Effects of rapid evolution on species coexistence

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Increasing evidence for rapid evolution suggests that the maintenance of species diversity in ecological communities may be influenced by more than purely ecological processes. Classic theory shows that interspecific competition may select for traits that increase niche differentiation, weakening competition and thus promoting species coexistence. While empirical work has demonstrated trait evolution in response to competition, if and how evolution affects the dynamics of the competing species—the key step for completing the required eco-evolutionary feedback—has been difficult to resolve. Here, we show that evolution in response to interspecific competition feeds back to change the course of competitive population dynamics of aquatic plant species over 10–15 generations in the field. By manipulating selection imposed by heterospecific competitors in experimental ponds, we demonstrate that (*i*) interspecific competition drives rapid genotypic change, and (*ii*) this evolutionary change in one competitor, while not changing the coexistence outcome, causes the population trajectories of the two competing species to converge. In contrast to the common expectation that interspecific competition should drive the evolution of niche differentiation, our results suggest that genotypic evolution resulted in phenotypic changes that altered population dynamics by affecting the competitive hierarchy. This result is consistent with theory suggesting that competition for essential resources can limit opportunities for the evolution of niche differentiation. Our finding that rapid evolution regulates the dynamics of competing species suggests that ecosystems may rely on continuous feedbacks between ecology and evolution to maintain species diversity.

biodiversity | eco-evolutionary dynamics | competition | character displacement | diversity maintenance

Classic theory suggests that natural selection arising from interspecific competition should generate phenotypic differences between species that weaken interspecific competition, favoring species coexistence (1–5). However, while this eco-evolutionary process has become central to explanations for diversity (6, 7), empirical evidence for such feedbacks between ecology and evolution remain equivocal for three reasons (8). First, evolution in response to interspecific competition is most commonly inferred from post hoc observational evidence that morphological differences between species are larger when species occur together (in sympatry) vs. apart (in allopatry) (8–10), with the strongest evidence coming from natural experiments (11, 12). While a few experimental studies demonstrate trait change in response to interspecific competition (13, 14), the causal influence of competition, the repeatability of the evolutionary change, and the speed of evolution relative to the rate of competitive population dynamics are often unknown (8).

Second, and maybe more importantly, while the feedback from evolutionary change to the population dynamics of the competing species is essential for contemporary evolution to affect diversity maintenance, this feedback is rarely empirically quantified (8, 15, 16). In lieu of direct empirical evidence, population dynamic consequences are typically assumed following the common theoretical expectation that evolved trait and behavioral differences should promote coexistence by increasing niche differences (7, 8, 11, 17–19). However, as emphasized in recent reviews, the assumption that evolution should increase niche differences may not always be justified (16, 20). Developments in species coexistence theory demonstrate an equally important role for differences between species in competitive ability in determining competitive outcomes (21–23). Indeed, theory suggests that evolution of competitive ability may be more likely when opportunities for the evolution of niche differentiation are limited, as occurs when species cannot substitute other resources for the ones used by their competitors (24, 25). In general then, it remains unclear how competitive population dynamics should change as a consequence of evolution, and the resulting eco-evolutionary feedbacks could be more complex than is generally appreciated (16, 20).

A third reason for poorly resolved empirical evidence for competitive, eco-evolutionary feedbacks relates to the concurrent nature of the ecological and evolutionary changes. If ecological and evolutionary processes simultaneously feed back on one another, this dynamic cannot be resolved by assuming a separation of timescales, and quantifying the population-dynamic consequences of past evolutionary change (15, 26). These three limitations have motivated recent calls for combining experimental evolution approaches (8) more typical of studies in laboratory microbial systems (27) with the tools of quantitative coexistence theory (16) to understand how rapid evolution in response to competition affects species coexistence in more natural systems.

Here, we demonstrate how eco-evolutionary feedbacks influence coexistence by experimentally manipulating the ability of aquatic plant species to evolve in response to interspecific competition while simultaneously quantifying their multigenerational competitive population dynamics. Our approach allows us to address three questions: (*i*) Does interspecific competition cause evolutionary change on ecological timescales? (*ii*) Is this evolutionary change consistent and large enough to alter the contemporary dynamics of the competing species? And, (*iii*) how

Significance

Understanding the dynamics of competing species is essential for explaining the origin and maintenance of species diversity. However, ecologists have typically ignored the potential for rapid evolution to alter the contemporary population dynamics of competing species. By disrupting the ability of aquatic plants to evolve in response to interspecific competition, we show that competition drives evolutionary change and this evolutionary change simultaneously feeds back to alter the abundance of competing species over just a few generations. Rather than increasing niche differences as classic theory predicts, evolution causes population trajectories to converge by changing the competitive hierarchy. Our results suggest that understanding how species diversity is maintained requires explicitly accounting for the effects of rapid evolution on competitive population dynamics.

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does this feedback influence coexistence via the evolution of niche differences and/or species' competitive abilities? To answer these questions, we studied two species of floating, aquatic plants—*Lemna minor* and *Spirodela polyrhiza*. Both species have fast life cycles with asexual reproduction every 3–7 d and ∼20 generations per growing season (28), providing an ideal system for understanding how eco-evolutionary feedbacks affect the contemporary dynamics of competing species.

We imposed two selection treatments on multigenotype populations of the two species competing in replicate experimental ponds in the field (*Materials and Methods*). In the "heterospecific selection" treatment, the two species competed with each other in competitive arenas and were free to evolve in response to interspecific competition. In the "conspecific selection" treatment, the two species also competed with each other, but in this treatment we prevented evolution in response to interspecific competition. We did so by replacing all individuals in these competitive arenas every 2 wk with the same number of individuals of each species, but drawn from multigenotype populations growing and evolving in single-species monocultures in the same ponds. Thus, our experimental manipulation preserves the ongoing effects of interspecific competition on the population sizes of the two species, but prevents evolution in response to interspecific competition, and thereby prevents this evolution from affecting the ecological dynamics of the competing species (29). Importantly, the species in both treatments were able to evolve to other biotic and abiotic selection pressures arising naturally in the field during the experiment. To quantify eco-evolutionary trajectories, we combined assessments of genotypic and phenotypic change with surveys of multigenerational competitive population dynamics. Finally, we did additional competition experiments using the evolved populations to quantify how evolution affects ecological dynamics by altering niche and competitive-ability differences.

Results and Discussion

Interspecific competition drove rapid evolutionary change (Fig. 1). Specifically, selection in response to conspecific vs. heterospecific competitors generated differences in the genotypic composition of the evolved populations of *L. minor* [permutational multivariate analysis of variance (PERMANOVA): $F_{(1,12)} = 2.80$, $P = 0.019$], but not of *S. polyrhiza* [$F_{(1,12)} = 0.1$, $P = 0.99$; *SI Appendix*, Fig. S1 and Table S1]. The different evolutionary trajectories for *L. minor* were driven most strongly by changes in the frequency of a single genotype (genotype 1 in Fig. 1). Selection for this genotype was positive in both treatments, but significantly less so when in competition with heterospecific competitors [$t_{(12)} = 4.94$, $P < 0.001$; *SI Appendix*, Fig. S2]. This genotype had the most extreme phenotypic trait values in the population (*SI Appendix*, Fig. S3), suggesting that interspecific competition was an agent of directional selection on *L. minor*. Importantly, differences in genotypic evolution caused differences in phenotypic evolution between treatments (described further below).

The evolutionary change was sufficiently large and rapid to affect the concurrent ecological dynamics of the competing species (Fig. 2). After a period of rapid growth from low density by both species, *L. minor* became numerically dominant in the conspecific selection treatment, with nearly twice as many individuals as *S. polyrhiza* (Fig. 2 and *SI Appendix*, Fig. S4). By contrast, competitor abundances were more even in the heterospecific selection treatment, with significantly lower final abundances of *L. minor* and significantly higher final abundances of *S. polyrhiza* (Fig. 2 and *SI Appendix*, Fig. S4 and Table S2; likelihood-ratio tests comparing population trajectories, *L. minor*, $\chi^2_{df=2} = 29.54$, $P < 0.001$; *S. polyrhiza*, $\chi^2_{df=2} = 8.02$, $P = 0.018$). Indeed, over the last third of the experiment, the average population size of *L. minor* was between 15 and 20% lower in the heterospecific selection treatment [$F_{(1,11.92)} = 8.16$, $P = 0.015$; Fig. 2].

Following coexistence theory, the observed changes in dynamics could be caused by the evolution of increased niche differences, a decrease in the competitive ability of *L. minor* relative to *S. polyrhiza*, or a combination of these effects (16, 20). Evaluating these scenarios requires quantifying niche and competitive-ability differences in each treatment. Expressions for these quantities can be derived from the mutual invasibility criterion of coexistence (21), and their values estimated based on a parameterized model of competitive population dynamics describing the species' interaction (23). We parameterized an appropriate competition model using data from a separate set of field competition experiments, which were required to disentangle the effects of intraspecific and interspecific competition on dynamics (*Materials and Methods*). These experiments involved measuring the population growth of individuals from the evolved populations of each species in each treatment, competing against a density gradient of conspecifics and (separately) heterospecifics from the same treatment (ref. 23 and *SI Appendix*, Figs. S5 and S6 and Table S3). We then used the parameter estimates from the competition model to quantify niche and competitive-ability differences in each treatment.

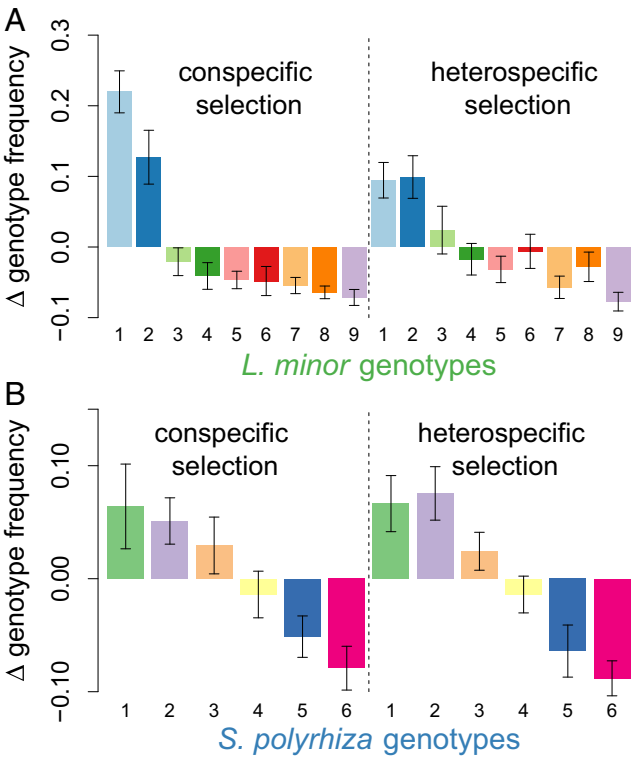

Fig. 1. Competition between species drives evolutionary change. Bars show the mean change in frequency of each genotype of (*A*) *L. minor* and (*B*) *S. polyrhiza* in the conspecific and heterospecific selection treatments. The change in genotype frequency is the change from the beginning of the experiment in June until the sampling date in August. Each color and number represents a different genotype. Errors are SEMs.

