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

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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

To give an example of how tracking and non-stationarity may be included in current models we modified a model from Chesson *et al.* (2004), which was originally conceptualized for annual plants with a seedbank. Although the model can be conceived of more generally, we use the language of annual plant germination for concreteness.

The model includes a suite of species traits, including (and particularly relevant for our aims) traits controlling species response to the environment via germination each year and traits related to how species may bet-hedge across years (via a seedbank), as well as traits relating to resource competition each year. Within-season dynamics are controlled by resource competition resulting in fitness differences, while interannual variation in the environment provides opportunities for coexistence via fluctuation-dependent mechanisms (i.e., niche differences resulting from different germination functions).

Across years, for a community of n species, the seedbank (N) of species i at time $t + 1$ is determined by the survival (s) of seeds that did not germinate in last season ($1 - g_i(t)$) plus new biomass (B_i) produced during the length of the growing season (δ) converted to seeds at rate ϕ:

$$N_i(t + 1) = sN_i(t)(1 - g_i(t)) + \phi B_i(t + \delta) \tag{1}$$

The production of new biomass each season follows a basic R* competition model: new biomass production depends on its resource uptake ($f(R)$ converted into biomass at rate c_i) less maintenance costs (m), with uptake controlled by a, u, and θ:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = c_i f(R) - mB_i \tag{2}$$

$$f(R) = \frac{aR^\theta}{1 + auR^\theta} \tag{3}$$

With the initial condition:

$$B_i(t + 0) = N_i(t)g_i(t)b_0 \tag{4}$$

where b_0 is the initial biomass per seed.

The resource (R) itself declines across a growing season due to uptake by all species and abiotic loss (ϵ):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = -\sum_{i=1}^{n} f_i(R)B_i - \epsilon R \tag{5}$$

Germination depends both on the traits of the species and on the environment that year. The fraction of seeds germinating for a species each year is determined by the distance between τ_i, a species characteristic, and $\tau_p(t)$, an attribute of the environment, which varies year-to-year. Germination fraction declines according to a Gaussian as the distance between τ_i and $\tau_p(t)$ grows (we refer to this distribution as the 'germination curve').

$$g_i(t) = g_{max}e^{-h(\tau_p(t) - \tau_i)^2} \tag{6}$$

The model is designed for multiple conceptualizations (Chesson *et al.*, 2004); given our focus here, we consider $\tau_p(t)$ to represent the environmental (abiotic) start of the growing season that varies from year-to-year and refer to it as the 'environmental start time.' τ_i represents the 'intrinsic biological start time' for species i. How well matched a species is to its environment each year can be measured as τ_i-$\tau_p(t)$, or the distance between the intrinsic (biological) start time and the environmental start time.

Adding phenological tracking to model:
We adjust the biological start time, τ_i so that it can respond to the environment dynamically through what we refer to as tracking. Tracking (α, which can vary between 0 to 1) decreases the distance between τ_i and $\tau_p(t)$, i.e., moving the intrinsic start time closer to the environmental start time in that year, resulting in a higher germination fraction (e.g., species B in Fig. S2b-c).

$$\alpha_i \in [0, 1]$$

$$\hat{\tau}_i = \alpha_i \tau_p(t) + (1 - \alpha_i)\tau_i \tag{7}$$

Thus,

$$\text{when } \alpha_i = 0, \hat{\tau}_i = \tau_i$$
$$\text{when } \alpha_i = 1, \hat{\tau}_i = \tau_p(t)$$

Simulations:
Using this model framework, we simulated a suite of two-species communities in stationary and non-stationary environments and examined persistence. As our interest is primarily in the role of environmental tracking, we focus on situations where species vary in their match to the environment through both the intrinsic biological start time (τ_i) combined with tracking (α), examining simulations where all species had some level of tracking. We also varied species' resource use efficiency (via c_i), yielding species with different R^* (where a lower R^* means a species can draw the resource down to a lower level and is thus considered the superior competitor). Each simulation was composed of two sequential parts: first, a 500-year stationary period where the underlying distribution of the environment does not change (but is stochastic, yielding year-to-year variation) followed by a 500-year non-stationary period where the underlying distribution of the environment shifts to an earlier start of season (see Fig. 3 in main text). Thus, only species that persisted through the first stationary period continued into the non-stationary period.

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

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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.

