

## Research



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# Adaptation reduces competitive dominance and alters community assembly

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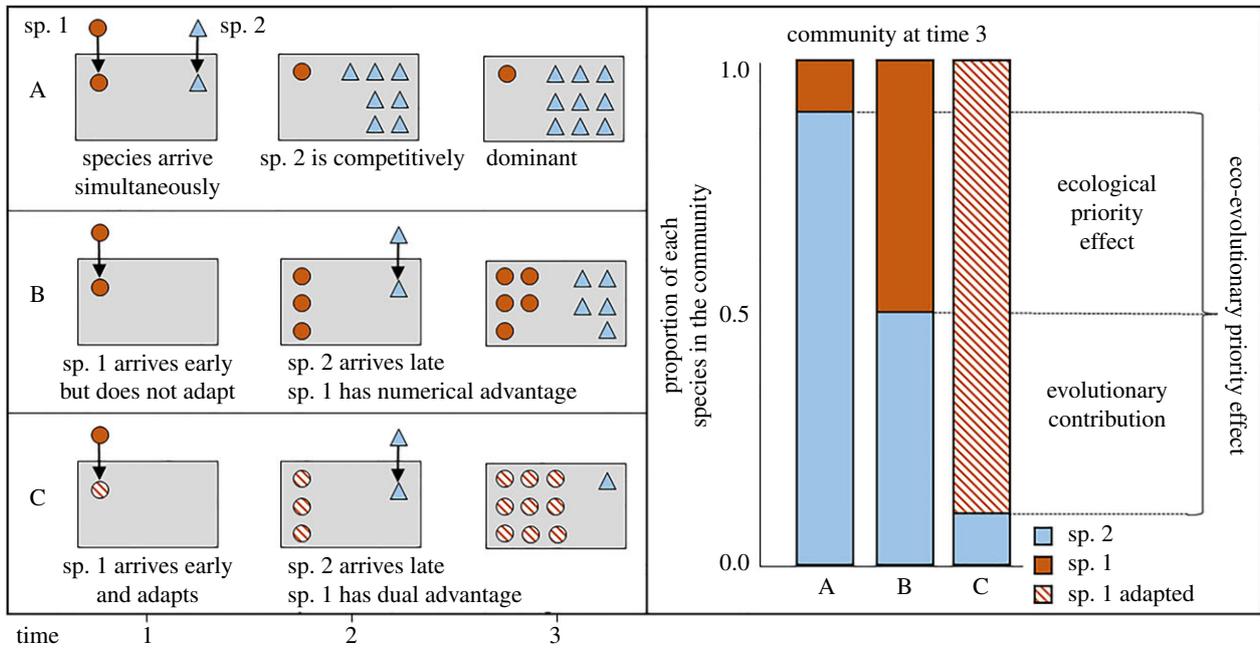
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A growing body of theory predicts that evolution of an early-arriving species in a new environment can produce a competitive advantage against later arriving species, therefore altering community assembly (i.e. the community monopolization hypothesis). Applications of the community monopolization hypothesis are increasing. However, experimental tests of the hypothesis are rare. Here, we provide a rare experimental demonstration of the community monopolization hypothesis using two archaeal species. We first expose one species to low- and high-temperature environments for 135 days. Populations in the high-temperature treatment evolved a 20% higher median performance when grown at high temperature. We then demonstrate that early arrival and adaptation reduce the abundance of a late-arriving species in the high-temperature environment by 63% relative to when both species arrive simultaneously and neither species is adapted to high temperature. These results are consistent with the community monopolization hypothesis and suggest that adaptation can reduce competitive dominance to alter community assembly. Hence, community monopolization might be much more common in nature than previously assumed. Our results strongly support the idea that patterns of biodiversity might often stem from a race between local adaptation and colonization of pre-adapted species.

## 1. Introduction

A central challenge in biology is to understand and predict the identity and abundance of species in ecological communities [1,2], which has become increasingly important as biologists predict the impacts of global change on biodiversity. Many theories attempt to explain the structure and composition of communities by focusing on ecological factors such as niches [3,4], dispersal [5,6], neutrality [7] and historical contingencies [8]. Although these theories and their recent syntheses have significantly improved our understanding of community assembly, many natural patterns are still unexplained [2,9]. For example, a meta-analysis of 158 datasets suggests that less than 50% of variation in community composition is explained by environmental and spatial processes [10]. The inability to explain community composition has led some researchers to suggest that community ecology is usually context-dependent and unpredictable, especially at the regional scales at which diversity is commonly studied [11].

