indicated	1 x	Yes	One time after harvesting	No	Ilumina Sequencing targeting 16S rRNA *gene*	Ma et al. (2018)
14	*Escherichia coli* O157:H7	Yes, fell below detection limit of 500 cells/g, 75 days after inoculation.	1 x	Yes	0 day (inoculation) and 28 days after	No	454 Pyrosequencing targeting bacterial 16S rRNA *gene* and CLPP	Mallon et al. (2018)
15	*Metarhizium brunneum* strain ART2825	Yes, increased from 56 to 144 CFU g−1 soil dry weight to 5569–17 596 CFU g−1 soil dry weight in pots treatment at week 7 after inoculation;	1x	Yes	0,7,15 weeks after inoculation for pot treatment and 0,9,16 weeks after inoculation for field treatment	No	Ilumina Miseq targeting 16S rRNA *gene* and ITS region	Mayerhofer et al. (2017)
16	FR140® (*Funneliformis mosseae*, MycAgro Ltd., France), Solrize® (Glomus sp., Agrauxine Ltd., France), *Septoglomus constrictum, Claroideoglomus lamellosum, Funneliformis geosporum,* and *Funneliformis mosseae*).	Yyes through root colonization percentage (28–70% for indigenous and 40–58% for commercial)	1x	Yes	24 weeks after inoculation	No	Ilumina Miseq targeting 16S rRNA *gene* and ITS region	Meglouli et al. (2018)

(*continued on next page*)

Table 1 (*continued*)

N°	Introduced microbial species	Inoculant survival monitoring	Inoculation number/ frequency	Microbial community change[a]	Time of measurements of soil community status	Resilience of soil community	Method to characterize the soil community	Authors
17	*Bacillus subtilis* PTS-394 and the GFP-tagged strain of *B.subtilis* PTS-394G containing the plasmid pGFP22	Yes, survived at 1.7×10^6 CFU/g root 9 days after inoculation	1x	Yes	1, 3, 7, 9 and 14 days after inoculation	Yes, after 3 days for bacterial community and 14 days for eukarya community	454 pyrosequencing targeting 16S rRNA *gene* and ITS region	Qiao et al. (2017)
18	*Glomus mosseae* M47V	Yyes 52% +- 6%	1x	Yes	at 40 days after transplantation	No	Ilumina Miseq targeting 16S rRNA *gene* sequencing	Qin et al. (2016)
19	Biofertilizer containing *Bacillus subtilis* SQR-9, *Paenibacillus polymyxa* SQR-21, *Trichoderma harzianum* SQR-T037	N/A	Continuous	Yes	40 days after inoculation	No	454 Pyrosequencing targeting 16S rRNA *gene*	Qiu et al. (2012)
20	*Pseudomonas jessenii* RU47	N/A	3x	Yes	3 weeks after planting in 2010 and 2 weeks after planting in 2011 and 2012	No	PCR DGGE and 454 pyrosequencing targeting 16S rRNA *gene*	Schreiter et al. (2014a)
21	*Mesorhizobium ciceri* ST282 and *Bacillus subtilis* Ch13	N/A	1x	Yes	at 40 days after sowing	No	454 pyrosequencing targeting 16S rRNA *gene*	Shcherbakova et al. (2017)
22	*Bacillus amyloliquefaciens* strain ZM9	Yes, survived at 1×10^7 CFU/g in the rizosphere	1x	Yes	at 1, 6, and 15 weeks after inoculation	No	Ilumina Miseq targeting 16S rRNA *gene*	Wu et al. (2016)
23	Biofertilizer containing *Bacillus amyloliquefaciens* W19 or *Trichoderma guizhounse* NJAU 4742	N/A	1 x	Yes	1 year after inoculation	No	Ilumina Sequencing targeting 16S rRNA *gene* and ITS	Xiong et al. (2017)
24	Biofertilizer *Bacillus amyloliquefaciens* W19 and *Trichoderma guizhouense* NJAU4742	N/A	1 x	Yes	1 year after inoculation	No	Ilumina Sequencing targeting 18S rRNA gene	Xiong et al. (2019)
25	*Pseudochrobactrum* sp. BSQ1 and *Massilia* sp. BLM18	Yyes but the level was not specified	1x	Yes	0,14, and 35 day after inoculation	No	Illumina HiSeq targeting 16S rRNA *gene*	Xu et al. (2018)
26	*Trichoderma harzianum* T-63	N/A	2x	Yes	at 30 days after second inoculation	No	16S rRNA *gene* and ITS region sequencing	Zhang et al. (2018)

[a] In order to determine the status of the impact on microbial community structure, it was assessed whether the changes are statistically significant or not: Yes means the changes are statistically significant whereas; No means otherwise.

