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Temporal dynamics of soil bacterial communities and multifunctionality are more sensitive to introduced plants than to microbial additions in a multicontaminated soil

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Abstract

Soil microbial communities are crucial for regulating the stability and degradation of contaminated land. However, the temporal response strategies of particular microbial groups to biotic introductions and their contributions to ecosystem functions and services (i.e., 'multifunctionality') in contaminated soils have yet to be investigated. Here, we present results from a 90-day microcosm experiment aiming to evaluate the temporal changes in bacterial communities and functions in response to microbial and plant additions in a contaminated agricultural soil. In addition, we quantified the contributions of specific bacterial taxa with different response strategies over time to alterations in ecosystem multifunctionality in pollutant degradation (polyphenol oxidase) and the cycling of carbon (dehydrogenase), nitrogen (urease and available nitrogen), phosphorus (available phosphorus), and potassium (available potassium). Results showed that native bacterial communities exhibited strong resilience to the introduced microbial consortium and were altered by plant growth. Plant-enriched bacterial taxa were located in the core and central positions of the co-occurrence networks and had considerable influence on the other nodes. Plant growth substantially influenced soil multifunctionality, in a process driven by specific bacterial taxa with different response strategies. The more tolerant taxa contributed most to multienzyme activities, whereas the more affected taxa largely determined multinutrient levels in the soil. These results provide a new perspective in disentangling the roles of plant-associated bacteria in the assembly of community interactions and ecosystem multifunctionality of contaminated agricultural soils.

KEYWORDS

biotic introduction, degraded land restoration, ecosystem multifunctionality, response strategy, soil contamination, temporal microcosm

1 | INTRODUCTION

Soil ecosystems worldwide are facing increasing environmental alterations and land degradation from anthropogenic pressures, global climate change, and biotic perturbations, which can profoundly influence ecosystem productivity and stability (Bardgett & van der Putten, 2014; Hassan et al., 2016; McGill et al., 2007; Philippot et al., 2013; Wagg, Bender, Widmer, & van der Heijden, 2014). Soil microorganisms represent one of the largest biodiversity reservoirs in terrestrial ecosystems. Microorganisms play key roles in maintaining multiple ecosystem functions and services simultaneously (hereafter 'multifunctionality'), such as primary production, litter decomposition,

nutrient cycling, and climate regulation (Delgado-Baquerizo et al., 2016; Delgado-Baquerizo et al., 2017; Haroon et al., 2013; Hicks Pries, Castanha, Porras, & Torn, 2017). In addition, microbial communities respond rapidly to environmental disturbances, and their sensitive responses can be monitored to assess the potential soil stability and degradation (Jiao et al., 2018). Therefore, it is of fundamental significance to understand the mechanism(s) involved in the maintenance of microbial communities and to discern their intrinsic dynamic processes occurring at the species-level following environmental disturbances.

Microorganisms exhibit remarkable stability in the face of disturbances, largely due to their high metabolic flexibility and physiological tolerance, as well as high abundance, widespread dispersal, rapid growth, and evolutionary adaptation (Allison & Martiny, 2008; Fuhrman, Cram, & Needham, 2015). Generally, the stability of microbial ecosystems is determined by three mechanisms (Allison & Martiny, 2008): (a) resistance, when the microbial community displays tolerance to a disturbance (Jiao et al., 2016; Jiao et al., 2016); (b) resilience, when the microbial community is changed by a disturbance yet rapidly recovers to its initial or alternative stable state (Griffiths & Philippot, 2013; Hodgson, McDonald, & Hosken, 2015); and (c) functional redundancy, when after a disturbance the ecosystem processes remain similar to their original state, despite the microbial community being substantially altered without recovery. Meanwhile, an individual microbial species can adopt three primary response strategies to environmental disturbances according to their apparent adaptations: (a) adapt and maintain the abundance unchanged (i.e., 'tolerant'); (b) become negatively affected and reduced in abundance (i.e., 'sensitive'); and (c) benefit from the new conditions and increase in abundance (i.e., 'opportunist'; Evans & Hofmann, 2012; Shade et al., 2012; Szekely & Langenheder, 2017). A previous study has identified specific phylogenetic groups of microorganisms with distinct response strategies to rainfall-induced carbon dioxide pulses in a terrestrial ecosystem (Placella, Brodie, & Firestone, 2012).

Environmental contamination is a global problem that causes damage to natural ecosystems and harms animal health (Jiao, Liu, et al., 2016). Due to wastewater irrigation or illegal discharges, an increasing influx of inorganic (e.g., heavy metals) and organic (e.g., petroleum hydrocarbons) contaminants could change soil physicochemical properties, leading to serious land degradation (Bayat et al., 2015; Dawson et al., 2007; Peterson et al., 2003; Wang, Zhao, Zeng, Hu, & Yu, 2015). Restoration ecology is a subject related to the "intentional human intervention in enhancing ecosystem recovery after disturbance" (Young, Petersen, & Clary, 2005), and the existing research has mainly focused on plants (Kardol & Wardle, 2010; Wardle & Peltzer, 2007). Given the influence of biodiversity losses upon ecosystem functioning and stability, the reintroduction of flora is considered the best approach for ecological restoration. During the restoration process, soil microorganisms may act as key engineers, mediating the re-establishment of biodiversity and ecosystem functions (Heneghan et al., 2008; Young et al., 2005). In addition, belowground microorganisms can promote plant establishment through symbiotic interactions (Requena, Perez-Solis, Azcon-Aguilar, Jeffries, & Barea, 2001; Smith et al., 2003). However, it is challenging to restore soil processes, because microbial ecosystem dynamics are complex, nonlinear, and only partly unpredictable (Nemergut et al., 2013). Moreover, historical contingency, known as priority effects, is typically an obstacle for soil colonization by newly introduced microbial species (Vannette & Fukami, 2014). Currently, there are a growing number of studies investigating the temporal dynamics of microbial communities in response to environmental contamination, defined as microbial succession (Fierer, Nemergut, Knight, & Craine, 2010; Jiao, Chen, et al., 2016; Jiao, Liu, et al., 2016). Yet we still lack basic knowledge of how microbial species interact and idiosyncratic effects influence biodiversity and ecosystem functioning during microbial community succession with one or more introduced microbial consortia (Calderon et al., 2017; Harris, 2009; Laughlin, 2014).

Soil microbe–plant interactions and feedbacks are closely associated with the multifunctionality of terrestrial ecosystems (Bagchi et al., 2014; Wagg et al., 2014). For example, aboveground plant richness plays a positive role in belowground ecosystem multifunctionality in global drylands (Maestre et al., 2012). Plants stimulate (select for) the evolution of new adaptive traits in root-associated bacteria, such as genes related to carbohydrate metabolism (Levy et al., 2018). Roots release exudates and mucilage into their surrounding soil environment and thus subsequently shape the associated microbial communities (Badri & Vivanco, 2009; Shi et al., 2011). Moreover, plant-associated microorganisms drive numerous ecosystem process, such as nutrient acquisition by plants and the cycling of resources between aboveground and belowground communities (De Vries et al., 2013; van der Heijden, Bardgett, & van Straalen, 2008). Species invasion is an important biotic and environmental perturbation that can alter soil nutrient cycling at the global scale (Rice, Westerman, & Federici, 2004). Restoration of biological invasions requires an active re-establishment of the native community (Kardol & Wardle, 2010), which should be a determinant for the restoration of ecological communities and ecosystem functions (Stinson et al., 2006). In addition, soil legacies can persist after the removal of invasive species and subsequently alter ecosystem processes (Marchante, Kjøller, Struwe, & Freitas, 2009). Invasive belowground microorganisms can also greatly alter aboveground and belowground ecosystem properties (Hendrix et al., 2008; Wardle & Peltzer, 2007). Currently, it is unclear how ecosystem multifunctionality is influenced jointly by reintroduced microbial flora and plants, particularly in contaminated soils.

