

Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities

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Decreasing species diversity is thought to both reduce community productivity and increase invasibility to other species. However, it remains unclear whether identical mechanisms drive both diversity–productivity and diversity–invasibility relationships. We found a positive diversity–productivity relationship and negative diversity–invasibility and productivity–invasibility relationships using microcosm communities constructed from spatial niche specialist genotypes of the bacterium *Pseudomonas fluorescens*. The primary mechanism driving these relationships was a dominance (or selection) effect: more diverse communities were more likely to contain the most productive and least invulnerable type. Statistical elimination of the dominance effect greatly weakened the diversity–invasibility relationship and eliminated the diversity–productivity relationship, but also revealed the operation of additional mechanisms (niche complementarity, positive and negative interactions) for particular combinations of niche specialists. However, these mechanisms differed for invasibility and productivity responses, resulting in the invasibility–productivity relationship changing from strongly negative to weakly positive. In the absence of the dominance effect, which may be an experimental artefact, decreasing diversity can have unexpected or no effects on ecosystem properties.

Keywords: bacteria; diversity; ecosystem function; invasibility; microcosm; productivity

1. INTRODUCTION

It has long been suggested that species diversity plays a critical role in ecosystem function (Darwin 1872; Elton 1958). Community construction experiments using plants, microbes and marine invertebrates provide support for this supposition, often demonstrating that more diverse communities are both more productive (Bell 1991; Tilman *et al.* 1997; van der Heijden *et al.* 1998; Hector *et al.* 1999; Cardinale *et al.* 2002) and more resistant to invasion by other species (McGrady-Steed *et al.* 1997; Stachowicz *et al.* 1999; Levine 2000; Hector *et al.* 2001). Three mechanisms have been invoked to explain the positive effect of diversity on productivity and the negative effect of diversity on invasibility in the absence of extrinsic covarying factors, such as disturbance, that may affect ecosystem functioning (Levine & D'Antonio 1999; Loreau & Hector 2001). First, more diverse communities will have a greater probability of containing particular species that contribute disproportionately to community invasibility or productivity (dominance or selection effect). Second, more diverse communities will occupy more niches and monopolize more resources. Such niche complementarity will exclude most invading species and optimize the use of a varied resource base. Third, particular species may facilitate each other's growth or invasion resistance (positive interactions).

Distinguishing between these mechanisms has been the focus of much recent research. A number of studies have successfully disentangled the dominance effect, sometimes

considered to be a statistical artefact rather than of biological significance (Aarssen 1997; Huston 1997; Huston *et al.* 2000), from the other two mechanisms (e.g. Stachowicz *et al.* 1999; Loreau & Hector 2001). Recent empirical work has also identified the significant role of positive interactions in shaping diversity–productivity relationships (Mulder *et al.* 2001; Cardinale *et al.* 2002). These data indicate that all three mechanisms can play a role in shaping experimental diversity–ecosystem function relationships.

Given that productivity and resistance to invasion can both increase with increasing species diversity, a key question remains: are they increased by identical mechanisms? Mechanistic links between ecosystem functions would greatly simplify general predictions of community responses to changes in diversity. However, any correlation between productivity and invasibility across a diversity gradient need not be causal. For example, an increase in productivity shaped by positive interactions may accompany an increased resistance to invasion caused by a dominance effect. Also possible would be an increase in productivity and a decrease in resistance to invasion caused by the addition of a particular species, despite an overall positive correlation between the two ecosystem functions. In this study we aimed to explicitly determine the role of all three mechanisms in shaping the relationships between diversity and productivity and invasibility, using experimental bacterial communities.