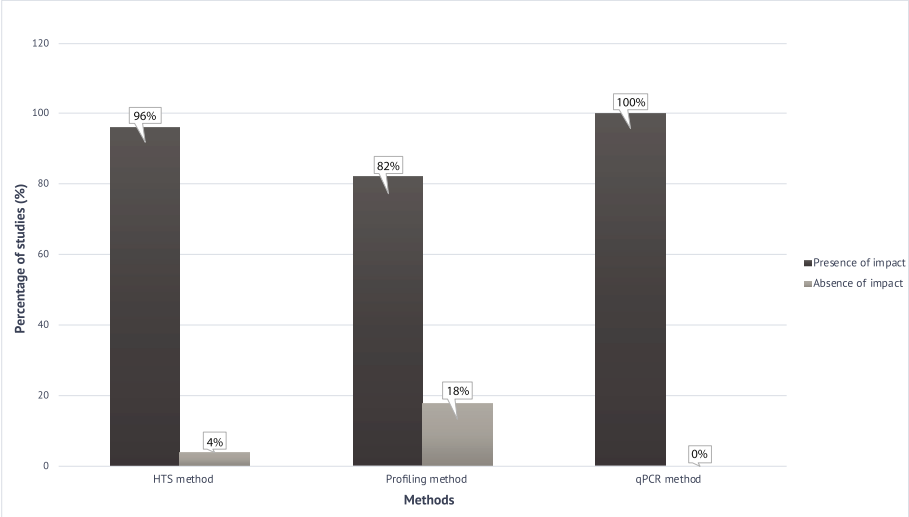


Fig. 2. Proportion of published studies that report presence or absence of microbial inoculation impact with respect to methodology used to detect such effects.

several studies, even though the number of inoculant cells declined following introduction into soil, changes in community composition persisted (Kozdrój et al., 2004; Renoud, 2016; Mallon et al., 2018).

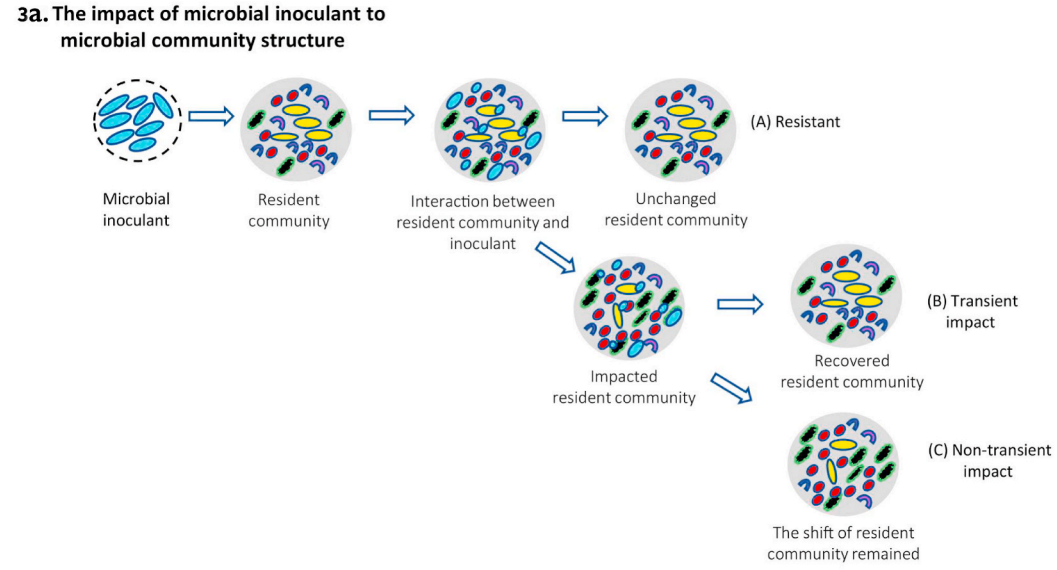
It remains unclear whether the measured changes are due to direct effects from the inoculants or indirect effects, for instance through nutrients released from dead or moribund inoculant cells. In the case where the inoculants survive to a level sufficiently high for the intended purposes, the effect is likely due to the inoculants themselves. For example, Fu et al. (2017) observed long-lasting changes in microbial composition when the inoculant, *Bacillus amyloliquefaciens* NJN-6, showed relatively stable abundance between 2.5 and 3.0 log copies of 16S rRNA gene/-gram soil within 3 years of experiment. On the other hand, one could argue that when survival is low due to biotic and abiotic factors, the observed changes in community structure could at least partly be due to the nutrient flush caused by dead (lysed) inoculant cells, which in turn could promote an increase in the abundance of some resident taxa (but see next section for an alternative explanation). Regardless of the potential mechanism, an impact can be observed in most cases.

