Resource availability modulates biodiversity-invasion relationships by altering competitive interactions

Tianjie Yang,[1,2] **Zhong Wei,**[1]* **Ville-Petri Friman,**[3]
Yangchun Xu,[1] **Qirong Shen,**[1]
George A. Kowalchuk[2] **and Alexandre Jousset**[1,2]

[1]*Jiangsu Provincial Key Lab for Organic Solid Waste Utilization, National Engineering Research Center for Organic-based Fertilizers, Jiangsu Collaborative Innovation Center for Solid Organic Waste Resource Utilization, Nanjing Agricultural University, 210095, Nanjing, People's Republic of China.*
[2]*Institute for Environmental Biology, Ecology & Biodiversity, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.*
[3]*Department of Biology, Wentworth Way, University of York, York, YO10 5DD, UK.*

Summary

Community diversity affects the survival of newly introduced species via resource competition. Competitive interactions can be modulated by resource availability and we hypothesized that this may alter biodiversity-invasion relationships. To study this, we assessed the growth of a bacterial invader, *Ralstonia solanacearum*, when introduced into communities comprised of one to five closely related resident species under different resource concentrations. The invader growth was then examined as a function of resident community richness, species composition and resource availability. We found that the relative density of the invader was reduced by increasing resident community richness and resource availability. Mechanistically, this could be explained by changes in the competitive interactions between the resident species and the invader along the resource availability gradient. At low resource availability, resident species with a high catabolic similarity with the invader efficiently reduced the invader relative density, while at high resource availability, fast-growing resident species became more important for the invader suppression. These results indicate that the

relative importance of different resident community species can change dynamically along to resource availability gradient. Diverse communities could be thus more robust to invasions by providing a set of significant species that can take suppressive roles across different environments.

Introduction

Species migrations between local populations are an essential driver of biodiversity and ecosystem functioning (Lundberg and Moberg, 2003; Venail *et al.*, 2008; Lindström and Östman, 2011; Lindström and Langenheder, 2012). Different communities are typically interconnected allowing species to disperse from one community to another. New migrating species can change community functioning by introducing for instance metabolic capabilities (Singh *et al.*, 2015) or creating new niches (Tilman, 2004). However, in some cases, effects of new species introductions can have undesirable effects on community functioning. This is true for example for pathogens that must first establish themselves in the host-associated microbial communities in order to cause a disease. A better understanding of the drivers that affect pathogen invasion success could thus potentially help to develop better disease management strategies (Jousset *et al.*, 2014; Wei *et al.*, 2015).

The success of invaders is likely to depend on the prevailing competitive interactions within the resident community, which are in turn affected by community richness and various environmental factors, such as resource availability. Species-rich communities may be able to occupy more niches and thereby outcompete invaders (Elton, 1958; Romanuk *et al.*, 2009; van Elsas *et al.*, 2012). Identity of the species composing the resident community could also affect the growth of the invader. For example, highly competitive resident species could inhibit invasions by consuming limiting resources that would be otherwise used by the invader (Fargione and Tilman, 2005; Jiang *et al.*, 2011). As a result, some resident species could be relatively more important for the invasion resistance than the others (Byun *et al.*, 2013).

Changes in resource availability could also have important effects on invader growth. Increases in the resource availability might facilitate invasions (Li and Stevens, 2012)

Table 1. ANOVA table summarizing the interactive effects of the species richness and the resource availability (*Model 1-'richness and resources'*) and the species identity and the resource availability (*Model 2-'identity effects'*) on the relative density of the invader (the log10-transformed relative mCherry fluorescence unit (RFU, mCherry/OD$_{600}$) after 48 h of incubation). The significant effects ($P < 0.05$) are highlighted in bold and the 'up' and 'down' arrows denote for positive and negative effects respectively.

	Df	F	P
Model 1-richness and resources			
Richness	1	89.72	**< 0.001 ↓**
Resource availability (RA)	1	109.89	**< 0.001 ↓**
Richness * RA		Non-significant and thus not retained in the final model	
Residuals	234		
Model summary	AIC: 144.31	R^2 = 0.46	
Model 2-identity effects			
QL-A2	1	84.59	**< 0.001 ↓**
QL-A3	1	122.67	**< 0.001 ↓**
QL-A6	1	81.62	**< 0.001 ↓**
QL-117	1	0.27	0.60
QL-140	1	1.28	0.26
Resource availability (RA)	1	221.07	**< 0.001 ↓**
QL-A2 * RA	1	40.52	**< 0.001 ↓**
QL-A3 * RA	1	40.55	**< 0.001 ↓**
QL-A6 * RA	1	42.55	**< 0.001 ↑**
QL-117 * RA	1	5.18	**0.024 ↑**
QL-140 * RA	1	7.45	**0.0068 ↑**
Residuals	225		
Model summary	AIC: −12.93	R^2 = 0.74	

if the resident community is not able to efficiently consume these additional resources, leaving free niche space for the invader (Davis *et al.*, 2000; Mallon *et al.*, 2015). Resource availability and species richness are likely to vary simultaneously. Understandinging their interactive effects on invasion may help better understand and manage ecosystems.

