PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Check for updates

Cite this article: Zee PC, Fukami T. 2018 Priority effects are weakened by a short, but not long, history of sympatric evolution. *Proc. R. Soc. B* **285**: 20171722. http://dx.doi.org/10.1098/rspb.2017.1722

Received: 2 August 2017
Accepted: 8 January 2018

Subject Category:
Ecology

Subject Areas:
ecology, evolution

Keywords:
priority effects, character displacement, community assembly, *Pseudomonas fluorescens*

Author for correspondence:
Peter C. Zee
e-mail: zee@olemiss.edu

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3980850.

THE ROYAL SOCIETY
PUBLISHING

Priority effects are weakened by a short, but not long, history of sympatric evolution

Peter C. Zee[1,2] and Tadashi Fukami[1]

[1]Department of Biology, Stanford University, Stanford, CA 94305, USA
[2]Department of Biology, University of Mississippi, Oxford, MS 38677, USA

PCZ, 0000-0003-2594-9602; TF, 0000-0001-5654-4785

Priority effects, or the effects of species arrival history on local species abundances, have been documented in a range of taxa. However, factors determining the extent to which priority effects affect community assembly remain unclear. Using laboratory populations of the bacterium *Pseudomonas fluorescens*, we examined whether shared evolutionary history affected the strength of priority effects. We hypothesized that sympatric evolution of populations belonging to the same guild would lead to niche differentiation, resulting in phenotypic complementarity that weakens priority effects. Consistent with this hypothesis, we found that priority effects tended to be weaker in sympatrically evolved pairs of immigrating populations than in allopatrically evolved pairs. Furthermore, priority effects were weaker under higher phenotypic complementarity. However, these patterns were observed only in populations with a relatively short history of sympatric evolution, and disappeared when populations had evolved together for a long time. Together, our results suggest that the evolutionary history of organismal traits may dictate the strength of priority effects and, consequently, the extent of historical contingency in the assembly of ecological communities.

1. Introduction

Priority effects, in which the order of species arrival at local habitat patches dictates the outcome of local species interactions, can result in historical contingency in community assembly, altering community structure and function [1–3]. Historical contingency caused by priority effects has been found in a range of organisms, including bacteria (e.g. [4]), fungi (e.g. [5]), plants (e.g. [6]) and animals (e.g. [7]), and increasing evidence indicates that the extent of historical contingency can be partly predicted from environmental conditions such as nutrient availability, disturbance frequency and temperature variability [8,9]. However, the strength of priority effects must be modulated not just by environmental conditions, but also by organismal traits that determine how species interact with one another [9]. These traits are often shaped by the evolutionary history of species [10], although only a limited number of studies have linked evolutionary history and priority effects [11–13]. Consider, for example, the evolutionary history of immigrants that colonize island communities. If all immigrants came to an island from the same mainland, immigrants might have traits that reflect a long history of shared, sympatric evolution. By contrast, if immigrants came from different, allopatric regions, some of the immigrants might encounter one another for the first time on the colonized island, with their traits having little shared evolutionary influence. These differences in the amount of prior evolutionary history that shapes species traits can determine the strength of priority effects, but the evidence needed to test this possibility is largely lacking.

In theory, shared evolutionary history can weaken priority effects if sympatric evolution results in niche differentiation, as expected from the concept of character displacement [14]. Niche differentiation can diminish priority effects because an early-arriving population might then exploit only the niche space it has specialized on, allowing other, late-arriving populations to use their own niche space. It is also possible, however, that shared, sympatric evolutionary history strengthens priority effects because sympatric evolution can cause populations to become similar in competitive ability, as expected from the neutral theory of biodiversity [15]. In this case, an early-arriving species could pre-empt local niche space, making it more difficult for subsequent species to establish. Which scenario is more likely may depend on the duration of evolutionary history. For example, niche partitioning can evolve rapidly in new environments (e.g. [10,16]), whereas trait convergence has been shown to evolve when species interact over longer time periods (e.g. [17,18]). Alternatively, either of these processes could operate exclusively, leading to either extreme niche differentiation or complete ecological neutrality, respectively.

In this paper, we report the first experimental test, to our knowledge, of the effects of both the presence and duration of shared evolutionary history on the strength of priority effects. Specifically, using the bacterium *Pseudomonas fluorescens* as an experimental system, we ask the following questions: does a history of sympatric evolution weaken or strengthen priority effects? If so, what is the biological mechanism underlying the role of evolutionary history and does the influence of evolutionary history on priority effects depend on the duration of prior evolution? Experimental populations of *P. fluorescens* are uniquely suited for asking these questions because of extensive knowledge on adaptive evolution in this bacterium. When founded from a single ancestral genotype, *P. fluorescens* populations rapidly diversify under static culture conditions into genetically based niche specialists, including multiple 'wrinkly spreader' (WS) types, which colonize the air–liquid interface to form a biofilm mat [19–24]. We used these multiple WS types for our experiments.

Based on previous research, we expected that the WS genotypes that evolved sympatrically in static culture conditions would display character displacement. If the air–liquid interface is an environment that can be divided into multiple niches, character displacement among WS genotypes may occur within biofilm mats through differentiation of surface attachment mechanisms ([11,22,25], see also [26]). For this reason, we predicted that sympatric pairs of WS genotypes would, on average, exhibit weaker priority effects than pairs that had evolved allopatrically. Alternatively, it is conceivable that WS genotypes have similar competitive abilities if they have evolved in sympatry [23]. If sympatrically evolved pairs were competitively more similar than allopatrically evolved pairs, one might expect stronger priority effects via niche pre-emption in sympatrically evolved pairs. As detailed below, our results support the first hypothesis, but only when the history of sympatric evolution was relatively short.

