

1 On eco-evolutionary dynamics of phenologies in competitive
2 communities and their robustness to climate change

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24 **Abstract**

25 **G**lobal changes currently cause temporal shifts in the favourable conditions for different
26 phases of species life cycles. Phenologies characterizing temporal presence, may adapt
27 through heritable evolution in response to these changes. Given a community context, this
28 evolution may cause a change in the phenology overlap and thus a change of interspecific
29 interactions such as competition. Using a model in which phenologies compete and coevolve,
30 we study the conditions under which diversity emerges, as well as their annual distribution.
31 We find that the environment richness (food quantity, light, pollinators...) and competition
32 constrain the diversity and spread of phenologies. A robust pattern of phenologies distribution
33 emerges consistent with Swedish flowering observations. Once a stable community is
34 reached, we apply a progressive change in environmental conditions. We found that
35 adaptation eventually restored diversity, but that the simulated change often led to numerous
36 extinctions due to increased competition. The percentage of diversity lost depends on the
37 speed of change and on the initial diversity. Phenologies already pre-adapted to the new
38 environmental conditions drive the restoration of diversity after the change. We finally study
39 a spatial version of the model in which local communities are organized along an
40 environmental gradient. Pre-change, allowing dispersal decreases the local adaptation of
41 phenologies to their local fixed environmental conditions. Dispersal however largely
42 enhances the maintenance of biodiversity in changing environments, though its benefits are
43 not homogeneous in space. Evolution remains the only rescue mechanism for southern
44 phenotypes.

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47 Keys words : Phenology, community ecology, evolutionary rescue, competition, adaptive
48 dynamics, dispersal

49 Introduction

50

51 Brittany, once a humid region favoring artichoke cultivation may well soon become a new
52 French wine-growing region. On the other hand, in traditional wine-growing regions,
53 grapes ripen earlier in the season. Such agricultural shifts immediately pinpoint how species
54 phenologies are currently affected by climate changes. Wild species undergo similar changes
55 and many recent shifts in phenology and distributions have been documented (Parmesan and
56 Yohe 2003).

57 Phenologies are simultaneously selected by environmental conditions and interspecific
58 interactions. Depending on the species life cycle and phenotypic traits, some parts of the year
59 may be more favorable for investment in growth, reproduction and resource acquisition.
60 Environmental factors favoring the presence of a species can be linked to fluctuations in
61 temperature, light or to the availability of certain limiting nutrients (J. Lloyd and Taylor
62 1994). For a given species, the combination of favorable abiotic conditions can be seen as a
63 temporal niche space or environmental window. The presence of other species however
64 constrains species phenology on an ecological and evolutionary scale. Within a functional
65 group, species present at the same time may find themselves in competition for resources or
66 space. Flowering plants may be in competition for pollinators (Mitchell et al. 2009), while
67 developing amphibian larvae may compete with breeding species within a pond (Alford and
68 Wilbur 1985). Mutualistic and trophic interactions similarly require overlapping phenologies
69 for the two species (Loeuille 2019; Waser 1979), so that the fitness of partner species largely
70 depends on their relative timing. Interspecific relationships thereby likely influence the
71 coevolution of species phenologies in natural communities.

72 Competition can cause phenologies to diversify. Assuming a suitable temporal window,
73 phenotypes active at different times partly avoid competition. Niche partitioning and limiting

74 similarity is then expected, so that a given diversity of phenologies may coexist (MacArthur
75 and Levins 1967; Chesson 2000). Such competitive effects are for instance well known for
76 flowering species. In the Arima Valley of Trinidad (tropical region), fruiting seasons of the 19
77 species of *Miconia* genus are spread out to cover the entire year. The staggered fruiting season
78 would have evolved through interspecific competition (Snow 1965). An annual temporal
79 partitioning of pollinators has also been reported many times as an important selective factor
80 of flowering phenologies (Appanah 1985; Botes, Johnson, and Cowling 2008; Wheelwright
81 1985).

82
83 Under current global changes, environmental conditions largely vary in space (warmer
84 conditions northward and at higher altitude) and in time (eg, earlier onset of phenologies,
85 (Sherry et al. 2007; Vitousek 1992)). Such changes in the abiotic conditions directly affect the
86 environmental window in which phenologies may coevolve. Evolution of phenological traits
87 or dispersal to colonize new parts of the changing environmental niche can both save a
88 population. Consistent with this view, many instances of rapid evolution of phenologies have
89 been recently reported (Carter, Saenz, and Rudolf 2018; Franks, Sim, and Weis 2007; Husby,
90 Visser, and Kruuk 2011; Jonzen 2006; Nusse 2005; Phillimore et al. 2010). Earlier arrival
91 dates of migratory birds have for instance been noted, with evolution likely playing a key role
92 (Jonzen 2006). If evolution is fast enough to keep a match between the species phenology, its
93 interactor and the environmental window, evolutionary rescue is expected (Gomulkiewicz and
94 Holt 1995). As global changes also shift the fundamental niche of species in space, dispersal
95 of phenologies to match the environmental niche could similarly offer a rescue mechanism.
96 Northward shifts and phenological shifts have been simultaneously noted in many groups of
97 species (Guisan and Thuiller 2005; Parmesan and Yohe 2003). The extent of dispersal or local
98 adaptation depends on the species ability to disperse and on the environmental fragmentation

99 (Kubisch et al. 2013; Loeuille 2019). For warm latitudes (equator, tropics), no source of
100 phenotypes adapted to warmer temperature may exist. When the environment changes, local
101 adaptation is then the only mechanism capable of saving biodiversity (Norberg et al. 2012;
102 Sinervo et al. 2010).

103

104 Changes in the environment are not simply abiotic and climatic, but also entail variations in
105 the community and interaction context. Reshuffling of interactions and local extinctions
106 largely restructure present-day communities (Tylianakis et al. 2008). As matching of
107 phenologies underpin ecological interactions, the restructuring of natural communities largely
108 impacts the fitness of coexisting phenologies and can cause diversity losses. For instance,
109 (Carter, Saenz, and Rudolf 2018) studied the phenology of 66 amphibian species on a 15 year
110 interval. They showed that phenology overlap increased and proposed that this may increase
111 competitive interactions by up to 25%. Eco-evolutionary consequences are intriguing. From
112 an ecological point of view, the increased competition may lead to species loss, due to
113 competitive exclusion. From an evolutionary point of view, given an increase in competitive
114 selective pressures, further displacement of phenologies is expected. Note that the two aspects
115 are in fact intertwined. If species have different abilities to evolve (population size, genetic
116 diversity...), evolutionary rescue may save species that evolve, but increase competition on
117 other species of the community (Loeuille 2019). Such asymmetric effects could make certain
118 species more vulnerable and cause their extinction (Johansson 2008). Interspecific
119 competition can also accentuate the selection gradient in certain situations and accelerate the
120 evolution (Osmond and de Mazancourt 2013). Finally, when local diversity is large, niche
121 packing constrains the possible evolution in response to environmental changes (de
122 Mazancourt, Johnson, and Barraclough 2008). Changing competitive interactions in a

123 community can therefore alter evolutionary rescue by changing the ability of species to track
124 environmental changes.

