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A comprehensive synthesis unveils the mysteries of phosphate-solubilizing microbes

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ABSTRACT

Phosphate-solubilizing microbes (PSMs) drive the biogeochemical cycling of phosphorus (P) and hold promise for sustainable agriculture. However, their global distribution, overall diversity and application potential remain unknown. Here, we present the first synthesis of their biogeography, diversity and utility, employing data from 399 papers published between 1981 and 2017, the results of a nationwide field survey in China consisting of 367 soil samples, and a genetic analysis of 12986 genome-sequenced prokaryotic strains. We show that at continental to global scales, the population density of PSMs in environmental samples is correlated with total P rather than pH. Remarkably, positive relationships exist between the population density of soil PSMs and available P, nitrate-nitrogen and dissolved organic carbon in soil, reflecting functional couplings between PSMs and microbes driving biogeochemical cycles of nitrogen and carbon. More than 2704 strains affiliated with at least nine archaeal, 88 fungal and 336 bacterial species were reported as PSMs. Only 2.59% of these strains have been tested for their efficiencies in improving crop growth or yield under field conditions, providing evidence that PSMs are more likely to exert positive effects on wheat growing in alkaline P-deficient soils. Our systematic genetic analysis reveals five promising PSM genera deserving much more attention.

Key words: agricultural sustainability, biogeography, phosphate-solubilizing microorganism, plant yield, population size, phenotype, biofertilizer, genotype

CONTENTS

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I. INTRODUCTION

Phosphorus (P) is one of the six elements that are essential for all organisms on Earth (Westheimer, 1987; Schlesinger, 1997; Elser, 2012). A huge amount of P is necessary to sustain Earth's life (Cordell, Drangert & White, 2009). On a geological timescale, the primary supply of P to the biota is largely from the weathering of P-containing rock (Walker & Syers, 1976). However, microbes also play a crucial role in the P cycle in the biosphere (Rodríguez & Fraga, 1999; Falkowski, Fenchel & Delong, 2008), as a majority of P in soil is present in insoluble forms that cannot be taken up directly by plants without assistance from microbes (Rodríguez & Fraga, 1999; Vitousek *et al*., 2010; Richardson & Simpson, 2011).

The discovery of phosphate-solubilizing microbes (PSMs), which are able to solubilize insoluble phosphates into free orthophosphate (Rodríguez & Fraga, 1999; Falkowski *et al*., 2008), dates back to 1908 (Sackett, Patten & Brown, 1908; Gerretsen, 1948). However, little attention was given to PSMs until the late 1980s (Goldstein, 1986; Rodríguez & Fraga, 1999). The past three decades have seen a dramatic rise in interest in PSMs for two reasons. One is the increasing depletion of extractable P rocks (Cordell *et al*., 2009). The other lies in the fact that an estimated 5.7 billion hectares of arable land worldwide contain too little free orthophosphate to achieve optimal crop production (Batjes, 1997; Hinsinger, 2001).

Several recent reviews have aimed to summarize major research achievements in the field of PSMs since the 1990s (Rodríguez *et al*., 2006; Sharma *et al*., 2013; Alori, Glick & Babalola, 2017; Pradhan *et al*., 2017*a*). For example, Rodríguez *et al*. (2006) integrated diverse information on a wide range of genes that encode enzymes responsible for microbial solubilization of either insoluble organic phosphates (e.g. *appA*, encoding phytase) or insoluble inorganic phosphates (e.g. *gcd*, encoding glucose dehydrogenase). However, many other important aspects of our current knowledge of PSMs have not yet been synthesized. First, no reviews have focused on the population density of PSMs in different habitats and the factors that influence this, despite the importance of such information for a better understanding of the role of PSMs in the biogeochemical cycling of P (Wang, Houlton & Field, 2007*b*). Second, there is no summary available of the overall diversity of PSMs, although a large number of PSM strains have been reported separately (e.g. Oliveira *et al*., 2009). Third, no efforts have been made to provide the comprehensive data compilation and synthesis that is needed for quantitative evaluation of the application potential of PSMs as P biofertilizers in different experimental settings, despite the wide range of laboratory and field experiments conducted to date (e.g. Zabihi *et al*., 2011). Additionally, little attention has been given to systematic screening of potentially promising PSM taxa for improving crop growth or yield by identifying microbial genotypes with genes that encode microbial enzymes responsible for phosphate solubilization, although the exponentially increasing availability of data on genome-sequenced microbes now allows such screening (Zimmerman, Martiny & Allison, 2013; Dunivin, Yeh & Shade, 2019).

Here, we present the first synthesis of the biogeography, diversity and utility of PSMs. To this end, we synthesize data from 399 papers published between 1981 and 2017, the results of a nationwide field survey in China consisting of 367 soil samples, and a genetic analysis of nearly 13000 genome-sequenced prokaryotic strains. Our findings provide a solid basis not only for further studies on basic aspects of PSMs but also for those addressing applied aspects of PSMs.

II. METHODS

(1) A global literature survey

To construct a comprehensive database of PSMs, we conducted a literature search on 31st December 2017 in the ISI *Web of Science* using the following combination of key words: phosphate-solubilizing microbe OR phosphate-solubilizing microorganism OR phosphate-solubilizing bacteria OR phosphate-solubilizing bacterium OR phosphate-solubilizing fungi OR phosphate-solubilizing fungus. We restricted our research to articles written in English and published between 1980 and 2017. We retrieved 761 hits. After an initial assessment based on careful reading of the abstracts, 646 full-text articles were downloaded for further analysis.

To be included in our database, articles were required to match at least one of the following three criteria: (*i*) presenting data on the population density of PSMs (phosphate-solubilizing bacteria, fungi or both) in environmental samples from a particular study site; (*ii*) reporting at least one new PSM strain and classifying it to genus or species; and (*iii*) determining the efficiency of a given PSM strain classified to genus or species in improving plant growth or yield in a laboratory or field experiment or both. A total of 399 papers matched our criteria.

For the papers matching the first criterion, we collected information on place name, geographic location (latitude and longitude), mean annual precipitation (MAP) and mean annual temperature (MAT) of the study sites, sample type (bulk soil, rhizosphere soil, sediment, etc.), and the population density of the PSMs (expressed as the number of colony-forming units per gram or per millilitre sample, i.e. CFU g^{-1} or CFU ml^{-1}), pH, and total and available P of the samples. We focused on these geographic, climatic and environmental parameters, as they are potentially important factors influencing the population density of PSMs in the environment (Kucey, 1983; Crowther *et al.*, 2019). Note, however, that full information on these parameters was generally presented in only a proportion of the targeted papers. Where this information was not provided, approximate values for the geographic and climatic factors were derived from *Google Earth* 7.0 (free version) and/or *WorldClim* by geocoding the place names of the study sites (Hijmans *et al.*, 2005). In cases where a given sample type for a study site consisted of samples collected at different time points, we combined all the data on the microbial and environmental parameters for different time points and calculated their averages for that sample type and study site. For example, if the 'bulk soil' of a study site comprised samples collected at three different time points, we calculated an average population density of PSMs for the 'bulk soil' based on those averages of the corresponding samples collected at the three time points (because the raw data for individual samples collected at each time point were generally not available in the literature), and we recorded these as three data points ($n = 3$ in our database; see online Supporting Information, Table S1) for the population density of PSMs in the 'bulk soil' of that study site. However, for study sites where samples of a given sample type were collected at only one time point, data points for a sample type are equal to the sample size of that sample type (these values were always presented in the literature). In cases where the population densities of both phosphate-solubilizing bacteria and fungi were determined, we considered their sum as the population density of PSMs. We plotted the information on sample type and the number of data points on a world map using the R package ggplot2 (Wickham, 2016). A *post-hoc* multiple-comparison Tukey's HSD test was carried out to explore significant differences between sample types in the population density of PSMs. Rock and municipal solid waste were not included in this multiple comparison, as there were data for only one study site for each of these two sample types. To investigate the effects of geographic, climatic and environmental parameters on the population density of PSMs in the environmental samples, we analysed the relationships between these parameters and the population density of PSMs by using univariate linear regressions. Data on water samples were excluded from the regression analysis, given that the physical nature of water differs greatly from that of solid samples. The normality of all data was evaluated using the *shapiro.test* function in R, and a log transformation was performed to increase normality when necessary.

