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Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities

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Abstract:

Positive relationships between species diversity and productivity have been reported for a number of ecosystems[1, 2]. Theoretical and experimental studies have attempted to determine the mechanisms that generate this pattern over short timescales[1, 2], but little attention has been given to the problem of understanding how diversity and productivity are linked over evolutionary timescales. Here, we investigate the role of dispersal in determining both diversity and productivity over evolutionary timescales, using experimental metacommunities of the bacterium *Pseudomonas fluorescens* assembled by divergent natural selection. We show that both regional diversity and productivity peak at an intermediate dispersal rate. Moreover, we demonstrate that these two patterns are linked: selection at intermediate rates of dispersal leads to high niche differentiation between genotypes, allowing greater coverage of the heterogeneous environment and a higher regional productivity. We argue that processes that operate over both ecological and evolutionary timescales should be jointly considered when attempting to understand the emergence of ecosystem-level properties such as diversity–function relationships.

Current understanding of the relationship between diversity and productivity is based on the ecological effects of "complementarity" and "sampling"[1]. The former suggests that species richness enhances productivity because of niche differentiation (e.g., complementarity) or positive interactions (e.g., facilitation) between species and therefore more of the available resources are exploited. In "sampling", more diverse communities are, by chance, more likely to contain species with a higher average productivity than communities with low diversity. Disentangling these two effects has been a major challenge in biodiversity research because both lead to a positive relationship between diversity and productivity, but differ considerably in their implications for understanding the consequences of diversity loss[1]. It is less clear, however, how the ecological mechanisms driving species coexistence (e.g., environmental heterogeneity, dispersal) are responsible for the shape of this relationship[3,4] and the underlying evolutionary mechanisms remain largely unexplored.

Population genetic[5] and ecological models[6] consider environmental heterogeneity and intermediate dispersal as central both to the emergence and the maintenance of genetic polymorphism within metapopulations and/or species diversity within metacommunities[7-10]. Given that diversity and productivity are likely to be correlated[1], dispersal rate should also play a key role in determining community structure and function (e.g., productivity) over both ecological and evolutionary time scales. Some experimental studies support the idea that dispersal in heterogeneous environments is important in the emergence and maintenance of diversity[11,12], but the simultaneous consideration of ecological and evolutionary mechanisms controlling diversity has yet to be considered. Here we report the results of a long-term experiment in heterogeneous metacommunities where the level of dispersal between patches was manipulated. This experimental design enabled us to investigate the effect of dispersal on both biodiversity and productivity.

Bacteria offer the unique opportunity to obtain rapid ecological and evolutionary responses using experimental designs that fulfill the assumptions of theoretical models[13]. We allowed a single clone of *Pseudomonas fluorescens SBW25* to evolve for ~500 generations in a highly spatially heterogeneous environment (i.e., Biolog® GN2 microplates containing 95 unique sources of carbon) under four levels of dispersal. All the genetic and metabolic variability that appeared during the experiment evolved *de novo* by mutation so that each emerging genotype with its own functional properties can be considered equivalent to an ecological "species" and the contents of a Biolog microplate therefore represent a metapopulation of genotypes or a metacommunity of species[14,15]. Performance on each carbon source was estimated every 24h (+/- 20 min) by measuring optical density with a spectrophotometer. The sum of absorbances over a Biolog microplate therefore reflects the resource use capacity of each metacommunity, considered as a proxy for its productivity (for further details see Methods)

Metacommunity productivity significantly increased during the selection period in all treatments (Fig. 1a) and this increase was greatest at an intermediate dispersal rate, as determined by quadratic regression and multiple means comparison tests (Fig. 1b). Frequency distributions of productivity on individual substrates help to link this result to the pattern of resource utilization. Distributions were initially bimodal (Fig. 1c to f), revealing high inequality in resource exploitation by the ancestral genotype and a source-sink like structure of the metacommunity. The distribution of productivity on individual substrates remained bimodal in the non-dispersal treatment (Fig. 1c), revealing that selection could not generate local adaptation on "poor" substrates in the absence of dispersal. The increase in productivity in metacommunities with dispersal (Fig. 1b) was primarily driven by an increase in productivity on substrates that were initially poorly exploited, as revealed by the switch to unimodality in the distribution of productivity on individual substrates (Fig. 1d, e and f).

