How phenological tracking shapes species and communities in non-stationary environments

E. M. Wolkovich & M. J. Donahue

Appendix S1. Additional methods and results for: literature review (traits and tracking), Figure 3, and model with tracking presented in Section IV.

1. Literature review of studies examining tracking and other traits

To examine current evidence of what traits may trade off with tracking, we systematically reviewed the literature for studies examining tracking and other traits together. 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*modelling

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. 4). 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 analysed (50 papers), single-species studies focused on intra-specific variation (55 papers), modelling 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; Sherwood *et al.*, 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 S1-S2.

Most studies examined tracking as how a phenophase related to temperature (85% of all tracking metrics), precipitation (10%, includes snow removal), photoperiod (3%), the North Atlantic Oscillation 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, although some measured many versions of temperature and/or precipitation metrics (e.g. 15 precipitation and/or temperature metrics considered in Munson & Long, 2017).

2.   Methods used to construct Fig. 3

We used NEON data from two sites (Site 1 – Abbey Road, Washington, USA and Site 2 – Moab, Utah, USA) to construct filters to model measured environmental tracking, environmental tracking, and fundamental tracking. In this example, we illustrate the contrasting multivariate environment (shown on left side of Fig. 3), including air temperature, cumulative photosynthetically active radiation (PAR), and precipitation. Ecologists often use a measurement filter to estimate tracking. For example, regressing the timing of a phenological event against monthly temperature to identify a threshold is effectively applying a simple, univariate measurement filter that we illustrate on the top right of Fig. 3 as the exceedance of a threshold by the 30-day mean daily air temperature. The cue system of an organism can also be conceptualized as a filter; for example, the requirement for winter chilling hours, as well as spring warming hours before budburst, is an example of a multivariate cue filter, illustrated on the centre right of Fig. 3 as a changing probability of an event (e.g. budburst) as a function of accumulated degree chilling hours and degree heating hours. Ultimately, fitness is determined by the joint distribution of many environmental variables through time, a complex fitness filter that ecologists understand in detail for only a few, well-studied organisms. On the bottom left of Fig. 3, we illustrate the end-of-season fitness as a function of the timing of a start-of-season life-history event, where the fitness filter includes: (i) growth as a unimodal function of temperature, a saturating function of PAR, and a saturating function of soil moisture, and (ii) survival as a function of early-season frost and summer heat stress.

3. 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 previous 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 resource uptake controlled by species-level parameters that define how the uptake increases as R increases (a), the inverse of the maximum uptake (u), and the shape of the uptake (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,

3

a species characteristic, and $\tau_p(t)$, an attribute of the environment, which varies year-to-year. Germination fraction declines according to a Gaussian curve as the distance between τ_i and $\tau_p(t)$ grows, with the rate of decline determined by h (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. S1B-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^* (a metric of resource competition 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. 5 in main text). Thus, only species that persisted through the first stationary period continued into the non-stationary period.

4

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 non-stationary periods. Species-specific parameters (c_i, τ_i, and α_i) were drawn from uniform random distributions with the ranges given in Table S3. All other parameters were identical between species (Table S3). 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.

Table S1. 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	linked	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 bird traits	1	1
other leaf traits	4	3
other lepidopteran traits	3	4
other plant traits	1	1
overwintering	2	1
range traits	1	4
root traits	3	0
seed mass/size/number	1	2
woody/herbaceous	1	0

Table S2. Summary of results from literature on phenological tracking showing which phenophases researchers found were linked to which traits, or not.

Taxa	Phenophase	Trait	linked	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 mass/size/number	1	2
plants	flowering/fruiting	woody/herbaceous	1	

Table S3. Parameter values, definitions, and units.

Parameter	Value(s)	Definition	Unit
N_i	initial conditions $N_i(0) = 100; min(N_i(t)) = 10^{-4}$	census of seedbank of species i	seeds per unit area
s	0.8	survival of species i	unitless
B_i	see 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 maximum 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	maximum 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	see 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	$\frac{biomass}{seeds}$
$f(R)$	see Eqn 3	resource uptake rate for species i	$\frac{resource}{(days)(biomass)}$
t	1	annual timestep	years
$0 \to \delta$	determined by rate of resource depletion	time during the growing season	days

