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Resource stoichiometry shapes community invasion resistance via productivity-mediated species identity effects

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Abstract

The diversity-invasion resistance relationships are often variable and sensitive to environmental conditions such as resource availability. Resource stoichiometry, the relative concentration of different elements in the environment, has been shown to have strong effects on the physiology and interactions between different species. Yet, its role for diversity-invasion resistance relationships is still poorly understood. Here we explored how the ratio of nitrogen and phosphorus affect the productivity and invasion resistance of constructed microbial communities by plant pathogenic bacterium, *Ralstonia solanacearum*. We found that resource stoichiometry and species identity effects affected the invasion resistance of communities. Both high nitrogen concentration and resident community diversity constrained invasions, and two resident species, in particular, had strong negative effects on the relative density of the invader and the resident community productivity. While resource stoichiometry did not affect the mean productivity of the resident community, it favored the growth of two species that strongly constrained invasions turning the slope of productivity-invasion resistance relationship more negative. Together our findings suggest that alterations in resource stoichiometry can change the community resistance to invasions by having disproportionate effects on species growth potentially explaining changes in microbial community composition under eutrophication.

Key words:

Resource stoichiometry, diversity-invasion resistance relationship, nitrogen, phosphorus, productivity, species identity effects

1. Introduction

Microbial biodiversity plays an important role in ecosystem functioning by offering sets of functions that cannot be provided by single species [1–3]. For example, host-associated microbial communities can ward off pathogens thereby protecting their associated host organism [4–6]. This process can also be viewed from the perspective of biological invasions where the members of resident microbial communities facilitate or constrain the establishment of the invader [7,8]. Several studies have shown that increasing community diversity reduces the likelihood of invasions by promoting a more comprehensive use of available niches in the given environment [3,9,10]. Such diversity-invasion resistance relationships are however often sensitive to environmental conditions such as resource availability [11] or temperature [12]. As a result, we still poorly understand how environmental contexts shape diversity-invasion resistance relationships.

Resource availability has been shown to be an important factor affecting the outcome of biological invasions [13–15]. Mechanistically, concentration or composition of resources can alter the physiology and interactions between different species within communities which can then lead to changes in community invasion resistance. Moreover, changes in resource availability may change the significance of species identity effects, i.e. the contribution of resident community members to the invasion, by promoting the growth of species that grow either slow or fast [16,17]. Species identity effects could thus explain positive diversity-invasion resistance relationships across environmental gradients where different species contribute to the invasion resistance under specific environmental conditions [1,18]. Here we studied how resource stoichiometry, the relative concentration of different elements in the environment, shapes invasions via diversity, productivity and species identity effects.

Resource stoichiometry is a broad and active research field in ecology that has been extensively used to understand predator-prey interactions [19,20]. While several studies have highlighted the importance of resource stoichiometry for the ecology and functioning of communities [21,22], its effects have been less studied in the context of diversity-ecosystem functioning relationships. Environmental stoichiometry can be used to link tissue composition of organisms with trophic level interactions [23–25] and it plays important role in determining which species are able to grow in any given ecosystem affecting consumer-resource interactions [26,27]. For example, low C:P ratio has been shown to favour fast-growing species leading to an increase in microbial diversity [28]. Resource stoichiometry can also affect invasions by altering species biomasses and growth dynamics [29]. However, it is unclear how resource stoichiometry shapes the diversity-invasion resistance and productivity-invasion resistance relationships.

In the present study, we used experimental approach to directly expose model microbial communities with varying levels of diversity to invasions by a single invader species under different resource stoichiometry treatments. The model 'resident' community was constructed by using five different bacterial species that have previously been shown to constrain invasions in a diversity-dependent manner [4,17]. As an invader, we used a plant pathogenic *Ralstonia solanacearum* bacterium whose life cycle is directly linked to biological invasions of the plant rhizosphere microbiome. *Ralstonia solanacearum* causes bacterial wilt disease [30,31] and is a major threat to global food production [32]. Before infecting its host, *R. solanacearum* must first get through microbial communities surrounding the plant roots. It has previously been shown that competition for resources between the invader and resident community members is important for the outcome of invasions [4,17]. How these invasion outcomes are affected by dynamic changes in nutrient levels typical for rhizosphere microbiomes [33,34] and resident community diversity remains unclear. To study this, we manipulated both resident community diversity gradient (richness levels of 1 to 5 species in all possible combinations) and the resource stoichiometry of the environment by changing the relative concentration and ratio of nitrogen (N) and phosphorus (P) orthogonally by following the Redfield ratio. Redfield ratio is the atomic ratio of carbon, nitrogen and phosphorus found in phytoplankton and throughout the deep oceans [35] and a general baseline of element composition for both aquatic and terrestrial ecosystems [36,37]. Communities were then exposed to *R. solanacearum* invasions and the invasion success was determined as the relative density of *R. solanacearum* invader after 72h growth in the resident community (indicative of the reproductive success of the invader): higher the final relative abundance of *R. solanacearum*, higher the invasion success. We expected that resident community diversity-invasion resistance relationship could be sensitive to resource stoichiometry having either positive or negative effects on invasions depending on specific changes in species ability to grow under different N:P ratios. Mechanistically, changes in invasion outcomes could potentially be explained via effects on community productivity or changes in the relative contribution of community members to invasions via species identity effects.

2. Methods

(a) Bacterial strains and plasmids

We used *Ralstonia solanacearum* species QL-Rs1115 tagged with pYC12-mCherry plasmid as a model invader in our experiments [38]. Five avirulent, but closely related, *Ralstonia spp.* isolates (*Ralstonia mannitolilytica* QL-A2, *Ralstonia mannitolilytica* QL-A3, *Ralstonia pickettii* QL-A6, *Ralstonia taiwanensis* QL-117 and *Ralstonia pickettii* QL-140) were used to construct our model resident communities [4]. None of these bacteria showed direct antagonism towards each other or the invader, which suggests that they likely interact indirectly through competition for shared resources. A more detailed description of the bacteria and used plasmid can be found in Table S1. All bacteria were stored at -80 °C in 20 % glycerol prior to the experiments.

(b) Assembly of resident communities

The resident communities were assembled by using all five avirulent species in substitutive design so that the final communities covered all possible species combinations and richness levels (total of 31 communities with equal initial bacterial biomasses, Table S2). Prior to the experiments, bacteria were pre-cultured from frozen stocks on Nutrient Agar plates (NA, 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}, agar 15.0 g L^{-1}, pH 7.0) and single colonies were picked and re-grown in liquid nutrient broth (NA medium without agar) at 30 °C for 12 h with 170 r.p.m. agitation. Bacterial isolates were washed three times in 0.85 % NaCl to remove nutrient residues and re-suspended in 0.85 % NaCl with final densities of 10^7 cells mL^{-1}.

(c) Manipulation of resource stoichiometry

To manipulate the resource stoichiometry, we first set up a minimal salt medium, which did not contain carbon, nitrogen or phosphorus (MOPS 30mM, $CaCl_2$ 0.1mM, $FeSO_4$ 3 mM, KCl 20mM, $MgCl_2$ 2mM, Na_2SO_4 14mM and NaCl 51mM, pH 7.0). The minimal medium was then supplemented with a mixture of carbons (fructose, glucose, sucrose, maltose, arabinose and galactose) in equal concentrations to yield a total concentration of 10 mM for all combined carbon resources as described previously [4]. The concentration of total carbon resources (10 mM) was held constant for all resource stoichiometry treatments. To manipulate the concentration and ratio of nitrogen and phosphorus, we added NH_4Cl or $NaH_2PO_4 \cdot 2H_2O$ as the sole nitrogen and phosphorus resource, respectively. A total of six resource stoichiometry treatments with four unique N:P ratios were established for the experiment where low, intermediate and high nitrogen levels were established within both low and high phosphorus levels (Table 1). Each media was then used to establish replicate treatments on 96-well microtiter plates in triplicate (18 microplates in total) for each resident community combination.

