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Supplementary Information for

Earlier phenology of a nonnative plant increases impacts on native competitors

Jake M. Alexander, Jonathan M. Levine

Corresponding author: Jake M. Alexander

Email: jake.alexander@usys.ethz.ch

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Supplementary Information Text

Supplementary Materials and Methods

Estimation of focal plant fecundity. To estimate fecundity, we counted flower heads of all focal individuals in the field. Native species were sampled between early-April and mid-May when focal individuals had completed flowering and senesced. For some species we noted considerable variation in the size of flower heads, which we accounted for in our estimates of total plant fecundity. To do so, we measured the length (*P. erecta*, *V. microstachys*) or diameter (*N. atractyloides*, *S. columbariae*) of every inflorescence per focal individual, and for each taxon collected 16–32 (mean 25.2) mature inflorescences that had not dehisced to count seed number per inflorescence. For *P. erecta*, *S. columbariae* and *V. microstachys* we predicted seed number per inflorescence from linear models of seed number on inflorescence size (R^2 = 0.80-0.92, seed number square-root transformed for *S. columbariae*). For *N. atractyloides* we estimated seed numbers within three size classes, and for *L. californica* and each *L. serriola* population we simply estimated the average seed number per inflorescence. The fecundity of each focal individual was then calculated as the sum of the seed numbers in each inflorescence.

L. serriola plants (both focal individuals and background competitors) were harvested before their seeds had ripened to prevent release of seed into the environment. Inflorescence counts of focal *L. serriola* individuals included both mature flowers/ripening seed heads and immature buds. To confirm that this approach did not lead to an underestimation of lifetime fecundity, we covered 20 individuals with netting to prevent seed release until the plants had senesced, at which time we counted the number of inflorescences that had produced seeds. The intercept of the relationship between initial and final (bagged) inflorescence counts was not significantly different from 0 (linear model, P = 0.295), and the slope not significantly different from 1 (t-test, P = 0.987), so we conclude that early harvesting did not bias fecundity estimates for *L. serriola*.

Estimating native species persistence. To test the hypothesis that differences in *L. serriola* phenology affect the ability of native species to persist with *L. serriola*, we parameterised a mathematical model describing how competition affects the population growth of annual plants. Full details of the model are given by Godoy and Levine (17) and are summarized here. The per capita population growth rate of an annual plant can be described by:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + g_i F_i \qquad (1)$$

where N_i is the population size (seed number) of focal species i prior to germination in year t, g_i is the germination rate of those seeds, s_i is the annual survival of ungerminated seeds in the soil seed bank, and F_i is the per germinant fecundity of species i. F_i is a Beverton-Holt function of both intra- and interspecific competitors as follows:

$$F_i = \frac{\lambda_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \qquad (2)$$

where λ_i is the per germinant fecundity in the absence of competition, and α_{ij} is the per capita effect of species j on the fecundity of species i.

From this model we can derive the low-density growth rate (LDGR; also known as the invasion growth rate) of a focal species i, that is its ability to recover from low density when its competitor j is at its single species equilibrium abundance (equation A.14 in ref. 17):

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)(s_i) + \frac{\lambda_i g_i}{1 + \alpha_{ij} g_j \left(\frac{1}{\alpha_{jj} g_j} \left[\frac{\lambda_j g_j}{1 - (1 - g_j)(s_j)} - 1 \right] \right)} \qquad (3)$$

We used equation 3 and the parameters estimated in the field experiment to calculate the LDGR of each native species i in the presence of each *L. serriola* population j. We obtained the parameters λ_i and α_{ij} as described above. *L. serriola* focal individuals experienced high mortality, especially in the competition plots, and so we did not estimate α_{jj} for each *L. serriola* population separately. Instead we fitted a model including all *L. serriola* individuals, irrespective of origin, to estimate a common *L. serriola* intraspecific competition coefficient (α_{jj}), with λ_j taken to be the average per germinant fecundity across all individuals with data, weighted by survival probability. Models fitted with population-specific estimates of λ_j, and therefore population-specific estimates of α_{jj}, produced qualitatively similar results (Fig. S2). This latter analysis required that we estimate λ_j for the Swiss population, for which there were no surviving plants growing without neighbours, as twice the 99th percentile of the fecundity of plants growing across the experiment, which approximated the upper estimate of λ_i based on the other populations.