Results show that, while the predicted coexistence outcome did not change between treatments, the more even abundances of the competing species under heterospecific selection were more consistent with a change in species' competitive abilities than with an increase in niche differences (Fig. 3). Specifically, we found little difference between treatments in the estimated niche difference, especially compared with the decrease in competitive ability of *L. minor* relative to *S. polyrhiza* (Fig. 3*A*). To evaluate the likelihood that these two alternative pathways contributed to the more even population abundances observed in our main experiment, we used Monte Carlo simulations to draw 10^6 possible combinations of the competition model parameters for each species in each treatment, based on the uncertainty in the original parameter estimates. We then calculated equilibrium population abundances, and niche and competitive-ability differences for each parameter combination within this set. For the parameter combinations that gave more even population abundances in the heterospecific vs. conspecific selection treatment—a situation that matches the observed abundances

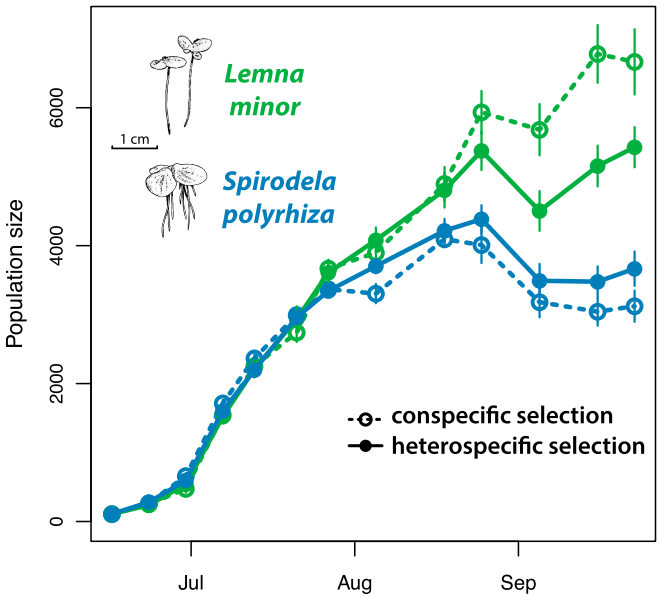

Fig. 2. Evolution in response to competition alters the population dynamics of competing species. Population trajectories of the competing species, *L. minor* (green) and *S. polyrhiza* (blue), when they were able to evolve in response to interspecific competition (heterospecific selection, solid line) or unable to evolve to interspecific competition (conspecific selection, dashed line). Errors are SEMs.

that we are aiming to explain (Fig. 2)—the competitive ability of *L. minor* decreased relative to *S. polyrhiza* in 96.4% of cases. By contrast, more even abundances were equally likely to be associated with increases or decreases in niche differences (46.3% and 53.7% of cases, respectively), suggesting little consequence of evolved changes in niche differences as a driver of the observed dynamics.

The lower competitive ability of *L. minor* occurred despite this species evolving a greater maximum finite rate of growth in the heterospecific selection treatment (Fig. 3*B*). All else being equal, a higher maximum finite rate of growth will increase competitive ability (23). However, the positive effect of this demographic change was more than counteracted by a large decrease in the ability of *L. minor* to maintain offspring production under crowded conditions [i.e., evolution caused *L. minor*'s sensitivity to competition (23) to increase because of increases in this species' response to both intraspecific (α_{LL}) and interspecific (α_{LS}) competition; Fig. 3*C*]. While existing theory accommodates the possibility of evolutionary changes in competitive ability (24), it does not generally consider separate (and contrasting) effects of evolution on these different components of competitive ability. Regardless of the specific evolutionary constraints driving these effects, the findings exposed here by combining experimental evolution with quantitative coexistence theory highlight the potential for complex evolutionary responses to competition.

Finally, we asked whether phenotypic traits differed between heterospecific and conspecific competitive environments in a manner consistent with the evolved competitive dynamics. *S. polyrhiza* traits did not differ between treatments (Fig. 4), consistent with the lack of genetic differences between treatments (Fig. 1). By contrast, *L. minor* had greater specific-leaf area under heterospecific selection [Fig. 4*A*; $F_{(1,12)} = 20.98$, $P < 0.001$]. This increase is consistent with the large decrease in the heterospecific selection treatment of the *L. minor* genotype that had the lowest specific-leaf area (genotype 1 in Fig. 1; *SI Appendix*, Fig. S3). Importantly, for each species, the differences in specific-leaf area between treatments in the field were consistent with those found under common-garden conditions in the laboratory (*SI Appendix*, Fig. S7), confirming that the observed differences in the field had a genetic component.

Traditionally, the evolution of traits in response to interspecific competition would be interpreted as evidence for changes in niche differences (7, 8, 11, 17–19). However, given that our demographic analyses suggest that competitive ability and not niche differences evolved in response to interspecific competition (Fig. 3), trait change in our study is more consistent with a relationship between trait evolution and changes in competitive ability. Indeed, higher specific-leaf area tends to be associated with higher growth rate (30) and greater sensitivity to resource depletion (31), both of which are consistent with the evolved changes in *L. minor*'s maximum finite rate of growth (Fig. 3*B*) and sensitivity to competition (Fig. 3*C*), respectively. The differences in trait values at the individual level also had some important implications for the differences in the structure of the evolving populations between treatments. While the population size of *L. minor* was lower in the heterospecific selection treatment (Fig. 2), as was total biomass [$F_{(1,12)} = 10.32$, $P = 0.008$; *SI Appendix*, Fig. S8], the total frond area of *L. minor* did not differ between treatments [$F_{(1,12)} = 1.33$, $P = 0.271$; *SI Appendix*, Fig. S8], because the area of individual fronds was greater under heterospecific selection [$F_{(1,12)} = 5.84$, $P = 0.033$; *SI Appendix*, Fig. S9]. By contrast, the increase in population size of *S. polyrhiza* in the heterospecific selection treatment translated directly into an increase in both the total (population-level) area [$F_{(1,12)} = 12.01$, $P = 0.005$] and

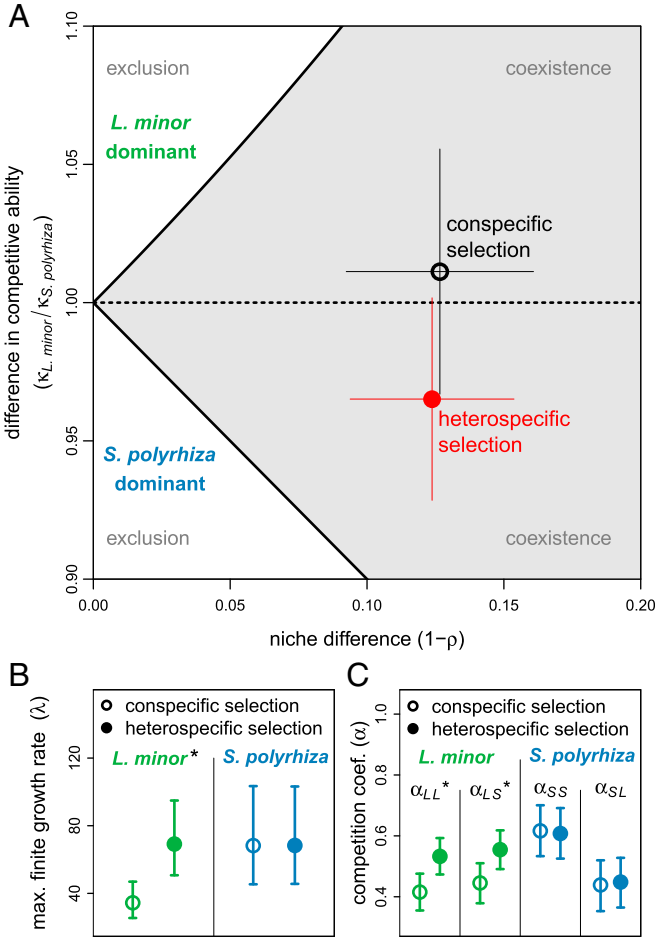

Fig. 3. The niche and competitive-ability differences between *L. minor* and *S. polyrhiza* after evolution in response to conspecific and heterospecific selection. (*A*) Stable coexistence occurs when the stabilizing niche difference $(1-\rho)$ exceeds the magnitude of the competitive-ability difference (κ_i/κ_j), shown by the gray shaded region defined by the inequality $\rho < \kappa_L/\kappa_S < 1/\rho$ (*Materials and Methods*). (*B*) The effects of the selection treatments on species' maximum finite rate of growth (λ). (*C*) The effects of the selection treatments on intraspecific (α_{ii}) and interspecific (α_{ij}) competition coefficients. Lines in *A* show 1 SD. Lines in *B* and *C* show 95% confidence intervals. The asterisk (*) indicates that the difference is significant (*SI Appendix*, Table S3).

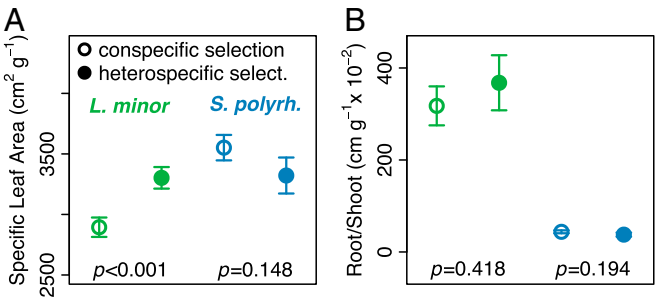

Fig. 4. The effects of the conspecific and heterospecific selection treatments on phenotypic trait evolution. (*A*) Specific-leaf area. (*B*) Root length-to-frond mass ratio. Errors are SEMs.

total (population-level) biomass of fronds [$F_{(1,12)} = 17.11$, $P = 0.001$; *SI Appendix*, Fig. S8] in the competitive arenas.

In sum, our results suggest that evolution in response to interspecific competition resulted in more even population sizes of the competitors (Fig. 2) and did so via evolved changes in competitive ability rather than the evolution of greater niche differences (Fig. 3). In general, evolved changes in competitive ability are predicted by theory when species cannot substitute other resources for the ones used by their competitors (i.e., the same resources are essential for both competing species; refs. 24 and 25), conditions that may characterize our system. In the experimental ponds, as in nature, *L. minor* and *S. polyrhiza* likely compete most strongly for space, light, and essential nutrients, resources that may not be substitutable. The degree of limitation by these factors is unknown, and even space may be less limiting than expected as plants can overlap on the surface of the water before populations equilibrate. Nonetheless, a potential explanation for our results is that competition for these nonsubstitutable resources constrained opportunities for the evolution of niche differences, while allowing changes in the efficiency with which shared resources are exploited (24, 25). Our system is unlikely to be unusual in this respect, because competition for nonsubstitutable resources is likely to structure other functionally sessile and/or autotrophic communities, including terrestrial plant and marine benthic communities (32, 33). While our experiment likely captures nonspatial opportunities for niche differences that occur in natural ponds—and captured sufficient opportunities for niche differentiation to allow coexistence in both treatments (Fig. 3*A*)—it is possible that more complex spatially varying environments would provide additional opportunities for the evolution of niche differences, as well as competitive abilities, in response to interspecific competition (12, 34, 35).

Our study has a number of limitations to consider when relating our findings to the evolution of competing species more generally. First, our results reflect the effects of selection on standing genetic variation. While our study does not, therefore, account for evolutionary dynamics arising from de novo mutations (27), selection on standing genetic variation is likely to be a more important driver of evolution rapid enough to alter concurrent ecological dynamics (36). Second, the competing species in our experiment began with a random selection of nine and six genotypes of *L. minor* and *S. polyrhiza*, respectively. Our results suggest that even with these low levels of genotypic variance, evolution in response to competition can alter competitive dynamics. Nevertheless, it is possible that higher levels of genotypic diversity or different combinations of genotypes may have generated different results, including the evolution of niche differentiation. Future work quantifying competition at the genotype level may be able to quantify levels of additive genetic variance in niche and competitive-ability traits, and thus quantify the potential for evolution along these axes as a function of genotypic diversity. Third, because the individuals in our study are clonal, traits are perfectly linked. Nonetheless, it is unclear how recombination would affect the speed and direction of evolution in our system. Fourth, while our experiment allowed us to attribute the differences between treatments to the influence of interspecific competition, it is unknown how the contribution of evolution in both treatments in response to selection pressures other than competition affected the observed dynamics of the competing species. Understanding these effects would be a worthy goal for future work (37). Finally, phenotypic plasticity, including via maternal effects, could have contributed to our results. While we cannot rule this possibility out, additional experiments testing for these effects demonstrate that plasticity tends to increase the overall competitive performance of *L. minor* in heterospecific competitive environments, and so, if anything, is likely to have counteracted the overall decrease in competitive performance we observed in our evolution experiment (*SI Appendix*, Fig. S10).