2. Material and methods

(a) Generation of sympatrically and allopatrically evolved pairs

To generate sympatrically and allopatrically evolved pairs of strains, we independently propagated 12 replicated pairs of *P. fluorescens* in static 6 ml cultures of standard King's B (KB) liquid media at 28°C for seven weeks, with weekly transfers of 60 μl of homogenized culture to fresh media. Each of these 12 microcosms was founded with the same pair of two ancestral clones: a wild-type SBW25 clone [19] and a SBW25::*lacZ* mutant clone [27]. Use of the mutant with a neutral *lacZ* marker ensured that derived strains were easily distinguishable when plated on KB agar supplemented with 50 μg ml^{-1} 5-bromo-4-chloro-3-indolyl-β-D-galactopyranoside (X-gal) [23,27].

Each week, immediately after the transfer to fresh media, the cultured medium of each microcosm was plated, and two WS strains (one strain with LacZ and one without) isolated and stored in 70% glycerol at −80°C. This treatment resulted in 24 populations with neutral markers (e.g. one strain with LacZ, and one without; two strains per selection line). Pairings of these *lacZ*+ and *lacZ*− WS types were used in the community assembly experiments described below, to determine how shared evolutionary history influenced the strength of priority effects during community assembly. Since reproduction is completely asexual in *P. fluorescens*, different genetically based morphotypes are analogous to species in a community [28]. As such, we will refer to vials with multiple morphotypes as communities. See the electronic supplementary material for a diagrammatic representation of the design of the generation of the strain used in the immigration experiments (electronic supplementary material, figure S1*a*), and the pairing of strains for sympatric and allopatric pairs (electronic supplementary material, figure S1*b*).

(b) Community assembly

We used replicated pairs of strains to assess how evolutionary history influences priority effects after one, two and seven weeks of prior evolution. This experiment followed the general methods of Fukami *et al*. [23] and Knope *et al*. [12]. The strains for these pairs were isolates from the selection lines described above. For each pairing, microcosms for community assembly were independently initiated with one *lacZ*+ and one *lacZ*− strain for easy enumeration of ancestral state. For each duration of evolution, the two treatments were pairs with and without history of sympatric evolution. Sympatrically evolved pairs consisted of alternatively marked WS isolates (i.e. *lacZ*+ and *lacZ*−) from the same microcosm of the experiment described above. Allopatrically evolved pairs consisted of alternatively marked WS isolates from separate microcosms. For both sympatrically and allopatrically evolved pairs, all strains used were derived from the evolution experiment described above (electronic supplementary material, figure S1). In other words, for each duration of evolutionary history, all strains used for the community assembly experiment were evolved for the same amount of time.

For both sympatrically and allopatrically evolved pairs, each replicated 12 times for a total of 24 pairs, we had two treatments of immigration order: the strain of one *lacZ* status was introduced to 6 ml of sterile, static KB media on day 0 (first strain), with the opposite *lacZ* marker introduced to the same microcosm 24 h later (second strain). After both strains were introduced, abundance (colony forming units, or CFU) was quantified through destructive harvesting and dilution plating on days 0, 1, 2, 4, 6, 8 and 10. Each of the 24 replicated pairs were sampled at each of these time points. For each duration of evolutionary history (i.e. one, two or seven weeks), the strain pairs used were independent of other weeks. In other words, at each week, strain pairs were isolated from different propagated selection lines.

(c) Quantifying priority effects

We calculated the strength and direction of priority effects, P_{ij}, by comparing how much a specific strain grew when it was introduced before another strain to how much it grew when it was introduced after. Following Vannette & Fukami [29], we quantified P_{ij} as the log of the ratio between the abundance of strain i, time-averaged over days 4 through 10, when introduced after strain j, $D(i)_{ji}$, and the abundance of strain i, also time-averaged over days 4 through 10, when it was introduced before j, $D(i)_{ij}$:

$$P_{ij} = \ln\left(\frac{D(i)_{ji}}{D(i)_{ij}}\right),$$

where P_{ij} values of zero indicate the absence of a priority effect, positive P_{ij} values indicate a facilitative priority effect, and negative P_{ij} values indicate an inhibitory priority effect [29].

(d) Quantifying complementarity: biofilm phenotypes

We expected sympatric evolution to result in phenotypic complementarity (a form of character displacement), and that pairs with more complementary phenotypes would in turn show weaker priority effects. To test this expectation, we characterized the phenotype of the biofilm formed at the air–liquid interface in static culture of each strain in independent monoculture. We measured biofilm thickness and the presence of a webbed appearance in the biofilms. The emergence of biofilms with this webbed appearance in *P. fluorescens* has previously been described [22,25]. Spiers & Rainey [22] found that cellulose increases cell–cell attachment and that a proteinacous attachment factor results in attachment to the glass walls of the vial. The webbed phenotype corresponds to more cell–cell adhesion, whereas the non-webbed phenotypes are more adhesive to the glass [25]. When inoculated together, the resulting biofilms are stronger than either phenotype alone [22,25]. We scored thickness as one of three categories of thin (scored as 0), medium (1) and thick (2), and webbing as either zero (not webbed) or one (webbed). For each strain, mat phenotypes were averaged from two replicates of independently formed air–liquid interface mats. From these two mat characteristics, we assigned a mat phenotype from which all pairwise distances among strains could be calculated using Euclidean distance. For any given pair of strains, we used values of this distance as an index of mat phenotypic dissimilarity and, more generally speaking, a proxy for phenotypic complementarity.