(d) Measuring resident community invasion resistance and productivity in microcosms

To quantify invasion resistance, all communities (10^6 cells mL^{-1} in 200 μL of final volume) were exposed to invasion by *R. solanacearum* QL-Rs1115 (10^5 cells mL^{-1} in 200 μL of final volume) under different resource stoichiometry environments. Replicate communities without invader were used as control treatments. All communities were incubated for 72 h at 30 °C with 170 r.p.m. orbital agitation. To measure invader density relative to resident community density, we measured the mCherry fluorescence signal (Excitation: 587 nm, Emission: 610 nm, gain: 60) of the invader and calculated the invasion success as mCherry relative fluorescence unit against total bacterial density of the community (RFU, mCherry/OD_{600}) at the end of the experiment (after 72 h of incubation). To quantify the total productivity of different communities in each resource environment, we used optical density (OD_{600}) as a measure of total bacterial growth (invader and the resident community). We used the control communities without the invader to blank the fluorescence signal background and optical density of the culture media to blank the OD_{600} background.

In order to verify plasmid stability during the invasion experiments, we grew gentamycin-tagged mCherry plasmid carrying *R. solanacearum* invader (10^6 cells mL^{-1} in 200 μL of final volume) in four N:P ratios (0.16, 1.6, 16 and 160) in the absence and presence of gentamycin antibiotic (30 μg mL^{-1}) for 72 h. Gentamycin was added only at the beginning or at every 24 h to create a strong selective pressure on the plasmid. The plasmid stability was determined as fluorescent signal intensity, which is indicative of bacterial growth and expression of the plasmid-encoded mCherry fluorescent protein (Figure S1). No difference was observed between different antibiotic treatments in any of the N:P ratios after 72 h of incubation (Figure S1; The main effect of antibiotic treatment in 0.16, 1.6, 16 and 160 N:P ratios, respectively: $F_{1,\,194} = 0.08$, $P = 0.77$; $F_{1,\,381} = 0.2$, $P = 0.65$, $F_{1,\,371} = 1.57$, $P = 0.21$ and $F_{1,\,190} = 0.08$, $P = 0.77$). This suggests that the plasmid was stably maintained during the invasion experiments in the absence of gentamycin.

(e) Measuring the growth and consumption of nitrogen and phosphorus by each bacterial species

The growth rate and productivity of all bacterial species were measured in monoculture at four N:P ratios. Bacterial were inoculated at an initial density of 10^6 cells mL^{-1} in 96-well microtiter plates as described above. Each monoculture was grown in triplicates under each of the N:P ratios at 30 ℃ with agitation (170 r.p.m.) for 72 h. To determine growth rates, we measured bacterial growth with spectrophotometer (OD_{600}) at every 8 h to fit in Logistics model function ("gcFitModel" in package "grofit" in R 3.3.1) [39] and the Maximum slope (μ, h^{-1}) of the Logistic model was considered as the maximum growth rate [40]. The productivity of each species was determined as the bacterial biomass after 72 h. Culture media without bacteria was used to determine the background absorbance before determining growth rates and productivity. To test the consumption of nitrogen and phosphorus by all bacteria, we obtained cell-free supernatant by centrifugation (10 000 rpm for 10 min) and filtration (0.22 μm filters) after 72 h incubation. Nitrogen and phosphorus concentrations were measured using a continuous-flow analyzer (AA3, SEAL, Germany) and compared with unconsumed media (no bacterial inoculation).

(e) Statistical analyses

Invasion success (RFU, mCherry/OD_{600}) and resource stoichiometry ratios (N:P) were $\log_{10}$–transformed before statistical analyses to fulfill model assumptions. All comparisons between the growth of individual species were analyzed using ANOVA and linear regression. General Linear Mixed Models (GLMs) were used to examine the resident species identity effects and resource stoichiometry as a function of invader relative density (invasion success). Model 1 ("Richness-ratio") and Model 2 ("Identity-ratio") were used to identify how individual species contributed to the invasion success as a function of resource stoichiometry. Model 3 ("Richness-concentration", Table S3) was used to analyze whether N and P concentrations had interactive effects with species richness in determining invasion success and resident community productivity. Model 4 ("Productivity-ratio", Table S4) was used to study the interactive effects between productivity and resource stoichiometry on the invasion success, while Models 5 ("Richness-ratio", Table S4) and 6 ("Identity-ratio", Table S4) were used to explore the effects of community diversity and species identity on the resident community productivity. In some cases, we used the means of community treatment replicates for simplified analysis (e.g. species presence effects in Figure 2).

Structural Equation Model (SEM; 'lavaan' package in R) was used to investigate the relative importance of resource stoichiometry, species identity effects, species maximum growth rates, nitrogen and phosphorus consumption and resident community productivity on the invasion success (the *prior* model is shown in Figure S2). All analyses were performed with R 3.3.1 [41].

3. Results

(a) Effects of resource stoichiometry on the diversity-invasion relationship

We found that increasing resident species richness had a negative effect on invasions across all N:P ratios (Figure 1; Model 1 in Table 2, the main effect of species richness on invader relative density). Similarly, the relative density of the invader decreased with increasing N:P ratio and N concentration (Model 1 in Table 2, the main effect of N:P ratio on invader relative density), while P concentration alone had no effect (Model 3 in Table S3). No interactive effect between species richness and N:P ratio on the relative density of the invader was found (Model 1 in Table 2). These results suggest that both species richness and N:P ratio constrained invasions independently, while N concentration alone had a stronger effect than P concentration.

(b) The effect of resident species identities on resident community productivity and invasions

We found that *R. mannitolilytica* QL-A2, *R. mannitolilytica* QL-A3 and *R. taiwanensis* QL-117 resident species had no significant species identity effects on the relative density of the invader (Model 2 in Table 2). In contrast, *R. pickettii* QL-A6 and *R. pickettii* QL-140 resident species were very effective at reducing the relative density of the invader (Model 2 in Table 2). To examine this in more detail, we compared the invasion resistance of resident communities with and without these two species. As expected, resident communities were less resistant to invasions in the absence of these two species (Figure 2, comparison on communities with and without *R. pickettii* QL-A6: panel a, $F_{1,184} = 400.4$, $P < 0.001$, comparison on communities with and without *R. pickettii* QL-140: panel b, $F_{1,184} = 4.47$, $P = 0.036$). Mechanistically, this could be explained by relatively more efficient consumption of nitrogen and phosphorus compared to the other resident species (Figures S3 and S4; Species main effects at 0.15, 1.5 and 15 mM nitrogen concentrations, respectively: $F_{6, 35} = 254.6$, $P < 0.001$; $F_{6, 35} = 3196$, $P < 0.001$ and $F_{6, 35} = 55.69$, $P < 0.001$. Species main effects at 0.09 and 0.9 mM phosphorus concentrations, respectively: $F_{6, 56} = 20.92$, $P < 0.001$ and $F_{6, 56} = 6.00$, $P < 0.001$). However, no clear differences were found in comparison with the invader, which suggests that *R. pickettii* QL-A6 and QL-140 were equally good at consuming nitrogen and phosphorus ($P > 0.05$ in all pairwise comparisons).

Even though increasing N:P ratio constrained invasions, no significant interactions with species identities were found in the full-scale invasion experiment (Model 2 in Table 2). To explore this further we compared the growth of resident species and the invader separately in monocultures. Growth rate of *R. pickettii* QL-A6, *R. pickettii* QL-140 and the invader *R. solanacearum* did not increase linearly with increasing N:P ratio. While *R. pickettii* QL-140 had the highest growth rate when N:P ratio was 0.16 ($F_{5,\ 12} = 9.87$, $P < 0.001$, Figure S5), *R. pickettii* QL-A6 grew the fastest at 16 and 160 N:P ratios ($F_{5,\ 30} = 24.87$, $P < 0.001$ and $F_{5,\ 12} = 26.77$, $P < 0.001$, respectively in Figure S5). No difference in the maximum growth rate of these species was found at 1.6 N:P ratio ($F_{5,\ 30} = 8.23$, $P < 0.001$, Figure S5).

However, clear positive correlations were found between the productivity (population density after 72 h of growth) of the invader, QL-A6 and QL-140 species and the increasing N:P ratio (Figure 3B). While *R. pickettii* QL-140 had the highest productivity at the lowest N:P ratio (0.16), the *R. pickettii* QL-A6 became more competitive relative to the invader at 16 and 160 N:P ratio treatments. This suggests that differences in species ability to grow under increasing N:P ratios were likely important in explaining diversity-productivity-invasion resistance relationships.

(c) The effect of resource stoichiometry on the resident community productivity and invasions

We found that increasing N:P ratio had a hump-shaped (non-linear) relationship with the resident community productivity (Figure S6, $F_{1,\ 184} = 1.28$, $P = 0.26$; the mean productivity of all resident communities in all richness levels), and only the resident community richness correlated positively with resident community productivity (Model 5 in Table S4). However, resident community productivity was positively affected by both *R. pickettii* QL-A6 and QL-140 species and QL-A6 had a positive effect on community productivity with increasing N:P ratio (Model 6 in Table S4), which is in line with their ability to efficiently consume nitrogen and phosphorus (Figures S3 and S4) and to reach higher biomasses (productivity) with increasing N:P ratios in monocultures (Figure 3B).