We conducted additional experiments to estimate germination rates, g_i, and seed-bank survival rates, s_i. First, we established the viability of seeds used in the experiment by germinating 100–150 seeds per species on filter paper in a climate cabinet for 2–3 weeks. A subset of ungerminated seeds were stained with 0.25 % tetrazolium solution to estimate the fraction of viable but dormant seeds. We then summed the number of germinated and dormant seeds to estimate the viable seed proportion. We estimated g_i in the field as the fraction of germinants emerging from 13–15 (mean 14.5) stations per species, where each station was sown with 100 viable seeds in plots without competitors. To estimate s_i, we buried nylon mesh bags each containing 100 viable seeds of one of the species (n=6 per species) at the field site in November 2014. Seed bags were retrieved at the end of the growing season in August 2015, and the fractions of surviving seed were calculated from the number of viable seeds before and after a year of burial (based on germination trials and tetrazolium staining as previously described). For *N. atractyloides*, we counted more viable seeds after than before burial, so we set its seed-bank survival to $s = 1$.

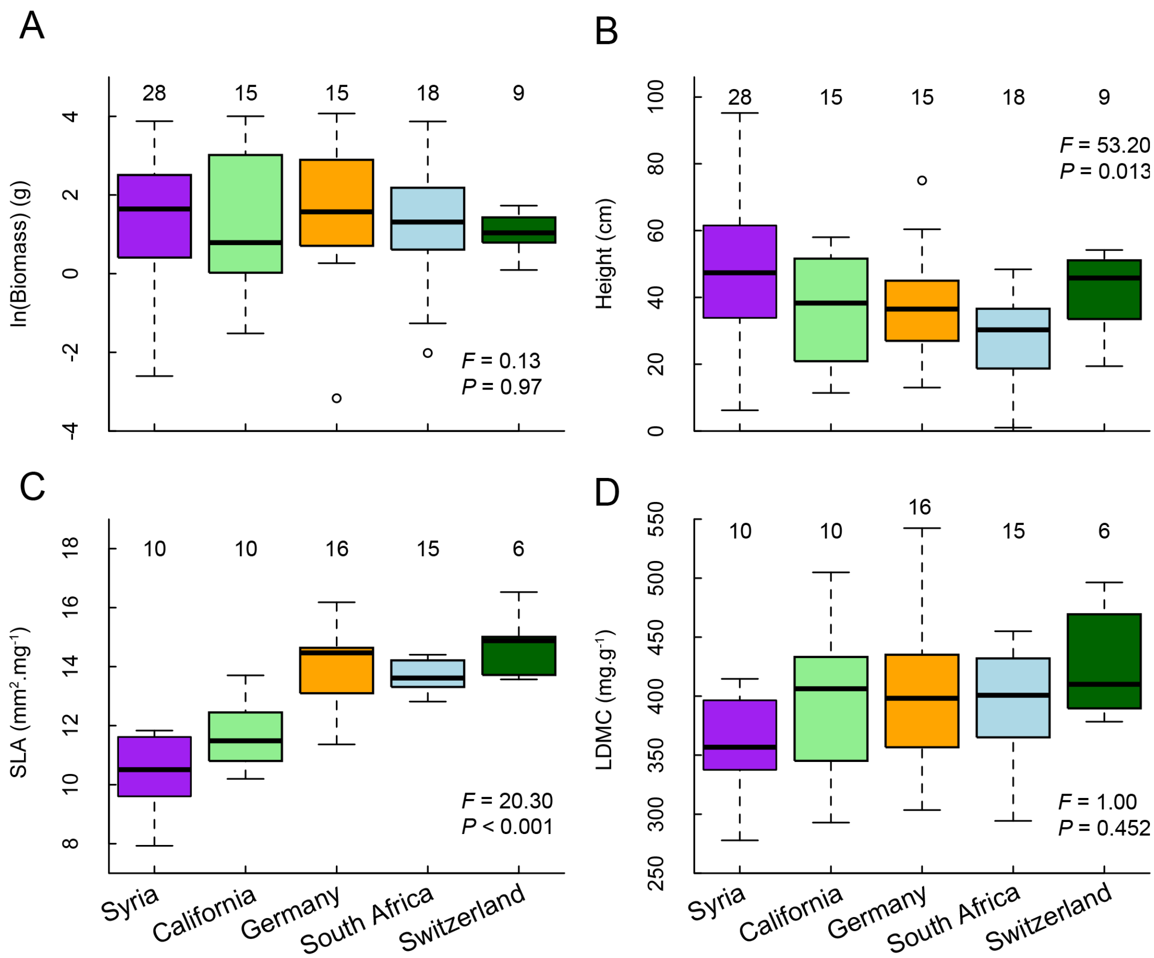

Fig. S1. Variation in aboveground biomass, height, specific leaf area (SLA) and leaf dry matter content (LDMC) between *L. serriola* plants originating from five populations (countries/USA states) and grown in a field site in southern California. Aboveground biomass and total plant height were determined from 9–28 (mean 17) flowering *L. serriola* individuals from each population that were harvested before they released seeds. SLA and LDMC were determined from 2–4 (mean 2.9) undamaged leaves from 6–16 (mean 11.4) individuals per population, collected in June 2015 from background competitor plants that had bolted or were flowering. Statistics indicate support for differences in population means from mixed effects models accounting for experimental plot as a random effect. Sample sizes for each population and trait are indicated above the box-and-whisker plots.

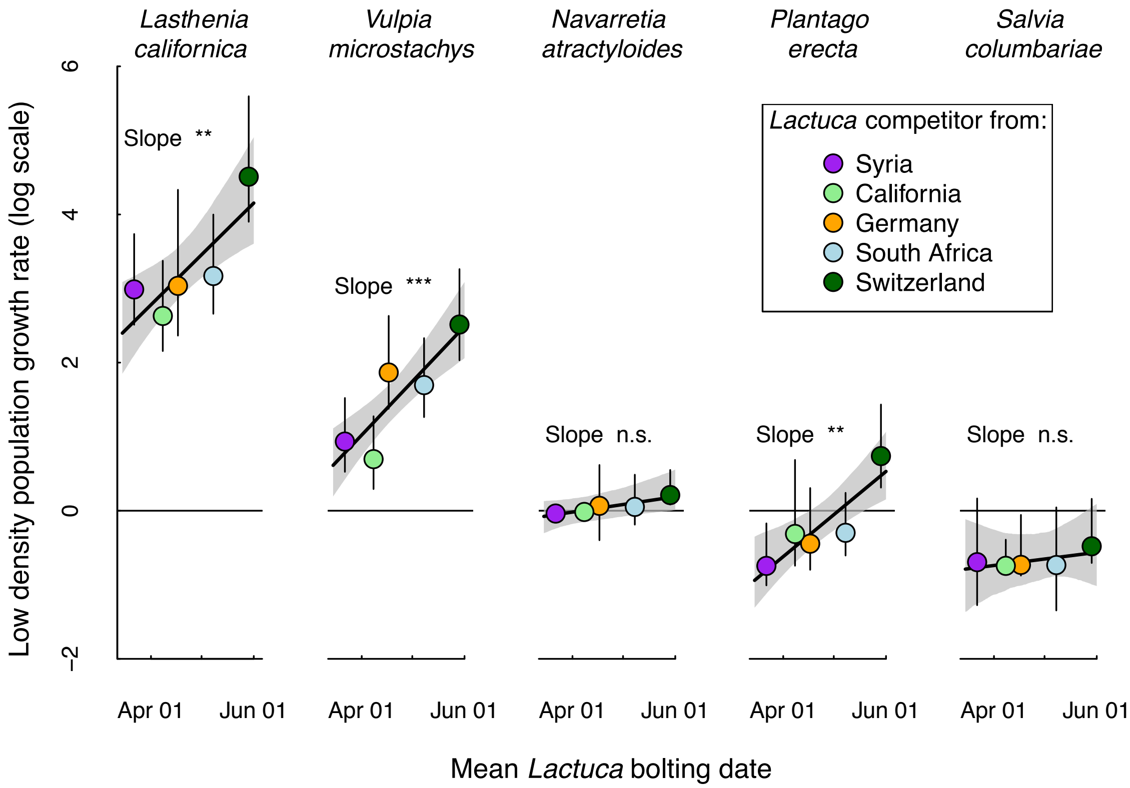

Fig. S2. Predicted low-density growth rates (LDGR) of five native species in competition with five *L. serriola* populations in an experimental garden in southern California, plotted against the mean bolting date of the *L. serriola* population. The estimates differ from those shown in Fig. 5 in that here LDGRs are calculated accounting for differences between *L. serriola* populations in fecundity in the absence of competition (λ_j) and in per capita intraspecific competitive effects (α_{jj}; see Materials & Methods). LDGR estimates are log-transformed, so that positive values predict that a focal species will persist with *L. serriola*, whilst negative values predict that they will be competitively excluded. Error bars and grey shading indicate the 95 % confidence intervals around estimates of LDGR and the regression slopes, respectively, accounting for variance in estimates of each *L. serriola* population's competitive effect on a native species (see Materials and Methods). *** $P < 0.001$; ** $P < 0.01$; n.s. $P > 0.05$.