Microcosms of the common plant-colonizing bacterium *Pseudomonas fluorescens* (Rainey & Travisano 1998) are a useful system to study the effects of diversity on ecosystem function. When propagated in spatially heterogeneous environments (a static glass microcosm containing nutrient-rich medium), *P. fluorescens* populations rapidly diver-

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sify, generating numerous niche specialist genotypes that are readily distinguished by their heritable colony morphologies on agar plates. The genotypes can be grouped into three distinct classes, or functional groups, based on colony morphology and resource use. Smooth (SM) morphs resemble the ancestral genotype and inhabit the liquid phase; wrinkly-spreading (WS) morphs form a biofilm at the air–broth interface, and less common fuzzy-spreader (FS) morphs colonize the bottom of the vials (Rainey & Travisano 1998). It is therefore possible to create communities that vary in both genotypic diversity and clearly defined functional group diversity, and determine their productivity and invasibility. Furthermore, the precise control over both environment and genetics and the ease of replication make this system well suited to identify mechanisms driving any observed relationships.

It is necessary to justify our use of asexual genotypes, rather than species, to create diversity gradients in this study. The proposed mechanisms linking reduced species diversity to reduced productivity and increased invasibility rely on variation in resource use within the community (more than one functional group) as well as variation within functional groups (Loreau 2000). As this variation exists between genotypes in this system (variation within and between spatial niche specialists), the same mechanisms linking species diversity to ecosystem function can theoretically operate to link genotypic diversity with population productivity and invasibility. Indeed, experimental demonstration of the mechanisms linking diversity to productivity and invasibility at the genotypic level would lend considerable weight to the generality of these mechanisms.

2. MATERIAL AND METHODS

(a) *Isolation of genotypes and community assembly*

Six populations of *P. fluorescens* strain SBW25 (wild-type) and 18 populations of SBW25 *panB*, a mutant strain that requires an exogenous source of pantothenic acid (Rainey 1999), were cultured in a static incubator at 28 °C in 25 ml glass universals with loose plastic lids, containing 6 ml of King’s Medium B (KB) supplemented with 0.0024% pantothenic acid to negate any fitness cost of the *panB* mutation (Rainey & Travisano 1998; Buckling *et al.* 2000). Wild-type and *panB* strains can be distinguished on selective media, allowing precise invasion assays. After 4 days, cultures were plated onto KB agar, and a single colony was isolated from each plate after 2 days’ growth at 28 °C. We obtained six *panB* and two wild-type SM, WS and FS genotypes. Correspondence between colony morphology and niche occupation was confirmed by inoculating half the colony into static microcosms and observing whether bacteria colonized predominantly the broth phase (SM), air–broth interface (WS) or the bottom (FS) of a static microcosm after 24 hours’ growth. High density populations of these genotypes were produced by 18 hours’ propagation at 28 °C in a 400 r.p.m. orbital shaker, and frozen at –80 °C in cryotubes in 20% glycerol/80% KB.

We used the *panB* genotypes to construct mixtures that varied in genotypic diversity (two, three and six genotypes) and functional group diversity (one to three). Each combination of genotypic and functional group diversity was replicated to the extent that, within each combination, all communities were independent and all genotypes were equally represented, resulting in a total of 45 mixtures (table 1). All 18 genotypes were also

Table 1. Details of constructed mixtures and their genotypic and functional group diversities. The 18 monocultures are not shown.
(s, smooth; f, fuzzy spreader; w, wrinkly spreader.)

| community | genotypic diversity | functional group diversity |
|--------------|---------------------|----------------------------|
| s1s6 | 2 | 1 |
| s2s4 | 2 | 1 |
| s5s3 | 2 | 1 |
| f3f5 | 2 | 1 |
| f1f2 | 2 | 1 |
| f4f6 | 2 | 1 |
| w3w6 | 2 | 1 |
| w5w4 | 2 | 1 |
| w1w2 | 2 | 1 |
| s6w4 | 2 | 2 |
| s4w2 | 2 | 2 |
| w6f5 | 2 | 2 |
| w5f4 | 2 | 2 |
| s3f1 | 2 | 2 |
| s1f2 | 2 | 2 |
| s2w1 | 2 | 2 |
| s5f3 | 2 | 2 |
| f6w3 | 2 | 1 |
| s5s3s1 | 3 | 1 |
| s2s6s4 | 3 | 1 |
| w1w2w3 | 3 | 1 |
| w4w5w6 | 3 | 1 |
| f3f4f6 | 3 | 1 |
| f1f2f5 | 3 | 1 |
| s1s6w1 | 3 | 2 |
| s4s5f1 | 3 | 2 |
| w2w3f3 | 3 | 2 |
| w4w5s3 | 3 | 2 |
| f4f5s2 | 3 | 2 |
| f2f6w6 | 3 | 2 |
| s2f3w5 | 3 | 3 |
| s4f2w4 | 3 | 3 |
| s3f6w6 | 3 | 3 |
| s5f4w2 | 3 | 3 |
| s6f5w3 | 3 | 3 |
| s1f1w1 | 3 | 3 |
| s1s2s3s4s5s6 | 6 | 1 |
| w1w2w3w4w5w6 | 6 | 1 |
| f1f2f3f4f5f6 | 6 | 1 |
| s2s3s6w1w5w6 | 6 | 2 |
| w2w3w4f3f4f5 | 6 | 2 |
| s1s4s5f1f2f6 | 6 | 2 |
| s1s6f1f4w4w5 | 6 | 3 |
| s3s5f2f6w1w3 | 6 | 3 |
| s2s4f3f5w2w6 | 6 | 3 |

