

Niche dimensionality links biodiversity and invasibility of microbial communities

Nico Eisenhauer^{*,†,1,2}, Wiebke Schulz³, Stefan Scheu³ and Alexandre Jousset^{†,3}

¹Department of Ecology and Ecosystem Management Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354, Freising, Germany; ²Institute of Ecology, Friedrich Schiller University of Jena, Dornburger Str. 159, 07743 Jena, Germany; and ³J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Str. 28, 37073, Göttingen, Germany

Summary

1. Biodiversity is a central factor driving community invasibility. Diverse communities exploit resources more efficiently, leaving less free niche space available to invaders. Niche partitioning, however, is only possible in complex resource environments, and we hypothesized that resource richness drives the biodiversity–invasibility relationship.

2. We tested the effect of two biodiversity indices, taxonomic richness and functional dissimilarity, on the invasibility of *Pseudomonas fluorescens* communities in microcosms of varying resource richness, herein used as a proxy for niche dimensionality, because different *P. fluorescens* genotypes differed in their ability to use those resources.

3. Invader success was negatively correlated with the diversity of the resident community, with functional dissimilarity being of greater significance than taxonomic richness. Varied niche dimensionality revealed different mechanisms determining community invasibility: at low niche dimensionality, invasibility was driven by the presence of particular genotypes (identity effect) rather than by the biodiversity of the resident community. At high niche dimensionality, functional dissimilarity increased community productivity and reduced invasion, most likely through complementarity effects.

4. The results show that functionally dissimilar bacterial strains efficiently exploit their environment, reducing the resources available for invasive species. These findings call for the preservation of functionally dissimilar taxa to warrant resistance of communities against invasive species, in particular, in environments of high niche dimensionality.

Key-words: biodiversity–ecosystem functioning, biological invasion, complementarity effect, identity effect, niche preemption

Introduction

Human actions are causing species gains and losses with sometimes drastic effects on ecosystem functioning (Wardle *et al.* 2011). Biodiversity is widely recognized to influence the invasibility of natural communities (Kennedy *et al.* 2002; Fargione & Tilman 2005; Van Elsas *et al.* 2012), but the conclusions of former experiments are sometimes contradictory and disputed. [Correction added after online publication 23 Oct 2012: the following sentence has been altered.] On one hand, observational studies have reported increased success of invasive species in more diverse communities (Levine & D'Antonio 1999; Stohlgren *et al.* 1999; Cleland *et al.* 2004), but on the other, biodiver-

sity has been reported to reduce invasion success (Hector *et al.* 2001; Kennedy *et al.* 2002; Fargione & Tilman 2005), with contrasting results likely depending in part on the spatial scale (Fridley *et al.* 2007). Other findings may be unified by including niche dimensionality as a factor driving community invasibility (Moles *et al.* 2012). Environmental complexity, which may also reflect the number of niches available, is likely to be an important driver of biodiversity–ecosystem functioning relationships (Dimitrakopoulos & Schmid 2004; Jousset *et al.* 2011a).

A complex (or multidimensional) environment may reduce niche overlap between competitors and allow more native as well as exotic species to coexist. Thus, resource complexity, as a major factor determining niche dimensionality, has been shown to be a central factor linking community diversity and productivity (Langenheder *et al.* 2010), and may also drive invader success (Melbourne

*Correspondence author. E-mail: nico.eisenhauer@web.de

†Authors contributed equally to this work.

et al. 2007). Environmental complexity may favour positive interactions between coexisting taxa, increasing the performance (mostly measured as community productivity) of diverse communities (Jousset *et al.* 2011a). More species within a given community may also cause more effective niche preemption, the more complete use of resources in space and time by diverse communities, thereby reducing invasion success (Mwangi *et al.* 2007; Jousset *et al.* 2011b). Here, we use the term niche dimensionality to describe the number of resources being differentially used by different taxa within a community and which may therefore represent distinct niches.

Species within a community compete for resources and resident species which may also hinder invasive species from establishing, particularly functionally similar ones (Tilman 2004; Fargione & Tilman 2005; Violle *et al.* 2011). Consequently, invaders are more likely to successfully establish when the resident community offers vacant niches (Tilman 2004; Mwangi *et al.* 2007). In contrast, resident communities exploiting resources efficiently (Roscher *et al.* 2005; Fargione *et al.* 2007) will leave fewer vacant niches and reduce invader fitness (Fargione, Brown & Tilman 2003; Tilman 2004). Resource use patterns are driven not only by the number of taxa present in the community (taxonomic richness), but also by their ecological differentiation: two functionally similar taxa competing for the same niche will leave most other niches vacant, while a mixture of functionally differentiated taxa will occupy most of the niches. This mean niche differentiation between the members of a community can be described as the functional dissimilarity, the mean ecological distance between competitors (Heemsbergen *et al.* 2004; Jousset *et al.* 2011a, b; Violle *et al.* 2011).