In this study, we examined how changes in resident community diversity (species richness) and composition (species identity effect) affects pathogen invasion success along a resource availability gradient. We specifically sought to explain the invasion in the context of resource competition between the members of model resident bacterial communities and an invading plant pathogenic bacterium, *Ralstonia solanacearum*, in liquid microcosms. We have previously demonstrated that the richness of the resident bacterial communities can reliably predict pathogen dynamics both in lab microcosms and plant rhizosphere (Wei *et al.*, 2015). In this study, we wanted to specifically explore if biodiversity-invasibility relationships are shaped by resource availability. Based on the resource competition theory (Tilman, 1999), we hypothesized that

increasing the resident community richness could constrain invasions by intensifying the strength of bacterial competition as less niches will be available for the invader. This relationship could however change along the resource availability gradient if the relative importance of different resident species depends on the environmental conditions, or with the resident community composition if the invasion resistance is driven by species identity effects.

Results

### Invasion success in microcosms

Increasing resident community richness and resource availability reduced the relative density of the invader (GLM, Table 1, *Model 1-'richness and resources'*, Fig. 1). No interactive effect between resource availability and community richness on the relative density of the invader was found (Table 1, *Model 1-'richness and resources'*).

Resident species identity effects on invasion

In line with the first analysis, increasing resource availability reduced the relative density of the invader, also when the resident species identity effects were included in the model (Table 1, *Model 2-'identity effects'*). The resident species identities had also clear effects on the relative density of the invader. While the species QL-A2, QL-A3 and QL-A6 reduced the relative density of invader across the resource availability gradient (negative main effect of QL-
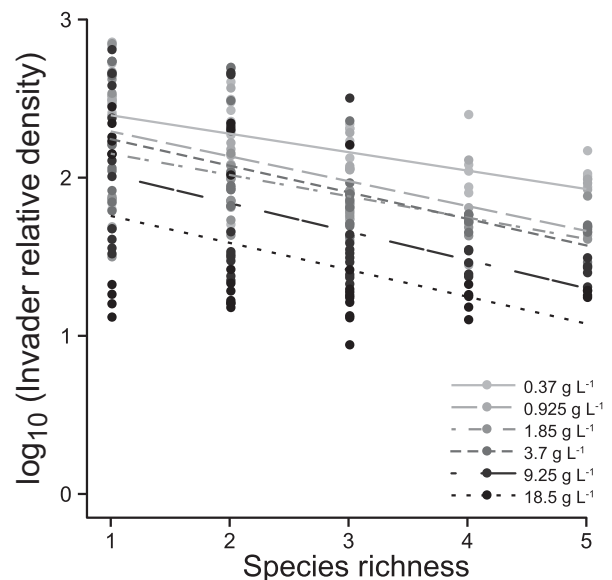
Fig. 1. The effect of resident community richness and resource availability on the relative density of the invader (the log$_{10}$-transformed relative mCherry fluorescence unit (RFU, mCherry/OD$_{600}$) after 48 h incubation. Different lines show richness-invasion resistance relationship at different resource availability levels.
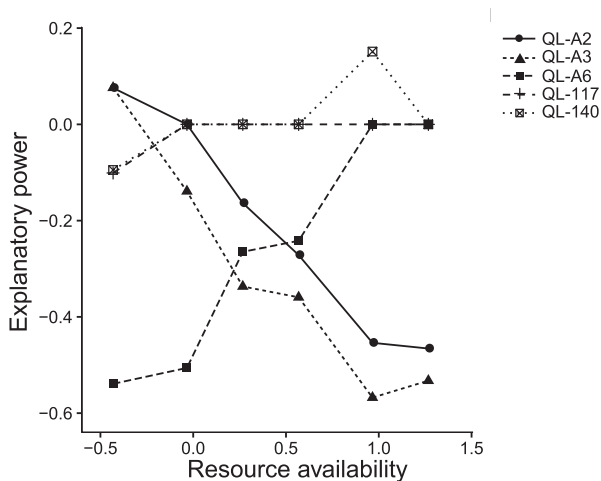
Fig. 2. The relationship between resource availability and explanatory power of the presence of each resident species on the relative density of the invader (the $\log_{10}$-transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 48 h incubation. The explanatory power was defined as the general coefficient of the presence of a given species in the resident community. A value lower than 0 denotes for a negative effect of certain species on the relative density of the invader, a value higher than 0 denotes for a positive effect and value of 0 denotes for a neutral effect. Separates analyses were performed within each resource availability level and the resource availability values were $\log_{10}$-transformed.