125

126 We build a model of a community of competing phenologies in a temporal niche potential
127 which we will call an environmental window. The environmental window is first fixed, then
128 altered to mimic global changes. Phenologies are characterized by two traits, the spread and
129 the mean date. Fitnesses of the different phenologies depend not only on abiotic constraints
130 (environmental window) but also on surrounding phenologies (competition). Using this
131 model, we investigate the following questions. (1) Given a fixed environmental window, and
132 starting with just one phenology, we investigate the conditions of diversification. When it
133 occurs, we characterize both the ecological (total diversity, community structure) and the
134 evolutionary state (phenology distribution). Phenological traits distribution is then compared
135 to an empirical dataset of flowering plants from Sweden. (2) We then study the impact of a
136 change of the environmental window on traits and on local diversity. We link the loss of
137 phenological trait diversity with the ability of species to evolve for both date and spread. We
138 expect greater losses of biodiversity when evolutionary potential are decreased. (3) Finally,
139 we undertake metacommunity simulations along a continuum of latitudes and investigate
140 whether dispersal or phenology evolution better explain evolutionary rescue events.

141

142 **I Construction of the eco-evolutionary model**

143

Variable	Significance	Unit
n_i	Population density of the i^{th} phenotype phenology	n
μ_i	Average date of the i^{th} phenotype phenology	<i>date</i>

σ_i	Spread of the i^{th} phenotype phenology in days	<i>days</i>
$R(\mu_i, \sigma_i)$	Intrinsic reproduction rate of the population	t^{-1}
$C(\mu_i, \mu_j, \sigma_i, \sigma_j)$	Per capita competition rate between phenotypes i and j	t^{-1}, n^{-1}

144 Table 1 : Model variables and their associated units.

Parameter	Significance	Unit	Value
m	The threshold for intrinsic reproduction to reach a overall positive reproduction rate	t^{-1}	200000
G	Ability of a species to exploit the environment	<i>days</i> . t^{-1}	200
P_{max}	Richness of the environment	t^{-1}	[3;64]
C	Competition	t^{-1}, n^{-1}	0.01
λ	The slope of the resource function at the inflection point.	<i>date</i> $^{-1}$	0.1
$j_{1/2}$	The date of the inflection of the sigmoid.	<i>date</i>	[60;120]
P_{dep}	Richness depletion in summer	t^{-1}	[0;0.9 P_{max}]
λ_{dep}	The slope of inflection	<i>date</i> $^{-1}$	0.5
$j_{1/2dep}$	The date of inflection of the depletion.	<i>date</i>	[170;120]
β_μ, β_σ	Poisson expectation of mutations per individual every dt_{mut} for μ and σ	$n_{mut} \cdot n^{-1}$	[0;10]* 10^{-6}
dt_{mut}	The time steps between mutations	t	0.1
T_{ch}	The duration of environmental change	t	[40;9000]
$\omega_\mu, \omega_\sigma$	The variance of the mutation distribution for μ and σ	<i>date, days</i>	0.1,0.01
r_{disp}	Poisson expectation of dispersers per individual every dt_{disp}	$n_{disp} \cdot n^{-1}$	[10^{-7} ; 10^{-4}]
dt_{disp}	The time step between dispersal events	t	0.01

145 Table 2 : The parameters of the model, their meaning and their associated unit. The values

146 reported are those used in the simulations. The intervals correspond to the variation of this

147 parameter for the analyses.

148 **I.1 Population dynamics of a given phenology** (μ_i, σ_i)

149

150 For a given phenotype (μ_i, σ_i) , population density n_i follows a simple Lotka-Volterra system.

151 Assuming that k phenologies coexist in the environment:

152

$$\frac{dn_i}{dt} = n_i \left(R(\mu_i, \sigma_i) - \sum_{j=0}^k n_j C(\mu_i, \mu_j, \sigma_i, \sigma_j) - m \right) \quad (1)$$

153

154

155 Here, R embodies the *per capita* reproduction rate and C the competition kernel, explained

156 below. All parameters are detailed in table 1.

157

158 **I.2 Phenological traits and associated trade-offs**

159 Phenological traits (μ_i, σ_i) define a temporal occupancy function g , modeled using a gaussian

160 function centered on μ_i (Equation 2, Figure 1a). Note that this function is normalized, so that

161 when activity is spread on a larger time window (higher σ), it is also reduced (fig 1c):

162

$$g(x) = \frac{G}{\sigma 2\pi} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (2)$$

$$R(\mu, \sigma) = \int_x \min(P(x), g(x)) dx \quad (3)$$

163

164

165 The match between the temporal occupancy function and the environmental window defines
166 the *per capita* reproduction rate R (equation 3, fig1a). As displayed on figure 1c, this creates a
167 trade-off acting on the spread σ , linking generalism and environmental use. When
168 phenologies are spread on little time (small σ), the quality of the environment may not be
169 sufficient to support this intense activity (narrow gaussian function overshoots the
170 environmental window). However, plants may swamp their herbivores by producing
171 vulnerable organs in concentrated bursts (Augspurger 1981). For large σ (spread phenology)
172 on the other hand, energy may be too limiting at extreme dates. Exploiting an environment to
173 reproduce can be resource-intensive (Primack and Stacy 1998).

174 Note that the environmental window (equation 4, fig 1a) summarizes biotic and abiotic
175 conditions (excluding competition) suitable for the development of the considered phenotype.
176 Such factors include temperature, rainfall, and resource availability. Taking the example of
177 plants, vegetative phenologies often depend on the photoperiod, humidity and temperature
178 (Chuine and Régnière 2017). Flowering phenology is constrained by the presence of
179 pollinators and resource accumulation (Rathcke and Lacey 1985) while fruiting phenology
180 may depend on the temporal availability of seed dispersers (Wheelwright 1985). We consider
181 several scenarios for the environmental window. First, the environmental niche is fixed and
182 made of two stuck sigmoids (first part of equation 4, fig 1A) and we let emerge the
183 community from the diversification of phenologies. Suitability is maximum in the middle of
184 the year at 180.

