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Resource stoichiometry shapes community invasion resistance via

productivity-mediated species identity effects

4

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18

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

27   bacterium, *Ralstonia solanacearum*. We found that resource stoichiometry and

28   species identity effects affected the invasion resistance of communities. Both high

29   nitrogen concentration and resident community diversity constrained invasions, and

30   two resident species, in particular, had strong negative effects on the relative density

31   of the invader and the resident community productivity. While resource stoichiometry

32   did not affect the mean productivity of the resident community, it favored the growth

33   of two species that strongly constrained invasions turning the slope of

34   productivity-invasion resistance relationship more negative. Together our findings

35   suggest that alterations in resource stoichiometry can change the community

36   resistance to invasions by having disproportionate effects on species growth

37   potentially explaining changes in microbial community composition under

38   eutrophication.

39

40   **Key words:**

41   Resource stoichiometry, diversity-invasion resistance relationship, nitrogen,

42   phosphorus, productivity, species identity effects

43

44   **1.   Introduction**

45   Microbial biodiversity plays an important role in ecosystem functioning by offering

46   sets of functions that cannot be provided by single species [1–3]. For example,

47   host-associated microbial communities can ward off pathogens thereby protecting

48   their associated host organism [4–6]. This process can also be viewed from the

49   perspective of biological invasions where the members of resident microbial

50   communities facilitate or constrain the establishment of the invader [7,8]. Several

51   studies have shown that increasing community diversity reduces the likelihood of

52   invasions by promoting a more comprehensive use of available niches in the given

53   environment [3,9,10]. Such diversity-invasion resistance relationships are however

54   often sensitive to environmental conditions such as resource availability [11] or

55 temperature [12]. As a result, we still poorly understand how environmental contexts

56 shape diversity-invasion resistance relationships.

57   Resource availability has been shown to be an important factor affecting the

58 outcome of biological invasions [13–15]. Mechanistically, concentration or

59 composition of resources can alter the physiology and interactions between different

60 species within communities which can then lead to changes in community invasion

61 resistance. Moreover, changes in resource availability may change the significance of

62 species identity effects, i.e. the contribution of resident community members to the

63 invasion, by promoting the growth of species that grow either slow or fast [16,17].

64 Species identity effects could thus explain positive diversity-invasion resistance

65 relationships across environmental gradients where different species contribute to the

66 invasion resistance under specific environmental conditions [1,18]. Here we studied

67 how resource stoichiometry, the relative concentration of different elements in the

68 environment, shapes invasions via diversity, productivity and species identity effects.

69   Resource stoichiometry is a broad and active research field in ecology that has been

70 extensively used to understand predator-prey interactions [19,20]. While several

71 studies have highlighted the importance of resource stoichiometry for the ecology and

72 functioning of communities [21,22], its effects have been less studied in the context of

73 diversity-ecosystem functioning relationships. Environmental stoichiometry can be

74 used to link tissue composition of organisms with trophic level interactions [23–25]

75 and it plays important role in determining which species are able to grow in any given

76 ecosystem affecting consumer-resource interactions [26,27]. For example, low C:P

77 ratio has been shown to favour fast-growing species leading to an increase in

78 microbial diversity [28]. Resource stoichiometry can also affect invasions by altering

79 species biomasses and growth dynamics [29]. However, it is unclear how resource

80 stoichiometry shapes the diversity-invasion resistance and productivity-invasion

81 resistance relationships.

82   In the present study, we used experimental approach to directly expose model

83 microbial communities with varying levels of diversity to invasions by a single

84 invader species under different resource stoichiometry treatments. The model

85   'resident' community was constructed by using five different bacterial species that

86   have previously been shown to constrain invasions in a diversity-dependent manner

87   [4,17]. As an invader, we used a plant pathogenic *Ralstonia solanacearum* bacterium

88   whose life cycle is directly linked to biological invasions of the plant rhizosphere

89   microbiome. *Ralstonia solanacearum* causes bacterial wilt disease [30,31] and is a

90   major threat to global food production [32]. Before infecting its host, *R.*

91   *solanacearum* must first get through microbial communities surrounding the plant

92   roots. It has previously been shown that competition for resources between the

93   invader and resident community members is important for the outcome of invasions

94   [4,17]. How these invasion outcomes are affected by dynamic changes in nutrient

95   levels typical for rhizosphere microbiomes [33,34] and resident community diversity

96   remains unclear. To study this, we manipulated both resident community diversity

97   gradient (richness levels of 1 to 5 species in all possible combinations) and the

98   resource stoichiometry of the environment by changing the relative concentration and

99   ratio of nitrogen (N) and phosphorus (P) orthogonally by following the Redfield ratio.

100 Redfield ratio is the atomic ratio of carbon, nitrogen and phosphorus found in

101 phytoplankton and throughout the deep oceans [35] and a general baseline of element

102 composition for both aquatic and terrestrial ecosystems [36,37]. Communities were

103 then exposed to *R. solanacearum* invasions and the invasion success was determined

104 as the relative density of *R. solanacearum* invader after 72h growth in the resident

105 community (indicative of the reproductive success of the invader): higher the final

106 relative abundance of *R. solanacearum*, higher the invasion success. We expected that

107 resident community diversity-invasion resistance relationship could be sensitive to

108 resource stoichiometry having either positive or negative effects on invasions

109 depending on specific changes in species ability to grow under different N:P ratios.

110 Mechanistically, changes in invasion outcomes could potentially be explained via

111 effects on community productivity or changes in the relative contribution of

112 community members to invasions via species identity effects.

113

114   **2.   Methods**

115   **(a) Bacterial strains and plasmids**

116   We used *Ralstonia solanacearum* species QL-Rs1115 tagged with pYC12-mCherry

117   plasmid as a model invader in our experiments [38]. Five avirulent, but closely

118   related, *Ralstonia spp.* isolates (*Ralstonia mannitolilytica* QL-A2, *Ralstonia*

119   *mannitolilytica* QL-A3, *Ralstonia pickettii* QL-A6, *Ralstonia taiwanensis* QL-117 and

120   *Ralstonia pickettii* QL-140) were used to construct our model resident communities

121   [4]. None of these bacteria showed direct antagonism towards each other or the

122   invader, which suggests that they likely interact indirectly through competition for

123   shared resources. A more detailed description of the bacteria and used plasmid can be

124   found in Table S1. All bacteria were stored at -80 °C in 20 % glycerol prior to the

125   experiments.

126   **(b) Assembly of resident communities**

127   The resident communities were assembled by using all five avirulent species in

128   substitutive design so that the final communities covered all possible species

129   combinations and richness levels (total of 31 communities with equal initial bacterial

130   biomasses, Table S2). Prior to the experiments, bacteria were pre-cultured from

131   frozen stocks on Nutrient Agar plates (NA, glucose 10.0 g L^{-1}, tryptone 5.0 g L^{-1}, beef

132   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

133   were picked and re-grown in liquid nutrient broth (NA medium without agar) at 30 °C

134   for 12 h with 170 r.p.m. agitation. Bacterial isolates were washed three times in

135   0.85 % NaCl to remove nutrient residues and re-suspended in 0.85 % NaCl with final

136   densities of 10^7 cells mL^{-1}.

137   **(c) Manipulation of resource stoichiometry**

138   To manipulate the resource stoichiometry, we first set up a minimal salt medium,

139   which did not contain carbon, nitrogen or phosphorus (MOPS 30mM, $CaCl_2$ 0.1mM,

140    $FeSO_4$ 3 mM, KCl 20mM, $MgCl_2$ 2mM, Na_2SO_4 14mM and NaCl 51mM, pH 7.0).

