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Species phylogenetic relatedness, priority effects, and ecosystem functioning

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Abstract. Species immigration history can structure ecological communities through priority effects, which are often mediated by competition. As competition tends to be stronger between species with more similar niches, we hypothesize that species phylogenetic relatedness, under niche conservatism, may be a reasonable surrogate of niche similarity between species, and thus influence the strength of priority effects. We tested this hypothesis using a laboratory microcosm experiment in which we established bacterial species pools with different levels of phylogenetic relatedness and manipulated the immigration history of species from each pool into microcosms. Our results showed that strong priority effects, and hence multiple community states, only emerged for the species pool with the greatest phylogenetic relatedness. Community assembly also resulted in a significant positive relationship between bacterial phylogenetic diversity and ecosystem functions. Interestingly, these results emerged despite a lack of phylogenetic conservatism for most of the bacterial functional traits considered. Our results highlight the utility of phylogenetic information for understanding the structure and functioning of ecological communities, even when phylogenetically conserved functional traits are not identified or measured.

Key words: bacteria; community assembly; ecosystem function; multiple community states; phylogenetic relatedness; priority effects.

Introduction

Understanding mechanisms underlying the assembly of ecological communities is one of the central goals of community ecology (Gleason 1927, Diamond 1975). Ecologists now recognize that both niche-based deterministic processes (Chase and Leibold 2003) and neutral stochastic processes (Bell 2001, Hubbell 2001) can operate during the process of community assembly. Niche-based processes involve the interaction between species' niches and the conditions of the environment where they live, which can jointly regulate the structure of the assembling communities. In habitats with similar environmental conditions and under the same regional species pool, such processes often result in convergent communities with similar species composition and abundance. Stochastic processes, highlighted by the neutral theory (Bell 2001, Hubbell 2001), can also strongly impact ecological communities. In particular, stochasticity in the order and timing of species colonization events, as demonstrated by both theoretical and empirical studies (e.g., Drake 1991, Law and Morton 1993, Jiang and Patel 2008, Fukami et al. 2010; reviewed by Chase 2003), can result in divergent communities dominated by different species. These multiple community states associated with different species colonization histories frequently arise from priority effects, in which early colonizing species affect the establishment and abundance of later colonizers.

One factor that can potentially influence the relative importance of deterministic and stochastic processes, and hence the strength of priority effects, is ecological similarity of species in the regional species pool. Both theory (e.g., MacArthur and Levins 1967) and experiments (e.g., Gause 1934) have demonstrated the difficulty for species with similar niches to coexist, which prompted Hardin (1960) to coin the competitive exclusion principle. A corollary of this principle, applying to community assembly, is that increasing ecological similarity of species in the regional pool may make it more likely for species already established at a locality to have strong negative impacts on newly colonizing species, promoting inhibitive priority effects. As species niches are often difficult to quantify and phylogenetically closely related species tend to possess similar niches (i.e., phylogenetic niche conservatism; Harvey and Pagel 1991, Prinzing et al. 2001, Webb et al. 2002, Donoghue 2008), we suggest that species phylogenetic relatedness may be used as a surrogate of niche similarity to predict the strength of competition and priority effects. The positive relationship between species phylogenetic relatedness and competition was in fact first hypothesized by Darwin (1859), and supported by a recent experiment (Violle et al. 2011). However, whether phylogenetic relatedness of the region-

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al species pool influences the strength of priority effects during community assembly remains an open question.

Phylogenetic relatedness of the regional species pool may also have consequences for the functioning of the assembled communities. For example, if phylogenetic relatedness serves as a reasonable surrogate for species ecological similarity, then low phylogenetic relatedness (i.e., high phylogenetic diversity) may translate into increased niche complementarity among species in the assembled communities, potentially resulting in high levels of ecosystem functioning (Cavender-Bares et al. 2009). On the other hand, high phylogenetic relatedness among species within the regional species pool would indicate possible redundancy in species' niches, likely leading to reduced ecosystem functioning. So far only a handful of studies have investigated the relevance of species phylogenetic relatedness for ecosystem functioning (Maherali and Klironomos 2007, Cadotte et al. 2008, 2009, Jiang et al. 2010), but the potential interactive effects of phylogenetic relatedness and assembly history on ecosystem functions have not been explored.

Here, we describe an experimental study examining how species phylogenetic relatedness affects priority effects and ecosystem functioning by using a laboratory model of bacterial communities. We established bacterial species pools with different levels of species phylogenetic relatedness and manipulated the immigration history of bacteria from each species pool into the assembled communities. We showed that significant dissimilarity among communities subjected to different assembly histories emerged only when bacteria in the species pool were phylogenetically closely related. We also found significant effects of phylogenetic relatedness and assembly history on bacterial ecosystem functions (i.e., bacterial production and decomposition).