A2, QL-A3 and QL-A6 (Table 1, *Model 2-'identity effects'*), the other resident species did not appear to have clear effects on the relative density of the invader (no effect of QL-117 and QL-140, Table 1, *Model 2-'identity effects'*).

Crucially, changes in the resource availability altered the relative importance of different resident species on the relative density of the invader. While the importance of species QL-A2 and QL-A3 became more important with increasing resource availability (slope decreased, Table 1, *Model 2-'identity effects'* and explanatory power increased, Fig. 2), the role of the other resident species (QL-A6, QL-117 and QL-140) became less important (slope increased, Table 1, *Model 2-'identity effects'* and explanatory power decreased, Fig. 2). This suggests that different resident bacterial species affected the invader relative density in resource-dependent manner (see ANOVA table in Supporting Information Table S6). When investigated further, we found that at low resource availability (NB concentration of 0.37 g L^{-1} and 0.925 g L^{-1}) the communities that included species QL-A6 explained most of the variance related to invasion (Fig. 2, Supporting Information Table S6). In contrast, at high resource availability (NB concentration more than 1.85 g L^{-1}) the communities that included species QL-A2 or QL-A3 had relatively largest effects on the invasion success (Fig. 2, Supporting Information Table S6). Together these results suggest that resource availability can change the relative importance of

resident species on invasions: invader relative density was reduced by resident communities containing the species QL-A6 at low and communities containing species QL-A2 and QL-A3 at high resource availability levels.

Impact of resident communities' resource use metrics on invasion

In order to investigate the cause behind the changing species identity effect along the resource availability gradient, we fitted a linear model expressing the relative density of the invader as function of two resource use metrics of the resident communities (catabolic similarity and growth rate). Both catabolic similarity and growth rate had significant negative effects on the relative density of the invader (Table 2, *Model 3-'resource use metrics'*). More specifically, increasing the resource availability gradually decreased the effect of catabolic similarity on the relative density of the invader, whereas the relative importance of resident community growth rate increased with increasing resource availability (slope of the catabolic similarity increased and slope of the growth rate decreased, Table 2, *Model 3-'resource use metrics'*).

In addition to summarizing the interactive effects of catabolic similarity and growth rate on the relative density of the invader, we also assessed the explanatory power (R^2 value of each linear model) of these resource use metrics on the invasion success. In line with the previous results, the explanatory power of the resident community growth rate increased linearly, while the explanatory power of catabolic similarity decreased with the increasing resource availability (Fig. 3).

In summary, communities that contained species with high catabolic similarity with the invader suppressed the invader more clearly at low and communities that contained fast-growing species at high resource availability levels (Fig. 4).

Discussion

Resource competition can have important effects on the biodiversity-invasion relationships (Mallon *et al.*, 2015). While species-rich communities may constrain the invader growth via intensified resource competition (Tilman, 1999; van Elsas *et al.*, 2012; Mallon *et al.*, 2015), it is less clear how biodiversity-invasion relationships are modulated by resource heterogeneity in space and time. In this study, we explored how changes in resource availability affects biodiversity-invasion relationships and if these changes could be explained by shifts in the strength of competitive interactions between the resident community species and the invader. We found that both the resident community richness and resource availability had a negative effect on the relative density of the invader. Mechanistically, these results could be explained by dynamic changes in the

Table 2. ANOVA table summarizing the interactive effects of the catabolic similarity and the growth rate of resident communities on the relative density of the invader (transformed relative mCherry fluorescence unit (RFU, mCherry/OD$_{600}$). The significant effects ($P<0.05$) are highlighted in bold and the 'up' and 'down' arrows denote for positive and negative effects respectively.

	Df	F	P
Model 3-resource use metrics			
Catabolic similarity	1	38.75	**< 0.001** ↓
Growth rate	1	178.43	**< 0.001** ↓
Resource availability (RA)	1	0.061	0.80
Catabolic similarity * RA	1	28.54	**< 0.001** ↑
Growth rate * RA	1	6.02	**0.015** ↓
Residuals	231		
Model summary	AIC: 121.70	R^2 = 0.52	

competitive asymmetry and the relative contribution of different resident species on the invader relative density along the resource gradient. First, increasing the resource availability favoured the fast-growing resident species over the invader, leading to less successful invasions. Second, increasing the resident community richness increased the likelihood that the communities contained species that were good at competing with the invader across the whole resource gradient, leading to less successful invasions also when the resource availability was low. Understanding the role of species identity effects across a range of environmental conditions is thus important for predicting the dynamics and outcomes of biological invasions in a changing world.

