

**Supporting Information.** David W. Armitage, Stuart E. Jones. 2019. Negative frequency-dependent growth underlies the stable coexistence of two cosmopolitan aquatic plants. *Ecology*.

## APPENDIX S1

### S1.1 Formulation of Growth Medium

This medium was originally formulated by Docauer (Docauer 1983) to approximate the buffering system (bicarbonate), pH (6.5), conductivity (440  $\mu\text{S}/\text{cm}$ ), and nutrient contents of natural waters containing *Lemna minor* and *Spirodela polyrhiza*. Below, we reproduce Docauer's original formulation from his dissertation.

Compound	Stock concentration	Stock per liter media	Final media concentration	
	g/L	mL	mg/L	mM
Na <sub>2</sub> EDTA	20.00	2.0		0.107
NaNO <sub>3</sub>	25.00	2.0	8.2 N	0.586
K <sub>2</sub> HPO <sub>4</sub>	3.68	1.0	1.3 P	0.042
KCl	50.00	1.0	26.0 K	0.671
CaCl <sub>2</sub>	25.00	2.0	18.0 Ca	0.450
MgSO <sub>4</sub> • 7H <sub>2</sub> O	37.50	0.5	13.5 Mg	0.555
Micronutrients	See below	1.0	See below	
NaHCO <sub>3</sub>	60.00	1.0*	48.0 HCO <sub>3</sub>	0.785

Micronutrient stock:

Compound	Stock concentration	Final media concentration	
	g/100 mL	mg/L	mM
FeSO <sub>4</sub> • 7H <sub>2</sub> O	0.995	2.0 Fe	0.036
MnCl <sub>2</sub> • 4H <sub>2</sub> O	0.072	0.2 Mn	0.004
Na <sub>2</sub> MoO <sub>4</sub> • 2H <sub>2</sub> O	0.044	0.1 Mo	0.001
H <sub>3</sub> BO <sub>3</sub>	0.057	0.1 B	0.009
ZnSO <sub>4</sub> • 7H <sub>2</sub> O	0.044	0.1 Zn	0.002
Na <sub>2</sub> EDTA	2.000		0.054

Mix the following separately and add 1 mL per 100 mL micronutrient stock:

CuSO <sub>4</sub> • 5H <sub>2</sub> O	0.004	0.0001 Cu	0.0000016
CoCl <sub>2</sub> • 6H <sub>2</sub> O	0.400	0.01 Co	0.00017
Na <sub>2</sub> EDTA	0.400		0.00010

\*Slowly add NaHCO<sub>3</sub> while bubbling to desired pH; 1.0 mL gives pH 6.5.

We used MilliQ ultrapure water as the base of our media. Stock solutions are added in the order they appear to avoid precipitation. The sodium bicarbonate is added last. At this point, the medium is supersaturated with CO<sub>2</sub> and is therefore more acidic than it would be when at equilibrium with air. To remedy this, the solution is vigorously bubbled with air for 30 minutes

until the pH stabilizes at 6.5. The solution is then autoclaved and can be used for growth experiments.

## S1.2 Specifying the Inter- and Intraspecific Competition Function

To choose the appropriate functional form of our population dynamic models, we needed to appropriately specify a species' growth responses to the densities of conspecifics and heterospecifics, and the interaction of these responses with the environment. For notational simplicity, we remove the time ( $t$ ) subscripts but note that all states and parameters save mortality rates can be time-variant. For our duckweed model with vegetative ( $N_j$ ) and dormant turion ( $S_j$ ) stages and variable temperatures ( $T$ ), we can model the total population growth rates by summing the turion and vegetative sub-populations:

$$r_j = \frac{\left(\frac{dN_j}{dt} + \frac{dS_j}{dt}\right)}{N_j + S_j} = \frac{N_j[\mu_j(T)f(\alpha_{jk}, N_k) - m_j]}{N_j + S_j}, \quad (j = 1, 2) \quad (\text{S1})$$

where  $f(\alpha_{jk}, N_k)$  describes the strength of intraspecific (when  $j=k$ ) and interspecific (when  $j \neq k$ ) competition. We compared related forms for  $f(\alpha_{jk}, N_k)$ : the standard Lotka-Volterra competition model (MacArthur 1970), and versions modified with log-transformed abundances (Turchin 2003). Likewise, a subset of models allowed for covariation between ambient temperature and the interaction parameters. For two species, *Spirodela* and *Lemna*, our models took the general form:

$$f(\alpha_{jk}, N_k) = 1 - \alpha_{jj}(T)N_j - \alpha_{jk}(T)N_k, \quad (j \neq k) \quad (\text{S2})$$

which, when combined with eq. S.1 and rearranged, yields the linear regression equation

$$\begin{aligned} \mathbb{E}[r_j | N_j, N_k, T] &= \beta_{j0} + \beta_{jT}T + (\beta_{jj} + \beta_{jjT}T) \log(N_j + 1) \\ &+ (\beta_{jk} + \beta_{jkT}T) \log(N_k + 1) + \varepsilon_j. \end{aligned} \quad (\text{S3})$$