Here, we characterized the temporal change in bacterial communities to biotic introductions (an introduced microbial consortium and three legume plants) in a multicontaminated agricultural soil. We also assessed the contributions of particular bacterial taxa with different response strategies to alterations in ecosystem multifunctionality. Phenanthrene, *n*-octadecane, and cadmium were used to prepare the contaminated soil, because they are prevalent in oil-contaminated areas. A contaminant-degrading microbial consortium enriched from an oil-contaminated soil was obtained from our previous work, as it could utilize phenanthrene and *n*-octadecane as the sole carbon under the stress of cadmium chloride ($CdCl_2$; Jiao et al., 2017). Three legume plants capable of forming nodules via symbiosis with N_2-fixing

rhizobia were selected, and these plants could generate specific associations with their root-associated microbiomes (Xiao et al., 2017). Soil bacterial communities were analyzed by high-throughput sequencing of the 16S ribosomal RNA gene in temporal microcosms over a 90-day period. We hypothesized that the temporal turnover of soil bacterial communities exhibits distinct trends in response to biotic introductions, whereas particular bacterial taxa with different response strategies influence the community assembly and ecosystem multifunctionality of the experimentally contaminated soil.

2 | MATERIALS AND METHODS

2.1 | Contaminated soil preparation

In July 2014, approximately 50 kg of soil sample was taken from a depth of 0–20 cm in a cornfield in Yangling, Shaanxi Province, Northwest China (108°4′51″E, 34°17′31″N). This soil had a sandy loam texture, and its detailed properties are shown in Table S1. The soil was sieved (5-mm mesh size) to remove any plant debris and large clods. Subsamples of the original soil were spiked with a mixture of phenanthrene and *n*-octadecane in dichloromethane at a concentration of 1,000 mg kg^{-1}, and also $CdCl_2$ in water at 50 mg kg^{-1}. The dichloromethane solution containing the organic contaminants was first mixed with 200 g of soil. Then, after the complete evaporation of the dichloromethane under a fume hood, the residual was thoroughly mixed with a further 800 g of soil and a $CdCl_2$ solution to a final concentration of 50 mg kg^{-1}. The spiked soil subsamples were incubated for 5 days in the dark with sterile water at ~15% soil moisture to reach equilibrium.

2.2 | Microbial enrichment consortium

The contaminant-degrading microbial consortium used in this study was enriched from contaminated soil surrounding an oil refinery in Yulin, Shaanxi Province, Northwest China (Jiao, Zhang, et al., 2017). The enrichment culture was obtained by using a basal salt medium supplemented with 250 mg L^{-1} phenanthrene + 250 mg L^{-1} *n*-octadecane + 50 mg L^{-1} $CdCl_2$, with 10 successive subcultures established at 10-day intervals. This microbial consortium was cultured in the same medium supplemented with the corresponding levels of organic and inorganic contaminants and was incubated on a rotating shaker for 10 days (28°C, 140 rpm). Then cells were harvested by centrifugation (6,000×g) for 30 min, washed twice, and resuspended in a 0.9% NaCl solution (~10^9 CFU ml^{-1}) for use as inoculum. This microbial consortium could degrade 90% of phenanthrene (250 mg L^{-1}) and *n*-octadecane (250 mg L^{-1}) in the presence of $CdCl_2$ (50 mg L^{-1}) within 10 days (Jiao, Zhang, et al., 2017). It was mainly composed of bacterial taxa belonging to the genera *Aquabacterium* (23.5%), *Naxibacter* (8.6%), *Dokdonella* (3.9%), and *Novosphingobium* (3.3%; Figure S1).

2.3 | Experimental design and sampling

The experiment tested four treatments: (a) unplanted soil with the microbial consortium inoculum sterilized by autoclave at 120°C for 30 min (control); (b) unplanted soil with the microbial consortium inoculum (bacteria); (c) soil with legumes planted and the microbial consortium inoculum sterilized (plant); and (d) soil with legumes and the microbial consortium inoculum (bacteria + plant [BP]). To analyze the temporal succession of microbial communities in microcosms, each treatment was sampled at five time points after introduction of microbial consortium and/or transplanting of legume plants: 10, 20, 30, 60, and 90 days.

The contaminated soils (~2 kg) were distributed into pots (20-cm diameter) that had a depth of 15 cm. The control and bacteria treatments received 10 ml of sterilized and active inoculum, respectively. For the plant and BP treatments, the three common legumes were *Robinia pseudoacacia* (woody), *Medicago sativa* (herbaceous), and *Vicia villosa* (herbaceous). Seeds of *R. pseudoacacia* (robinia), *M. sativa* (alfalfa), and *V. villosa* (vetch) were surface sterilized and germinated at 28°C for 36 hr under aseptic conditions. Five robinia, 20 alfalfa, and 20 vetch seedlings (each 1 cm in length) were transplanted per pot. All pots were incubated in a greenhouse (16-hr day [25°C]:8-hr night [20°C]) for 90 days. Pots were given sterile water three times per week to maintain their soil moisture at ~15%. Pots assigned to the different treatments were arranged randomly and rotated regularly throughout the incubation period.

At the designated time points, the soils in pots without any plants were collected from a depth of 3–15 cm. For pots with plants, we adopted destructive sampling; after plant roots with soil attached were carefully removed, the remaining soil without roots was mixed and collected. Although the rhizosphere consists of the soil most affected by plants, the volume collected here was much too small. Therefore, we focused on the soil microbial responses to the impact of plant growth at a larger scale. At each time point, four replicates were sampled in the control and bacteria treatments, whereas six replications (two biological replicates × three legume species) were generated in the plant and BP treatments by pooling three of six replicate pots for each of the three legume species. In this way, 20 soil samples were generated at each time point for the treatments of control (n = 4), bacteria (n = 4), plant (n = 6), and BP (n = 6). In total, 100 soil samples were obtained from the five sampling time points for all treatment, and 10 g of each sample was stored at −80°C for microbial analysis.