For the papers matching the second criterion, we collected information on species name (for strains that were classified only to the genus level, the genus name plus 'sp.' was recorded), strain name, domain name (i.e. archaea, bacterium or fungus), habitat type, growth medium for isolation of the strain, and the presence of inorganic or organic phosphate in the growth medium. To provide an overview of the diversity of the PSM strains identified in the literature, we counted the total number of these strains and the number of species/genera they represented. In addition, we divided these strains into subgroups according to their domain (i.e. archaea, bacterium or fungus) or their ability to solubilize different types of phosphates (i.e. insoluble organic or inorganic phosphates or both) and counted the number of species/genera represented by the corresponding strains within individual subgroups. To show the genera represented by the identified prokaryotic strains of PSMs, the representative full-length 16S ribosomal RNA (rRNA) gene sequences of these genera (one sequence per genus) retrieved from the SILVA database (release 138.1; Quast *et al.*, 2012) were used to construct a phylogenetic tree with RAxML (Stamatakis, 2006). Similarly, the representative full-length 18S rRNA gene sequences retrieved from the SILVA database were used to construct a phylogenetic tree for the fungal genera represented by the identified fungal strains of PSMs. The contributions of individual genera to the total number of identified PSM strains or to the total number of identified PSM strains that can solubilize both inorganic and organic phosphates (hereafter referred to as $PSM^{I\&O}$) were calculated and then visualized on the phylogenies using iTOL v4 (Letunic & Bork, 2019).

For the papers matching the third criterion, we collected information on the strain name, species name and domain name of each PSM strain under investigation, experiment type (field or laboratory), plant name (Latin and cultivar names were recorded when applicable), pH, total and available P of the plant growth substrate used in the experiment, and the effect of each PSM strain on plant growth or yield (compared to the non-inoculated control). To obtain information about the factors influencing the performance of the tested strains, we divided the reported experiments into subgroups in a stepwise manner according to experiment type, plant type (crop or non-crop) and measure of effect (edible part or non-edible part for crops and biomass for non-crop plants). In cases where more than one measure of effect was available, we used only the one that was most relevant to the shoot biomass of non-crop plants or the yield of crops (edible parts). For example, when shoot and root biomasses of wheat (*Triticum aestivum*) were determined as measures of the effect of a given PSM strain in an experiment, we used shoot biomass as the measure of the effect of that strain on wheat in that experiment. We calculated the proportions of different effect types (i.e. positive, negative, or no effect) of experiments for the finest-level subgroups under consideration. In cases where it was not clear whether a difference between an inoculated treatment and its non-inoculated control in plant growth or yield was statistically significant, we considered a decrease or increase no greater than 10% compared to the control as 'no effect'. Regarding 'positive effect' cases for each of the finest-level subgroups, we further calculated an average improvement (%) (i.e. the arithmetic mean of the increases observed in all relevant cases). The average improvement of all field experiments showing a positive effect was calculated and compared with that of all laboratory experiments showing a positive effect based on an independent sample *t*-test. To obtain a better understanding of the application potential of PSM strains, the results from field experiments were selected for further analysis. We compared soil pH and available P between the experiments showing a positive effect and those showing a negative effect with a Student's *t*-test. In cases where data on available P were not present in mg kg^{-1}, they were transformed assuming that soil has a bulk density of 1.3 g cm^{-3}. This analysis was not done for total soil P, as only 11 experiments reported this parameter. We also calculated the percentages of positive effect cases for individual subgroups of experiments divided according to crop type [i.e. wheat, maize (*Zea mays*) and chickpea (*Cicer arietinum*)]; other crops were not considered, as the number of experiments for each of these were <10) or PSM type (i.e. bacteria and fungi; data on archaea were not available).

(2) A nationwide field survey

To obtain more insights into the biogeography of PSMs, a nationwide field survey of the population density of PSMs in soil was conducted in China from July to August 2018. Forty sites distributed across 22 provinces (Table S2) were selected to be representative of the geographic, climatic and edaphic variations present across China. At each site, two to three representative habitats that were approximately five kilometres apart were chosen for the collection of soil samples. In sum, four desert (Gobi) regions, nine grasslands, 27 forests, 29 farmlands and 40 mined lands were sampled. We paid considerable attention to mined lands, as they are widespread in China and pose serious threats to soil quality and functioning (Chen *et al*., 2014*a*). For each habitat, four soil samples were collected at a depth of 0–20 cm. Each soil sample consisted of three subsamples, which were collected from three randomly distributed locations. To avoid the potential effects of plants, soils located approximately 1 m away from the plant rhizosphere were sampled. After sampling, we recorded the geographic parameters (coordinates and elevation) of each habitat and transported the samples to laboratories as soon as possible.

Phosphate-solubilizing bacterial and fungal populations in our soil samples were enumerated according to methods described previously (Leaungvutiviroj *et al*., 2010). As described in Section II.1, we considered the population density of PSMs to be the sum of those of the densities of phosphate-solubilizing bacteria and fungi. Note that 15% of our soil samples failed to form clear zones on the plates used for counting PSM colonies within an incubation period of 7 days, of which nearly 80% were soil samples from mined lands. This is in agreement with the well-known observation that the edaphic conditions of mined lands are generally unfavourable for soil microbes responsible for soil nutrient cycling (Sheoran, Sheoran & Poonia, 2010). As a result, a total of 367 soil samples whose PSM populations could be counted after 7 days of incubation were included for further analysis. Selected soil properties, including pH, electrical conductivity (EC), total and available (Olsen) P, nitrate-nitrogen (NO_3^--N), ammonia-nitrogen (NH_4^+-N), dissolved organic carbon (DOC), and water-soluble organic carbon (WSOC), were determined using standard methods (Sparks & Sparks, 1996).

We compared the population density of soil PSMs among habitat types using a *post-hoc* multiple-comparison Tukey's HSD test. The climatic parameters (MAP and MAT) for each habitat were obtained from *WorldClim* by using its geographic coordinates. To explore the effects of geographic, climatic and edaphic parameters on the population density of soil PSMs, univariate linear regressions were used to analyse the relationships between these parameters and the population density of soil PSMs. The *shapiro.test* function in R was employed to evaluate the normality of the data. Where necessary, data were log-transformed to increase their normality.