established as monocultures. Genotypes were grown for 18 hours as above and inoculated into 6 ml of KB at equal densities within microcosms, with total mixture density 100-fold less than the maximum afforded by the microcosms.

(b) *Measurement of productivity and invasibility*

Productivity was defined as mean bacterial cell density of three replicates after 2 days’ growth in KB media; long enough for maximal density to be reached. Density was determined by counting the number of colony forming units (CFUs) per unit volume after 2 days’ growth on KB agar. Relative frequencies of different functional groups were also determined. Cell den-

sity, not biomass, was employed as a measure of productivity because it allowed a direct comparison with invasibility, which could only be measured in terms of cell density. Furthermore, there are no detectable differences in cell size between representative SM, WS and FS genotypes using electron microscopy (Kahn 1998; Spiers *et al.* 2002).

Invasibility was measured as the average ability of the six wild-type genotypes (two each of SM, WS and FS) to independently invade each *PanB* mixture when the invading genotype was initially at a 100-fold lower frequency (Crawley 1987). Note that we use a general definition of invasibility, the average ability of non-resident 'species' to invade the community, rather than the traditional ecological meaning of the ability of foreign species to invade. The theory linking diversity to both definitions of invasibility is identical (e.g. Case 1990; Law & Morton 1996), but our methodology aided the identification of the mechanisms behind diversity–invasibility relationships. Invading genotypes were simultaneously inoculated with the residents, but at 100-fold lower density. Simultaneous inoculation of residents and invaders was necessary to prevent disturbance of the microcosms during the growth phase, and to allow quantifiable levels of invasion before growth rates slowed at the microcosm's carrying capacity. Immediately prior to inoculation, and 2 days later when maximal density had been reached, cell densities of the invading genotype, the resident genotype(s), and the different morphotypes within the resident mixture, were determined by counting at least 2000 CFUs after 2 days' growth on vitamin-free casein agar (Proteose peptone No. 3 substituted with vitamin-free acid-hydrolysed casein in standard KB) supplemented with $4.8 \times 10^{-6}\%$ pantothenic acid (Buckling *et al.* 2000). On this medium the *panB* resident genotypes were readily distinguished from the invading wild-type genotypes by their greatly reduced colony size. Relative fitness of the invading genotype was calculated from the ratio of the estimated Malthusian parameters (m) of the invading-to-resident genotypes, $m = \ln(N_f/N_0)$, where N_0 is the starting density and N_f the final density (Lenski *et al.* 1991).