2.4 | Soil ecosystem multifunctionality analysis

We used the soil samples taken at the 90-day time point to analyze soil ecosystem multifunctionality because of the relatively large impact the plants had on the environment surrounding their roots by this time. We assessed six ecosystem functions related to pollutant degradation (polyphenol oxidase) and the cycling of carbon (dehydrogenase), nitrogen (urease and available nitrogen [AN]), phosphorus

(available phosphorus [AP]), and potassium (available potassium [AK]). These functions were chosen because they deliver some of the fundamental supporting and regulating ecosystem services (Bradford et al., 2014; Delgado-Baquerizo et al., 2016; Jing et al., 2015; Maestre et al., 2012), particularly in contaminated soils. Activities of the enzymes polyphenol oxidase (PPO), dehydrogenase (DHA), and urease (UE) were assayed by the methods of Chen, Wang, Wang, and Huang (2004), Singh and Singh (2005), and Li et al. (2009), respectively. Physicochemical properties of the soils, including their pH, organic matter, total nitrogen, AN, AP, and AK, were all measured using standard soil testing procedures (Bao, 2000). Because of the disparate soil enzyme activities and physicochemical properties, we divided soil ecosystem multifunctionality into two groups: multienzyme activities (PPO, DHA, and UE) and multinutrient levels (AN, AK, and AP). We then quantified the multifunctionality index for each soil sample using the first axis of a principal component analysis (this explained 80% of the variation in these two groups of variables) according to Laforest-Lapointe, Paquette, Messier, and Kembel (2017).

2.5 | DNA extraction, polymerase chain reaction amplification, and 16S rRNA gene sequencing

Genomic DNA was extracted from the soil samples with the MP FastDNA SPIN Kit for soils (MP Biomedicals, Solon, OH) according to the manufacturer's instructions. The V4–V5 region of the 16S rRNA gene was amplified by using the primer pair 515F/907R (Jiao, Liu, et al., 2016). These amplified polymerase chain reaction products were sequenced on the Illumina HiSeq 2500 platform (Illumina Inc., San Diego, CA) using 250-bp paired-end reads. The acquired sequences were filtered for quality according to Caporaso et al. (2011), and any chimeric sequences were removed with the USEARCH tool on the basis of the UCHIME algorithm (Edgar, Haas, Clemente, Quince, & Knight, 2011). Then, the remaining sequences were grouped according to their taxonomy and assigned to operational taxonomic units (OTUs) at a 3% dissimilarity level, by using the UPARSE pipeline (Edgar et al., 2011). OTUs with less than two sequences were removed, and representative sequences of OTUs were taxonomically assigned using the RDP classifier (Caporaso et al., 2011).

2.6 | Data analyses

To characterize the temporal response strategies of particular soil bacteria, the obtained OTUs were grouped according to how they responded to the four treatments. For each treatment, changes in relative abundance were interpreted as a measure of this response and used to categorize the OTUs. To do this, pairwise comparisons (using *t* tests) of the relative abundance of each OTU in the control versus other treatment samples were performed at each sampling time point. Based on this exercise, (a) the OTUs that did not significantly differ in their relative abundance were categorized as tolerant OTUs, (b) those that had a significantly lower abundance in the noncontrol treatment samples were deemed sensitive OTUs, and (c) those that had higher abundance were categorized as opportunist OTUs.

Prior to the data analysis, each sample was rarefied to correct for sampling effort using a subsample with a minimum of 23,378 sequences (according to the sample size). To assess microbial diversity and abundance, we evaluated the α-diversity of OTU richness and the Shannon–Wiener index, as well as the changes in community composition using the Bray–Curtis distance between the samples. A principal coordinate analysis was performed on the distance matrices to visualize the relationships among the soil samples. A similarity analysis (ANOSIM) and a permutational multivariate analysis of variance (ADONIS) were performed to determine significant differences among the sample classifications (i.e., four treatments). To quantify the relative importance of α-diversity of different response groups on soil multifunctionality, we adopted a multiple regression model and a variance decomposition analysis with the lm and calc.relimp functions in the 'relaimpo' package, respectively.

Network analysis was performed to identify the bacterial co-occurrence patterns. Three networks were constructed on the basis of the correlation analysis corresponding to the bacteria, plant, and BP treatments. Spearman's correlation between two OTUs was estimated. Robust correlations with Spearman's correlation coefficients > 0.8 (strong) and false discovery rate-corrected P values < 0.01 (significant) were identified to form the networks, in which each node represents one OTU and each edge represents a strong and significant correlation between two nodes. Network-level topological features were estimated for a set of metrics: average path length, average degree, graph density, clustering coefficient, and modularity. In addition, four node-level topological features were calculated for each node, namely, degree, betweenness, closeness, and eigenvector centrality. These topological features provide indicators for evaluating the roles of nodes in a network (Eiler, Heinrich, & Bertilsson, 2012; Steele et al., 2011). High values of these topological features indicate the core and central position of a node in the network, whereas low values indicate a peripheral position (Jiao, Chen, & Wei, 2017; Ma et al., 2016). For example, degree represents the number of direct connections for an individual node (Greenblum, Turnbaugh, & Borenstein, 2012), and betweenness centrality reflects the potential influence of a particular node on the connections of other nodes (Greenblum et al., 2012). Networks were visualized using the interactive Gephi platform (Bastian, Heymann, & Jacomy, 2009; Newman, 2003, 2006).

All statistical analyses were conducted using R v3.2.2 (http://www.r-project.org/) unless otherwise stated.

3 | RESULTS

3.1 | General characteristics of the bacterial dataset

After quality filtering and the removal of chimeric sequences, the Illumina V4–V5-derived 16S rRNA dataset contained 3,381,179 high-quality sequences, which clustered into 4,173 OTUs on the basis of a 97% similarity cutoff. Because the soil bacterial communities were

similar among the three legumes ($P > 0.1$; estimated via ANOSIM and ADONIS analysis), the subsequent analysis considered the influence of plant growth by taking the three legume species as a whole rather than individually.

3.2 | Temporal effects of introduced microbial consortium and legume plants on bacterial communities

First, we determined the OTU richness and diversity of the sequencing data for each time point (Figure S2). For treatments without plants (control and bacteria), the overall α-diversity increased remarkably in the early phase (0–30 days) of the experiment but reached a plateau in its later phase (30–90 days). Compared with microcosms treated without plants, the plant growth treatments (plant and BP) showed a higher OTU richness from 60 days onward. At 90 days, microcosms grown with alfalfa showed the highest α-diversity, followed by vetch and robinia (Figure S3). Overall, introducing the microbial consortium did not significantly change the α-diversity of soil bacteria throughout the incubation period ($P > 0.05$).

For the compositional β-diversity, we estimated the temporal variation of community similarity between each treatment and control microcosms via the fitted quadratic ordinary least squares models (Figure 1a,c,e). The similarities between the bacteria treatment and control microcosms increased significantly during the incubation period, indicating a recovery of native bacterial communities. By contrast, the similarities between plant treatment and control microcosms significantly decreased as the incubation progressed, indicating an increasing impact of plant growth. Interestingly, the similarities