Increasingly, evidence suggests that evolution often acts on short time scales and, therefore, alters ecological processes [12,13]. The integration of ecological and evolutionary perspectives might, therefore, shed new light on the predictability of ecological communities. Indeed, an eco-evolutionary perspective has



**Figure 1.** Three examples of community assembly over time (left) demonstrating ecological and eco-evolutionary priority effects. A. Two species (sp. 1, orange circles and sp. 2, blue triangles) arrive to an open habitat patch (grey square) at the same time. Species 2 has a competitive advantage and, therefore, occupies a much larger portion of the community in time 3 (bars on right). B. Species 1 arrives early and gains a numerical advantage prior to the arrival of species 2, which allows species 1 to occupy half the community in time 3. The difference between A and B is an ecological priority effect (right). C. Species 1 arrives early and adapts to novel conditions in the habitat patch prior to the arrival of species 2. Now, species 1 has a numerical and an adaptive advantage, which allows it to occupy a larger portion of the community in time 3. The difference between A and C is owing to an eco-evolutionary priority effect and the difference between B and C is the evolutionary contribution. (Online version in colour.)

already provided new insights about species coexistence, food-web assembly, invasion biology and the redistribution of biodiversity under climate change [14–16]. In particular, by combining evolution with the metacommunity concept, the evolving metacommunity framework proposes an integrated role for dispersal, colonization, niche evolution and species interactions in determining biodiversity patterns [17,18].

An important hypothesis advanced by the evolving metacommunity framework is the contribution of evolution to priority effects (figure 1). A priority effect occurs when the order in which species arrive to a patch alters community assembly, usually because the first species to colonize a location gains a competitive advantage over later-arriving species (figure 1: A,B). Purely ecological priority effects often explain patterns of community assembly, stability and composition [8]. However, evolution can also create or enhance priority effects (i.e. evolutionary and eco-evolutionary priority effect, respectively). Specifically, if a species arrives to a patch to which it is initially maladapted and evolves increased fitness (i.e. adapts) prior to the arrival of competing species, this adaptation can provide advantages against later arriving species that results in a priority effect (figure 1: C). Evolutionary and eco-evolutionary priority effects (hereafter eco-evolutionary priority effects for simplicity) differ from well-known ecological priority effects in that rapid evolution of the early-arriving species causes or enhances the competitive advantage that alters community assembly (figure 1). Eco-evolutionary priority effects, therefore, depend on a race between adaptation of the first species arriving to a patch and colonization by pre-adapted species [19,20]. The three step eco-evolutionary process—early arrival, adaptation and altered assembly—is known as the community monopolization hypothesis [19].

The community monopolization hypothesis has engendered a suite of recent theoretical explorations that suggest eco-evolutionary priority effects could be common in nature [19]. Original theory suggested that community monopolization effects were only likely when dispersal probability was low [21] and could be thwarted if pre-adapted species occurred in the metacommunity [22]. However, subsequent theory has added a number of complicating factors and demonstrated that eco-evolutionary priority effects can occur under commonly observed dispersal probabilities, when pre-adapted species occur in the metacommunity, in the presence of gene flow, under many landscape structures and with both sexual and asexual reproduction [20,23]. Applications of the community monopolization hypothesis are also providing novel insights about observed adaptive radiations on remote islands [20,24], and about the response of biodiversity to global change [19,21,25]. Most recently, theory has demonstrated how unexplained variation in communities and neutral-like characteristics can arise from eco-evolutionary priority effects [26].