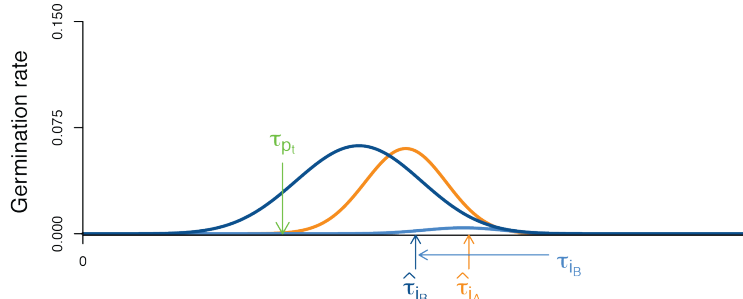**(A) Distributions of resource timing under stationary and non-stationary periods**
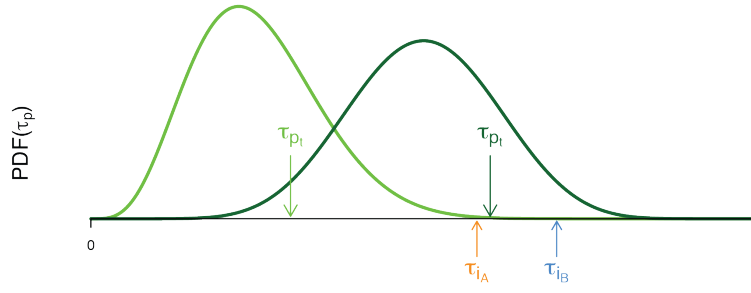
(B) Realized germination rates (drawn from stationary period)
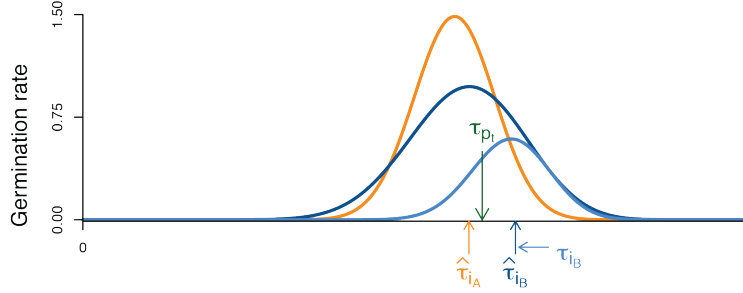
(C) Realized germination rates (drawn from end of non-stationary period)

Timing of resource pulse, τ_p

Fig. S1. The distributions of the environment (A, showing probability density function, PDF) 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 non-stationary 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 non-stationary period. Note the change in axes between (B) and (C) shows the decline in overall germination rate as the environment moves away from the preferred germination time of both species.
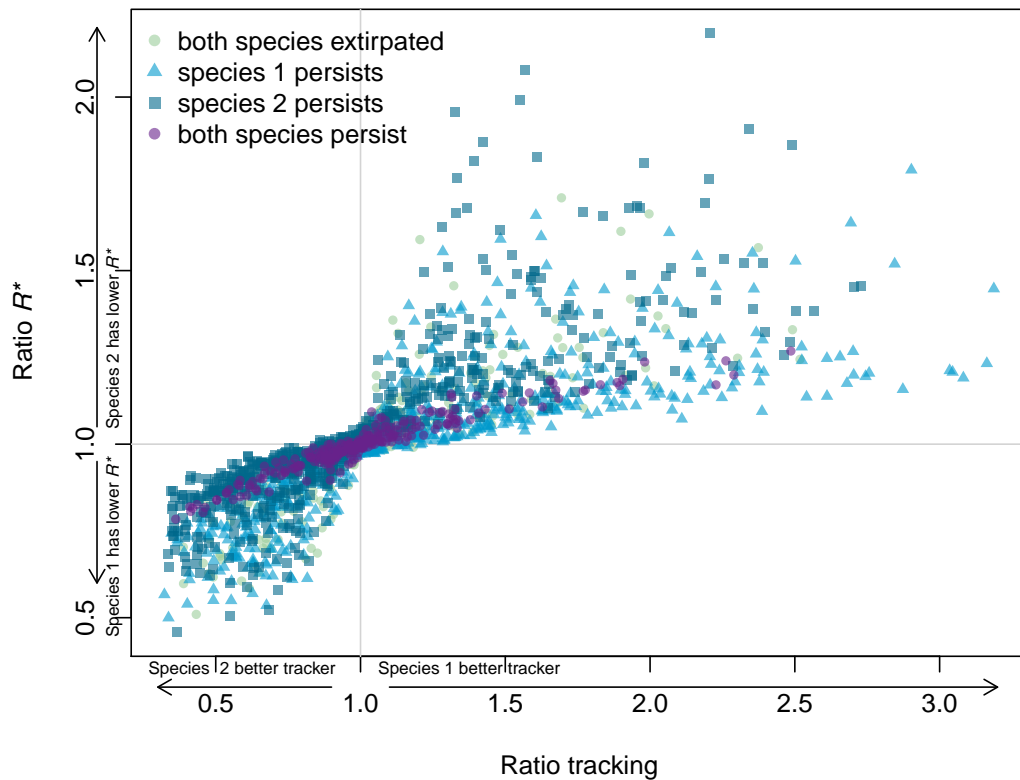
9

Fig. S2. 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 colour represent the outcome for that two-species community of 500 years of non-stationarity, where the abiotic start of the season shifts earlier.