185 In equation 4, P_{max} represents the quality of the environment. Parameter $j_{1/2}$ is inversely
186 related to the width of the environmental window. Parameter λ affects the steepness of the
187 environmental window early and late in the year.

$$P(x) = \frac{P_{max}}{1 + e^{\lambda(|x-180|-j_{1/2})}} \quad (4)$$

188

189 **I.3 Linking phenologies and competitive interactions**

190

191 When phenologies co-occur within the environmental window, they are assumed to compete
192 for available resources. Following classical frameworks (MacArthur and Levins 1964), we
193 assume that competition is larger when phenologies are more similar, so that competition is
194 proportional to the integral of the product of the two presence functions (equation 5).

$$C(\mu_i, \mu_j, \sigma_i, \sigma_j) = G^2 e^{\frac{-(\mu_i - \mu_j)^2}{2(\sigma_i^2 + \sigma_j^2)}} \quad (5)$$

195

196 Note that individuals having exactly the same phenology compete at a maximum and constant
197 rate G^2 .

198

199 **II Ecological dynamics**

200 Consider first that all individuals have the same phenology. Equation (1) then simply
201 corresponds to a logistic equation and the population reaches its carrying capacity (6).

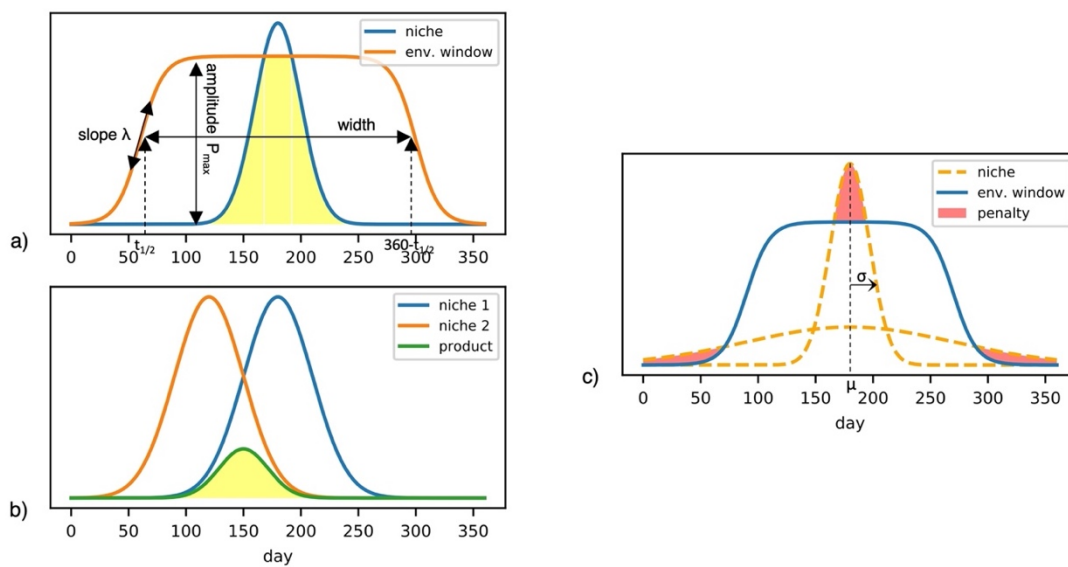
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$$n^* = \frac{R - m}{G^2} \quad (6)$$

203

204 The population then exists whenever the intrinsic reproduction rate is higher than intrinsic

205 mortality rate m .



206

207 Figure 1 : Defining the population dynamics of phenologies : a) The temporal occupancy

208 function (equation 2, blue) and environmental window (equation 4, orange) define the

209 intrinsic reproduction rate (equation 3, yellow integral). b) Competition between two

210 phenologies (yellow integral) increases with their similarity (equation 5). c) Note that because

211 of our definition of the reproduction rate, phenologies that are too narrow or too wide

212 (variations in σ) pay a cost here represented by the red integral.

213 III Evolution, coevolution and diversification of phenologies in a fixed environment

214

215 Evolution of phenologies is studied using a numerical implementation of adaptive dynamics
216 (Dieckmann and Law 1996). Mutations occur independently, either on the phenological
217 spread σ or on the mean date μ .

218 The equations of population dynamics (equation 1) are integrated, and at fixed time
219 intervals dt_{mut} , the number of mutants is drawn in a poisson distribution that depend on the
220 *per capita* mutation probability (β_μ for μ , β_σ for σ) and on the size of the populations
221 currently present in the community. While we typically consider rare mutations, we allow
222 variations in the frequency of mutation dt_{mut} to modulate the evolutionary potential of
223 evolving phenologies. Whenever a population mutates, a rare mutant population is introduced
224 (at density 1). Mutations are of small amplitude and the mutant trait is drawn in a normal
225 distribution centered on the parent trait. The variance of this normal distribution is the
226 parameter ω_μ for μ and ω_σ for σ . When integrating equation (1) any population passing
227 below the extinction threshold (<1) is assumed extinct and dropped from the system.

228 While we are able to give a few mathematical results for simpler cases (see below), most
229 scenarios are not mathematically trackable so that we mostly rely on simulations. A benefit of
230 this simulation choice is that it allows us a large flexibility as we can make the environmental
231 window take very diverse forms to investigate climate change, but also systematically vary
232 the relative speed of ecology and evolution.

233 To uncover how the evolution of each trait (μ, σ) depends on the value of the other trait, but
234 also on other parameters of the system, we first fix the environment and study the evolution of
235 each trait separately, the other being fixed.

236 **III.1 Evolution and diversification of μ**

237 We start with a single resident population of phenology (μ, σ) and consider the evolution of
238 the mean date μ . The relative fitness of a mutant μ' that differs slightly from the resident
239 population μ is given by its invasion fitness (equation 7), ie, its growth rate when rare and the
240 resident at equilibrium (Metz, Nisbet, and Geritz 1992):

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$$s(\mu, \mu', \sigma, \sigma) = R(\mu', \sigma) - m - \frac{(R(\mu, \sigma) - m) * C(\mu, \mu', \sigma, \sigma)}{C(\mu, \mu, \sigma, \sigma)} \quad (7)$$

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Because we assume no depletion, the first term of the equation will be maximum mid-year (creating stabilizing selection). On the contrary, the last term will be larger when phenological niches have less overlap, i.e. when μ' differs from μ . This will favor disruptive selection, creating diversification when the environmental window is wide enough or when the spread σ is small enough.

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Since the maximum of the environmental window is mid-year ($x=180$), the penalty of a wide or narrow phenological niches (fig 1c) will be minimal at this date. Evolutionary dynamics of the trait can be visualized using pairwise invasibility plots (PIPs, (Geritz et al. 1998)). A PIP (figure 2b) shows the sign of the invasive fitness (equation 7) of a mutant μ' (y-axis) in a resident population μ (x-axis). Black areas show positive values where corresponding mutants invade the resident population. The direction of evolution can then be deduced (blue

258 trajectories, red trajectories correspond to failed invasions). On figure 2b (left), note that for
259 narrow phenologies ($\sigma = 30$), evolution eventually leads to a singularity at which both earlier
260 and later mean dates are able to invade (blue dots at the end of the trajectory). Such situations
261 correspond to branching points that allow diversification around $\mu = 180$ (fig2a). Because the
262 environmental window is much larger than the phenology here, the fitness landscape is rather
263 flat (large black areas along the diagonal from 100 to 260). Conversely, for wide phenologies
264 (fig 2b, right), evolution leads to a unique singular strategy at $\mu = 180$ that cannot be invaded
265 (read crosses). Such situations are called CSS (Continuously Stable Strategies, (Eshel 1983))
266 and are indicative of stabilizing selection. Evolution stops there and no diversification occurs.