Despite the potential importance and its increasing application, empirical tests of the community monopolization hypothesis are rare. Early experiments and observations supporting the hypothesis fail to demonstrate all three steps of the eco-evolutionary process [27,28] or test the related single-species version of the hypothesis, the population monopolization hypothesis [29,30]. Within-species demonstrations might be more likely to result in eco-evolutionary priority effects owing to the functional equivalence between the invading and adapted ecotypes, given their genetic similarity and rapid evolution of traits caused by simple genetic changes [31]. Greater differences among highly diverged species might reduce eco-evolutionary priority effects if competing

species diverge into separate niches [32] or compete so asymmetrically that no level of adaptation can overcome competition. Only one study has demonstrated the dynamic nature of colonization, adaptation and altered community assembly described by the community monopolization hypothesis. Gómez *et al.* [33] demonstrated that community structure in a warm compost environment differed depending on whether an early-arriving species, *Pseudomonas fluorescens*, had adapted to the novel environment. However, in this experiment, an entire community containing many species arrived simultaneously after adaptation of the early-arriving species [33]. The simultaneous invasion by many species represents a special case in nature and is not a scenario that has been explored in mathematical models used to develop the community monopolization hypothesis. Moreover, the simultaneous invasion by many species probably favours an eco-evolutionary priority effect owing to sampling, where an increase in the number of invading species increases the likelihood that at least one species is affected by evolution of the early-arriving species. Hence, direct tests of theoretical predictions are still needed to demonstrate the generality of the community monopolization hypothesis.

Here, we provide a direct test of the community monopolization hypothesis as described by theory using two highly diverged archaeal species in the genus *Haloferax* that compete for resources in aquatic environments: *Haloferax volcanii* and *Haloferax mediterranei*. *Haloferax volcanii* and *H. mediterranei* have on average 84.6% nucleotide identity among shared orthologues [34] and are estimated to have diverged approximately 80 Ma [35], which is similar to humans and mice [36,37]. Hence, a test of the community monopolization hypothesis with these two species moves beyond testing the single-species version of the hypothesis. Also, *H. mediterranei* has characteristics of a ‘microbial weed’, including the most rapid rate of cell division among halophilic archaeon and broad environmental tolerances [38]. These characteristics probably make *H. mediterranei* a superior competitor under common laboratory conditions (see below). Hence, evaluating whether adaptation of *H. volcanii* can overcome this competitive dominance and alter community assembly provides a strong and novel test of the community monopolization hypothesis. We first test if *H. mediterranei* is indeed a dominant competitor under our laboratory conditions. We then allow *H. volcanii* to adapt to high-temperature conditions in the laboratory and test if this adaptation alters the colonization ability of *H. mediterranei* at high temperature.

## 2. Methods

### (a) Study system and laboratory conditions

*Haloferax* (Class: *Halobacteria*) is a genus of aerobic, heterotrophic Archaea that live in hypersaline aquatic habitats such as the Dead Sea. *Haloferax* are mesophilic and have one generation approximately every 2–4 h at temperatures between 40 and 50°C. We grew cultures in a low-temperature (42°C) environment to represent ideal conditions and a high-temperature (48°C) environment to represent suboptimal conditions. We chose these temperatures based on preliminary experiments that suggested 42°C is ideal and 48°C is suboptimal for *H. volcanii*. For this study, we used an auxotroph of each focal species: *H. volcanii* strain H98, developed as a uracil and thymidine auxotroph [39–41], and *H. mediterranei* strain WR646, developed as a uracil and tryptophan auxotroph [42]. These auxotrophs facilitated selective plating to count the relative abundance of each species in mixed cultures (see below).

We grew laboratory populations in rich medium supplemented with thymidine (see the electronic supplementary material for recipe). Except where we state otherwise, we grew laboratory populations in 2 ml, 96-well plates containing 320 µl of medium, and sealed the plates with adhesive foil. We interspersed wells containing isolated populations with empty wells or wells containing only medium to avoid cross-contamination among isolated populations. Preliminary tests indicated no signs of cross-contamination using these techniques. We kept cultures in exponential phase by transferring 20 µl of homogenized culture from the most recently created plate to 300 µl of fresh medium in a new plate every 2–5 days. Following methods described by Lenski [43] and Van den Bergh *et al.* [44], this serial dilution protocol results in an average generation time of approximately one generation per day.