(c) Statistical analyses

All data were analysed as generalized linear models using GLIM v. 4 (Crawley 1993). Log (productivity) and invasibility were regressed onto genotypic diversity and functional diversity, and the correlation between productivity and invasibility determined. To determine if mechanisms above and beyond the dominance effect were driving diversity–productivity relationships, we calculated the standard 'overyielding' measure, $D_{\max} = (O_T - \max(M_i))/\max(M_i)$, where O_T is total observed mixture productivity and $\max(M_i)$ is productivity of the genotype within the mixture that showed the greatest productivity in monoculture (Loreau 1998). Values greater than zero unambiguously demonstrate that dominance effects alone are insufficient to explain a positive effect of diversity on productivity. The same D_{\max} measure was used to determine 'overresistance' for invasibility data, replacing productivity with invasibility, with the dominance effect insufficient to explain a negative effect of diversity on invasibility if D_{\max} values were less than zero. Note that this method is likely to overestimate the importance of the dominance effect; it is possible, for example, that niche complementarity may be operating even if mixture productivity is not greater than that of the most productive monoculture (Loreau & Hector 2001). Furthermore, complementarity effects may be cancelled out by inhibitory effects. More sophisticated and less conservative methods for partitioning dominance effects from

the other mechanisms have recently been developed for productivity data (Loreau & Hector 2001). However, such partitioning is not possible for invasibility data.

These D_{\max} values were regressed onto genotypic and functional group diversity as above, to determine if relationships existed between diversity and productivity and diversity and invasibility, in the absence of the dominance effect. We next determined if particular functional group combinations were consistently overyielding or overresistant. Significance testing of D_{\max} values for particular functional group combinations was carried out using one-tailed one-sample *t*-tests (against zero), corrected, where appropriate, for carrying out multiple tests on the different functional group combinations using the sequential Bonferroni test (Rice 1989).

We next attempted to disentangle niche complementarity from positive interactions in overyielding and overresistant mixtures. Distinguishing between these mechanisms is extremely difficult, as the operation of one mechanism does not exclude the other. Here, we identified the operation of positive interactions by considering situations where niche complementarity alone could not explain the data. In the light of this, we define the two mechanisms as follows. In positively interacting communities, at least one community member contributes more to productivity or invasibility than when in monoculture. Where niche complementarity occurs no community member exceeds its performance in monoculture. We calculated the difference between the density of a particular functional group in the presence of other functional groups, and as a monoculture. If this difference was greater than zero, this unambiguously demonstrated positive interactions; if not, niche complementarity was deemed to operate. To identify the mechanism of overresistance, we considered resistance to invasion by individual functional groups, rather than by the 'average' of all three functional groups. We determined the difference between each functional group's ability to invade a functionally diverse mixture, and its ability to invade monocultures of the least invulnerable member of the mixture. If this value was significantly less than zero for any of the three invading functional groups, positive interactions were contributing to the overresistance of the mixture. If not, overresistance was caused by niche complementarity.

It is also possible that organisms can interact negatively. To identify negative interactions, we calculated the expected productivity and invasibility of diverse mixtures from the averages of the contributing genotypes when in monoculture, weighted by their final proportions in the mixture. If mixture values were significantly less than this expected value, particular functional group combinations must be inhibiting the productivity or increasing the invasibility of the mixture.

3. RESULTS

Consistent with most previous controlled studies of species diversity, productivity increased ($F_{1,61} = 4.05$, $p < 0.05$) and invasibility decreased ($F_{1,61} = 4.92$, $p < 0.05$) with increasing genotypic diversity. These relationships were explained by the increase in functional group diversity that accompanied increasing genotypic diversity ($p > 0.4$ for the effect of genotypic diversity within functional diversity on both productivity and invasibility). Thus, productivity increased ($F_{1,60} = 6.35$, $p = 0.01$) and invasibility decreased ($F_{1,60} = 15.5$, $p < 0.001$) with increasing functional group diversity (figure 1).