267

268 We now detail further situations in which diversification occurs. Figure 2c shows the quasi-
269 equilibrium situations for different sets of simulations where spread is systematically
270 manipulated. Note that the wider phenology ($\sigma = 50$) has only one date (yellow) and makes
271 the limit beyond which no diversification occurs. When the spread is more limited ($\sigma = 30$,
272 light green), the system eventually settles at two phenological dates (close to 150 and 210).
273 Smaller phenological spreads lead to increasingly more phenological niches with
274 heterogeneous densities. We quantified diversity using Shannon indices to account for
275 density asymmetries. The equilibrium diversity of phenologies increases when the (fixed)
276 phenological spread is smaller (figure 2d), which is consistent with niche packing
277 expectations (MacArthur and Levins 1967).

278 Note that diversity also depends on characteristics of the environmental window (fig2e).

279 While it varies rather little with the maximum richness of the environmental window P_{max}
280 (blue), it increases with the width of the environmental window (orange). Intuitively, given
281 the phenological spread σ is fixed, it is possible to pack more phenologies when a wider
282 environmental window exists.

283 **III.2 σ is evolving to accommodate the richness of the environment**

$$s(\mu, \sigma, \sigma') = R(\mu, \sigma') - m - \frac{(R(\mu, \sigma) - m) * C(\mu, \mu, \sigma, \sigma')}{C(\mu, \mu, \sigma, \sigma)} = R(\mu, \sigma') - R(\mu, \sigma) \quad (8)$$

284 We now fix the phenology mean date μ and study the evolution of phenological spread σ . As
285 before, evolution can be understood by analyzing the invasion fitness of a rare mutant σ' in a
286 resident population σ :

287 Remembering that mutants can invade when this quantity is positive, equation 8 means that
288 evolution will simply follow variations of the intrinsic reproduction rate. Penalties shown on
289 figure 1c then simply have to be minimized. To minimize the first penalty, for a given date,
290 the optimal phenology should match the environmental quality, not overshoot the window.
291 Such a perfect match however happens for a given σ that may induce penalties early and late
292 in the year. This last penalty can often be neglected if the phenology is not too spread or too
293 close from the edge of the window. The optimal strategy under these conditions is stable and
294 can be explicitly computed:

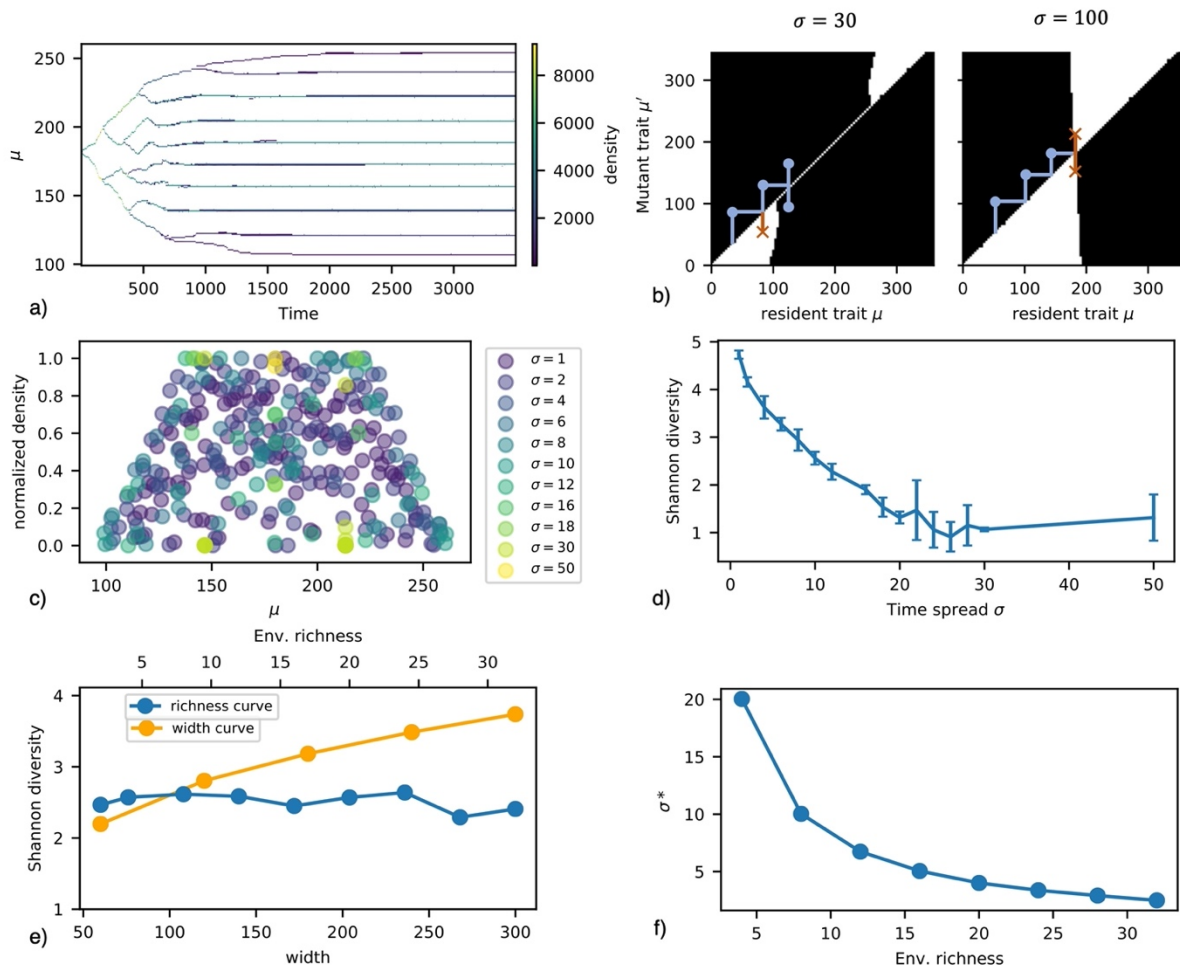
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$$\sigma^*(\mu) = \frac{G}{2\pi P(\mu)} \quad (9)$$

296

297 Equation 9 shows that the selected spread is inversely proportional to the quality of the
298 environment, given the (fixed) mean phenological date μ . Phenologies are therefore more
299 spread when the environment is poor (low P_{max}). A direct consequence is that phenologies at