In addition to complementarity effects of functionally dissimilar communities (Fargione & Tilman 2005; Jousset *et al.* 2011b), key species may also disproportionately contribute to invasion resistance (Hodgson, Rainey & Buckling 2002; Jiang, Brady & Tan 2011; Messmer *et al.* 2011) if they efficiently consume resources required by the invader. Such identity effects, however, are more likely to play a significant role at low niche dimensionality due to the stochastic match or mismatch of resource identity and species-specific resource requirements, whereas invasion at high niche dimensionality may rather be explained by complementarity effects (Jousset *et al.* 2011a) due to higher functional dissimilarity and resulting higher community resource use efficiency.

In this study, we used microbial microcosms to test if niche dimensionality (resource richness) mediates the relationship between biodiversity and invasibility. We grew defined resident *Pseudomonas fluorescens* communities of varying biodiversity (taxonomic richness and functional dissimilarity) in microcosms containing one to five carbon sources, representing environments of different niche dimensionality. Each resource can be considered as an environmental axis, and we define the niche of each species on the base of its usage of the different resources. All these

'resource axes' are orthogonal, so that the environment can be seen as an n-dimensional Euclidian space. These communities were subjected to invasion by the model invader *Pseudomonas putida*. We orthogonally crossed the diversity of the resident community with niche dimensionality to investigate interactive effects. We hypothesized that niche dimensionality drives the biodiversity–invasibility relationship. More specifically, we expected biodiversity of the resident community to reduce invader success at high niche dimensionality via complementary niche preemption (Fig. 1). At low niche dimensionality, in contrast, where complementary interactions are restricted, we expected invader success to be driven by identity effects, that is, by pairwise interactions between invaders and resident taxa (Fig. 1).

Materials and methods

NICHE DIMENSIONALITY AND BACTERIAL DIVERSITY

Resident bacterial communities were assembled from eight *P. fluorescens* strains CHA0, PF5, Q2-87, 1M1-96, MVP1-4, F113, Phl1C2 and Q8R1-96 [see Appendix S1, Supporting Information and the study by Jousset *et al.* (2011b) for more details]. We set up 21 different bacterial communities by randomly assembling

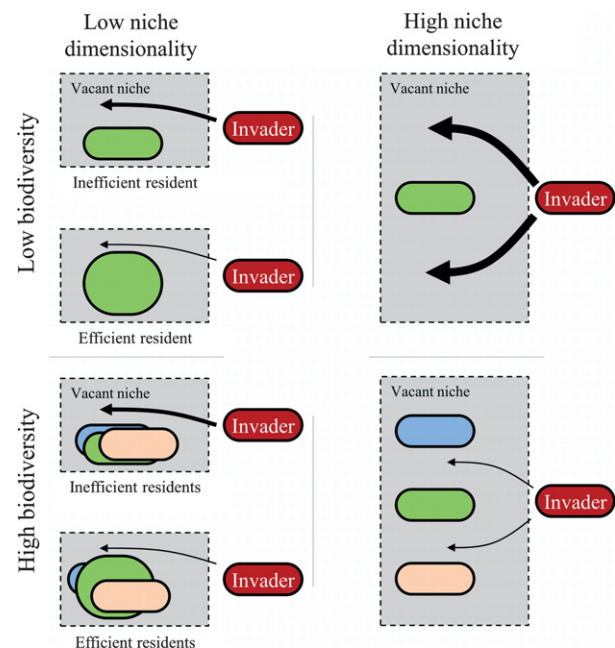


Fig. 1. Schematic representation of the hypotheses. At low niche dimensionality, as in the case of a degraded environment, the success of an invader is driven by identity effects: if resident species efficiently occupy the niche, small niche space will be available for the invader. Biodiversity will have few effects on invader success. At high niche dimensionality (complex or heterogeneous environment), low diverse communities will leave niche space free, and thereby be vulnerable to invasion. If resident species are complementary in their niche occupation, less niches will be vacant, limiting the success of invaders. The efficiency of single species may be less important at high niche dimensionality. Thickness of the arrows symbolises invader success.