Here, the regression coefficients ( $\beta$ 's) relate to the coefficients of eqs. 5 and S.2 as follows:

$$\begin{aligned} \beta_{j0} + \beta_{jT}T &= v_j(\mu_j(T) - m_j), \\ \beta_{jj} + \beta_{jjT}T &= v_j\mu_j(T)\alpha_{jj}(T), \\ \beta_{jk} + \beta_{jkT}T &= v_j\mu_j(T)\alpha_{jk}(T), \end{aligned} \quad (\text{S4})$$

and

$$\begin{aligned} v_j &= N_j / (N_j + S_j), \\ \alpha_{jj}(T) &= \alpha_{jj}(\bar{T}) + \phi_{jj}T, \\ \alpha_{jk}(T) &= \alpha_{jk}(\bar{T}) + \phi_{jk}T. \end{aligned} \quad (\text{S5})$$

We assume that the scaling parameter,  $v_j$ , is equal to one for both species. This simplification did not significantly change our parameter estimates, as these values were very close to 1 for populations during most census periods. We then used our empirical estimates for  $\mu_j(T)$  and  $m_j$  to solve for the model parameters. For convenience, thermal responses of competition parameters were assumed to be linear functions of temperature where  $\alpha_{jk}(T)$  are competition coefficients at average ambient temperatures (here, 20°C) and  $\varphi_{jk}$  are the temperature-dependent slope parameters in  $\alpha_{jj}(T)$ . While this assumption has some empirical support (reviewed in Amarasekare and Coutinho 2014), we note that our sampling design did not permit the recovery of nonlinear or non-monotonic response surfaces. Regression models were fit to data from the fluctuating environment experiment using least squares (lm) in R (ver. 3.3). Best-fitting models were selected based on coefficients of determination ( $R^2$ ). We ultimately selected model 4, with log-transformed populations and temperature-dependent competition for our species interaction term. Parameters and fit statistics for each model are presented in Table S2.

### S1.3 Quantifying the temporal storage effect

The temporal storage effect (Chesson 1994) is one of two potential fluctuation-dependent coexistence mechanisms. We used the Monte Carlo-based approach introduced by Ellner *et al.* (2016) to quantify the contribution of the temporal storage effect to invaders' *per capita* growth rates in fluctuating environments. This technique begins by defining a function that describes species' growth rates in terms of an environmentally-dependent parameter,  $E_j$ , and competition parameter,  $C_j$ . Many formulations for  $f(E_j, C_j)$  are possible, but here we use

$$r_j = f(E_j, C_j) = v_j(E_j C_j - m_j), \quad j = (1, 2), \quad (\text{S6})$$

where

$$E_j = \mu_j(T), \quad C_j = 1 - \alpha_{jj}(T)N_j - \alpha_{jk}(T)N_k, \quad j \neq k. \quad (\text{S7})$$

Using these equations, we generated environmental sequences for  $E_j(t)$  across a range of different average temperatures and amplitudes by simulating the dynamics of a resident species in monoculture and saving its model parameters and states at each time step once it had reached equilibrium with its environment (i.e.,  $\bar{r}_{j\setminus r} = 0$ ). These values were then used to calculate both species' long-term average resident and invasion growth rates,  $\bar{r}_{j\setminus r}$  and  $\bar{r}_{j\setminus i}$ , respectively, where  $\bar{r}_j = \mathbb{E}[r_j(t)]$ . Because a storage effect requires nonzero covariance between  $E_j(t)$  and  $C_j(t)$ , its contribution to an invader's growth rate (and therefore coexistence) is proportional to the contribution of  $\text{cov}(E_j, C_j)$  to the invader's growth rate,  $\bar{r}_{j\setminus i}$ . To remove the signature of  $\text{cov}(E_j, C_j)$  from  $\bar{r}_{j\setminus i}$ , we generated a second vector of environmental parameters,  $E_j^\#(t)$ , by randomly subsampling without replacement from the original  $E_j(t)$  vectors. This step makes  $E_j^\#$  and  $C_j$  independent of one another, and allows us to estimate  $\bar{r}_j^\# = \mathbb{E}[r_j^\#(t)]$ . With these values, we estimated the contribution of the storage effect ( $\Delta I_{j\setminus i}$ ) to the growth rate of invading species ( $\bar{r}_{j\setminus i}$ ) using the equation

$$\Delta I_{j \setminus i} = (\bar{r}_{j \setminus i} - q_{jk} \bar{r}_{k \setminus r}) - (\bar{r}_{j \setminus i}^{\#} - q_{jk} \bar{r}_{k \setminus r}^{\#}), \quad (\text{S8})$$

where  $q_{jk}$  are species-specific scaling factors relating to the relative sensitivity to competition experienced by resident species compared to the invading species (Chesson 1994). These scaling factors can be estimated by defining new environmental and competition parameters  $E_j$  and  $C_j$ :

$$E_j = f(E_j, C_j^*), \quad C_j = -f(E_j^*, C_j), \quad (\text{S9})$$

where  $C_j^*$  and  $E_j^*$  equal their baseline (i.e., mean or median) values. Thus, for our model, by defining  $E_j^* = \overline{\mu_j(T)}$ , we arrive at

$$C_j = v_j(m_j - \overline{\mu_j(T)})[1 - \alpha_{jj}(T) \log(N_j + 1) - \alpha_{jk}(T) \log(N_k + 1)]. \quad (\text{S10})$$