300 the edge of the environmental window are expected to be more spread out. Numerical
 301 simulations confirm the mathematical analysis (figure 2f). We find that evolutionary
 302 equilibrium σ^* decreases in richer environments, so that phenologies specialize in time.
 303



304
 305 Figure 2 : Evolution of the phenology mean date (panels a-e) and spread (panel f)
 306 depending on the environmental conditions and the other trait. a) Diversification of μ in time
 307 ($\sigma = 10$) b) Pairwise invasibility plot (PIP) showing the evolutionary dynamics of the mean
 308 date for two (fixed) values of σ (black: mutant μ' can invade resident μ , white: mutant μ'
 309 cannot invade resident μ). Example evolutionary trajectories are in blue while examples of
 310 failed invasions are in red. ($P_{max} = 3$) c) Distribution of equilibrium phenology mean dates for
 311 several σ values. d) Shannon diversity at equilibrium according to σ with μ evolving (the

312 error bars are the standard deviation for 10 replicates). e) Diversity of phenologies at
313 equilibrium depending on the characteristics of the environmental window (amplitude and
314 width) with μ evolving. f) Stable evolutionary equilibrium for phenology spread (σ)
315 depending on the richness of the environmental window. ($\beta_\mu, \beta_\sigma = 10^{-5}$ for panels (acdef), $j_{1/2}$
316 = 120 for panels (acdf))

317
318 We stress that no diversification is possible at σ^* (CSS) so that in our model the diversification
319 only happens for mean dates μ . This diversification is however constrained by both the
320 environment and the spread of phenology σ (fig2d, e). The spread therefore potentially allows
321 an adaptation to the abundance of the resource when μ has evolved. To confirm this, we now
322 investigate the coevolution of the two traits.

323

324 **III.4 Coevolution of phenological traits**

325 We now allow mutations to occur on both traits (σ and μ). We investigate how the shape of
326 the environmental window affects the evolutionary equilibrium. An example simulation
327 showing the emergence of seven different phenologies is displayed on fig3a. In link with
328 previous analyses (equation 9), we observe that phenologies that evolve at central (high
329 quality) dates evolve narrow phenologies, while phenologies evolving at extreme date become
330 spread. This pattern of phenology distribution is robust to variations in the environmental
331 window. For instance, on fig 3b, for nine different maximum qualities of the environment, we
332 observe that the further the phenologies evolve from central dates, the greater their temporal
333 spread (figure 3b). In summary, phenologies adapt to the environment richness at the date of
334 their phenology which constrains the diversification indirectly through interspecific
335 competition and the availability of ressources on both sides.

336

337 Emerging diversity depends on the shape of the environmental window (figure 3d).
338 Particularly, higher quality of the environmental window leads to higher diversity levels. The
339 richer the environment, the more phenologies evolve to restricted temporal presence thereby
340 avoiding competition with surrounding phenologies. The width of the environmental window
341 here plays a minor role for diversity.

342

343 **Empirical analysis of flowering phenological spread**

344

345 We test whether the pattern of more spread phenologies at extreme dates (figure 3b) is
346 relevant for species constrained by the same environmental window. We investigate how the
347 flowering interval of 63 plant species in Sweden depends on their flowering time. For this
348 dataset, the seasonality of the conditions favorable to the development of flowers (light,
349 pollinators...) is very marked and reduced in time. 30 specimens per species were collected in
350 the herbarium of the Swedish Natural History Museum (Weinbach 2015).

351 The number of flowers per specimen was reported for each observation. We fit a Gaussian on
352 the counting of flowering observations through the year of each species. It is assumed that the
353 sampling effort was the same for all species over time. Each sampling corresponds to a count
354 of the number of flowers. Having count data, we use a generalized linear model with a
355 poisson-like error:

356

$$\log(Y_{ij}) = a_i X_j^2 + b_i X_j + c_i + \varepsilon_{ij}, \varepsilon_{ij} \sim N(0, \sigma^2) \quad (10)$$

357

358 (10) X_j being the day of the year, Y_{ij} being the count of the flowering-species i on day j . a_i , b_j
359 and C_j are estimated for each species.

360 The mean date of i correspond to: $\frac{-b_i}{2a_i}$

361 The temporal spread: $\frac{1}{\sqrt{-a_i}}$

362 For the different species, we want to link the estimated spread to the estimated mean date.

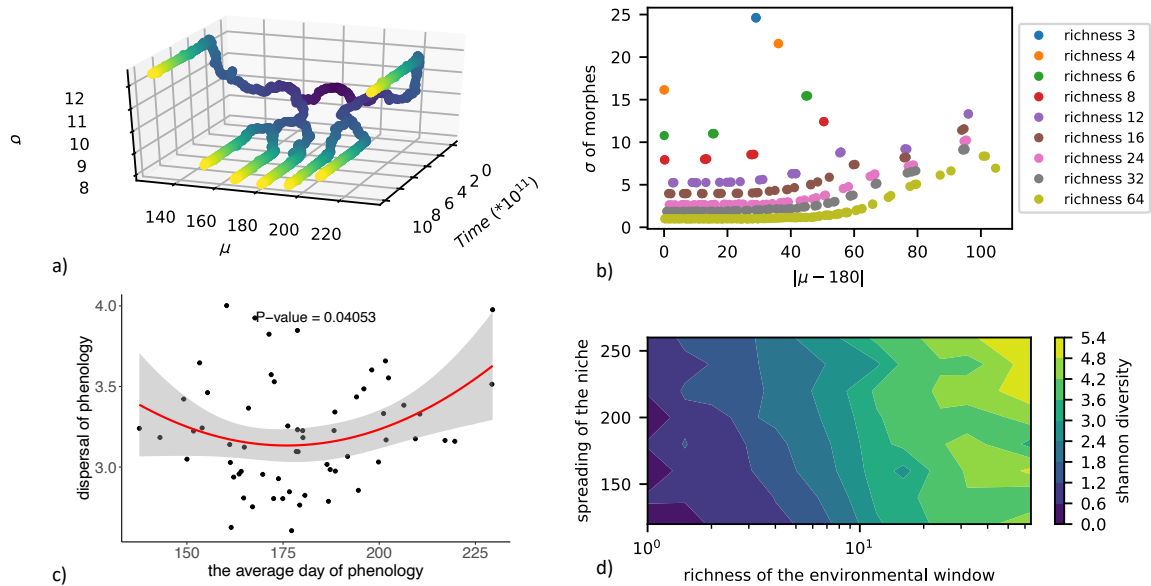
363 Equation (11) shows the statistical model with X_i the mean date of species i and Y_i its spread.

$$\log(Y_i) = dX_i^2 + eX_i + f + \varepsilon_i, \varepsilon_i \sim N(0, \sigma^2) \quad (11)$$

364

365 Consistent with our expectation, Figure 3c shows that plants flowering in the middle of the
366 summer have shorter phenologies than those flowering at more extreme dates. Short spread
367 flowering is more common in the summer when the competition might be stronger. An
368 explanation could be the low presence of pollinators at the beginning of the season limiting
369 the rate of visitation per flower or competition for other resources (nutrient, light) on a short
370 suitable period.