Resident community productivity had a clear negative effect on the relative density of the invader (Figure 3A, Model 4 in Table S4), and crucially, the negative relationship between the resident community productivity and the density of the invader became stronger with increasing N:P ratio (Figure 3A, Model 4 in Table S4). This can be explained by resident species identity effects, in particular, the ability of *R. pickettii* QL-140 to increase its growth with increasing N:P ratio, which then turned the productivity-invasion resistance relationship more pronounced.

(d) Linking species identity and resource stoichiometry effects with productivity-invasion resistance relationship

To further study how invasions and community productivity were shaped by resource stoichiometry and species identity effects, we built a Structural Equation Model (SEM) describing direct and indirect relationships between these variables. The final SEM model explained 76 % of the variance of the relative density of the invader (Figure 4). The species *R. pickettii* QL-A6 had a significant negative effect on the relative density of the invader, while the species *R. pickettii* QL-140 promoted both community productivity and reduced the relative density of the invader. Similar to previous analyses, resource stoichiometry did not change the species identity effects in the SEM. However, resource stoichiometry had negative effects on both resident community productivity and the relative density of invader, while the resident community productivity itself had a negative effect on invasions. Together these results suggest that species identity and resource stoichiometry had both direct and indirect negative effects on invasions and that the indirect effects were mediated by resident community productivity.

4. Discussion

Biodiversity is an important determinant of ecosystem functioning having significant effects on community resistance to biological invasions [5,42,43]. Here we addressed how changes in environmental stoichiometry (N:P ratio) affects invasion resistance of model microbial communities. We found that changes in resource stoichiometry had clear effects on invasion outcomes via productivity-mediated species identity effects. First, increasing N:P ratio lowered the intercept of diversity-invasion resistance relationship, which suggests that increasing the input of nitrogen reduced the likelihood of invasions regardless of the community diversity. Second, two resident species, *R. pickettii* QL-A6 and QL-140, played key roles in having negative effects on the invader and positive effects on resident community productivity. Crucially, increasing the N:P ratio turned the slope of productivity-invasion resistance relationship much steeper because the species *R. pickettii* QL-A6 and *R. pickettii* QL-140 grew better and constrained invasions more efficiently when nitrogen became more abundant. Together these results suggest that resource stoichiometry can change the outcome of microbial invasions via productivity-mediated species identity effects.

In line with the previous studies, increasing resident community diversity decreased the likelihood of successful invasions [4,5,44]. While resource stoichiometry did not interact with resident species richness, it lowered the intercept of diversity-invasions resistance relationship. This suggests that an increase in the relative concentration of nitrogen improved the resident community invasion resistance regardless of the species richness but that this effect was stronger in more diverse communities. One simple explanation for this is that increasing community diversity increased the likelihood that one or both of the species that were effective at constraining invasions (*R. pickettii* QL-A6 and QL-140) were included in communities. To study this in more detail, we concentrated on exploring the relative importance of resident species identities on invasions.

Two resident species, *R. pickettii* QL-A6 and QL-140, played key roles in having negative effects on the invader relative density and positive effects on the resident community productivity. Both of these species were effective at consuming nitrogen and phosphorus across all N:P ratios (Figures S3 and S4), and hence, their contribution to invasion resistance likely overshadowed the effects of the other resident community members. However, no difference was found in the consumption of nitrogen and phosphorus among the invader, *R. pickettii* QL-A6 and QL-140 (Figures S3 and S4), which suggests that these three species were equally efficient at sequestering N and P. However, either the *R. pickettii* QL-A6 or QL-140 was clearly faster at growing than the invader in three out of four N:P ratios used in our experiments (Figure S5), which could have helped them to outcompete the invader in these conditions. Moreover, while these species constrained invasions across all N:P ratios (Figure 4), we found that the importance of species QL-A6 on community productivity increased along increasing N:P ratio, while species QL-140 had the highest productivity at low N:P ratios (Figure 3B). Together these results suggest that resource stoichiometry changed invasion outcomes via productivity-mediated species identity effects by favoring resident species that were efficient at growing when the nitrogen was abundant. This finding is in line with a previous study where these two species were observed to have highly negative effects on the same invader used in this study due to high catabolic similarity [17] and supports the idea that individual contribution of resident community members on invasions can change according to resource availability [17]. In the future, it would be interesting to study if environmental stoichiometry can drive changes in the elemental stoichiometry of bacterial and other microbial cells. For example, it has been shown that the effects of resource stoichiometry can be species-specific [46] where environmental stoichiometry favor species with similar biomass composition [25,26]. In this case, the similarity in biomass composition between the resident species and the invader could be important determinant for invasions.

Furthermore, we found that increasing N:P ratio had a hump-shaped effect on community productivity that peaked at intermediate N:P ratios, which can optimize species coexistence or community productivity [19,22,47]. However, this relationship was not very strong and was only visible when all the communities with different richness levels were included in the analysis. Interestingly, resident community productivity correlated negatively with the relative density of the invader only within 16 and 160 N:P ratios. Mechanistically, this could be explained by the fact that the importance of *R. pickettii* QL-A6 on resident community productivity and invasions resistance increased along increasing N:P ratio (Figure 3B and Model 2 in Table 2). This suggests that increasing the input of N can increase the invasion resistance of communities via productivity, but that these effect might be driven by certain important 'key stone' species instead of changes in the total community productivity [9,17]. Several previous studies have suggested that resource stoichiometry of the environment is a good predictor of species growth capacity [46,48]. For example, both N and P are important for species growth via effects on production and expression of proteins, enzymes and cell structures [27,49,50] and could often be limiting resources in the environment. Furthermore, it is possible that invasion resistance is not only mediated by nitrogen uptake but also by carbon metabolism, which is known to be interconnected with nitrogen regulation [51]. In support for this, a previous study has shown that the same resident species used in this study had higher growth rates, productivity and high resource niche overlap with the same invader used in this experiment when measured in various carbon media [4,17]. As a result, it is possible that competition for both carbon and nitrogen affected the observed invasion outcomes also in this experiment.

Here we link the high N:P ratio to improved community functioning in terms of increased invasion resistance. Our results suggest that resource stoichiometry can have positive effects on resident community productivity by favoring species that are very efficient at constraining invasions. Interestingly, resource stoichiometry did not change the shape of diversity-invasion resistance relationship even though invasions were less successful in more diverse communities in general. In contrast, resource stoichiometry turned the slope of the productivity-invasion resistance more negative, because increase in nitrogen availability potentially intensified the competitive interactions between resident community members and the invader by favoring the growth of certain resident community members (*R. pickettii* QL-A6 and *R. pickettii* QL-140). This is in line with studies showed that competition becomes stronger under higher N:P ratio [28,52]. In the future, it will be important to better understand the effects of resource stoichiometry on invasions in more natural environments. For example, more information is needed how the presence of more complex microbial community, multi-trophic interactions with predators and parasites, root exudation and spatially uneven distribution of particulate organic matter shape the elemental stoichiometry and their effects on invasions in complex plant-soil ecosystems.

We conclude that resource stoichiometry is an important determinant of community invasion resistance. Human activities continue to have a huge effect on global elemental cycling [53], nitrogen leaching and eutrophication, which are causing growing problems and having devastating effects on the functioning of ecosystems [54,55]. In the case of eutrophication, our results suggest that resource stoichiometry could drive changes in microbial community composition potentially affecting the likelihood of biological invasions. In the agricultural context, resource stoichiometry could affect the severity of disease epidemics via effects on microbial competition. A better understanding of this process could potentially help to control plant pathogen invasions via modulation of soil nutrient availability and balance (N:P ratios) to maintain relatively stable and invasion resistant microbial community. In broader perspective, understanding how changes in global element balances affect the interactions within and between communities is crucial for predicting ecosystem-level responses to environmental change.

Authors contributions. Alexandre Jousset, Zhong Wei and Tianjie Yang designed the experiment and Tianjie Yang carried out the laboratory work with the help of Gang Han and Qingjun Yang and analyzed all the data. All authors wrote the manuscript and gave final approval for publication. We have no competing interests.