For much of the last century, most ecologists have treated the maintenance of species diversity as a purely ecological process (21, 38, 39). In addition, while evolution was commonly thought to shape the traits of competing species, the simultaneous feedbacks between these ecological and evolutionary processes, as expected from theory, have been difficult to empirically evaluate. Only by experimentally disrupting the eco-evolutionary feedback through altering species' abilities to evolve in response to their competitive environment were we able to directly show that evolution concurrent with ecological dynamics strongly affects the population dynamics of competing species over just a few generations. The outcome of this approach, coupled with the principles of quantitative species coexistence theory, gives a unique process-level view of the eco-evolutionary dynamics expected to shape contemporary patterns of biodiversity. Our results suggest that understanding competitive population dynamics—a cornerstone of ecological knowledge—may require accounting for the simultaneous influence of rapid evolutionary change.

Materials and Methods

Species, Collection, and Culturing. *Lemna minor* and *Spirodela polyrhiza* are small, globally distributed, floating, aquatic plants belonging to the Lemnoideae subfamily of the Araceae family (28). The plants are morphologically simple, composed of a floating frond with small rootlets attached to the underside (Fig. 2). Flowering is rare, and instead, reproduction occurs every 3–7 d via asexual budding of daughter fronds. Populations often contain multiple genotypes (40). *L. minor* and *S. polyrhiza* likely compete most strongly for space, light, and essential nutrients. Populations vary greatly in density, and where nutrient availability is high, they can grow at high densities in overlapping layers. Our experiment used six genotypes of *S. polyrhiza* and nine genotypes of *L. minor* (*SI Appendix*, Tables S4 and S5). Genotypes were collected from ponds in central Europe in 2015, and two genotypes of *S. polyrhiza* from the same region were obtained from the collection of M. Huber and S. Xu (then at the Max Planck Institute for Chemical Ecology, Jena, Germany). To distinguish between genotypes, we developed microsatellite markers for each species (*SI Appendix*, Table S6). To generate sufficient numbers of individuals to initiate the experiment, we cultured each genotype for 8 wk in a greenhouse, in large (36 × 64 × 32 cm), green, plastic tubs containing ∼45 L of tap water and a layer (∼1–3 cm) of general purpose potting soil (GO/ON flower soil with 100–300 mg/L N, 150–450 mg/L P_2O_2, and 1,200–2,000 mg/L K_2O).

Field Setup. The experiment was done in 13, 1,260-L green, fiberglass cattle tanks (140 × 100 × 90 cm), which were regularly arranged in a field at the University of Zurich (47.3743°N, 8.5510°E). In May 2016, we distributed 80 L of general purpose potting soil (details as above) across the bottom of each tank, and then each was two-thirds filled with tap water (∼840 L). One liter of pond water (containing plankton) and three to five snails collected from nearby natural ponds were then added to each experimental pond. Diverse and abundant zooplankton, algal, and insect communities were observed in the experimental ponds during the experiment. To mimic the shaded conditions under which the plants commonly occur, each pond was shaded with two layers of 45% shade cloth. Competitive population dynamics and evolution of the two plant species occurred in small competitive arenas in each pond. Competitive arenas were white plastic containers (122-mm diameter, 1,100 mL) attached to a wooden frame floating on the surface of the water in each pond, with a single frame supporting a 5 × 6 array of 30 containers. Each container was attached to the frame with ∼3 cm of the container protruding above the surface of the water. The bottom of each container was punctured, allowing exchange of water and plankton between container and pond.

Experimental Manipulation. There were two treatments in the main experiment, one in which both species competed and were able to respond to selection imposed by interspecific competition (heterospecific selection), and

one in which both species competed but were unable to respond to selection imposed by interspecific competition (conspecific selection). There was one replicate of each treatment in each of the 13 ponds. Both treatments were initialized by placing 108 fronds of each species into each of two competitive arenas within each pond. At the beginning of the experiment, there were 12 individuals of each genotype of *L. minor* in each replicate of each treatment, and there were 12 individuals of three genotypes of *S. polyrhiza* and the remaining three genotypes had 24 individuals each (we initially thought each of the latter clones were two separate clones but genotyping subsequent to the establishment of the experiment revealed them to be a single genotype, hence their higher initial density). The two-species experimental communities were established in June 2016, and the component populations were allowed to grow and compete.

To prevent evolution in response to interspecific competition in the conspecific selection treatment, we replaced all individuals of both species in this treatment every 2 wk with individuals from multigenotype but single-species source populations that were not subject to selection from their heterospecific competitor, but were subject to selection from conspecific competitors. For each replicate, the single-species source populations were initiated at the same time, in the same pond, with the same genotypes, each with the same number of individuals as in the two-species communities, but with only one species per container. Thus, these single-species populations, which were used as a source of individuals for the conspecific selection treatment (described next), were free to evolve to the same abiotic and biotic conditions as the populations in the heterospecific selection treatment, but they were unable to evolve in response to competition from heterospecific individuals, to which they were not exposed.

To execute a single experimental replacement, we counted and then discarded all individuals of both species from a replicate of the conspecific selection treatment. We then replaced these individuals with same number of individuals of each species in that replicate, but using individuals from a single-species source population for each species from the same pond. We repeated this procedure every 2 wk for all replicates. There were 11 single-species source populations for each species in each pond, giving us a fresh source population for each replacement. Because the replacement method retains the number of individuals of each species in each replicate of the conspecific selection treatment, the manipulation preserves the ongoing effects of interspecific competition on the sizes of the populations of the two species in this treatment. However, the manipulation prevents evolution in response to interspecific competition, and therefore prevents such evolution from affecting the dynamics of the interaction. In the heterospecific selection treatment, the populations of the two species were able to compete and evolve in response to one another. The populations in both treatments were physically mixed during the weekly photographic censuses (described below). Single-species source populations were physically mixed with a plastic fork as a procedural control. We randomized the position of the treatments and single-species source populations within each pond.

Quantifying Evolutionary Change. Evolution—the change in genotype frequency over multiple generations—was quantified by genotyping between 24 and 32 individuals of each species in each replicate sampled 50 d (August 4, 2016) after the experiment was initiated. In total, we genotyped 1,280 individuals using four microsatellite markers for each species (*SI Appendix*, Table S6) in a single multiplex procedure (*SI Appendix*). To determine whether there were differences between treatments in genotypic composition, we used PERMANOVA (41). For each species, we first described compositional differences between populations across both treatments using Euclidean dissimilarity matrices. We used a symmetric distance measure (Euclidean distance) because including shared absences of genotypes provides important information about the effects of our treatments. We then implemented PERMANOVA using the "adonis" function in the "vegan" package in R (42), including pond as a random factor (41). Genotypic compositional differences were visualized using principal-coordinates analysis (41). We further assessed for consistency in the direction of evolutionary change with univariate analyses on the numerically dominant genotype (genotype 1 in Fig. 1). We first assessed the probability that this genotype consistently increased in frequency in both treatments using exact binomial tests. We then assessed if the magnitude of the change in the frequency differed between treatments using a paired *t* test.

Quantifying and Analyzing Population Trajectories. We photographed all individuals in each replicate of each treatment approximately every week (8.6 ± 2.9 d) for the duration of the experiment. So that all individuals could be distinguished in each photograph, we carefully removed all individuals from each competitive arena with a plastic fork and placed them in larger containers for photographing before returning them to their original competitive arena within each pond. Individuals of both species were then manually counted in the photographs using ImageJ (43). To test for differences in the population trajectories between treatments, we fit a two-parameter logistic function to phenomenologically describe the time-series data for each species in each treatment. The function took the form $N_i(t) = a/(1+(a/N_{i,0}-1)e^{-bt})$, where N_i, the population size of species *i*, was modeled as a function of time, *t*, and where *a* is the predicted asymptotic population size and *b* is the population growth rate. This model was fit to the time-series data using the "nlme" package in R. We included pond as a random effect and used an autoregressive correlation error structure to account for repeated counts over time. To determine whether the trajectories differed between treatments, we used likelihood-ratio tests to compare full models including treatment effects with reduced models where treatment effects were excluded. As an additional test for whether the selection treatments caused differences in population sizes, we compared the mean population size for each species between treatments across the last five census dates. These tests were done using linear mixed-effects models with treatment as a fixed factor and pond as a random effect.

Additional Competition Experiments and Competition Model. To quantify niche and competitive-ability differences between the species in each treatment, we parameterized a two-species competitive population dynamics model describing the interaction between the evolved populations of *L. minor* and *S. polyrhiza*. The aim here was not to describe the population trajectories in the two treatments (as described above), but rather to understand if the differences in dynamics between treatments could be explained by evolved differences in niche differences and/or in species competitive abilities. Parameterizing an appropriate competition model requires estimating the maximum finite rates of growth, and the per capita strength of intraspecific and interspecific competition, but estimating these quantities from observed population trajectories in mixture (i.e., in our main experiment) is difficult to do with confidence. Therefore, we identified and parameterized an appropriate competition model using data from a separate set of competition experiments, done under the same field conditions, using individuals sampled from the evolved populations of each species in the main experiment. These separate competition experiments began on August 10, 6 d after the genotype sampling. To initiate the experiments, a small number of individuals of both species were haphazardly sampled from each replicate of each treatment in the main experiment. Fronds collected from different replicates of the same treatment were then combined, providing the material for the separate competition experiments. We took this approach because parameterizing the competition model separately for each replicate of the main experiment was not feasible.

The separate competition experiments involved measuring population growth in response to a range of densities of conspecific and heterospecific individuals (23). To enable accurate estimates of the competition model parameters while limiting the total number of individuals required in these experiments, we did these competition trials in smaller competitive arenas (open-ended pipes, 46-mm diameter), attached vertically to the inside wall of one of the same type of container used in the main experiment, which was itself attached to a wooden frame floating within one of five experimental ponds. These five ponds were maintained from the beginning of the season to have similar conditions as the 13 experimental ponds used in the main experiment. To quantify the strength of intraspecific competition, we measured population growth of *S. polyrhiza* at densities of 1.6, 2.1, 4.9, 10.3, 30.9, 50.9, 76.9, and 96.9 individuals·cm^{-2}, and of *L. minor* at 1.6, 2.7, 7.6, 15.2, 52.5, 89.4, 126.7, and 163.5 individuals·cm^{-2}. To quantify the strength of interspecific competition, we measured population growth of individuals of the focal species at low density (1.6 cm^{-2}) competing against their heterospecific competitor at each of the densities listed above. These competitor densities were chosen because they covered a range of densities up to levels beyond the maximum densities observed in the main experiment (111.89 fronds·cm^{-2}), as has been shown to be optimal for accurately estimating model parameters (44). Note also that the lowest densities (1.6 fronds·cm^{-2}) still contained 27 individuals, allowing for sufficient representation of each of the genotypes at even the lowest densities. The treatments containing only low densities of conspecifics were replicated three times, and there was one replicate of each of the remaining density combinations. The treatment densities were randomly distributed across the five ponds. Photographs of all individuals in all treatments were taken 2 wk after the experiment was initiated. Individuals in the photographs were then counted to estimate population growth over 2 wk, the same duration as the evolution manipulation in the main experiment. Data from these competition experiments were fit to the Law–Watkinson competition model (45), which takes the following form:

$$N_{i,t+1} = \frac{N_{i,t}\lambda_i}{1 + N_{i,t}^{\alpha_{ii}} + N_{j,t}^{\alpha_{ij}}}, \quad [1]$$

where $N_{i,t}$ is the population size of species *i* at time *t*, and $N_{i,t+1}$ is the population size of species *i* 2 wk later. The parameter λ_i is the maximum

finite rate of growth, and the parameters α_{ii} and α_{ij} are the intraspecific and interspecific competition coefficients, respectively. Data from the competition experiments were fit to this model using nonlinear least-squares regression using the "nls" function in R. We included the selection treatments as a factor in our model fits, allowing separate estimates of each of the competition model's parameters in each treatment. We used likelihood-ratio tests to compare full models allowing a separate estimate of each parameter for each treatment, with reduced models allowing only a single estimate of each parameter across both treatments. For details of the competition model assumptions, see *SI Appendix*.