(e) Statistical analyses

Using general linear mixed models (GLMMs), we tested for the effects of evolutionary history, i.e. sympatric versus allopatric evolution (referred to as Evolutionary Treatment), the duration of evolutionary history, i.e. one, two or seven weeks (referred to as Week), and the timing of observation, i.e. days 4 through 10, during community assembly (referred to as Day) on the difference in abundance between first- and second-arriving strains. Similarly, we also tested for the effects of Evolutionary Treatment, Week and the biofilm phenotypic distance (referred to as Distance) on the strength of priority effects (P_{ij} values). In addition, we tested for the effects of Evolutionary Treatment and Week on the difference in the strength of priority effects between sympatrically evolved and allopatrically evolved pairs (ΔP). In each of these analyses, we included all possible two- and three-way interactions among factors in a full initial model. In each of the models, we included the identity of the selection lines from which strains were isolated as random effects. We performed model selection based on corrected AIC (AICc) rankings to determine the best-fit models [30] (see electronic supplementary material for AICc tables).

We complemented these analyses with two additional approaches: (i) t-tests that tested for the differences in abundances between the first- and second-arriving strains, (ii) t-tests that tested for the differences in the strength of priority effects between sympatrically and allopatrically evolved pairs and (iii) linear regressions that tested for significant relationships between biofilm phenotypic differences and the strength of priority effects.

For all analyses, we assumed that the density of any strain for which we found no colonies on the dilution plates was 10^6 CFU ml^{-1}, a value that is roughly an order of magnitude lower than the detection threshold for our plates. The actual density could have been lower than 10^6 CFU ml^{-1} in some cases, but we used this value as a conservative method that could underestimate, but not overestimate, the strength of priority effects. As an alternative method, we also did the analyses after discarding all of the replicates where no colony was found for a strain. This alternative method yielded qualitatively identical results to the ones we present here. For each of the three weeks (one, two and seven weeks of prior evolution), the tested strain pairs were not the same continued evolutionary lineages. Instead, independent sets of strain pairs were used for each of the three weeks. All data analyses were performed in R [31].

3. Results

(a) Abundance through time

In all replicates of one week of evolutionary history, the first strain rose to high density by day 1, and the second strain remained at a lower abundance for the majority of the experiment (figure 1*a*). However, by the end of the experiment (day 10), the second strain of sympatrically evolved pairs reached higher density than the first strain, whereas in allopatrically evolved pairs, the second strain remained at a lower density (figure 1*a*). Surprisingly, in sympatrically evolved pairs, all second-arriving strains rose to higher density by day 10 of the experiment.

For each time point, the difference in abundance between the first- and second-arriving strains provides a metric of establishment success of the second immigrant (figure 2). Higher positive values indicate that the first species remains dominant in the community, while smaller (or negative) values indicate more successful establishment by the second immigrant. This metric was higher for allopatrically evolved pairs than for sympatrically evolved pairs at day 10 (t-test, $p = 0.0002$), confirming that late-arriving immigrants attained higher relative abundance when they had evolved sympatrically with the first immigrant (figure 2*a*).

For all replicates of both two and seven weeks of prior evolution, the first-arriving strain rose to high density, and