141   The minimal medium was then supplemented with a mixture of carbons (fructose,

142   glucose, sucrose, maltose, arabinose and galactose) in equal concentrations to yield a

143   total concentration of 10 mM for all combined carbon resources as described

144   previously [4]. The concentration of total carbon resources (10 mM) was held

145   constant for all resource stoichiometry treatments. To manipulate the concentration

146   and ratio of nitrogen and phosphorus, we added NH_4Cl or $NaH_2PO_4 \cdot 2H_2O$ as the sole

147   nitrogen and phosphorus resource, respectively. A total of six resource stoichiometry

148   treatments with four unique N:P ratios were established for the experiment where low,

149   intermediate and high nitrogen levels were established within both low and high

150   phosphorus levels (Table 1). Each media was then used to establish replicate

151   treatments on 96-well microtiter plates in triplicate (18 microplates in total) for each

152   resident community combination.

153   **(d) Measuring resident community invasion resistance and productivity in**

154   **microcosms**

155   To quantify invasion resistance, all communities (10^6 cells mL^{-1} in 200 μL of final

156   volume) were exposed to invasion by *R. solanacearum* QL-Rs1115 (10^5 cells mL^{-1} in

157   200 μL of final volume) under different resource stoichiometry environments.

158   Replicate communities without invader were used as control treatments. All

159   communities were incubated for 72 h at 30 °C with 170 r.p.m. orbital agitation. To

160   measure invader density relative to resident community density, we measured the

161   mCherry fluorescence signal (Excitation: 587 nm, Emission: 610 nm, gain: 60) of the

162   invader and calculated the invasion success as mCherry relative fluorescence unit

163   against total bacterial density of the community (RFU, mCherry/OD_{600}) at the end of

164   the experiment (after 72 h of incubation). To quantify the total productivity of

165   different communities in each resource environment, we used optical density (OD_{600})

166   as a measure of total bacterial growth (invader and the resident community). We used

167   the control communities without the invader to blank the fluorescence signal

168   background and optical density of the culture media to blank the OD_{600} background.

169   In order to verify plasmid stability during the invasion experiments, we grew

170   gentamycin-tagged mCherry plasmid carrying *R. solanacearum* invader (10^6 cells

171   mL^{-1} in 200 μL of final volume) in four N:P ratios (0.16, 1.6, 16 and 160) in the

172   absence and presence of gentamycin antibiotic (30 μg mL^{-1}) for 72 h. Gentamycin

173   was added only at the beginning or at every 24 h to create a strong selective pressure

174   on the plasmid. The plasmid stability was determined as fluorescent signal intensity,

175   which is indicative of bacterial growth and expression of the plasmid-encoded

176   mCherry fluorescent protein (Figure S1). No difference was observed between

177   different antibiotic treatments in any of the N:P ratios after 72 h of incubation (Figure

178   S1; The main effect of antibiotic treatment in 0.16, 1.6, 16 and 160 N:P ratios,

179   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

180    $F_{1, 190} = 0.08$, $P = 0.77$). This suggests that the plasmid was stably maintained during

181   the invasion experiments in the absence of gentamycin.

182   **(e) Measuring the growth and consumption of nitrogen and phosphorus by each**

183   **bacterial species**

184   The growth rate and productivity of all bacterial species were measured in

185   monoculture at four N:P ratios. Bacterial were inoculated at an initial density of 10^6

186   cells mL^{-1} in 96-well microtiter plates as described above. Each monoculture was

187   grown in triplicates under each of the N:P ratios at 30 ℃ with agitation (170 r.p.m.)

188   for 72 h. To determine growth rates, we measured bacterial growth with

189   spectrophotometer (OD$_{600}$) at every 8 h to fit in Logistics model function

190   ("gcFitModel" in package "grofit" in R 3.3.1) [39] and the Maximum slope (μ, h^{-1}) of

191   the Logistic model was considered as the maximum growth rate [40]. The

192   productivity of each species was determined as the bacterial biomass after 72 h.

193   Culture media without bacteria was used to determine the background absorbance

194   before determining growth rates and productivity. To test the consumption of nitrogen

195   and phosphorus by all bacteria, we obtained cell-free supernatant by centrifugation

196   (10 000 rpm for 10 min) and filtration (0.22 μm filters) after 72 h incubation.

197   Nitrogen and phosphorus concentrations were measured using a continuous-flow

198   analyzer (AA3, SEAL, Germany) and compared with unconsumed media (no

199   bacterial inoculation).

200

201   **(e) Statistical analyses**

202   Invasion success (RFU, mCherry/OD_{600}) and resource stoichiometry ratios (N:P) were

203   log_{10}–transformed before statistical analyses to fulfill model assumptions. All

204   comparisons between the growth of individual species were analyzed using ANOVA

205   and linear regression. General Linear Mixed Models (GLMs) were used to examine

206   the resident species identity effects and resource stoichiometry as a function of

207   invader relative density (invasion success). Model 1 ("Richness-ratio") and Model 2

208   ("Identity-ratio") were used to identify how individual species contributed to the

209   invasion   success   as   a   function   of   resource   stoichiometry.   Model   3

210   ("Richness-concentration", Table S3) was used to analyze whether N and P

211   concentrations had interactive effects with species richness in determining invasion

212   success and resident community productivity. Model 4 ("Productivity-ratio", Table

213   S4) was used to study the interactive effects between productivity and resource

214   stoichiometry on the invasion success, while Models 5 ("Richness-ratio", Table S4)

215   and 6 ("Identity-ratio", Table S4) were used to explore the effects of community

216   diversity and species identity on the resident community productivity. In some cases,

217   we used the means of community treatment replicates for simplified analysis (e.g.

218   species presence effects in Figure 2).

219   Structural Equation Model (SEM; 'lavaan' package in R) was used to investigate

220   the relative importance of resource stoichiometry, species identity effects, species

221   maximum growth rates, nitrogen and phosphorus consumption and resident

222   community productivity on the invasion success (the *prior* model is shown in Figure

223   S2). All analyses were performed with R 3.3.1 [41].

224

225   **3. Results**

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

227   We found that increasing resident species richness had a negative effect on invasions

228   across all N:P ratios (Figure 1; Model 1 in Table 2, the main effect of species richness

229 on invader relative density). Similarly, the relative density of the invader decreased

230 with increasing N:P ratio and N concentration (Model 1 in Table 2, the main effect of

231 N:P ratio on invader relative density), while P concentration alone had no effect

232 (Model 3 in Table S3). No interactive effect between species richness and N:P ratio

233 on the relative density of the invader was found (Model 1 in Table 2). These results

234 suggest that both species richness and N:P ratio constrained invasions independently,

235 while N concentration alone had a stronger effect than P concentration.

236 **(b) The effect of resident species identities on resident community productivity**

237   **and invasions**

238 We found that *R. mannitolilytica* QL-A2, *R. mannitolilytica* QL-A3 and *R.*

239 *taiwanensis* QL-117 resident species had no significant species identity effects on the

240 relative density of the invader (Model 2 in Table 2). In contrast, *R. pickettii* QL-A6

241 and *R. pickettii* QL-140 resident species were very effective at reducing the relative

242 density of the invader (Model 2 in Table 2). To examine this in more detail, we

243 compared the invasion resistance of resident communities with and without these two

244 species. As expected, resident communities were less resistant to invasions in the

245 absence of these two species (Figure 2, comparison on communities with and without

246 *R. pickettii* QL-A6: panel a, $F_{1,184} = 400.4$, $P < 0.001$, comparison on communities

247 with and without *R. pickettii* QL-140: panel b, $F_{1,184} = 4.47$, $P = 0.036$).