Quantifying Niche and Competitive-Ability Differences. Using our parameter estimates for the Law–Watkinson competition model, we can define expressions that quantitatively describe the niche difference, which stabilizes species coexistence, and differences between species in their competitive abilities, which promote competitive exclusion (21). Both these quantities are based on the mutual invasibility criterion of species coexistence (*SI Appendix*). Following the methods of earlier studies (21, 23), the niche overlap for the Law–Watkinson model is $\rho = \sqrt{\alpha_{ij}\alpha_{ji}/\alpha_{jj}\alpha_{ii}}$, and the stabilizing niche difference is $1-\rho$. This expression quantifies the degree to which the per capita strength of intraspecific competition (the denominator) exceeds the per capita strength of interspecific competition (the numerator). The difference between species in their competitive abilities in the Law–Watkinson model is $\kappa_i/\kappa_j = \ln(\lambda_i - 1)/\ln(\lambda_j - 1) \cdot \sqrt{\alpha_{jj}\alpha_{ji}/\alpha_{ij}\alpha_{ii}}$ (23). This expression determines who will win in competition in the absence of niche differences. The first term of this ratio quantifies the difference between the species in their productivity in the absence of competition, and the second term quantifies the difference between species in their sensitivity to competition from both heterospecific and conspecific competitors (23). Coexistence occurs when $\rho < \kappa_i/\kappa_j < 1/\rho$ (21). For more information on the derivation of these quantities from the mutual invasibility criterion, and their relationship to population abundances, see *SI Appendix*.

We used our estimates for the parameters in the Law–Watkinson model to estimate niche ($1 - \rho$) and competitive-ability differences (κ_i/κ_j) in both selection treatments. To estimate the SD of these composite variables, and to evaluate the likelihood that niche vs. competitive-ability differences were responsible for the differences in dynamics between treatments, we used error propagation methods based on Monte Carlo simulations, using the "propagate" package in R (*SI Appendix*).

Trait Measurements. We sampled 25–60 individuals of each species from each replicate of the two treatments in September 2016. We photographed these fronds and quantified total frond area in each sample using ImageJ. We quantified area per frond by dividing the total frond area by the number of fronds in the sample. We measured dry mass by first removing all roots and turions (dormant resting stages in *S. polyrhiza*) and then dried the remaining fronds at 70 °C for 24 h before weighing. We assessed root length as the longest root of a single haphazardly chosen cluster of fronds from each replicate. With these data, we calculated for each replicate and species, specific-leaf area and the ratio of root length to dry mass. Population-level estimates of frond area and biomass were calculated by multiplying the individual-level estimates of these variables by the population sizes of the species on the final census date. We compared the value of each individual-level trait, and area and biomass traits at the population level, for each species between treatments using linear mixed-effects models, with treatment as a fixed effect and pond as a random effect. To determine whether the observed phenotypic changes had a genetic component, morphological traits of individual clones were also assessed after growth in common-garden conditions in the laboratory (*SI Appendix*).

ACKNOWLEDGMENTS. We thank Ariane Le Gros, Laura Stefan, Cyrill Hess, Renato Guidon, Andrea Reid, and other members of the Plant Ecology Group for assistance; and Sabine Güsewell, Jacob Usinowicz, and Marti Anderson for analytical advice. We thank Josh van Buskirk and the University of Zurich for use of their field infrastructure. We thank Walter Lämmler, Shuqing Xu, and Meret Huber for providing clones and advice. M.M.T. was supported by the ETH Zürich Center for Adaptation to Changing Environments.

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SI Appendix: Figures

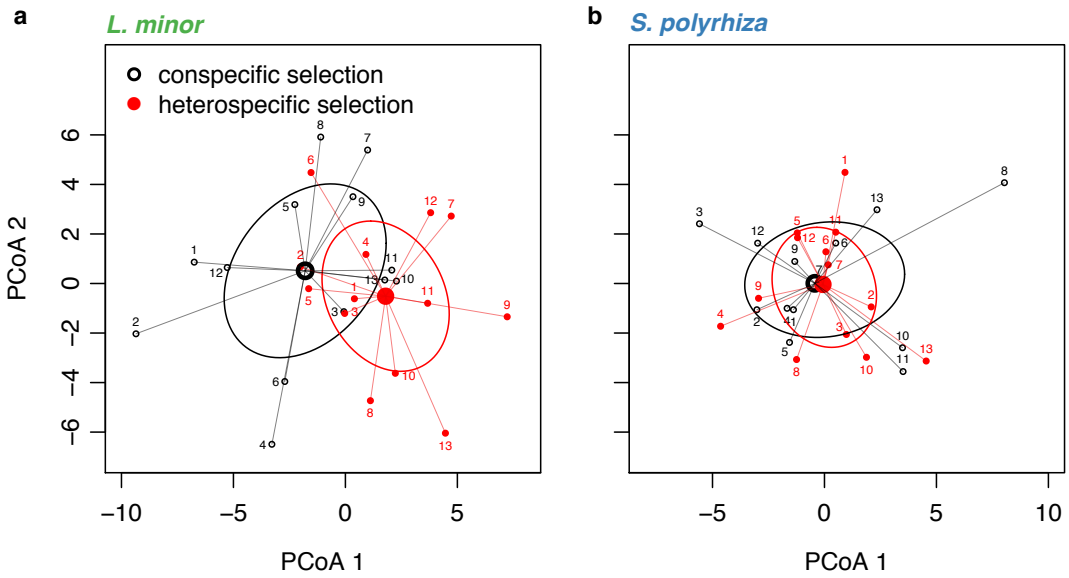

Fig. S1. Principal Coordinates Analysis (PCoA) of the genotypic composition of the evolved populations of (**a**) *L. minor* and (**b**) *S. polyrhiza* in the conspecific and heterospecific selection treatments. Large points show treatment centroids and small points show populations in each treatment in each experimental pond. Ellipses show one standard deviation confidence ellipses around treatment centroids. Each pond is labelled with a unique pond number (noting that there is one replicate of each treatment within each pond) so that the consistency of the direction of the compositional differences between treatments within ponds can be assessed along the two PCoA axes. In (**a**), 12 out of 13, and 9 out of 13 experimental ponds show consistent, directional, compositional differences between treatments along PCoA axis one and two, respectively. The first two principal coordinates (plotted) account for 60.85 % of the variation in genotypic composition in (**a**) and 61.05 % of the variation in genotypic composition in (**b**). The PCoA analysis for each species is based on a Euclidean dissimilarity matrix describing differences in genotypic composition between each population across both treatments. The visual representation shown here is accompanied by formal tests for differences between treatments using PERMANOVA (Table S1). PCoA best represents the compositional differences assessed by PERMANOVA, and faithfully represents the distances between populations without distortion (1).

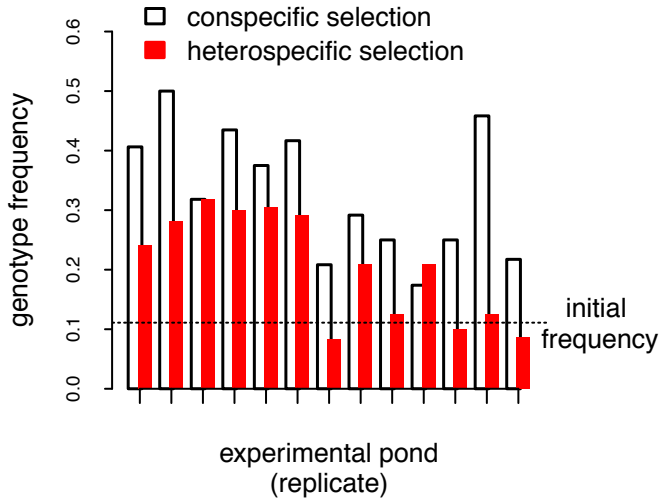

Fig. S2. Genotype frequencies of the 'light-blue' *L. minor* genotype (genotype 1 in Fig. 1) in each replicate of each selection treatment in each experimental pond, 60 days after the experiment was initiated. Each pair of red and open bars represents a single experimental replicate. The horizontal dotted line indicates the initial genotype frequency at the beginning of the experiment. The dominant genotype consistently increased in frequency in both treatments (binomial exact test in the conspecific selection treatment: probability = 1, p = 0.0002; and in the heterospecific selection treatment: probability = 0.77, p = 0.0923). The final genotype frequency was consistently and significantly higher in the conspecific vs. the heterospecific selection treatment (paired, two-sided t-test: $t_{12} = 4.936$ $p = 0.0003$).