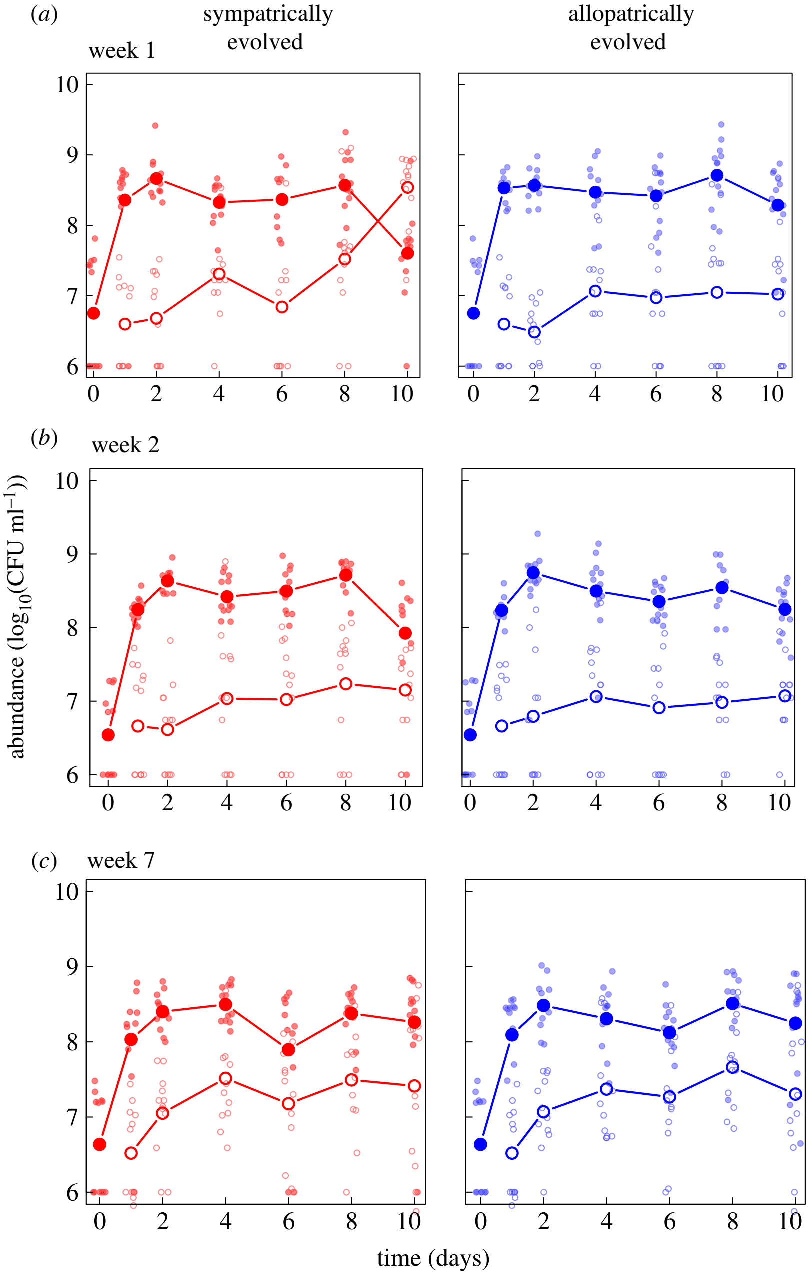

Figure 1. Abundance dynamics in assembled communities. Points represent the abundances of first- (closed circles) and second- (open circles) arriving strains for sympatrically evolved (red, left) and allopatrically evolved (blue, right) pairs of strains. Each row of panels shows results for strain pairs that had the following duration of sympatric or allopatric evolution: (*a*) one week, (*b*) two weeks or (*c*) seven weeks.

the second-arriving strain remained at relatively low density (figure 1*b*,*c*). For all time points, we found no significant difference in the abundances of the first and second immigrants for sympatrically evolved and allopatrically evolved pairs (*t*-tests, $p > 0.05$; figure 2*b*,*c*). The week two replicates showed an apparent trend towards reduced priority effects at day 10 in sympatrically evolved pairs, but this trend was not statistically significant (*t*-test, $p > 0.05$; figures 1*b* and 2*b*).

Analyses of GLMMs suggest differences in abundance between first- and second-arriving strains were significantly predicted by both Day and Week. In models with interactions among Day, Week and Evolutionary Treatment, the Evolutionary Treatment alone was not a significant predictor, but the interactions between Day and Week and between Day and Evolutionary Treatment were significant (electronic supplementary material, tables S1–S3). These GLMM analyses corroborate the observation that evolutionary history influenced abundances, but that this effect was evident only at late time points during community assembly and only when the strains had undergone a short duration of sympatric evolution (figure 2).

(b) Strength of priority effects

To compare the strength of priority effects between the two evolutionary history treatments, we calculated the difference in P_{ij} between allopatrically evolved and sympatrically evolved pairs for each given strain i (i.e. $\Delta P = [P_{\{i,\text{allopatrically evolved } j\}} - P_{\{i,\text{sympatrically evolved } k\}}]$) for one, two and seven weeks of evolutionary history. Subscripts j and k correspond to the second strain in the experiment from the allopatric or sympatric evolution treatment, respectively. After one week, mean ΔP was marginally lower than zero (two-tailed *t*-test, $p = 0.065$), indicating that priority effects in allopatrically evolved pairs tended to be more negative than in sympatrically evolved pairs (figure 3*a*). The

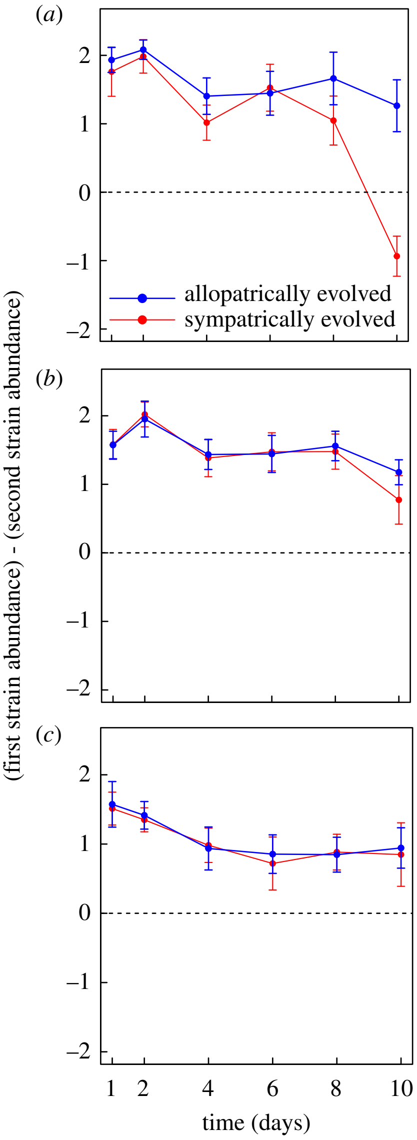

Figure 2. Differences between the log-transformed abundances of first- and second-arriving strains. Points represent the mean differences between first- and second-arriving strain abundances for sympatrically evolved (red) and allopatrically evolved (blue) pairs of strains. Duration of sympatric or allopatric evolution: (*a*) one week, (*b*) two weeks or (*c*) seven weeks.

general linear mixed model analysis did not reveal significant effects of either Week or Evolutionary Treatment (electronic supplementary material, table S4). However, after two and seven weeks of evolutionary history, ΔP did not differ significantly from zero (*t*-tests, $p > 0.1$; figures 3*b*,*c*). The GLMM did not show significant treatment effects for Week or Evolutionary Treatment, suggesting that the lack of treatment effect at weeks 2 and 7 overwhelmed the signal that we found for treatment differences in the strength of priority effects at week 1.

