Supplemental materials: How environmental tracking shapes communities in stationary & non-stationary systems

E. M. Wolkovich & M. J. Donahue

1 Literature review

We systematically reviewed the literature for studies examining tracking and other traits. We searched ISI in August 2019 for:

1. Topic: 'phenolog* chang*' and Title: phenolog* AND trait*

2. Topic: 'warming shift*' AND trait* and Title: phenolog*

3. Topic: 'phenolog* track*' AND trait* and Title: phenolog*

4. Topic: 'phenolog* sensitiv*' AND trait* and Title: phenolog*

which resulted in 231 papers (83% of which were published in 2011 or later, see Fig. S1). From here we used the following criteria to determine from which papers we could not extract data: no phenology or phenological change measured (73 papers), no trait(s) measured or analyzed (49 papers), single-species studies focused on intra-specific variation (55 papers), modeling or theory studies without data (12 papers), or papers without new data presented (reviews, etc.: 4 papers), or miscellaneous reasons leading to no data relevant to our aims (7 papers). This left us with 30 papers including relevant data (Suzuki & Kudo, 1997; Post & Stenseth, 1999; Adrian *et al.*, 2006; Xu *et al.*, 2009; Goodenough *et al.*, 2010; Diamond *et al.*, 2011; Moussus *et al.*, 2011; Szilvia *et al.*, 2012; Dorji *et al.*, 2013; Ishioka *et al.*, 2013; Xia & Wan, 2013; Bock *et al.*, 2014; Kharouba *et al.*, 2014; Vegvari *et al.*, 2015; Bell *et al.*, 2015; Jing *et al.*, 2016; Lasky *et al.*, 2016; McDermott & DeGroote, 2016; Zhu *et al.*, 2016; Brooks *et al.*, 2017; Du *et al.*, 2017; Munson & Long, 2017; Arfin Khan *et al.*, 2018; Zhang *et al.*, 2018; Ladwig *et al.*, 2019; Park *et al.*, 2019; Sharma & Upadhyaya, 2019; Xavier *et al.*, 2019; Zettlemoyer *et al.*, 2019), nine of which did not test for a relationship between tracking and the other studied traits (Suzuki & Kudo, 1997; Adrian *et al.*, 2006; Xu *et al.*, 2009; Szilvia *et al.*, 2012; Bell *et al.*, 2015; McDermott & DeGroote, 2016; Sherwood *et al.*, 2017; Sharma & Upadhyaya, 2019; Xavier *et al.*, 2019). We present data from the remaining papers in Tables S2-S3.

Most studies examined tracking as how a phenophase related to temperature (85% of all tracking metrics), followed by precipitation (10%, includes snow removal), followed by photoperiod (3%), the climate mode NAO (1%), water table depth (0.5%), and year (0.5%). Four of the 30 studies examined more than one major climate metric, though some measured many versions of temperature and/or precipitation metrics (e.g., 15 precipitation and/or temperature metrics considered in Munson & Long, 2017).

2 Model

The two species coexistence model (see Equations 1-6 in main text) includes both interannual variation in the environment and intra-annual resource competition. The model was modified from Chesson *et al.* (2004), which was originally conceptualized for annual plants with a seed-bank. Although the model can be conceived of more generally, we use the language of annual plant germination for concreteness.

In the model, the population census of seeds, N, occurs at time t at the end of the growing season (Equation 1). Seeds survive over winter at rate s and are lost from the population at rate $(1-s)$. Surviving seeds germinate at rate $g_i(t)$. Seeds that do not germinate remain in the seed bank until the next census at $t+1$. Germination rate is a Gaussian function that declines with the distance between τ_i, the species-specific preferred germination time, and $\tau_p(t)$, the timing of the resource pulse in year t, with maximum germination when $\tau_i = \tau_p(t)$ (Equation 6, Fig. 2a,b). In cases that include tracking, the distance between τ_i and $\tau_{p(t)}$ can be reduced by tracking, α_i, resulting in greater germination fraction (Equation 7).