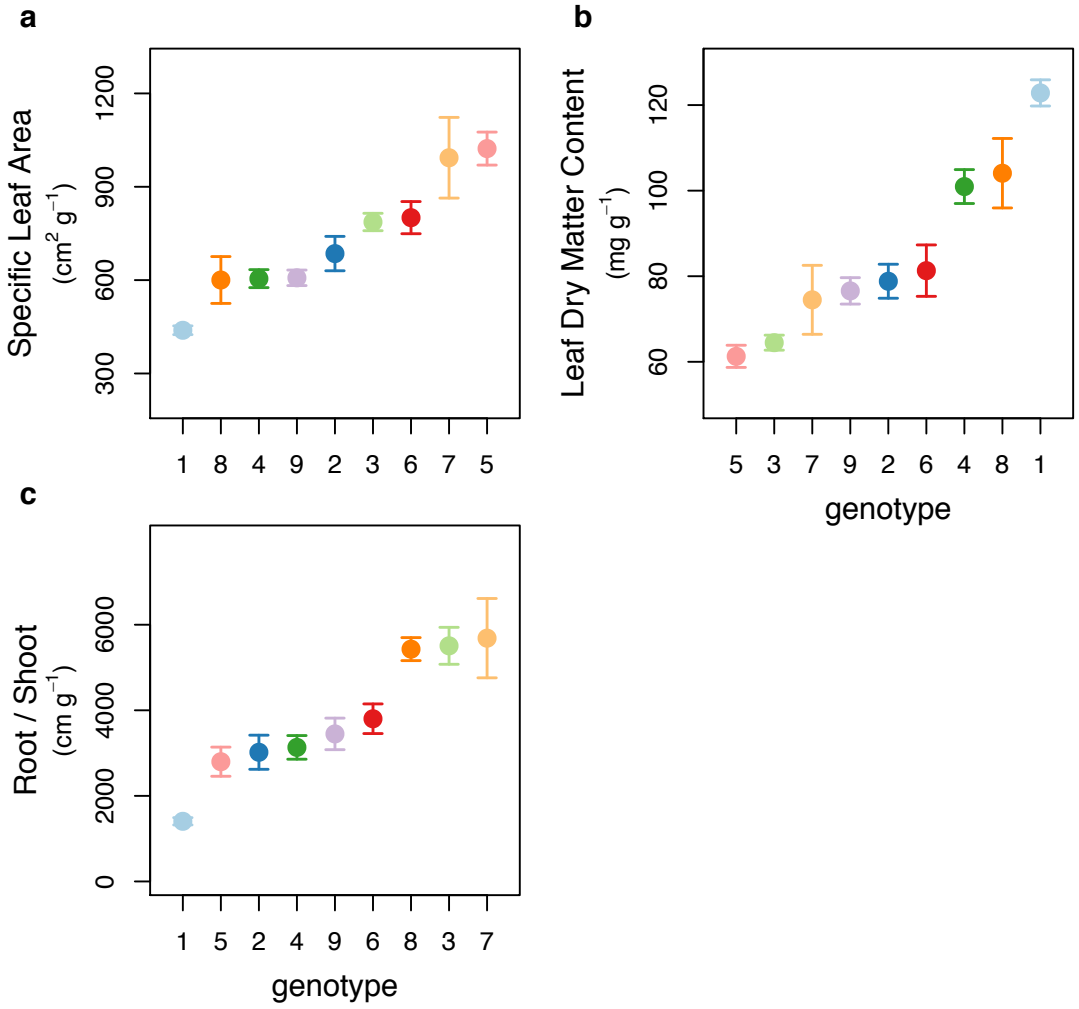

Fig. S3. Trait values for each of the nine *L. minor* clones used in the experiment. (**a**) specific-leaf area (SLA) (**b**) leaf-dry-matter content (LDMC), and (**c**) the ratio of root-length to frond-dry-mass. Colors and genotype numbers on x-axes for each genotype match those used in Fig. 1 in the main text. Traits of each genotype were measured after two weeks of growth and reproduction in controlled laboratory conditions (SI Methods), and so reflect genetically-based differences in phenotypic trait values independent of the influence of competition and environmental conditions. Error bars are standard errors (SEM).

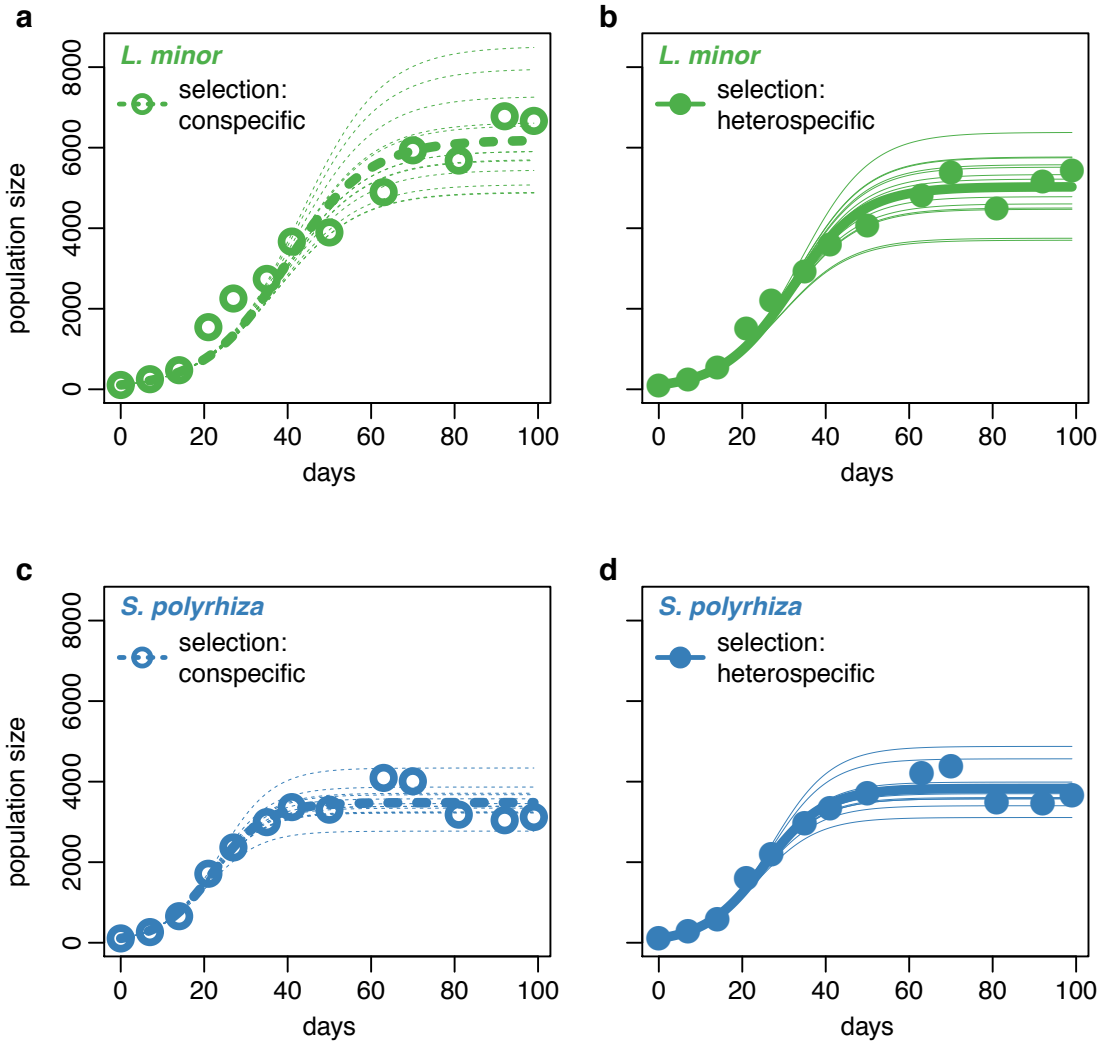

Fig. S4. The fit of a two-parameter sigmoid (logistic) model to the population trajectories (time-series) of each species in the two evolution treatments in the main experiment. Each panel shows the predicted logistic curve (bold curve) from the best-fit nonlinear mixed model (Table S2), and the mean population size at each census date (points, which are the same as those in Fig. 2 in the main text). Thin lines show pond-level random effects. Note that while the trajectories of each species in each treatment are here shown in separate panels for clarity, the *L. minor* populations in (a) and the *S. polyrhiza* populations in (c) are competing against each other. The same is the case for the *L. minor* populations in (b) and the *S. polyrhiza* populations in (d). We note that we only use the logistic curves to get a quantitative sense of the trajectories and their differences between treatments across the entire time series. These functions do not relate to the Law-Watkinson model of competition (Equation 1, Figs S5 and S6, Table S3), which we parameterized to generate estimates of niche and competitive-ability differences after evolution had occurred (shown in Fig. 3).

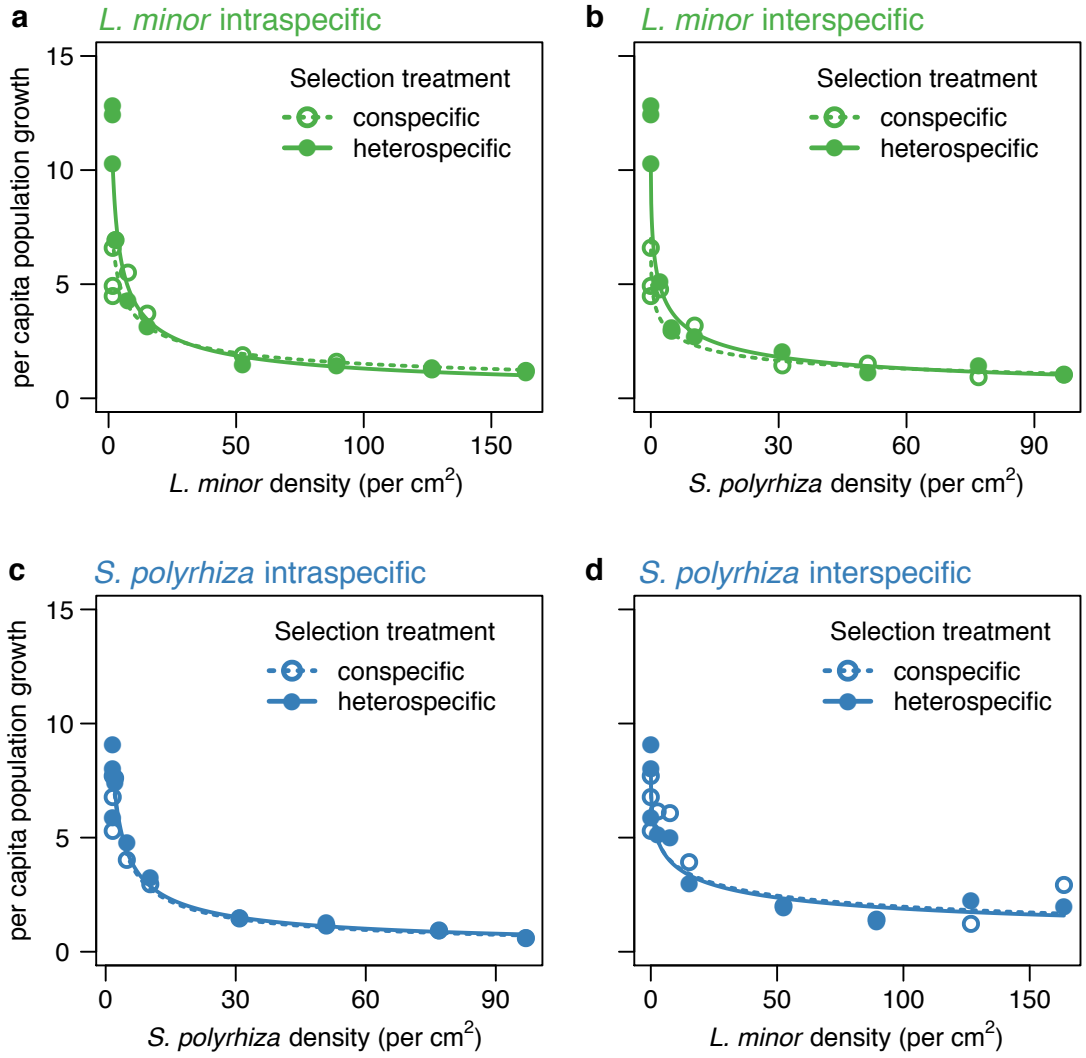

Fig. S5. Fit of the Law-Watkinson competition model to the data from the separate set of competition experiments. These experiments were done in mid-August using individuals taken from the evolved populations in each treatment in the main experiment. (**a**) and (**b**) show the effect of increasing densities of conspecific and heterospecific individuals, respectively, on the per capita population growth of *L. minor*. (**c**) and (**d**) show the effect of increasing densities of conspecific and heterospecific individuals, respectively, on the per capita population growth of *S. polyrhiza*. Points are raw data from the competition experiments and curves are predicted values from the fits of the Law-Watkinson competition model (Equation 1) to the experimental data. Our estimates for lambda shown in Fig. 3b are the projected y-intercepts of the curves shown here, however in these figures we have restricted the visualization to the range of the data only (down to the minimum density included in these experiments of 1.6 individuals per cm^2 on the x-axis). We note that the Law-Watkinson competition model describes a steep decline in offspring production as competitor density increases above zero, and so the y-intercepts are higher than would appear to be the case given the range of the data and curves shown in this figure.