To investigate the mechanisms underlying the hump-shaped dispersal-productivity relationship (Fig. 1b), we estimated the functional composition of evolved metacommunities at the end of the selection period by assaying the productivity of 16 randomly chosen genotypes from each metacommunity on each substrate. One potential explanation for this hump shaped pattern is that highly productive genotypes are selected at intermediate dispersal rates. To test this hypothesis, we estimated the genotypic productivity for each clone as the sum of productivity scores from each individual substrate. Across all dispersal treatments, average genotypic productivity was lower than that of the ancestral clone (Fig. 2) and there were no significant differences in mean genotypic performances between dispersal treatments or between replicates within treatments.

Alternatively, it is possible that productivity peaks at intermediate dispersal rate because of increased diversity at the scale of the metacommunity. To test this hypothesis, we partitioned the total within-metacommunity variance of individual performances into effects of genotype (G), environment (E), and genotype-by-environment interaction (GxE). The E component measures variation in growth between substrates (i.e., environmental heterogeneity) while the G component measures variation in mean individual productivity among genotypes[16,17]. The GxE component reflects differences in the response

of different genotypes to different environmental conditions; this is a measure of the amount of niche variation within metacommunities. GxE variance can be further decomposed into inconsistency (I), which measures niche differentiation (i.e., complementarity) or functional diversity within the metacommunity[17] and responsiveness (R), which measures diversity of niche breadth within the metacommunity (see Box 1).

The absolute quantities of G, E, and GxE do not differ between dispersal treatments (Fig. 3a). However, the proportion of total variance attributable to inconsistency varies among dispersal treatments, with maximal functional diversity (i.e., inconsistency) at an intermediate dispersal rate (Fig. 3b). The proportion of total variance attributable to responsiveness declines with increasing dispersal (see Supplementary Figure) but only represents 2 to 3 % of total phenotypic variance. Given that both functional diversity and productivity peak at an intermediate dispersal rate, this analysis supports the idea that differences between metacommunities in productivity stem from differences in diversity. Further support for this comes from the observation that the rank-order diversity and productivity of individual metacommunities are reasonably well correlated (Fig. 4; n = 12, $P = 0.04$, $r^2 = 0.34$).

In the absence of dispersal, the community present on each substrate behaves as a closed system, where *in situ* mutation is the only source of variation. Under such conditions, adaptation to poorly exploited habitats is obstructed by low effective population size, which reduces the rate of supply of beneficial mutations and increases the effect of genetic drift. Evidence for this constraint can be seen by the observation that adaptation to 'poor' substrates was impossible without dispersal (Fig. 1c). At the metacommunity scale, this results in low productivity, because only a minority of substrates make substantial contributions to total production, and low diversity, because the metacommunity is dominated by genotypes that are specialized on a narrow range of productive resources. With dispersal, beneficial mutations generated *ex situ* are constantly introduced by migration, allowing adaptation to 'poor' quality habitats[18] (see Supplementary Discussion).We argue that the consequences of adaptation to poor substrates, in terms of both diversity and productivity, depend on the strength of selection for specialists with high productivity on a narrow range of substrates, and generalists with intermediate productivity on a wide range of substrates.

At low and intermediate dispersal rates, selection favors resource specialization[15]. At the scale of the metacommunity this results in high diversity because of substrate specialists, and high productivity since each substrate is exploited efficiently. Consistent with this argument, functional diversity (i.e., inconsistency) is high in the 10% migration treatment (Fig. 3b) and average niche breadth is low, reflecting resource specialization (Fig. 3c). At high dispersal rates, selection favors generalists across multiple substrates instead of resource specialists[15], resulting in intermediate diversity and productivity at the scale of the metacommunity. In support of this argument, inconsistency is low in the 100% dispersal treatment (Fig. 3b), reflecting lower functional diversity, and average niche breadth is high (Fig. 3c), demonstrating the presence of generalists.