248 Mechanistically, this could be explained by relatively more efficient consumption of

249 nitrogen and phosphorus compared to the other resident species (Figures S3 and S4;

250 Species main effects at 0.15, 1.5 and 15 mM nitrogen concentrations, respectively: $F_{6,}$

251 $_{35} = 254.6$, $P < 0.001$; $F_{6, 35} = 3196$, $P < 0.001$ and $F_{6, 35} = 55.69$, $P < 0.001$. Species

252 main effects at 0.09 and 0.9 mM phosphorus concentrations, respectively: $F_{6, 56} =$

253 20.92, $P < 0.001$ and $F_{6, 56} = 6.00$, $P < 0.001$). However, no clear differences were

254 found in comparison with the invader, which suggests that *R. pickettii* QL-A6 and

255 QL-140 were equally good at consuming nitrogen and phosphorus ($P > 0.05$ in all

256 pairwise comparisons).

257   Even though increasing N:P ratio constrained invasions, no significant

258   interactions with species identities were found in the full-scale invasion experiment

259   (Model 2 in Table 2). To explore this further we compared the growth of resident

260   species and the invader separately in monocultures. Growth rate of *R. pickettii*

261   QL-A6, *R. pickettii* QL-140 and the invader *R. solanacearum* did not increase linearly

262   with increasing N:P ratio. While *R. pickettii* QL-140 had the highest growth rate when

263   N:P ratio was 0.16 ($F_{5, 12}$ = 9.87, *P* < 0.001, Figure S5), *R. pickettii* QL-A6 grew the

264   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,

265   respectively in Figure S5). No difference in the maximum growth rate of these species

266   was found at 1.6 N:P ratio ($F_{5, 30}$ = 8.23, *P* < 0.001, Figure S5).

267   However, clear positive correlations were found between the productivity

268   (population density after 72 h of growth) of the invader, QL-A6 and QL-140 species

269   and the increasing N:P ratio (Figure 3B). While *R. pickettii* QL-140 had the highest

270   productivity at the lowest N:P ratio (0.16), the *R. pickettii* QL-A6 became more

271   competitive relative to the invader at 16 and 160 N:P ratio treatments. This suggests

272   that differences in species ability to grow under increasing N:P ratios were likely

273   important in explaining diversity-productivity-invasion resistance relationships.

274

275   **(c) The effect of resource stoichiometry on the resident community productivity**

276   **and invasions**

277   We found that increasing N:P ratio had a hump-shaped (non-linear) relationship with

278   the resident community productivity (Figure S6, $F_{1, 184}$ = 1.28, *P* = 0.26; the mean

279   productivity of all resident communities in all richness levels), and only the resident

280   community richness correlated positively with resident community productivity

281   (Model 5 in Table S4). However, resident community productivity was positively

282   affected by both *R. pickettii* QL-A6 and QL-140 species and QL-A6 had a positive

283   effect on community productivity with increasing N:P ratio (Model 6 in Table S4),

284   which is in line with their ability to efficiently consume nitrogen and phosphorus

285   (Figures S3 and S4) and to reach higher biomasses (productivity) with increasing N:P

286   ratios in monocultures (Figure 3B).

287   Resident community productivity had a clear negative effect on the relative

288   density of the invader (Figure 3A, Model 4 in Table S4), and crucially, the negative

289   relationship between the resident community productivity and the density of the

290   invader became stronger with increasing N:P ratio (Figure 3A, Model 4 in Table S4).

291   This can be explained by resident species identity effects, in particular, the ability of

292   *R. pickettii* QL-140 to increase its growth with increasing N:P ratio, which then turned

293   the productivity-invasion resistance relationship more pronounced.

294

295   **(d) Linking species identity and resource stoichiometry effects with**

296   **productivity-invasion resistance relationship**

297   To further study how invasions and community productivity were shaped by resource

298   stoichiometry and species identity effects, we built a Structural Equation Model

299   (SEM) describing direct and indirect relationships between these variables. The final

300   SEM model explained 76 % of the variance of the relative density of the invader

301   (Figure 4). The species *R. pickettii* QL-A6 had a significant negative effect on the

302   relative density of the invader, while the species *R. pickettii* QL-140 promoted both

303   community productivity and reduced the relative density of the invader. Similar to

304   previous analyses, resource stoichiometry did not change the species identity effects

305   in the SEM. However, resource stoichiometry had negative effects on both resident

306   community productivity and the relative density of invader, while the resident

307   community productivity itself had a negative effect on invasions. Together these

308   results suggest that species identity and resource stoichiometry had both direct and

309   indirect negative effects on invasions and that the indirect effects were mediated by

310   resident community productivity.

311

312   **4. Discussion**

313   Biodiversity is an important determinant of ecosystem functioning having significant

314   effects on community resistance to biological invasions [5,42,43]. Here we addressed

315   how changes in environmental stoichiometry (N:P ratio) affects invasion resistance of

316   model microbial communities. We found that changes in resource stoichiometry had

317   clear effects on invasion outcomes via productivity-mediated species identity effects.

318   First, increasing N:P ratio lowered the intercept of diversity-invasion resistance

319   relationship, which suggests that increasing the input of nitrogen reduced the

320   likelihood of invasions regardless of the community diversity. Second, two resident

321   species, *R. pickettii* QL-A6 and QL-140, played key roles in having negative effects

322   on the invader and positive effects on resident community productivity. Crucially,

323   increasing the N:P ratio turned the slope of productivity-invasion resistance

324   relationship much steeper because the species *R. pickettii* QL-A6 and *R. pickettii*

325   QL-140 grew better and constrained invasions more efficiently when nitrogen became

326   more abundant. Together these results suggest that resource stoichiometry can change

327   the outcome of microbial invasions via productivity-mediated species identity effects.

328   In line with the previous studies, increasing resident community diversity

329   decreased the likelihood of successful invasions [4,5,44]. While resource

330   stoichiometry did not interact with resident species richness, it lowered the intercept

331   of diversity-invasions resistance relationship. This suggests that an increase in the

332   relative concentration of nitrogen improved the resident community invasion

333   resistance regardless of the species richness but that this effect was stronger in more

334   diverse communities. One simple explanation for this is that increasing community

335   diversity increased the likelihood that one or both of the species that were effective at

336   constraining invasions (*R. pickettii* QL-A6 and QL-140) were included in

337   communities. To study this in more detail, we concentrated on exploring the relative

338   importance of resident species identities on invasions.

339   Two resident species, *R. pickettii* QL-A6 and QL-140, played key roles in having

340   negative effects on the invader relative density and positive effects on the resident

341   community productivity. Both of these species were effective at consuming nitrogen

342   and phosphorus across all N:P ratios (Figures S3 and S4), and hence, their

343   contribution to invasion resistance likely overshadowed the effects of the other

344   resident community members. However, no difference was found in the consumption

345   of nitrogen and phosphorus among the invader, *R. pickettii* QL-A6 and QL-140

346   (Figures S3 and S4), which suggests that these three species were equally efficient at

347   sequestering N and P. However, either the *R. pickettii* QL-A6 or QL-140 was clearly

348   faster at growing than the invader in three out of four N:P ratios used in our

349   experiments (Figure S5), which could have helped them to outcompete the invader in

350   these conditions. Moreover, while these species constrained invasions across all N:P

351   ratios (Figure 4), we found that the importance of species QL-A6 on community

352   productivity increased along increasing N:P ratio, while species QL-140 had the

353   highest productivity at low N:P ratios (Figure 3B). Together these results suggest that

354   resource stoichiometry changed invasion outcomes via productivity-mediated species

355   identity effects by favoring resident species that were efficient at growing when the

356   nitrogen was abundant. This finding is in line with a previous study where these two

357   species were observed to have highly negative effects on the same invader used in this

358   study due to high catabolic similarity [17] and supports the idea that individual

359   contribution of resident community members on invasions can change according to

360   resource availability [17]. In the future, it would be interesting to study if

361   environmental stoichiometry can drive changes in the elemental stoichiometry of

362   bacterial and other microbial cells. For example, it has been shown that the effects of

363   resource stoichiometry can be species-specific [46] where environmental

364   stoichiometry favor species with similar biomass composition [25,26]. In this case,

365   the similarity in biomass composition between the resident species and the invader

366   could be important determinant for invasions.