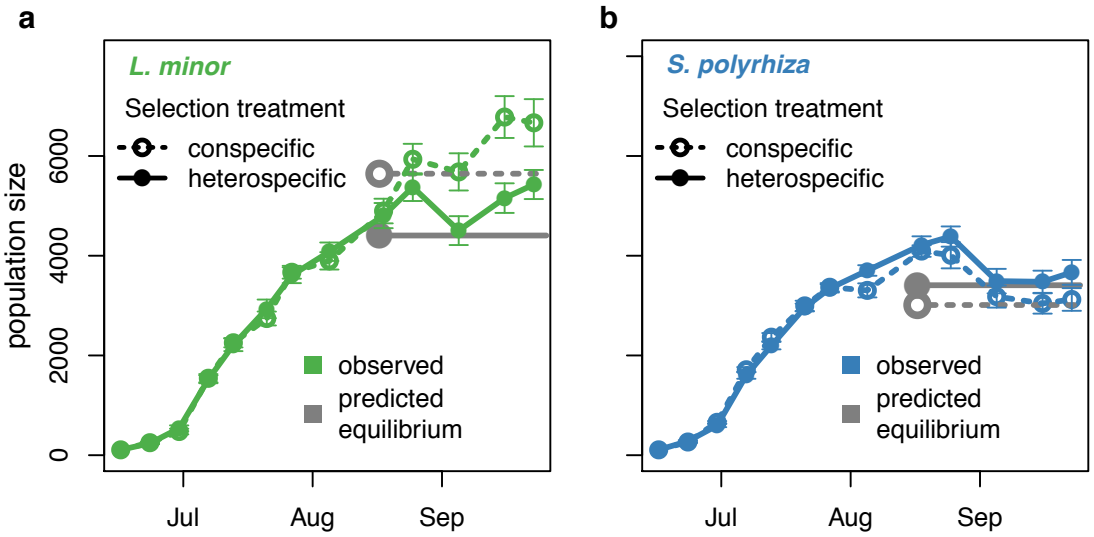

Fig. S6 Observed population trajectories and predicted equilibrium population sizes of (**a**) *L. minor* and (**b**) *S. polyrhiza*. Predicted equilibrium population sizes were calculated using the parameter values estimated by fitting the Law-Watkinson competition model (Equation 1) to the data from the separate competition experiments done in mid-August 2016 (Materials and Methods, Table S3, Fig. S5). The predicted equilibrium values in grey are shown as a line beginning August 10, the date the competition experiments used to parameterize the Law-Watkinson competition model were initiated. The equilibrium population sizes shown here in grey account for the competition occurring within and between the species, as in the main experiment. Note that the observed trajectories are those shown in Fig. 2 in the main text, but are here shown in separate panels for each species for clarity.

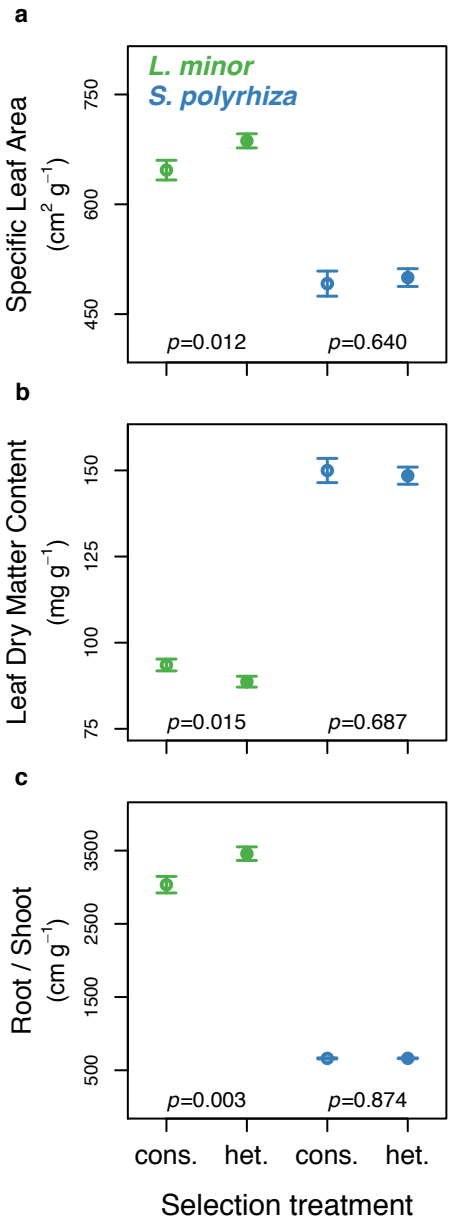

Fig. S7 The effects of the conspecific and heterospecific selection treatments on genetically-based trait evolution in *L. minor* and *S. polyrhiza*. (**a**) specific-leaf area, (**b**) leaf-dry-matter content, and (**c**) the ratio of root-length to frond-dry-mass. Data shown are the population-level trait values in each treatment based on lab-measured traits for each genotype, weighted by their observed frequency in each replicate of the conspecific and heterospecific selection treatments. *p*-values are from linear mixed effects models with treatment modeled as a fixed effect and experimental pond (n = 13) as a random effect. Error bars are standard errors (SEM). We note that these traits are measured under controlled conditions in growth chambers and so reflect genetically-based phenotypic differences. While the mean trait values for each species can differ between lab and field (cf. Fig. 4), consistency in the direction of the phenotypic differences between treatments for a particular species shown in this figure, and for the same traits measured in the field (Fig. 4), suggest that the observed differences in the field had a genetic component.

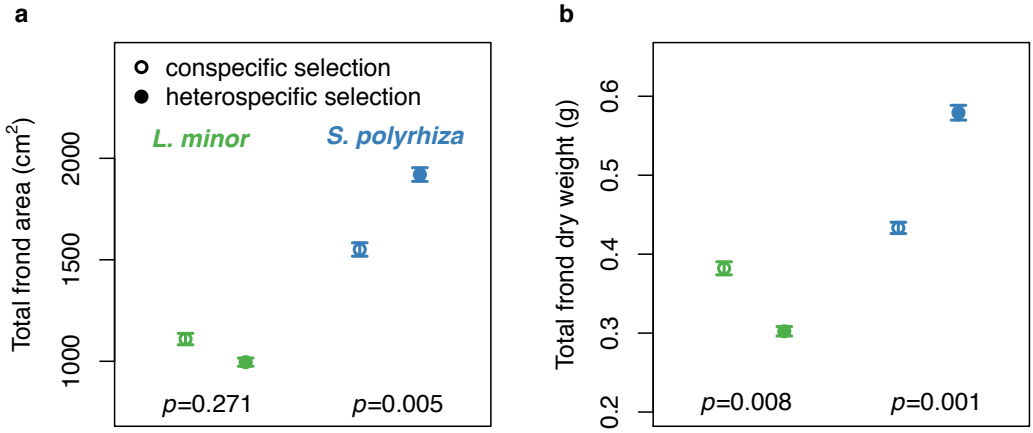

Fig. S8. The effect of the conspecific and heterospecific selection treatments on (**a**) the total frond area within competitive arenas, and (**b**) total frond dry weight (biomass) within competitive arenas, of *L. minor* and *S. polyrhiza* on the last sampling date of the experiment. To be clear, these plots do not show differences in mean trait values, but rather show the total frond area and total frond mass summing over all individuals in a each competitive arena. Error bars around mean estimates are standard errors (SEM).

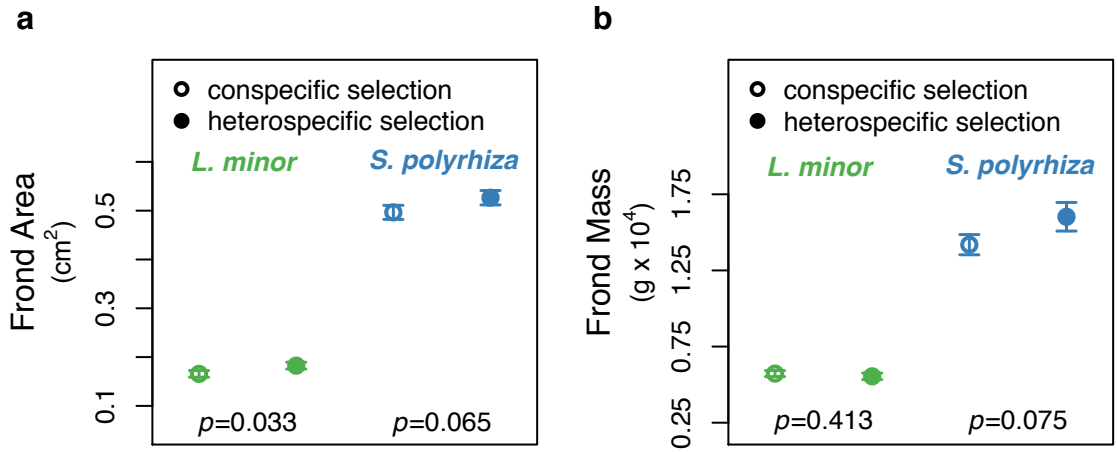

Fig. S9 The effects of the conspecific and heterospecific selection treatments on (**a**) area and (**b**) biomass of individual fronds. *p*-values are from the results of linear mixed-effects modeling with 12 degrees of freedom. Error bars around mean estimates are standard errors (SEM).

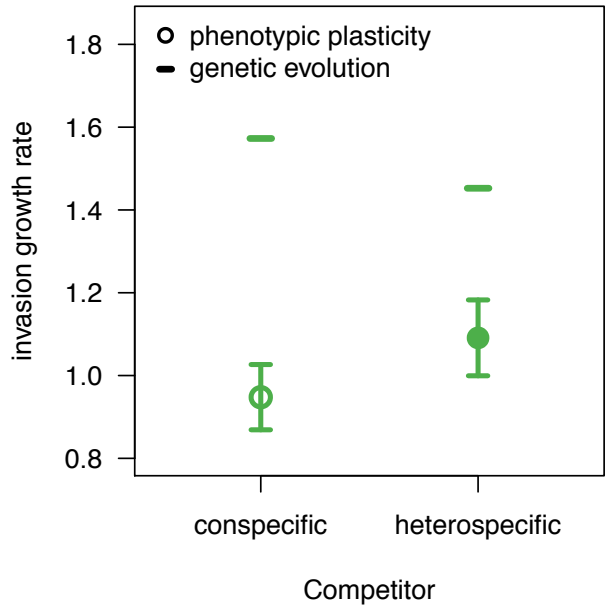

Fig. S10 Invasion growth rates of *L. minor* competing against *S. polyrhiza* as a consequence of plasticity in response to conspecific vs. heterospecific competitive environments (circles). Invasion growth rates were calculated using equation S2.2. For reference, the horizontal green lines show the effect of genetic evolution on the estimated invasion growth rates due to conspecific or heterospecific selection in the evolution experiment (based on the parameter estimates from the fit of the Law-Watkinson competition model as described in the methods of our main evolution experiment). The phenotypic plasticity result suggests that plasticity improves *L. minor's* ability to coexist with *S. polyrhiza*, which is opposite to the effects of genetic evolution (shown by the lines). Error bars are standard errors (SEM). See SI Appendix on phenotypic plasticity for a detailed description of the phenotypic plasticity experiment.

SI Appendix: Tables

Table S1 Results of permutational multivariate analysis of variance (PERMANOVA) testing for genotypic compositional differences between populations for each species in the conspecific and heterospecific selection treatments. Analyses were based on Euclidean dissimilarities of the sampled genotypic abundances between each replicate of each treatment. The analyses were implemented according to a randomized block design, with one replicate of each treatment within each of 13 experimental ponds (blocks).