In summary, we have shown that both functional diversity and productivity peak at an intermediate dispersal rate in bacterial communities assembled by natural selection resulting in a positive correlation between diversity and productivity (Fig. 4). The productivity of individual genotypes did not differ between dispersal treatments (Fig. 2), implying that a "sampling" effect cannot account for this pattern. Instead, our results indicate that communities with higher functional diversity evolve at an intermediate dispersal rate (Fig. 3b), demonstrating that "niche differentiation" (i.e., complementarity) contributes to the observed differences in productivity between dispersal treatments (Fig.4).

It is important to point out, however, that the correlation between diversity and productivity is not perfect: we estimate that 34% of the variation in productivity among communities can be accounted for by variation in functional diversity. An intriguing possibility is that facilitative interactions between genotypes[19,20] play an important role in determining productivity. Distinguishing the effects of niche differentiation (i.e., functional diversity) and facilitation is difficult in practice, and they are usually referred to collectively as complementarity[21]. Disentangling these two effects may be an interesting prospect for future research. It is important to note, however, that facilitation via biochemical mechanisms such as cross-feeding[22] requires niche differentiation into different metabolic phenotypes, suggesting that the potential for facilitation was also greatest at an intermediate dispersal rate.

1. Methods Summary

We selected populations derived from a single clone of *Pseudomonas fluorescens* SBW25 on Biolog GN2 microplates under 4 different dispersal treatments (3 replicate lines per treatment). Every 24

hours (+/-20 minutes) we measured the absorbance at 590 nm on each line on every substrate, which provides an accurate measure of both cell density and productivity on each substrate. Following the assay migration was allowed to occur between substrates in each line such that 0%, 1%, 10%, or 100% of the population on each substrate was derived from a pool of immigrants derived from all substrates (further details in Methods). Finally, we transferred 1uL from each substrate to a fresh Biolog plate. Microplates were incubated at 28C in a humidified incubator.

We measured the growth of 16 randomly sampled genotypes from each selection line at transfer 40 across all 95 Biolog substrates in 2 large assays (8 clones/line/assay). As a control, we also assayed 6 colonies of the ancestral clone in each assay. The ancestral clone gave equivalent growth scores in both assays across all substrates.

2. Methods

2.1. Ancestral Strain

To initiate our experiment we used an isolate of a *Pseudomonas fluorescens* SBW25 isogenic strain that had previously evolved for *c.* 900 generations in a complex environment of 8 carbon sources[16].

2.2. Selection Experiment

Biologs contain 95 different carbon sources from 11 different chemical families: polymers, carbohydrates, esters, carboxylic acids, amides, amino acids, aromatic compounds, amines, alcohols, phosphorylated compounds and bromhydric acid.

A single colony of our ancestral strain was used to found three replicates for each selection line (i.e., dispersal level). Each colony was initially grown for 24h in 6 ml of M9KB media (NH_4Cl 0,1 g/L; Na_2HPO_4 0,6 g/L; KH_2PO_4 0,3 g/L; NaCl 0,05 g/L; Glycerol 1 g/L, Proteose peptone # 2 2g/L) under constant orbital shaking (200 r.p.m.). One ml of this culture was centrifuged (1min at 13000 rpm) and washed by eliminating the M9KB and adding 1ml of M9 minimal salts (NH4Cl 1g/l; Na2HPO4 6g/l; KH2PO4 3g/l; NaCl 0,5g/l). 125 µl of this solution was diluted into 25ml of M9 minimal salts and starved for two hours at 28°C. 140 µl of this "starved cells" solution was then used to inoculate each well of the Biolog. The Biologs were incubated in the dark at 28°C during 24 hours in humid chambers. Daily transfers to new Biologs maintained maximal growth rate and allowed control of the amount of dispersal between wells. A transfer consisted of inoculating each well of a new recipient Biolog with 1µl of the content of an old donor Biolog. Before each transfer, new Biologs were prepared by adding 140 µl of M9 minimal salts to each well. In the 0% dispersal treatment, transfers from old wells to new wells were directly carried out with a 96 pin replicator (Boekel 96 pin/well model #140500) that transfers 1µl of culture and 'prints' the populations grown on each selection Biolog to the new selection Biolog. We did not wash the cultures before each transfer since we estimated that after 24 hours the carbon remaining in the used Biolog was rather small and/or the volume of substrate transferred was also very small (1µl) to have any effect. For the 1% treatment we serially filled each well of a sterile 96 well microplate (Falcon 96 well microplate) with 99 µl of each old well plus 1 µl of immigrants obtained by mixing the content of each old well of the same Biolog. We then used the pin replicator to inoculate the new Biolog with the content of this intermediate microplate. For the 10% dispersal treatment we followed the same procedure, but with 90µl plus 10µl immigration. For the 100% dispersal treatments, we sampled all 140 µl from each old well to prepare a mixture. We then refilled the old wells with 140µl of that mixture and used the pin replicator to inoculate the new Biologs. All treatments thus result in the same quantity of culture (1µl) transferred every 24h into new Biologs.