Material and Methods

Our experiment used eight strains of common environmental bacteria from freshwater ecosystems (Fig. 1), all of which can form colonies with unique morphological characteristics on agar plates. To estimate phylogenetic relatedness between these bacteria, we constructed phylogeny based on bacterial 16S rRNA sequences (Fig. 1a). We sequenced the 16S rRNA gene of each bacterial strain, aligned the sequences with Clustal X (version 2.0; Larkin et al. 2007), selected the best sequence evolution model, GTR+G with MrModeltest (version 2.3; Nylander 2004), by using the Akaike information criterion, and built the phylogenetic tree with Bayesian method in MrBAYES (version 3.1.2; Huelsenbeck and Ronquist 2001). Three archaea were used as the out-group. The phylogenetic distance between bacteria was obtained by summing lengths of the intervening branches between the two species on the phylogeny; smaller phylogenetic distance between bacteria indicates greater phylogenetic relatedness. Using these eight strains of bacteria, we established four species pools: *Serratia*, *Staphylococcus*, *Bacillus*, and a mixed-genus pool with one bacterium randomly selected from each of the single-genus pools (Fig. 1a; see Plate 1). The phylogenetic diversity (hereafter PD) of each species pool was calculated by summing the lengths of all the intervening branches of all the species in each pool (Faith 1992). PD is thus an aggregate measure of the phylogenetic relatedness of each species pool; higher PD values indicate larger phylogenetic distances and thus weaker phylogenetic relatedness among species.

We estimated functional trait diversity of each species pool based on the bacteria's ability to utilize a variety of carbon substrates that may appear in the bacterial growth medium used in our experiment. We measured 55 bacterial traits with Biolog MicroPlates (Biolog, Hayward, California, USA). Following the manufacturer's instructions, we prepared and inoculated Gram-positive and Gram-negative bacterial cultures into their corresponding type of Biolog MicroPlates. Gram-positive and Gram-negative microplates, each containing 96 wells, share 55 carbon substrates in common, so we only recorded the results of these 55 traits. We scored positive results, indicating that the species was able to use carbon sources in the wells, as 1 and negative results as 0. In addition, we tested the ability of these bacteria to utilize two common carbon substrates: cellulose and starch. We spread diluted cultures of each bacterial strain on carboxymethylcellulose (Wohl et al. 2004) and starch agar plates, incubated them at room temperature (~22°C) for 5 days, and flooded plates with 1% Gango Red and Lugol's iodine solutions, respectively. Colorless zones around bacterial colonies on agar plates were observed if bacteria utilize cellulose or starch. Based on the total 57 traits, we calculated functional trait diversity of each species pool in two ways. First, we calculated functional richness (hereafter FR) by counting the total number of carbon substrates that bacteria from a species pool could utilize. Second, we calculated functional diversity (hereafter FD) of each species pool. We performed a UPGMA-based cluster analysis (unweighted pair group method with arithmetic mean) with the Euclidean distance between bacteria in the 57-dimensional trait space to produce the functional dendrogram (Fig. 1b), and calculated FD of each species pool as the total intervening branch lengths of all the species in the pool on the dendrogram (Petchey and Gaston 2002). To test for phylogenetic conservatism of the measured traits, we conducted a Mantel test based on 10 000 permutations that evaluated the correlation between bacterial phylogenetic distance and trait Euclidean distance. We also tested the phylogenetic signal of each trait with Blomberg's K (Blomberg et al. 2003), using the multiPhylosignal function in the Picante package (Kimbel et al. 2010).

Our experiment used 25-mL capped test tubes as microcosms, each of which contained 10 mL of medium. The medium contained 0.55 g of crushed protozoan pellets (Carolina Biological Supply, Burlington, North Carolina, USA) per liter of deionized water. Protozoan