Source	SS	df	MS	*F*	*p*
A. *Lemna minor*					
experimental pond	457.62	12	38.135	1.0587	0.4026
selection treatment	100.77	1	100.769	2.7976	0.0193
residuals	432.23	12	36.019		
total	990.62	25			
B. *Spirodela polyrhiza*					
experimental pond	269.31	12	22.442	0.871	0.721
selection treatment	2.35	1	2.346	0.091	0.995
residuals	309.15	12	25.763		
total	580.81	25			

Table S2 Parameter estimates from the fits of a two-parameter sigmoid (logistic) function to the population trajectories of *L. minor* and *S. polyrhiza* in each of the two experimental treatments (see Fig. S4 for visualization). The parameter *a* estimates the asymptotic population size, and *b* estimates the *per capita* population growth rate. For each species we tested for significant differences in the parameter estimates between the conspecific and heterospecific selection treatments using likelihood-ratio tests. **Note** that the logistic function was used to phenomenologically describe the trajectories of the competing species in each treatment over the entire experiment. These functions do not relate to the Law-Watkinson competition model (equation 1, Figs S5 and S6, Table S3), which we used to generate estimates of niche and competitive-ability differences after evolution had occurred (Fig. 3).

Function	parameter	estimate	SE	$\chi^2_{df=1}$	*p*
A. *Lemna minor*					
$N_{L.minor}(\text{days}) = \frac{a}{1+\left(\frac{a}{N_{L.minor,0}}-1\right)e^{-b(\text{days})}}$	$a_{\text{conspecific selection}}$	6189.90	329.9		
	$a_{\text{heterospecific selection}}$	5027.90	333.3	8.78	0.003
	$b_{\text{conspecific selection}}$	0.102	0.0018		
	$b_{\text{heterospecific selection}}$	0.120	0.0033	24.16	<0.001
B. *Spirodela polyrhiza*					
$N_{S.poly.}(\text{days}) = \frac{a}{1+\left(\frac{a}{N_{S.poly.,0}}-1\right)e^{-b(\text{days})}}$	$a_{\text{conspecific selection}}$	3478.20	124.11		
	$a_{\text{heterospecific selection}}$	3831.04	168.34	3.85	0.050
	$b_{\text{conspecific selection}}$	0.156	0.0053		
	$b_{\text{heterospecific selection}}$	0.140	0.0066	5.28	0.022

Table S3 Tests for whether the demographic rates and competition coefficients for *L. minor* and *S. polyrhiza* from the Law-Watkinson competition model differ between the two selection treatments. The Law-Watkinson competition model was fit to data from a separate series of competition experiments done in mid-August using individuals taken from the treatments in the main experiment at this time (see Materials and Methods for details). The parameters in the model are the focal species' finite rate of increase, λ_i, and competition coefficients α_{ii} and α_{ij}, which describe the per capita competitive effects of species *i* and *j* on species *i*'s offspring production, respectively. Each line of the table shows the results of a likelihood-ratio test comparing a full model with separate estimates of the parameter for each treatment with a reduced model with only one estimate of the parameter across both treatments. Models were fit using nonlinear least-squares regression, with residual standard errors of 0.155 and 0.179 for the full model for *L. minor* and *S. polyrhiza* respectively, with 28 degrees of freedom. Parameter estimates and their confidence intervals for each treatment are shown in Figs 3b and 3c, fits of the competition model to the data are shown in Fig. S5, and the predicted equilibrium abundances based on the parameter estimates are compared with the observed population trajectories in Fig. S6.

parameter	$\chi^2_{\mathrm{df}=1}$	p
A. *Lemna minor*		
λ_L	10.937	0.001
α_{LL}	8.578	0.003
α_{LS}	6.670	0.009
B. *Spirodela polyrhiza*		
λ_S	<0.001	0.996
α_{SS}	0.028	0.868
α_{SL}	0.034	0.854

Table S4 The multilocus microsatellite genotypes of the *Lemna minor* clones used in the experiment. Values represent allele sizes in base pairs.

Clone	Fig. 1 color	Fig. 1 num.	Collection location	Microsatellite loci			
				R5C	R15A	R15B	R15C
R.20		1	Leuggern, Aargau, CH	346/350/446	225/267	188/190	370/376
R.70		2	Lenzburg, Aargau, CH	334/342/438	225/270	180/192	374/376
R.27		3	Leuggern, Aargau, CH	326/330	225	178/192	368/388
R.12		4	Urdorf, Zürich, CH	334	225/264	180/198	368/376
R.36		5	Urdorf, Zürich, CH	326/330	225/276	178/180	368/390
R.49		6	Zofingen, Aargau, CH	346/394	225	180	368/386
R.55		7	Kleindöttingen, Aargau, CH	326/354	225	174/188	368/384
R.50		8	Zofingen, Aargau, CH	330	225/270	170/180	382/384
R.83		9	Rüschlikon, Zürich, CH	342/346	252/258	180/190	376/382

Table S5 The multilocus microsatellite genotypes of the *Spirodela polyrhiza* clones used in the experiment. Values represent allele sizes in base pairs.

Clone	Fig. 1 color	Fig. 1 num.	Collection location	Microsatellite loci			
				7814	Pso31	7286	1035
S.20.29		1	Lenzburg, Aargau, CH	228	242	388	368
S.9622		2	Freiburg, Breisgau, DE	224	242	388	368/370
S.9607		3	Rämibühl, Zürich, CH	228	242/263	392	368/370
S.21		4	Delfgauw, S. Holland, NL	224	242	388	368
S.8.26		5	Urdorf, Zürich, CH	224/228	242	388	368/370
S.5.18		6	Irchel, Zürich, CH	228	242/266	392	368/370

Table S6 Microsatellite markers used to genotype *Lemna minor* and *Spirodela polyrhiza*. Allele size ranges are based only on the clones used in this experiment.

Locus	Primer sequence (5' – 3')	Repeat motif	Allele size range (bp)
A. *Lemna minor*			
R5C	F: TGATGCCAGTAGATCCGGC R: ACGCCTGAACACGATTGATG	AGAT	326-446
R15A	F: GTGACAGCGTATCCTTGTGC R: TCAGCGGCAAGATCATCAAG	ATC	225-276
R15B	F: TCGAGCTAATCAGTGGAGCC R: TGAGTGCTCGGCTTGACTTTC	AG	170-198
R15C	F: TGTTCCCACCCACTTGAC R: AAAGGAAGAGGGAGCAAGGG	AT	368-390
B. *Spirodela polyrhiza*			
7814	F: TAGTGTAGGGTGCAGCTGTG R: GTTCGTGAAAGGCCTAGCAC	AG	224-228
Pso31	F: TCCACCGTCTCCCTGTAATG R: CCACTCCCTCGTCGTGAAG	AAG	242-266
7286	F: CCGAATATGCCGAGGAATGC R: TCCTCGATCTGCCGCTTTAG	CG	388-392
1035	F: TGCTTGGTCACTCTTGTCTG R: ACGATTCCTAGCTCCTCTGC	AT	368-370

SI Appendix: Technical Details and Methods

Microsatellite development and identification of genotypes. We developed microsatellite markers to identify unique clonal lineages of *L. minor* and *S. polyrhiza*. Sequence data was obtained for *S. polyrhiza* from Wang et al. 2014 (2), genbank accession ATDW01000001.1, and from lemna.org (genome draft lm8627.ASMv0.1, downloaded on October 16th 2015) for *L. minor*. Microsatellite loci were identified and primers developed using *msatcommander* v.1.0.8 (3) with the default settings but excluding mononucleotide repeat motifs. Microsatellite primers selected to genotype the clonal lineages used in the experiment are described in Table S6 and the genotypes of each species are shown in Tables S4 and S5. Genotyping was done on at least three independent samples of each clonal lineage during the testing phase.

Genotyping in the main experiment. In order to obtain sufficient DNA for genotyping, individuals sampled from each treatment were allowed to multiply for one week in separate individual 1.2 mL tubes filled with nutrient media (4). Samples were then freeze-dried and DNA was extracted using a modified CTAB procedure (5). Each species had their own unique set of fluorescently labeled microsatellite markers (Microsynth, Switzerland; Table S6), which were pooled in a 15µL multiplex PCR and included 1 unit of GoTaq G2 Flexi DNA polymerase (Promega AG, Switzerland), 3µL of 5x Mg-free reaction buffer, 1.2mM MgCl2, 0.2mM of each dNTP, between 0.15 and 0.5 µM of each forward and reverse primer pair (exact concentrations depended on the strengths of the fluorescent dye and optimized per multiplex primer set), and 3µL of DNA template.

The PCR cycling program for *S. polyrhiza* included an initial denaturation of 94 °C for 5 min, followed by 35 cycles of denaturation (94 °C, 1 min), annealing (60 °C, 1 min), and extension (72 °C, 1 min), and a final extension of 72 °C for 10 min. For *L. minor*, we used touchdown PCR with an initial denaturation of 94 °C for 5 min, followed by five cycles of denaturation (94 °C, 1 min), annealing (65 °C, 1 min; decreasing by 1 °C per cycle), and extension (72 °C, 1 min). This was followed by 30 cycles with an annealing temperature of 60 °C, and a final extension of 72 °C for 15 min. Fragment length analyses were conducted on an ABI 3730 Genetic Analyzer (Applied Biosystems) at the ETH Genetic Diversity Center and visualized using the software *Geneious* version 9.1.6 (6).

Competition model assumptions. As described in the Materials and Methods in the main text, to quantify niche and competitive-ability differences between the species in each treatment, we parameterized a two-species competitive population dynamics model – the Law-Watkinson competition model (7) – using a separate series of competition experiments done under the same conditions in the field and using the evolved populations in each treatment from our main experiment. Importantly, we used these separate competition experiments to identify and parameterize this model because estimating model parameters from the observed trajectories in mixture is not possible (Materials and Methods).

The Law-Watkinson model is a simple, phenomenological model of competitive population dynamics. The model itself does not explicitly describe the mechanisms underpinning population growth and competition, nor does it explicitly describe the influence

of structure within populations, such as age or size-structure or plasticity, on dynamics. Importantly however, the separate competition experiments that we used to identify and parameterize the Law-Watkinson model do include these potentially important influences on dynamics. Therefore, to the extent that particular mechanisms of competition or structure within populations influence dynamics, these influences will be captured in the results of our competition experiments, and therefore by our model parameterization. Of course, if the influence of population structure, for example, changes over time, predictions from our phenomenological model would miss these factors. We note that the Law-Watkinson model provided a significantly better fit to the experimental data than a Beverton-Holt (8, 9) form of density dependence, where the competition coefficients are scalars rather than exponents on N (*L. minor*: ΔAIC = 25.36; *S. polyrhiza*: ΔAIC = 10.93). Regardless, all of the subsequent results were similar if we use the Beverton-Holt form. We also note that we fit a discrete-time competition model to a continuous-time process (plant population growth) because the former best matches the time interval of our experimental measurements. Importantly, the Law-Watkinson model fit our competition experiment data well (Fig. S5), and our parameterizations based on these fits do a good job of predicting both qualitatively and quantitatively the abundance of the competing species in our main experiment (Fig. S6). This provides confidence that the model and parameterization, and the inferences we make based on this model (i.e. niche and competitive ability differences), accurately capture features of the study system that influence competition between these species.

Niche and competitive-ability differences. The quantitative expressions for niche overlap (ρ) and the ratio of competitive abilities (κ_i/κ_j) are derived directly from the mutual invasibility criterion of species coexistence (10-14). The mutual invasibility criterion determines if species coexistence is possible by assessing the ability of each species at low density to 'invade' a 'resident' species (the heterospecific competitor) that is at its single-species equilibrium density (10, 11). If both species involved in the interaction have positive invasion growth rates, then the mutual invasibility criterion is met, and the species are predicted to coexist. Equivalently, this criterion is met when $\rho < \frac{\kappa_i}{\kappa_j} < \frac{1}{\rho}$ (11, 13, 15, 16), an inequality we introduce in the main text. In words, this expression states that for coexistence to occur via mutual invasibility, the niche overlap between species must be less than the ratio of their competitive abilities, a criterion we visualize in Fig. 3a.