We measured light absorbance at 590 nm (absorbance peak of tetrazolium) every 24 hours (+/- 20 minutes) prior to each transfer, using a FLUOstar Optima spectrophotometer (BMG®). Usually absorbances measured in Biolog microplates are corrected by a blank well (with no carbon source but very few nutrients and tetrazolium). However, in our experiment the correction against the control well was not possible, because the genetic composition of the control wells varied during the selection period. For each metacommunity, the sum of absorbances measures the total catabolic performances over the substrates of the Biolog. Because this corresponds to the quantity of carbon metabolised during 24h it can be used as a proxy of metacommunity productivity. The experiment ran for 40 transfers (*c.* 500 bacterial generations). At the 40^{th} transfer, the content of all wells of each Biolog were mixed and frozen at -80 °C in 50% glycerol (w/v).

2.3. Assays

The assays measured individual genotypic performances on each carbon source at the end of the experiment. Prior to the assays, frozen mixtures from the end of the selection period were reconditioned in 6 ml of M9KB media for 24 h at 28°C under constant orbital shaking (200 r.p.m.). Sixteen genotypes (after serial dilution and plating) were randomly chosen from each replicate of each dispersal treatment (192 genotypes in total). We individually amplified these genotypes in M9KB media for 24 h at 28°C under constant orbital shaking (200 r.p.m.). For each genotype, 1 ml of culture was sampled, centrifuged and cells were washed by eliminating the M9KB and adding 1ml of M9 minimal salts. Then, 125 µl of washed culture was diluted in 25 ml of M9 minimal salts and starved for two hours (at 28°C) before their inoculation into the 96 wells of the Biologs (140µl). We scored absorbance at 590 nm for each genotype in each carbon source (16 genotypes $\times$ 4 dispersal treatments $\times$ 3 replicates $\times$ 95 carbon sources) after 24h of incubation in the dark at 28°C in humid chambers. We also reconditioned and assayed (same protocol) 12 genotypes of the ancestral clone used to inoculate the Biologs at the beginning of the selection period. We corrected absorbances by subtracting control well scores, because the genotypic composition of each well was the same.

2.4. Statistical analysis

On the first day of the selection period, we calculated the mean coefficient of variation in absorbances for each carbon source. Forty-one substrates were excluded because repeated measurements on the ancestor were statistically unreliable (coefficient of variation >1; see ref. 27), leaving 54 informative substrates. Analysis with all 95 substrates showed no qualitative differences to that used in this study with the 54 informative substrates (data not shown). For each dispersal treatment, we analyzed the total phenotypic variance in absorbances within metacommunities by partitioning environmental, genotypic and genotype-by-environment interaction components[28]. The interaction component ($G \times E$) can be further decomposed into *responsiveness* and *inconsistency*[16,28] as described in Box 1. We calculated the proportions of each component of total phenotypic variance to compare dispersal treatments (One-way ANOVA). To compare relative proportions of *inconsistency,* we used an angular transformation of the data. To link metacommunity productivity at the end of the selection period vs. functional diversity we performed a Spearman rank correlation test (because the data were not normally distributed) and present the ranked data in Fig. 4. Data were analyzed with JMP 5.0 software (SAS Institute, Cary, NC).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

BOX 1: Responsiveness and Inconsistency as relative measures of the diversity of resource exploitation strategies and niche differentiation (functional diversity).