Germinating seeds are converted to seedling biomass at rate b_0 (Equation 4). Within year dynamics of the two species follows R^* competition for a single resource. The growing season begins with a single resource pulse $R_0(t)$. Both species consume the resource at rate $f(R)$ (Equation 3), and the resource undergoes abiotic loss (e.g., evapotranspiration) at rate ϵ (Equation 5). Differences in R_i^* were generated by differences in conversion efficiency, c_i. Species were otherwise identical in resource update parameters (a, u, and θ) and in metabolic loss (m). Biomass at the end of the season is converted into seeds at rate ϕ, and the population of seeds is censused at $t+1$.

Interannual variation occurs in both the timing and the amount of the resource pulse. The timing of the resource pulse varies from year to year and is given by $\tau_p(t)$, which is drawn from a β distribution. The amount of resource available at the beginning of each season, $R_0(t)$, varies from year to year and is drawn from a log-normal distribution. Each model run is comprised of a 500 year stationary period and a 500 year nonstationary period. During the stationary period, $R_0(t)$ and $\tau_p(t)$ are each drawn from a stationary distribution. During the nonstationary period, the timing of the resource pulse, $\tau_p(t)$, gradually shifts earlier in the season (Fig. S2). For the model runs displayed in Fig. 3 and Fig. 4, this shift in the timing of the resource pulse is the only change in the environment during the nonstationary period. We also discuss model runs in which the amount of resource, $R_0(t)$, declines during the nonstationary period along with the shift in timing, $\tau_p(t)$ (Fig. S2).

To simulate competitive dynamics, both species were initialized with a census size of $N(0) = 100$ per unit area, and the temporally varying parameters $R_0(t)$ and $\tau_p(t)$ were generated for the stationary and nonstationary periods. Species-specific parameters (c_i,τ_i, and α_i) were drawn from uniform random distributions with the ranges given in Table S1. All other parameters were identical between species (Table S1). Within-year R^* competition dynamics were solved using an ode solver (`ode` in the R package `deSolve`) and ended when the resource was drawn down to $min(R^*)$, i.e., the R^* value of the better resource competitor. The end of season biomass of each

species was converted to seeds, and the populations were censused. At each census, a minimum cutoff was applied to define extinction from the model. Note that "coexistence" in this model is defined by joint persistence through time and not by low density growth rate.

3 References

Adrian, R., Wilhelm, S. & Gerten, D. (2006). Life-history traits of lake plankton species may govern their phenological response to climate warming. *Global Change Biology*, 12, 652–661.

Arfin Khan, M.A.S., Beierkuhnlein, C., Kreyling, J., Backhaus, S., Varga, S. & Jentsch, A. (2018). Phenological sensitivity of early and late flowering species under seasonal warming and altered precipitation in a seminatural temperate grassland ecosystem. *Ecosystems*, 21, 1306–1320.

Bell, J.R., Alderson, L., Izera, D., Kruger, T., Parker, S., Pickup, J., Shortall, C.R., Taylor, M.S., Verrier, P. & Harrington, R. (2015). Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology*, 84, 21–34.

Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M. & Menzel, A. (2014). Changes in first flowering dates and flowering duration of 232 plant species on the island of guernsey. *Glob Chang Biol*, 20, 3508–19.

Brooks, S.J., Self, A., Powney, G.D., Pearse, W.D., Penn, M. & Paterson, G.L.J. (2017). The influence of life history traits on the phenological response of british butterflies to climate variability since the late-19th century. *Ecography*, 40, 1152–1165.

Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley, L.B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, 92, 1005–1012.

Dorji, T., Totland, O., Moe, S.R., Hopping, K.A., Pan, J. & Klein, J.A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, 19, 459–472.

Du, Y.J., Chen, J.R., Willis, C.G., Zhou, Z.Q., Liu, T., Dai, W.J., Zhao, Y. & Ma, K.P. (2017). Phylogenetic conservatism and trait correlates of spring phenological responses to climate change in northeast china. *Ecology and Evolution*, 7, 6747–6757.

Goodenough, A.E., Hart, A.G. & Stafford, R. (2010). Is adjustment of breeding phenology keeping pace with the need for change? linking observed response in woodland birds to changes in temperature and selection pressure. *Climatic Change*, 102, 687–697.

Ishioka, R., Muller, O., Hiura, T. & Kudo, G. (2013). Responses of leafing phenology and photosynthesis to soil warming in forest-floor plants. *Acta Oecologica-International Journal of Ecology*, 51, 34–41.