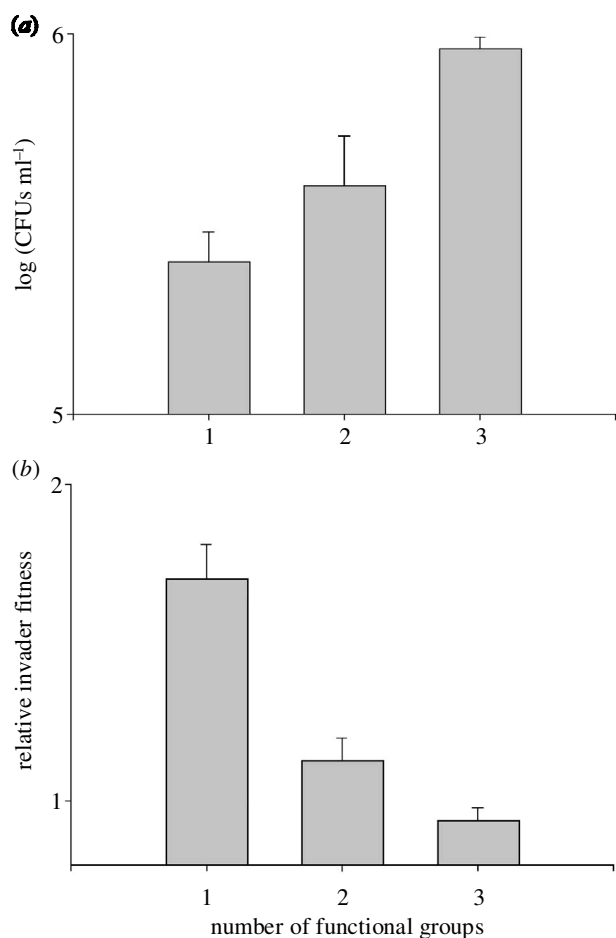


Figure 1. Relationships between number of functional groups present in a community and (a) mean (+1 s.e.m.) productivity (log (CFUs ml⁻¹)) and (b) mean (+1 s.e.m.) relative fitness of invading genotypes.

We next addressed the importance of dominance effects in determining the relationships between functional group diversity and productivity and invasibility. Replacing the raw productivity/invasibility data with D_{\max} caused the effect of functional diversity to become non-significant for both productivity ($F_{1,43} = 0.85$, $p > 0.1$) and invasibility ($F_{1,43} = 3.00$, $p = 0.09$). Visual inspection indicated that mixtures containing WS were more productive and less invulnerable (figure 2). This was confirmed by fitting the presence or absence of WS as a binary factor to the original data, which explained 62% of the total productivity deviance ($F_{1,60} = 72.92$, $p < 0.001$) and 69% of the total invasibility deviance ($F_{1,60} = 92.4$, $p < 0.001$). Observed relationships between functional diversity, productivity and invasibility were largely because diverse mixtures were more likely to contain WS.

These results do not exclude the operation of other mechanisms: niche complementarity and positive interactions may operate for particular functional group combinations. From our analysis, we found WS–FS and WS–FS–SM combinations were significantly more productive than the most productive genotypes in monoculture ($t = 3.33$, d.f. = 5, $p = 0.01$; and $t = 3.01$, d.f. = 8, $p = 0.03$ respectively; figure 3a). Positive interactions explained the overyielding of WS–FS combinations: WS gained higher densities in the presence of FS than in isolation ($t = 3.3$, d.f. = 5, $p = 0.04$), indicating that FS somehow facilitated