these strains, establishing richness levels of one (all eight monocultures), two (eight communities), four (four communities) and eight genotypes (four replicates; 24 treatments; Appendix S2, Supporting Information). Each genotype was present in the same number of communities at each richness level. This bacterial diversity gradient allows testing general ecological questions, even if the bacterial diversity in natural systems may be higher, even at small spatial scales (Jessup, Forde & Bohannan 2005). We used *P. putida* IsoF as model invader (Schuhegger *et al.* 2006), chromosomally tagged with green fluorescent protein (GFP; Koch, Jensen & Nybroe 2001).

Bacteria were grown in a gradient of resource richness to modulate niche dimensionality. Microcosms contained 14 different combinations (16 treatments; Appendix S2, Supporting information) of glucose, mannose, fructose, sucrose and citrate, mixed to a total of one (all single carbon sources), two (four combinations), three (four combinations) and five carbon sources (three replicates). Total substrate concentration was always 5 g substrate L⁻¹. To keep bacterial diversity and resource richness orthogonal, each bacterial community was grown in each of the resource treatments (24 bacterial treatments × 16 resource treatments, that is a total of 384 combinations).

BIODIVERSITY INDICES

We used two indices for the biodiversity of the resident communities: taxonomic richness was defined as the number of genotypes present at the beginning of the experiment. Further, we estimated the functional dissimilarity of bacterial communities to account for niche differentiation among resident taxa (Cadotte *et al.* 2009; Jousset *et al.* 2011b). First, each genotype was grown in minimal medium supplemented by one of the used carbon sources (see below). Growth was recorded as the optical density (OD₆₀₀) of the culture after 24 h incubation at 26 °C. For each treatment, three replicates were set up. We used these data to compute pairwise Euclidian distances between all genotypes as follows:

$$D_{(x,y)} = \sqrt{\sum_{i=1}^5 (x_i - y_i)^2},$$

where, x_i and y_i are the OD₆₀₀ of the genotypes x and y on the substrate i . The functional dissimilarity of the community was then defined as the average pairwise distance between the genotypes present in the community (Walker, Kinzig & Langridge 1999).

CULTURE CONDITIONS

Bacteria were pregrown overnight in Lysogeny Broth (LB), pelleted by centrifugation (10 000 g, 1 min), washed twice in 0.85% NaCl and adjusted to an OD₆₀₀ of 0.5. Bacteria were grown at 25 °C in 384-well microtiter plates (Brand, Wertheim, Germany). Each well contained 40 µL OS minimal medium (Schnider-Keel *et al.* 2000) supplemented with one to five carbon sources at a total concentration of 5 g L⁻¹. We chose glucose, mannose, fructose, sucrose and citrate as carbon source because each of these sources supports the growth of at least one genotype and the invader. The total OD₆₀₀ was 0.05 in all treatments. Resident communities were then grown either alone or in the presence of the model invader *P. putida* (5% of total start biomass). Communities were grown for 24 h, a duration allowing all communities to reach the plateau phase under the tested conditions. We measured the optical density (OD₆₀₀, proxy for total community biomass) and the green fluorescence (Ex: 485 nm, Em: 520 nm, gain 80, as proxy for the biomass of the

GFP-tagged invader) in a M200 Plate reader (Tecan, Crailsheim, Germany). Invader success was estimated as the relative fluorescence (RFU, GFP/OD₆₀₀). The fluorescence signal was blanked on the basis of the background signal from the invader-free treatment, and pure cultures of GFP-tagged *P. fluorescens* IsoF were used to calibrate the RFU to biomass relationships.

Note that resident genotypes and the invader were inoculated simultaneously following the approach of Hodgson, Rainey & Buckling (2002) and Jousset *et al.* (2011b). As detailed above, the model invader was added at much lower density than the resident genotypes. We chose to use this approach because adding invaders at a later stage would have caused major disturbances of the microcosms which may have affected the growth phase of resident genotypes.

