



## Short communication

## Resource utilization capability of bacteria predicts their invasion potential in soil



Chao Ma <sup>a, b, c</sup>, Manqiang Liu <sup>a, b, c, \*</sup>, Hui Wang <sup>a, b</sup>, Chenying Chen <sup>a, b</sup>, Wenqing Fan <sup>a, b</sup>, Bryan Griffiths <sup>d</sup>, Huixin Li <sup>a, b</sup>

<sup>a</sup> Soil Ecology Lab, College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing, 210095, China

<sup>b</sup> Jiangsu Collaborative Innovation Center for Solid Organic Waste Resource Utilization, Nanjing, 210014, China

<sup>c</sup> State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing, 210008, China

<sup>d</sup> SRUC, Crop and Soil Systems Research Group, Edinburgh, EH9 3JG, UK

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## ABSTRACT

Biological invasion is governed by intrinsic and extrinsic factors, but few studies have explored the interactive roles of species traits and disturbance in soil microbial invasion. A microcosm experiment was conducted to compare the survival of four non-indigenous bacteria in soil previously subjected to heating disturbance (60 °C, 24 h). The survival of non-indigenous bacteria was positively correlated with their utilization capability of saccharose and glucose 3 days after inoculation, and positively with maltose, saccharose, D-mannitol, glycerol, glucose and amylose 42 days following inoculation. Disturbance increased resource availability and also reduced diversity of the native microbial community. Bacteria survival was significantly increased in disturbed soil, especially for the bacteria with weak resource utilization capability. Bacterial invasion potential was determined by resource utilization capability, with that dependence increased with incubation duration and reduced if soil was initially disturbed.

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Biological invasions have become a serious threat to ecological, economic and social systems worldwide (Sala et al., 2000). A better understanding of the mechanisms that govern biological invasion will provide knowledge controlling their negative effects (Vitousek et al., 1996; Pyšek and Richardson, 2010). One mechanism receiving considerable attention is the specific traits that enable a species to invade a new habitat (Kolar and Lodge, 2001). Studies have shown the importance of phenotypic, physiological and biochemical traits such as size (Matz and Kjelleberg, 2005), growth rate (Mächler and Altermatt, 2012) and resource utilization capability (Dawson et al., 2012) for the performance of invasive species. Such species specific traits in invasiveness are often ecosystem dependent (Kolar and Lodge, 2001). However, few studies have focused on the traits of non-indigenous microorganisms that determine invasiveness in soil ecosystems, especially following disturbance (Litchman, 2010).

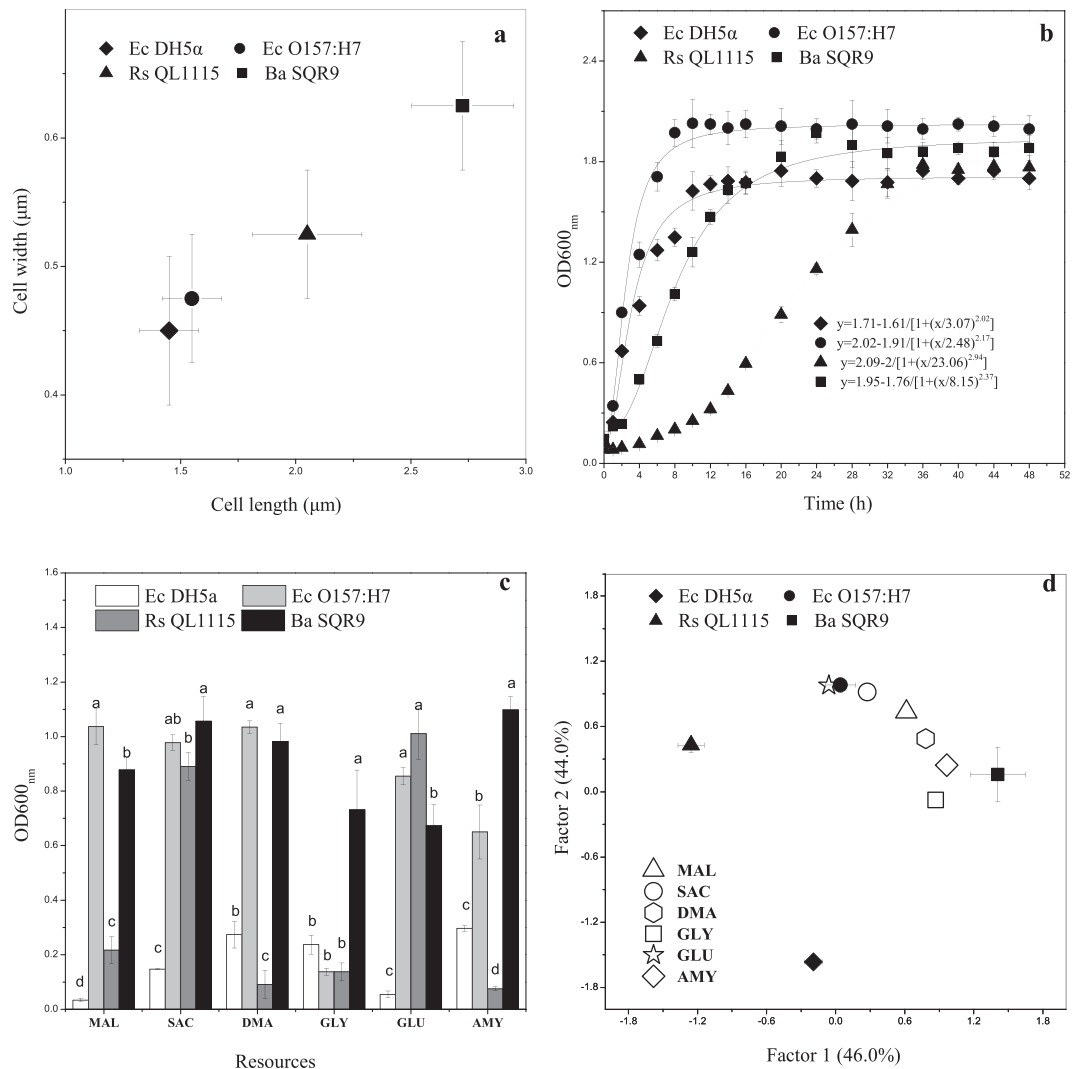
Disturbance could change ecosystem properties (e.g. eliminating native community competition and altering resource