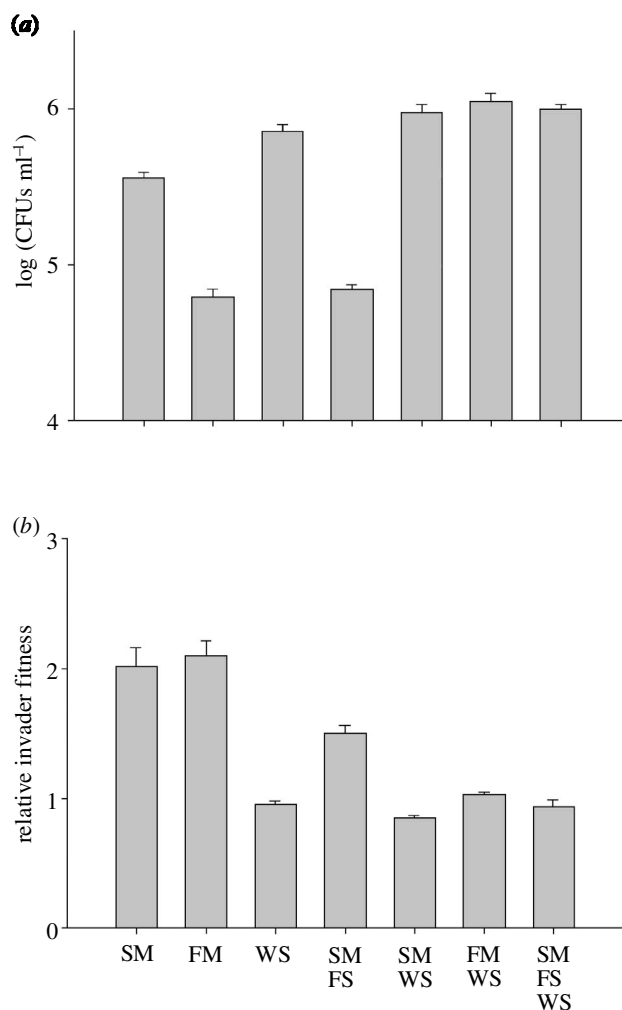


Figure 2. (a) Mean (+1 s.e.m.) productivity (log (CFUs ml⁻¹)) and (b) mean (+1 s.e.m.) relative fitness of invading genotypes; for functional groups and functional group combinations.

the growth of WS. No such enhancement of growth occurred for either WS, SM or FS in SM–WS–FS combinations ($p > 0.1$ in all cases): niche complementarity caused overyielding in these mixtures.

The only overresistant mixtures were SM–FS combinations ($t = 3.06$, d.f. = 5, $p = 0.05$; figure 3b), and this was the result of niche complementarity. Although SM–FS combinations were overall more resistant to invading genotypes than the least invulnerable SM and FS monocultures, they were not more resistant than SM monocultures to SM or WS invaders or FS monocultures to FS invaders ($p > 0.4$ in all cases). There was therefore no evidence for positive interactions. Overresistance was simply caused by resident SM preventing other SM genotypes invading, and FS preventing invasion by other FS.

We found no evidence of negative interactions affecting invasibility. However, SM–FS combinations were significantly less productive than predicted by their average monoculture performance, weighted by their final proportion in the mixture ($t = 10.39$, d.f. = 5, $p < 0.001$), demonstrating a negative interaction. This was the result of FS inhibiting SM (SM densities were significantly less than expected from their monoculture yields, weighted by

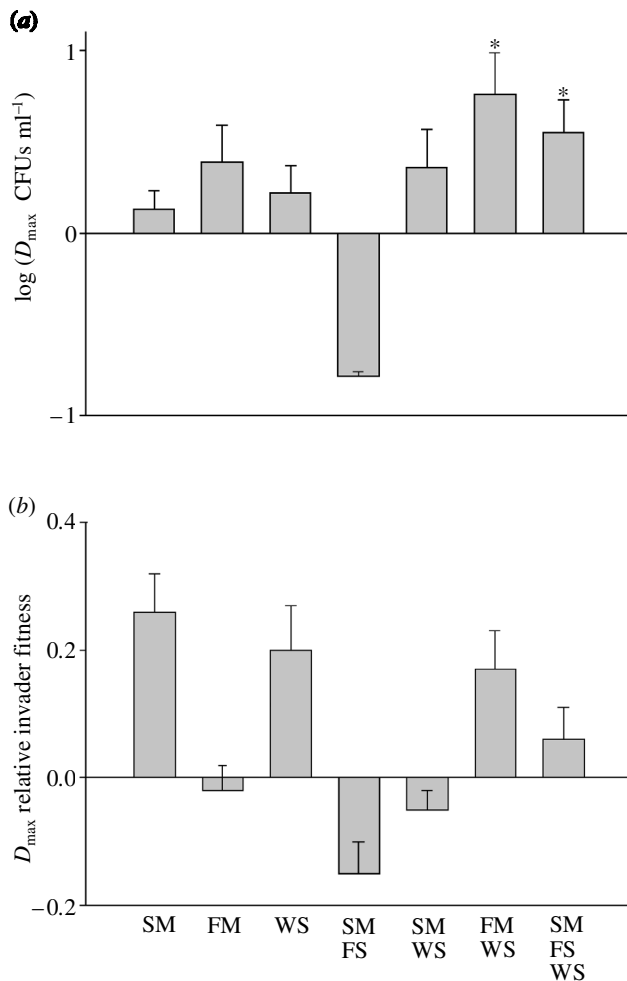


Figure 3. (a) Mean (± 1 s.e.m.) D_{\max} productivity (log CFUs ml⁻¹) and (b) mean (± 1 s.e.m.) D_{\max} relative fitness of invading genotypes; for functional groups and functional group combinations. Monoculture data are by definition excluded. Asterisks indicate D_{\max} values significantly greater (a) or less (b) than zero.