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Table 1. Concentration of nitrogen (NH_4Cl) and phosphorus (NaH_2PO_4) and their ratios (N:P) in different treatments

Treatment	Nitrogen (mM)	Phosphorus (mM)	N:P ratio
1	1.5	0.09	16:1 (Redfield ratio)
2	15	0.09	160:1
3	0.15	0.09	1.6:1
4	1.5	0.9	1.6:1
5	15	0.9	16:1
6	0.15	0.9	1.6:10

Table 2. ANOVA table summarizing the species richness, N:P ratio and species identity effects on the relative density of the invader (Models 1 – 2). Significant effects ($P < 0.05$) are highlighted in bold and the “up” and “down” arrows denote for positive and negative effects on the relative density of invader, respectively. Non-significant terms were not retained in the final models (“Not retained”).

	Relative density of the invader		
	Df	F	*P*
Model 1 (“Richness-ratio”)			
Species richness (Richness)	1	28.50	**< 0.001** ↓
N:P ratio (Ratio)	1	9.71	**0.0021** ↓
Richness * Ratio	1	0.0072	0.93
Residuals	182		
Model summary	AIC: 368.45, $R^2 = 0.17$		

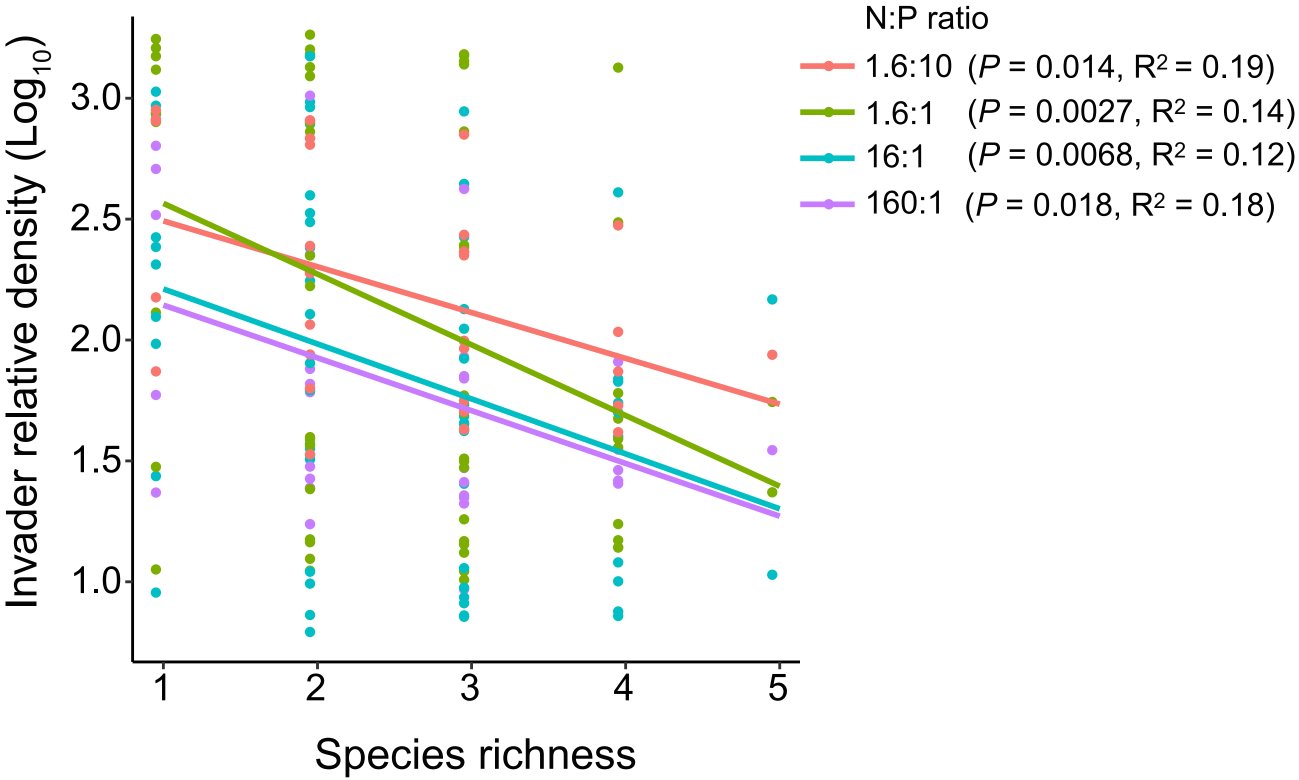
Model 2 ("Identity-ratio")			
QL-A2		Not retained	
QL-A3		Not retained	
QL-A6	1	524.41	**< 0.001 ↓**
QL-117		Not retained	
QL-140	1	25.27	**< 0.001 ↓**
N:P ratio (Ratio)	1	33.74	**< 0.001 ↓**
QL-A2 * Ratio		Not retained	
QL-A3 * Ratio		Not retained	
QL-A6 * Ratio		Not retained	
QL-117 * Ratio		Not retained	
QL-140 * Ratio		Not retained	
Residuals	182		
Model summary		AIC: 136.72, $R^2 = 0.76$	

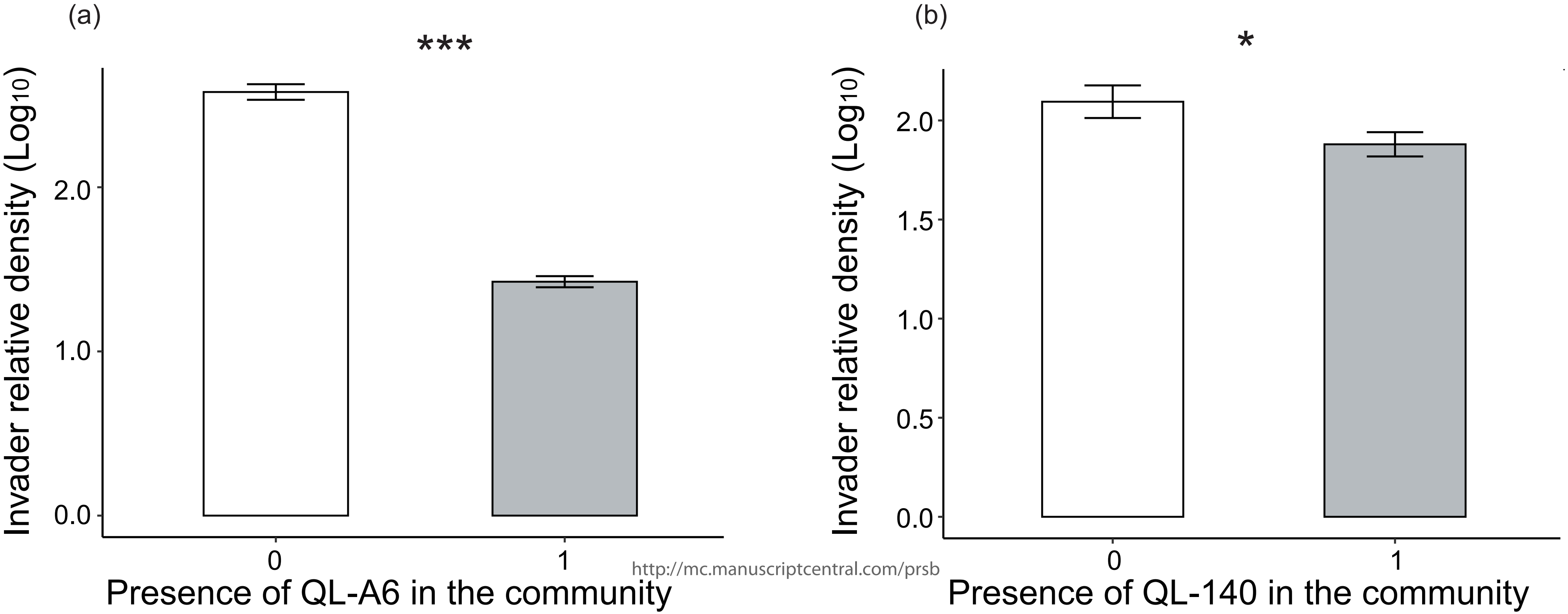
Figure 1. The effects of species richness and N:P ratio on invasion success (relative invader density). The relative density of the invader was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 72 h incubation.