We found that resident community richness and resource availability both had a negative effect on the relative density
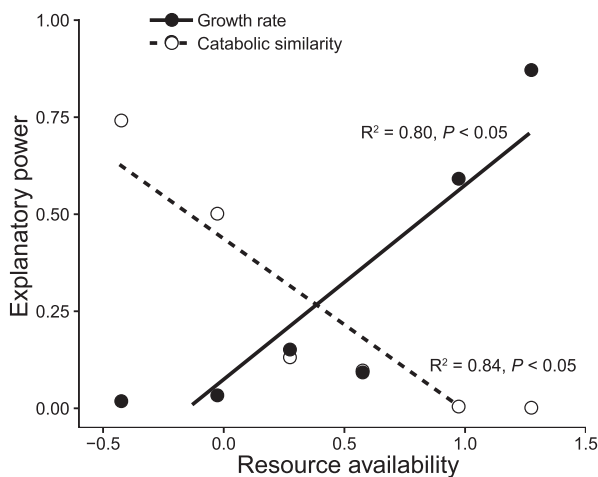
Fig. 3. The explanatory power of the growth rate (closed symbols, plain line) and the catabolic similarity (open symbols, dashed line) for predicting the relative density of the invader (the log$_{10}$-transformed relative mCherry fluorescence unit (RFU, mCherry/OD$_{600}$) within all resource availability levels. Explanatory power is defined as R^2 of linear regression between the growth rate or the catabolic similarity and the invader relative density. Values of resource availability levels were log$_{10}$-transformed.
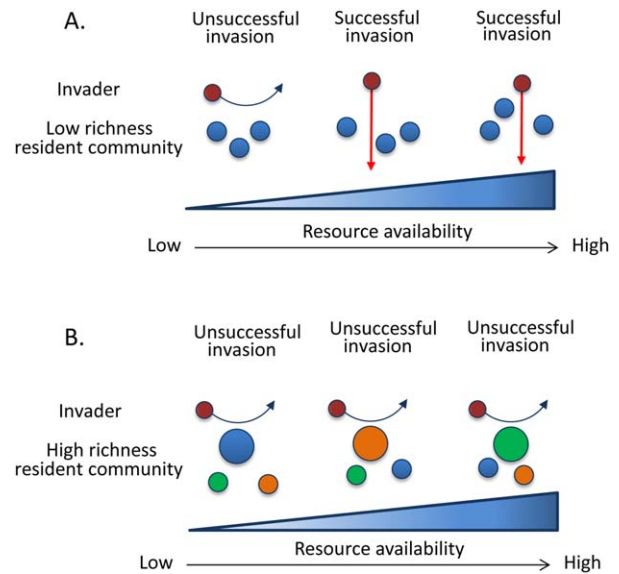
Fig. 4. A schematic figure on invasions as a function of resident community richness across resource availability gradient. In panel (A), resident communities with low richness can suppress invader only under certain levels of resource availability as community Is likely to possess only few suppressive functions. In panel (B), resident communities with high richness can suppress invader across the resource availability gradient because different community members (large circles) can take suppressive roles at different resource availability levels. [Colour figure can be viewed at wileyonlinelibrary.com]

of the invader. The observed negative relationship between the resident community richness and the invasion success is in line with some previous studies (Naeem *et al.*, 2000; Roscher *et al.*, 2009; Byun *et al.*, 2013) and theoretical models (Elton, 1958; Tilman, 1999). However, the reduction in the relative density of invader with increasing resource availability is in contrast with some other studies (Davis *et al.*, 2000; Kuebbing *et al.*, 2013; Mallon *et al.*, 2015). For example, Mallon *et al.* (2015) found that increasing resource availability can promote invasions due to relaxed resource competition. In our case, this discrepancy may be explained by the fact that bacteria were likely able to consume all the resources during the experiment without addition of new external resources. As a result, even though the increase in resource availability boosted community density, in general, it unlikely opened up vacant niches for the invader because the experimental system was 'closed'. In supporting this, we found that even though the total community density at the end of the experiment (in terms of optical density) were around 150-fold higher in the highest compared with lowest resource availability level (Supporting Information Fig. S3), the relative density of the invader was the lowest in the highest resource availability level. Interestingly, no interactive effect was found between the resident community richness and resource availability on the invader relative density. This suggests that richness

independently constrained the relative density of the invader regardless of the resource availability (and vice versa).

To study the effect of resident community richness on the relative density of the invader more closely, we examined how the relative contribution of each resident community species changed across the resource availability gradient (i.e. species identity effect). We found that the presence of certain three species (QL-A2, QL-A3 and QL-A6) had especially important role for constraining the relative density of the invader. This is in line with previous studies showing that species identity effects can play a fundamental role for invasions in communities, and that species-specific traits may be very important for the suppression of invaders (Eisenhauer *et al.*, 2012; Byun *et al.*, 2013). The two other species (QL-117 and QL-140) had no significant effect on the relative density of the invader. This result can be explained by the relatively poor growth of these species in the microcosm conditions during the experiment. The NB media contains a large amount of glucose (approximate 54% of the total dry weight), and QL-117 and QL-140 species are unable to utilize this resource as efficiently as the other resident community species (Supporting Information Table S3). Such asymmetries in the resource use efficiency has previously been shown to be important for the competition with invaders (Tilman, 1982). Crucially, while species QL-117 and QL-140 species had weak effects on the invasion regardless of the resource availability, species QL-A2, QL-A3 and QL-A6 played an important role and their relative contribution changed along the resource availability gradient.