367   Furthermore, we found that increasing N:P ratio had a hump-shaped effect on

368   community productivity that peaked at intermediate N:P ratios, which can optimize

369   species coexistence or community productivity [19,22,47]. However, this relationship

370   was not very strong and was only visible when all the communities with different

371   richness levels were included in the analysis. Interestingly, resident community

372   productivity correlated negatively with the relative density of the invader only within

373   16 and 160 N:P ratios. Mechanistically, this could be explained by the fact that the

374   importance of *R. pickettii* QL-A6 on resident community productivity and invasions

375 resistance increased along increasing N:P ratio (Figure 3B and Model 2 in Table 2).

376 This suggests that increasing the input of N can increase the invasion resistance of

377 communities via productivity, but that these effect might be driven by certain

378 important 'key stone' species instead of changes in the total community productivity

379 [9,17]. Several previous studies have suggested that resource stoichiometry of the

380 environment is a good predictor of species growth capacity [46,48]. For example, both

381 N and P are important for species growth via effects on production and expression of

382 proteins, enzymes and cell structures [27,49,50] and could often be limiting resources

383 in the environment. Furthermore, it is possible that invasion resistance is not only

384 mediated by nitrogen uptake but also by carbon metabolism, which is known to be

385 interconnected with nitrogen regulation [51]. In support for this, a previous study has

386 shown that the same resident species used in this study had higher growth rates,

387 productivity and high resource niche overlap with the same invader used in this

388 experiment when measured in various carbon media [4,17]. As a result, it is possible

389 that competition for both carbon and nitrogen affected the observed invasion

390 outcomes also in this experiment.

391   Here we link the high N:P ratio to improved community functioning in terms of

392 increased invasion resistance. Our results suggest that resource stoichiometry can

393 have positive effects on resident community productivity by favoring species that are

394 very efficient at constraining invasions. Interestingly, resource stoichiometry did not

395 change the shape of diversity-invasion resistance relationship even though invasions

396 were less successful in more diverse communities in general. In contrast, resource

397 stoichiometry turned the slope of the productivity-invasion resistance more negative,

398 because increase in nitrogen availability potentially intensified the competitive

399 interactions between resident community members and the invader by favoring the

400 growth of certain resident community members (*R. pickettii* QL-A6 and *R. pickettii*

401 QL-140). This is in line with studies showed that competition becomes stronger under

402 higher N:P ratio [28,52]. In the future, it will be important to better understand the

403 effects of resource stoichiometry on invasions in more natural environments. For

404 example, more information is needed how the presence of more complex microbial

405   community, multi-trophic interactions with predators and parasites, root exudation

406   and spatially uneven distribution of particulate organic matter shape the elemental

407   stoichiometry and their effects on invasions in complex plant-soil ecosystems.

408   We conclude that resource stoichiometry is an important determinant of

409   community invasion resistance. Human activities continue to have a huge effect on

410   global elemental cycling [53], nitrogen leaching and eutrophication, which are

411   causing growing problems and having devastating effects on the functioning of

412   ecosystems [54,55]. In the case of eutrophication, our results suggest that resource

413   stoichiometry could drive changes in microbial community composition potentially

414   affecting the likelihood of biological invasions. In the agricultural context, resource

415   stoichiometry could affect the severity of disease epidemics via effects on microbial

416   competition. A better understanding of this process could potentially help to control

417   plant pathogen invasions via modulation of soil nutrient availability and balance (N:P

418   ratios) to maintain relatively stable and invasion resistant microbial community. In

419   broader perspective, understanding how changes in global element balances affect the

420   interactions within and between communities is crucial for predicting ecosystem-level

421   responses to environmental change.

422

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624   Table 1. Concentration of nitrogen (NH$_4$Cl) and phosphorus (NaH$_2$PO$_4$) and their ratios (N:P) in

625   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

626

627   **Table 2.** ANOVA table summarizing the species richness, N:P ratio and species identity effects on the

628   relative density of the invader (Models 1 – 2). Significant effects ($P < 0.05$) are highlighted in bold and

629   the "up" and "down" arrows denote for positive and negative effects on the relative density of invader,

630   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, $R^2 = 0.76$	

631

632   **Figure 1.** The effects of species richness and N:P ratio on invasion success (relative invader density).

633   The relative density of the invader was defined as log-10 transformed relative mCherry fluorescence

634   unit (RFU, mCherry/OD_{600}) after 72 h incubation.

635

636   **Figure 2.** The effect of *R. pickettii* QL-A6 and QL-140 species on the relative density of the invader

637   (panel a and b, respectively). Relative density of the invader was defined as log-10 transformed relative

638   mCherry fluorescence unit (RFU, mCherry/OD_{600}) after 72 h incubation. The 0 and 1 on X-axes denote

639   for the presence and absence of *R. pickettii* QL-A6 and QL-140 species in the bacterial community and

640   bars show ±1 standard error (n=186). Asterisks indicate significant differences (*, $P < 0.05$; **, $P <$

641 0.01; ***, $P < 0.001$).

642

643   **Figure 3.** (A) The effect of N:P ratio on the resident community productivity-invasion resistance

644   relationship. Resident community productivity was defined as optical density (OD_{600}) after 72 h

645   incubation and shows the mean of all resident communities across all richness levels. The relative

646   density of invader was defined as log-10 transformed relative mCherry fluorescence unit (RFU,

647   mCherry/OD_{600}) after 72 h incubation. (B) The productivity of resident species and the invader at

648   different N:P ratios measured in bacterial monocultures (OD_{600} at 72 h of incubation).

649

650   **Figure 4.** Structural Equation Model presenting direct and indirect effects of species identities and

651   resource stoichiometry on resident community productivity and relative density of the invader.

652   Resident community productivity was defined as optical density (OD_{600}) after 72 h incubation. Invasion

653   success was defined as log-10 transformed relative mCherry fluorescence unit (RFU, mCherry/OD_{600})

654   after 72 h incubation. Continuous and dashed arrows indicate positive and negative effects, respectively,

655   and the width of the arrows indicate relative effect sizes. Black circles indicate the proportion of the

656   total variance explained and asterisks indicate significant effects (*, $P < 0.05$; **, $P < 0.01$; ***, $P <$
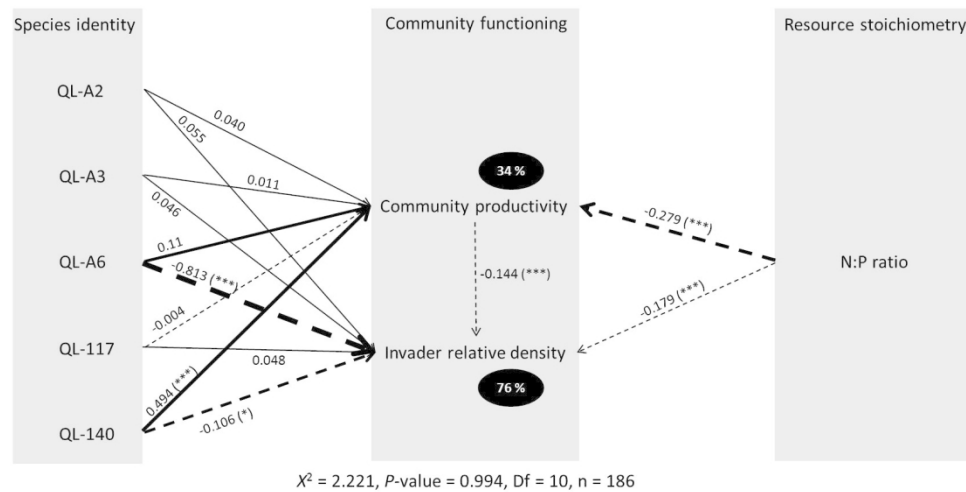
657   0.001).