(c) Phenotypic complementarity and priority effects

In the general linear mixed model analyses, we found that the best-fit model was one without interactions, revealing that Week was the most significant factor (electronic supplementary material, table S5). However, inclusion of the interaction between Evolutionary Treatment and Week did yield a well-fit model (electronic supplementary material, tables S5–S7).

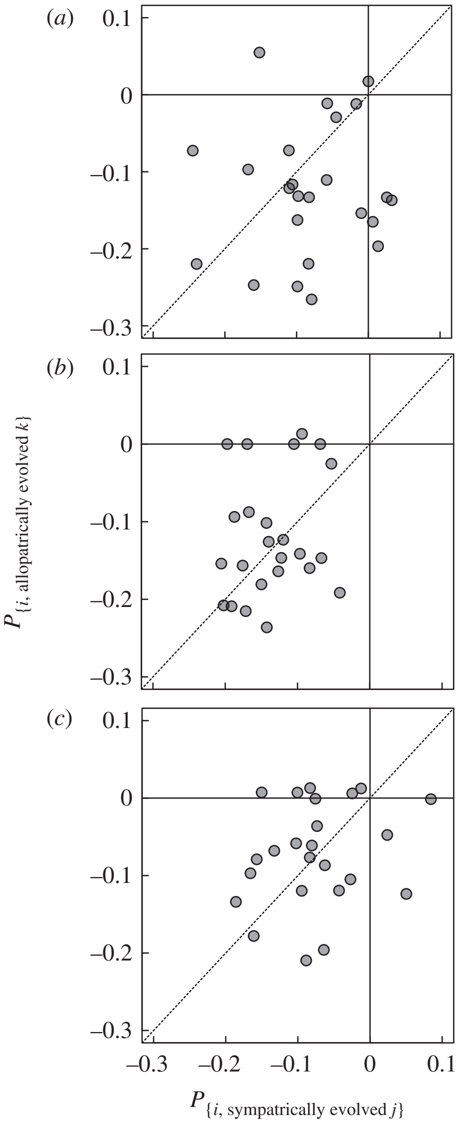

Figure 3. Comparison of the strength of priority effects between allopatrically and sympatrically evolved pairs. Each data point represents the priority effect experienced by focal strain *i* when introduced after a sympatrically evolved strain *j* and after an allopatrically evolved strain *k*. Diagonal lines represent the case where the strength of priority effects in sympatrically and allopatrically evolved pairs were the same ($\Delta P = 0$). Points falling below ($\Delta P > 0$) or above ($\Delta P < 0$) the diagonal line represent stronger priority effects in allopatrically and sympatrically evolved pairs, respectively. Duration of sympatric or allopatric evolution: (*a*) one week, (*b*) two weeks or (*c*) seven weeks.

With allopatrically and sympatrically evolved pairs for one week analysed together, inhibitory priority effects were weaker (i.e. P_{ij} was less negative) when the paired strains were more dissimilar (i.e. more complementary) in their biofilm characteristics (linear regression, $p = 0.004$). Analysed separately, this relationship was significant for both allopatrically evolved (linear regression, $p = 0.03$) and sympatrically evolved pairs (linear regression, $p = 0.03$) (figure 4*a*). After two weeks of shared evolutionary history, priority effects were weaker in more complementary pairs (linear regression, $p = 0.0014$) when sympatrically and allopatrically evolved pairs were analysed together. However, when analysed separately, only the relationship for allopatrically evolved pairs was significant (linear regression, $p = 0.004$) (figure 4*b*). No relationships (either combined or separately analysed) were significant between phenotypic complementarity and the strength of priority effects after seven weeks of evolutionary