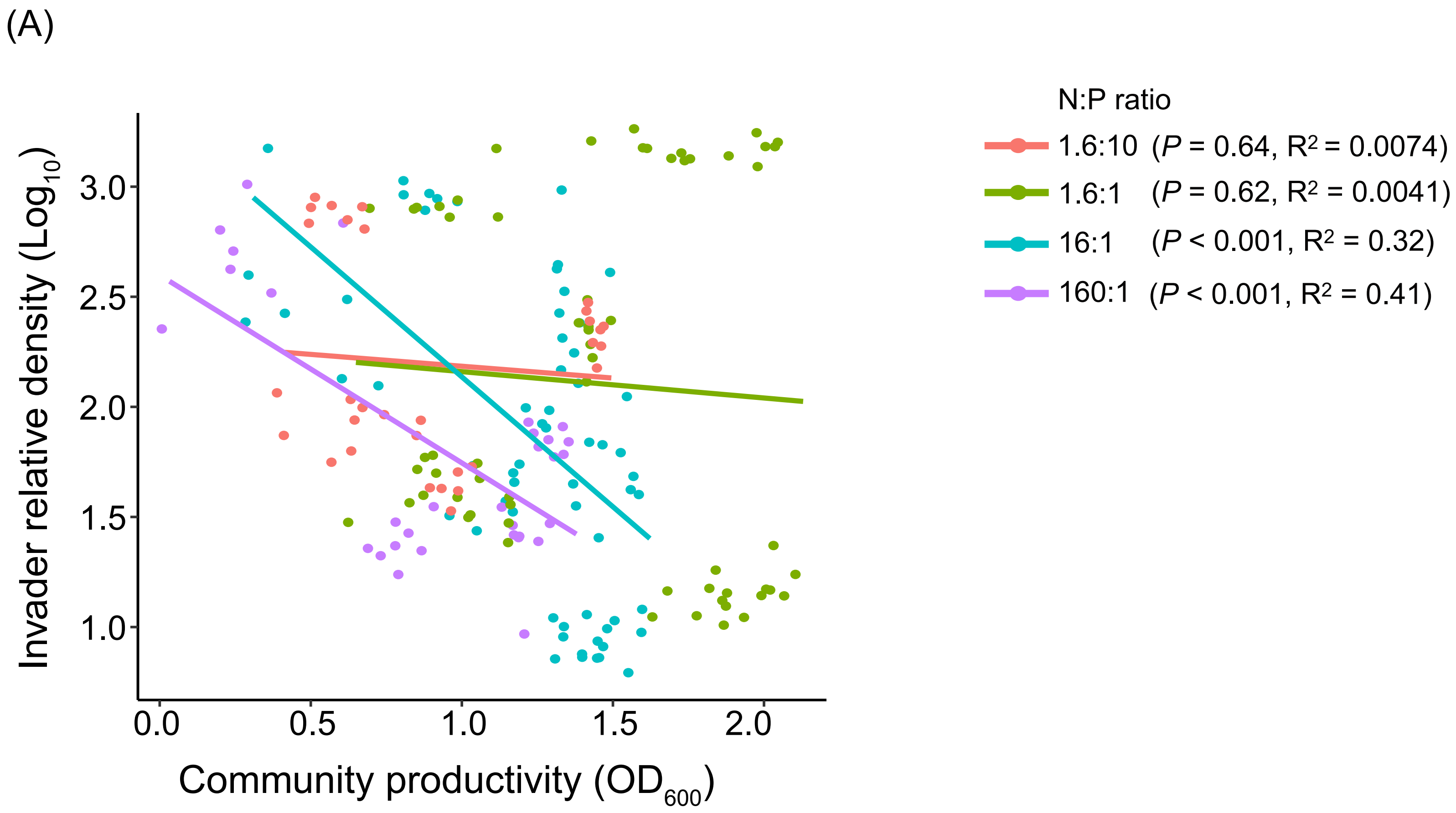
Figure 2. The effect of *R. pickettii* QL-A6 and QL-140 species on the relative density of the invader (panel a and b, respectively). Relative density of the invader was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 72 h incubation. The 0 and 1 on X-axes denote for the presence and absence of *R. pickettii* QL-A6 and QL-140 species in the bacterial community and bars show ±1 standard error (n=186). Asterisks indicate significant differences (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

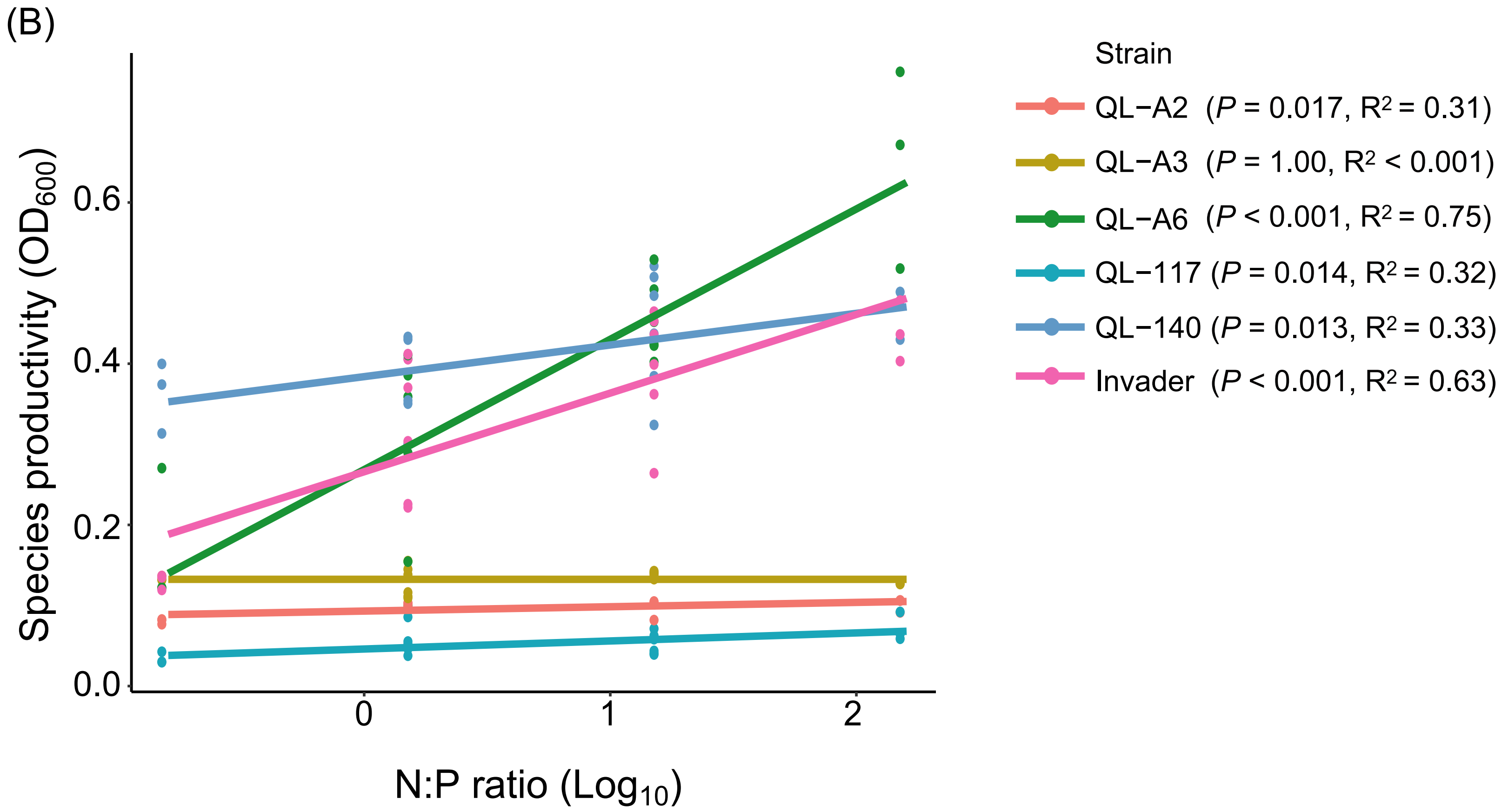
Figure 3. (A) The effect of N:P ratio on the resident community productivity-invasion resistance relationship. Resident community productivity was defined as optical density (OD_{600}) after 72 h incubation and shows the mean of all resident communities across all richness levels. The relative density of invader was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 72 h incubation. (B) The productivity of resident species and the invader at different N:P ratios measured in bacterial monocultures (OD_{600} at 72 h of incubation).