In our 'common garden' assays, the performances of different genotypes over different environments (V_P) can be decomposed into genotypic (V_G), environmental (V_E) and genotype-by-environment interaction (V_{GE}) components as follows:

$$V_P = V_G + V_E + V_{GE} \quad (1)$$

The genotypic variance is the variance of average performances of a given genotype across all environments, and the environmental variance is the variance of environmental deviations (deviation of each phenotypic value from the mean performance of the genotype across all environments). The covariance term arises if genotypic values and environmental deviations are correlated and the interaction component arises as genotypes react differently to different environments[28]. Furthermore, the interaction component (*G*×*E*) can be partitioned into *responsiveness* and *inconsistency*[16,28]: $V_{GE} = R + I$. The responsiveness component (R) indicates differences in environmental variances and thus measures diversity of resource exploitation strategies (specialists and generalists):

$$R = \sum \frac{\left(\sigma_{Ei} - \sigma_{Ej}\right)^2}{2G(G-1)} \qquad (2)$$

The inconsistency (I) component indicates non-correlations between genotypes over environments:

$$I = \sum \frac{\sigma_{Ei}\,\sigma_{Ej}\left(1 - \rho_{EiEj}\right)}{G(G-1)} \qquad (2)$$

where *G* is the number of genotypes tested, σ_{Ei} and σ_{Ej} the standard deviations of environmental responses for each genotype, and ρ_{EiEj} the environmental correlation among each pair of genotypes tested. The lack of correlation implies that each genotype is fittest in a different environment or, more generally, that reaction norms are negatively correlated over the different environments. The *inconsistency* is a measure of niche differentiation or functional diversity[17] since it reflects specialization on different resources. Measures of functional diversity based on trait diversity are probably more informative than simple measures of diversity *per se*[29].
We present in the figure various possible outcomes of selection in the simplest metacommunity, constituted of two wells (with different resources) and no dispersal. Depending on the reaction norms obtained after evolution, one can differentiate between situations with no responsiveness and/or no inconsistency, leading to contrasted ecological interpretations.