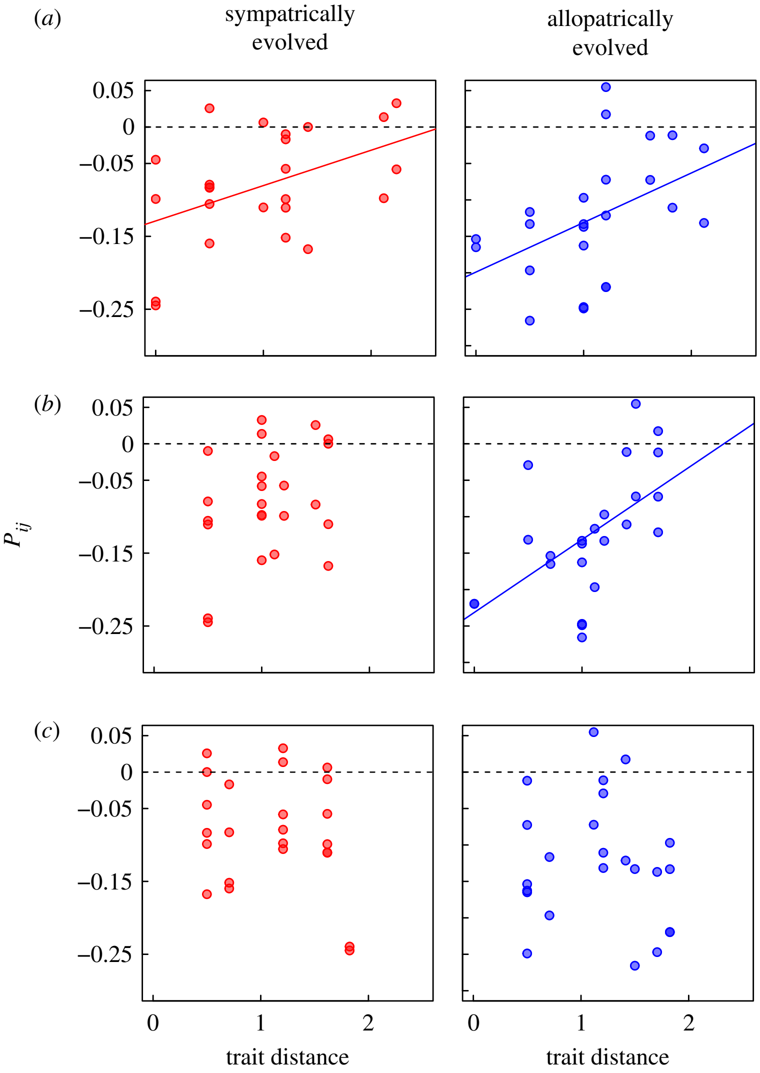

Figure 4. Relationship between phenotypic similarity (trait distance) and the strength of priority effects (P_{ij}). The x-axis is the Euclidean distance between strains i and j in mat phenotypes, as measured by webbing and thickness. The y-axis is the P_{ij} value for the corresponding strains i and j. Duration of sympatric or allopatric evolution: (*a*) one week, (*b*) two weeks or (*c*) seven weeks. For week 1 (*a*), the relationship was significant for both sympatrically and allopatrically evolved pairs (linear regression, $p = 0.03$). For week 2 (*b*), only allopatrically evolved pairs were significant (linear regression, $p = 0.004$). For week 7 (*c*), neither sympatrically nor allopatrically pairs showed a significant relationship.

history (figure 4*c*). This observation that the evolutionary treatment effect was mitigated with longer periods of evolutionary history was supported by the GLMM showing a significant interaction between Distance and Week (electronic supplementary material, table S7).

4. Discussion

In this laboratory experiment, we initially found a pattern suggesting weaker priority effects in pairs of populations that had evolved sympatrically prior to immigration than in those that had evolved allopatrically (figure 3*a*). However, as the duration of evolutionary history increased, this weakening of priority effects by sympatric evolution disappeared (figure 3*b*,*c*). These results provide the first experimental evidence, to our knowledge, that short-term, but not long-term, history of sympatric evolution might weaken the extent of historical contingency in community assembly. Our data further suggest that, in our experiment, the strength of priority effects was in part determined by the amount of phenotypic complementarity in interacting populations (figure 4), a finding consistent with the functional guild hypothesis demonstrated in grassland plants [32] and the niche component hypothesis proposed with nectar yeasts [29]. Our results are also consistent with those of Brockhurst *et al*. [11], who showed that evolution of character displacement in *P. fluorescens* biofilms allowed for higher productivity and invasion resistance. The novel aspect of our study, however, is that we examined the effect of the duration of evolutionary history, which revealed the time-sensitive influence of the history of sympatric evolution (figures 2 and 3).

Why was the effect of phenotypic complementarity lost over longer evolutionary periods? There are two potential explanations. First, two phases of trait evolution in competing populations may have resulted from the following scenario. Initially, sympatrically evolving pairs may have quickly achieved niche partitioning [14,22]. Subsequently, a longer period of sympatric evolution may have gradually led to increased competitive similarity among populations. Beyond theoretical support [15,17,33–36], empirical evidence for gradual convergence has been found in several taxonomic groups, including cichlid fishes [37], protozoans [38] and ovenbirds [18]. Second, both sympatrically and allopatrically evolving pairs may have initially diverged in traits, but sympatrically evolving pairs may have converged at a faster rate than allopatric pairs. More fine-grained temporal sampling at earlier time points, and longer periods of evolutionary history would help to distinguish the two alternative explanations. Either way, findings from our experiment suggest that slow trait convergence in sympatrically evolved species could influence how species interact ecologically when they colonize a new habitat.

One limitation of this study concerns how biofilm phenotypes were characterized. As in many other efforts to relate phenotypic variation to biotic interactions, it is unclear in this study how relevant our phenotypic characterization may be to explaining the strength of priority effects. For example, given the results for priority effects, one would expect sympatrically evolved pairs to be phenotypically more dissimilar than allopatrically evolved pairs in the week one replicates, but we did not observe this difference (t-test, $p = 0.6$, figure 4). Therefore, phenotypic similarity, as estimated in this study, does not really explain the difference that we observed in the strength of priority effects between sympatrically and allopatrically evolved pairs. Likewise, another expectation would be for allopatrically evolved pairs of week 2 and week 7 replicates to be more phenotypically similar to each other than sympatrically evolved pairs of week 1 replicates, but this expectation was not observed, either (figure 4). One possible explanation for these apparent discrepancies between expected and observed patterns is that the biofilms developed originally through mutations affecting the type of adhesion that we did not measure [22,25]. The thickness and webbing phenotypes we measured may have been a result of subsequent mutations that were of secondary importance to determining interactions between sympatrically evolved pairs. It is striking that significant relationships were still detected between phenotypic distance and the strength of priority effects even with crude phenotypic measurements like ours (figure 4). However, a more thorough trait characterization may enable a more mechanistic explanation of the weakened priority effects in sympatrically evolved pairs than is possible with our data.