### (b) Testing for competitive dominance

We first tested whether *H. mediterranei* was competitively dominant in the high-temperature environment as predicted by its high growth rate and broad environmental tolerances [38]. This experiment also represented a scenario where both species arrive to a high-temperature environment simultaneously and with equal abundance (figure 1: A, see below). We isolated four biological replicates of both species by picking four isolated colonies from an agar plate streaked from a stock culture. We then created mixed-species communities using one biological replicate from each species in a fully factorial design (i.e. 16 mixed-species communities). We inoculated 160 µl of medium with 20 µl of *H. volcanii* and 20 µl of *H. mediterranei* culture, each with a standardized density of  $1.1 \times 10^6$  colony forming units (CFUs) ml<sup>-1</sup>. We grew mixed-species cultures for 48 h in a 96-well optical plate placed in a 48°C shaking incubator. After 48 h, we measured the abundance of *H. volcanii* and *H. mediterranei* in each community using selective plating. We plated serial dilutions of all communities ranging from 10<sup>-5</sup> to 10<sup>-8</sup> onto 100 mm agar plates created with casamino acids medium supplemented with uracil, and either thymidine and hypoxanthine to allow *H. volcanii* growth or tryptophan to allow *H. mediterranei* growth (see the electronic supplementary material for media recipe). After incubation, we counted the CFUs growing on each plate type, and averaged the results to provide an estimate of density for each species in each of the 16 replicate communities. We predicted that *H. mediterranei* would have higher abundance than *H. volcanii* despite starting at equal densities (figure 1: A), which would demonstrate competitive dominance.

### (c) Experimental evolution of *Haloferax volcanii*

We isolated 12 biological replicates (hereafter ‘founding populations’) of *H. volcanii* by isolating 12 colonies from an agar plate streaked from a stock culture (electronic supplementary material, figure S1A). These biological replicates were independent of the replicates used in the competitive dominance experiment. We transferred each colony to 600 µl of medium in a 96-well plate and kept the founding populations at 42°C for 24 days to allow adaptation to the laboratory environment (electronic supplementary material, figure S1A). After 24 days, we replicated this initial plate six times in separate 96-well plates. Our design resulted in 72 isolated populations founded from 12 biological replicates (electronic supplementary material, figure S1A). We grew these replicate plates at 42°C for an additional 8 days prior to randomly assigning half the plates to a low-temperature treatment (42°C) and the other half to a high-temperature treatment (48°C; electronic supplementary material, figure S1B). At this time, we also preserved the 12 founding populations used to create the six replicates by combining 25 µl of homogenized culture with 25 µl of a 50% glycerol solution containing 14% NaCl and then froze the cultures at –80°C (electronic supplementary material, figure S1B). The low-temperature treatment remained constant at 42°C for the

remainder of the experiment (electronic supplementary material, figure S1B). The high-temperature treatment gradually increased from 42°C to 48°C over 57 days and then remained at 48°C for another 78 days (electronic supplementary material, figure S1B). We cycled the plates through four incubators during this time to avoid confounding treatment effects with potential incubator effects. We resurrected the founding populations 14 days prior to the end of the adaptation experiment and kept them at 42°C to allow for comparison with the adaptation treatments (electronic supplementary material, figure S1B). We kept all populations in exponential phase throughout the duration of the evolution experiment as described above. However, during the final 5 days, we did not provide populations with fresh medium to allow them to reach stationary phase (i.e. maximum density) and then moved all populations to room temperature to slow further adaptation. Because growth is slow at room temperature, storing the populations at room temperature in stationary phase effectively preserved the populations under common conditions and at a constant density, which facilitated standardizing density among populations for the competition experiments below.

#### (d) Testing for adaptation

We tested for divergent adaptation among treatments by evaluating the maximum density achieved by the founding, low-temperature and high-temperature populations when grown at 42°C and 48°C (electronic supplementary material, figure S1C). Maximum density is one of many, often correlated, components of fitness used in microbial growth experiments [45,46]. We first consolidated populations into two new plates: (i) a plate containing the 12 founding populations and the 36 low-temperature populations, which we put in a 42°C incubator; and (ii) a plate containing the 36 high-temperature populations, which we put in a 48°C incubator. After one week of growth, we moved all populations to 42°C for 48 h to provide a common acclimation temperature. Although this acclimation step could reverse potential evolution in the high-temperature treatments, we felt this step was necessary to demonstrate evolution because acclimation to different temperatures can substantially alter the results of common garden experiments [47]. After acclimation, we split both plates into two identical replicates by transferring 20 µl of homogenized culture into 80 µl of medium in 96-well optical plates. We sealed each plate with transparent plastic film and distributed the plates between a 42°C incubator and a 48°C incubator, such that both low-temperature and high-temperature populations were growing at 42°C and 48°C. After 9 days, we measured optical density by absorbance of light at 620 nm and used this as an assay of performance. We excluded four populations from our analysis because they did not grow on the final plate used to measure optical density. However, including these populations in the analysis did not change our main conclusions (electronic supplementary material).