Finally, we used a regression approach outlined in Ellner *et al.* (2016, Appendix S1) to estimate the scaling parameters. For two species, Chesson's (1994, 2000) definition of these parameters is given by the equation

$$q_{jk} = \frac{\partial C_{j \setminus i}}{\partial C_{k \setminus r}}. \quad (\text{S11})$$

This partial derivative can be estimated by evaluating the slope of a nonlinear regression (here, a smoothing spline) of  $C_{j \setminus i}(t)$  on  $C_{k \setminus r}(t)$  at  $C_{k \setminus r} = 0$ .

We used this approach to identify thermal regimes where the temporal storage effect rescues a species from competitive exclusion by satisfying the inequality

$$0 < \bar{r}_{j \setminus i} < \Delta I_{j \setminus i}. \quad (\text{S12})$$

We also identified regions where the storage effect was overall positive but not greater than an invader's growth rate. In this situation, the storage effect positively contributes to coexistence, but cannot be considered the sole operating coexistence mechanism.

## Supplementary Tables

**Table S1.** Model selection results for duckweed growth rates in monoculture and competition. Candidate models are listed for each experiment. Bolded models denote best fits based on parsimony, BIC, and  $R^2$ . Temperatures and frequencies were centered at their median values prior to fitting.

Environment	Model form	BIC	$\Delta$ BIC*	$R^2$
Static temperatures (monoculture) $n = 72$	$r_{period} \sim 1$ ( <i>intercept – only model</i> )	-690	319	0
	$r_{period} \sim$ species (S) (Spirodela = 1)	-690	319	0.02
	$r_{period} \sim$ S + temperature (T) + temperature <sup>2</sup>	-938	70	0.60
	<b><math>r_{period} \sim</math> S + T + T<sup>2</sup> + census period (C)</b>	<b>-1009</b>	<b>0</b>	<b>0.70</b>
Static temperatures (competition) $n = 40$	$r \sim 1$ ( <i>intercept – only model</i> )	-697	142	0
	$r \sim$ species (S) (Spirodela = 1)	-694	145	0.01
	$r \sim$ S + temperature (T) + temperature <sup>2</sup>	-830	9	0.63
	<b><math>r \sim</math> S + T + T<sup>2</sup> + frequency (F)</b>	<b>-840</b>	<b>0</b>	<b>0.67</b>
	$r \sim$ S + T + T <sup>2</sup> + F + (S $\times$ F)	-837	3	0.67
Fluctuating temperatures (competition) $n = 55$	$r_{period} \sim 1$ ( <i>intercept – only model</i> )	-2296	797	0
	$r_{period} \sim$ species (S) (Spirodela = 1)	-2295	798	0.01
	$r_{period} \sim$ S + census period (C)	-3039	54	0.80
	<b><math>r_{period} \sim</math> S + C + frequency (F)</b>	<b>-3091</b>	<b>2</b>	<b>0.83</b>
	$r_{period} \sim$ S + C + F + turion replace (TR) (Yes=1)	-3093	0	0.83
	$r_{period} \sim$ S + C + F + TR + (S $\times$ F)	-3087	6	0.83
	$r_{period} \sim$ S + C + F + TR + (S $\times$ TR)	-3091	1	0.83
	$r_{period} \sim$ S + C + F + TR + (S $\times$ F) + (S $\times$ TR)	-3085	7	0.83

\*Models with  $\Delta$ BIC  $\leq 4$  were considered well-supported, and from these, we favored the model with the smallest number of parameters.

**Table S2.** Mean parameter estimates and fit statistics for our four competition models where the response variable is a species' total growth rate ( $r_j$ ). The parameter  $\alpha_{jj}(\bar{T})$  and  $\alpha_{jk}(\bar{T})$  are the estimates for intra- and interspecific competition parameters at average temperatures (20 °C), respectively. The phi ( $\phi_{jk}$ ) parameters indicate the predicted change in competition ( $\alpha_{jk}$ 's) with an increase or decrease of 1 °C from the average.