their final proportion in the mixture proportion: $t = 11.76$, d.f. = 5, $p < 0.001$), but not vice versa ($p > 0.1$ for FS).

Analysis of the raw data revealed a highly significant negative correlation between the productivity and invasibility of mixtures of genotypes: the most productive mixtures tended to be the least invulnerable ($r_s = -0.7$, $n = 63$, $p < 0.001$; figure 4a). However, this correlation was due to the dominance effect of WS. When the dominance effect was controlled for by using D_{\max} values of productivity and invasibility, the relationship became weakly but significantly positive ($r_s = 0.361$, $n = 45$, $p = 0.015$; figure 4b). This positive relationship was largely due to SM-FS combinations showing niche complementarity for invasibility and negative interactions for productivity.

4. DISCUSSION

In this study we aimed to investigate the mechanisms driving a concomitant increase in productivity and decrease in invasibility with increasing diversity of bacterial mixtures. Despite the apparent ecological simplicity of bacterial microcosms, we found evidence for strong dominance effects, niche complementarity and both posi-

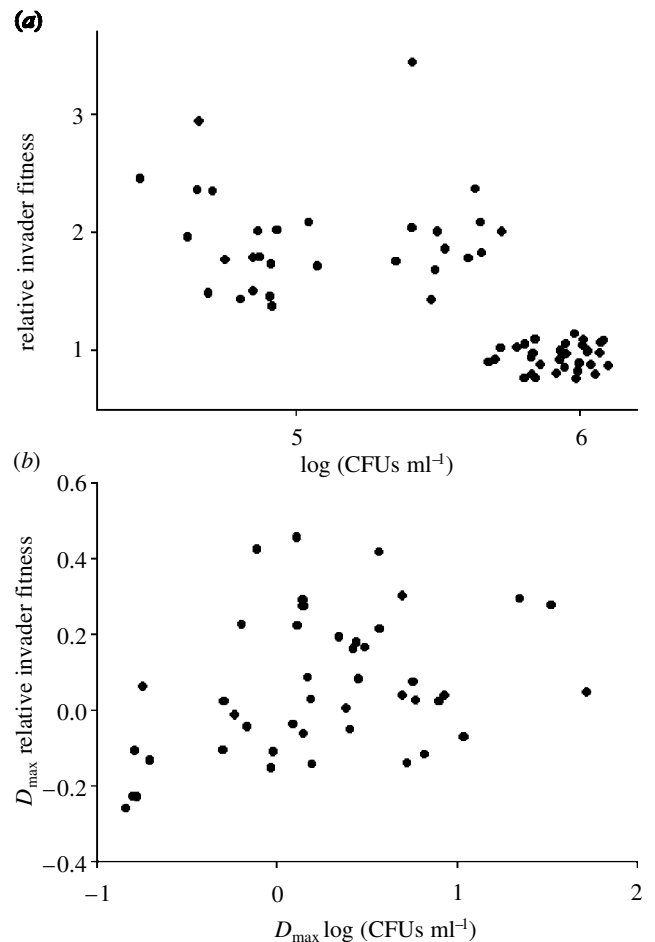


Figure 4. Relationships between: (a) productivity (log CFUs ml⁻¹) and relative fitness of invading genotypes and (b) D_{\max} productivity (log CFUs ml⁻¹) and D_{\max} relative fitness of invading genotypes.

tive and negative interactions. All these mechanisms are likely to operate in natural communities. The relationships between diversity and productivity and diversity and invasibility were driven by functional group diversity rather than genotypic diversity. This supports the prediction that interactions are more likely to occur with increasing ecological variation within a community (Loreau 2000). A similar result was obtained with microcosms of unicellular algae (*Chlamydomonas* spp.), where interactions in diverse microcosm communities were more apparent in mixed species communities compared with mixed genotype (within-species) communities (Bell 1990, 1991).