371



372

373 Figure 3 : Coevolution in a stable environment and comparison with empirical data. a)

374 Coevolutionary dynamics of the spread and average date of phenologies. The color yellows in

375 time. ($P_{max} = 8$) b) Distribution of evolved phenological spread σ depending on evolved mean

376 date μ at equilibrium. Nine simulations are shown, for different qualities of the

377 environmental window. In all cases, phenologies are more spread as the evolved dates

378 become less central. c) Relationship between phenological spread and mean date for the

379 flowering of 63 plant species in Sweden. d) Variations in Shannon diversity at coevolutionary

380 equilibrium depending on the environmental window parameters. ($\beta_\mu, \beta_\sigma = 10^{-5}$ for panels

381 (abd), $j_{1/2} = 120$ for panels (ab))

382

383

384 IV Eco-evolutionary dynamics under global changes

385

386 As a second step, we no longer consider the environmental window as fixed, but allow it to

387 change to reflect possible consequences of global changes. Specifically, we allow the system

388 to evolve toward quasi-equilibrium in a fixed environmental window (blue in fig 4a). We then

389 modify environmental conditions and study the consequences of this modification for eco-
390 evolutionary dynamics and for the maintenance of diversity. Modifications correspond to
391 changes in the onset and ending of the environmental window (parameter $j_{1/2}$) (eg, milder
392 conditions in early spring and late autumn) and to a depletion of up to 90% within summer
393 (second part of equation 4) to reflect harsher conditions mid-summer (drought, extreme
394 temperatures, (Spinoni et al. 2018)) (fig 4a). This change consists in a linear evolution of the
395 parameters of the environmental window for the time period T_{ch} . We keep the integral under
396 the curve constant, so that total environmental quality *per se* does not change in these
397 simulations.

$$P(x) = \frac{P_{max}}{1 + e^{\lambda(|x-180|-j_{1/2})}} - \frac{P_{dep}}{1 + e^{\lambda_{dep}(|x-180|-j_{dep1/2})}} \quad (12)$$

398

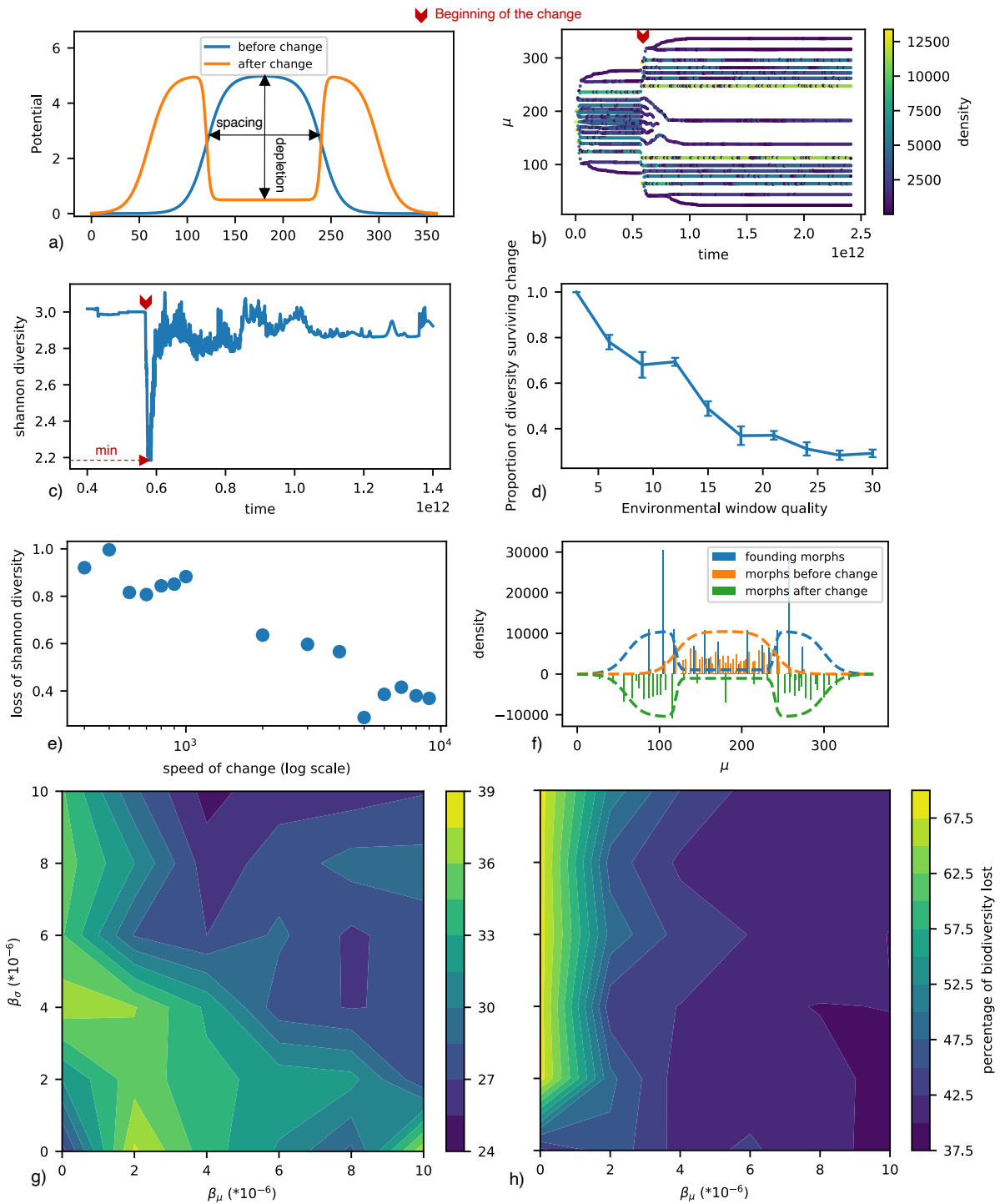
399 **IV.1 Evolutionary rescue of phenologies**

400

401 Based on evolutionary rescue (Gomulkiewicz and Holt 1995) we expect that a given
402 phenology may more easily persist when its evolutionary potential (here mutation rate and
403 amplitude) is larger, and when the disturbance is less intense. Evolutionary rescue theory is
404 however based on single species models and may not hold in complex communities where
405 indirect effects occur (Loeuille 2019). Surprisingly, we found that the tenets of evolutionary
406 rescue still apply to our communities of competing phenologies. Particularly, biodiversity is
407 saved when evolution is allowed to be faster and disturbances are slower.