Jing, J., Li, K. & Liu, Z.G. (2016). Effects of varying temperature on leaf phenology and herbivory of dominant tree species in subtropical evergreen broad-leaves forest in eastern china. *Polish Journal of Ecology*, 64, 53–69.

Kharouba, H.M., Paquette, S.R., Kerr, J.T. & Vellend, M. (2014). Predicting the sensitivity of butterfly phenology to temperature over the past century. *Global Change Biology*, 20, 504–514.

Ladwig, L.M., Chandler, J.L., Guiden, P.W. & Henn, J.J. (2019). Extreme winter warm event causes exceptionally early bud break for many woody species. *Ecosphere*, 10.

Lasky, J.R., Uriarte, M. & Muscarella, R. (2016). Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality. *Environmental Research Letters*, 11.

McDermott, M.E. & DeGroote, L.W. (2016). Long-term climate impacts on breeding bird phenology in pennsylvania, usa. *Global Change Biology*, 22, 3304–3319.

Moussus, J.P., Clavel, J., Jiguet, F. & Julliard, R. (2011). Which are the phenologically flexible species? a case study with common passerine birds. *Oikos*, 120, 991–998.

Munson, S.M. & Long, A.L. (2017). Climate drives shifts in grass reproductive phenology across the western USA. *New Phytologist*, 213, 1945–1955.

Park, D.S., Breckheimer, I., Williams, A.C., Law, E., Ellison, A.M. & Davis, C.C. (2019). Herbarium specimens reveal substantial and unexpected variation in phenological sensitivity across the eastern united states. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 374.

Post, E. & Stenseth, N. (1999). Climatic variability, plant phenology, and northern ungulates. *Ecology*, 80, 1322–1339.

Sharma, S. & Upadhyaya, H.D. (2019). Photoperiod response of annual wild cicer species and cultivated chickpea on phenology, growth, and yield traits. *Crop Science*, 59, 632–639.

Sherwood, J.A., Debinski, D.M., Caragea, P.C. & Germino, M.J. (2017). Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources. *Ecosphere*, 8.

Suzuki, S. & Kudo, G. (1997). Short-term effects of simulated environmental change on phenology, leaf traits, and shoot growth of alpine plants on a temperate mountain, northern Japan. *Global Change Biology*, 3, 108–115.

Szilvia, K., Fehervari, P., Krisztina, N., Andrea, H. & Tibor, C. (2012). Changes in migration phenology and biometrical traits of reed, marsh and sedge warblers. *Central European Journal of Biology*, 7, 115–125.

Vegvari, Z., Juhasz, E., Toth, J.P., Barta, Z., Boldogh, S., Szabo, S. & Varga, Z. (2015). Life-history traits and climatic responsiveness in noctuid moths. *Oikos*, 124, 235–242.

Xavier, R.D., Leite, M.B. & Matos, D.M.D. (2019). Phenological and reproductive traits and their response to environmental variation differ among native and invasive grasses in a neotropical savanna. *Biological Invasions*, 21, 2761–2779.

Xia, J.Y. & Wan, S.Q. (2013). Independent effects of warming and nitrogen addition on plant phenology in the inner mongolian steppe. *Annals of Botany*, 111, 1207–1217.

Xu, Z.F., Hu, T.X., Wang, K.Y., Zhang, Y.B. & Xian, J.R. (2009). Short-term responses of phenology, shoot growth and leaf traits of four alpine shrubs in a timberline ecotone to simulated global warming, eastern tibetan plateau, china. *Plant Species Biology*, 24, 27–34.

Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019). Phenology in a warming world: differences between native and nonâĂŘnative plant species. *Ecology Letters*.

Zhang, J.H., Yi, Q.F., Xing, F.W., Tang, C.Y., Wang, L., Ye, W., Ng, I., Chan, T.I., Chen, H.F. & Liu, D.M. (2018). Rapid shifts of peak flowering phenology in 12 species under the effects of extreme climate events in macao. *Scientific Reports*, 8.

Zhu, J.T., Zhang, Y.J. & Wang, W.F. (2016). Interactions between warming and soil moisture increase overlap in reproductive phenology among species in an alpine meadow. *Biology Letters*, 12, 4.

4 Tables & figures

Table S1: Table of parameter values, definitions, and units.