We could also predict well which species would constrain the invasion at each resource availability level based on simple resource use metrics of the resident community. For instance, species with a high catabolic similarity with the invader were the most efficient at controlling invader relative density at low resource availability levels (QL-A6 especially important). Catabolic similarity between two species is a good proxy of the intensity of the resource competition (Bøhn and Amundsen, 2001; Ji and Wilson, 2002). The observed negative correlation between the catabolic similarity and the relative density of the invader confirms that resident species with a highly similar resource use pattern with the invader are likely to increase invasion resistance at low resource availability levels (Wilson and Lindow, 1994; Ji and Wilson, 2002; Dianese *et al.*, 2003). However, the effect of catabolic similarity rapidly vanished with the increasing resource availability. Instead, the presence of fast-growing species in the resident community (QL-A2 and QL-A3 especially important) became more important to prevent invader relative density. We propose the following explanation for this shift. At low resource availability, most resources are likely to be present at low abundance. Hence, community ability to use multiple different resources is likely important to leave few niches open for the invader. However, increase in resource availability will increase the abundance of all different resources and even communities with a broad catabolic potential will unlikely be able to consume all of them (Mallon *et al.*, 2015). Instead, the presence of fast-growing species may be decisive. Even without consuming all resources, fast growing species may cause limitation on other resources, such as oxygen or space. Our results could be thus explained based on classical r- vs. K-strategist theory (Pianka, 1970). For example, species QL-A2 and QL-A3 could be classified as r-strategist as they are able to grow fast when the resources are abundant, while species QL-A6 with a broad niche breadth could be classified as K-strategist, which is able to grow and compete with the invader efficiently when the resource availability and the amount of every individual resource is low. Together these results suggest that at low resource availability negative biodiversity–invasion relationship are likely driven by functional diversity of the resident community. However, at high resource availability the main driver shifts to the inclusion of a species able to rapidly grow under the experimental setting. Understanding the functional variation across environmental gradients is thus likely to be important to develop predictive biodiversity-invasion relationship framework in changing environments (Wardle 2001, Hodgson *et al.* 2002; Fargione and Tilman, 2005).

We conclude that resource availability can modulate biodiversity-invasion relationships by changing the relative importance of different resident species in the invasion process. Our key finding is that the functioning of invasion-resistant communities may be stable if different species are able to adopt suppressive roles under different environmental conditions. Even though we conducted this experiment in relatively simple laboratory conditions, the results could be used to mechanistically understand patterns of invasions in natural soil (Wei *et al.*, 2015; Hu *et al.*, 2016). Resource competition could thus be an important underlying factor shaping pathogen invasions in the rhizosphere, where the resource availability is determined by the supply of plant-derived exudates and carbon (Kuzyakov, 2002). Constructing functionally dynamic and redundant microbial communities that can efficiently outcompete invaders under temporally and spatially changing environmental conditions could thus improve the efficiency and consistency of future biocontrol applications.

Experimental procedures

Bacterial strains and plasmids

We used plant pathogenic *Ralstonia solanacearum* QL-Rs1115 (GenBank accession GU390462) constitutively tagged with mCherry, using the stable plasmid pYC12-mCherry, as the invading bacterium (Wei *et al.*, 2011). The resident communities comprised of one to five avirulent, but

closely related *Ralstonia* species, deposited under the accession number JN699058 (strain QL-A2, *Ralstonia mannitolilytica*), KJ780056 (strain QL-A3, *Ralstonia mannitolilytica*), HQ267096 (strain QL-A6, *Ralstonia pickettii*), KJ780054 (strain QL-117, *Cupriavidus taiwanensis*, formerly *Ralstonia sp.*) and KJ780055 (strain QL-140, *Cupriavidus sp.*, formerly *Ralstonia sp.*) (Wei *et al.*, 2015). None of the bacteria showed antagonism towards each other or *R. solanacearum* QL-Rs1115 on nutrient agar plates, suggesting that resource competition was the main driver of competitive interactions with the invader. All information on the bacterial strains and plasmid can be found in Supporting Information Table S1.

Construction of resident communities

The resident species communities were constructed by using all five avirulent species in all possible richness levels (between 1 to 5 species) and combinations (31 communities in total, Supporting Information Table S2). We used a substitutive design so that all communities were set up at same initial total bacterial densities (10^7 cells mL^{-1}) and evenness (i.e. multispecies communities had equal ratio of each species). All resident communities were then invaded by *R. solanacearum* QL-Rs1115 (initial density of 10^7 cells mL^{-1}) while a set of same communities were grown as controls without the invader.