Table S1. Estimates of low-density population growth rates (LDGR) of native California species competing with *L. serriola* originating from one of five geographic areas. Values in parentheses are 95 % confidence intervals accounting for uncertainty in estimates of *L. serriola*'s competitive effect on native species (α_{ij}; shown in Fig. 5), or propagating uncertainty in all eight parameters of the expression for LDGR (equation 3 in Supplementary Materials and Methods).

Focal taxon (i)	Source of uncertainty	$LDGR_{i,Germany}$	$LDGR_{i,South\ Africa}$	$LDGR_{i,Syria}$	$LDGR_{i,California}$	$LDGR_{i,Switzerland}$
L. californica	α_{ij} only	2.99 (2.32, 4.29)	3.51 (3.00, 4.34)	2.65 (2.18, 3.40)	2.83 (2.36, 3.58)	4.48 (3.87, 5.56)
	All parameters	2.57 (-1.31, 6.88)	3.09 (-0.96, 7.29)	2.22 (-1.48, 6.34)	2.40 (-1.38, 6.55)	4.10 (-0.27, 8.36)
N. atractyloides	α_{ij} only	0.06 (-0.40, 0.60)	0.10 (-0.01, 0.65)	-0.05 (-0.06, 0.01)	0.00 (-0.04, 0.12)	0.20 (0.08, 0.53)
	All parameters	0.07 (-1.01, 1.88)	0.09 (-1.07, 2.05)	-0.05 (-0.46, 0.42)	-0.01 (-0.74, 0.99)	0.16 (-1.19, 2.31)
P. erecta	α_{ij} only	-0.47 (-0.82, 0.27)	-0.05 (-0.40, 0.53)	-0.90 (-1.12, -0.40)	-0.17 (-0.63, 0.87)	0.71 (0.29, 1.41)
	All parameters	-0.69 (-3.01, 2.61)	-0.34 (-2.90, 3.23)	-1.04 (-3.09, 1.69)	-0.43 (-2.93, 3.18)	0.34 (-2.62, 4.26)
S. columbariae	α_{ij} only	-0.74 (-0.88, -0.08)	-0.65 (-0.86, 0.28)	-0.76 (-1.35, -0.06)	-0.70 (-0.83, -0.30)	-0.49 (-0.71, 0.14)
	All parameters	-0.83 (-2.79, 1.30)	-0.73 (-2.78, 1.79)	-0.84 (-2.80, 1.28)	-0.81 (-2.78, 1.27)	-0.63 (-2.73, 2.00)
V. microstachys	α_{ij} only	1.82 (1.33, 2.59)	2.04 (1.61, 2.67)	0.59 (0.18, 1.18)	0.90 (0.50, 1.48)	2.48 (2.00, 3.23)
	All parameters	1.50 (-2.56, 5.61)	1.72 (-2.34, 5.80)	0.25 (-3.71, 4.31)	0.56 (-3.44, 4.61)	2.17 (-1.89, 6.23)

Table S2. Parameters (± standard error) derived from the competition experiment and used to fit models of competitive population dynamics. Parameters include estimates of the mean survival-weighted fecundity of plants growing without neighbours (λ_i), and competition coefficients (α_{ij}) describing the per capita effects of competitor *j* (*L. serriola* originating from one of five geographic areas) on focal taxon *i* (one of five native Californian species, or *L. serriola* population). *L. serriola* individuals from each population were also pooled ("*Lactuca*") to estimate parameters at the species level.