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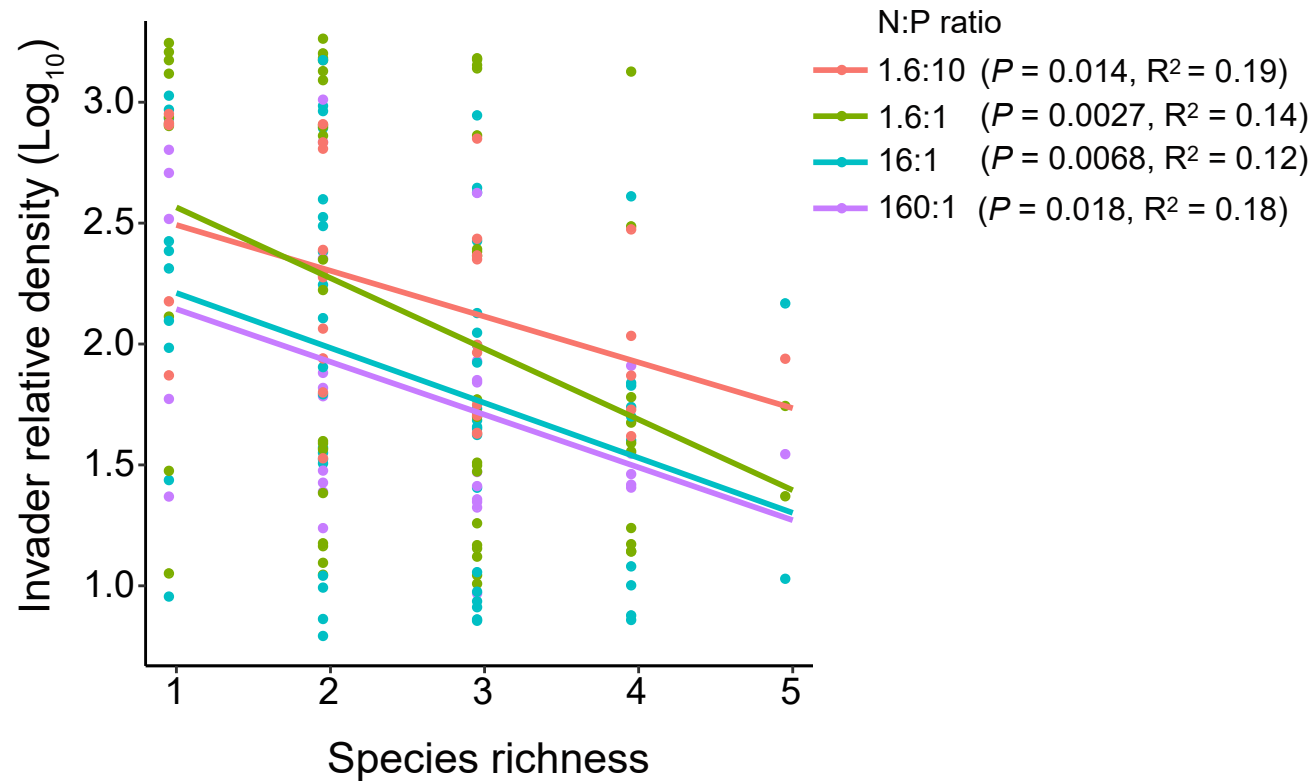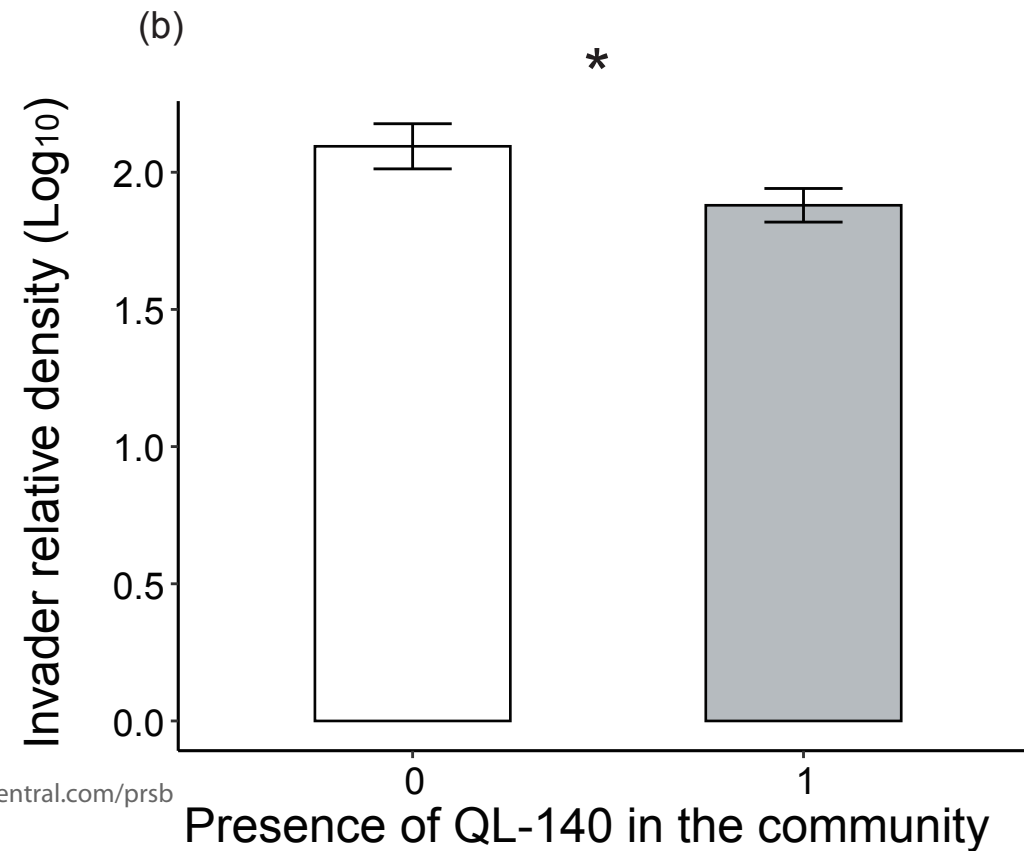