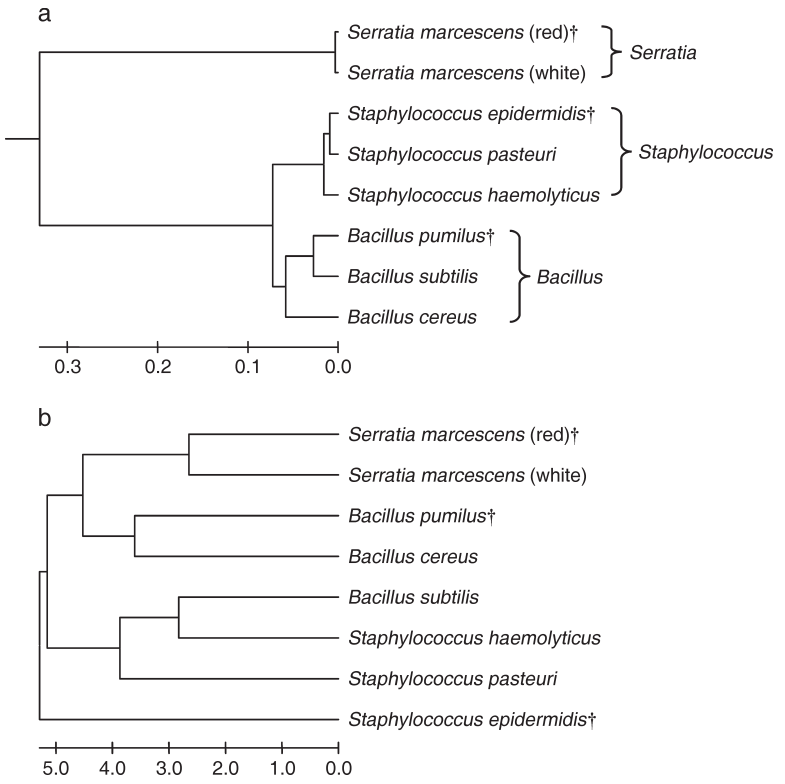

FIG. 1. (a) Phylogeny based on Bayesian methods and (b) functional dendrogram based on cluster analysis (via unweighted pair group method with arithmetic mean [UPGMA]) of 57 traits for the study bacteria. Four species pools, *Serratia* (initial phylogenetic diversity [PD], 0.0065; initial functional richness [FR], 36; initial functional diversity [FD], 2.645), *Staphylococcus* (initial PD, 0.0274; initial FR, 42; initial FD, 7.224), *Bacillus* (initial PD, 0.0959; initial FR, 35; initial FD, 6.959), and the mixed-species pool (initial PD, 0.4854; initial FR, 50; initial FD, 7.550) were formed by these bacteria. Daggers indicate the bacteria constituting the mixed species pool. The scales for branch lengths are shown beneath the phylogenetic tree (panel a) and the functional dendrogram (panel b).

pellets are made from grass and include a variety of common carbon resources for bacterial growth. Medium was autoclaved in large flasks and filtered to remove insoluble particles, then transferred into experimental microcosms and autoclaved again before the experiment started. The microcosms were incubated on a shaker at 200 rpm under room temperature (~22°C).

The experiment included all the possible assembly sequences for each bacterial pool. Thus, we had two sequential assembly history treatments for the *Serratia* pool that contained two species, and six for the *Staphylococcus, Bacillus*, and mixed pools that each contained three species (Fig. 1). Each treatment was replicated three times. Prior to the experiment, we prepared stock cultures of each bacterial strain in 8% nutrient broth. At the beginning of the experiment (day 0), we introduced the first species into microcosms by transferring a small volume (<5 μL) of stock culture with an aseptic loop. In the same way, on days 7 and 14, we introduced the second and third immigrants (no third immigrant for the *Serratia* communities), respectively. The weekly interval between species introduction allowed the assembled communities to equilibrate before the next introduction event. Our pilot experiment, albeit using only half of the eight bacterial strains used in this study, indicated that bacterial populations of individual species, initiated at small size in isolation from other species, require 2–3 days to reach carrying capacity and persist at the stationary phase for at least our experimental duration; bacterial communities containing multiple species generally reach equilibrium in one week and can persist for similarly long periods of time (J. Tan, *unpublished data*). On day 21, we added a dried, weighed, and autoclaved wheat seed to each microcosm. On day 49, we terminated the experiment and destructively sampled the microcosms. The samples from microcosms were serially diluted and spread on nutrient agar plates. After 7-day incubation, we counted the number of bacterial colonies on plates to determine population density (colony formation units per milliliter [CFU/mL]) of each bacterial strain. Wheat seeds were retrieved from microcosms, oven dried, and weighed. Two ecosystem functions were recorded. Total bacterial production in each microcosm was obtained by summing the density of each bacterial strain. Decomposition was measured as the fraction of wheat seed mass lost during the experiment.

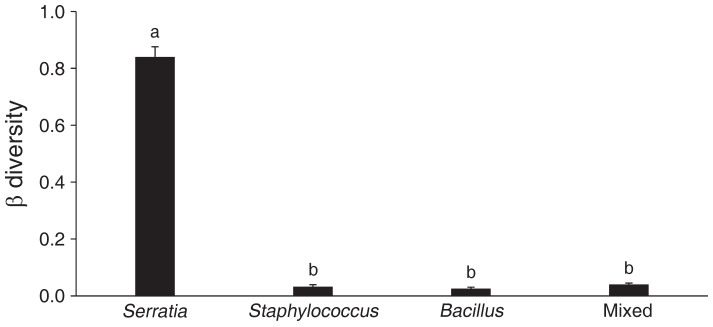

FIG. 2. The β diversity among communities assembled from the four species pools with varying phylogenetic relatedness; β diversity is calculated as 1 − (Morisita similarity index). Values are means + SE. Treatments sharing the same letters do not differ according to Tukey's HSD test.