(3) A systematic genetic analysis

To assess the genetic potential of cultured and whole genome-sequenced prokaryotic microbes for phosphate solubilization, we performed a phylogenomic analysis to retrieve genes encoding orthologous proteins of acid phosphatase (AP), alkaline phosphatase (ALP), phytase and glucose dehydrogenase (GCD) from all 12986 complete bacterial and archaeal genomes from NCBI GenBank (updated on 3rd May 2019). These four enzymes were selected as they are considered the major enzymes responsible for organic and inorganic phosphate solubilization by microbes (especially prokaryotes; Rodríguez *et al*., 2006). One representative protein sequence for each gene family, AP (*phoN*, *aphA* and *olpA*), ALP (*phoD*, *phoX* and *phoA*), phytase (*appA* and *phy*) and GCD (*gcd*), was retrieved from KEGG according to its corresponding KEGG Ontology (KO) number. The homologues of each gene family were obtained through an initial BLASTp search against 2764 manually curated representative genomes of prokaryotes with a broad range of phylogenetic diversity (e-value cut-off 1e-15; Wang & Wu, 2017). The sequences of each gene family were aligned using MAFFT v7.427 (Katoh *et al*., 2002) and trimmed using ZORRO (Wu, Chatterji & Eisen, 2012). A phylogenetic tree of each gene family was constructed using FastTree 2.1.10 (Price, Dehal & Arkin, 2010) and was manually inspected to resolve orthologues and potential paralogues into different subfamilies. A hidden Markov model was built for each subfamily using HMMer 3.2 (Eddy, 1998).

Selecting the proper HMM search threshold is key to obtaining orthologous proteins for each gene family at a large scale. Instead of using arbitrary thresholds as in previous studies (e.g. Dunivin *et al*., 2019), we calibrated the threshold from known orthologous sequences for each gene family. We performed an HMM search using the orthologous HMM of each gene family against the known orthologous proteins in the 2764 representative genomes from manual tree inspection. The lowest bitscore of all hits was recorded as the threshold for all orthologous matches of the gene family. A full HMM search was performed for each gene family using all of its orthologous and paralogous HMMs against the protein sequences of all 12,986 genomes. Protein sequences that showed the best hit with the orthologous HMM with (*i*) a bitscore greater than the calibrated threshold for the gene family, and (*ii*) more than 90% sequence coverage, were retained as the orthologues for each gene family.

The numbers of orthologous proteins for each gene family among all 12986 genomes were tabulated. For each of the four enzymes, the proportion of enzyme-positive genomes within a given genus to all genomes within that genus was calculated. Given the important role of pyrroloquinoline quinone (PQQ, a cofactor of GCD) in the microbial solubilization of inorganic phosphates (Rodríguez *et al.*, 2006), only genomes with *gcd* plus at least one gene encoding PQQ (*pqq*) were considered GCD-positive genotypes. Genes encoding orthologous proteins of PQQ were retrieved from the 12986 genomes according to the method described above. For each of the four enzymes, we also assessed the contribution of each genus to the total enzyme-positive genotypes by dividing the number of enzyme-positive genomes within each genus by the total number of enzyme-positive genomes of all 12986 genomes. The phylogenetic distribution of the two measurements mentioned above and the genera with enzyme-positive genomes were visualized in iTOL v4 (Letunic & Bork, 2019). The phylogenies were constructed as described above.

III. RESULTS

(1) Global patterns of the population density of PSMs in the environment

We found 63 studies quantifying the population density of PSMs in a total of 1053 environmental samples collected from 117 geographical locations distributed across 19 countries around the world (Fig. 1A, Table S1). On average, rhizosphere and bulk soils harboured more PSMs than sediments and water bodies ($P < 0.05$, Fig. S1A) but not more PSMs than composts and plant roots. The population density of PSMs in the environmental samples was positively related to the total P and MAT of the study site ($P < 0.05$, Fig. 1B, D) but was not correlated with pH, available P, latitude, longitude or MAP ($P > 0.05$, Fig. 1C, Fig. S1B–E).

(2) Continental patterns of the population density of soil PSMs

Our nationwide field survey including 367 soil samples (Fig. 2A, Table S2) showed that both farmland and forest soils exhibited a higher PSM population density than those from the other habitats ($P < 0.05$, Fig. S2A). Positive relationships were found between the population density of soil PSMs and total P, available P, NO_3^--N, DOC, MAT, MAP and longitude of the study sites ($P < 0.05$, Fig. 2B, C, E–G, Fig. S2E, G). Negative relationships existed between the population density of soil PSMs and EC, latitude and elevation ($P < 0.05$, Fig. S2B, F, H). The population density of soil PSMs was not correlated with pH, NH_4^+-N or WSOC ($P > 0.05$, Fig. 2D, Fig. S2C, D).

(3) Overall diversity of PSMs isolated worldwide

More than 20 archaeal, 398 fungal and 2286 bacterial strains were identified as PSMs (Fig. 3A, Table S3). Five fungal and 25 bacterial genera were found to be rich in PSMs (i.e. >10 strains; Fig. 3C, D, Table S3). Among these, *Bacillus*, *Pseudomonas*, *Enterobacter*, *Burkholderia*, *Penicillium* and *Aspergillus* individually had more than 100 identified PSM strains and thus could be considered significant PSM genera (Fig. 3C, D, Table S3).

At least 214 and 2580 strains were found to be able to solubilize organic and inorganic phosphates (hereafter referred to as PSM^O and PSM^I, respectively; Fig. 3B). Among these, only 90 strains were $PSM^{I\&O}$, the majority of which were affiliated with *Paenibacillus*, *Bacillus*, *Pseudomonas*, *Lactococcus*, *Enterobacter* and *Alcaligenes* (Fig. 3C). These six genera, of which three overlapped with those containing >100 PSM strains, were also considered significant PSM genera. The resultant nine main PSM genera belonged to three bacterial phyla and one fungal phylum (Fig. 3C, D).

(4) Performance of PSMs in improving plant growth and yield

A total of 724 records on the performance of individual PSM strains in improving plant growth and yield were reported in 185 studies (Fig. 4A, Table S4). Regardless of plant type and measure of effect, the proportion of positive effect cases (records) in laboratory-based experiments was nearly 80%, which was much higher than that of field-based experiments. When only positive effect cases were taken into account, the average improvement observed in laboratory-based experiments was 91.7%, which was 2.37 times higher than that of field-based experiments ($P < 0.01$, Fig. 4A).

The average soil pH of field-based experiments showing a positive effect of PSMs was 7.23, which was higher than that showing no effect ($P < 0.05$, Fig. 4B). Lower available soil P was recorded in field-based experiments showing a positive effect of PSMs ($P < 0.001$, Fig. 4C). A total of 76.5% of field-based experiments conducted with wheat showed a positive effect of PSMs, which was much higher than for experiments with maize and chickpea (Fig. 4D). A total of 37.5% of experiments focusing on fungi reported a positive effect, which was almost equal to that of bacteria ($P > 0.05$, Fig. 4E).