We tested for divergent adaptation using a Bayesian mixed-effects model with the 'R2jags' package in the R statistical software v. 3.6.0. We used maximum optical density as the response variable and the following independent variables: treatment (founder, low-temperature and high-temperature treatments), common garden temperature (42 and 48°C), and their interaction. We also included random intercept terms for biological replicate to account for the replication of biological replicates across plates and treatments, and plate to account for any potential differences among plates within treatments. We used weakly informative normal priors with a mean of zero and a variance of 1000 for all coefficients and a uniform prior ranging between 0 and 100 for the standard deviation of the error terms [48]. We ran three chains in the Markov chain Monte Carlo (MCMC) sampling each for 100 000 iterations with a burn-in period of 50 000 iterations and retained every tenth draw, which resulted

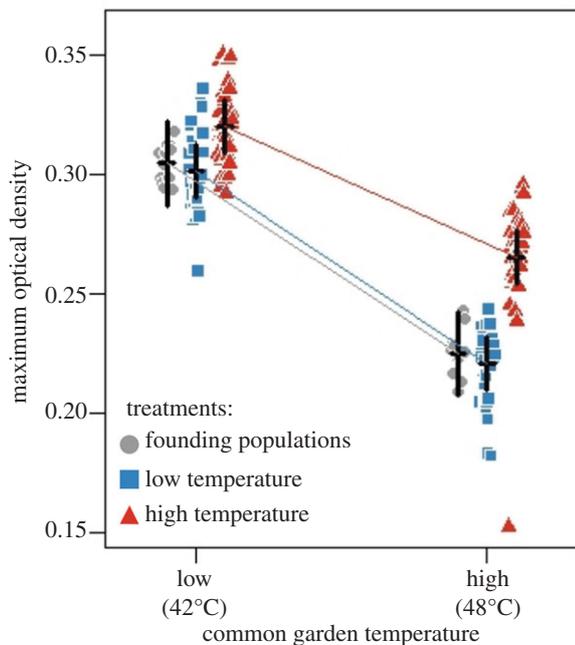
in well-mixed chains for all parameters (i.e. Gelman–Rubin statistics < 1.01). Posterior predictive checks of the mean and variance of the data suggested the model fit the data well (Bayesian  $p_{\text{mean}} = 0.564$ , Bayesian  $p_{\text{variance}} = 0.507$ ). We calculated the posterior for all pairwise differences among treatments at each temperature to evaluate adaptation. We considered pairwise differences significant if the 95% credible interval (CI) of the difference did not overlap zero.

#### (e) Testing for priority effects

We tested for ecological and eco-evolutionary priority effects (figure 1) by allowing *H. mediterranei* to invade low- and high-temperature adapted populations of *H. volcanii* growing at the high temperature (48°C). Invasion of *H. volcanii* populations adapted to the low temperature (but growing in the high temperature) represents a scenario where *H. volcanii* arrives first, gains a numerical advantage, but does not adapt to the high temperature (figure 1: B). The numerical advantage could result in an ecological priority effect (figure 1). Invasion of *H. volcanii* populations adapted to and growing at the high temperature represents a scenario where *H. volcanii* arrives first and adapts to the high temperature prior to the arrival of *H. mediterranei* (figure 1: C), which could result in an eco-evolutionary priority effect (figure 1). The community monopolization hypothesis predicts that the abundance of the second colonist should be lowest when it invades adapted populations of the first colonist (figure 1).