Figure 4. Structural Equation Model presenting direct and indirect effects of species identities and resource stoichiometry on resident community productivity and relative density of the invader. Resident community productivity was defined as optical density (OD_{600}) after 72 h incubation. Invasion success was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 72 h incubation. Continuous and dashed arrows indicate positive and negative effects, respectively, and the width of the arrows indicate relative effect sizes. Black circles indicate the proportion of the total variance explained and asterisks indicate significant effects (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).


Invader relative density (Log10)
3.0
2.5
2.0
1.5
1.0
1
2
3
4
5
Species richness
N:P ratio
1.6:10 (P = 0.014, R² = 0.19)
1.6:1 (P = 0.0027, R² = 0.14)
16:1 (P = 0.0068, R² = 0.12)
160:1 (P = 0.018, R² = 0.18)


(a)
***
Invader relative density (Log10)
2.0
1.0
0.0
0
1
Presence of QL-A6 in the community
(b)
*
Invader relative density (Log10)
2.0
1.5
1.0
0.5
0.0
0
1
Presence of QL-140 in the community


(A)
Invader relative density (Log10)
3.0
2.5
2.0
1.5
1.0
0.0
0.5
1.0
1.5
2.0
Community productivity (OD600)
N:P ratio
1.6:10 (P = 0.64, R² = 0.0074)
1.6:1 (P = 0.62, R² = 0.0041)
16:1 (P < 0.001, R² = 0.32)
160:1 (P < 0.001, R² = 0.41)


(B)
Species productivity (OD600)
0.6
0.4
0.2
0.0
0
1
2
N:P ratio (Log10)
Strain
QL−A2 (P = 0.017, R² = 0.31)
QL−A3 (P = 1.00, R² < 0.001)
QL−A6 (P < 0.001, R² = 0.75)
QL−117 (P = 0.014, R² = 0.32)
QL−140 (P = 0.013, R² = 0.33)
Invader (P < 0.001, R² = 0.63)

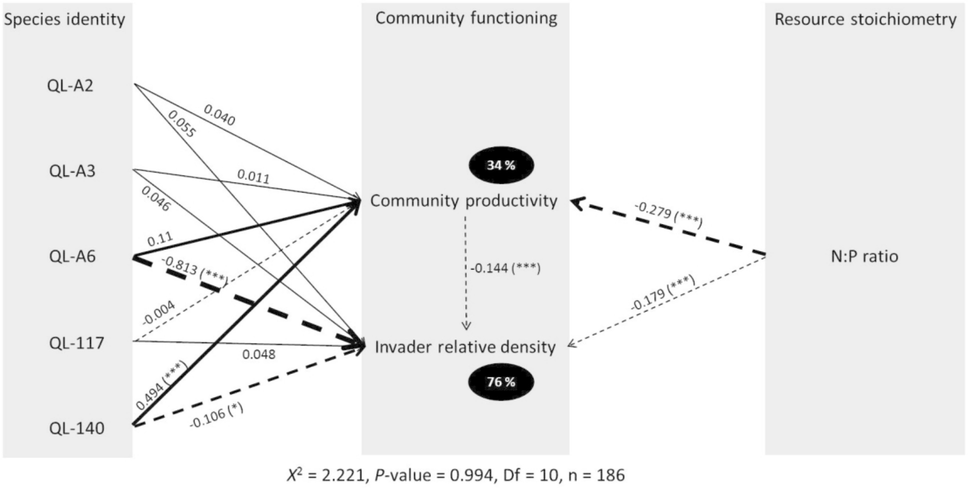
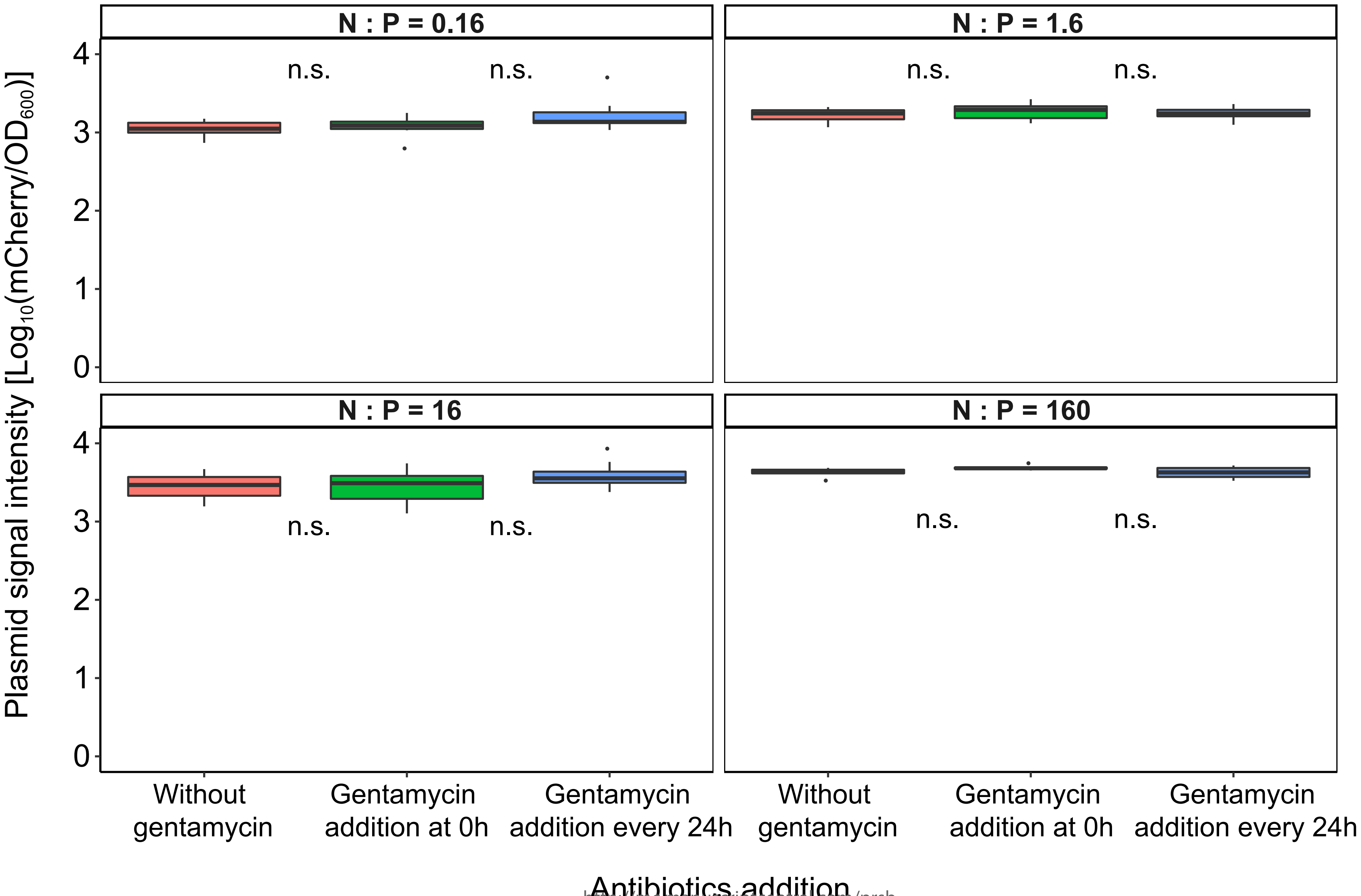


Figure 4. Structural Equation Model presenting direct and indirect effects of species identities and resource stoichiometry on resident community productivity and relative density of the invader. Resident community productivity was defined as optical density (OD600) after 72 h incubation. Invasion success was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD600) after 72 h incubation. Continuous and dashed arrows indicate positive and negative effects, respectively, and the width of the arrows indicate relative effect sizes. Black circles indicate the proportion of the total variance explained and asterisks indicate significant effects (*, P < 0.05; **, P < 0.01; ***, P < 0.001).