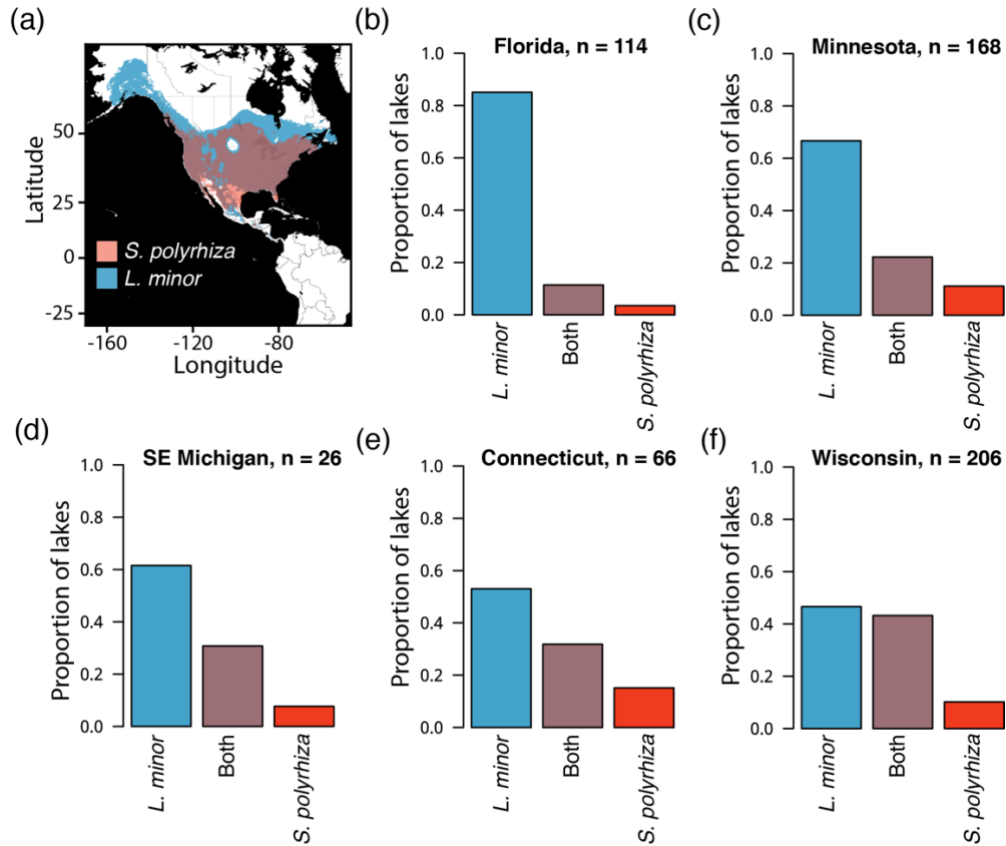
	<b>Model form</b>	<b>Species</b>	$\alpha_{jj}(\bar{T})$	$\alpha_{jk}(\bar{T})$	$\phi_{jj}$	$\phi_{jk}$	$R^2$
1	$\mu_j(T) \left[ 1 - \sum_{k=1}^2 \alpha_{jk} N_k \right] - m_j$	<i>Spirodela</i>	$7.27 \times 10^{-5}$	$3.99 \times 10^{-5}$	n/a	n/a	0.55
		<i>Lemna</i>	$5.15 \times 10^{-5}$	$5.83 \times 10^{-5}$	n/a	n/a	0.61
2	$\mu_j(T) \left[ 1 - \sum_{k=1}^2 \alpha_{jk} \log(N_k + 1) \right] - m_j$	<i>Spirodela</i>	$1.14 \times 10^{-1}$	$6.38 \times 10^{-2}$	n/a	n/a	0.73
		<i>Lemna</i>	$1.07 \times 10^{-1}$	$6.16 \times 10^{-2}$	n/a	n/a	0.76
3	$\mu_j(T) \left[ 1 - \sum_{k=1}^2 \alpha_{jk}(T) N_k \right] - m_j$	<i>Spirodela</i>	$1.23 \times 10^{-3}$	$6.86 \times 10^{-4}$	$4.80 \times 10^{-5}$	$2.08 \times 10^{-5}$	0.56
		<i>Lemna</i>	$8.23 \times 10^{-4}$	$8.86 \times 10^{-4}$	$3.01 \times 10^{-5}$	$3.50 \times 10^{-5}$	0.62
4	$\mu_j(T) \left[ 1 - \sum_{k=1}^2 \alpha_{jk}(T) \log(N_k + 1) \right] - m_j$	<i>Spirodela</i>	$1.07 \times 10^{-1}$	$6.46 \times 10^{-2}$	$6.22 \times 10^{-3}$	$3.09 \times 10^{-3}$	<b>0.77</b>
		<i>Lemna</i>	$1.01 \times 10^{-1}$	$5.91 \times 10^{-2}$	$6.34 \times 10^{-3}$	$3.04 \times 10^{-3}$	<b>0.80</b>

**Table S3.** Parameter values for duckweed competition model. Unless otherwise noted, values are empirically derived from monoculture and competition experiments.