We conducted the invasion experiments by first inoculating 160 µl of medium with 20 µl of *H. volcanii* culture with a standardized density of  $1.1 \times 10^7$  CFUs ml<sup>-1</sup>. We then immediately added 20 µl of *H. mediterranei* culture with a standardized density of  $1.1 \times 10^6$  CFUs ml<sup>-1</sup>. This procedure simulated early arrival of *H. volcanii* and a subsequent numerical advantage. We did not allow *H. volcanii* to gain a numerical advantage by waiting to add *H. mediterranei* (as would happen in nature) because we wanted to ensure the initial densities of both species were standardized across treatments and replicates. We replicated this invasion using eight *H. volcanii* populations from the low-temperature treatment and eight populations from the high-temperature treatment that originated from the same eight founding populations, which created a paired design. The single *H. mediterranei* culture used in these experiments was a homogenized mixture of populations that had been growing at 42°C for 65 days. We grew mixed-species cultures for 48 h in a 96-well optical plate placed in a 48°C shaking incubator. After 48 h, we measured the abundance of *H. volcanii* and *H. mediterranei* in each community using selective plating as described above, except we used 50 mm agar plates. We also plated a 10<sup>-3</sup> dilution of a subset of communities on plates lacking both thymidine and tryptophan (but containing uracil) to test for possible mating, recombination and loss of auxotrophy between congeners that could undermine the efficacy of selective media to facilitate measurement of species-specific abundances [42]. We observed no growth on uracil-only plates in this experiment, indicating no substantial recombination between species and no contamination of the communities with non-auxotrophic strains.

We used a Bayesian generalized mixed-effects model to test the predictions in figure 1. We modelled the proportion of *H. mediterranei* in mixed-species communities from each treatment, including the competitive dominance experiments described above. We used a beta regression with a factor identifying the three treatments and random effects for the *H. volcanii* founding population used in all experiments (i.e. accounting for the paired design) and *H. mediterranei* biological replicate used in the competitive dominance experiments. We used weakly informative priors as described above and a weakly informative gamma prior with shape and scale parameters set to 0.01 for the precision coefficient. We ran three chains in the MCMC sampling each for



**Figure 2.** Populations of *H. volcanii* exposed to high temperature for 135 days perform better than founding populations and populations from the low-temperature treatment when grown in the high-temperature (48°C) environment. Points show the maximum optical density (a measure of performance) for each founding population (grey dots), each population from the low-temperature treatment (blue squares) and each population from the high-temperature treatment (red triangles) when grown at 42°C and 48°C. Black crosses are the median (horizontal line) and 95% credible interval (vertical line) for each group estimated from a Bayesian mixed-effects model. See the electronic supplementary material, figure S2 for posterior plots of the differences among treatments. (Online version in colour.)

250 000 iterations with a burn-in period of 50 000 iterations and retained every tenth draw, which resulted in well-mixed chains for all parameters (i.e. Gelman–Rubin statistics < 1.01). Posterior predictive checks of the mean and variance of the data suggest the model fit the data well (Bayesian  $p_{\text{mean}} = 0.514$ , Bayesian  $p_{\text{variance}} = 0.594$ ). We calculated the posterior difference among treatments and considered the treatments different if the 95% credible interval of the difference did not overlap zero.

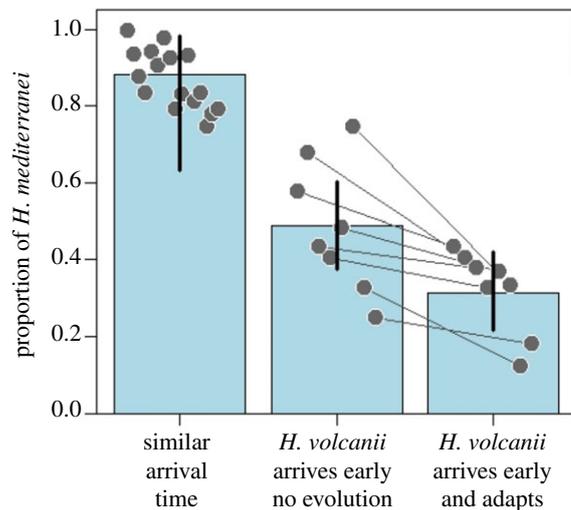
### 3. Results

#### (a) Competitive dominance

*Haloflex mediterranei* dominated the community with a median proportion of 0.88 when both species arrived simultaneously to the high-temperature environment at equal abundance (figure 3). This demonstrates the competitive dominance we expected in the absence of priority effects.