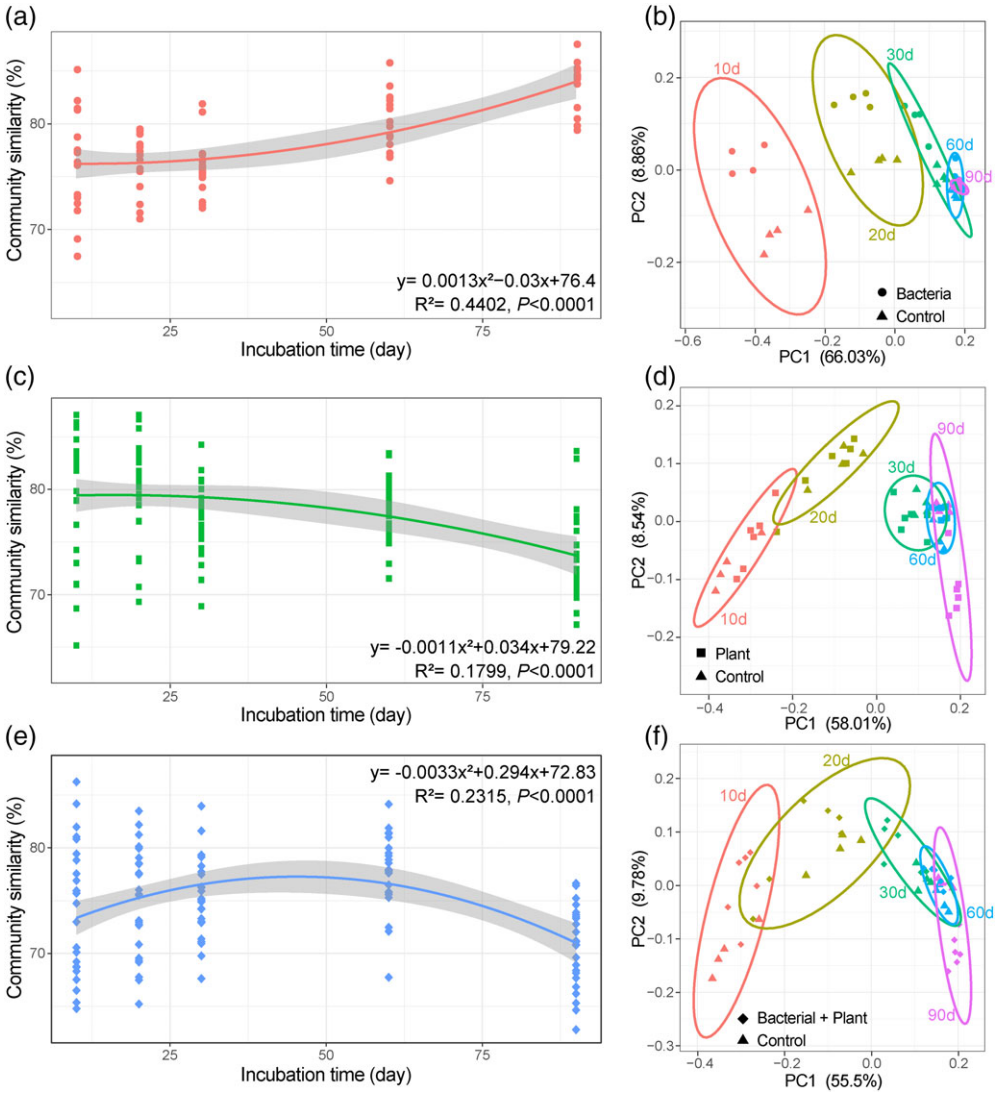

FIGURE 1 General patterns of bacterial β-diversity in response to biotic introductions in soil microcosms. Temporal variation of community similarities between the control versus bacteria, plant, and bacterial + plant treatments (a, c, and e), as estimated by the fitted quadratic ordinary least squares models. A principal coordinate analysis based on the Bray–Curtis dissimilarity among the samples between the control versus bacteria, plant, and bacterial + plant treatments (b, d, and f); 80% confidence ellipses are shown around the samples from each time point [Colour figure can be viewed at wileyonlinelibrary.com]

between the BP treatment and control microcosms first increased but then decreased, thus indicating a complex interaction effect of the introduced legume plants and microbial consortium on native bacterial communities. Furthermore, the principal coordinate analysis (Figure 1 b,d,f) based on the Bray–Curtis dissimilarity revealed that the confidence ellipses of the control and treatment samples gradually shrank, enlarged, and showed alternate trends for bacteria, plant, and BP, respectively. Additionally, differences in bacterial composition between control and treatments at each time point, as tested with ANOSIM and ADONIS, are presented in Tables S2 and S3. For the bacteria treatment, significant differences in the bacterial community were observed in the early phase (10–30 days), which gradually decreased along the incubation period; the differences were no longer significant in the later phase (60–90 days). For the plant and BP treatments, the bacterial community did not different significantly in the early phase (20–30 days), except for at 10 days, which may have been related to the disturbance generated by sowing the plants. By contrast, during the later phase (60–90 days), significant differences were observed, thought these were more pronounced at Day 60 than at Day 90.

Moreover, we estimated the temporal dynamics of the dominant bacterial phyla in control samples (Figure S4A). The relative abundance of Proteobacteria deceased with increasing incubation period, whereas that of Actinobacteria increased. Then the influence of different treatments was explored by taking the absolute values of relative phylum abundance between the control and treatment samples (Figure S4B). For the bacteria treatment, the differences in the dominant Proteobacteria, Actinobacteria, Chloroflexi, and Acidobacteria deceased with increasing incubation period. For the plant and BP treatments, the differences in most of the dominant phyla showed an increasing trend over the incubation period. These results confirmed the above observations in Figure 1.

The changes in bacterial community composition were coupled to an extensive turnover of OTUs. The individual members exhibited distinct response strategies to the different treatments (Figure 2; Table S4). For the bacteria treatment, the relative abundance of tolerant OTUs gradually increased over the incubation period, whereas opportunist and sensitive OTUs decreased. By contrast, the reverse trends were observed for the two treatments with plants. Moreover, different response OTUs to the BP treatment displayed alternate trends during the incubation period. The relative abundance of opportunist and sensitive OTUs first decreased and then increased, whereas tolerant OTUs first increased and then decreased. In addition, the final relative abundances of sensitive and tolerant OTUs were higher or lower than the initial levels, respectively, which indicated a stronger effect on them from the legume plants than from the microbial consortium introduced. Furthermore, we estimated the influence of the different treatments on the distributions of each response group (Figure S5). The BP-opportunist and sensitive OTUs had the highest relative abundances, yet the BP-tolerant OTUs had the lowest. There was no significant difference between bacteria and plant treatments, except for sensitive OTUs in the latter with a higher relative abundance.