Parameter	Value(s)	Definition	Unit
N_i	init cond $N_i(0) = 100; min(N_i(t)) = 10^{-4}$	census of seedbank of species i	seeds per unit area
s	0.8	survival of species i	unitless
B_i	cf. Eqn 2	biomass of species i	biomass
R_0	$\sim logN(\mu, \sigma) mu = log(2), \sigma = 0.2$	annually varying initial value of resource at the beginning of the growing season	resource
c_i	$\sim$Unif(8,20)	conversion efficiency of R to biomass of species i	$\frac{biomass}{resource}$
m	0.05	maintenance costs during growth season i	days^{-1}
a	20	uptake increase as R increases for species i	days^{-1}
u	1	inverse of max uptake for species i	$\frac{(days)(biomass)}{resource}$
θ	1	shape of uptake for species i	unitless
ϕ	0.05	conversion of end-of-season biomass to seeds	biomass^{-1}, but conceptually $\frac{seeds}{(biomass)(seeds)}$
ϵ	1	abiotic loss of R	days^{-1}
g_{max}	0.5	max germination rate of species	unitless
h	100	controls the the rate at which germination declines as τ_p deviates from optimum for species i	days^{-2}
g_i	cf. Eqn 6	germination rate	unitless
τ_p	$\sim \beta(10, 10)$	timing of pulse	days
τ_i	$\sim$ Unif(0.1,0.9)	timing of max germination of species i	days
α_i	$\sim$ Unif(0,1)	phenological tracking of species i	unitless
b_0	1	biomass of a seedling	$\frac{biomass}{seeds}$
$f(R)$	cf. Eqn 3	resource uptake rate for species i	$\frac{resource}{(days)(biomass)}$
t	1	annual timestep	years
$0 \rightarrow \delta$	determined by rate of resource depletion	time during the growing season	days

Table S2: Summary of traits related to phenological tracking in the literature and whether papers reported statistical evidence that they were linked or not. See Table S2 for an extended version.

Trait	n linked	n not linked
diet traits	0	3
early/late phenophase	10	4
habitat traits	1	3
height	1	0
hibernation stage	0	3
leaf/shoot size	1	0
migration traits	3	2
mobility	1	3
nativeness	1	3
niche breadth	3	2
other Lepidopteran traits	3	4
other bird traits	1	1
other leaf traits	4	3
other plant traits	1	1
overwintering	2	1
range traits	1	4
root traits	3	0
seed weight/size/number	1	2
woody/herbaceous	1	0

Table S3: Summary of results from literature on phenological tracking showing which phenophases researchers found were linked to which traits, or not.