Two other aspects of our experiment point to future research directions. First, the abiotic environment for our evolutionary treatments was the same as the environment for our assembly experiment. If the environment for community assembly was different from the historical environment in which populations had evolved, prior sympatric evolution might not have the same effects that we found (see also [12]), an idea that we believe deserves experimental tests. Second, our experiment focused on immigration by pairs of populations as a simplest case to study the role of arrival order. In more diverse communities, sympatric evolution affecting species traits can involve not only competitive interactions, but also other types of antagonistic and mutualistic interactions (e.g. predator–prey, host–parasite, plant–herbivore, plant–pollinator, habitat modification). Sympatric evolution involving these other ecological interaction types should also be studied to better understand evolutionary influences on priority effects.

Although results of microbial experiments like ours should not be uncritically extrapolated to other systems, the basic idea we have considered here may be broadly applicable, particularly for communities that assemble on islands, lakes and other isolated habitat patches with discrete boundaries. As these communities assemble by immigration and *in situ* diversification [39–41], deterministic sets of ecomorphs are expected to emerge through ecological niche filling [42]. However, this expectation is not always met, as shown in Anolis lizards [43], cichlid fishes [44] and Hawaiian spiders [45]. Our results suggest that variation in the evolutionary history of immigrants relative to one another may sometimes explain why we see a pattern of more deterministic assembly in some cases and more historically contingent assembly in others.

Data accessibility. Data are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.63t3d [46].

Authors' contributions. P.C.Z. and T.F. conceived and designed the study; P.C.Z. performed the experiments and analyses; and P.C.Z. and T.F. wrote the manuscript.

Competing interests. We have no competing interests.

Funding. This work was funded by an NSF Postdoctoral Research Fellowship (P.C.Z.) and a Stanford University Terman Fellowship (T.F.).

Acknowledgements. We thank Julia Tsai and Anna Wietelmann for laboratory assistance and Benjamin Callahan, Matthew Knope, Rachel Vannette, Andrew Letten, and other former and current members of the community ecology group at Stanford for comments. Michael Brockhurst and two anonymous reviewers also provided comments that improved the paper.

References

1. Palmgren A. 1926 Chance as an element in plant geography. In *Proceedings of the International Congress of Plant Sciences* (ed. BM Duggar), pp. 591–602. Menasha, WI: George Banta Publishing Company.
2. Sutherland JP. 1974 Multiple stable points in natural communities. *Am. Nat.* **108**, 859–873. (doi:10.1086/282961)
3. Drake JA. 1991 Community-assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.* **137**, 1–26. (doi:10.1086/285143)
4. Devevey G, Dang T, Graves CJ, Murray S, Brisson D. 2015 First arrived takes all: inhibitory priority effects dominate competition between co-infecting *Borrelia burgdorferi* strains. *BMC Microbiol.* **15**, 61. (doi:10.1186/s12866-015-0381-0)
5. Kennedy PG, Peay KG, Bruns TD. 2009 Root tip competition among ectomycorrhizal fungi: are priority effects a rule or an exception? *Ecology* **90**, 2098–2107. (doi:10.1890/08-1291.1)
6. Sarneel JM, Kardol P, Nilsson C. 2016 The importance of priority effects for riparian plant community dynamics. *J. Veg. Sci.* **27**, 658–667. (doi:10.1111/jvs.12412)
7. Rasmussen NL, Van Allen BG, Rudolf VH. 2014 Linking phenological shifts to species interactions through size-mediated priority effects. *J. Anim. Ecol.* **83**, 1206–1215. (doi:10.1111/1365-2656.12203)
8. Chase JM. 2003 Community assembly: when should history matter? *Oecologia* **136**, 489–498. (doi:10.1007/s00442-003-1311-7)
9. Fukami T. 2015 Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23. (doi:10.1146/annurev-ecolsys-110411-160340)
10. Schluter, D. 2000 Ecological character displacement in adaptive radiation. *Am. Nat.* **156**, 4–16. (doi:10.1086/303412)
11. Brockhurst MA, Hochberg ME, Bell T, Buckling A. 2006 Character displacement promotes cooperation in bacterial biofilms. *Curr. Biol.* **16**, 2030–2034. (doi:10.1016/j.cub.2006.08.068)