STATISTICAL ANALYSES

The data on community productivity and invasion success were log₁₀ transformed and analysed with sequential general linear models to test the effects of taxonomic richness and functional dissimilarity of the resident community, resource richness, the two-way interactions between bacterial diversity indices and resource richness, as well as bacterial composition and resource composition on the productivity and invasibility of bacterial communities. All factors and interactions were tested in one statistical model for each response variable. The sequential approach allows testing of correlated predictor variables, such as taxonomic richness and functional dissimilarity ($r = 0.60$, $P = 0.0024$), and avoids the overestimation of explained variance (Schmid *et al.* 2002), because the variance explained by a given factor fitted first is removed from the remaining analysis, and thus the test of factors fitted afterwards. To prevent the usage of pseudo-replicates, factors were tested against specific error terms (Table 1): main effects of bacterial biodiversity were tested against bacterial composition, resource richness against resource composition and interactions between bacterial biodiversity indices and resource richness against bacterial composition × resource composition (Schmid *et al.* 2002). Bacterial communities and resource treatments with identical compositions received the same consecutive number to statistically separate biodiversity from composition effects. In separate sequential analyses, we tested if taxonomic richness effects depend on functional dissimilarity (by fitting taxonomic richness after functional dissimilarity), that is, testing the richness effect while holding functional dissimilarity constant, and vice versa. If this approach renders the diversity index fitted second nonsignificant, most of the variance is explained by the first index. However, if the diversity index fitted second remains significant, the first index is a poor predictor of the second one. We also altered the sequence of bacterial composition and resource composition in separate models, but this did not change the results significantly.

In additional sequential analyses, we determined the significance of genotype identity effects by testing the significance of the presence of genotypes (1–8; either 0 = absent or 1 = present) in affecting community invasibility. Similarly, we tested the significance of resource identity effects in further analyses, which showed that resource richness effects were not only due to resource identity effects (i.e. resource richness remained significant when fitted after each of the resource types in sequential analyses).

We calculated the explanatory power of the presence of particular genotypes (identity effects) and of the functional dissimilarity by linear regression for each resource treatment. Explanatory power was defined as R^2 of the variable [SS (variable)/SS (total)] when fitted first. Linear regressions were used to investigate the relationship between community productivity and invasibility, as well as between resource richness and the explanatory power (R^2) of functional dissimilarity and the sum of genotype identity effects on community invasibility. In addition, we used linear regressions

Table 1. Effects of bacterial diversity of the resident community of *Pseudomonas fluorescens* and resource richness on community productivity and invasibility by the model invader *Pseudomonas putida*

Factor	Df	Error term	Productivity		Invasibility	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Taxonomic richness (TR)						
Fitted 1st	1,18	BC	4.08	0.0585	8.36	0.0097
Fitted 2nd	1,18	BC	0.08	0.7782	0.93	0.3476
Functional dissimilarity (FDissim)						
Fitted 1st	1,18	BC	14.02	0.0015	12.47	0.0024
Fitted 2nd		BC	10.03	0.0053	5.04	0.0376
Resource richness (RR)	1,14	RC	5.01	0.0420	2.19	0.1609
TR × RR	1,298	BC × RC	10.18	0.0016	6.48	0.0114
FDissim × RR	1,298	BC × RC	6.74	0.0099	8.43	0.0040
Bacterial composition (BC)	18,32	BC × RC	9.43	<0.0001	8.43	<0.0001
Resource composition (RC)	14,32	BC × RC	22.75	<0.0001	33.32	<0.0001
BC × RC	298,32	Residuals	8.85	<0.0001	14.80	<0.0001
Residuals	32					
Model	335		27.58	<0.0001	49.59	<0.0001

Significant ($P < 0.05$) bacterial diversity and resource richness effects are given in bold. Df, degrees of freedom.

to investigate the relationship between invasion success and the functional distance between the resident community and the invader in the different resource richness treatments. All analyses were performed using SAS 9.2 (SAS Institute, Cary, NC, USA). Although we were unable to mathematically differentiate selection from complementarity effects as proposed by Loreau & Hector (2001), we regarded functional dissimilarity effects as proxy for complementarity, and identity effects to indicate selection effects (Jousset *et al.* 2011a). Moreover, we regarded transgressive overyielding as indication of complementarity effects.

Results

COMMUNITY PRODUCTIVITY

The productivity of the resident community increased with resource richness and with increasing bacterial diversity (Table 1, Fig. 2). The biodiversity effect could be attributed to functional dissimilarity rather than to taxonomic

richness (Table 1). The impact of both taxonomic richness and functional dissimilarity increased with resource richness, that is, the slopes of the relationships between diversity indices and community productivity increased with increasing number of resources (Table 1, significant two-way interactions; Fig. 2). The effect of functional dissimilarity on community productivity remained significant when fitted after taxonomic richness, whereas the taxonomic richness effect was nonsignificant when fitted second (Table 1) indicating that biodiversity effects were mainly due to functional dissimilarity.