| Taxa	Phenophase	Trait	n linked	n not linked
Lepidoptera	activity length	hibernation stage		1
Lepidoptera	activity length	migration traits		1
Lepidoptera	activity length	other Lepidopteran traits	1	
Lepidoptera	appearance/collection date	diet traits		1
Lepidoptera	appearance/collection date	early/late phenophase	2	
Lepidoptera	appearance/collection date	habitat traits		2
Lepidoptera	appearance/collection date	hibernation stage		1
Lepidoptera	appearance/collection date	migration traits	1	
Lepidoptera	appearance/collection date	mobility		2
Lepidoptera	appearance/collection date	niche breadth	2	1
Lepidoptera	appearance/collection date	other Lepidopteran traits	1	2
Lepidoptera	appearance/collection date	overwintering	2	
Lepidoptera	appearance/collection date	range traits	1	2
Lepidoptera	flight timing	early/late phenophase	1	1
Lepidoptera	flight timing	mobility	1	1
Lepidoptera	flight timing	niche breadth		1
Lepidoptera	flight timing	other Lepidopteran traits		1
Lepidoptera	flight timing	overwintering		1
Lepidoptera	flight timing	range traits		1
Lepidoptera	last/median emergence dates	diet traits		1
Lepidoptera	last/median emergence dates	habitat traits		1
Lepidoptera	last/median emergence dates	hibernation stage		1