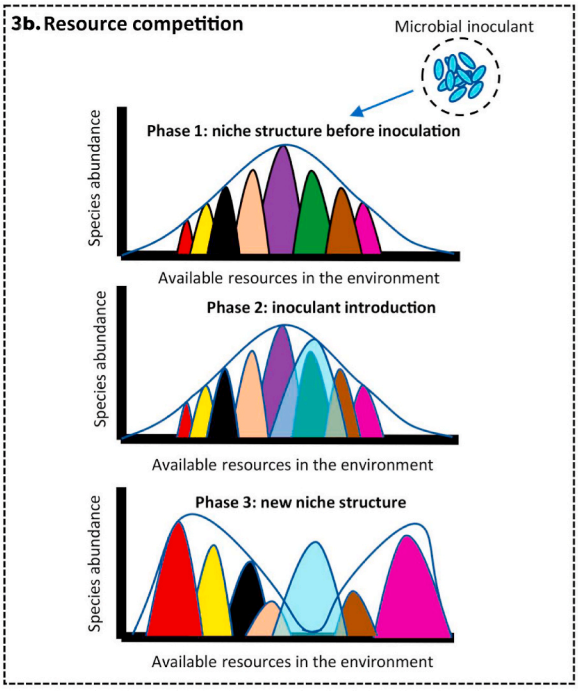
We hypothesized that the level of inoculation might positively determine the magnitude of inoculation impact as higher inoculation level might render longer inoculant survival. However, it was not possible to test any direct relationship between inoculation level and impact since the studies referred to releases of different microbial species with distinct experimental set up. Moreover, each study also applied different inoculation methods such as soil amendment, direct introduction, seed coating, etc. Hence, inferring general conclusions about the relationship between inoculation level and impact would be invalid and requires a more systematic testing of the inoculant level across a broad range of strains, soils and inoculation methods. However, in a recent study, Dong et al. (2019) revealed that increasing inoculated biofertilizer concentrations led to a greater impact on soil resident microbial diversity, providing evidence for our hypothesis.

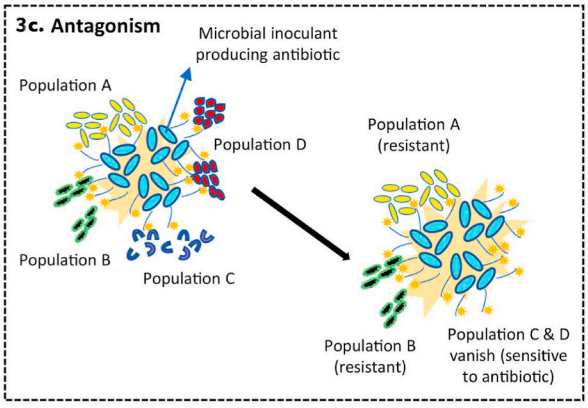
3. Resilience of soil microbial communities in response to inoculation