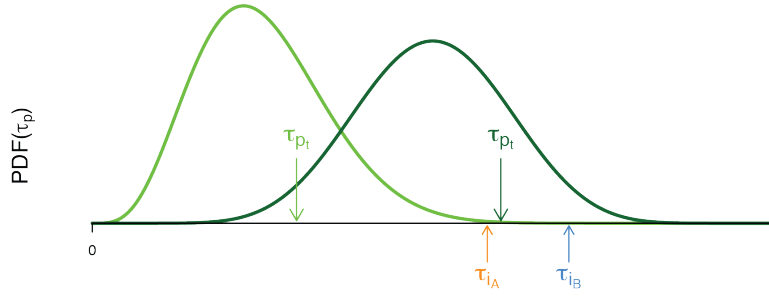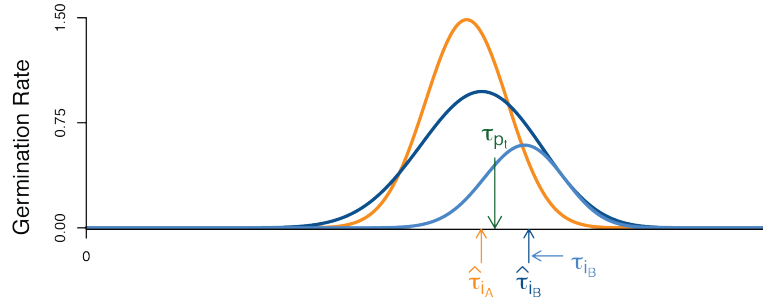| Taxa	Phenophase	Trait	n linked	n not linked
Lepidoptera	activity length	hibernation stage		1
Lepidoptera	activity length	migration traits		1
Lepidoptera	activity length	other Lepidopteran traits	1	
Lepidoptera	appearance/collection date	diet traits		1
Lepidoptera	appearance/collection date	early/late 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	
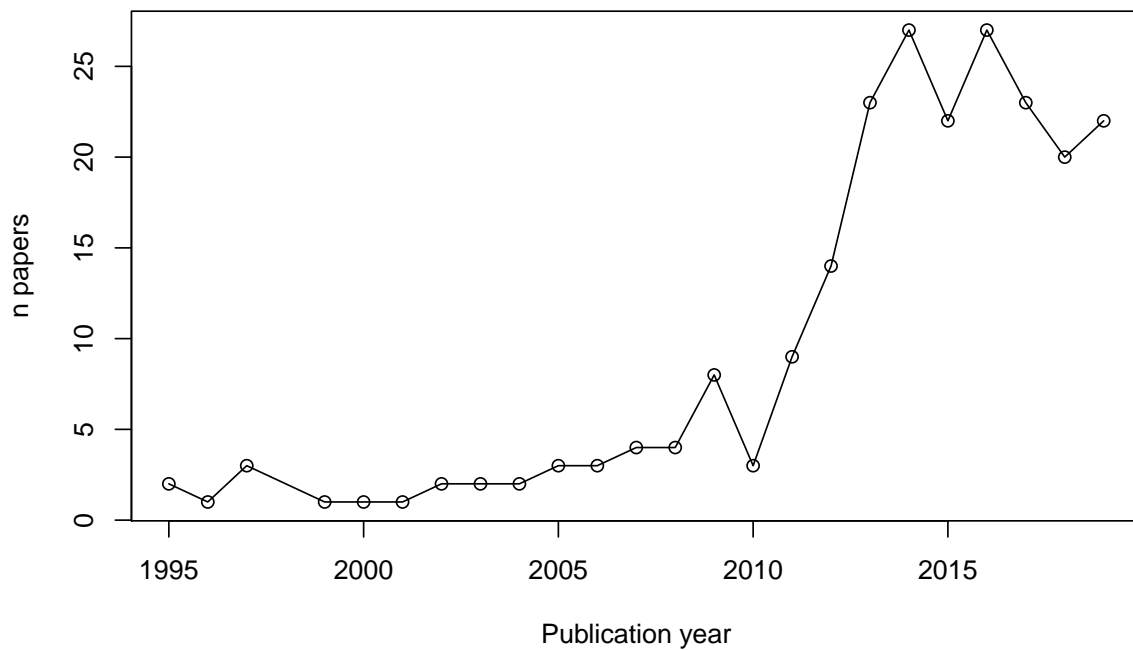
Figure S1: Trends in all papers using search terms over time. Of papers from which we could extract data all 25 of 30 were published in 2011 or onward.
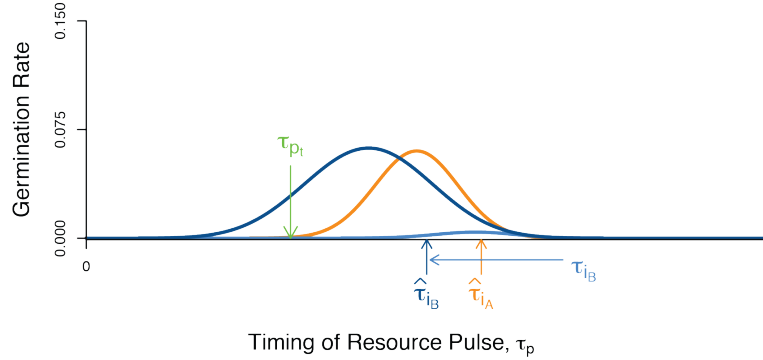
Figure S2: The distributions of the environment (a) and species' germination for two sample years (b-c) in our seed germination model. (a) The timing of the resource pulse ($\tau_p(t)$), which defines the environmental start of season, is β-distributed with parameters $\beta(10, 10)$ during the stationary period (dark green) shifting to $\beta(5, 15)$ through the nonstationary period (light green). (b) Realized germination rate as a function of $\tau_p(t)$ for two species