#### (b) Adaptation to high temperature

*Haloflex volcanii* populations that grew in the high-temperature environment for 135 days adapted to the high temperature. *Haloflex volcanii* populations from the high-temperature treatment had an 18% higher median performance than the founding populations (95% CI of the difference in performance = 0.021–0.060) and a 20% higher median performance than populations from the low-temperature treatment (95% CI of the difference in performance = 0.030–0.059) when grown at the high temperature (figure 2; electronic supplementary



**Figure 3.** Arrival time and evolution affect community assembly between two species of *Halobacteria*—*H. volcanii* and *H. mediterranei*—when grown in a high-temperature environment. When both species arrive to an open high-temperature environment at similar times, *H. mediterranei* is competitively dominant (left bar). However, if *H. volcanii* arrives first and gains a numerical advantage, the proportion of *H. mediterranei* in the population is reduced by a median of 45% (middle bar), which is an ecological priority effect. If *H. volcanii* arrives first and adapts to the high temperature, the proportion of *H. mediterranei* is further reduced by 36% (right bar), which is the signature outcome of an eco-evolutionary priority effect. The blue bars show the median proportion of *H. mediterranei* 48 h after invading populations of *H. volcanii*. Error bars are 95% credible intervals from a Bayesian generalized mixed-effects model. Points show the proportion of *H. mediterranei* in each of the 32 competition experiments. Diagonal lines between points over the right two bars join paired points based on the founding populations of *H. volcanii* used to start the low- and high-temperature treatments. See the electronic supplementary material, figure S3 for posterior plots of the differences among treatments. (Online version in colour.)

material, figure S2). Populations from the high-temperature treatment also had a 6% higher median performance than populations from the low-temperature treatment when grown at low temperature (95% CI of the difference in performance = 0.004–0.033), but performance did not differ from the founders when grown at low temperature (95% CI of the difference in performance = –0.004 to 0.035; figure 2; electronic supplementary material, figure S2). The median performance did not differ between the founding populations and populations from the low-temperature treatment when grown at the low temperature (95% CI of the difference in performance = –0.023 to 0.017) or high temperature (95% CI of the difference in performance = –0.024 to 0.015), suggesting no evolution in response to laboratory conditions other than temperature (figure 2; electronic supplementary material, figure S2).

#### (c) Ecological and eco-evolutionary priority effects

When unadapted *H. volcanii* arrived early to the high-temperature environment and gained a numerical advantage, the proportion of *H. mediterranei* in the community decreased by a median of 45% relative to when the two species arrived simultaneously (i.e. in the competitive dominance experiment), demonstrating an ecological priority effect (figure 3). The median difference in the proportion of *H. mediterranei* in the community between these two scenarios was 0.38 (95% CI = 0.11–0.54; figure 3; electronic supplementary material,

figure S3). When *H. volcanii* arrived early and adapted to the high-temperature environment, the proportion of *H. mediterranei* in the community decreased by a median of 36% relative to when *H. volcanii* did not adapt, demonstrating an eco-evolutionary priority effect consistent with the community monopolization hypothesis. The median difference in the proportion of *H. mediterranei* in the community between these two treatments was 0.17 (95% CI = 0.07–0.27; figure 3; electronic supplementary material, figure S3). Overall, early arrival and adaptation resulted in a 63% median reduction in the proportion of *H. mediterranei* in the community, and 31% of this change was owing to evolution (figure 3).

#### 4. Discussion

We provide, to our knowledge, the first experimental example of an eco-evolutionary priority effect between two highly diverged species and, therefore, strong experimental support of the community monopolization hypothesis. By focusing on two highly diverged species, our work builds on prior examples that provided within-species demonstrations of eco-evolutionary priority effects. Moreover, our work suggests eco-evolutionary priority effects can occur under strong asymmetric competition. Most theory on eco-evolutionary priority effects assumes species are neutral at either the local or meta-community scale prior to evolution [20,23]. In nature, however, species often exhibit strong asymmetric competition, which is often thought to negate priority effects [8]. Our results demonstrate that evolution can reduce this asymmetric competition and alter community assembly, which significantly broadens the contexts where eco-evolutionary priority effects might be important in nature. Our work, therefore, opens the door for a fuller exploration of eco-evolutionary priority effects among a wide variety of species in natural communities.