Invasion in microcosms

Prior to each experiment, one colony of each strain, recovered from −80°C 20% glycerol stocks, was selected and grown in nutrient broth (NB, glucose 10.0 g L^{-1}, tryptone 5.0 g L^{-1}, beef extract 3.0 g L^{-1}, yeast extract 0.5 g L^{-1}, pH 7.0) with 170 r.p.m. agitation at 30°C for 12 h. Bacteria were then washed three times by centrifugation (6000 rpm, 5 min), resuspended in 0.85% NaCl and adjusted to a density of 10^7 cells mL^{-1}. Bacterial communities constructed according to the scheme provided in Supporting Information Table S2.

We set up six different resource availability treatments by diluting NB to a concentration of 18.5, 9.25, 3.7, 1.85, 0.925 and 0.37 g L^{-1} (See Supporting Information Table S4) with sterile water. Each resident community was first inoculated to each resource availability treatment in a full factorial design. The invader *R. solanacearum* QL-Rs1115 (tagged with the pYC12-mCherry plasmid) was subsequently introduced into all communities (with a final concentration of 10^5 cells mL^{-1}). Communities were incubated at 30°C with 170 r.p.m. orbital agitation for 48 h (200 μL together with bacteria and medium per well), a time chosen to allow all communities to reach stationary phase. Total bacterial growth was then estimated by measuring the optical density (OD$_{600}$) of communities. The invader density was estimated based on the mCherry fluorescence signal (Excitation: 587 nm, Emission: 610 nm) with a SpectraMax M5 Plate reader (Molecular Devices, Sunnyvale, CA, USA). The relative density of the invader was defined as the mCherry relative fluorescence unit (RFU, mCherry/OD$_{600}$) at the end of the experiment. We used communities without invader to blank the fluorescence signal and control wells containing culture medium only to blank the OD$_{600}$. The wells contained a total of 200 μL of liquid: 180 μL of media, 15 μL inoculum of constructed resident community and 5 μL

inoculum of the invader. In order to prevent evaporation, we inserted a wet paper tissue on the top of the microplates, which were then placed individually inside of sealable plastic bags (minigrip). We did not observe noticeable evaporation in any of the wells by using this procedure.

Determining the resident bacterial resource use metrics

We selected the catabolic similarity and the growth rate as explanatory variables to infer the bacterial competitive interactions as both variables are representative of resource use across several taxa. The catabolic similarity was used as a proxy for the potential nutrient competition between the resident species and the invader in terms of similarity of species resource use (Ji and Wilson, 2002; Wei *et al.*, 2015).

We determined bacterial resource use patterns by growing each species separately on minimal medium supplemented by one out of 48 different resources (Supporting Information Table S3) representative of nutrients available around tomato roots, which is the original habitat of studied bacteria (Wei *et al.*, 2015). Briefly, overnight cultures of each strain were washed three times with 0.85% NaCl, adjusted to a density of 10^7 cells mL^{-1} and grown on OS minimal medium (Schnider-Keel *et al.*, 2000) with a single resource from 48 resources in 96-well microtiter plates. Bacterial density was estimated as optical density (OD$_{600}$) of each well after incubation for 48 h at 30°C with agitation. Resource use was scored positive in all wells with an OD$_{600}$ > 0.05. The catabolic similarity was calculated based on the resource use patterns of all the communities and the invader (*R. solanacearum* QL-Rs1115 with mCherry). In a previous study, we demonstrated that this metric provides a robust estimate of competitive interactions in various conditions ranging from liquid microcosms to the soil (Wei *et al.*, 2015). Since catabolic similarity was calculated as bacterial growth across various different media, same value was used for different resource availabilities. Values of catabolic similarity are shown in supporting information (Supporting Information Table S5).

We further determined the intrinsic growth rate of each single species and all the communities in mono- and polycultures. All resident communities were combined as described (31 communities in total, Supporting Information Table S2) with initial total cell densities of 10^7 per mL^{-1} and inoculated in 96-well microtiter plates. All communities were grown in triplicates under each of the six tested resource availability levels (18.5, 9.25, 3.7, 1.85, 0.925 and 0.37 g L^{-1} NB) at 30°C with agitation (170 r.p.m.) for 48 h. To obtain bacterial growth rates, we used OD$_{600}$ value from thirteen time points to fit in Logistics model function ('gcFitModel' in package 'grofit' in R 3.3.1), which is descriptive of both gram positive and negative bacterial growth (Kacena *et al.*, 1999). The maximum slope (μ) in Logistic model was used as bacterial growth rate (Kahm *et al.*, 2010) (with unit h^{-1}) and mean growth rate of three replicates was used in the further analyses.