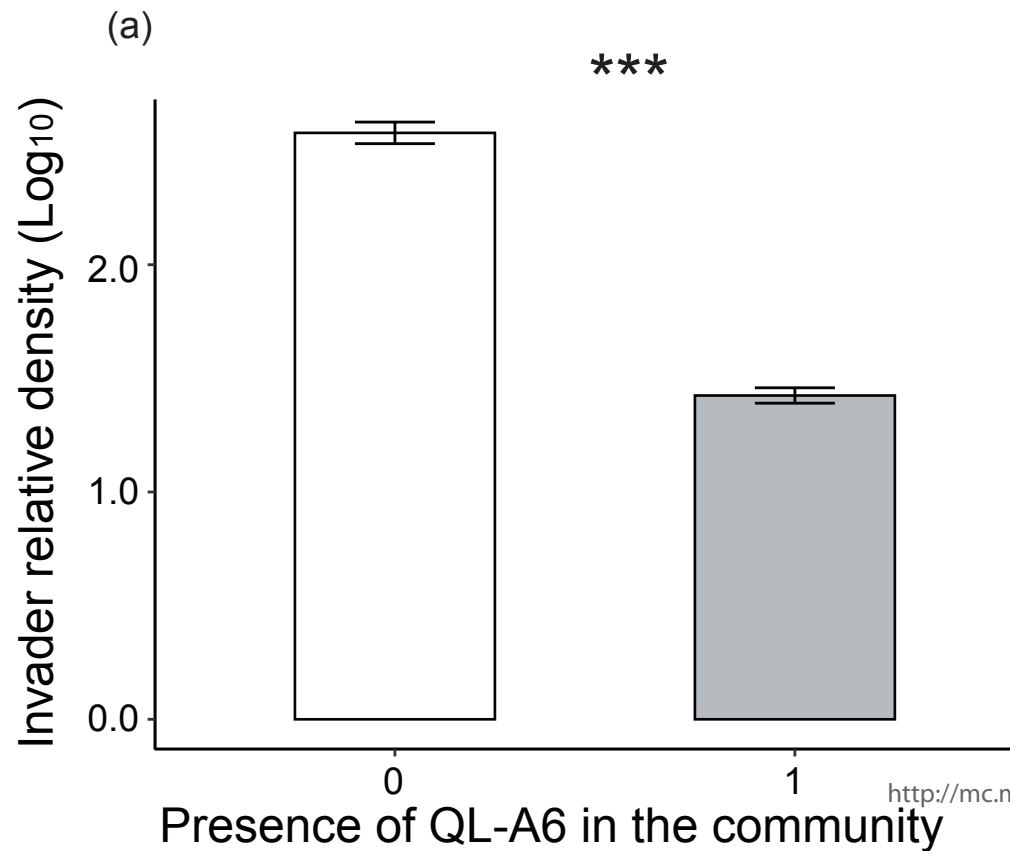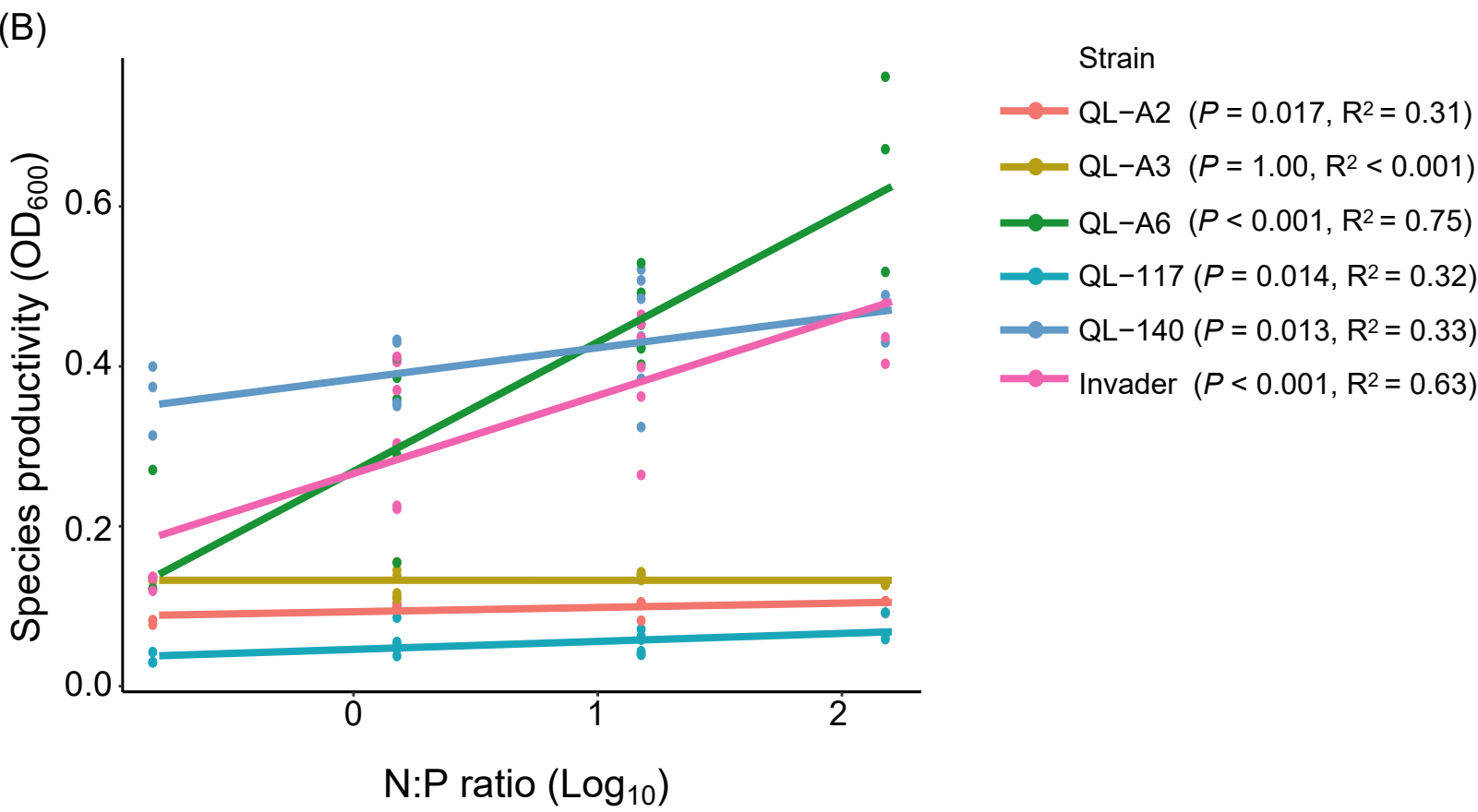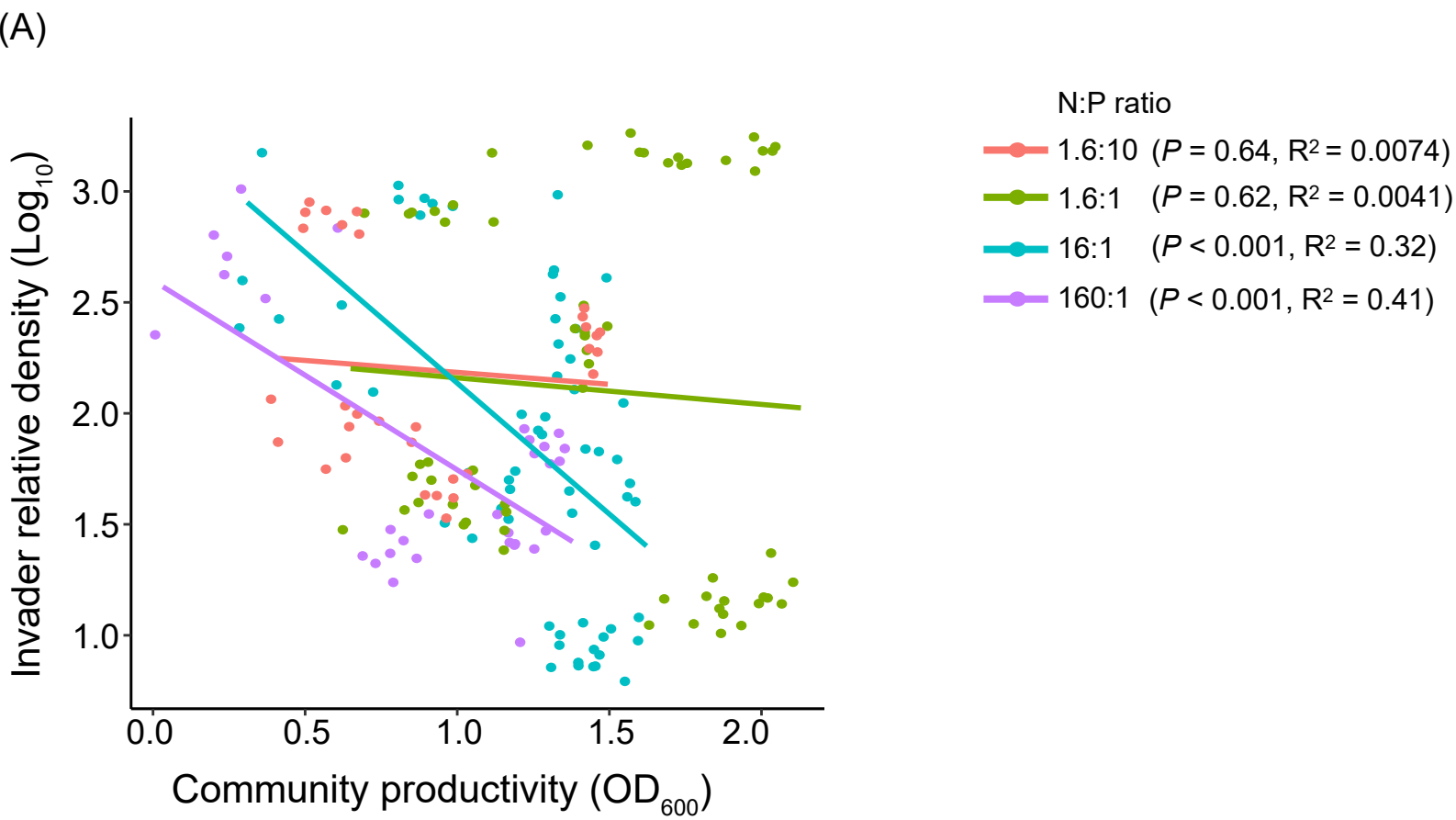
(a)