Focal taxon (*i*)	λ_i	$\alpha_{i,Germany}$	$\alpha_{i,South\ Africa}$	$\alpha_{i,Syria}$	$\alpha_{i,California}$	$\alpha_{i,Switzerland}$	$\alpha_{i,Lactuca}$	Seed viability	Seed bank survival (*s*)	Germinatio rate (*g*)
L. californica	15339 (2460)	0.79 (0.32)	0.45 (0.14)	1.06 (0.30)	0.88 (0.25)	0.17 (0.06)	NA	0.67	0.50 (0.12)	0.35 (0.06)
N. atractyloides	751 (197)	1.25 (0.77)	0.99 (0.56)	7.71 (3.31)	2.59 (1.01)	0.53 (0.18)	NA	0.50	1.00	0.07 (0.02)
P. erecta	647 (96)	1.26 (0.44)	0.65 (0.18)	2.87 (0.95)	0.83 (0.33)	0.26 (0.07)	NA	0.98	0.32 (0.05)	0.26 (0.05)
S. columbariae	2646 (494)	17.14 (9.77)	11.34 (7.25)	18.92 (12.04)	13.74 (5.57)	6.50 (2.64)	NA	0.96	0.47 (0.09)	0.18 (0.04)
V. microstachys	950 (156)	0.25 (0.07)	0.20 (0.05)	0.85 (0.20)	0.62 (0.15)	0.13 (0.04)	NA	0.78	0.01 (0.01)	0.60 (0.07)
Germany	1167 (681)	NA	NA	NA	NA	NA	0.98 (0.34)	0.95	0.58 (0.13)	0.16 (0.04)
South Africa	904.05 (400)	NA	NA	NA	NA	NA	0.75 (0.25)	0.85	0.73 (0.05)	0.18 (0.07)
Syria	2501 (714)	NA	NA	NA	NA	NA	2.17 (0.67)	0.97	0.67 (0.09)	0.09 (0.03)
California	1026 (378)	NA	NA	NA	NA	NA	0.86 (0.34)	0.97	0.73 (0.11)	0.15 (0.05)
Switzerland	228	NA	NA	NA	NA	NA	0.16 (0.07)	0.99	0.67 (0.11)	0.10 (0.03)
Lactuca	1607 (353)	NA	NA	NA	NA	NA	1.38 (0.52)	NA	0.68 (0.04)	0.14 (0.02)

Table S3. Origins of the 26 *L. serriola* populations included in the common garden experiment. The five populations included in the competition experiment are indicated w asterisks. Population codes ("Pop") correspond to codes used in ref. 20.

Pop	Country	Range	Latitude	Longitude
Ls002	Australia	Introduced	-35.4300	149.7800
Ls004	Australia	Introduced	-42.6800	147.3200
Ls005	Australia	Introduced	-37.8194	145.0000
Ls006	Canada	Introduced	49.1247	-123.1784
Ls007	Canada	Introduced	49.9397	-119.3930
Ls008	Canada	Introduced	49.1482	-116.5349
Ls021	France	Native	43.7432	4.7925
Ls026*	Germany	Native	51.3117	12.2377
Ls029	Italy	Native	41.2889	13.9839
Ls032	Netherlands	Native	51.6667	5.3333
Ls039	Spain	Native	36.6392	-4.4958
Ls040	Sweden	Native	56.6164	16.4579
Ls049	Switzerland	Native	46.8298	9.4095
Ls051	UK	Native	51.3811	-2.6444
Ls060	South Africa	Introduced	-33.9553	18.8086
Ls064	South Africa	Introduced	-33.8828	18.6333
Ls066*	South Africa	Introduced	-28.0003	24.7500
Ls074	Syria	Native	33.4500	36.2833
Ls075*	Syria	Native	34.7167	36.4000
Ls077	Armenia	Native	40.2000	44.2500
Ls087	Azerbeijan	Native	39.2667	48.4833
Ls093	Israel	Native	31.9896	34.8982
Ls096	Oregon	Introduced	45.4138	-117.8291
Ls099	Oregon	Introduced	45.4093	-117.8933
Ls112*	California	Introduced	34.7389	-120.0261
Ls114*	Switzerland	Native	47.4031	8.5489

Database S1. Fecundity and neighbour density data for focal individuals of *L. serriola* and native species in the competition experiment, including bolting date for *L. serriola*.

ID:	Unique identifier for each focal individual.
Plot:	Unique identifier for each experimental plot.
Background:	"Lactuca" if plot was sown with *L. serriola* as a background competitor, else "none".
Lactuca_background:	Origin of the *L. serriola* background competitor: "CA", California; "CH", Switzerland; "DE", Germany; "SA", South Africa; "SY", Syria; "none" if no background competitor.
Focal_taxon:	Identity of the focal individuals; native species: "Las", *Lasthenia californica*; "Nav", *Navarretia atractyloides*; "Pla", *Plantago erecta*; "Sal", *Salvia columbariae*; "Vul", *Vulpia microstachys*. *L. serriola* origins as for "Lactuca_background".
Neighbour_abundance:	The number of seedlings counted within a 7.5 cm radius of the focal individual.
Date_bolting:	For *L. serriola* focal individuals, the date when bolting was first observed.
Fecundity:	The estimated seed production of a focal individual.
Survival:	Whether or not a focal individual survived to produce seeds.

Additional database S1 (separate file)