12. Knope ML, Forde SE, Fukami T. 2012 Evolutionary history, immigration history, and the extent of diversification in community assembly. *Front. Microbiol.* **2**, 273. (doi:10.3389/fmicb.2011.00273)
13. Tanentzap AJ, Brandt AJ, Smissen RD, Heenan PB, Fukami T, Lee WG. 2015 When do plant radiations influence community assembly? The importance of historical contingency in the race for niche space. *New Phytol.* **207**, 468–479. (doi:10.1111/nph.13362)
14. Brown WL, Wilson EO. 1956 Character displacement. *Syst. Zool.* **5**, 49–64. (doi:10.2307/2411924)
15. Hubbell SP. 2006 Neutral theory and the evolution of ecological equivalence. *Ecology* **87**, 1387–1398. (doi:10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2)
16. Streelman JT, Danley PD. 2003 The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol.* **18**, 126–131. (doi:10.1016/S0169-5347(02)00036-8)
17. terHorst CP, Miller TE. 2010 When can competition for resources lead to ecological equivalence? *Evol. Ecol. Res.* **12**, 843–854.
18. Tobias JA, Cornwallis CK, Derryberry EP, Claramunt S, Brumfield RT, Seddon N. 2014 Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* **506**, 359–363. (doi:10.1038/nature12874)
19. Rainey PB, Travisano M. 1998 Adaptive radiation in a heterogeneous environment. *Nature* **394**, 69–72. (doi:10.1038/27900)
20. Spiers AJ, Kahn SG, Bohannon J, Travisano M, Rainey PB. 2002 Adaptive divergence in experimental populations of *Pseudomonas fluorescens*. I. Genetic and phenotypic bases of wrinkly spreader fitness. *Genetics* **161**, 33–46.
21. Spiers AJ, Bohannon J, Gehrig SM, Rainey PB. 2003 Biofilm formation at the air–liquid interface by the *Pseudomonas fluorescens* SBW25 wrinkly spreader requires an acetylated form of cellulose. *Mol. Microbiol.* **50**, 15–27. (doi:10.1046/j.1365-2958.2003.03670.x)
22. Spiers AJ, Rainey PB. 2005 The *Pseudomonas fluorescens* SBW25 wrinkly spreader biofilm requires attachment factor, cellulose fibre and LPS interactions to maintain strength and integrity. *Microbiology* **151**, 2829–2839. (doi:10.1099/mic.0.27984-0)
23. Fukami T, Beaumont HJ, Zhang XX, Rainey PB. 2007 Immigration history controls diversification in experimental adaptive radiation. *Nature* **446**, 436–439. (doi:10.1038/nature05629)
24. Tan J, Yang X, Jiang L. 2017 Species ecological similarity modulates the importance of colonization history for adaptive radiation. *Evolution* **71**, 1719–1727. (doi:10.1111/evo.13249)
25. McDonald MJ. 2009 The genetics of *Pseudomonas fluorescens* SBW25: adaptation to a spatially structured environment. PhD thesis, Massey University, New Zealand.
26. Ellis CN, Traverse CC, Mayo-Smith L, Buskirk SW, Cooper VS. 2015 Character displacement and the evolution of niche complementarity in a model biofilm community. *Evolution* **69**, 283–293. (doi:10.1111/evo.12581)
27. Zhang X-X, Rainey PB. 2007 Construction and validation of a neutrally-marked strain of *Pseudomonas fluorescens* SBW25. *J. Microbiol. Meth.* **71**, 78–81. (doi:10.1016/j.mimet.2007.07.001)
28. Kassen R, Llewellyn M, Rainey PB. 2004 Ecological constraints on diversification in a model adaptive radiation. *Nature* **451**, 984–988. (doi:10.1038/nature02923)
29. Vannette RL, Fukami T. 2014 Historical contingency in species interactions: towards niche-based predictions. *Ecol. Lett.* **17**, 115–124. (doi:10.1111/ele.12204)
30. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.
31. R Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
32. Fargione J, Brown CS, Tilman D. 2003 Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl Acad. Sci. USA* **100**, 8916–8920. (doi:10.1073/pnas.1033107100)
33. MacArthur R, Levins R. 1967 The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385. (doi:10.1086/282505)
34. Abrams PA. 1987 Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution* **41**, 651–661. (doi:10.1111/j.1558-5646.1987.tb05836.x)
35. Scheffer M, van Nes EH. 2006 Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc. Natl Acad. Sci. USA* **103**, 6230–6235. (doi:10.1073/pnas.0508024103)
36. Grether GF, Losin N, Anderson CN, Okamoto K. 2009 The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biol. Rev. Camb. Philos. Soc.* **84**, 617–635. (doi:10.1111/j.1469-185X.2009.00089.x)
37. Muschick M, Indermaur A, Salzburger W. 2012 Convergent evolution within an adaptive radiation of cichlid fishes. *Curr. Biol.* **22**, 2362–2368. (doi:10.1016/j.cub.2012.10.048)
38. Miller TE, Moran ER, terHorst CP. 2014 Rethinking niche evolution: experiments with natural communities of protozoa in pitcher plants. *Am. Nat.* **184**, 277–283. (doi:10.1086/676943)
39. MacArthur RH, Wilson EO. 1963 An equilibrium theory of insular zoogeography. *Evolution* **17**, 373–387. (doi:10.1111/j.1558-5646.1963.tb03295.x)
40. Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
41. Hubbell SP. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
42. Mahler DL, Ingram T, Revell LJ, Losos JB. 2013 Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science* **341**, 292–295. (doi:10.1126/science.1232392)
43. Losos JB, Jackman TR, Larson A, de Queiroz K, Rodríguez-Schettino L. 1998 Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118. (doi:10.1126/science.279.5359.2115)
44. Seehausen O. 2006 African cichlid fish: a model system in adaptive radiation research. *Proc. R. Soc. B* **273**, 1987–1998. (doi:10.1098/rspb.2006.3539)
45. Gillespie R. 2004 Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359. (doi:10.1126/science.1091875)
46. Zee PC, Fukami T. 2018 Priority effects are weakened by a short, but not long, history of sympatric evolution. Dryad Digital Repository. (https://doi.org/10.5061/dryad.63t3d)