Parameter	Description	Species ( <i>j</i> )	Value ( $\pm$ 95% CI)
$T_{\max,j}$	Species' maximum temperature for growth (eq. 2)	<i>Spirodela</i>	38.93 ( $\pm$ 0.86)
		<i>Lemna</i>	36.82 ( $\pm$ 1.43)
$T_{\min,j}$	Species' minimum temperature for growth (eq. 2)	<i>Spirodela</i>	2.56 ( $\pm$ 4.53)
		<i>Lemna</i>	0.00 ( $\pm$ 4.02)
$c_j$	Scaling constant for thermal growth model (eq. 2)	<i>Spirodela</i>	$1.60 \times 10^{-5}$ ( $\pm$ $4.33 \times 10^{-6}$ )
		<i>Lemna</i>	$2.18 \times 10^{-5}$ ( $\pm$ $6.27 \times 10^{-6}$ )
$T_{d,j}$	Temperature at which 50% of growth is devoted to turions (eq. 3)	<i>Spirodela</i>	15 °C*
		<i>Lemna</i>	n/a
$T_{g,j}$	Temperature at which 50% of turions germinate at 20 days (eq. 4)	<i>Spirodela</i>	25 °C*
		<i>Lemna</i>	n/a
$\alpha_{jj}(\bar{T})$	Intraspecific competition parameter (at 20 °C) (eq. S.5)	<i>Spirodela</i>	0.1069 ( $\pm$ 0.016)
		<i>Lemna</i>	0.1005 ( $\pm$ 0.015)
$\alpha_{jk}(\bar{T})$	Interspecific competition parameter (at 20 °C) (eq. S.5)	<i>Spirodela</i>	0.0646 ( $\pm$ 0.009)
		<i>Lemna</i>	0.0591 ( $\pm$ 0.010)
$\varphi_{jj}$	Effect of $\pm 1^\circ\text{C}$ temperature change on $\alpha_{jj}$ (eq. S.5)	<i>Spirodela</i>	$6.22 \times 10^{-3}$ ( $\pm$ $1.93 \times 10^{-3}$ )
		<i>Lemna</i>	$6.34 \times 10^{-3}$ ( $\pm$ $1.73 \times 10^{-3}$ )
$\varphi_{jk}$	Effect of $\pm 1^\circ\text{C}$ temperature change on $\alpha_{jk}$ (eq. S.5)	<i>Spirodela</i>	$3.09 \times 10^{-3}$ ( $\pm$ $1.12 \times 10^{-3}$ )
		<i>Lemna</i>	$3.04 \times 10^{-3}$ ( $\pm$ $1.10 \times 10^{-3}$ )
$m_j$	Species' average <i>per capita</i> mortality rate (eq. 5)	<i>Spirodela</i>	0.0134 ( $\pm$ $7.46 \times 10^{-4}$ )
		<i>Lemna</i>	0.0107 ( $\pm$ $6.86 \times 10^{-4}$ )

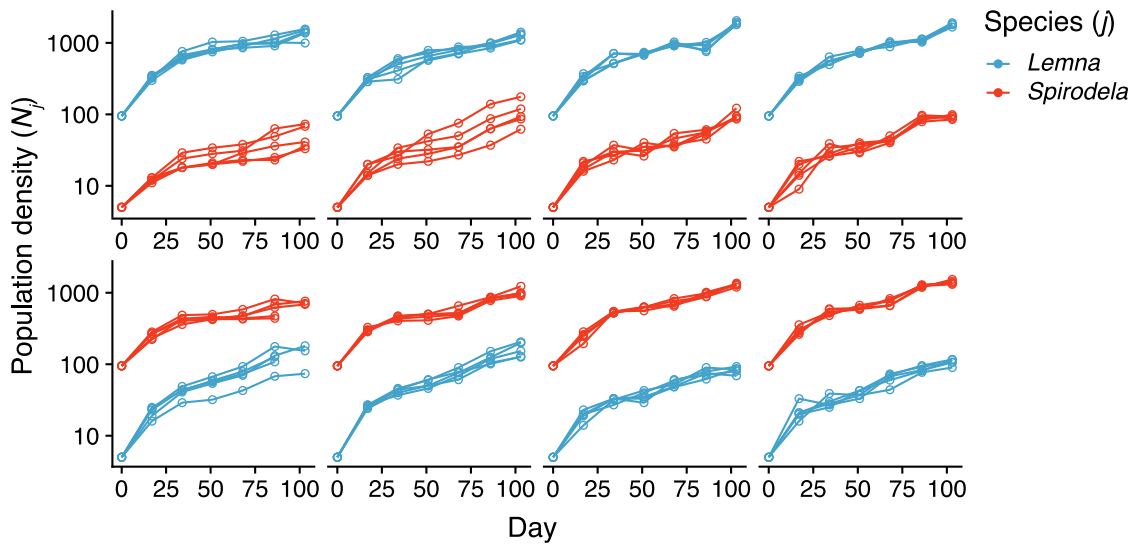
\* Values from Docauer (1983).