Statistical analyses

We log$_{10}$–transformed the relative density of the invader (RFU, mCherry/OD$_{600}$) and resource availability prior to further analyses. In the first step, we set up three separate general linear models (GLM) expressing the invader relative

density as a function of the interactive effects between resident community composition and the resource availability. The first model (*Model 1-'richness and resources'*) expressed the relative density of the invader as a function of the interactive effect of richness (continuous predictor) and resource availability (continuous predictor). The second model (*Model 2-'identity effects'*) expressed the relative density of the invader as a function of the presence of each species (binary predictors) and resource availability (continuous predictor). The third model (*Model 3-'resource use metrics'*) expressed the relative density of the invader as a function of the growth rate and catabolic similarity of the communities.

In the second step, we sought to explain the contribution of each species to the relative density of the invader, catabolic similarity and growth rate separately at each resource availability level. The 'overlap' approach was used to remove the overlapping effects between each resident species. We used a function 'sAICfun' in the library 'devtools' (Byrnes *et al.*, 2014) to examine the independent coefficient values and the effects of single species presence for the relative density of the invader. The explanatory power was defined as the general coefficient of the single species presence in the community. Similarly, we investigated the identity effects on growth rate at each resource availability level. Resident species identity effects on catabolic similarity were also analysed with the same method. Model analyses and figures showing identity effect on growth rate and the catabolic similarity are presented in supporting information respectively (identity effect on the growth rates: Supporting Information Table S7, Fig. S1, identity effect on the catabolic similarity: Supporting Information Fig. S2).

In order to summarize how the contribution of resource use metrics on the relative density of the invader changed across the resource gradient, we used separate linear models to correlate the resource use metrics (growth rate and catabolic similarity) with the relative density of the invader within each resource availability level. The explanatory power was defined as R^2 of the variable at each resource availability level. All analyses were performed with R 3.3.1.

Acknowledgements

References

Bøhn, T., and Amundsen, P.-A. (2001) The competitive edge of an invading specialist. *Ecology* 82: 2150–2163.

Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., *et al.* (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods Ecol Evol* 5: 111–124.

Byun, C., de Blois, S., and Brisson, J. (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *J Ecol* 101: 128–139.

Davis, M.A., Grime, J.P., and Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88: 528–534.

Dianese, A.C., Ji, P., and Wilson, M. (2003) Nutritional similarity between leaf-associated nonpathogenic bacteria and the pathogen is not predictive of efficacy in biological control of bacterial spot of tomato. *Appl Environ Microbiol* 69: 3484–3491.

Eisenhauer, N., Schulz, W., Scheu, S., and Jousset, A. (2012) Niche dimensionality links biodiversity and invasibility of microbial communities. *Funct Ecol* 27: 282–288.

van Elsas, J.D., Chiurazzi, M., Mallon, C. A., Elhottova, D., Kristufek, V., and Salles, J.F. (2012) Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proc Natl Acad Sci* 109: 1159–1164.

Elton, C.S. (1958) The Ecology of Invasions by Plants and Animals, Vol. 18. *Methuen, London*, UK.

Fargione, J.E., and Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecol Lett* 8: 604–611.

Hodgson, D.J., Rainey, P.B., and Buckling, A. (2002) Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities. *Proc Biol Sci* 269: 2277–2283.

Hu, J., Wei, Z., Friman, V.-P., and Gu, S. (2016) Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. *MBio* 7: e01790-16.

Ji, P., and Wilson, M. (2002) Assessment of the importance of similarity in carbon source utilization profiles between the biological control agent and the pathogen in biological control of bacterial speck of tomato. *Appl Environ Microbiol* 68: 4383–4389.

Jiang, L., Brady, L., and Tan, J. (2011) Species diversity, invasion, and alternative community States in sequentially assembled communities. *Am Nat* 178: 411–418.

Jousset, A., Becker, J., and Chatterjee, S. (2014) Biodiversity and species identity shape the antifungal activity of bacterial communities. *Ecology* 95: 1184–1190.

Kacena, M.A., Merrell, G.A., Manfredi, B., Smith, E.E., Klaus, D.M., and Todd, P. (1999) Bacterial growth in space flight: logistic growth curve parameters for Escherichia coli and Bacillus subtilis. *Appl Microbiol* 51: 229–234.

Kahm, M., Hasenbrink, G., and Ludwig, J. (2010) *Grofit: Fitting Biological Growth Curves with R*, Vol. 33.

Kuebbing, S., Rodriguez-Cabal, M.A., Fowler, D., Breza, L., Schweitzer, J.A., and Bailey, J.K. (2013) Resource availability and plant diversity explain patterns of invasion of an exotic grass. *J Plant Ecol* 6: 141–149.

Kuzyakov, Y. (2002) Review: factors affecting rhizosphere priming effects. *J Plant Nutr Soil Sci* 165: 382.

Li, W., and Stevens, M.H.H. (2012) Fluctuating resource availability increases invasibility in microbial microcosms. *Oikos* 121: 435–441.

Lindström, E.S., and Langenheder, S. (2012) Local and regional factors influencing bacterial community assembly. *Environ Microbiol Rep* **4:** 1–9.