during the stationary period: the orange line is a non-tracking species A with preferred germination time, τ_{iA}, that is close to the mean of the stationary period; the blue lines show the difference in realized germination rate of a tracking species with a preferred germination time, τ_{iB}, that is further from the mean of the stationary period both without (light blue) and with (dark blue) the effect of tracking; note the shift from τ_{iB} to $\hat{\tau}_{iB}$. (c) Realized germination rate of species A and species B at the end of the nonstationary period. Note the change in axes from (b) to (c) shows the decline in overall germination rate as the environment moves away from the preferred germination time of both species.
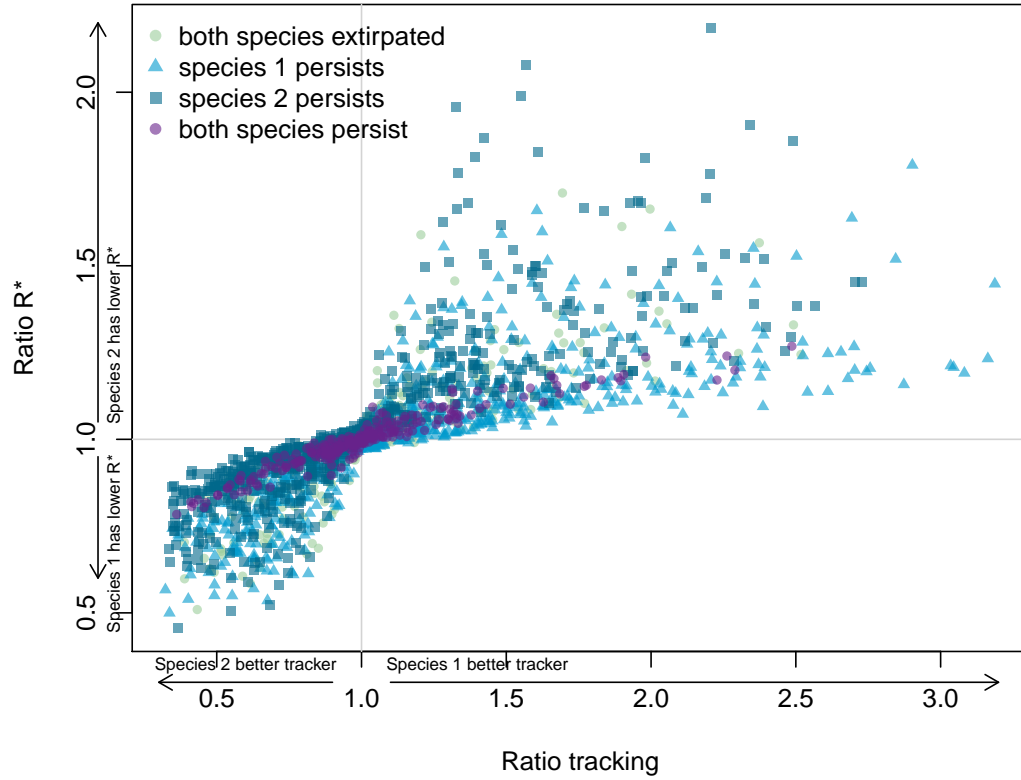
Figure S3: How non-stationarity reshapes two-species communities in a simple model where tracking (X axis: species 1/species 2) trades off with R^* (Y axis: species 1/species 2): each point represents one two-species community that persisted through 500 years of stationary dynamics while the shape and color represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.