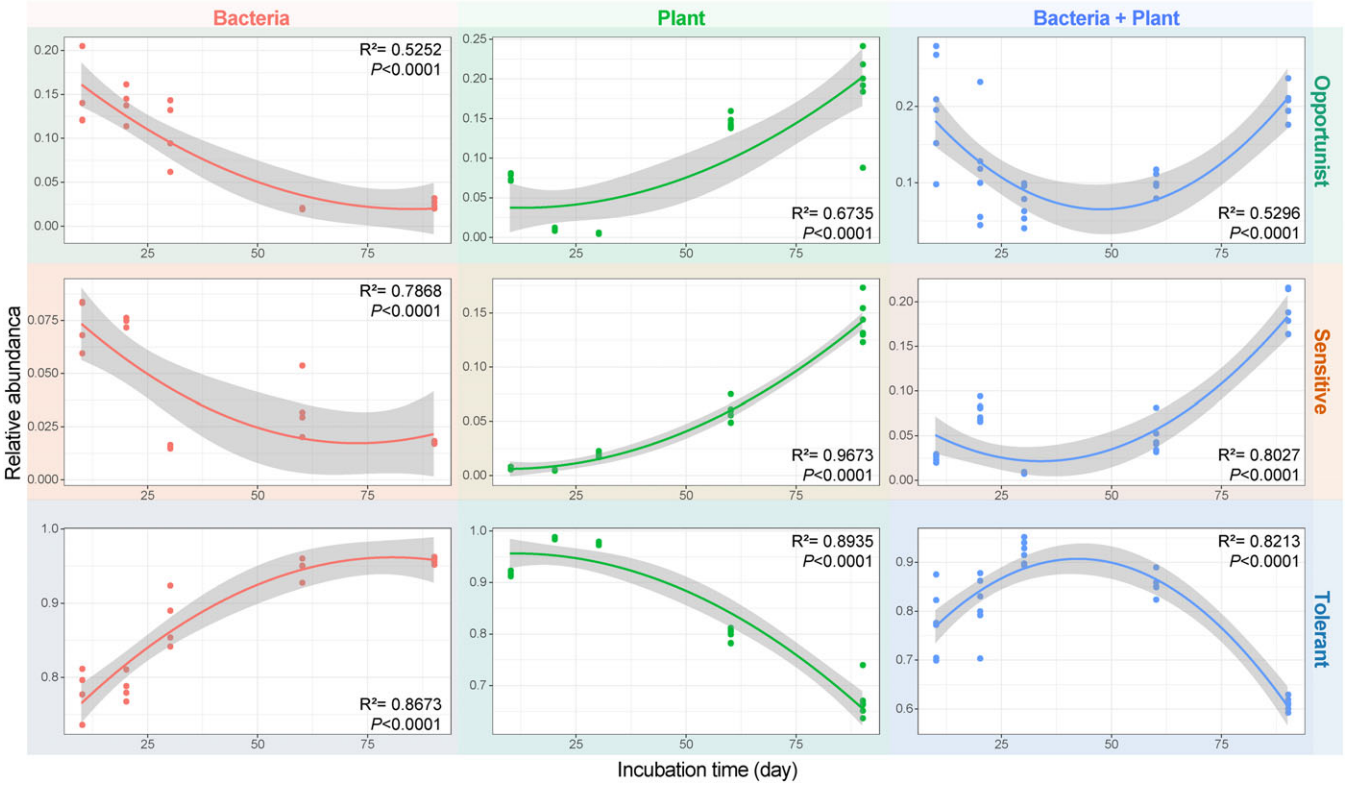

FIGURE 2 Temporal dynamics of specific bacterial taxa with distinct response strategies to biotic introductions. Relationships between the relative abundance of bacterial groups and the incubation period were determined by linear regression analysis ($P < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

Additionally, we explored the temporal dynamics of the dominant bacterial genera in different treatment samples (Figure S6). The relative abundances of *Janthinobacterium* and *Lysobacter* decreased over the incubation period in all treatments. By contrast, *Kaistobacter* and *Nocardioides* increased, with lower or higher abundances in plant growth treatments in the later phase (90 days), respectively. Interestingly, *Pseudoxanthomonas*, one of the major members in the introduced microbial consortium, had a higher relative abundance in the bacteria and BP treatments in the early phase (10–30 days), which decreased over the incubation period.

3.3 | Bacterial co-occurrence patterns in different treatment microcosms

The metacommunity co-occurrence networks were constructed for different treatment microcosms on the basis of correlations (Figure 3). Comparing the network-level topological features revealed substantially higher average degree and clustering coefficient and lower average path length in the plant and BP treatment networks than in the bacteria treatment network. This indicates that the plant growth networks were more connected and had closer relationships than does the microbial consortium network (Table S5). Opportunist OTUs were located in the core and central positions of the plant and BP treatment networks and exhibited extremely strong influence on other nodes (Figure 3). To confirm this observation, we examined four unique node-level topological features of different response OTUs, that is, the degree, betweenness, closeness, and eigenvector centrality (Figure 4). Although the values of these node-level topological features were similar among the different response groups in the bacteria network, they were significantly higher ($P < 0.05$) for opportunist OTUs than other nodes in the plant and BP networks. This suggests that compared with other response groups, opportunist OTUs were more often located in central positions within the plant and BP treatment networks, and less so in the bacteria treatment network.

Given this extremely strong influence of opportunist OTUs, we visualized their distribution at the genus level (Figure S7). Opportunist OTUs comprised diverse taxa, including Proteobacteria, Actinobacteria, and Firmicutes. Although there were no significant differences in bacterial community structure between the plant and BP treatments, the composition of opportunist OTUs did show slight differences. In the plant treatment, opportunist OTUs were mainly classified into the genera *Steroidobacter*, *Lysobacter*, *Iamia*, *Promicromonospora*, *Nitrospira*, and *Thiobacillus* (Figure S7A), whereas in the BP treatment, *Pseudoxanthomonas*, *Hydrogenophaga*, *Achromobacter*, *Stenotrophomonas*, and *Iamia* were predominant (Figure S7B).

3.4 | Main bacterial drivers of soil ecosystem multifunctionality

To explore the influence of plant growth on soil ecosystem multifunctionality, we estimated changes in soil enzyme activities and nutrient levels induced by plant growth (Figure S8). Soil DHA and total nitrogen were substantially increased by plant growth, whereas AN, AK, and AP were reduced. We also examined the associations between specific bacterial populations and soil enzyme activities and nutrient levels (Figure 5). Soil PPO and UE were positively associated with the relative abundance of *Arenimonas* and *Thermomonas*. Soil DHA and total nitrogen were positively associated with the relative abundance of *Iamia* and *Aeromicrobium*. Soil AN, AK,