availability) and thus influence biological invasion (Hobbs and Huenneke, 1992). The contribution of species traits to invasiveness varies when ecosystem properties change (Besaw et al., 2011; Mächler and Altermatt, 2012), so the interactive effects between disturbance and invasive species traits, particularly for non-pathogenic microorganisms, is important for understanding invasion success (Litchman, 2010). We conducted a microcosm experiment to investigate the roles of species traits on the invasion potential of four non-indigenous bacteria in soil initially disturbed or not. We hypothesized that strong resource utilization capability would facilitate bacterial survival while the bacteria with weak resource utilization would benefit more from the increase of resource availability and suppression of native competition induced by a heating disturbance, as simulating a possible climate change scenario.

The strains tested are *Escherichia coli* DH5 $\alpha$ -gfp (Ec DH5 $\alpha$ ), *E. coli* O157:H7-gfp (Ec O157:H7), *Ralstonia solanacearum* QLR51115-rfp (Rs QL1115) and *Bacillus amyloliquefaciens* SQR9-gfp (Ba SQR9). We selected these bacteria based on their different ecological functions and that they were non-indigenous to the soil tested (Fig. 1, Supplementary Fig. S1 and Supplementary Table S1).

\* Corresponding author. Soil Ecology Lab, College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing, 210095, China. Tel.: +86 25 84395104; fax: +86 25 84395815.

E-mail address: [liumq@njau.edu.cn](mailto:liumq@njau.edu.cn) (M. Liu).



**Fig. 1.** Phenotypic, physiological and biochemical traits of the studied non-indigenous bacteria including cell size (a), growth kinetics (b), resource utilization capability (c), and the overall differences of different bacteria regarding the utilization capability of different resources by Principle component analysis (PCA) (d). PCA provided the overall differences in resource utilization capability of non-indigenous bacteria (solid symbols) and the corresponding locations different carbon (hollow symbols) in the bi-plot based on correlations. Different letters on bars of each resource utilization indicated significant differences ( $P < 0.05$ ) based on the Duncan's test. MAL, SAC, DMA, GLY, GLU and AMY represented maltose, saccharose, D-mannitol, glycerol, glucose and amylose, respectively.

Seventy-two soil microcosms were established by weighing 45 g soil into 130 ml serum bottles. All the bottles were sealed with rubber plug. The half of the microcosms were subjected to heating at 60 °C for 24 h (i.e. disturbed treatment) and the other half were left at room temperature (i.e. non-disturbed treatment). And then all microcosms were unsealed and vented in a sterile fume hood for 2 h at room temperature to return the microcosms to ambient conditions (e.g. temperature and CO<sub>2</sub> concentration). Before inoculating bacteria to the soil following the 2 h of cooling down, four replicate disturbed and non-disturbed microcosms were destructively sampled to measure soil resource and community properties. All remaining microcosms were then sealed again and incubated at 25 °C for up to 42 days. During the incubation period, the bottles were vented in a sterile fume hood for 2 h when the CO<sub>2</sub> concentrations in the bottles were beyond 5%. Four replicate microcosms of each treatment were destructively sampled 3 and 42 days after inoculation. Information on soil tested, bacterial culture and inoculation, measurements and data analysis can be found online (Supplementary Methods).

The abundance of non-indigenous bacteria at both harvest dates were significantly different among the three species tested (3rd day  $F = 38.3$ ,  $P < 0.0001$ ; 42nd day  $F = 500.2$ ,  $P < 0.0001$ , Fig. 2), suggesting that the survival of non-indigenous bacteria in soil is trait dependent (Liang et al., 2011). We also observed that the key trait determining bacteria survival in soil was resource utilization capability, rather than strain gram stain, persistence of structures, cell size and growth rate (Fig. 1, Supplementary Fig. S1 and Table S2). The dependence on resource utilization capability positively correlated with saccharose and glucose utilization capability on the 3rd day, while positively with all substrates on the 42nd day (Supplementary Table S3), which might be attributed to the discrepancy of specific resource availability in soil relative to non-indigenous bacterial demands (Fig. 1c, d), indicating bacteria invasion would rely on the quality or composition of soil resource (Li and Stevens, 2012).

As expected, disturbance before inoculation significantly promoted soil resource availability and reduced soil community competition (Table 1), and the extent of disturbance-promoted

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