408 We vary the environmental window for different time periods T_{ch} to simulate various speeds
409 of current changes (fig 4e). This speed of the environmental change is to be contrasted with
410 the adaptation capacity of phenologies, that is also systematically manipulated (fig 4gh).

411 Finally, we investigate whether consequences of global changes are similar in poor (fig 4h) vs
 412 rich environments (fig 4g).
 413



414

415 Figure 4 : Consequences of environmental for community eco-evolutionary dynamics a)

416 Modeling environmental changes through modifications of the environmental window b) an

417 example of coevolutionary dynamics of mean dates under environmental changes. Densities
418 of the phenologies are reported through variations in colors. c) Diversity dynamics in time. d)
419 Proportion of the phenologies that contribute to diversity post change depends on the quality
420 of the environmental window. e) Percentage of diversity loss as a function of the rate of
421 change. Loss is measured based on the difference between Shannon diversity at the onset of
422 environmental change and the minimum of Shannon diversity following it. ($T_{ch} \in [40:9000]$)
423 f) The funding phenotypes: dashed lines represent the environmental windows. Bars are the
424 densities of each phenotype with their associated mean date. The orange bars are the ones
425 before the change, the green ones are the phenotypes after the change. In bleu are the funding
426 phenotypes, the density associated is the cumulated density of all its descendants. g,h)
427 biodiversity loss (in percentage) as a function of evolutionary capacity for μ and σ in a rich
428 (g) and in a poor environment (h). ($P_{max} = 12$ for panels (bcdfg), $P_{max} = 8$ for panel (h), β_{μ} ,
429 $\beta_{\sigma} = 10^{-5}$ for panels (bcdef), $T_{ch} = 2000$ for panels (bcd fgh), $j_{1/2} = 120$ for panels (ab), $j_{1/2} =$
430 120 for panels (abcdefgh), $j_{1/2dep} = 60$ for panels (abcdefgh))
431
432 Following the environmental change, we observe that phenologies evolve toward newly
433 suitable early and late dates, while most go extinct mid-year due to the depletion (Fig 4b). As
434 expected from previous results (eg, equation 9), mid-year phenologies have large spreads
435 (light blue, sup fig 1) as they evolve in a deteriorated environment (summer depletion).
436
437 In spite of this continuous adaptation of phenologies, modeled changes have large impacts on
438 the maintenance of diversity. Diversity decreases drastically during the environmental change,
439 then partially recovers (Fig4c). Diversity loss is quantified based on the difference between
440 the diversity level observed just before the change and the minimum diversity observed post-

441 change. We confirm the intuition that the faster the change, the greater diversity losses
442 (Fig4e).

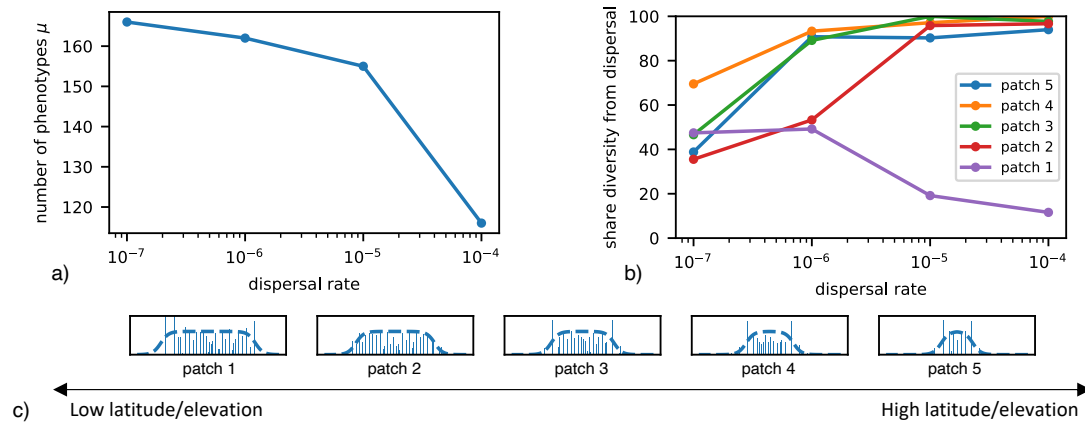
443 Fast evolution of the two traits allows a better resistance of the community (fig 4g,h). In poor
444 environments (Fig4h), fast evolution of mean dates μ is particularly important. Evolution of
445 spread σ alone is detrimental as phenologies adapt to the local environmental quality thereby
446 widening and increasing competition with surrounding phenologies (low β_{μ} on Fig 4g,h).

447 Mean date evolution allows phenologies to move to new suitable parts of the environmental
448 window. In rich environments, however, evolutionary potentials of both traits jointly favor the
449 maintenance of diversity (Fig 4g), emphasizing a stronger interaction between the two
450 dimensions of phenologies. A possibility is that in such rich environments selection of larger
451 spread (hence increased competition) is less prevalent.

452 Phenologies existing pre-change contribute differently to biodiversity post-change. Founding
453 phenologies are mostly at the edge of the environmental window, pre-change (Fig 4f). Early
454 and late season phenology could better maintain themselves in the face of change and drive
455 future diversity. The proportion of initial lineages founding post-change diversity is smaller
456 for high quality environments that have high pre-change diversity (Fig 4d). Competition has a
457 greater effect on the loss of diversity in such systems, as they initially have many high density
458 phenologies mid-summer. Coevolved changes in the timing and spread of phenologies in
459 response to change then increase competition between phenologies and cause extinctions.

460

461 **IV.2 Phenology coevolution in heterogeneous space**



462
 463 Figure 5 : Implications of dispersal for metacommunity eco-evolutionary dynamics a) Global
 464 diversity at the evolutionary equilibrium decreases with dispersal rate. b) Share of final (post-
 465 change) diversity attributable to dispersal versus local evolution for the 5 patches c) Gradient
 466 of environmental windows (thick dashed lines) and evolved phenologies (light blue) from low
 467 latitudes (left) to high latitudes (right). ($j_{1/2} \in [60,80,100,120,140]$ for (a) , $j_{1/2dep} \in$
 468 $[30,40,60,70]$ for (b))

469
 470 As a final step, we extend our eco-evolutionary model to account for spatial aspects
 471 (metacommunity). This will allow us to discuss the relative contribution of spatial dynamics
 472 (dispersal) vs local evolution in determining diversity maintenance. Our model has 5 patches
 473 along a gradient of the environmental windows (latitudinal or elevation gradient, figure 5c).
 474 Patches at the lower end of the gradient have a large environmental window (eg, temperature
 475 allows activity for a large part of the year), while at the other extreme of the gradient, the
 476 environmental windows are narrower. Local ecological and evolutionary dynamics are similar
 477 to previous sections. Phenologies have a certain probability P_m of dispersing to the adjacent
 478 patch every fixed time step dt_m . Phenologies at the edge can only migrate inward. Once the