(5) Promising PSMs revealed by genetic analysis

Among the 12986 prokaryotic genomes, 4367, 6377, 2401 and 1524 were found to have AP-, ALP-, phytase- and GCD-positive genotypes, respectively (Tables S5–S8). We

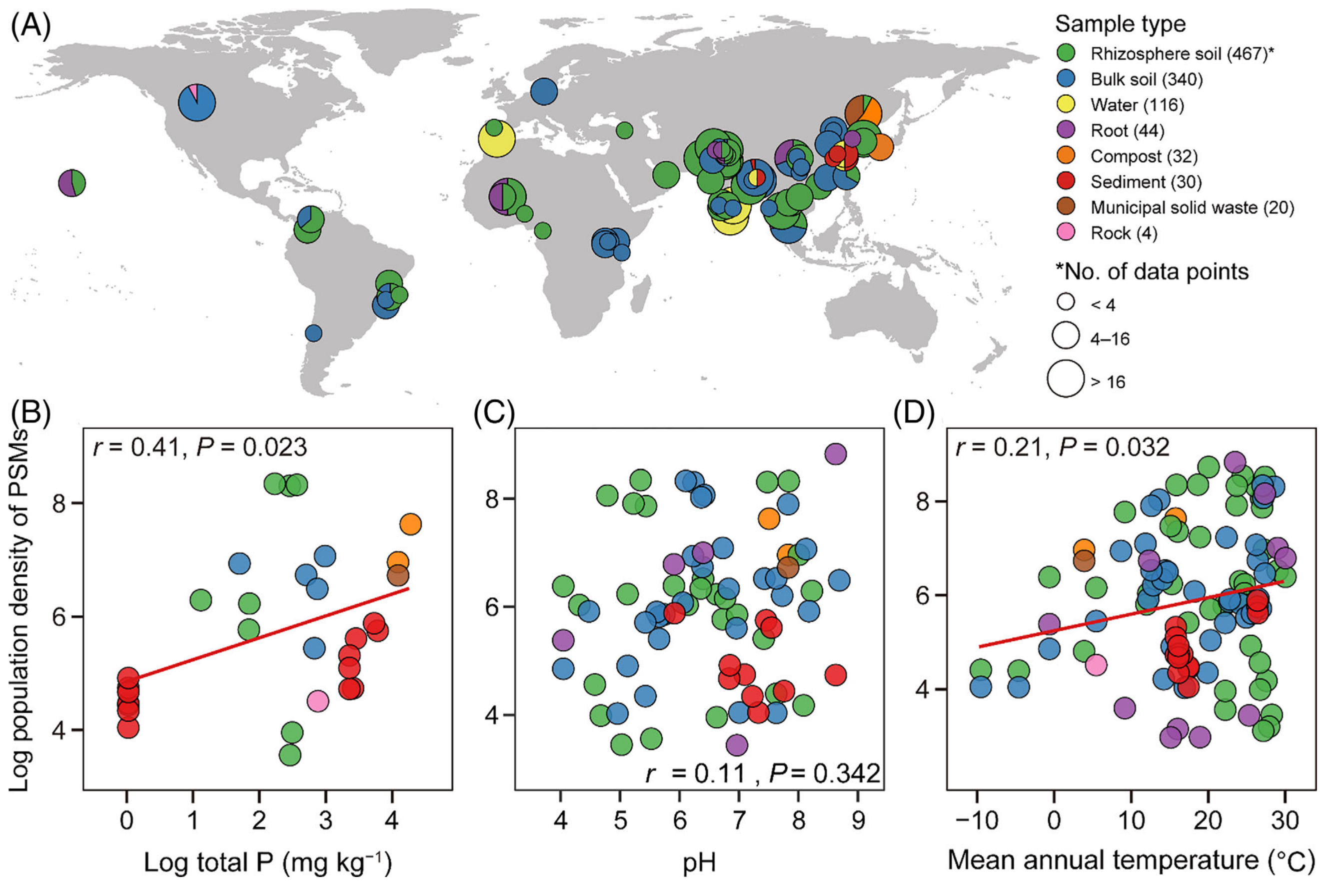


Fig 1. Global patterns of the population density of phosphate-solubilizing microbes (PSMs) in the environment. (A) Locations of the 117 sites at which the population density of PSMs in environmental samples was determined. Sample types are indicated by coloured circles. The numbers of data points for the indicated sample types are given in parentheses in the key. The size of a circle on the map is proportional to the number of data points for a given sample type at that site. Circles with more than one colour indicate that more than one type of sample was collected from these sites. Some sites are close to each other, leading to overlaps among circles. (B–D) Effects of total P (B), pH (C) and mean annual temperature (D) of the study sites on the population density of PSMs. Colour coding of symbols is as in A. See Table S1 for source data.

focused on the genera rich in enzyme-positive genotypes, each of which had no less than 30 sequenced genomes, and ≥50% of the sequenced genomes contained at least one gene encoding an enzyme of interest. In this context, 17, 29, nine and eight genera were found to be rich in AP-, ALP-, phytase- and GCD-positive genotypes, respectively (Fig. 5, Tables S5–S8). We identified six genera rich in both GCD-positive and AP-/ALP-/phytase-positive genotypes (i.e. with genetic potential for solubilization of both inorganic and organic phosphates) as promising PSM genera (Fig. 5). Remarkably, *Klebsiella* and *Xanthomonas* were the only two genera rich in genotypes for all four enzymes. For *Klebsiella*, 99.5, 99.0, 98.1 and 91.3% of genomes were AP-, ALP-, phytase- and GCD-positive, respectively.

IV. DISCUSSION

The roles of PSMs in driving the biogeochemical cycling of P and mediating plant uptake of P are comparable to those of nitrifying microbes in the N cycle (Rodríguez & Fraga, 1999; Crowther *et al.*, 2019). However, research on PSMs has lagged far behind that on nitrifying microbes. This is especially the case for the past decade, when great advances have been made in the study of nitrifying microbes (Kuypers, Marchant & Kartal, 2018). In comparison, the number of studies currently available on PSMs is tiny (Alori, Glick & Babalola, 2017; Kuypers, Marchant & Kartal, 2018). More surprisingly, these studies have not yet been synthesized either at a global scale or in a quantitative way, representing a major constraint on the development of PSM research.

(1) Factors determining the geographic distribution of PSMs

The population density of PSMs in environmental samples and its determinants are critical to understanding not only their population ecology but also their roles in regulating the biogeochemical cycling of P and mediating the plant uptake of this element (Goldstein, 1986; Rodríguez &