We calculated realized community PD, FR, and FD, based on the realized species composition measured at the end of the experiment. We calculated β diversity between communities sharing the same species pool but subjected to different assembly histories, by first calculating the modified Morisita similarity index (Horn 1966), then subtracting it from 1. Calculation of Morisita indices was based on untransformed bacterial density data. For subsequent statistical analyses, all the bacteria density data were $\log_{10}$-transformed ($\log_{10}[x + 1]$) to improve normality. We used one-way ANOVA with β diversity as the dependent variable and species pool as the class variable to assess the effect of varying phylogenetic relatedness among species pools on history-induced differences in community structure, as represented by β diversity. Tukey's HSD was further conducted as the post hoc test. To test the effect of assembly history on the density of bacteria in communities sharing the same species pool, we used MANOVA with bacteria densities for each species pool as the dependent variable and history sequence as the class variable. To test the effect of assembly history on bacterial production and decomposition in different species pools, we used nested ANOVA with production and decomposition as the dependent variables and history sequences as a factor nested within species pools. To further test the effect of assembly history, we used one-way ANOVA within each species pool, with production and decomposition as the dependent variables and assembly history sequence as the independent variable. To test the effect of phylogenetic and functional diversity on bacterial production and decomposition, we used simple and backward-selection multiple linear regressions to model the ecosystem functions (i.e., bacterial production and decomposition) as functions of realized PD, FR, and FD. In all the regressions, explanatory variables were deemed significant if $P \leq 0.05$.

RESULTS

Our study bacteria did not exhibit significant phylogenetic conservatism when all the 57 traits were considered together (Mantel test, $P = 0.152$). When examined individually, 9 of 57 traits (15%), including D-fructose, L-fucose, α-D-glucose, α-D-lactose, D-melibiose, D-alanine, D, L, α-glycerol phosphate, α-D-glucose-1-phosphate, and D-glucose-6-phosphate, showed significant phylogenetic signals (multiPhylosignal function, $P < 0.05$).

The β diversity among communities subjected to different histories varied significantly among the four species pools (ANOVA, $F_{3,411} = 443.081$, $P < 0.001$). This significant variation mainly resulted from the larger values of β diversity observed in the *Serratia* pool (see Fig. 2; Tukey's HSD). The dominant species in communities of the *Serratia* pool differed depending on history treatments (Fig. 3a). In contrast, in the *Staphylococcus*, *Bacillus*, and mixed-species pools, the dominant species remained the same in different history treatments (Fig. 3b–d). Nevertheless, MANOVA still revealed a significant effect of assembly history on species densities in those species pools (*Staphylococcus*, Wilks' lambda = 0.010, $F_{15,28} = 7.882$, $P < 0.001$; *Bacillus*, Wilks' lambda = 0.029, $F_{15,28} = 4.867$, $P < 0.001$; mixed, Wilks' lambda = 0.018, $F_{15,28} = 6.097$, $P < 0.001$), in addition to the significant effect of history for the *Serratia* pool (Wilks' lambda = 0.017, $F_{1,4} = 234.1$, $P < 0.001$).

Nested ANOVA revealed a significant effect of assembly history on bacterial production ($F_{5,40} = 14.449$, $P < 0.001$), but no effect of assembly history on decomposition ($F_{5,40} = 0.886$, $P = 0.499$). One-way ANOVA indicated that assembly history had a significant effect on bacterial production in communities of the *Staphylococcus* ($F_{5,12} = 30.086$, $P < 0.001$), *Bacillus* ($F_{5,12} = 16.888$, $P < 0.001$), and mixed ($F_{5,12} = 3.601$, $P = 0.032$) pools, but had no effects in communities of the *Serratia* pool ($F_{1,4} = 1.136$, $P = 0.346$). In contrast, assembly history significantly affected decomposition in the *Staphylococcus* communities only (*Staphylococcus*, $F_{5,12} = 37.615$, $P < 0.001$; *Serratia*, $F_{1,4} = 1.136$, $P = 0.346$; *Bacillus*, $F_{5,12} = 0.670$, $P = 0.654$; mixed, $F_{5,12} = 2.348$, $P = 0.105$). Nested ANOVA also revealed that ecosystem function level differed significantly in communities of different species pools (production, $F_{14,40} = 41.161$, $P < 0.001$; decomposition, $F_{14,40} = 6.288$, $P < 0.001$).