294x146mm (150 x 150 DPI)


N : P = 0.16
N : P = 1.6
N : P = 16
N : P = 160
n.s.
Plasmid signal intensity [Log$_{10}$(mCherry/OD$_{600}$)]
0
1
2
3
4
Without gentamycin
Gentamycin addition at 0h
Gentamycin addition every 24h
Antibiotics addition

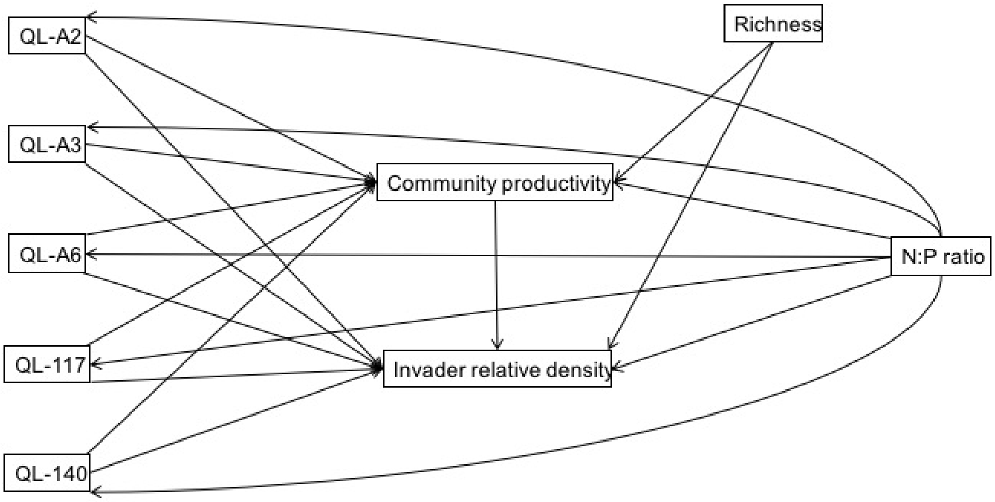
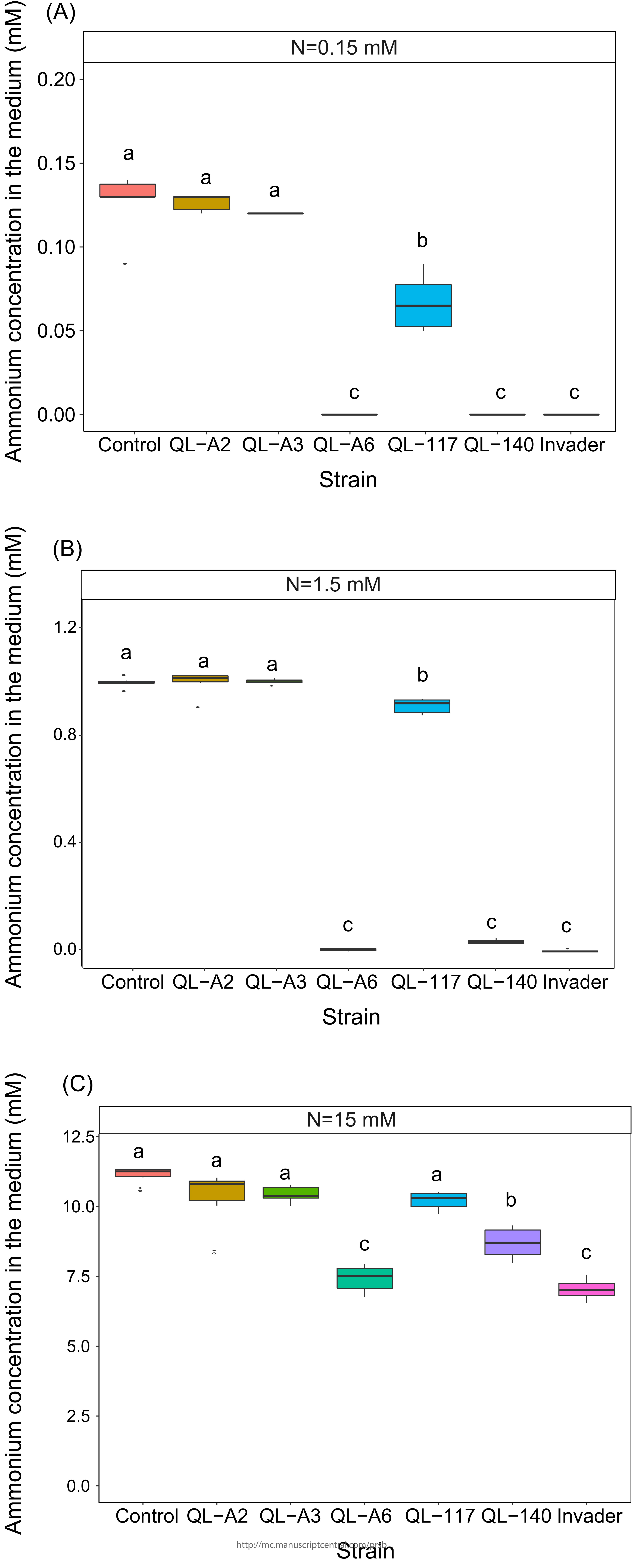
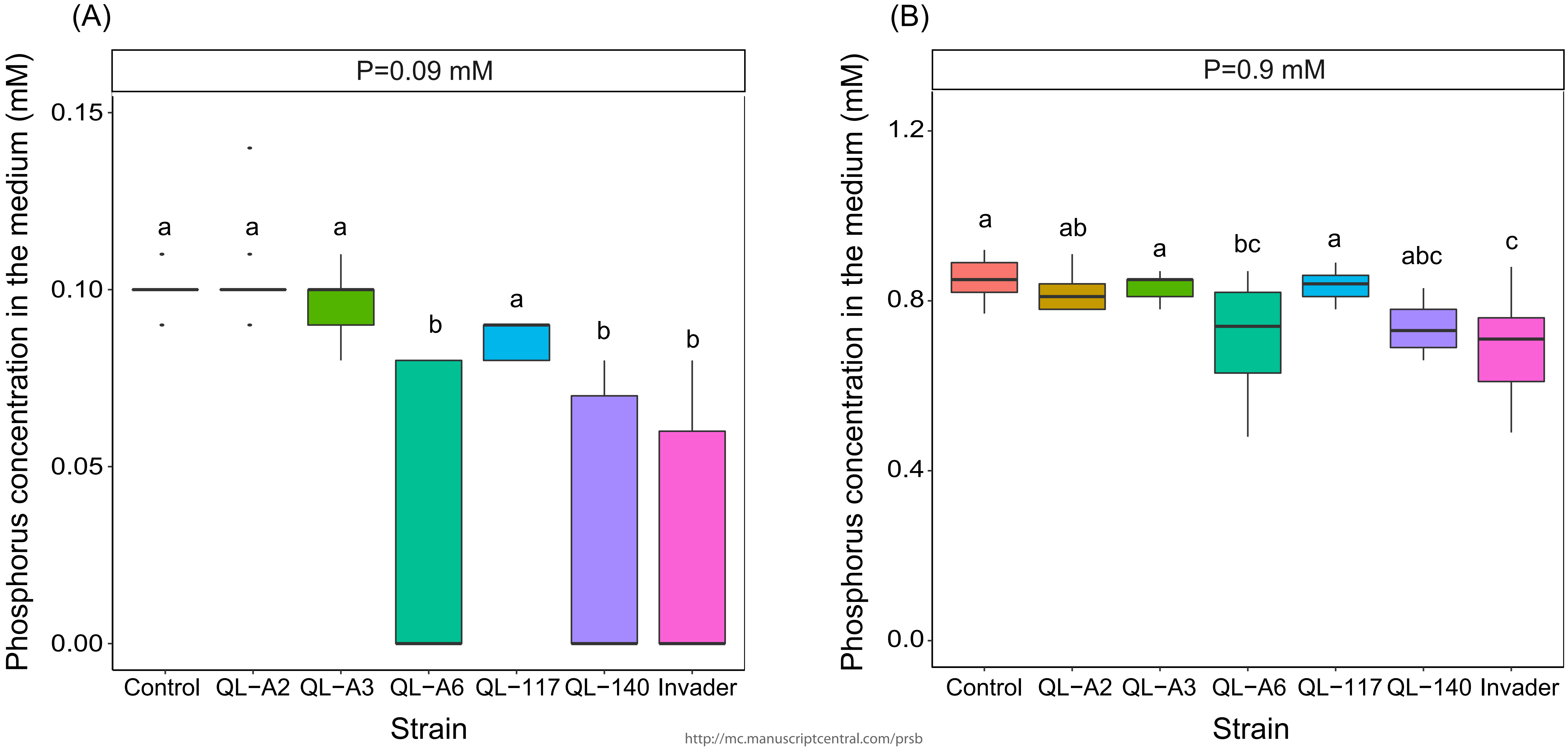
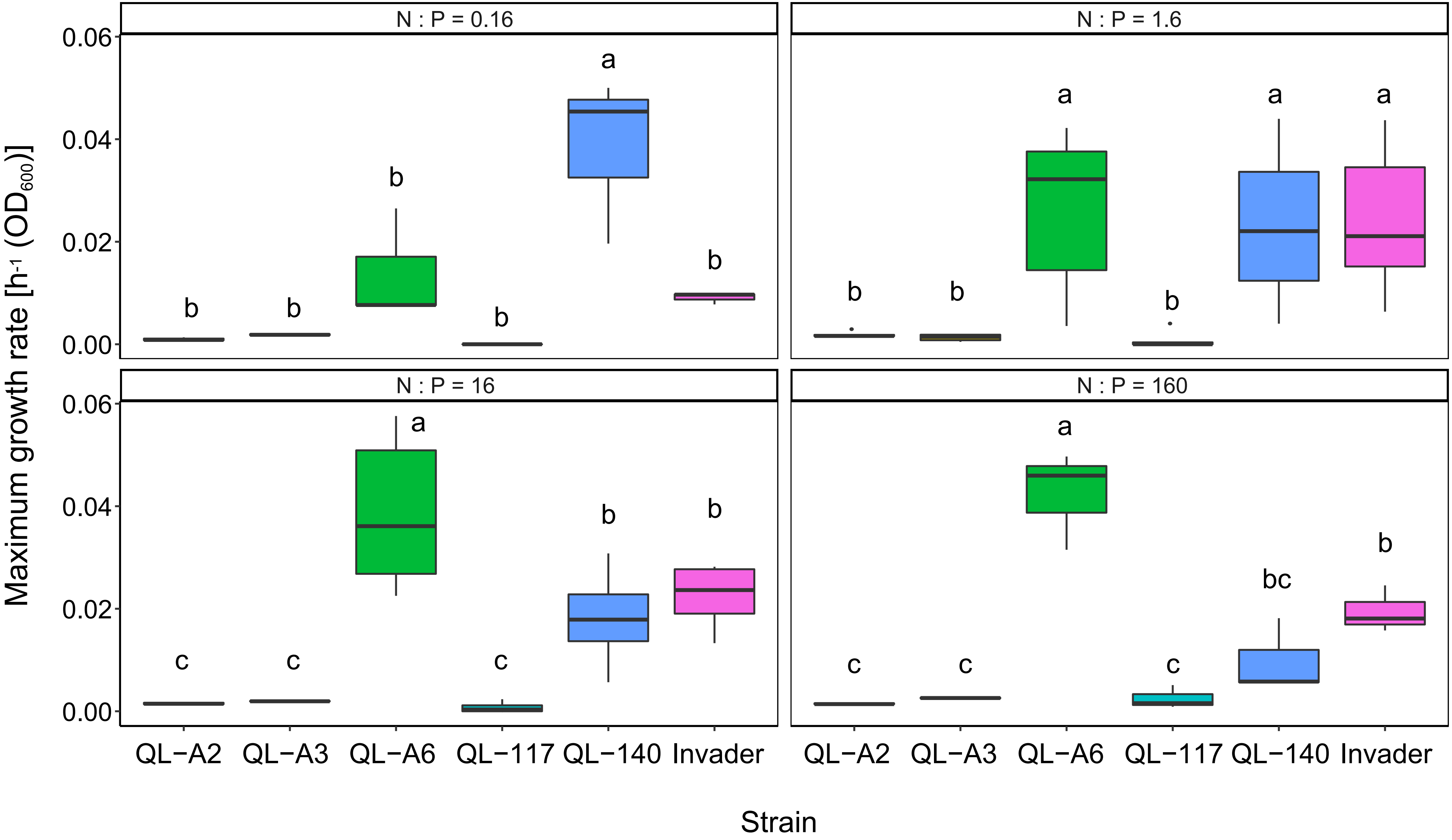