## Supplementary Figures

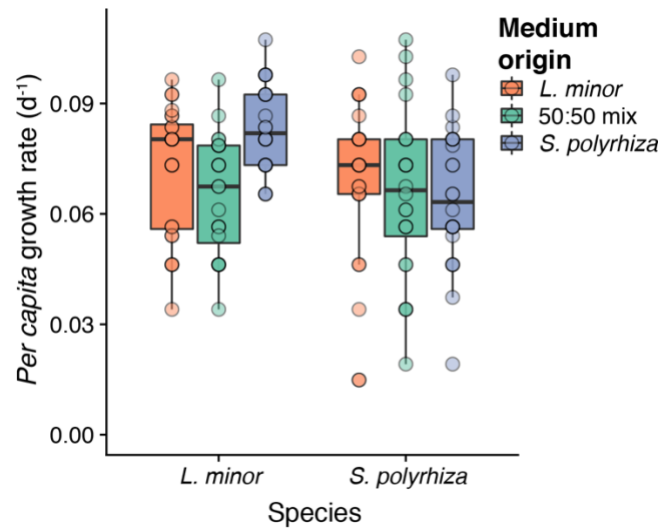


**Figure S1.** (a) Geographic ranges of *Lemna minor* and *Spirodela polyrhiza* in the Americas show broad, but not complete overlap (note: both species occur in Eurasia and Africa, as well). (b-f) Multiple independent lake and pond surveys show that *L. minor* is frequently encountered in the absence of *S. polyrhiza*, but *S. polyrhiza* rarely occurs in the absence of *L. minor*. Data sources are as follows: Minnesota, Muthukrishnan Ranjan et al. (2018); Florida, Alahuhta et al. (2017); Connecticut, McCann (2015); and SE Michigan, Docauer (1983). Range maps were obtained from the BIEN 3.0 database (Enquist et al. 2016).

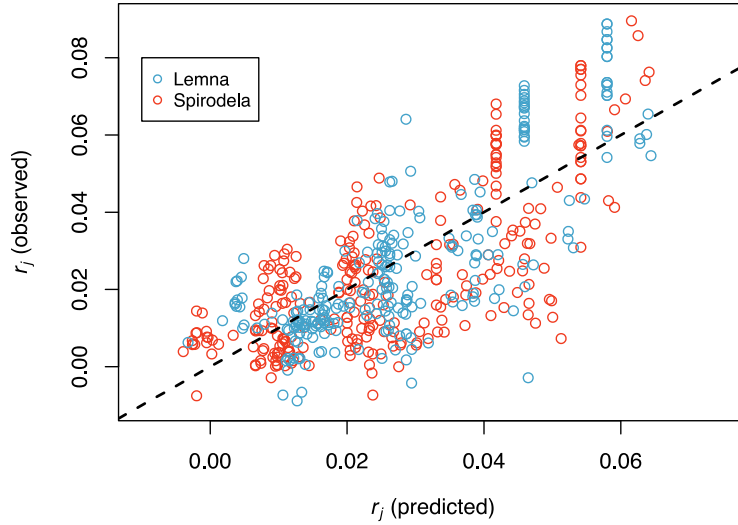




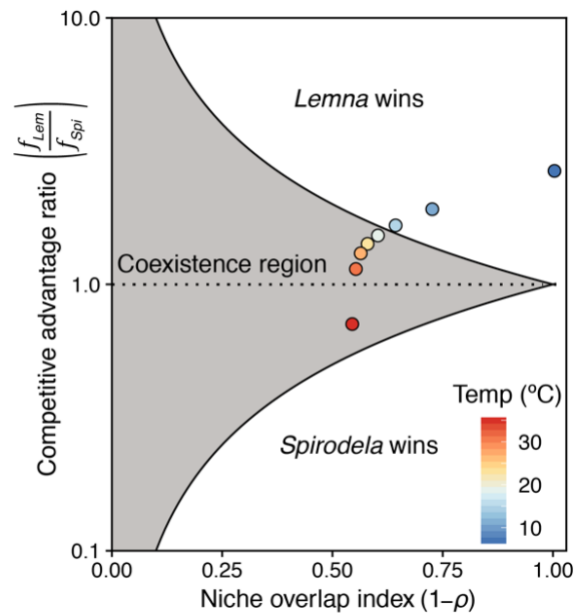
**Figure S2.** Population dynamics for duckweed cultures in fluctuating temperature experiment. Graph is faceted to more clearly display individual cultures.



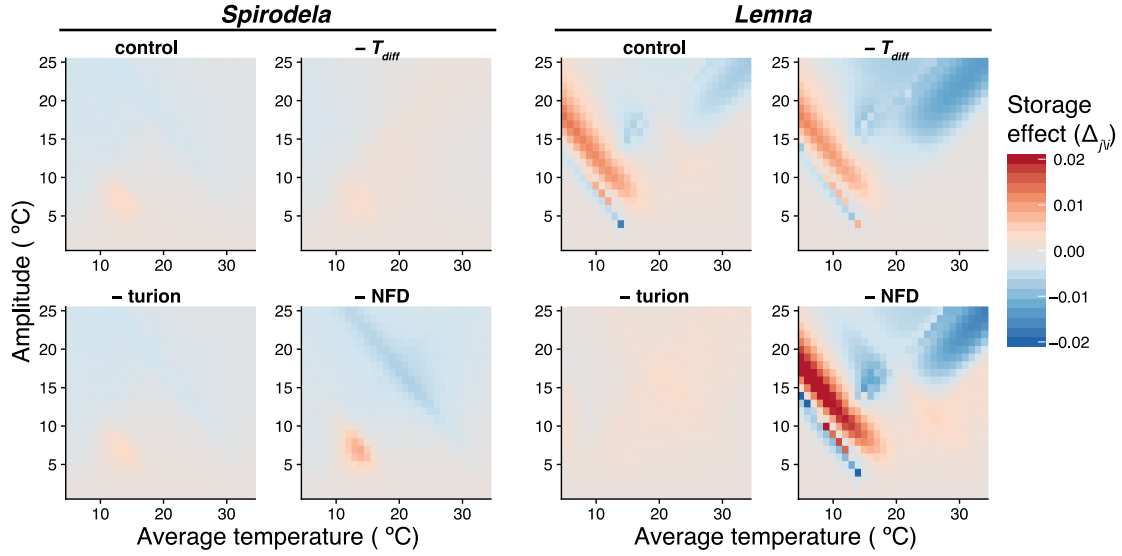
**Figure S3.** Low-abundance growth responses of each duckweed species when grown in media pre-conditioned by either conspecifics, heterospecifics, or a mixture of both. With the exception of *Lemna* growing in media conditioned by *Spirodela*, there is no significant effect of pre-conditioning on species' growth rates.