Simple linear regressions showed that both bacterial production and decomposition increased with realized

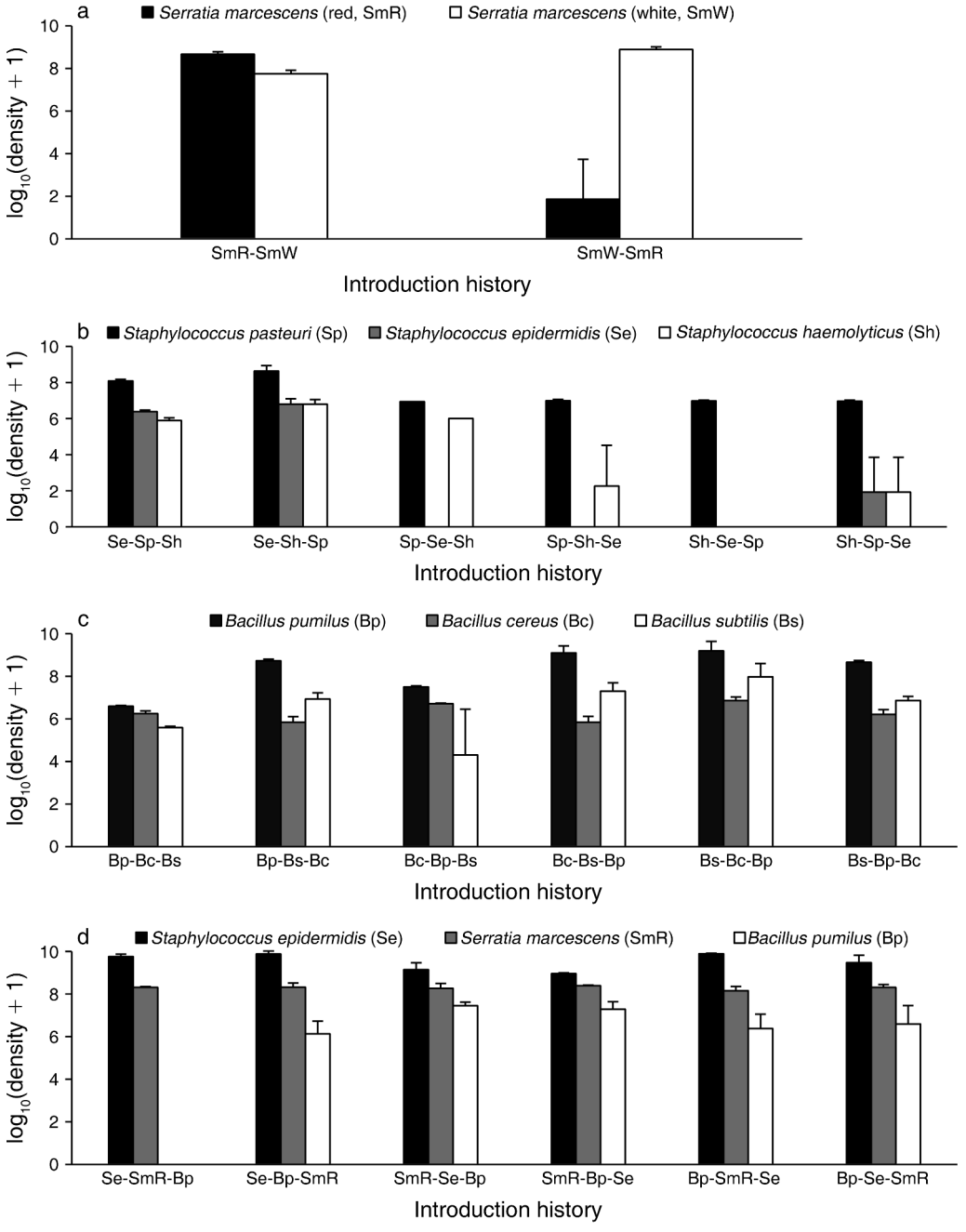

FIG. 3. Population density of each bacterium from the four species pools: (a) *Serratia*, (b) *Staphylococcus*, (c) *Bacillus*, and (d) mixed-species pool, at the end of the experiment. Values are means + SE with density measured as colony formation units (CFU) per mL and was $\log_{10}(x + 1)$-transformed prior to analysis.

PD (Fig. 4a; $R^2 = 0.461$, $P < 0.001$; Fig. 4b; $R^2 = 0.212$, $P < 0.001$), FR (Fig. 4c; $R^2 = 0.586$, $P < 0.001$; Fig. 4d; $R^2 = 0.410$, $P < 0.001$), and FD (Fig. 4e; $R^2 = 0.268$, $P < 0.001$; Fig. 4f; $R^2 = 0.415$, $P < 0.001$), respectively. Multiple regression models retained realized FR and FD as best predictors of both bacterial production and decomposition.

DISCUSSION

The results of our experiment demonstrated the importance of understanding species phylogenetic relatedness when predicting the strength of priority effects. We observed the highest β diversity among communities in the *Serratia* pool (Fig. 2), which contained phylogenetically most closely related bacterial strains (Fig. 1a).