The expressions quantifying niche and competitive-ability differences are composite variables of the parameters in Law-Watkinson model. Therefore, we used error propagation methods to estimate the uncertainty in these composite variables based on the uncertainty in the underlying parameter estimates (17). Specifically, for each treatment we used Monte Carlo simulations to generate 10^6 possible combinations of each of the parameter values in the Law-Watkinson model based on their estimated values, and their variances and covariances, from the underlying model fits. We then used each unique parameter combination to generate a unique estimate of the niche ($1-\rho$) and competitive ability difference (κ_i/κ_j). This process generates a probability distribution (based on 10^6 values) for both the niche and competitive-ability difference in each treatment, from which we can estimate an expected value and standard deviation for each of these composite variables in

each treatment (17). For this procedure, we used the 'propagate' package in R (18). The expected values and their standard deviations are shown in Fig. 3a.

We emphasize that it is not our goal to test for significant differences in niche and competitive-ability differences between our selection treatments, but rather to identify which of these alternative (but not mutually exclusive) pathways resulted in the differences in the population dynamics we observed between our selection treatments (Fig. 2). To do this we first identified which of the 10^6 simulated parameter combinations (described above) resulted in more even equilibrium population abundances in the heterospecific selection treatment, which is what we observed in our main experiment (Fig. 2). For example, we excluded simulated parameter combinations that would have resulted in an increase in *L. minor* abundance under heterospecific selection, because such a change is inconsistent with the dynamics that we observed in our main experiment and that we are aiming to explain (Fig. 2). Then, for each parameter combination that resulted in more even abundances in the heterospecific vs. conspecific selection treatment (consistent with our main result) we calculated niche ($1-\rho$) and competitive ability (κ_i/κ_j) differences according to the expressions for calculating these quantities that we introduced in the Materials and Methods. We then calculated the proportion of these cases where niche differences ($1-\rho$) were higher vs. lower in the heterospecific versus conspecific selection treatment, and the proportion of cases where competitive ability differences ($\kappa_{L.\ minor}/\kappa_{S.\ polyrhiza}$) were higher vs. lower in the heterospecific vs. conspecific selection treatment. If higher vs. lower values occur in equal proportion, this suggests that the difference between treatments in abundance in our main experiment were unlikely to be explained by a particular directional change in this term. By contrast, if more even abundances in the heterospecific selection treatment were always associated with a particular directional change in either the niche or competitive ability difference, this suggests that this directional change was likely to be an important driver of the differences in abundance between treatments.

We note that because niche and competitive-ability differences are derived based on the mutual invasibility criterion of species coexistence, there is not a 1:1 match between these quantities and population abundances away from the invasion boundary. While niche and competitive ability differences directly determine invasion success (13), population abundances away from the invasion boundary are also determined by single-species' carrying capacities, for example (12). Thus, while decreasing the competitive ability of one species over another will cause a decrease in its relative abundance (as we found for *L. minor*), the relationship between the magnitude of the competitive ability differences (defined at the invasion boundary and shown in Fig. 3a) and the magnitude of the difference in population sizes away from the invasion boundary (shown in Fig. 2) is not expected to be 1:1.

Trait measurements in the lab. Measuring traits of each clone under controlled conditions allowed us to isolate the effects of selection on genetically-based trait differences. A few mother fronds of each clone were marked and placed in glass jars containing nutrient media (19), and covered with a punctured plastic lid to avoid excessive evaporation. These fronds were kept in climate cabinets at 25 deg. C on a 14-10 hr. light-dark cycle for two weeks, and produced 2-3 generations of daughter fronds during this time. The original mother fronds

were then discarded and the same morphological traits measured on the plants in the field were measured on the lab-reared individuals (for between 5-15 fronds for *S. polyrhiza* and 10-30 fronds for *L. minor*). We used the same methods for measuring traits as for the field-based trait measurements (described in the Materials and Methods in the main text) and we also measured frond wet weight, which allowed us to assess leaf dry matter content (dry mass/wet mass) for each clone. We used the measurements of each clone-level trait to reconstruct the change in trait values due to genotypic change in the main experiment. We did this by weighting the clone-level mean trait values by the known frequency of each clone in each replicate in each treatment in the main experiment (Fig. 1, Fig. S7).

Phenotypic Plasticity Test. To check that phenotypic plasticity was not the major driver of our results, we examined how a plastic response of *L. minor* to conspecific and heterospecific competitive environments affects its ability to coexist with *S. polyrhiza*. *S. polyrhiza* did not show evidence of trait (Fig. 4), demographic (Fig. 3b), or competitive rate (Fig. 3c) change in our experiments. In combination with the lack of genotypic change across treatments (Fig. 1), these results suggest that plasticity in this species was unlikely to have contributed to our results.

We assessed the effects of plasticity on the ability of *L. minor* to coexist with *S. polyrhiza* using a common coexistence criterion – the low-density 'invasion' growth rate (11). We note that competitive ability (as estimated in our evolution experiment, Fig. 3a) is derived from the mutual invasibility condition of species coexistence, which means that a decrease in competitive ability as we found for *L. minor* in our main evolution experiment will be mirrored by a decrease in the low-density invasion growth rate for this species, all else being equal. Therefore, if phenotypic plasticity is responsible for the decrease in competitive ability observed in our evolution results (Fig. 3a), then phenotypic plasticity in response to heterospecific competitive environments should decrease *L. minor*'s invasion growth rate, relative to the effects of phenotypic plasticity in response to conspecific competitive environments. We describe our methods and results in more detail below, but the end result is that phenotypic plasticity in response to heterospecific competitive environments tends to increase *L. minor*'s invasion growth rate (Fig. S10), a result that is opposite to what would be expected if phenotypic plasticity was responsible for our evolution results.

Phenotypic plasticity test: experimental design. We allowed the dominant *L. minor* clone from our main experiment (genotype 1 shown in light blue in Fig. 1, Table S4) to grow for five weeks either in conspecific or heterospecific (i.e. with *S. polyrhiza*) competitive environments. These 'plasticity induction' treatments mirrored the selective environments in the two treatments in our main evolution experiment, but without genotypic variation in *L. minor* such that evolution via changes in genotype frequencies could not occur. Thus, if there are differences in *L. minor* growth rates after being exposed to the two the different induction treatments, we can attribute these to plastic changes in response to the competitive environment.

Individuals in both plasticity induction treatments (heterospecific and conspecific induction) were grown in a climate chamber at ETH Zürich in large containers (210 mm diameter, 195 mm height) containing 1250 ml Hoagland's nutrient solution (4) (replenished

weekly) under a 16/8 hour, 23/21°C day/night cycle. There were nine replicates of each treatment. After five weeks, we used the individuals from each replicate of each treatment in competition experiments designed to parameterize a model of competitive population dynamics (12), which we then used to estimate invasion growth rates. For the competition experiments, we exposed low densities (0.65 individuals per cm^2) of *L. minor* that had been growing in either conspecific or heterospecific competitive environments to a range of densities (0, 1.3, 3.3, 7.4, 15.8, ~23.3, ~28.7 and ~34 individuals per cm^2) of a single clone of *S. polyrhiza* that itself had been growing in only conspecific competitive environments. In addition, we grew the same clone of *S. polyrhiza* across the same range of densities growing by itself. Each density combination was placed in a competitive arena – an open-ended vertical tube 2.8 cm in diameter – that was inserted into a frame floating in a large rectangular plastic tub (64 x 36 cm x 20 cm) that was filled to 15 cm depth with nutrient solution. For each replicate of the plasticity induction treatment (n = 9) there were a total of 22 density combinations in the subsequent competition experiment, enabling us to parameterize separate competition models for each replicate. All 22 density combinations for a single replicate were attached and randomly positioned within a floating frame placed in a single plastic tub. Individuals in each density combination were allowed to compete for seven days after which the final population sizes were quantified from photographs.

Phenotypic plasticity test: analyses and results. We fit population growth data for each replicate to a Beverton-Holt model of competitive population dynamics taking the following functional form (8, 9):

$$\frac{N_{L,t+1}}{N_{L,t}} = \frac{\lambda_L}{1 + \alpha_{LS} N_{S,t}} \qquad \text{(S2.1)}$$

where $N_{L,t}$ describes the population size of *L. minor* (*L*) at time *t*, λ_L is the per capita population growth rate in the absence of competitors (i.e. the finite rate of increase), and α_{LS} quantifies the per capita competitive effect of *S. polyrhiza* (*S*) on offspring production in *L. minor*. We also fit equation S2.1 to the *S. polyrhiza* data for each replicate to estimate the finite rate of increase (λ_S) and intraspecific competition coefficient (α_{SS}) for this species.

For this experiment, comparison of ΔAIC values indicated that the Beverton-Holt competition model (Equation S2.1) provided a better fit to the data than the Law-Watkinson competition model used in the genetic evolution experiment (Equation 1, described in the main text). We note that although different models best fit the data from the plasticity (Beverton Holt) and the genetic evolution (Law-Watkinson) experiments, in each case the model used was clearly the one that best fit the data, and so is most likely to provide accurate inference about dynamics and coexistence. Moreover, when we compare the effects of conspecific versus heterospecific treatments between the plasticity and evolution experiments, it is the direction of the difference between treatments within each experiment – i.e. a comparison based on data fit with the same model – that provides the information required to identify the contrasting effects of plasticity vs. evolution on performance.

The ability of species to coexist can be quantified by assessing the mutual invasibility criterion for species coexistence (11). As explained above, this criterion quantifies the ability of each species to recover from low density in the presence of their heterospecific competitor,

which is at its single-species equilibrium density. In our case, we are interested in the change in the magnitude of *L. minor*'s invasion growth rate after having had the opportunity to plastically respond to either heterospecific or conspecific competitors.

Following equation S2.1, we quantified the invasion growth rate of *L. minor* invading *S. polyrhiza* using the following equation:

$$N_{L,t+1} = \frac{\lambda_L}{1+\alpha_{LS}\left(\frac{\lambda_S - 1}{\alpha_{SS}}\right)} \quad \text{(S2.2)}$$

which is the same as equation S2.1, but where *L. minor* is at vanishingly small density and $N_{S,t}$ has been replaced by the expression $\frac{\lambda_S - 1}{\alpha_{SS}}$, which quantifies the equilibrium population density of *S. polyrhiza*. Fitting equation S2.1 to the data from each replicate of the competition experiments provided replicate estimates of each parameter in equation S2.2, allowing nine independent estimates of *L. minor*'s invasion growth rate for each phenotypic plasticity treatment (conspecific vs. heterospecific induction).

As shown in Fig. S10, *L. minor* invasion growth rates tended to be higher when this species was able to plastically respond to heterospecific compared with conspecific competitors. By contrast, *L. minor* invasion growth rates showed exactly the opposite pattern as a consequence of genetic evolution to heterospecific competitors (Fig. S10), which mirrors the decline in *L. minor* competitive ability shown in Fig. 3a in the main text. These contrasting effects of plasticity vs. evolution on competitive performance of *L. minor* suggest that, if anything, plasticity in response to conspecific vs. heterospecific competitive environments is likely to have counteracted the effects of evolution in response to those same competitive environments. Subsequent analyses indicated that the higher invasion growth rate as a consequence of plasticity in heterospecific competitive environments (Fig. S10) occurred as a consequence of an increase in *L. minor*'s competitive ability, which is again opposite to the effects of genetic evolution, which reduced *L. minor*'s competitive ability, as shown in Fig. 3a in the main text.

SI Appendix: References

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