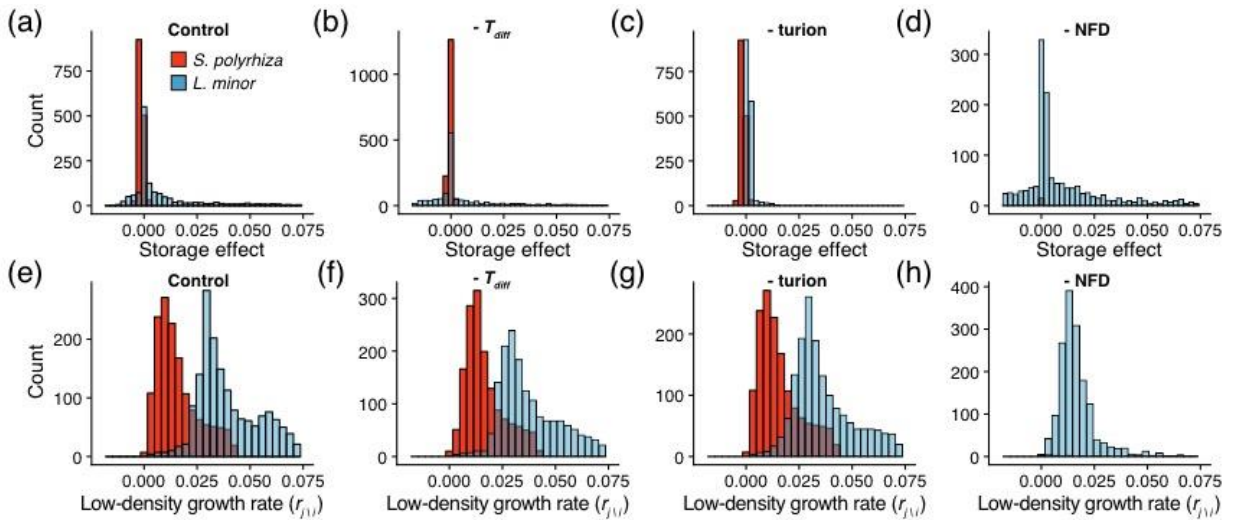
**Figure S4.** Plot of observed versus model-predicted growth rates (from Table S2) for each species. Perfect 1:1 relationship is denoted by the dashed black line.



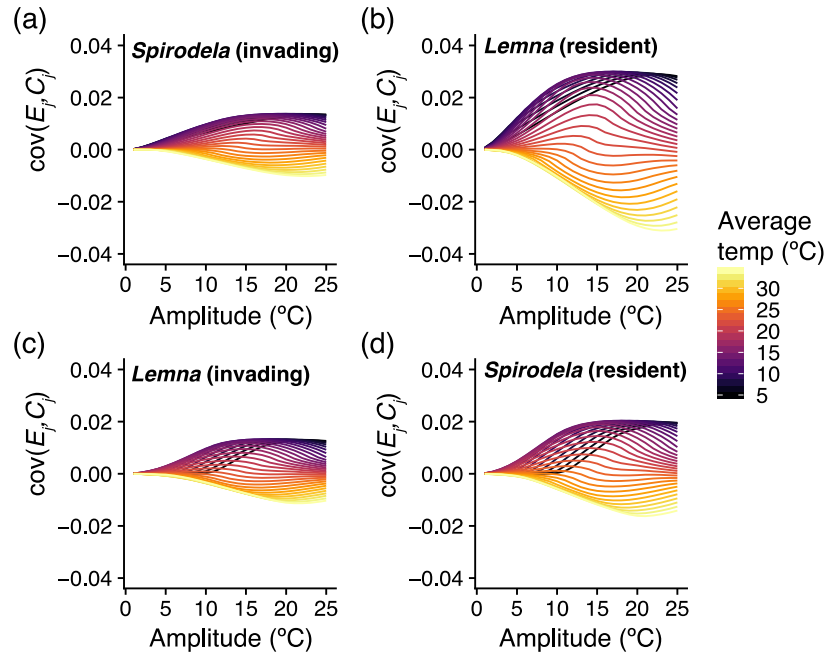
**Figure S5.** Plot of coexistence outcomes in static temperatures as a function of niche overlap,  $1 - \rho(T)$  (Eq. 6), and competitive advantage ratio  $f_2/f_1 = (\mu_2/\mu_1)\sqrt{\alpha_{11}\alpha_{12}/\alpha_{22}\alpha_{21}}$ , where temperature indices are dropped for notational simplicity (for details, see Barabás et al. 2018). This ratio compares the performance of both species in the absence of coexistence-promoting mechanisms. Coexistence occurs when  $1 - \rho(T) < f_2(T)/f_1(T) < [1 - \rho(T)]^{-1}$ , as illustrated by the shaded region. Points denote where on this plane *Spirodela-Lemna* communities fall at particular static temperatures, illustrating how coexistence critically depends on ambient temperature.