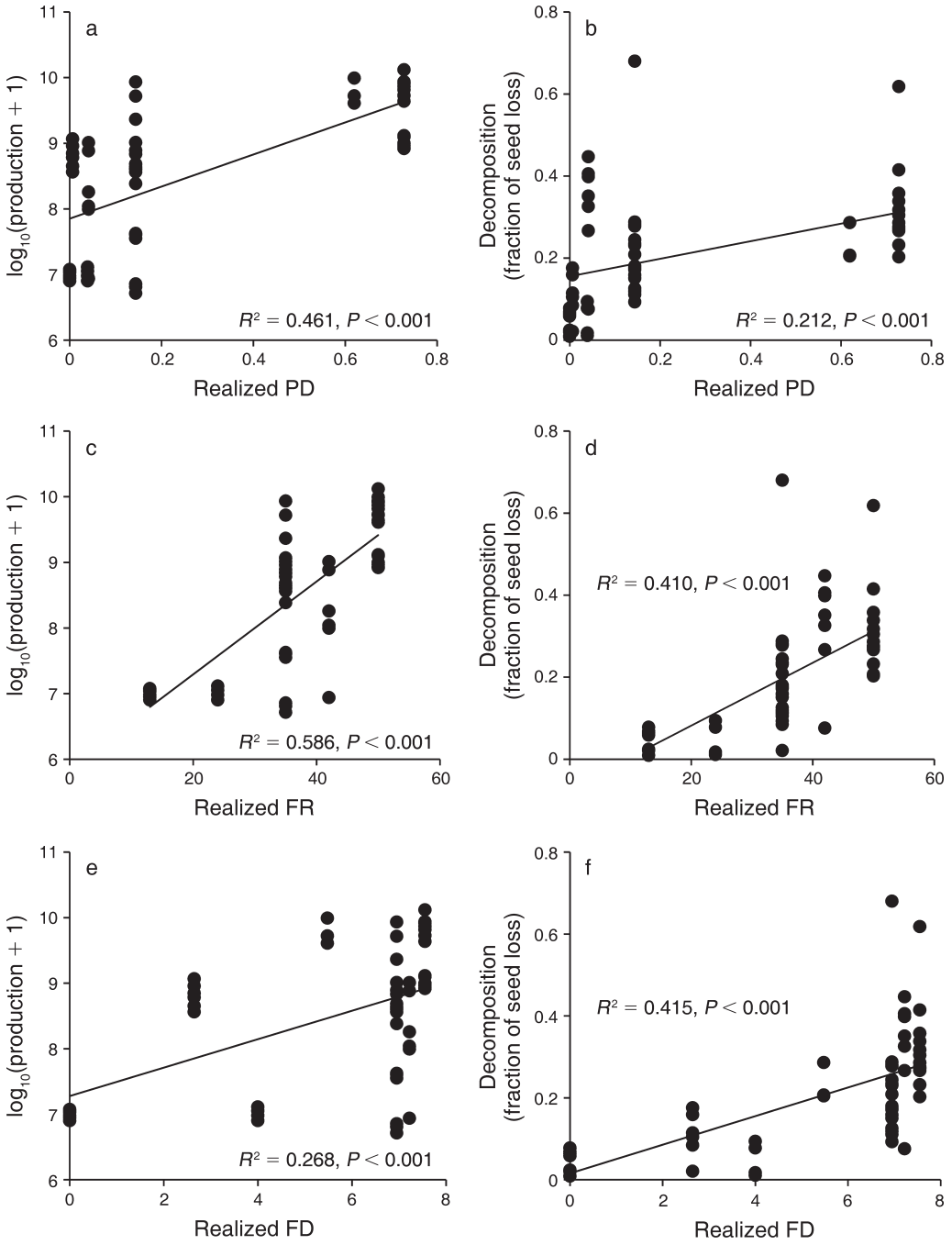

FIG. 4. Relationships between (a, b) realized phylogenetic diversity (PD), (c, d) functional richness (FR), (e, f) functional diversity (FD) and (a, c, e) bacterial production and (b, d, f) decomposition. PD and FD attained zero values in communities with one species. Data are plotted with linear regression lines. Bacterial production was measured as colony formation units (CFU) per mL and was $\log_{10}(x + 1)$-transformed prior to analysis.

Different *Serratia marcescens* strains were dominant in these communities when subjected to different assembly histories (Fig. 3a). In contrast, communities from each of the other pools with lower phylogenetic relatedness were structurally similar (Fig. 2), containing the same dominant species regardless of history (Fig. 3b–d). This difference emerged despite the fact that history had a significant effect on the structure of the assembled communities for all species pools, as revealed by MANOVA. These results appear consistent with our hypothesis that stronger competition may occur between species that are more closely related phylogenetically