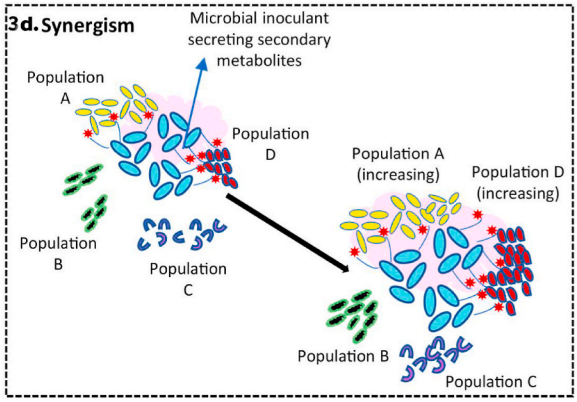
Regardless of the main mechanism through which inoculation impacts the native soil microbiome, it remains unclear whether the impact persists for longer periods of time or vanishes more or less quickly, i.e. how resilient the native communities are. We advocate that it is logical to assume that persisting microbial inoculants will have longer impact compared to short-lived inoculants. Given the paucity of current information, further studies need to consider the long-term assessment of community resilience, next to the impact of recurrent application of microbial inoculants, specifically whether the soil microbiome (i) retains function and structure regardless the amount of inoculum added (resistance); (ii) shows capacity to self-organize after disturbance, returning to its original state (resilience); or (iii) is capable of building and enhancing its learning and adaptation capacity, by reaching an alternative stable state (Carpenter and Brock, 2008) (Fig. 3a). A careful examination of the studies listed in Table 1 and Supplementary Tables S1 and S2 showed that the time span for a soil microbial community to recover and return to its initial composition after microbial release varies a lot. For instance, the release of *Pseudomonas fluorescens* DR54 affected the structure of resident microbiome associated with barley rhizosphere up to 6 days after inoculation but the latter returned to its original structure at day 9 (Johansen and Olsson, 2005). Other studies observed resilience only several months after inoculation (Yin et al., 2013; Wang et al., 2018). However, to the best of our knowledge, studies on the impact of microbial inoculation on the soil microbiome have targeted resilience from a compositional perspective only. Thus, key aspects of microbial function have remained unaddressed. Here, we argue that addressing resilience from a functional perspective is key to determine whether the invaded communities could still retain their functioning despite changes in their composition. Further exploration of multi-omics studies is needed to foster our understanding in the impact and resilience of the resident microbiome facing microbial inoculation from functional point of view.

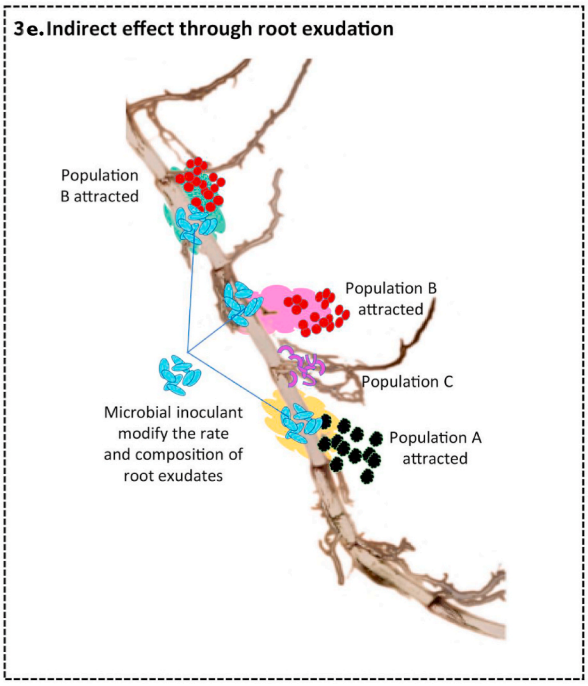
Microbial ecology concepts outline that microbial resilience can be linked to specific population traits, such as the ability to grow rapidly and to exhibit physiological plasticity (Allison and Martiny, 2008). Previous studies confirmed that these are some of the features that allow microbial communities to recover from environmental perturbation (Schimel et al., 2007; Shade et al., 2012). Based on this concept, we propose that these traits play important roles in promoting the resilience of microbial community following inoculation, albeit experimental work should be done to prove the hypothesis. For instance, from an ecological perspective, the effect of introducing microbes to soil might be related to the physiological capacity of resident communities to withstand antagonistic effects from the invaders (see next section). Studies focusing on the transcription and regulation of genes associated with resistance or tolerance traits could provide evidence of potential resistance mechanisms. The methods and tools to study gene transcription and regulation regarding physiological tolerance and adaptation towards toxic and antibiotic compounds are available (Ramos et al., 2009; Blair et al., 2015). When applied in the context of microbial invasion, they could indicate whether defence mechanisms triggered after inoculation could nurture the survival of the invader or help recovery of











(caption on next page)