(b)

(A)

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X^2 = 2.221, *P*-value = 0.994, Df = 10, n = 186

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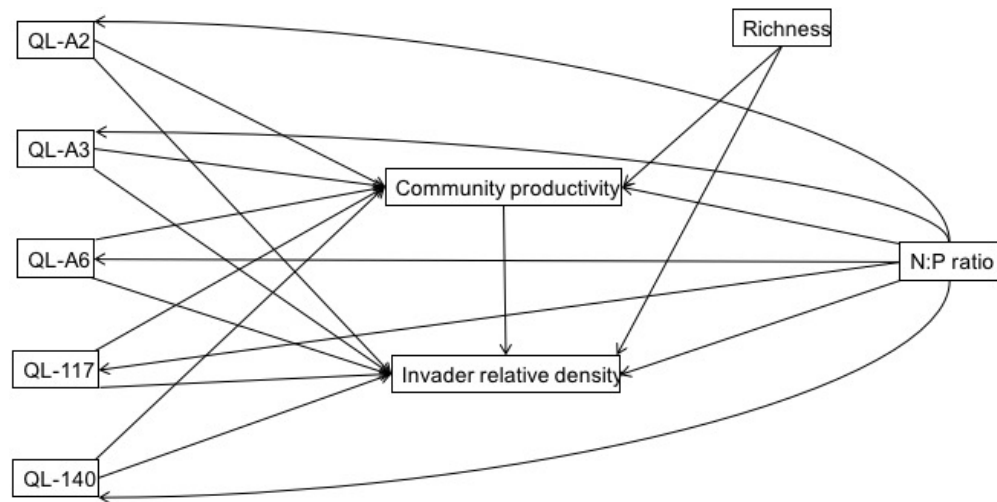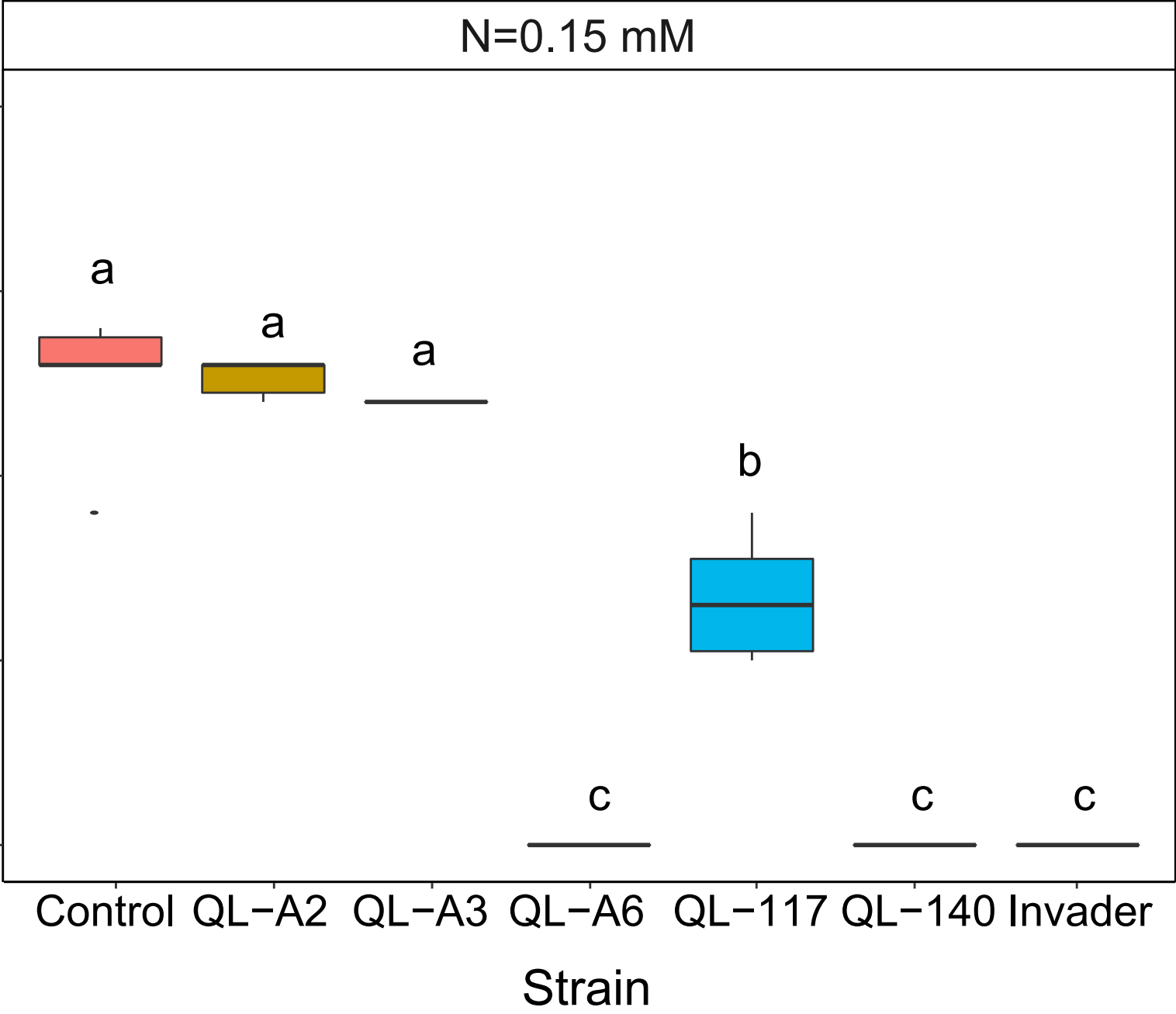
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