The dominance effect was the main mechanism driving relationships between diversity and both productivity and invasibility. After controlling for the dominance effect, there was no relationship between diversity and productivity, and only a weak relationship between diversity and invasibility. The dominance effect operated at the level of functional groups rather than genotypes: the presence or absence of WS genotypes was the best predictor of both productivity and invasibility (figure 2). The dominance of the WS genotype is probably attributable to its ability to colonize the air-broth interface, where it monopolizes both nutrients and oxygen (Rainey & Travisano 1998). Pumping oxygen into the broth phase of the microcosm would help to elucidate this mechanism.

Controlling for the dominance effect resulted in the negative relationship between productivity and invasibility to become positive, but only weakly so (figure 4). We conclude that the same mechanism, the dominance effect of WS, is largely responsible for both the increased productivity and decreased invasibility of diverse mixtures. However, it has been strongly argued that the dominance effect is a statistical artefact of assembling random communities, and will have less impact on the productivity and invasibility of natural communities (Aarssen 1997; Huston 1997; Huston *et al.* 2000). We therefore determined the relative influence of other mechanisms in shaping the remaining weak relationship between productivity and invasibility.

We identified three out of four functional group combinations that differed in productivity from expectations based on monoculture results (figure 3). The first, a positive interaction between FS and WS, caused an increased WS yield but no change in FS. We propose that the presence of FS in the harsher, oxygen-depleted conditions of the microcosm floor may release extra nutrients (via cell movement or metabolism) that directly benefit WS growth. Second, SM, FS and WS combinations produced higher total yields than expected. Based on our definitions, this was due to niche complementarity, although we cannot completely exclude the potential influence of positive interactions. Third, negative interactions between SM and FS resulted in reduced mixture yields when they were combined. This negative effect was manifested as a repression of SM growth in the presence of FS; presumably FS produces a metabolite that inhibits SM growth. We were surprised not to observe niche complementarity between SM and WS, given their clear spatial niche separation. This indicates that the occupation of distinct niches is not sufficient to produce a net niche complementarity effect. In our system, we suggest that spatial niche occupation does not affect the division of media nutrients, or that antagonistic interactions between SM and WS balance any benefits of niche partitioning. In combination, these different mechanisms resulted in no net relationship between functional group diversity and productivity.

The mechanisms causing deviation from expected productivity in these three functional group combinations did not translate to changes in invasibility (figure 3). Niche complementarity caused a reduction in the invasibility of FS–SM combinations, simply because FS and SM prevented invasion by FS and SM, respectively. Neither positive nor negative interactions were identified as being important to invasibility. The decreased invasibility of FS–SM combinations was sufficient to produce an almost significant relationship between functional group diversity and invasibility.

Ignoring the strong influence of the dominance effect, our results have two important implications for the interrelationships between diversity and ecosystem functions. First, we demonstrate that different mechanisms may drive diversity–productivity and diversity–invasibility mechanisms. In other words, the consequences of particular genotype interactions differed for productivity and invasibility. Second, although certain genotypes (or species) combinations can interact positively in their contribution to ecosystem functions, others can interact negatively. The probable increase in frequency of both positive

and negative interactions with increasing diversity will complicate predictions of their influence on ecosystem function. Taken together, these results show that decreasing diversity may not adversely affect all ecosystem functions. This is consistent with recent work on plant communities that demonstrates that diversity can have a positive effect on productivity, but a negative effect on another ecosystem property: resistance to environmental perturbations (Pfisterer & Schmid 2002). The importance of diversity to ecosystem function in this and other studies largely hinges on the dominance effect (Huston *et al.* 2000; Wardle 2001). It is therefore critical to determine the importance of the dominance effect in natural populations and communities, which are clearly more complex than the microcosm communities used here.

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