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Figures

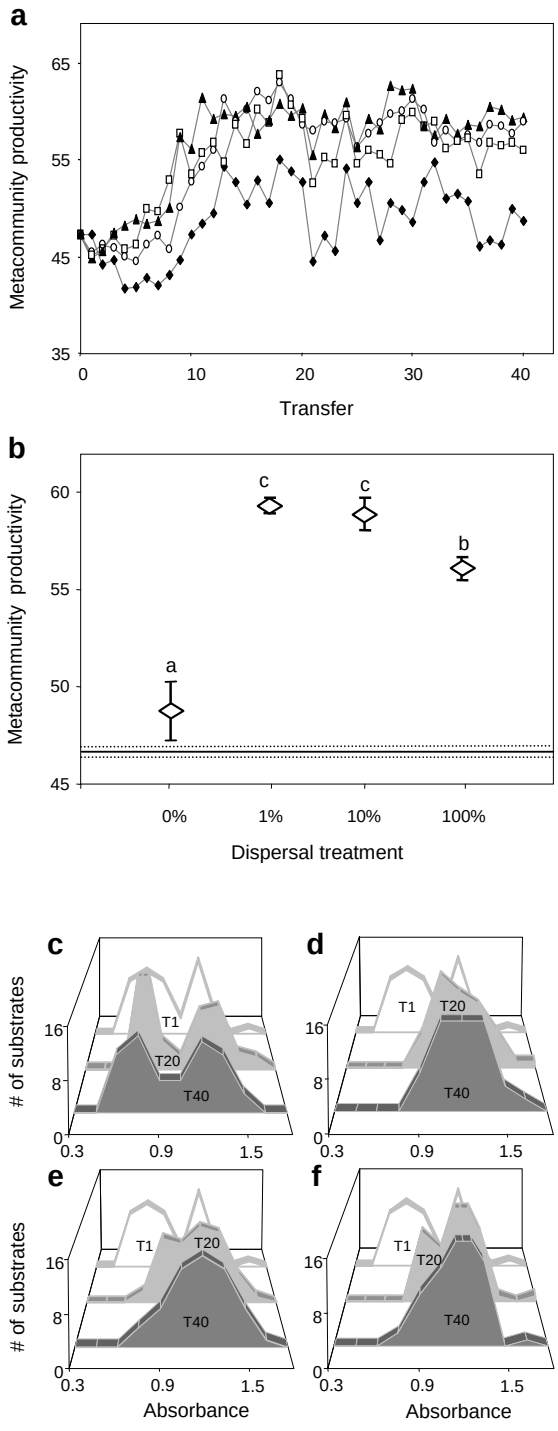

Figure 1

Figure 1: Metacommunity productivity as a function of dispersal rate

a) Plotted points show the temporal variation in mean productivity of metacommunities (n = 3) with 0% dispersal (♦), 1% dispersal (▲), 10% dispersal (○), and 100% dispersal (□). In all cases a plateau in productivity was observed in the second half of the selection period suggesting that maximal metacommunity productivity was attained. **b)** Mean metacommunity productivity (+/- s.e.m; n = 3) as a function of dispersal rate at the end of the selection period. Productivity peaks at intermediate dispersal rates as judged by quadratic regression (i.e., transfer 40; Quadratic test: $F_{2,9} = 47.8$, $P < 0.0001$, quadratic parameter $t = -7.98$, $P < 0.0001$) and multiple means comparison (Tukey's test, $q = 3.2$; $\alpha = 0.05$). The solid line represents the mean productivity of the replicate measures of the ancestral clone (+/- s.e.m; dotted lines, n = 12). This pattern is consistent over the plateau period (i.e., summed metacommunity productivity values over the 20 last transfers; Quadratic test: $F_{2,9} = 34.337$, $P < 0.0001$, quadratic parameter $t = -6.52$, $P = 0.0001$; Tukey's test, $q = 3.202$; $\alpha = 0.05$) **c** to **f)** Frequency distribution of mean productivity on individual substrates of the three replicates of each dispersal treatment at the beginning (T1), middle (T20) and at the end of the selection period (T40) for **c**) no dispersal, **d**) 1% dispersal, **e**) 10% dispersal and **f**) 100% dispersal treatments.

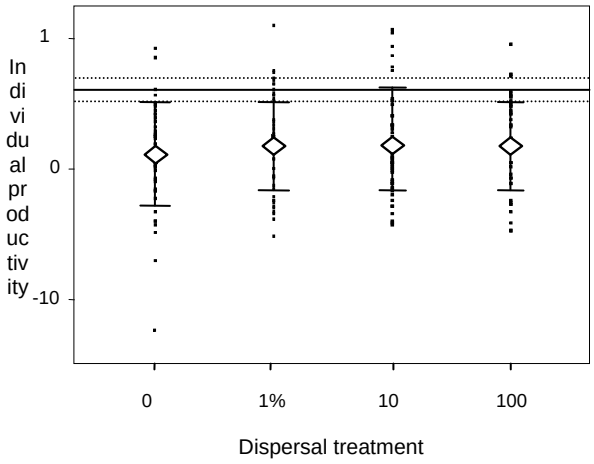

Figure 2

Figure 2: Individual genotypic productivity for each dispersal level

Plotted points represent the productivity of individual genotypes at the end of the selection period for each dispersal treatment (n = 48); diamonds are the mean genotypic productivity for each dispersal treatment (+/- s.e.m; n = 3) and the solid line represents the mean productivity of replicate measures of the ancestral clone (+/- s.e.m; n = 12). We observed no differences in mean individual genotypic performances between dispersal treatments or between replicates within treatments (Nested ANOVA: $F_{3,180} = 0.46$, $P = 0.46$ and $F_{8,180} = 1.75$, $P = 0.09$, n = 192).