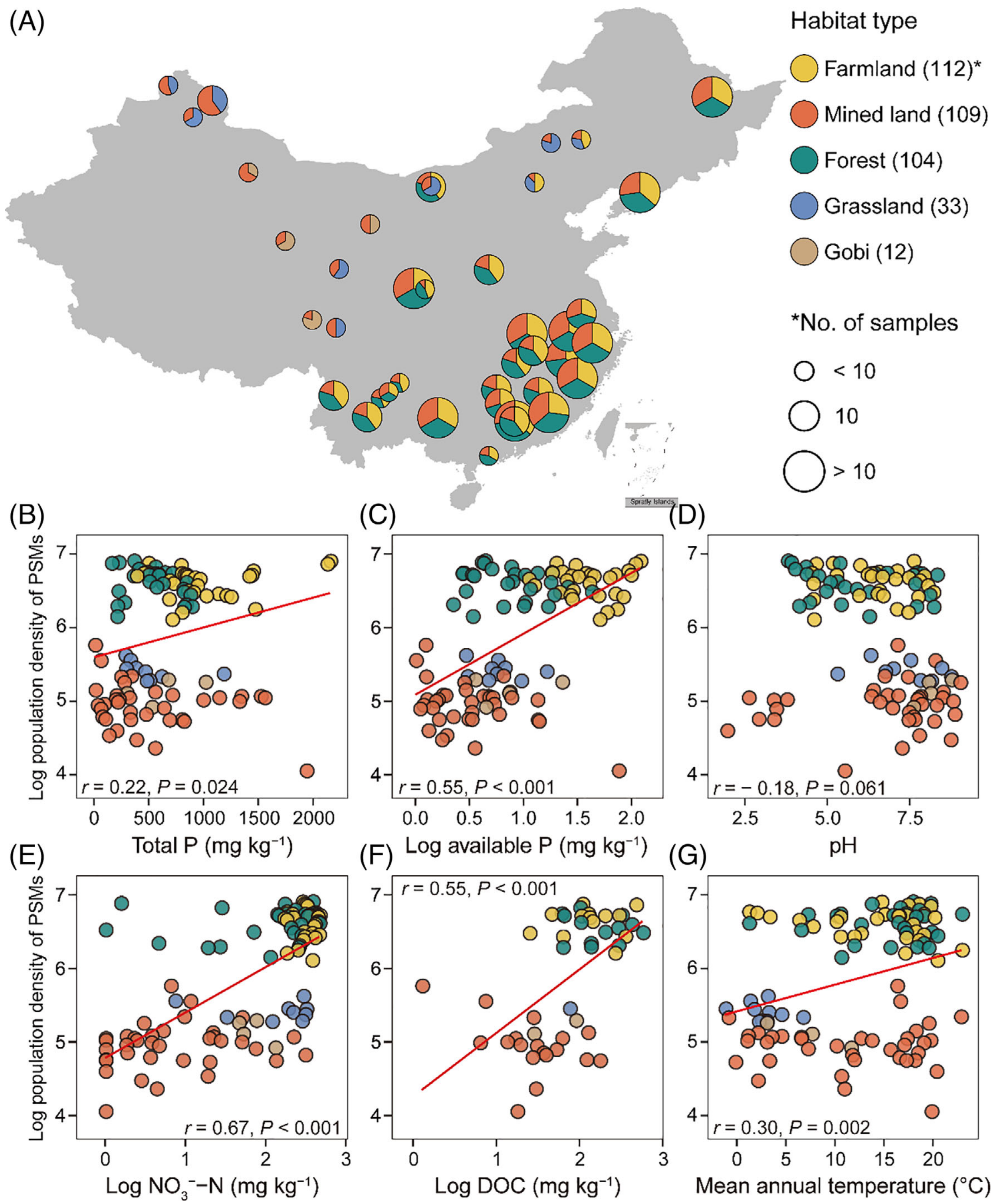


Fig 2. Patterns of the population density of soil phosphate-solubilizing microbes (PSMs) across China. (A) Locations of the 40 sites at which the population densities of soil PSMs were investigated in our field survey. Habitat types are indicated by coloured circles. The numbers of soil samples for the indicated habitat types are given in parentheses in the key. The area of a circle on the map is proportional to the number of soil samples for a given habitat type at that site. Circles with more than one colour indicate that soil samples were collected from more than one type of habitat at these sites. Some sites are close to each other, leading to overlaps between some circles. (B–G) Effects of total P (B), available P (C), pH (D), nitrate-nitrogen (NO_3^--N, E), dissolved organic carbon (DOC, F) and mean annual temperature (G) of the study sites on the population density of soil PSMs. See Table S2 for source data.

Fraga, 1999). Indeed, due to its strong association with soil P solubilization potential (e.g. Hu *et al.*, 2009), the population density of soil PSMs can be used as a proxy to represent the overall function of soil microbial communities responsible for P cycling. While a growing body of evidence suggests that exploring the functional biogeography of soil microbial

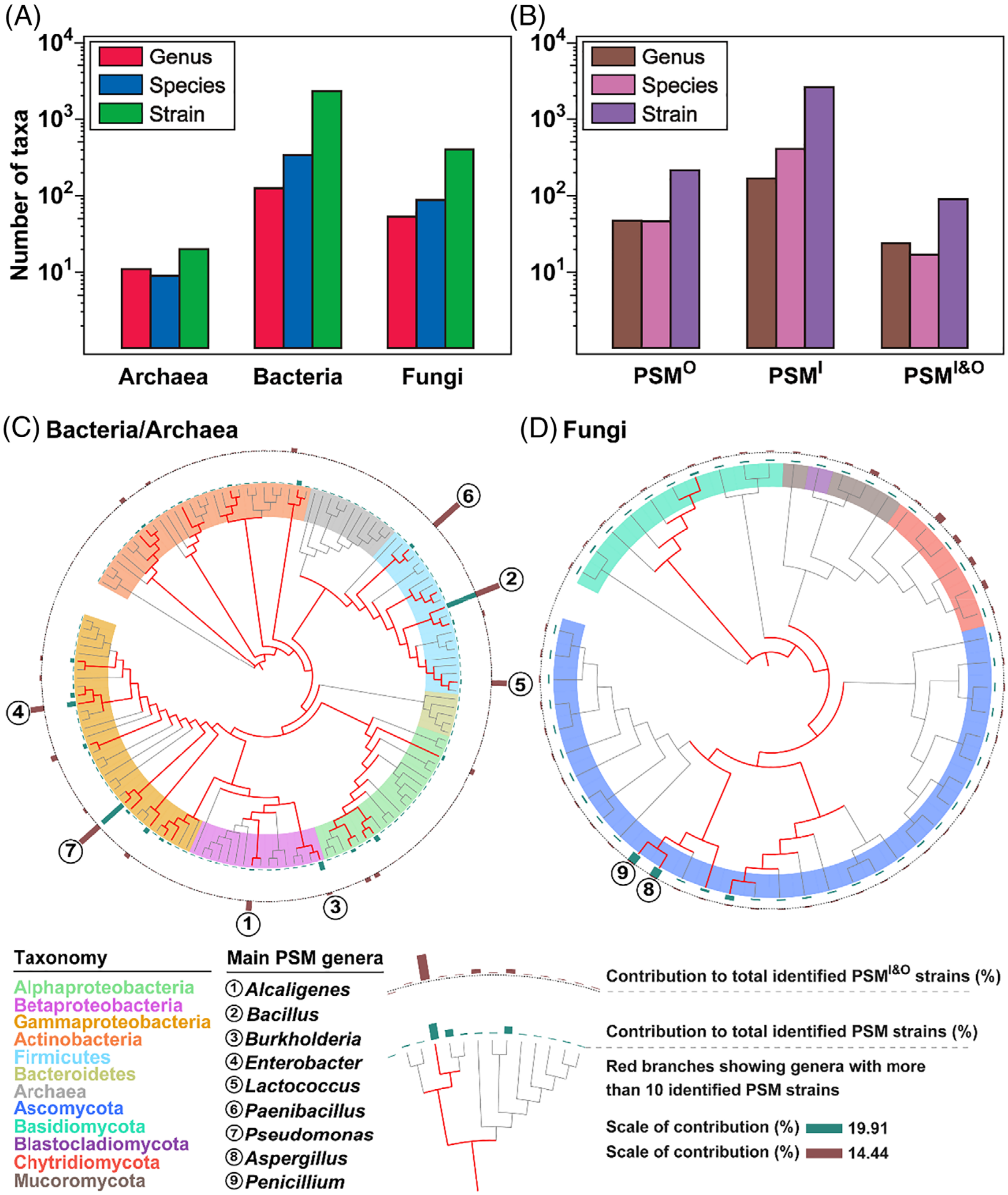


Fig 3. Overall diversity of phosphate-solubilizing microbes (PSMs) reported in the literature. (A, B) The number of taxa of PSM subgroups divided according to domain (A) and substrate preference for phosphate solubilization (B). PSM^O and PSM^I represent microbes that can solubilize organic and inorganic phosphates, respectively; $PSM^{I\&O}$ represents those that can solubilize both organic and inorganic phosphates. (C, D) Phylogenies showing genera represented by all 2704 identified PSM strains. The genera with more than 10 PSM strains are highlighted with red branches in the phylogenies. The two rings outside the phylogenies indicate the contributions of individual genera to the total identified PSM (inner ring) and $PSM^{I\&O}$ strains (outer ring). Seven bacterial and two fungal genera (each with >100 identified PSM strains or >5 identified $PSM^{I\&O}$ strains) considered the main PSM genera are identified with numbers on the outermost ring. See Table S3 for source data.