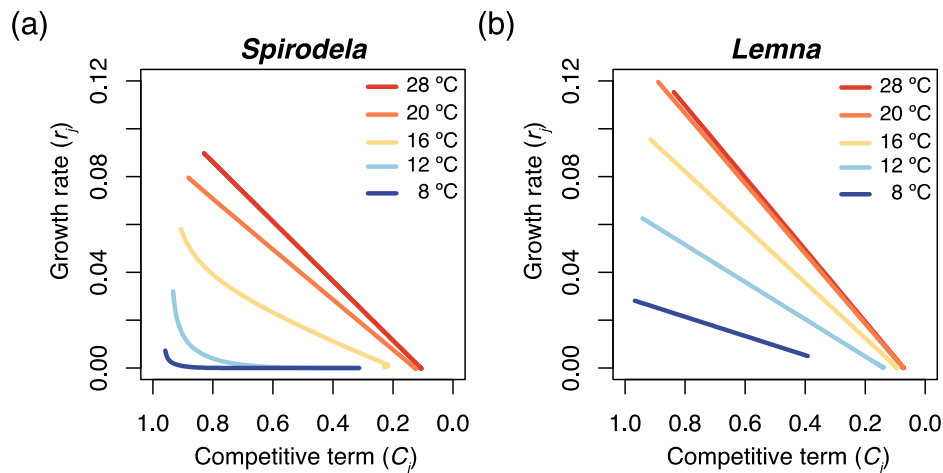
**Figure S6.** Contributions of the temporal storage effect to species' growth rates in the presence or absence of different interspecific differences. Comparing these values to species' invasion growth rates (Fig. 4) suggests that, overall, the storage effect's contributions to invader growth rates are minimal. However, removal of turion production weakens the contribution of the storage effect to the growth of *Lemna*. Control = standard conditions with all species-level differences (Eq. 5);  $-T_{diff}$  = species' thermal growth differences removed;  $-\text{turion}$  = turion production by *Spirodela* removed;  $-\text{NFD}$  = differences between inter- and intraspecific competition removed and replaced with average values.



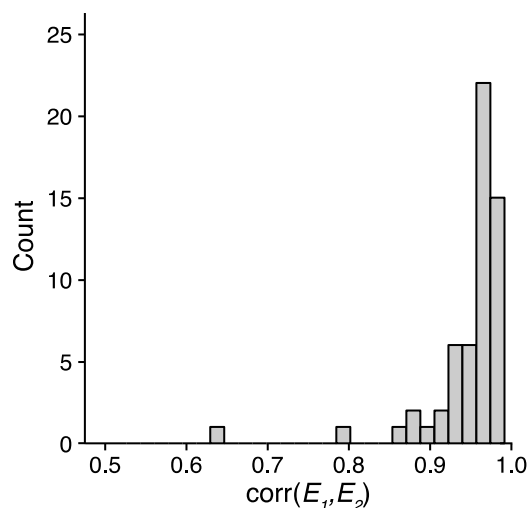
**Figure S7.** (a-d) Contributions of the temporal storage effect to species' growth rates in the presence or absence of different interspecific differences. Comparing these values to species' invasion growth rates (e-h) (censored to cases where  $r_{ji} > 0$ ) suggests that, overall, the storage effect's contributions to invader growth rates are minimal. Control = standard conditions with all species-level differences (Eq. 5);  $-T_{diff}$  = species' thermal growth differences removed;  $-\text{turion}$  = turion production by *Spirodela* removed;  $-\text{NFD}$  = differences between inter- and intraspecific competition removed and replaced with average values. Here, removal of turion production weakens the contribution of the storage effect to the growth of *Lemna*.



**Figure S8.** Illustration of covariance between environmental response and the strength of competition for (a) *Spirodela polyrhiza* and (b) *Lemna minor*. Overall, these values remain close to zero for both species in most environments. More positive  $\text{cov}(E, C)$  values will increase the strength of the storage effect. This is consistent with our observation that the largest storage effects for both species occurred at low temperatures and intermediate-to-high amplitudes.



**Figure S9.** Illustration of subadditivity between environmental that response and competition for (a) *Spirodela polyrhiza* and (b) *Lemna minor*. Lines represent values obtained from oscillating equilibria in the standard interspecific competition model (Eq. 5). Models were fit to static environments with both species at starting densities of 1. Results are robust to the addition of temperature fluctuations. Note that the X-axis is reversed to illustrate that the impact of competition increases from left to right. These results imply that the impacts of competition on species' growth rates decrease as temperatures move away from species' optima.



**Figure S10.** Histogram depicting the correlation coefficients of species' environmental parameters,  $E_j$ , simulated under different average temperatures and amplitudes.

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