Our experiments provide support for a growing number of theoretical, conceptual and observational studies using eco-evolutionary priority effects to explain biodiversity patterns in nature. For example, recent studies have provided phylogenetic support for the long-held idea that adaptive radiations by initial colonists can affect community assembly [49–52]. Plants in the Canary Islands and Macaronesia are probably monophyletic because early colonists radiated to fill empty niches and restricted the colonization of other species via niche preemption [53,54]. Molecular phylogenies and palaeo-reconstruction of available niches provide strong support for similar macro-evolutionary priority effects for alpine plants in New Zealand [55–57]. Models and phylogenetics also provide compelling evidence that *Tetragnatha* spiders often diversify and monopolize habitat on newly formed Hawaiian islands, therefore limiting colonization by other species [20,24].

Our results are also relevant to thinking more critically about the joint ecological and evolutionary processes that determine future communities in response to anthropogenic disturbances such as climate change. To date, most predictions of the redistribution of biodiversity under global change take a single-species, niche-focused approach and suggest that many species will simply shift their distribution to track suitable habitat [58,59]. However, theory has already suggested that the redistribution and loss of biodiversity owing to global change might depend on a race between local adaptation and the movement of pre-adapted species

[16,22,25,60]. For example, if a species adapts to changing climates in its current range or in newly encountered environments as it expands its range, it could prevent other species from shifting their ranges and lead to higher levels of extinction than predicted without evolution [16,25,61]. Our results demonstrate such eco-evolutionary species interactions owing to warming. However, an important next step is to determine how quickly evolution can result in a priority effect. In our experiments, adaptation occurred over 135 days (i.e. approx. 135 generations following calculations from Lenski [43] and Van den Bergh *et al.* [44] that account for our serial transfer protocol, or 1620 generations using a 2 h generation time), which is certainly relevant to microbial responses to climate change, but probably too slow to alter climate change responses for species with longer generation times. However, cases of rapid evolution in response to climate change are accumulating quickly for a wide variety of species [16,62]. Thus, it seems likely that eco-evolutionary priority effects could occur under climate change and alter species responses.

Highly controlled laboratory experiments in simple communities like ours are required to demonstrate proof-of-concept, but necessarily exclude important details that could alter results in nature. Future experiments should test how quickly evolution can alter priority effects under different biological contexts such as sexual versus asexual reproduction or with varying levels of genetic diversity [19,20]. Environmental contexts, such as varying degrees of isolation might also be important [19,20,25]. Moreover, experiments should evaluate how eco-evolutionary dynamics in mixed-species communities play out over longer timeframes. We only maintained mixed-species communities for 48 h and we do not know how eco-evolutionary dynamics would play out over longer periods. Indeed, competition for resources over longer time frames can have complex effects on eco-evolutionary dynamics [63]. Moreover, co-evolution among species can affect the outcome of invasions [64,65]. Continued adaptation to high temperature by *H. volcanii* could result in the eventual exclusion of *H. mediterranei*, which would enhance the results presented here. Alternatively, the eco-evolutionary priority effects we observed could be transient, and eventually *H. mediterranei* could exclude *H. volcanii*. Nevertheless, transient eco-evolutionary priority effects will slow ecological dynamics, which could explain biodiversity patterns in nature, such as why species are often not responding to climate change as predicted [16,66]. Last, future experiments should incorporate a fully factorial design including all combinations of adaptation of the early-arriving species (i.e. adapted or unadapted) and arrival time of the late-arriving species (i.e. simultaneous or late), which would provide a more comprehensive understanding of whether the contributions of ecology and evolution are additive or interactive. Ultimately, the next step in understanding the importance of eco-evolutionary priority effects is experiments in nature with a diversity of taxa [13,67]. Such experiments will help predict where and when evolution could win the race against colonization by pre-adapted species.

Overall, our results provide experimental support for the idea that the joint processes of dispersal, niche evolution and local species interactions act together in ways that determine community assembly and ultimately affect the abundances of competing species. Accounting for these interacting processes could alter explanations for observed patterns and predictions in diverse fields of ecology and

evolution, including biogeography, community ecology, restoration ecology and climate change biology [8,19]. The evolving metacommunity concept, from which the community monopolization hypothesis stems, offers a complementary and synergistic view of the tension between the dominant biodiversity theories ruled by either niche-based determinism or neutral stochasticity. Joining these views suggests that understanding arrival times and adaptation could allow us to forecast outcomes of community assembly and contribute to a more predictive community ecology.

**Data accessibility.** All the data and code used to produce the results presented in this paper are included in the electronic supplementary material.

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