communities can improve the predictions of global biogeochemical models for C and N (Crowther *et al.*, 2019), little is known about the biogeography of the population density of soil PSMs. To our knowledge, there has been only one prior study that determined the population density of PSMs in environmental samples at a spatial scale larger than the

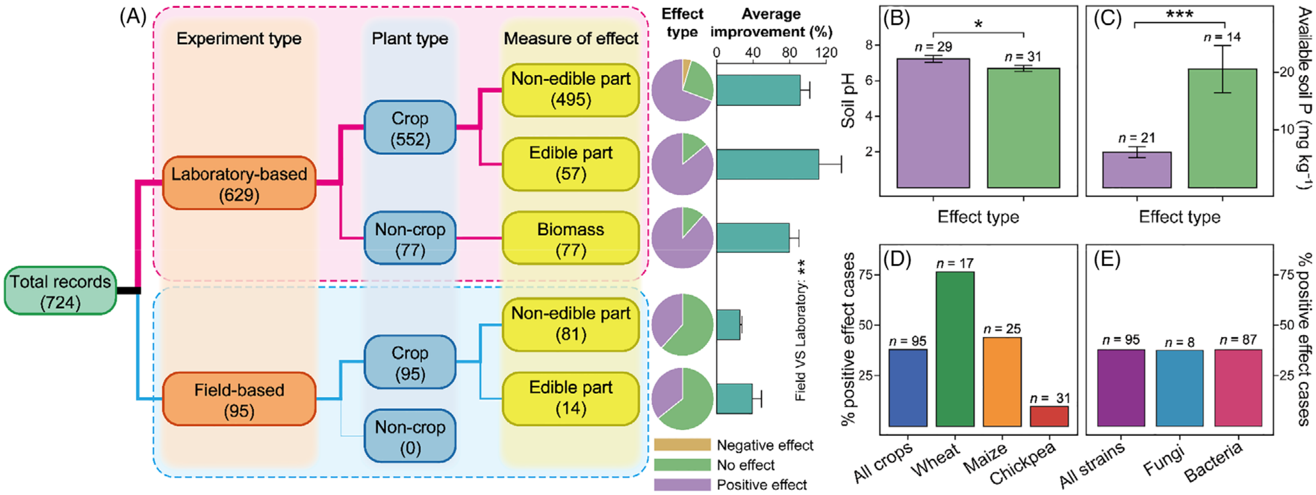


Fig 4. Performance of phosphate-solubilizing microbes (PSMs) in improving plant growth or yield. (A) Overview of reported experiments addressing the performance of PSMs in improving plant growth or yield. The number of experiments for a given subgroup according to experiment type, plant type or measure of effect is given in parentheses. (B–E) Important factors influencing the performance of PSMs on crop growth or yield in field experiments. (B, C) There are significant differences between experiments showing positive effects of PSMs and those showing no effects for soil pH (B) and available P (C). (D, E) Potential effects of crop and PSM types on the performance of PSMs. In A–C the results of a Tukey's HSD test and a Student's *t*-test are shown: *, ** and *** represent $P < 0.05$, 0.01 and 0.001, respectively. Numbers above the bars in B–E indicate the numbers of experiments for the respective subgroups. See Table S4 for source data.

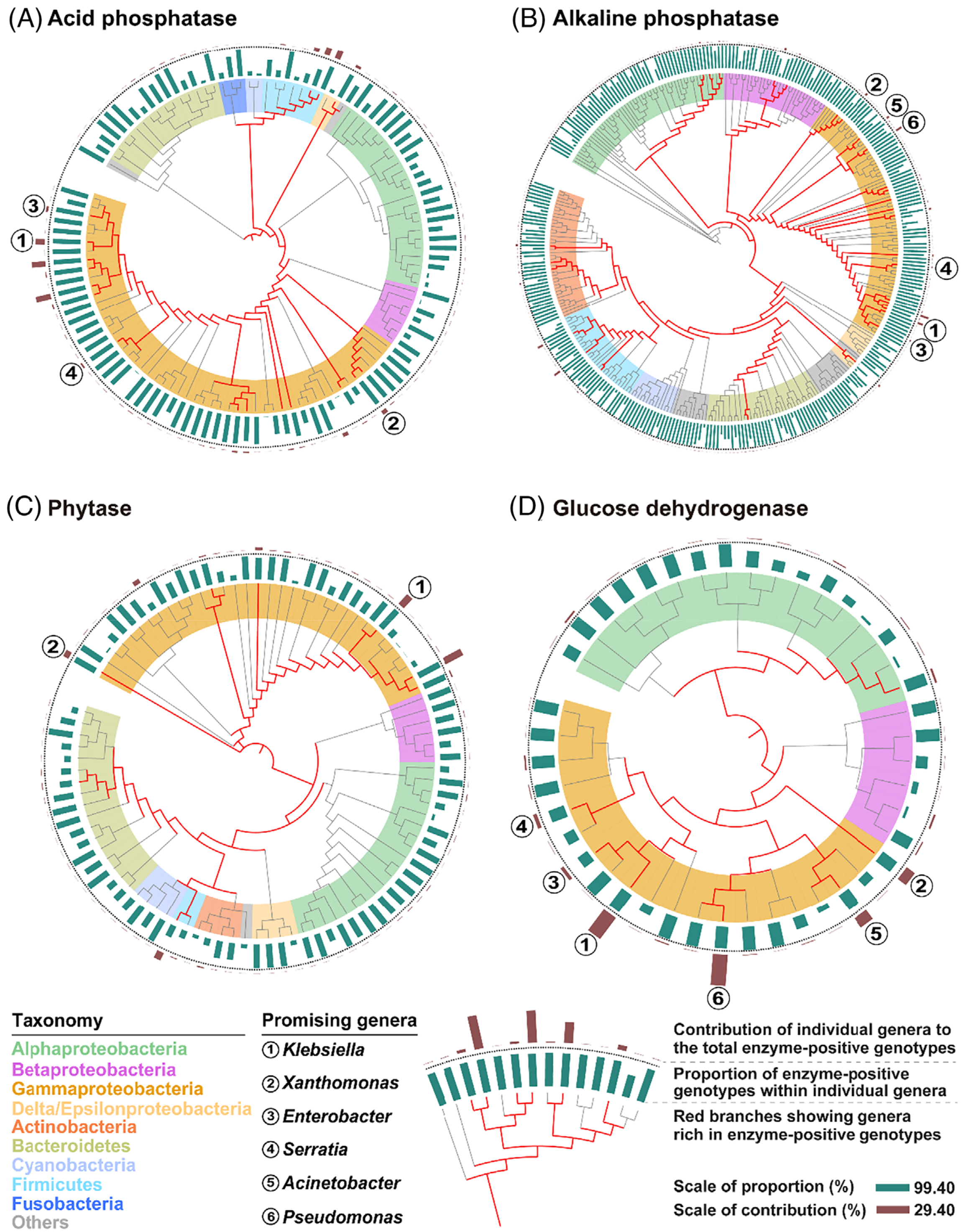
plot level. In that study, the population density of phosphate-solubilizing fungi in 29 soils collected from 17 sites located in southern Alberta, Canada, was found to be positively correlated with total soil P but was not related to available soil P (Kucey, 1983). In agreement with this pattern, we showed that at a global scale, there was a positive relationship between the population density of PSMs in environmental samples and total P in the environment, but not with available P (Fig. 1B, Fig. S1B). We speculate that the lack of correlation between the population density of PSMs and available P is likely attributable to: (*i*) the sample size of the study conducted in southern Alberta was too small to capture sufficient variation in available soil P at that spatial scale, and (*ii*) different analysis methods were used to determine available P in the environment of about half of the 117 sites synthesized in this study (Table S1), with the variations in available P arising from different analysis methods likely obscuring any correlation. Intriguingly, these suggestions are supported by the results of our nationwide field survey in which we analysed available P in soils across China using a uniform method and found a positive relationship between the population density of soil PSMs and available soil P (Fig. 2C). This finding reinforces the importance of PSMs as a driver of the biogeochemical cycling of P (Rodríguez & Fraga, 1999; Falkowski *et al.*, 2008).