Fig. 3. The impact of microbial inoculants on soil community structure and four possible mechanisms explaining how they can modify the soil microbial community composition. Fig. 3a summarizes the possible temporal dynamics of microbial community structure following microbial inoculation. In the first scenario (A), after inoculation the community resists, i.e. the community structure does not change. In the second scenario (B), the microbial inoculants change the initial composition of resident community. Here the initial invasion by the inoculants increases the abundances of red and black resident microbial populations but decreases yellow and purple populations. After the exclusion of inoculants, the initially impacted microbial composition can recover and return to its initial state (i.e. complete resilience). In the third scenario (C), the microbial inoculants will permanently change the initial composition of resident community, i.e. the inoculation-induced shift in community composition remains and the community reaches alternative stable state. In addition, we illustrate four possible mechanisms on how microbial inoculants alter resident community composition, beginning with resource competition (Fig. 3b). The introduced microbes (blue circles) are inoculated to a native community which consists here of eight taxa. The thick blue line indicates the entire niche of the native community. When microbial inoculant (blue peak) is introduced into the community, an overlapping zone is created as the invader and some resident taxa compete for similar resources. The initial population size of inoculant (blue peak) is high enough to outcompete resident taxa which compete for resources of similar preference, which then alters the community structure. The niche structure is altered in such a way that residents would preferentially occupy those niches on which the invader has little or no competitive advantage. The second mechanism explaining inoculation effect on soil microbial community composition is associated with antagonism (Fig. 3c). In the case where the inoculants produce antibiotics (depicted in orange), they eliminate some microbial taxa sensitive to antibiotics (Populations C and D) while resistant taxa (Populations A and B) will maintain their abundance. The third mechanism is related to synergism where the inoculants excrete secondary metabolites (in red) serving as nutrients for some resident taxa, which stimulates their growth (Fig. 3d). In this Fig., the secondary metabolites are able to increase the abundance of populations A and D while populations B and C remain unaffected. The fourth is indirect mechanism through which inoculation can affect soil microbial community by modifying the rate and composition of root exudates (Fig. 3e). Different organic compounds exuded by roots (depicted by clouds in pink, green, and orange) will then favour some microbial taxa. In Fig. 3e, populations A, B, and D are favoured by the inoculation-induced modification of exudates. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the resident communities.

From the resilience perspective, two additional points associated with technical issues and ecological concepts should be considered. Regarding the latter, even if soil microbiomes tend to return to their initial composition after invasion, we speculate that the abundance and diversity of some taxa might remain changed. Although this hypothesis needs to be further investigated in the context of inoculation impact, it has been verified in a study using another type of disturbance. Jurburg et al. (2017) measured the alteration of soil microbial community composition following heat disturbance and found that even though the majority of resident bacteria tend to be resilient (resilience at community level 49 days after disturbance), the abundance of slow-growing *Conexibacter* and some *Phenylobacterium* strains were two times higher compared to those observed in the community prior to disturbance. Meanwhile *Nitrosomonadaceae, Nitrospira, Xanthomonadaceae, Lysonacter*, and *Chitinopagaceae* remained largely supressed after disturbance, indicating a lack of resilience. These results also highlight the importance of evaluating the impact of inoculation in a temporal context since the effects might change overtime. However, to what extent these changes affect soil ecosystem functioning remains largely unknown.

Microbial inoculants will have a direct effect promptly after being introduced into the new habitat. This effect is interesting for those who gauge the changes' magnitude and sensitivity in a short-term duration. As time goes by, environmental change is likely to influence ecological and evolutionary processes. When they come into force, chronic impacts will be most likely detected and long-term evaluation is needed especially when the inoculants survive. However, most of the 108 studies addressing the impact of microbial releases on soil community (Table 1 and Supplementary Tables S1 and S2) only measured the effects over short durations. Around 50% of HTS-method, 75% of qPCR method, and 77% of profiling-method based studies presented in these tables monitored the soil community status over less than 3 months after inoculation. For instance, the inoculation impact of *Arthrobacter chlorophenolicus* A6L to microbial communities in 4-chlorophenol contaminated soil was only measured for 13 days (Jernberg and Jansson, 2002). Chen et al. (2013) measured the impact of *Burkholderia* sp J62 and *Pseudomonas thivervalensis* Y-1-3-9 on the microbiomes of cadmium contaminated soil at day 60 only. In both cases, the inoculation led to changes in the structure of the resident communities, but it remains unclear whether the impact persisted for longer period of time. In Fig. 1b, from 26 HTS studies, 11 performed multiple measurements on soil community status and only 2 of them reported resilience capacity following inoculation. For profiling method, multiple measurements of the impact were conducted in 40 studies and only 10 of them showed tendencies to return to its original state (see Fig. 1c) In qPCR-based method, none of those studies indicated resilience capacity (see Fig. 1d). Thus, one faces the possibility that release-induced changes in community structure might be permanent (do not, or not easily, return to the initial composition). If the shift is irreversible, the altered community may undergo alternative stable state and potentially affect soil functioning; for instance, if a key narrow function like ammonia oxidation is affected. This is related with the phenomenon called hysteresis where a system is unable to recover to its initial state after perturbation (Beisner et al., 2003). For instance, Sun et al. (2013) showed increasing and decreasing relative abundance of *Nitrosomonas* and *Nitrosospira* respectively in the soil with intercropping combined with *Rhizobium* inoculation treatment. The community composition did not return to its original state even after 2 years since the *Sinorhizobium meliloti* CCBAU01199 was introduced.