Lindström, E.S., and Östman, Ö. (2011) The importance of dispersal for bacterial community composition and functioning. *PLoS One* **6:** e25883.

Lundberg, J., and Moberg, F. (2003) Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems* **6:** 0087–0098.

Mallon, C., Poly, F., Le Roux, X., Marring, I., van Elsas, J.D., and Salles, J.F. (2015) Resource pulses can alleviate the biodiversity – invasion relationship in soil microbial communities. *Ecology* **96:** 915–926.

Naeem, S., Knops, J.M., Tilman, D., Howe, K.M., Kennedy, T., and Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91:** 97–108.

Pianka, E.R. (1970) On r- and K-Selection. *Am Nat* **104:** 592–597.

Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J., and Martinez, N.D. (2009) Predicting invasion success in complex ecological networks. *Philos Trans R Soc Lond B Biol Sci* **364:** 1743–1754.

Roscher, C., Beßler, H., Oelmann, Y., Engels, C., Wilcke, W., and Schulze, E.-D. (2009) Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *J Ecol* **97:** 32–47.

Schnider-Keel, U., Seematter, A., Maurhofer, M., Blumer, C., Duffy, B., Gigot-Bonnefoy, C., *et al.* (2000) Autoinduction of 2,4-diacetylphloroglucinol biosynthesis in the biocontrol agent Pseudomonas fluorescens CHA0 and repression by the bacterial metabolites salicylate and pyoluteorin. *J Bacteriol* **182:** 1215–1225.

Singh, M., Awasthi, A., Soni, S.K., Singh, R., Verma, R.K., and Kalra, A. (2015) Complementarity among plant growth promoting traits in rhizospheric bacterial communities promotes plant growth. *Sci Rep* **5:** 15500.

Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci U S A* **101:** 10854–10861.

Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80:** 1455–1474.

Venail, P.A., MacLean, R.C., Bouvier, T., Brockhurst, M.A., Hochberg, M.E., and Mouquet, N. (2008) Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. *Nature* **452:** 210–214.

Wardle, D.A. (2001) Experimental demonstration that plant diversity reduces invasibility – evidence of a biological mechanism or a consequence of sampling effect?. *Oikos* **95:** 161–170.

Wei, Z., Yang, X., Yin, S., Shen, Q., Ran, W., and Xu, Y. (2011) Efficacy of Bacillus-fortified organic fertiliser in controlling bacterial wilt of tomato in the field. *Appl Soil Ecol* **48:** 152–159.

Wei, Z., Yang, T., Friman, V.-P., Xu, Y., Shen, Q., and Jousset, A. (2015) Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. *Nat Commun* **6:** 8413.

Wilson, M., and Lindow, S.E. (1994) Ecological similarity and coexistence of epiphytic Ice-nucleating (Ice+) Pseudomonas syringae strains and a non-Ice-nucleating (Ice-) biological control agent. *Appl Environ Microbiol* **60:** 3128–3137.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Information of the bacterial strains and plasmid used in this study.
Table S2. The composition of resident species communities used in the study. In the table, "1" denotes for the presence of the species in the community and "0" for the absence of species in the community. Richness denotes for species richness.
Table S3. The resource use patterns of each resident species and the invader on 48 different resources. The plus sign denotes for species ability to grow on specific resources.
Table S4. Composition of Nutrient Broth (NB) medium through each resource availability level.
Table S5. The catabolic similarity (number of resources both the invader and at least one resident community species can utilize) between the invader and the resident communities. High index values denote for high catabolic similarity.
Table S6. Table summarizing the effects of resource availability and resident species identity effects on the invader relative density at each resource availability level. On the effect column, the "1" denotes for a positive effect, "0" for neutral effect, and "−1" for a negative effect. Coefficient was calculated by function "sAICfun" in R 3.3.1.
Table S7. Table summarizing the effects of resource availability and resident species identity effects on the growth rate of resident communities at each resource availability. On the effect column, the "1" denotes for a positive effect, "0" for neutral effect, and "−1" for a negative effect. Coefficient was calculated by function "sAICfun" in R 3.3.1.
Fig. S1. Explanatory power of the presence of each resident species on the growth rate of all the communities at all resource availability levels. Explanatory power is defined as the general coefficient of the presence of a given resident species in the community (values lower than "0" denote for a negative effect of certain species on invader relative density, values higher than "0" denote for a positive effect and "0" denote for a neutral effect). Separates analyses were performed at each resource availability level.
Fig. S2. The effect of resident species identity effects (the presence in the community) on the catabolic similarity with the invader. Explanatory power is defined as the general coefficient of the presence of a given resident species in the community (values lower than "0" denote for a negative effect of certain species on invader relative density, values higher than "0" denote for a positive effect and "0" denote for a neutral effect).
Fig. S3. The effect of resident species richness and resource availability on the growth of the uninvaded communities (OD_{600}) after 48 h incubation. Different lines show richness-productivity relationships through all resource availability levels.