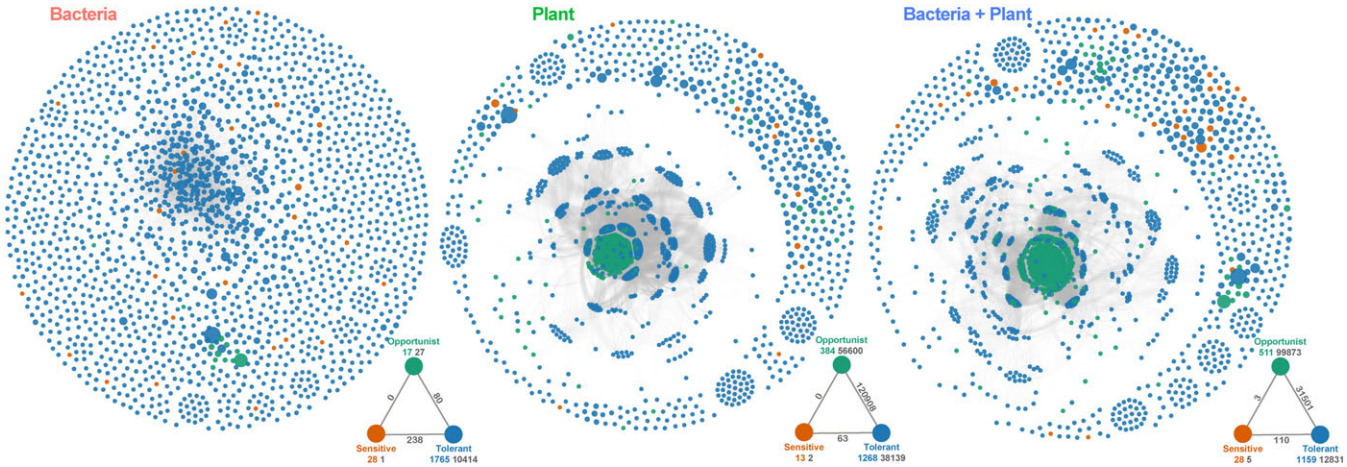

FIGURE 3 Metacommunity co-occurrence networks of bacterial taxa from soil microcosms with biotic introductions based on a correlation analysis. Networks are colored for the categories of distinct response strategies. A connection indicates a strong (Spearman's $\rho > 0.8$) and significant (false discovery rate-corrected P value < 0.01) correlation. The size of each node is proportional to the relative abundance of the operational taxonomic units; the thickness of a connection between two nodes (i.e., an edge) is proportional to the value of Spearman's correlation coefficient. The external associations (black numbers) among each subcommunity are displayed on the bottom right of each graph. The numbers in black below each node represent the inner associations of each subcommunity, and the numbers of nodes in each subcommunity are coloured according to the categories [Colour figure can be viewed at wileyonlinelibrary.com]

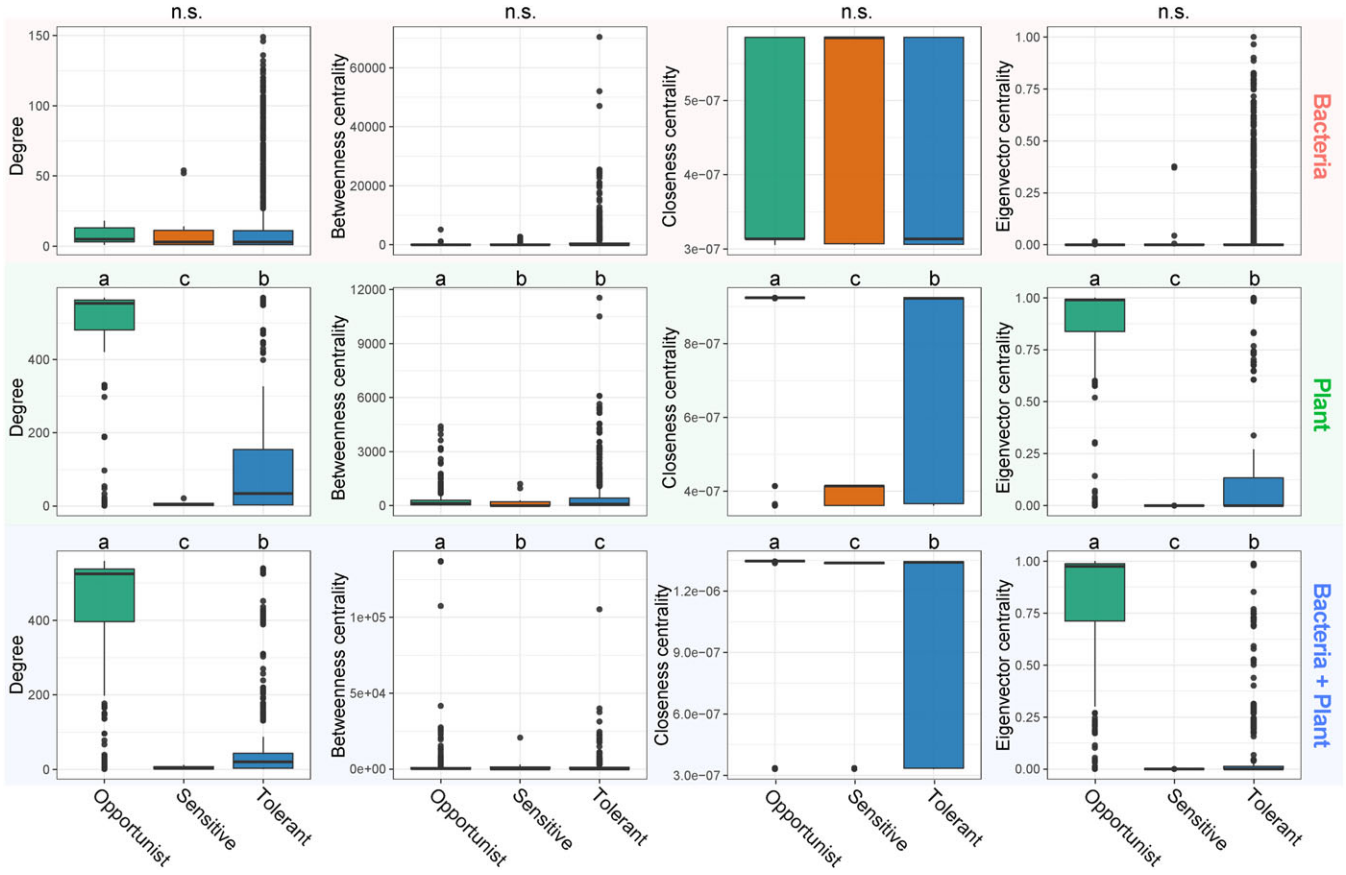

FIGURE 4 Unique node-level topological features of specific bacterial taxa with different response strategies to biotic introductions in the co-occurrence networks. Significance was estimated for differences in these features among different response strategies, on the basis of multiple comparisons with Kruskal–Wallis. n.s., not statistically significant ($P > 0.05$); bars that do not share a letter are significantly different ($P < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

and AP were all positively associated with the relative abundance of *Janthinobacterium*, *Kaistobacter*, *Ramlibacter*, and *Cupriavidus*.

Given the substantial influence of plant growth we detected in the experiment, we then uncovered the main bacterial drivers of soil ecosystem multifunctionality in the plant growth treatments. Specifically, we performed a multivariate regression analysis that included OTU richness, Shannon diversity, and the relative abundance of different response OTUs, to quantify their respective contribution to multienzyme or multinutrient functions in soil (Table 1). The α-diversity of tolerant OTUs contributed most towards explaining the variation in soil multienzyme activities; likewise, the diversity and relative abundance of opportunist and sensitive OTUs contributed most to the soil multinutrient levels. Furthermore, we estimated the correlations of compositional β-diversity with the dissimilarities of soil multifunctionality based on their Euclidean distances. There were no significant correlations between compositional β-diversity and the dissimilarities of soil multienzyme index ($P > 0.1$). Nonetheless, the dissimilarities of soil multinutrient index were significantly correlated with the compositional β-diversity of opportunist and sensitive OTUs, rather than with that of tolerant OTUs. This result indicates that the compositional β-diversity of opportunist and sensitive OTUs made important contributions to soil multinutrient functions (Figure 6).