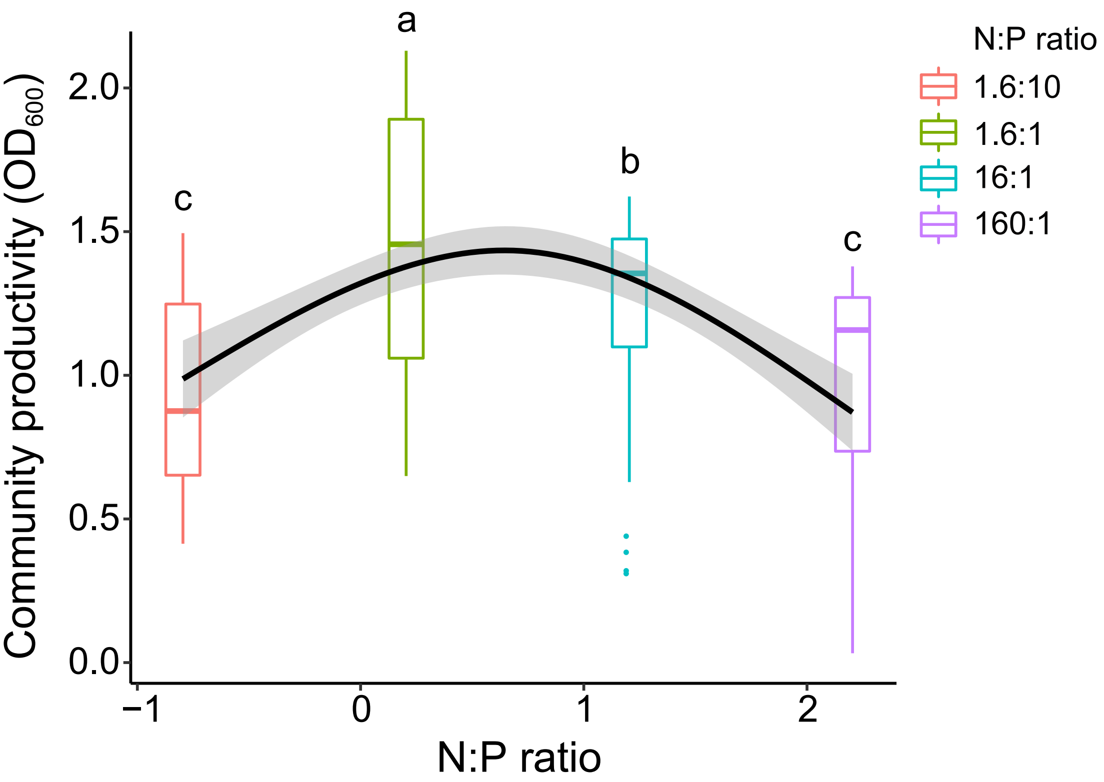
Figure S2. A priori structural equation models including species identity, N:P ratio, community productivity and the relative density of the invader.

230x115mm (72 x 72 DPI)


(A)
N=0.15 mM
Ammonium concentration in the medium (mM)
0.20
0.15
0.10
0.05
0.00
a
a
a
b
c
c
c
Control QL−A2 QL−A3 QL−A6 QL−117 QL−140 Invader
Strain
(B)
N=1.5 mM
Ammonium concentration in the medium (mM)
1.2
0.8
0.4
0.0
a
a
a
b
c
c
c
Control QL−A2 QL−A3 QL−A6 QL−117 QL−140 Invader
Strain
(C)
N=15 mM
Ammonium concentration in the medium (mM)
12.5
10.0
7.5
5.0
2.5
0.0
a
a
a
c
a
b
c
Control QL−A2 QL−A3 QL−A6 QL−117 QL−140 Invader
Strain


(A)
P=0.09 mM
Phosphorus concentration in the medium (mM)
0.15
0.10
0.05
0.00
a
a
a
b
a
b
b
Control
QL−A2
QL−A3
QL−A6
QL−117
QL−140
Invader
Strain
(B)
P=0.9 mM
Phosphorus concentration in the medium (mM)
1.2
0.8
0.4
0.0
a
ab
a
bc
a
abc
c
Control
QL−A2
QL−A3
QL−A6
QL−117
QL−140
Invader
Strain


N : P = 0.16
N : P = 1.6
N : P = 16
N : P = 160
Maximum growth rate [h-1 (OD600)]
0.06
0.04
0.02
0.00
QL−A2
QL−A3
QL−A6
QL−117
QL−140
Invader
Strain
b
b
b
b
a
b
b
b
a
b
a
a
c
c
a
c
b
b
c
c
a
c
bc
b


a
b
c
c
Community productivity (OD_{600})
2.0
1.5
1.0
0.5
0.0
−1
0
1
2
N:P ratio
N:P ratio
1.6:10
1.6:1
16:1
160:1