A common pattern revealed by our global literature review and nationwide field survey is that the population density of PSMs is not correlated with pH (Figs 1C and 2D), indicating a wide range of pH values over which PSMs can thrive. This finding appears reasonable, as a major mechanism underlying microbial solubilization of insoluble phosphates is that PSMs can acidify their extracellular environment by secreting organic acids (Rodríguez & Fraga, 1999). By contrast, the relative abundance of *Nitrospirae* (a major group of microbes governing the biogeochemical cycling of N) in the global topsoil microbiome was reported to increase with soil pH (Bahram *et al.*, 2018). This differential response of PSMs and *Nitrospirae* to environmental pH could be interpreted as pH-related niche partitioning between these two important functional microbial groups. On the other hand, we obtained the first evidence for synergistic interactions between PSMs and nitrifying microbes and potentially those driving C cycling: the population density of soil PSMs across China was positively correlated with not only soil NO_3^--N but also soil DOC (Fig. 2E, F).

In addition to confirming the positive effect of MAT on the population density of PSMs (Figs 1D and 2G), our nationwide field survey showed further that the population density of soil PSMs across China was positively correlated with MAP and longitude but negatively correlated with latitude (Fig. S2E–G). It is thus clear that soil PSMs tended to reach larger population sizes and thereby likely a higher metabolic activity responsible for P cycling in warm and moist regions than in dry and cold regions. Similar patterns have been observed for microbes governing the biogeochemical cycling of N and C (Bahram *et al.*, 2018; Crowther *et al.*, 2019). Taken together, these findings provide further evidence for functional coupling between soil PSMs and microbes governing soil nitrification and organic matter degradation (Crowther *et al.*, 2019).

(2) **Are we observing the whole picture of PSM diversity?**

A traditional viewpoint has been that rhizosphere soil will have a higher population density of PSMs than bulk soil (Goldstein, 1986). However, the results from our global-scale literature review (Fig. S1A) do not support this viewpoint. This discrepancy may be attributed at least partly to the considerable variations in population density of PSMs among the studies synthesized herein. These variations could be



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derived from complex sources. For example, plant identity was reported previously to have a considerable effect on the population density of PSMs in rhizosphere soil (Leaungvutiviroj *et al.*, 2010). Additional studies focusing on pairwise comparisons of the population density of PSMs between the rhizosphere and bulk soil from the same plant species are needed to examine the generality of this finding, as such studies remain relatively rare.

Although a large proportion of early efforts to isolate PSMs were focused on rhizosphere soil (Goldstein, 1986), an increasing number of PSM strains have been isolated from a wide range of other habitats (including bulk soil, water, sediment, rock, compost, plant tissue and even animal tissue; Table S3). Here, for the first time, we provide a comprehensive list of all PSM strains reported in the literature. The total number of PSM strains (i.e. 2704) was somewhat smaller than expected, which could partly be due to exclusion of strains without genus- level taxonomic information available. The six main PSM genera (*Bacillus*, *Pseudomonas*, *Enterobacter*, *Burkholderia*, *Penicillium* and *Aspergillus*; each with >100 PSM strains) identified herein have also frequently been mentioned in previous reviews (e.g. Rodríguez & Fraga, 1999; Alori *et al.*, 2017). However, we showed also that the number of bacterial genera rich in PSM strains and their contribution to the total number of PSM strains far exceeded the corresponding values for fungal genera (Fig. 3). These results clarify a popular misconception regarding the numerical predominance of fungal PSM genera (Alori *et al.*, 2017). The great difficulty in culturing archaea is likely a major reason for the finding that only 20 archaeal strains belonging to 11 genera were able to solubilize inorganic phosphates. Nonetheless, it is interesting to explore whether archaea can solubilize organic phosphates, considering that their phylogenetic and functional diversities are much higher than previously thought (Schleper, Jurgens & Jonuscheit, 2005).

Remarkably, 90 strains were found to have the ability to solubilize both inorganic and organic phosphates (i.e. $PSM^{I\&O}$ strains; Fig. 3B), of which 93.3% were bacteria. Among the 19 bacterial genera containing $PSM^{I\&O}$ strains, *Paenibacillus*, *Bacillus*, *Pseudomonas*, *Lactococcus*, *Enterobacter* and *Alcaligenes* together contributed 70% of the total number of $PSM^{I\&O}$ strains. To date, they have received much less attention than they deserve, especially considering the widespread cooccurrence of inorganic and organic insoluble phosphates in the environment (Walker & Syers, 1976; Vitousek *et al.*, 2010) and that many members of these genera (e.g. *Bacillus*) show a broad spectrum of antagonistic activity against phytopathogens (Fira *et al.*, 2018). Despite the existence of these main $PSM^{I\&O}$ genera and those rich in PSM strains, it is often observed that different strains from the same species can have strong, weak or even no ability to solubilize phosphates (e.g. Baldan *et al.*, 2015; Brígido, Glick & Oliveira, 2017). In agreement with this, a previous phylogenetic analysis revealed that the average level of phylogenetic conservation for genes encoding ALP was less than the species level (Zimmerman *et al.*, 2013). These findings raise another key question about the relative importance of vertical inheritance and other factors for a given strain to acquire the ability to solubilize either inorganic or organic phosphates. Indeed, our recent study provided evidence that phage-related horizontal gene transfer can assist some soil microbes in acquiring new genes encoding GCD (Liang *et al.*, 2020). Nonetheless, the polyphyletic nature of PSM strains makes it difficult to develop a universal molecular tool for analysing all PSMs in environmental samples.