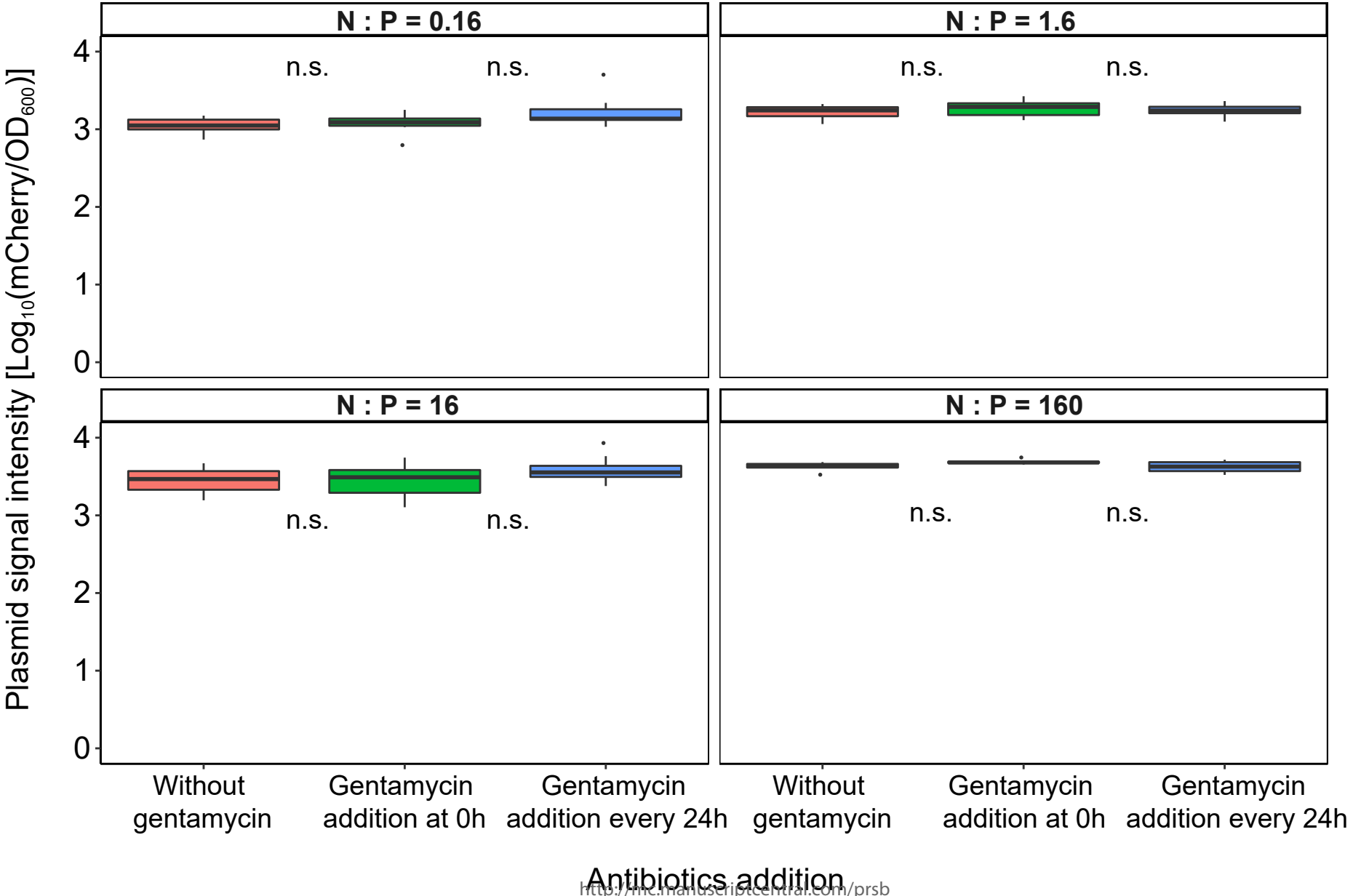
Figure S2. A priori structural equation models including species identity, N:P ratio, community productivity and the relative density of the invader.
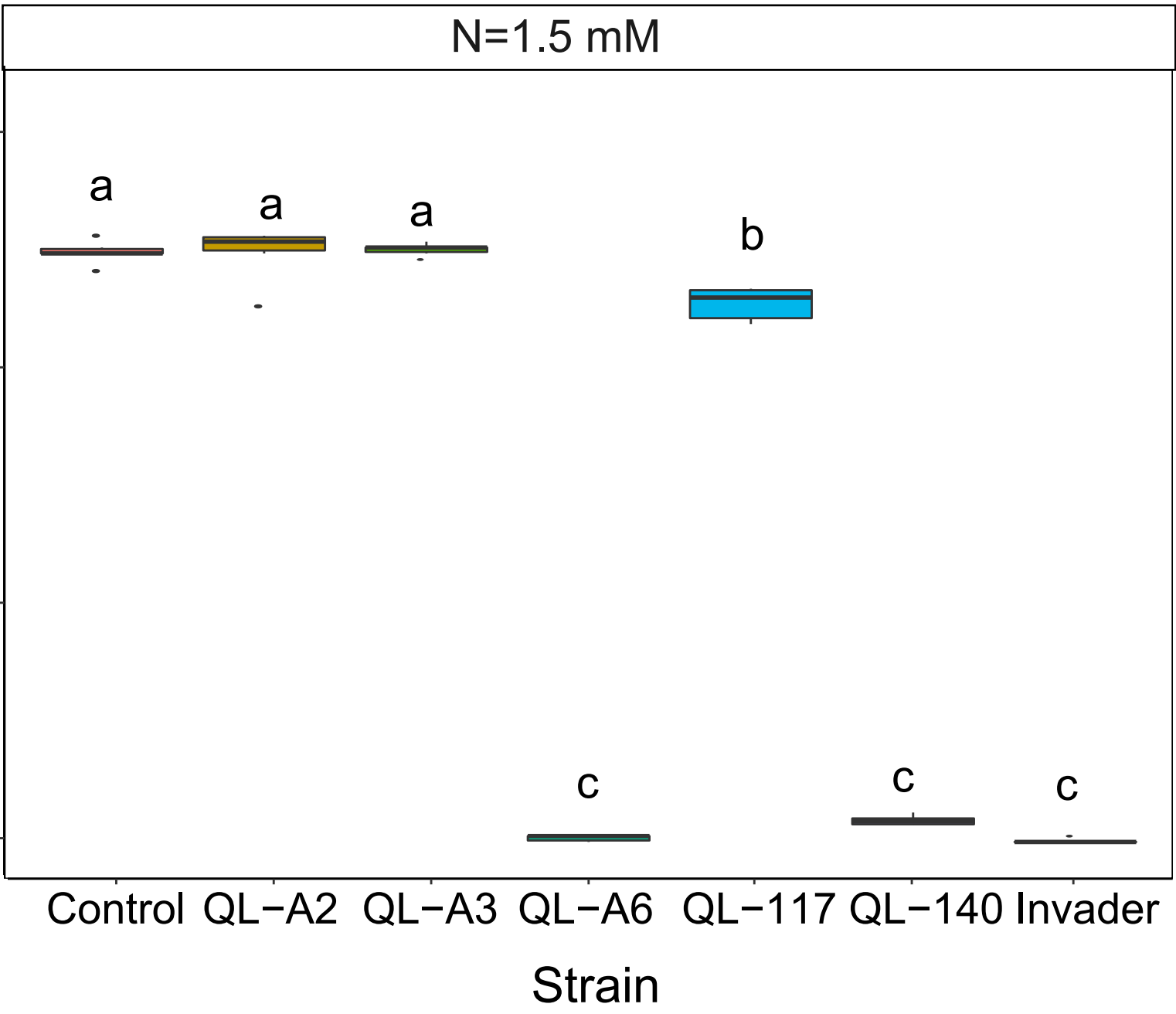
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