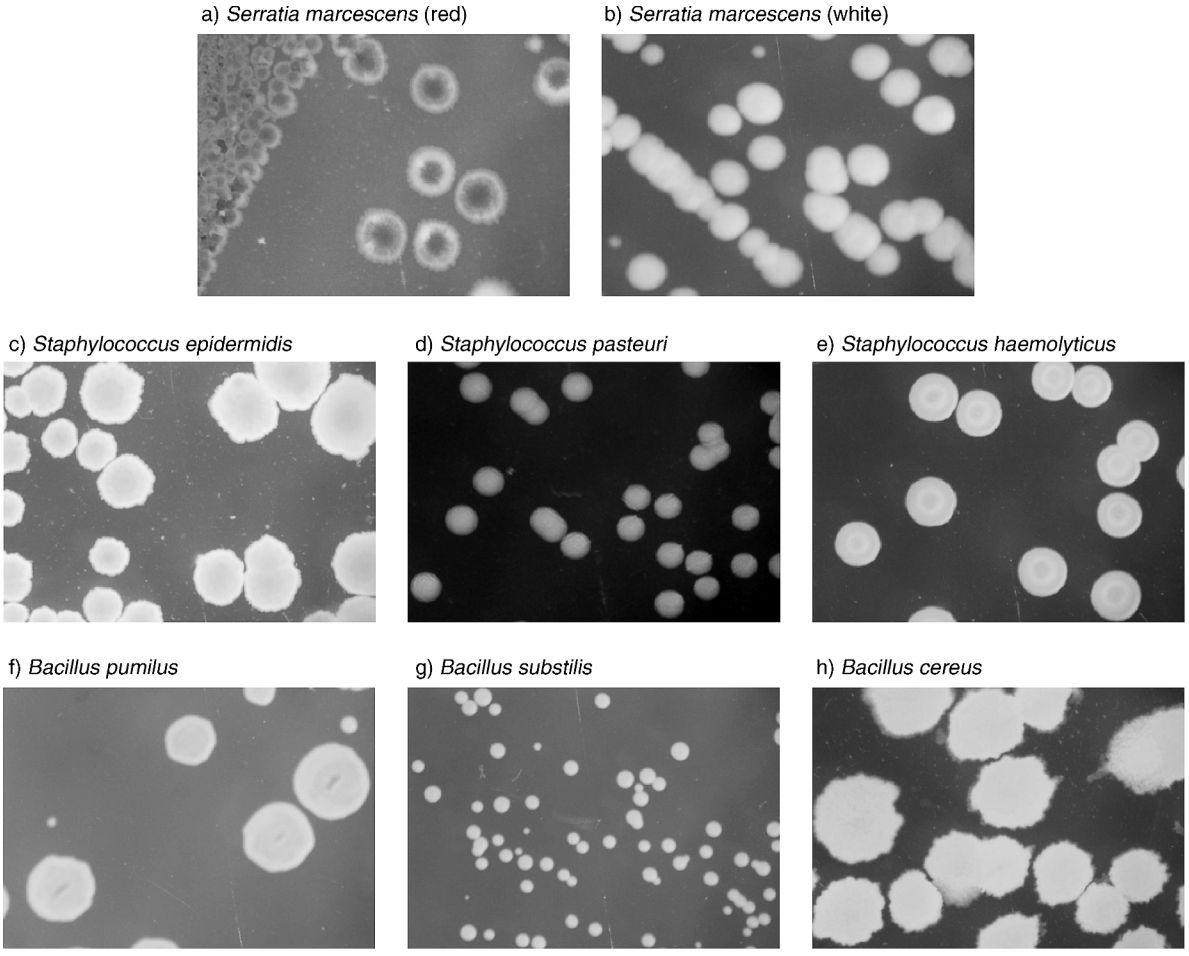

PLATE 1. Colonies of the eight bacteria studied, on agar plates. Photo credits: J. Tan and L. Jiang.

(Maherali and Klironomos 2007, Violle et al. 2011), leading to stronger priority effects that generate multiple community states (Chase and Leibold 2003, Fukami and Lee 2006). However, phylogenetic conservatism was not detected when all bacterial traits were considered together, and nonsignificant phylogenetic signals were detected for the majority of measured traits. At least three mutually nonexclusive explanations can account for these results. One possibility is that at least some of the phylogenetically conserved traits that we measured are important in defining the ecological niches of our study bacteria in our experiment. This is supported by the fact that phylogenetic diversity and functional diversity based on measured traits (including FR and FD) were both positively related to bacterial production and decomposition in our experiment. Another possibility is that some unmeasured traits that are important in defining species niches may be phylogenetically conserved, making phylogenetic relatedness a reasonable proxy of functional similarity with regard to these traits. A third explanation is that phylogenetic relationships based on the 16S rRNA gene, which is known to be highly conserved between different species of bacteria (Coenye and Vandamme 2003), may not adequately capture the potentially large variation in traits coded by less conserved genes (see Dahle et al. 2011 for a counterexample). Note that this issue can be circumvented in the future by constructing phylogeny based on whole genomes, which are currently unavailable for most organisms. Regardless, our results highlight the utility of phylogenetic information for understanding the structure and functioning of ecological communities, even when phylogenetically conserved functional traits are not identified or measured.