(3) Determinants of PSM performance in improving plant growth and yield

The importance of field experiments in evaluating the application potential of PSM strains as P biofertilizers has long been recognized (Goldstein, 1986). To date, however, there are only 95 such experiments (Fig. 4A), among which 70 strains were tested. Nonetheless, these experiments have several critical implications for further estimation of PSM strain efficiencies in improving crop growth or yield under field conditions. First, regardless of the different experimental conditions used, laboratory experiments overestimated the actual efficiencies of PSM strains in field experiments by an average of 237%. Second, PSM strains were more likely to exhibit positive effects in alkaline P-deficient soils (average pH of 7.23 and an average available P of 6.16 mg kg^{-1}; Fig. 4B, C). This appears reasonable, given that acidification of their surrounding environment is a major mechanism for phosphate solubilization by PSMs (Rodríguez & Fraga, 1999) and that a soil available P level lower than 10 mg kg^{-1} is considered insufficient to meet the growth demands of many crops (Syers, Johnston & Curtin, 2008).

(Figure legend continued from previous page.)

Fig 5. Phylogenetic distribution of prokaryotic genomes with the genetic potential for phosphate solubilization. Genera represented by prokaryotic genomes with (A) acid phosphatase (AP)-, (B) alkaline phosphatase (ALP)-, (C) phytase- and (D) glucose dehydrogenase (GCD)-positive genotypes, respectively. The genera rich in genotypes of interest (i.e. groups of genera that contain no less than 30 sequenced genomes individually, and 50% of these genomes contain genes encoding an enzyme of interest) are highlighted by red branches in the phylogenies. Singletons (i.e. genera with only one genome containing genes encoding an enzyme of interest) were excluded from our analysis and are not shown in the phylogenies. The inner ring with blue bars surrounding the phylogenies indicates the proportion of enzyme-positive genomes of a given genus to the total sequenced genomes of that genus. The outer ring with brown bars indicates the contribution of individual genera to the total enzyme-positive genotypes of interest. Six genera rich in AP/ALP/phytase-positive and GCD-positive genotypes (i.e. genomes with genetic potential for both organic and inorganic phosphate solubilization), considered promising PSM genera, are marked by numbers in the outermost ring. See Tables S5–S8 for source data.

Third, the benefits of using inoculation with PSM strains seem to be higher for wheat than for maize and chickpea (Fig. 4D). This phenomenon may be attributed partly to the higher P requirement of wheat compared to the other two crops (Rose, Hardiputra & Rengel, 2010; Singh *et al.*, 2016), while other possible reasons remain to be explored. Another remarkable issue is that only five field-based observations of the positive effects of PSM strains on crop yield (edible part, Fig. 4A) have been reported, highlighting the urgent need for more such experiments. To that end, $PSM^{I\&O}$ strains deserve more attention, given the preliminary evidence that the probability of the occurrence of an increase in crop yield driven by $PSM^{I\&O}$ strains is higher than that of PSM^{I} and PSM^{O} strains (12.5% *vs.* 6.45%; Table S4).

(4) New hopes from previously unknown PSMs

In an attempt to identify promising microbial taxa for future research, we found that bacteria with the genetic potential for solubilization of organic phosphates outnumbered those of inorganic phosphates (Fig. 5, Tables S5–S8). This result is in contrast to the numerical inferiority of PSM^{O} strains identified in the literature (Fig. 3B), indicating that a large number of PSM^{O} strains exist that remain to be characterized. More importantly, six promising genera rich in genotypes of $PSM^{I\&O}$ strains were revealed by our systematic genetic analysis (Fig. 5). Among these, *Klebsiella* and *Xanthomonas* were the most remarkable, as they were rich in genotypes with genes encoding all four enzymes of interest (Fig. 5). While most *Xanthomonas* strains are plant pathogens (Ryan *et al.*, 2011), *Klebsiella* should be a priority for future research. This is especially the case, given that many strains of this genus were reported to enhance plant growth by producing indole acetic acid (e.g. Sachdev *et al.*, 2009). However, only five PSM^{O} and 56 PSM^{I} strains from this genus have been reported, with no $PSM^{I\&O}$ strains identified to date (Table S3), perhaps explaining why *Klebsiella* has received little attention in recent reviews (e.g. Alori *et al.*, 2017). On the other hand, although the other four of our promising genera are well recognized in the literature (e.g. Alori *et al.*, 2017), the potential of their members as $PSM^{I\&O}$ strains has been poorly explored (especially for *Acinetobacter* and *Serratia*).

V. CONCLUSIONS

(1) Taking advantage of a comprehensive quantitative synthesis approach, this study provides the most complete picture of the biogeography, diversity and utility of PSMs to date.
(2) We revealed that the population density of PSMs in environmental samples at continental to global scales is regulated by total P rather than pH, presenting novel evidence for pH-related niche partitioning between PSMs and nitrifying microbes.
(3) The significant positive relationships between the population density of soil PSMs and available P, NO_3^--N and DOC in soil suggest functional couplings between soil PSMs and microbes driving soil nitrification and organic matter degradation.
(4) PSMs tend to occur at a higher population density in warm and moist regions than in dry and cold regions.
(5) We compiled an inclusive list of PSMs, which included 2704 strains characterized by their polyphyletic nature.
(6) We showed that currently available field-based experiments conducted to estimate the application potential of the reported PSM strains are still limited but provide evidence for a tendency of PSMs to have positive effects on wheat growing in alkaline P-deficient soils.
(7) Six promising genera for future research were identified by our systematic genetic analysis (*Klebsiella*, *Xanthomonas*, *Enterobacter*, *Serratia*, *Acinetobacter*, and *Pseudomonas*).

VI. ACKNOWLEDGEMENTS, AUTHOR CONTRIBUTIONS AND DATA ACCESSIBILITY

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Author contributions: J.-T.L., J.-L. Liang, P.J. and W.-S.S. developed and framed the research questions; J.-L. Lu, H.-Y.W., Z.F., X.-J.W., S.-W.F., T.Y., S.-C.Z., S.-N.O., X.-D.Y., Z.-H.W., X.-D.D., L.-Y.T. and B.L. conducted the experiments and collected the data; P.J., J.L. Lu, J.-L. Liang and Z.W. performed the data analyses; J.-T.L., J.-L. Liang, P.J. and Z.W. wrote the first draft; all authors contributed to revisions.

Data accessibility: scripts used to produce figures and links to original are available in GitHub (https://github.com/scnupjia/psm).

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VIII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Effects of sample type (A), available P (B), mean annual precipitation (C), latitude (D) and longitude (E) of the study site on the population density of phosphate-solubilizing microbes (PSMs).

Fig. S2. Effects of habitat type (A), electrical conductivity (EC, B), ammonia-nitrogen (NH_4^+-N, C), water-soluble organic carbon (WSOC, D), mean annual precipitation (E), latitude (F), longitude (G) and elevation (H) of the study site on the population density of soil phosphate-solubilizing microbes (PSMs).

Table S1. Characteristics of the study sites in which the population density of phosphate-solubilizing microbes (PSMs) was reported in the literature.

Table S2. Characteristics of study sites from which soil samples were collected during the nationwide field survey in China to determine the population density of soil phosphate-solubilizing microbes (PSMs).

Table S3. List of phosphate-solubilizing microbe (PSM) strains reported in the literature.

Table S4. List of experiments conducted to determine the effects of phosphate-solubilizing microbe (PSM) strains on plant growth or yield.

Table S5. Occurrence of the genetic potential to produce acid phosphatase among prokaryotic genera.
Table S6. Occurrence of the genetic potential to produce alkaline phosphatase among prokaryotic genera.
Table S7. Occurrence of the genetic potential to produce phytase among prokaryotic genera.
Table S8. Occurrence of the genetic potential to produce glucose dehydrogenase among prokaryotic genera.

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