COMMUNITY INVASIBILITY

The success of *P. putida* was not significantly influenced by the main effect of resource richness (Table 1; but see significant interactions between resource richness and

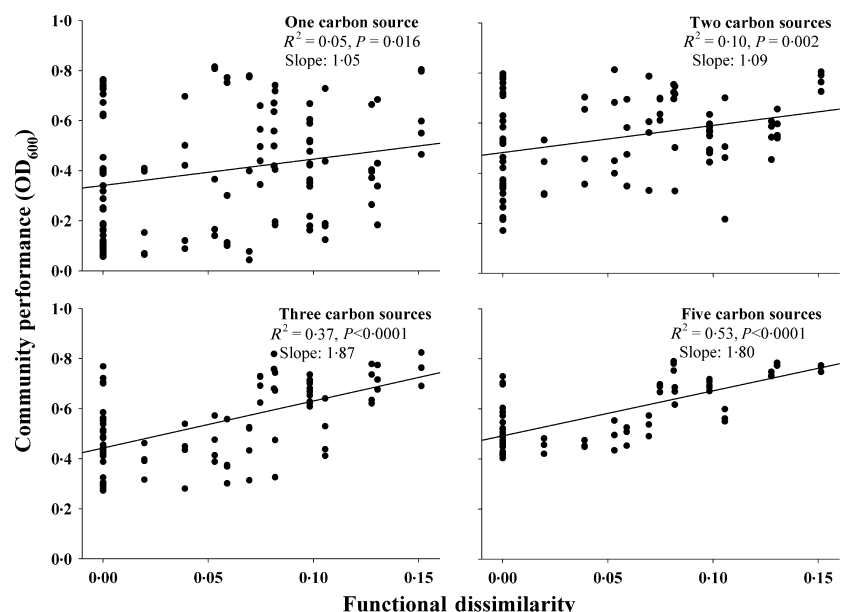


Fig. 2. Productivity (defined as the log-transformed density after 24 h) of resident *Pseudomonas fluorescens* communities as affected by functional dissimilarity of the resident bacterial community and resource richness (1, 2, 3 and 5 resource species).

diversity indices). Invader success decreased significantly with increasing taxonomic richness and functional dissimilarity. The effect of functional dissimilarity on community invasibility remained significant when fitted after taxonomic richness, whereas the taxonomic richness effect was nonsignificant when fitted second (Table 1), suggesting that the observed biodiversity effects were mainly due to functional dissimilarity of the resident community. Functional dissimilarity of the resident community did not significantly affect invasion at low resource richness (one and two carbon sources), but reduced invasion considerably at high resource richness (three and five carbon sources; Table 1, significant two-way interaction; Fig. 3).

Conversely, the mean functional mismatch between the resident community and the invader, that is, mean functional distance, influenced invader success significantly at low resource richness (one carbon source; $P < 0.05$), but not at higher resource richness (two, three and five carbon sources; all $P > 0.2$). Invader success was positively correlated with the functional distance to the resident community in the presence of one resource only ($r = 0.21$, $P = 0.049$), indicating that the presence of certain functionally similar taxa in the resident community in comparison with the invader was most influential at low environmental complexity.

Community productivity and invasibility were negatively correlated ($r = -0.28$, $P < 0.0001$). The predictive power of functional dissimilarity and taxonomic richness (the latter not shown) increased linearly with resource richness, whereas identity effects decreased (Fig. 4), confirming the hypothesis that complementarity effects need high niche dimensionality to play a significant role.

The presence of certain genotypes significantly decreased invasibility in most cases: CHA0 (−30%, $P < 0.001$), PF5 (−7%, $P = 0.36$), Q2-87 (−31%, $P < 0.001$), 1M1-96 (−17%, $P < 0.019$), MVP1-4 (−9%, $P = 0.26$), F113 (−28%, $P < 0.001$), Phl1C2 (−31%, $P < 0.001$) and

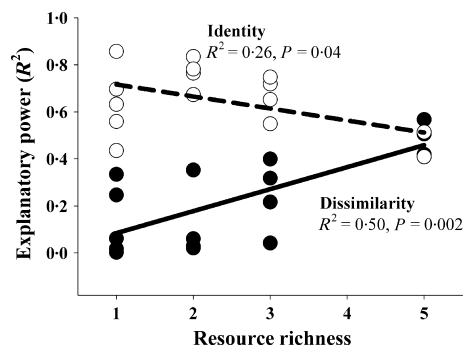


Fig. 4. Relationship between resource richness (1, 2, 3 and 5 resource species) and the explanatory power (R^2 value for parameter fitted first in a sequential GLM) of identity effects (open symbols, dashed regression line) and functional dissimilarity (closed symbols, plain regression line) on community invasibility.