Finally, technical issues influence our perception of inoculant effects and post inoculation resilience of the resident community. As shown in Table 1 and the supplementary tables, different approaches ranging from profiling methods to advanced molecular techniques such as HTS have been used for evaluating inoculation effects over the short and longer term. The numbers of studies employing the different methods to detect possible inoculant effects are very different and restrict analysis of a possible effect of the method used on our capacity to detect an inoculant effect. For example, 100 and 80% of the studies employing phospholipid-fatty acid (PLFA) method and automated ribosomal intergenic spacer analysis (ARISA), respectively, detected an impact. However, we cannot say that the PLFA method allowed better detection of inoculant impact compared to ARISA because there were only 5 studies employing ARISA for 14 studies based on PLFA. Actually, to make a fair comparison, a study should be conducted with the same experimental setup, same inoculation level, and same microbial inoculant, comparing which methods are the most sensitive to detect an effect.

The sensitivity of techniques such as micro-respiration metabolic profiling (biology based CLPP), fatty acid approaches (FAME and PLFA) or molecular fingerprint techniques (DGGE, ARISA, [T]RFLP) might limit our ability to detect changes to the most abundant microbial populations. Although this issue can be solved by using HTS approaches (the strength and limitation of each technique are discussed in Kirk et al. (2004)), they lack information on microbial activities or phenotypic characteristics. Further, when using DNA-based methods one cannot distinguish the origin of the DNA as it might come from living cells, lysates, dead cells, or free DNA. We thus advocate using a combination of HTS and other phenotypical methods, as impact and resilience can only be properly tackled when both taxonomic and functional community traits are concomitantly assessed.

4. Proposed mechanisms of how inoculation drives resident microbial community changes

Although our literature search showed that microbial inoculation often affects the resident soil microbial communities, the mechanisms underlying the impact are still poorly understood. Some of the studies analyzed pointed to a possible mechanism explaining inoculant effect on soil microbial community, but none of studies comprehensively discusses the relative importance of the different possible mechanisms at stake. Thus, here we present and discuss four mechanisms that can govern the changes in the soil native microbiome upon microbial inoculation (Fig. 3).

The first mechanism refers to resource competition (Fig. 3b), which has been studied to dissect the relationship between biodiversity and invasibility in microbes (van Elsas et al., 2012; Eisenhauer et al., 2013; Mallon et al., 2015). Several studies have shown that the amount of (limiting) resources that are left unconsumed by native species and the consumption rate of resources by the native and invader species control the fate of invading species (van Elsas et al., 2012; Mallon et al., 2015; Wei et al., 2015; Yang et al., 2017). This means that the higher the number of vacant niches (not used by the resident community), the higher the chance of the inoculant to successfully establish in their new habitat. More precisely, Mallon et al. (2015) reported that low level of overlap between the soil community niche and the niche of an inoculated bacteria is a good predictor for the capacity of the inoculated bacteria to maintain high abundance following inoculation. Similarly, Wei et al. (2015) observed that soil communities with high connectance, low nestedness, and a clear niche overlap with the invader, reduce invasion success.

Once establishment takes place, the introduced microbial inoculant might be able to outcompete some taxa and use existing resources to spread and grow (Fig. 3b). This would be applicable if the invaders possess special traits that make them competitively superior in utilizing resources, for instance by promoting soil acidification (Zhang et al., 2009) or by having higher access to iron in soil due to siderophore production (Wandersman and Delepelaire, 2004). Once the invaders get established, their abundance could suppress functionally similar taxa from the resident communities – i.e. taxa that compete for similar resources – and facilitate the enhancement of taxa that are functionally unrelated to the inoculants.