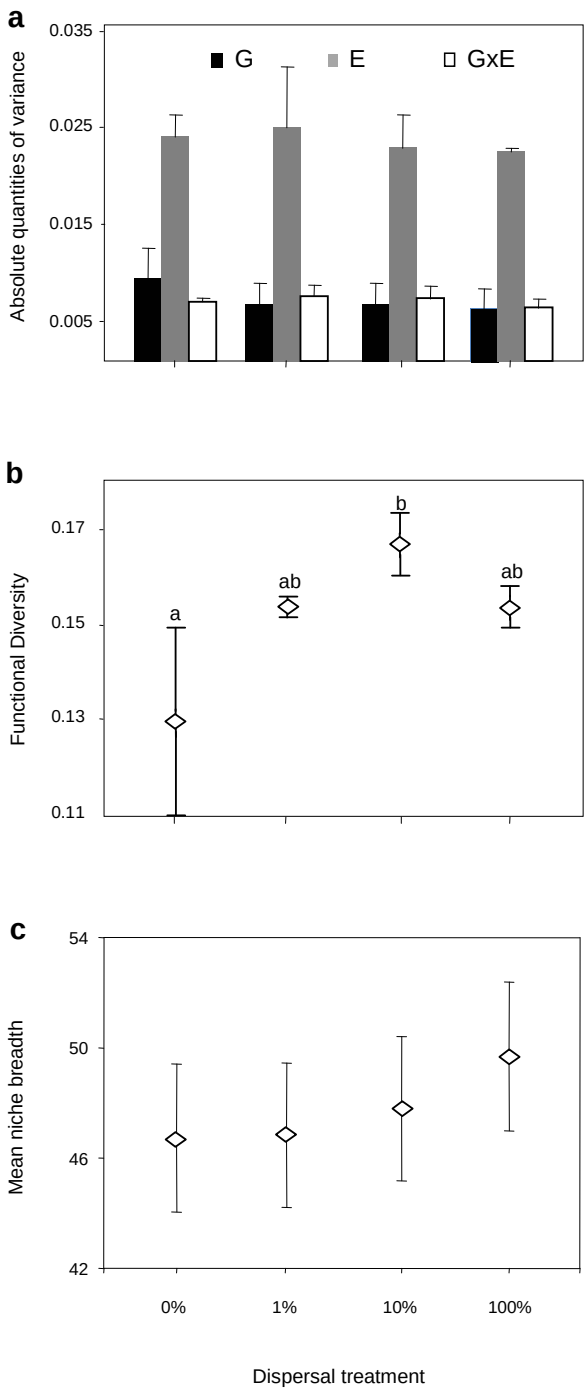
a
Absolute quantities of variance
0.035
0.025
0.015
0.005
G
E
GxE
b
Functional Diversity
0.17
0.15
0.13
0.11
a
ab
b
ab
c
Mean niche breadth
54
50
46
42
0%
1%
10%
100%
Dispersal treatment

Figure 3

Figure 3: Phenotypic variance partitioning and niche breadth for each dispersal treatment

a) Bars show the mean quantity of phenotypic variance (+/- s.e.m; n = 3) attributable to effects of genotype (G), environment, (E) and genotype by environment interaction (GxE). The absolute quantities of G, E, and GxE do not differ between dispersal treatments (one-way ANOVA, n = 12, $P > 0.05$) **b)** Plotted points show functional diversity measured as a percentage of total phenotypic variance attributable to inconsistency. Functional diversity peaks an intermediate dispersal level as judged by quadratic regression (Quadratic test: $F_{2,9} = 9.84$, $P = 0.05$, n = 12; quadratic parameter $t = -3.16$, $P = 0.012$) and multiple means comparison (Tukey's test, $q = 3.2$; $\alpha = 0.05$). **c)** Diamonds show the average genotypic niche breadth for each dispersal treatment (+/- s.e.m; n = 48), calculated as the number of substrates giving positive growth scores for each genotype. Average niche breadth increases exponentially with dispersal rate ($F_{1,3} = 420$, $P = 0.0024$, $r^2 = 0.99$) and there are no differences in mean niche breadth among replicate lines nested within treatments ($F_{3,8} = 1.43$, $P = 0.19$).