Q8R1-96 (−26%, $P < 0.001$); however, fitting the presence of genotypes before functional dissimilarity did not render the effect of the latter nonsignificant (all $P < 0.05$), indicating that – in addition to identity effects – interactions between genotypes determined invasibility.

Discussion

We showed that niche dimensionality links community biodiversity and invasibility, most likely due to varying importance of complementarity effects at low (identity effects prevail) and high niche dimensionality (complementarity effects prevail). This notion is supported by inverse effects of bacterial diversity on community productivity, that is, positive effects of functional dissimilarity on community productivity were highest at high niche dimensionality.

At low niche dimensionality, functional dissimilarity, an index indicating complementarity effects (Heemsbergen et al. 2004; Jousset et al. 2011a), had little if any impact

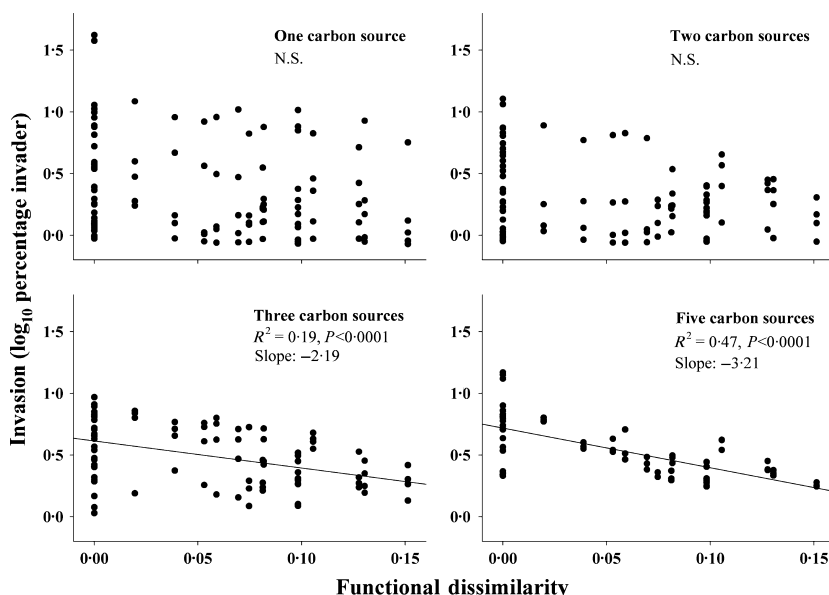


Fig. 3. Community invasibility (defined as the log-transformed relative abundance of the invader *Pseudomonas putida* after 24 h) as affected by functional dissimilarity of the resident bacterial community and resource richness (1, 2, 3 and 5 resource species).

on community productivity and invasibility. In contrast, genotype identity significantly affected invasibility, that is, invasion success depended on the presence of certain genotypes exploiting the same or a similar complement of resources as the invader (Fargione, Brown & Tilman 2003; Tilman 2004).

In contrast, at high niche dimensionality, biodiversity became a significant predictor of community invasibility. In parallel, niche dimensionality increased biodiversity effects on community productivity. The observed biodiversity effects likely are due to the functional dissimilarity of the resident community, indicating niche differentiation between bacterial strains (Walker, Kinzig & Langridge 1999; Jousset *et al.* 2011a). This suggests that niche preemption essentially determines the success of invaders (Fargione, Brown & Tilman 2003; Mwangi *et al.* 2007) with diverse communities covering more niches than simple ones (Fargione, Brown & Tilman 2003; Fargione & Tilman 2005). This is supported by significant functional dissimilarity effects on community productivity at high niche dimensionality, and, in contrast to the findings of Jiang & Morin (2004), a significant negative correlation between productivity and invasibility. Our results, moreover, suggest that the pronounced effect of functional dissimilarity on invasibility was not due to the systematic inclusion of one dominant genotype in the resident community, but due to resource use complementarity within functional dissimilar communities, because communities with the highest functional dissimilarity had lower invasion rates than the monoculture with the lowest invasibility (Fig. 3). Similarly, several mixed communities were more productive than the most productive monoculture, indicating transgressive overyielding of functionally dissimilar communities at high niche dimensionality (Fig. 2), which – in turn – may have caused invaders to show transgressive underyielding (Becker *et al.* 2012) at high functional dissimilarity (Fig. 3).