Our results indicated that phylogenetic diversity positively affected ecosystem functions (i.e., bacterial production and decomposition), but that ecosystem functioning was better predicted by functional diversity. Using data from plant experiments, Cadotte et al. (2008, 2009) also showed that primary productivity was positively correlated with both plant phylogenetic and functional diversity. However, their results indicated that phylogenetic diversity explained more variation in plant productivity than several measurements of functional diversity. This discrepancy between the results of the two studies may be due to the fact that horizontal

gene transfer, which may increase trait similarity among distantly related species and weaken the correlation between phylogenetic relatedness and trait similarity, is much more common for bacteria than for plants (Andersson 2005, Richardson and Palmer 2007). Note that phylogenetic diversity nevertheless remained significant in explaining the functioning of bacterial communities in our experiment.

Our results also showed that community assembly history had significant effects on bacterial production in the *Staphylococcus*, *Bacillus*, and mixed communities, and on decomposition in the *Staphylococcus* communities. Likewise, Fukami et al. (2010) manipulated the assembly history of wood-decay fungal communities and found a significant effect of assembly history on fungal decomposition. They showed that community divergence in species richness and composition, resulting from different assembly histories, led to the differentiation of ecosystem functioning. However, this mechanism cannot explain the divergence/convergence of ecosystem functioning in communities subjected to different assembly histories in our study. Two distinct alternative states were formed in communities of the *Serratia* pool (Fig. 3a), but ecosystem functions of these two community states were similar. In contrast, a single community state was observed in the *Staphylococcus* pool, but ecosystem functions differed among the assembled communities (Fig. 3b). One explanation for the lack of historical effects on ecosystem functioning in the *Serratia* communities is that the two strains of *Serratia marcescens* may play similar ecological roles since they are phylogenetically closely related (99% similarity based on phylogeny) and functionally similar (sharing 50 of 57 traits). The two *Serratia* strains may thus be largely functionally substitutable, resulting in the same levels of ecosystem functions in communities dominated by different *Serratia* strains. In other species pools, although the historical effect was not strong enough to generate multiple community states, the abundance of subdominant species differed under different assembly histories (hence the significant effect of assembly history on species densities in MANOVA), especially in the *Staphylococcus* pool (Fig. 3b), which may have caused the differentiation of ecosystem functioning in those species pools. All together, our results showed that assembly history affected ecosystem functioning in some communities, but not in others. Understanding the conditions that promote the relationship between assembly history and ecosystem functioning remains an important topic of future research.

One concern is that each phylogenetic relatedness level in our experiment included only one species combination, so one could argue that the effect of phylogenetic relatedness may have been confounded with the effect of species identity. An ideal solution to this problem would be to use as many species combinations at each phylogenetic level as possible, but this may not be logistically possible. In particular, finding many combinations of phylogenetically closely related bacteria with different colony morphologies (e.g., the red and white *Serratia marcescens*) is difficult. In this experiment, although we cannot exclude the possibility that the effects of species phylogenetic relatedness and identity are confounded, results from a related experiment suggests that this is not the case. That experiment produced results similar to the current experiment. In particular, strong priority effects were also observed in bacterial communities containing closely related species, specifically those with three strains of *Bacillus pumilus*; weaker priority effects were detected in communities with less related species (J. Tan, *unpublished data*). In the present experiment, weak priority effects also emerged in all communities of the three species pools with relatively low levels of phylogenetic relatedness, resulting in single community states. Together, these results strongly suggest a linkage between species phylogenetic relatedness and the strength of priority effects. Nevertheless, future studies that manipulate phylogenetic relatedness or diversity should aim to establish multiple species combinations within each treatment, in order to eliminate the potential confounding effects from species identity.

In this study, different bacterial species pools exhibited different levels of phylogenetic relatedness, permitting an evaluation of how phylogenetic relatedness might govern the relative contributions of niche-based deterministic processes (Chase and Leibold 2003) and neutral stochastic processes (Bell 2001, Hubbell 2001) to community assembly. In the experiment we conducted to accomplish this evaluation, multiple community states resulting from strong stochastic assembly processes (i.e., priority effects) were only observed in the species pool with the highest phylogenetic relatedness and highest functional similarity. Alternatively, single-community states resulting from strong deterministic assembly processes were observed in communities assembled from less phylogenetically related species pools. As such, these observations support our hypothesis that priority effects are stronger between species that are more closely related phylogenetically, although some caution must be exercised when generalizing these results given the limitation of our experimental design (see last paragraph). Further, our study demonstrates a positive relationship between phylogenetic diversity and ecosystem functions in an experiment that directly manipulated phylogenetic diversity. Importantly, we obtained these results despite the fact that many functional traits measured in our experiment exhibited nonsignificant phylogenetic signals. Our results thus highlight the difficulty of identifying species functional traits relevant for community assembly and ecosystem functioning, and at the same time, the utility of basic phylogenetic information in predicting the structure and functioning of ecological communities.

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