4 | DISCUSSION

Land degradation is a global problem that is leads to substantial changes in soil biodiversity and ecosystem functions and services (Caravaca, Lozano, Rodriguez-Caballero, & Roldan, 2017; Delgado-Baquerizo et al., 2016). Revealing the temporal responses of particular bacterial groups to soil perturbations and their contributions to ecosystem multifunctionality is pivotal to understand the maintenance of microbial diversity and microbe-driven ecosystem processes (Delgado-Baquerizo et al., 2017). In this study, we found that native bacterial communities exhibited stronger resilience to the introduced microbial consortium than to the legume plants growing in a multicontaminated agricultural soil. In particular, the temporal turnover of particular bacterial taxa with different response strategies influenced the community assembly and ecosystem multifunctionality of the experimentally contaminated soil. These findings suggest that developing policies to protect microbial diversity with different response strategies is crucial for the preservation of soil ecosystem multifunctionality under global environmental contamination scenarios.

Counteracting human-induced transformation and degradation of natural ecosystems necessitates active ecological restoration and intervention (Wardle & Peltzer, 2007). Aboveground–belowground

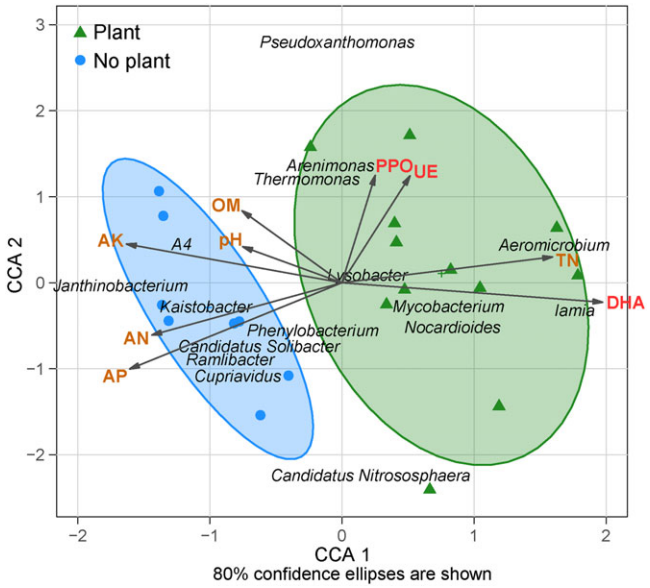

FIGURE 5 Influence of plant growth on the ecosystem multifunctionality of contaminated soil, estimated by canonical correspondence analysis. In total, 80% confidence ellipses are shown around the samples with and without plant growth. Green triangles represent samples with plant growth, and blue circles represent samples without plant growth. Arrows represent a different ecosystem multifunctionality. Only genera with a relative abundance higher than 0.5% are shown. OM, organic matter; TN, total nitrogen; AN, available nitrogen; AP, available phosphorus; AK, available potassium; PPO, polyphenol oxidase; DHA, dehydrogenase; UE, urease [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Variation explained by the variables of different response groups of soil bacteria to legume plant growth in the regression models of soil ecosystem multifunctionality

		Soil ecosystem multifunctionality (%)	
Group	Variable	Multienzyme	Multinutrient
Tolerant	Shannon	14.80	
	Richness	25.52	
	Relative abundance		
Opportunist	Shannon		19.06
	Richness		14.10
	Relative abundance		10.25
Sensitive	Shannon		
	Richness		9.08
	Relative abundance		9.49
Total		40.32	61.99

Note. NA: not statistically significant ($P > 0.05$).

linkages have important implications for restoration ecology in that they play vital roles in driving ecosystem structure and functioning, including the cycling of carbon and nutrients (Kardol & Wardle, 2010). Microbial ecosystems can exhibit remarkable resistance and resilience in response to various environmental alterations, such as global climate change (Delgado-Baquerizo et al., 2017; Szekely & Langenheder, 2017), soil contamination (Jiao, Chen, et al., 2016; Jiao, Liu, et al., 2016), and pH fluctuation (Feng et al., 2017). In our experiment, we found that soil microcosms were influenced by introducing the contaminant-degrading microbial consortium in the early phase, but they quickly recovered their compositional β-diversity. This might be explained by the priority effect of native bacterial members, which is regarded as an obstacle hindering the colonization by newly introduced species (Vannette & Fukami, 2014). In addition, the introduced microbial consortium was obtained via an enrichment culture of an artificially contaminated soil, thus likely providing tightly regulated and less complex conditions in comparison with what occurs in the field (Jiao, Chen, et al., 2016; Jiao, Liu, et al., 2016). In this case, the microbial consortium may not have been well adapted to the complex soil environment and therefore was less competitive than the native bacterial community.

Previous studies have found that colonization by newly added species was restricted to just a small fraction of available niche space, possibly due to a low amount of available resources or intense competition with the resident species in the community (Calderon et al., 2017; Nemergut et al., 2013). Under the latter scenario, there is evidence that interspecific interactions could impede the ability of new species to exploit the niches available to them during the colonization process (Calderon et al., 2017; Martorell & Freckleton, 2014). This hindrance, however, may be strengthened by the temporal responses of particular bacterial taxa with different resource-use strategies. For example, after introducing the microbial consortium, we found the relative abundance of tolerant bacterial taxa gradually increased, whereas a decrease occurred in sensitive bacterial taxa. These temporal response processes indicated a high resistance and resilience of soil microcosms towards counteracting the colonization of new, potentially invasive species. Microorganisms can adopt distinct response strategies to perturbations, which could be related to their phylogenetically conserved ecological traits (Placella et al., 2012; Szekely & Langenheder, 2017). Although the compositional β-diversity did recover, some bacterial taxa colonization did ensue over the incubation period from introducing the consortium. This may have resulted from niche sharing between the new invaders and resident species. The resource-based niche theory associates the establishment of potential invaders with local resource availabilities and the ecological traits of resident species (Tilman, 2004). These results also provide evidence for a habitat filtering process, that is, the nonrandom establishment and colonization of individuals with respect to abiotic local characteristics, and this would suggest that the microbial communities were assembled via deterministic rather than stochastic processes (Calderon et al., 2017; Placella et al., 2012).

In contrast to the treatment with the introduced microbial consortium, we detected cumulative effects of legume plant growth during the experiment. In particular, we observed that gradual increases in the relative abundances of those bacterial taxa significantly influenced by plant growth, that is, opportunist and sensitive OTUs. In this context, the former were also defined as bacterial taxa enriched by plants; likewise, the sensitive ones were the bacterial taxa depleted by plants. Plant roots are known to exert a selective effect on the soil microbial community (Bulgarelli et al., 2012; Mendes et al., 2011), which could potentially promote their own growth and nutrition (Mendes,