Biodiversity effects on productivity increase with environmental complexity (Griffin *et al.* 2009; Replansky & Bell 2009; Langenheder *et al.* 2010), and we demonstrated that niche dimensionality is a major link between biodiversity and invasibility. Environmental heterogeneity can determine biodiversity–invasibility relationships (Jiang & Morin 2004; Melbourne *et al.* 2007), and we showed that the number of resources available can play a similar role even in homogeneous microcosms. Our results allow for improved predictions of the consequences of biodiversity loss (Kennedy *et al.* 2002) and habitat degradation (Messmer *et al.* 2011) on invasion processes. At high niche dimensionality, high resident biodiversity poses a barrier against invasive species, most likely due to complementary resource capture (Fargione & Tilman 2005) and niche preemption (Mwangi *et al.* 2007). In contrast, at low niche dimensionality, identity or selection effects (Loreau & Hector 2001; Hodgson, Rainey & Buckling 2002; Fargione & Tilman 2005) of resident species prevail.

Niche dimensionality was an important determinant of invasion success in the homogeneous microcosms used in this study. At high niche dimensionality, high biodiversity provides protection against invasive species, but if only few niches are present, invasion success heavily relies on the mismatch in resource use of the resident and invader species. This implies that invader success at low niche dimensionality strongly depends on the presence of certain key taxa in the resident community being able to use this resource efficiently. This assumption is further supported by the fact that invasion success correlated significantly positively with functional distance to the resident community at low niche dimensionality. Although the results derived from microbial microcosms may not be directly transferrable to natural communities, similar mechanisms are likely at play. We, therefore, propose that biodiversity of functionally dissimilar species needs to be preserved to maintain invasion resistance of habitats of high niche dimensionality.

Acknowledgement

Nico Eisenhauer gratefully acknowledges funding by the Deutsche Forschungsgemeinschaft (DFG; Ei 862/1, Ei 862/2).

References

- Becker, J., Eisenhauer, N., Scheu, S. & Jousset, A. (2012) Increasing antagonistic interactions cause bacterial communities to collapse at high diversity. *Ecology Letters*, **15**, 468–474.
- Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, **4**, e5695.
- Cleland, E.E., Smith, M.D., Andelman, S.J., Bowles, C., Carney, K.M., Horner-Devine, M.C., Drake, J.M., Emery, S. & Vandermaast, D.B. (2004) Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecology Letters*, **7**, 947–957.
- Dimitrakopoulos, P.G. & Schmid, B. (2004) Biodiversity effects increase linearly with biotope space. *Ecology Letters*, **7**, 574–583.
- Fargione, J.E., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA*, **100**, 8916–8920.
- Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604–611.
- Fargione, J.E., Tilman, D., Dybzinski, R., HilleRisLambers, J., Clark, C., Harpole, W.S., Knops, J.M.H., Reich, P.B. & Loreau, M. (2007) From selection to complementarity: shifts in the causes of biodiversity productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society: B*, **274**, 871–876.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, **88**, 3–17.
- Griffin, J.N., Jenkins, S.R., Gamfeldt, L., Jones, D., Hawkins, S.J. & Thompson, R.C. (2009) Spatial heterogeneity increases the importance of species richness for an ecosystem process. *Oikos*, **118**, 1335–1342.
- Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Lawton, J.H. (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research*, **16**, 819–831.
- Heemsbergen, D.A., Berg, M.P., Loreau, M., van Hal, J.R., Faber, J.H. & Verhoef, H.A. (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, **306**, 1019–1020.
- Hodgson, D.J., Rainey, P.B. & Buckling, A. (2002) Mechanisms linking diversity, productivity and invasibility in experimental bacterial communities. *Proceedings of the Royal Society: B*, **269**, 2277–2283.