Lepidoptera	last/median emergence dates	migration traits		1
Lepidoptera	last/median emergence dates	other Lepidopteran traits	1	1
passerine birds	breeding time	diet traits		1
passerine birds	breeding time	habitat traits	1	
passerine birds	breeding time	migration traits	2	
passerine birds	breeding time	niche breadth	1	
passerine birds	breeding time	other bird traits	1	1
plants	budbreak/leafing	early/late phenophase	3	1
plants	budbreak/leafing	nativeness		1
plants	budbreak/leafing	other leaf traits	2	1
plants	budbreak/leafing	range traits		1
plants	flowering/fruiting	early/late phenophase	4	2
plants	flowering/fruiting	height	1	
plants	flowering/fruiting	leaf/shoot size	1	
plants	flowering/fruiting	nativeness	1	2
plants	flowering/fruiting	other leaf traits	2	2
plants	flowering/fruiting	other plant traits	1	1
plants	flowering/fruiting	root traits	3	
plants	flowering/fruiting	seed weight/size/number	1	2
plants	flowering/fruiting	woody/herbaceous	1	
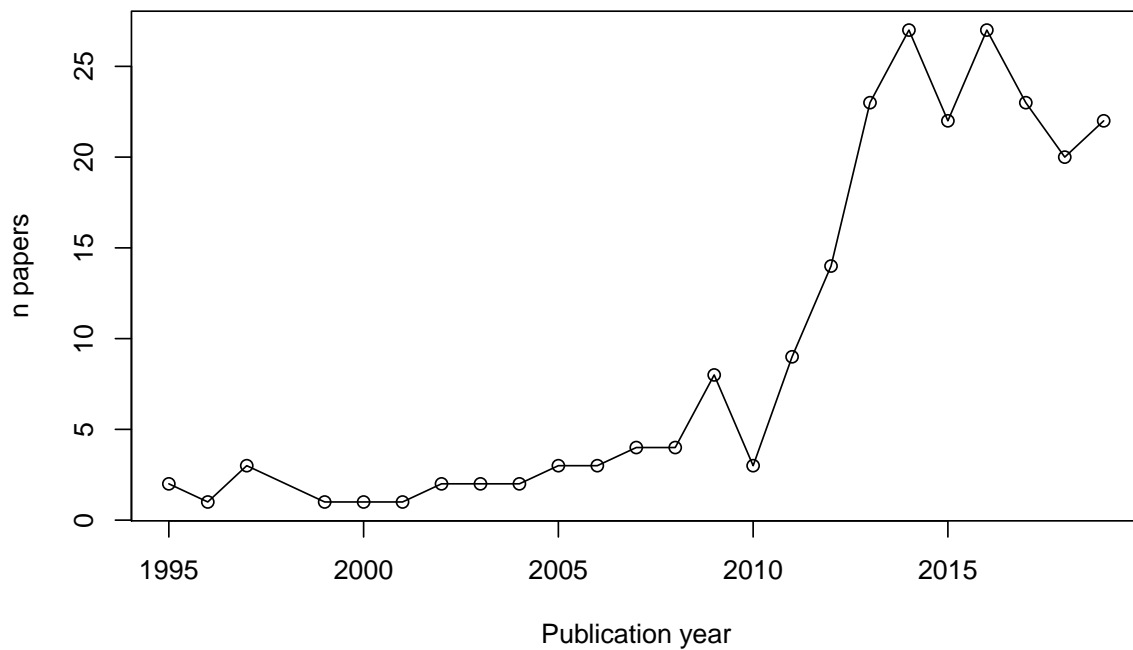
Figure S1: Trends in all papers using search terms over time. Of papers from which we could extract data all 25 of 30 were published in 2011 or onward.
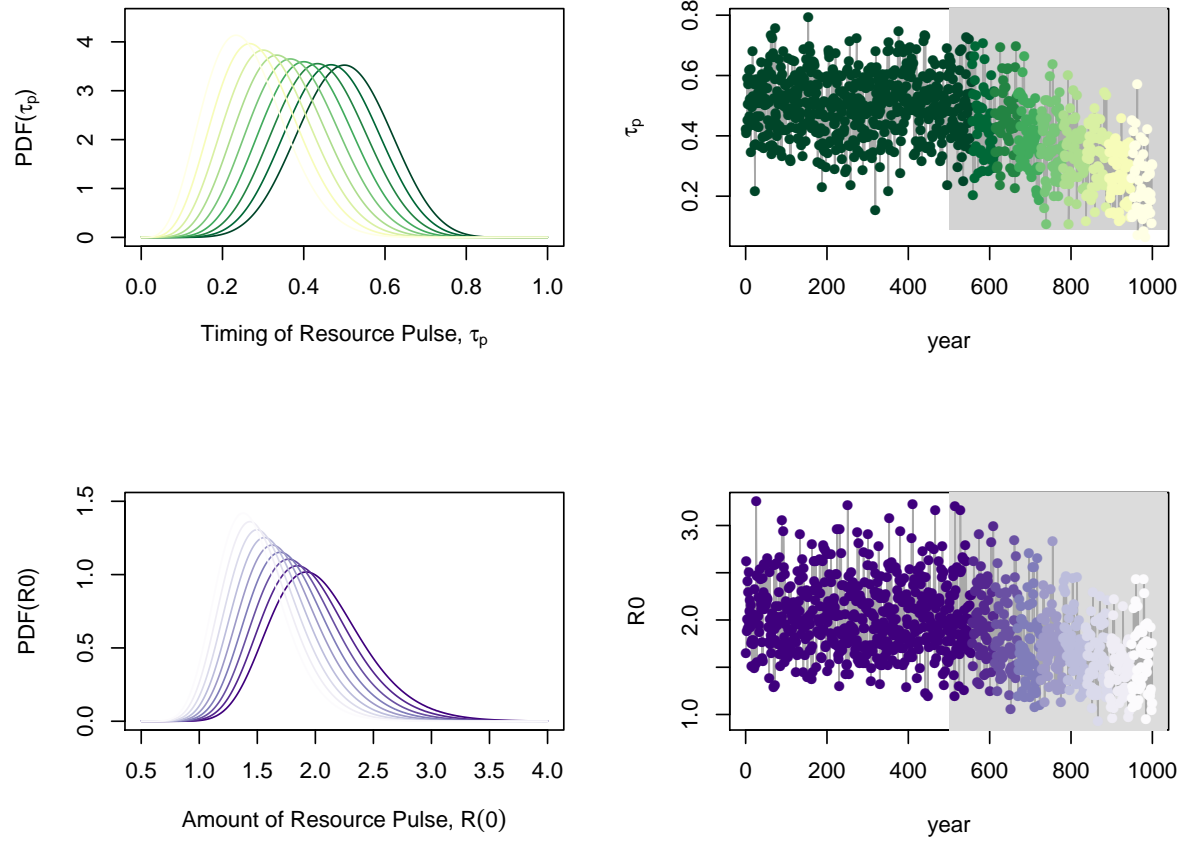