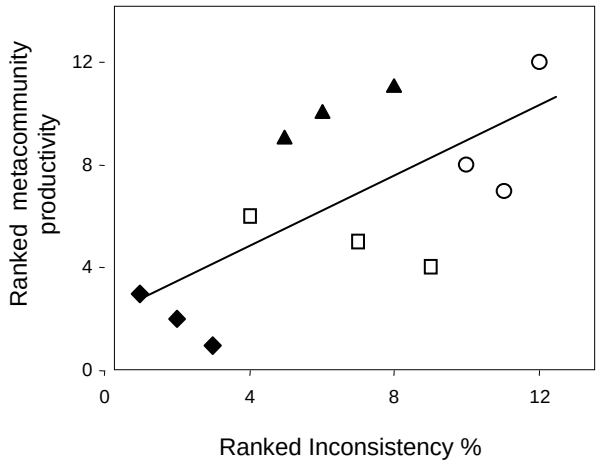

Figure 4

Figure 4: Metacommunity diversity and productivity

Plotted points show the rank-order productivity and functional diversity of metacommunities with 0% dispersal (♦), 1% dispersal (▲), 10% dispersal (○), and 100% dispersal (□). Diversity and productivity are positively correlated (Spearman's test: $F_{1,10} = 5.26$, $P = 0.04$, $r^2 = 0.34$, n = 12).

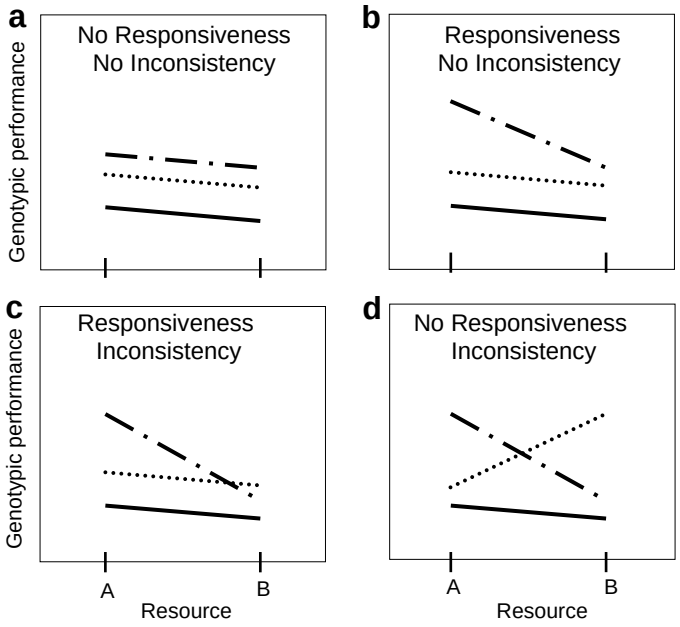

Fig. Box.1

Figure Box 1: Each dashed line represents the reaction norm over resources A and B of two genotypes that have evolved in A and B respectively from the same isogenic population (solid line). In **a**) the evolved genotypes have parallel reaction norms and there is no *GxE* interaction. The environmental variances of two genotypes are equal (no *responsiveness*) and reaction norms are parallel (no *inconsistency*). In **b**) genotypes do not respond equally to different environments, they have different environmental variances (*responsiveness*) but their responses are highly correlated (no *inconsistency*). In both cases regional functional diversity is low because genotypes are regionally redundant in their resource utilization. In **c**) the reaction norms intersect (*inconsistency*) and environmental variances differ (*responsiveness*). In this case, *responsiveness* and *inconsistency* account for the interaction component of total phenotypic variance. Finally in **d**) the ranking of genotypes changes over resources (*inconsistency*), but in this case they have the same environmental variation (no *responsiveness*). In **c**) and **d**) regional functional diversity is high because genotypes exploit different resources.