It is interesting to note that inoculants that do not get established can also lead to shifts in the resident microbial communities. A recent study by Mallon et al. (2018) revealed that the soil invasion by *E. coli* led to important shifts in soil community composition and associated niche breadth, despite the fact that the invasive species declined dramatically in abundance 30 days after introduction. These authors concluded that resource competition played an important role and that the niche structure of the resident community got shifted away from invader's resources. The observed shifts in soil microbial community structure could thus be explained by an increase in the abundances of rare or subordinate taxa due to competitive release caused by the direct competition between invasive species and microbial taxa initially abundant in the resident communities. Despite the lack of success in establishing itself, *E. coli* left a legacy – a reduction in the niche overlap between resident community and invader, leaving the niches occupied by the invader partly vacant for the duration of the experiment (30 days). Since these shifts were consistently associated with a reduction in the use, by the resident community, of the niches used by the *E. coli*, the changes in community structure were likely due to competition for resources rather than utilization of nutrients that become available in response to dead cells. Moreover, the consistent response observed across the various community diversity levels, including those where *E. coli* was still present at higher densities, supported this conclusion. This finding raises two important points. From an applied perspective, it might provide a window of opportunity for a new invasion by the same species – or functionally similar inoculants – which should then encounter less competition, facilitating the establishment phase of additional inoculations. Thus, recurrent inoculations could represent a strategy for inoculants that do not survive well in soils. From an ecological perspective, it raises the questions of how long this legacy effect holds – i.e. how resilient is the resident soil community after inoculation? (see previous section) – and then what the potential impact of recurrent inoculations is.

The second and third mechanisms driving changes in the soil microbiome following inoculation relate to direct antagonism (Fig. 3c) and synergism (Fig. 3d) between some resident microorganisms and the inoculants, through which inoculants can affect community composition by suppressing or fostering other soil microbes, respectively. Regarding antagonism, inoculants can directly influence the growth and activity of the resident communities, in particular through antibiosis – i.e. by secreting chemical compounds that kill or inhibit resident microbes in their vicinity (Fig. 3c). Several microbial inoculants released for agricultural purposes, particularly those which intend to control the pathogens, have this capacity. For instance, particular species of *Bacillus, Pseudomonas, Streptomyces, Burkholderia, Pantoea, Lysobacter* and *Enterobacter*, are predominantly involved in antibiotic production (Dukare et al., 2018). Although these chemicals target certain pathogens, they might also have effects on non-target microbial taxa. For instance, the release of *Pseudomonas fluorescens* F113Rif producing antibiotic 2,4-diacetylphloroglucinol (Phl) decreased the genetic diversity of different rhizobia species in the sugar beet rhizosphere (Walsh et al., 2003). The residual impact was long-lasting, as indicated by the reduction of Phl sensitive taxa even after the field was disinfected and sown with uninoculated seeds from new plant species.

Introduced microorganisms can also influence resident microbial communities through synergism, where microorganisms cooperate from marginal support to absolute mutual dependence (Fig. 3d). In this case, the arrival of inoculants that produce signalling metabolites such as precursors, vitamins, and certain amino acids, stimulates the growth of resident microbial communities (Schink, 2002). In addition, some microbes can be extremely dependent on their mutual partners in such way that neither species can function optimally in the absence of its partner (Kato et al., 2012). The importance of synergism and antagonism has been recently emphasized by Li et al. (2019) who reported that antagonistic and facilitative pairwise interactions within resident microbial communities predict well invasion by the plant–pathogenic bacterium *Ralstonia solanacearum*.

The fourth mechanism explaining why inoculation can modify the soil microbial community is an indirect effect involving plant root exudates (Fig. 3e). Many microbial inoculants including PGPR indeed influence the growth and development of the root system through the production of phytohormones and other molecules. These compounds promote lateral root branching and modify root functioning (Vacheron et al., 2013). In particular, introduced PGPR increase the rates of root exudation which in turn can modify the rhizospheric microbial community. For instance, Florio et al. (2017) reported that the PGPR *Azospirillum lipoferum* CRT1, which is known to promote root exudation, induces an increase of the abundance of denitrifying heterotrophs only in soils where denitrifiers are limited by carbon availability. Further, Florio et al. (2019) showed that this PGPR inoculation effect on soil denitrifier functional groups was indeed modulated by manipulating the inputs of artificial root exudates to soil. Beyond exudate quantity, studies also showed that microbial inoculants can modify the composition of root exudates, in particular regarding amino acids and different groups of flavonoids (Matilla et al., 2010; Phillips, 2004). These exudates contain diverse organic compounds which favour specific microbes to metabolize these compounds. For instance, the introduction of *Chryseobacterium balustinum* Aur9 changed flavonoid concentrations exuded by soybean roots (Dardanelli et al., 2010). These changes alter the abundance of rhizobia in the rhizosphere since flavonoids initiate the symbiosis with legumes (Khan et al., 2012). In addition, increasing benzoxazinoids concentration in maize root exudates was observed as a