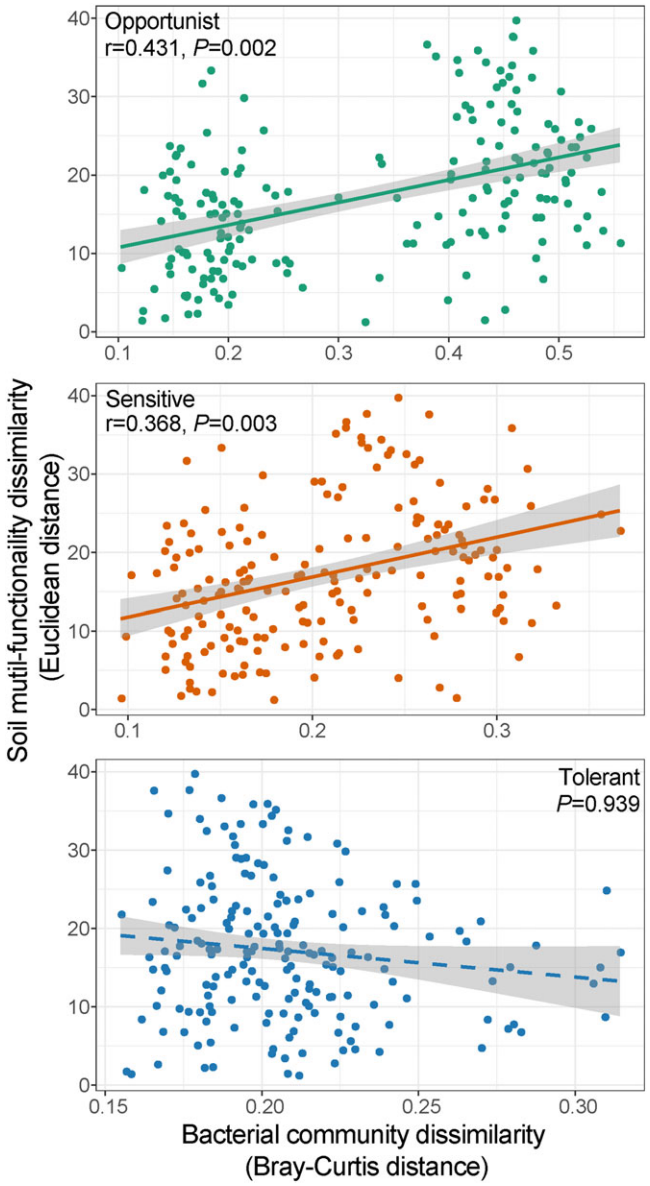

FIGURE 6 Correlations between compositional β-diversity of different response groups of soil bacteria and dissimilarities of soil multinutrient index based on Euclidean distance, estimated by Mantel test [Colour figure can be viewed at wileyonlinelibrary.com]

Kuramae, Navarrete, van Veen, & Tsai, 2014). Plants may also select a subset of microorganisms to interact at different stages of vegetative growth (Chaparro, Badri, & Vivanco, 2014). These potentially beneficial microorganisms that support nutrient acquisition for promoting plant growth are typically called plant growth-promoting rhizobacteria. Their occurrence may help explain why the plant-enriched bacterial taxa were located in the core and central positions of the networks and also strongly influenced the other nodes. The plant-enriched bacterial taxa might benefit from abundant nutrients such as root exudates and mucilage, thus enabling them to occupy the dominant ecological niches in the interaction network (Lange et al., 2015). Previous studies have demonstrated that plants' growth could increase soil network complexity and the coexistence of soil organisms via strengthening the efficiency of carbon uptake (Morrien et al., 2017; Shi et al., 2016; Stegen, Lin, Konopka, & Fredrickson, 2012).

Interestingly, the temporal responses of soil microcosms to the BP treatment were complicated. The β-diversity first increased and then decreased over the incubation period, and this was accompanied by alternating trends for different response OTUs. These complex responses might be linked to interactions between the priority effect of native bacterial members and the selective effect imposed by plant growth; the former mainly functions in the early phase, and the latter play roles in the later phase of incubation. Because the bacterial community structure was similar between the plant and BP treatments, introducing new species only might not influence the selective effect of plant growth on soil microcosms. Altogether, given their vital roles in promoting plant growth (Mendes et al., 2014), our results provide a new perspective: Plant-enriched bacteria may also act as keystone species to drive the assembly of the interaction web in soil.

Understanding the factors controlling how ecosystem multifunctionality is linked to plant production and nutrient cycling is critical to preserve and manage natural and human-dominated ecosystems (Delgado-Baquerizo et al., 2016). Recent research provides evidence that terrestrial ecosystem multifunctionality is driven by both plant and microbial diversity (Cardinale et al., 2011; Delgado-Baquerizo et al., 2016; Lefcheck et al., 2015; Maestre et al., 2012). In the present study, we assessed six ecosystem functions and particularly disentangled the main drivers behind soil ecosystem multifunctionality. We found that the diversity of tolerant OTUs contributed most to multienzyme functioning. Soil enzymes are involved in nutrient cycling, and almost all ecological reactions in soil are dependent on enzyme catalysis. DHA and PPO are two oxidoreductases that catalyze important metabolic processes, including the decomposition of organic inputs and the detoxification of xenobiotics (Wu et al., 2017; Xu et al., 2014). Urease hydrolyzes urea to release ammonium into soil (Nannipieri, Ceccanti, Cervelli, & Sequi, 1978). During the 3-month incubation period, most bacterial members in the microcosms could adapt to the contaminated conditions through their rapid growth; perhaps they also obtained an ability to degrade the organic contaminants via rapid evolutionary adaptation. In addition, urease activity was mainly functioned by the indigenous bacterial taxa because urea inherently existed in the original soil. Therefore, the plant-tolerant taxa, which had the greatest relative abundance in the community, largely determined the multienzyme functioning.

With regard to multinutrient functioning, plant-sensitive taxa were found to be the main drivers. Additionally, soil multinutrient functioning was significantly correlated with the compositional β-diversity of plant-sensitive taxa, but not with tolerant OTUs. Plant growth could considerably modify soil microbial communities and physiochemical properties, including nutrient factors, via the release of exudates and mucilage from roots (Badri & Vivanco, 2009; Shi et al., 2011). Thus, it would not be surprising to find that plant-associated taxa were somehow related to soil nutrient cycling. In particular, legumes used in the present work accumulated the total N in soils, while they depleted other available nutrients. This dynamic may be explained in two ways: (a) the legumes form nodules via

symbiosis with N_2-fixing rhizobia, which represent an important input for the nitrogen cycle (Vitkova, Tonika, & Mullerova, 2015); (b) the roots need to uptake available nutrients from soils for plant growth. These results suggested that plant-associated taxa were not only located in the core and central positions of the networks, but they also drove soil ecosystem multifunctionality, mainly by contributing to nutrient cycling. Prior work has indicated that soil microbial diversity is positively related to the multifunctionality in several terrestrial ecosystems (Delgado-Baquerizo et al., 2016; Jing et al., 2015). Our study highlights that the respective response strategies of bacterial taxa are an integral part of soil ecosystem multifunctionality. To the best of our knowledge, the present study based on temporal microcosms is the first demonstration of the roles of bacterial communities with distinct response strategies in driving ecosystem multifunctionality in a multicontaminated agricultural soil.

5 | CONCLUSIONS

We detected different response strategies of particular bacterial groups to biotic introductions in temporal soil microcosms and quantified their respective contributions to alterations in ecosystem multifunctionality. Native bacterial communities exhibited strong resilience to the introduced microbial consortium, accompanying the temporal turnover of particular bacterial taxa with different response strategies. Different response groups to plant growth determined the soil multifunctionality. By using temporal microcosms, our study provides a new perspective in disentangling the main drivers of ecosystem multifunctionality by quantitatively partitioning the response strategies of soil bacterial communities. It is pivotal to develop approaches and policies to protect soil microbial diversity with different response strategies from global environmental drivers, so that the overall multifunctionality of terrestrial ecosystems is better preserved for future generations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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