- Jessup, C.M., Forde, S.E. & Bohannan, B.J.M. (2005) Microbial experimental systems in ecology. *Advances in Ecological Research*, **37**, 273–307.
- Jiang, L., Brady, L. & Tan, J. (2011) Species diversity, invasion, and alternative community states in sequentially assembled communities. *The American Naturalist*, **178**, 411–418.
- Jiang, L. & Morin, P.J. (2004) Productivity gradients cause positive diversity – invasibility relationships in microbial communities. *Ecology Letters*, **7**, 1047–1057.
- Jousset, A., Schmid, B., Scheu, S. & Eisenhauer, N. (2011a) Genotypic richness and dissimilarity opposingly affect ecosystem functioning. *Ecology Letters*, **14**, 537–545.
- Jousset, A., Schulz, W., Scheu, S. & Eisenhauer, N. (2011b) Intraspecific genotypic richness and relatedness predict the invasibility of microbial communities. *ISME Journal*, **5**, 1108–1114.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P.B. (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.
- Koch, B., Jensen, J.E. & Nybroe, O. (2001) A panel of Tn7-based vectors for insertion of the *gfp* maker gene or for delivery of cloned DNA into Gram-negative bacteria at a neutral chromosomal site. *Journal of Microbiological Methods*, **45**, 187–195.
- Langenheder, S., Bulling, M.T., Solan, M. & Prosser, J.I. (2010) Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. *PLoS ONE*, **5**, e10834.
- Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.
- Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **412**, 72–76.
- Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., et al. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, **10**, 77–94.
- Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. (2011) Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, **92**, 2285–2298.
- Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L., Eldridge, D.J., Jurado, E., Hemmings, F.A., Reich, P.B., et al. (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, **100**, 116–127.
- Mwangi, P.N., Schmitz, M., Scherber, C., Roscher, C., Schumacher, J., Scherer-Lorenzen, M., Weisser, W.W. & Schmid, B. (2007) Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology*, **95**, 65–78.
- Replansky, T. & Bell, G. (2009) The relationship between environmental complexity, species diversity and productivity in a natural reconstructed yeast community. *Oikos*, **118**, 233–239.
- Roscher, C., Temperton, V.M., Scherer-Lorenzen, M., Schmitz, M., Schumacher, J., Schmid, B., Buchmann, N., Weisser, W.W. & Schulze, E.-D. (2005) Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. *Ecology Letters*, **8**, 419–429.
- Schmid, B., Hector, A., Huston, M.A., Inchausti, P., Nijis, I., Leadley, P. W. & Tilman, D. (2002) The design and analysis of biodiversity experiments. *Biodiversity and Ecosystem Functioning* (eds M. Loreau, S. Naeem & P. Inchausti), pp. 61–75. Oxford University Press, Oxford.
- Schnider-Keel, U., Seematter, A., Maurhofer, M., Blumer, C., Duffy, B., Gigot-Bonnefoy, C., Reimann, C., Notz, R., Défago, G., Haas, D. & Keel, C. (2000) Autoinduction of 2,4-diacetylphloroglucinol biosynthesis in the biocontrol agent *Pseudomonas fluorescens* CHA0 and repression by the bacterial metabolites salicylate and pyoluteorin. *Journal of Bacteriology*, **182**, 1215–1225.
- Schuhegger, R., Ihring, A., Gantner, S., Bahnweg, G., Knappe, C., Vogt, G., Hutzler, P., Schmid, M., van Breusegem, F., Eberl, L., Hartmann, A. & Langebartels, C. (2006) Induction of systemic resistance in tomato by N-acyl-L-homoserine lactone-producing rhizosphere bacteria. *Plant Cell and Environment*, **29**, 909–918.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.
- Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA*, **101**, 10854–10861.
- Van Elsas, J.D., Chiurazzi, M., Mallon, C.A., Elhottova, D., Krištufek, V. & Salles, F. (2012) Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proceedings of the National Academy of Sciences USA*, **109**, 1159–1164.
- Violle, C., Nemergut, D.R., Pu, Z. & Jiang, L. (2011) Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, **14**, 782–787.
- Walker, B., Kinzig, A. & Langridge, J. (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95–113.
- Wardle, D.A., Bardgett, R.D., Callaway, R.M. & van der Putten, W.H. (2011) Terrestrial ecosystem responses to species gains and losses. *Science*, **332**, 1273–1277.

Received 15 May 2012; accepted 20 August 2012

Handling Editor: Michael Pfender

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Strains of *Pseudomonas fluorescens* (resident community) and *P. putida* (invader) used in this experiment.

Appendix S2. Composition of bacterial communities and resource treatments.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.