response to inoculation with *Azospirillum lipoferum* CRT1, *Azospirillum brasilense* CFN-535, and UAP-154 (Walker et al., 2011). The increasing benzoxazinoid concentrations could increase the abundance of *Pseudomonas putida* in the maize rhizosphere (Neal et al., 2012) and the exudation of malic acid, ultimately stimulating the abundance of *Bacillus subtilis* (Rudrappa et al., 2008). From these examples, it is clear that changes in root exudation induced by microbial inoculants indirectly alter microbial composition in the rhizosphere. However, it is important to note that plant genotype, potentially via (shifted) exudation, can interfere with the inoculant and contribute to changes in soil microbial structure and composition (Aira et al., 2010; Andreote et al., 2010). A recent study by Xu et al. (2020) revealed a significant interaction effect between rhizobium inoculation and soybean genotype on rhizosphere fungal communities. Moreover, disentangling the complexity of who contributes what to whom remains challenging, as some microbial resident taxa altered by an inoculant can themselves induce cascading effects, e.g. on root exudation and the presence of complex cross-kingdom interactions between plants and microbial communities themselves.

5. Future perspectives and concluding remarks

In many countries, laws or regulations often require that any impacts of the release of microbial taxa on the environment, including soil and its microbial community, should be negligible (Scherwinski et al., 2008; Wu et al., 2008; Xiong et al., 2013), which is often overlooked. Our literature search reveals that the majority of published studies reported that inoculation does modify the composition of the resident soil community, with possible long-lasting effects. We thus advocate for studies that foster our understanding of the resistance and resilience of native soil microbial communities facing microbial inoculants. In particular, further studies are required to measure how big and long-lasting such impacts are, especially in an open field across seasons and years where conditions vary.

Although the impact of microbial release on soil microbial community has been assessed mostly from a compositional perspective, evaluating inoculant impact and community resilience from a functional perspective – using a broad range of *omic* approaches (metagenomics, metatranscriptomics, metabonomiics, metaproteomics) – will help determining whether the invaded communities retain their functioning despite inoculant-induced changes in their composition. This notion is related to the often observed functional stability due to the presence of functionally redundant microbes in the soil community (Jurburg and Salles, 2015). Whereas high functional redundancy can allow some microbial species that are insensitive to inoculation to compensate for the decrease or loss of the function provided by more sensitive ones – thus leading to similar functioning despite changes in community composition – changes in function can still be observed if sensitive microbial species are replaced by functionally inefficient and insensitive ones (i.e. species with lower specific activities than those present in the original community). Therefore, resilience will depend not only on redundancy but also on the physiological constraints of the affected species, ecological resilience, and recovery ability. In addition, the evaluation on root and soil phenomics should also be evaluated as soil inoculation might lead to changes in the phenotypical features (physical and biochemical traits) of plant and soil biomes (Bargaz et al., 2018; Durán et al., 2018).

Moreover, we need a better understanding of the mechanisms underlying the changes in the soil microbiome composition and functioning upon invasion, which may help us to improve the effectiveness of many practical microbiological applications. By enhancing our knowledge in this field, we could better engineer the way inoculants affect the abundance of beneficial taxa and those with negative properties, including those associated with inoculant survival in soil. This will aid us to develop inoculants with superior survival ability or increase the resistance of resident communities upon invasion by pathogenic invaders. Furthermore, application of microbial inoculants as environmental probiotics could be one way to harness soil microbial capabilities to mitigate the negative consequences of climate change (Jansson and Hofmockel, 2020). Engineering inoculants that foster the activity of resident taxa able to improve carbon sequestration and water retention in soil could contribute to mitigation and adaptation measures in the era of climate change. In sum, the value of understanding the impact of microbial inoculation on resident microbial community will be a meaningful and integrative development of microbiological theory paving the way to new practical applications.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107874.

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