Figure S2: How the environment shifts from the stationary period to the nonstationary period. The timing of the resource pulse shifts from $\tau_p \sim \beta(10, 10)$ for the 500 year stationary period to $\tau_p \sim \beta(5, 15)$ over the 500 year nonstationary period. For simulations where the amount of resource is also changing, $R(0) \sim logNormal(log(2), 2))$ during the 500 year stationary period and shifts to $R(0) \sim logNormal(log(2)/2, 2)$ during the nonstationary period.
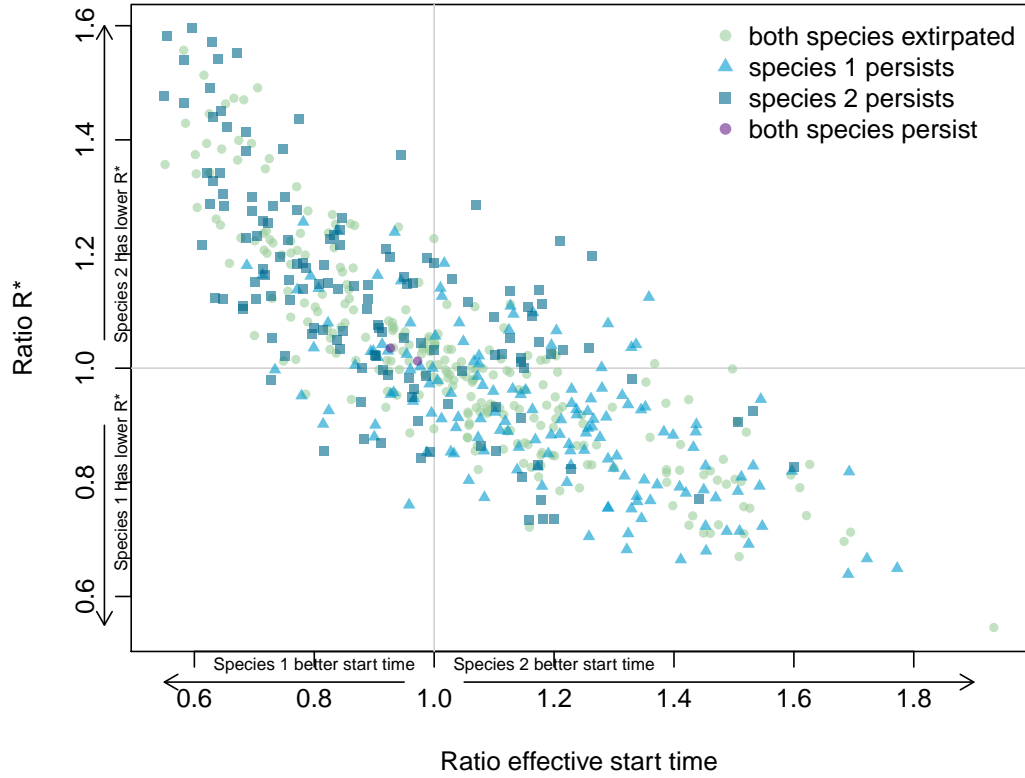
Figure S3: How non-stationarity reshapes two-species communities in a simple model where effective start time (X axis: species 1/species 2) trades off with R^* (Y axis: species 1/species 2): each point represents one two-species community that persisted through 500 years of stationary dynamics while the shape and color represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.
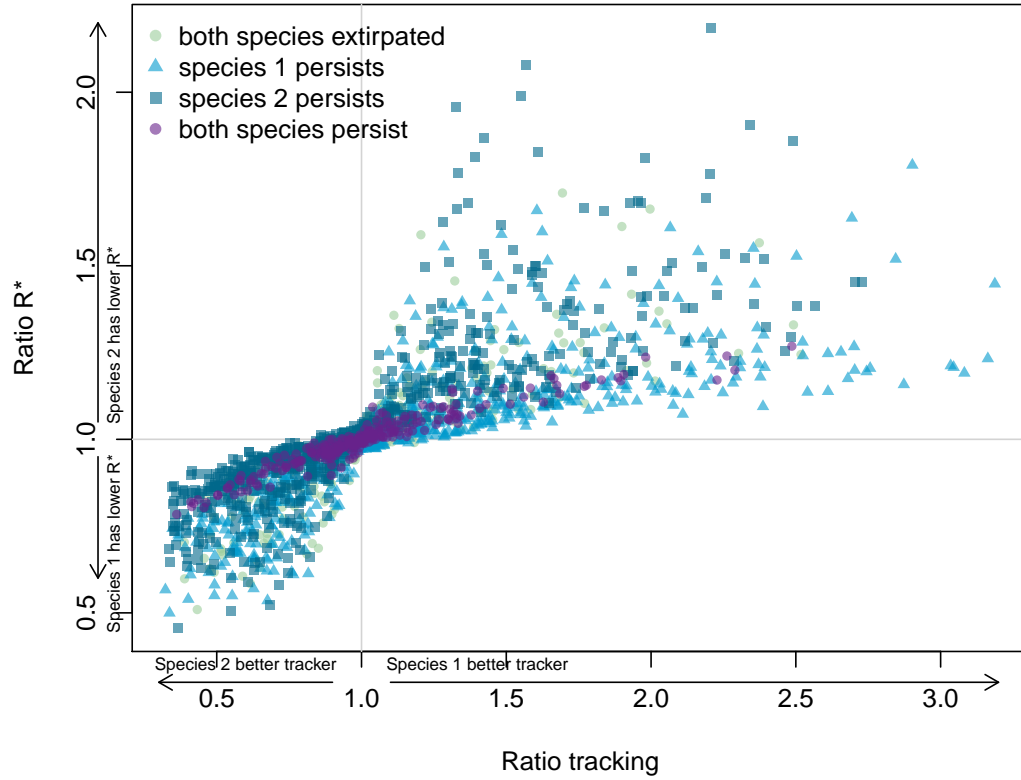
Figure S4: How non-stationarity reshapes two-species communities in a simple model where tracking (X axis: species 1/species 2) trades off with R^* (Y axis: species 1/species 2): each point represents one two-species community that persisted through 500 years of stationary dynamics while the shape and color represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.