479 metacommunity has settled on an eco-evolutionary dynamics quasi-equilibrium, we alter the
480 environmental windows to mimic global changes as we did in the previous section.
481 Before the environmental change, total diversity decreases as the dispersal rate increases
482 (figure 5a). Such increases in dispersal homogenise the competitive context at the
483 metacommunity scale. Consistent with previous metacommunity works, phenotypes that are
484 better adapted to this global context are favored, while others go extinct, which explains the
485 drop in diversity (de Mazancourt, Johnson, and Barraclough 2008; Mouquet and Loreau 2003;
486 Thompson and Fronhofer 2019).
487 We now turn to global change simulations and study whether phenologies maintained after
488 change come from another patch (dispersal contribution) vs *in situ* evolution (adaptation
489 contribution). At higher dispersal rates, the share of phenotypes resulting from dispersal
490 increases in high latitude/elevation patches 2,3,4 or 5 but decreases in the low
491 latitude/elevation patch 1 (Figure 5b). Phenologies that could have evolved on patches 2,3,4
492 to fill the new environmental window have been outcompeted by phenotypes coming from
493 lower latitudes. On patch 1 (low latitude), no pre-adapted disperser exists so that the
494 maintenance of diversity largely rely on adaptation (Figure 5b).

495

496 **VII Discussion**

497 Our simple model suggests that eco-evolutionary dynamics of competing phenologies often
498 allow the emergence of diversification, leading to communities whose diversity is constrained
499 by the available environmental window. Diversity may be partly maintained given
500 environmental changes due to evolutionary rescue, though competitive exclusion may be
501 intensified in some instances. The spatial model reveals that this maintenance of diversity
502 through local evolution is dominant at low latitudes or elevations, but that dispersal
503 contribution is dominant in other conditions.

504

505 For a fixed environment, we find that phenologies adapt to local environmental quality
506 through changes in the phenological spread while limiting similarity leads to partitioning of
507 the environmental window through evolution of different mean dates. Coevolution of the two
508 traits thereby lead to a robust pattern where long phenologies are favored early and late in the
509 year, while central phenologies are short. The empirical pattern we observe in the Swedish
510 flora is consistent with this prediction. Among these flowering plants likely sharing roughly
511 similar environmental windows, we find short flowering blooms during summer and longer
512 flowering periods at the beginning and the end of the year. Such variations may be related to
513 the abundance of pollinators, nutrient or light allowing for shorter flowering periods when
514 environments are more suitable during summer (Kehrberger and Holzschuh 2019). Short mass
515 blooming then increases the frequency of visits by pollinators (Ashman and Shoen 1996). On
516 the contrary, at the beginning of the season phenologies are more spread out. Such a spread,
517 selected in the model by competition in poor resource conditions, could be further enhanced
518 in nature as bet hedging strategy given the risks of an uncertain pollination (Kehrberger and
519 Holzschuh 2019; Rathcke and Lacey 1985). We want to stress that the study of flowering
520 phenology in Sweden is here provided as an illustration, a way to test one of the key results of
521 the model. We do not claim that such patterns will inevitably be found in nature. Among
522 pollinators in Corsica (sup fig 2), phenological spread increases linearly with the average
523 phenology date (Menegus 2018). One possibility is that the shape of the environmental
524 window differs in these locations. For instance, vegetation environmental windows seem to
525 vastly differ across Europe (Stöckli and Vidale 2004). In this article, authors observed very
526 abundant vegetation at the beginning of the season. Insect pollinators can be expected to have
527 a reduced phenology early in the year when vegetation is flourishing. However, in our model,
528 the minimum limit of phenological spread only depends on the environmental richness,

529 whereas this limit certainly also depends on physiological constraints related to development.
530 The phenologies can then be artificially infinitely fine if the environment is infinitely rich.
531 Some models explicitly take into account organism development as a function of the
532 environment (Johansson and Bolmgren 2019). This sets a more realistic minimum limit for
533 the phenological spread, but would not necessarily change our predictions.
534 Next to the hypothesis of variation in the shape of the environmental window, we want to
535 stress that the pattern we propose here is a signature of the coevolution of competing
536 phenologies. We do not expect to observe it when phenologies are mainly constrained not by
537 interspecific interactions, but directly by abiotic conditions. For instance, if late phenologies
538 were to be mostly determined by abiotic factors, competition playing a lesser role (few active
539 individuals), while competition decrease progressively in the year, we would expect an
540 increased phenological spread only late in the year, which would be consistent with the
541 pattern here reported in Corsica.
542 Our model often allows diversification, following a partitioning of the environmental window
543 that leads to a limiting similarity of phenologies, thereby reducing competition (Macarthur
544 and Levins 1967). Such a temporal partitioning of activity of species competing for common
545 resources has been reported in various contexts. Mediterranean amphibians share the use of
546 ponds for breeding (Richter-Boix, Llorente, and Montori 2006). Our competition term would
547 then correspond to competition for spawning space. In flowering plants, many examples of
548 exclusion through competition for pollinators have been shown (Willmer 2011). For systems
549 in which hybrids have low fitness (Waser 1978), competition for pollinator exclusivity may
550 cause the partitioning of phenologies. Conversely, having very distinct phenologies could be
551 indicative of limiting competition. The diversification process we report here maintains
552 various levels of diversity. We find that diversity mainly increases with the width of the
553 environmental window when spread is fixed and only phenological dates evolve. In case of

554 coevolution, diversity is not tightly linked to the width of the environmental window, but
555 rather increases the total quality of the environment. The difference has be explained by the
556 fact that high quality environments select for narrower spread, so that if spread can evolve,
557 more phenologies can be packed within the environmental window.

558 While current changes threaten biodiversity, evolution may play a key role in saving certain
559 species (evolutionary rescue, (Gomulkiewicz and Holt 1995)). It is however unclear whether
560 such a positive role of evolution may remain in a community context (Johansson 2008;
561 Loeuille 2019; Osmond and de Mazancourt 2013). For instance, in a competition context, fast
562 evolution of a phenology may allow it to outcompete neighbor phenologies. Theoretically, for
563 a given phenology, evolutionary rescue may happen due to changes on either dimensions:
564 changing dates to follow suitable conditions, or changing spread to cover more conditions.

565 Interestingly, we find that adaptive evolution tracks the new shape of the environmental
566 window mainly through the evolution of the mean date, particularly in poor environments.

567 Shifts in reproductive phenologies of plants in California towards earlier and later dates in the
568 year are similar to patterns observed in our model (Parmesan 2006; Sherry et al. 2007).

569 Phenological shifts of dates have been linked to adaptive evolution for plants (Franks, Sim,
570 and Weis 2007), for amphibians (Phillimore et al. 2010) and for pollinators (Duchenne et al.
571 2020). If this evolution is fast enough to match the speed of change, we observe an
572 evolutionary rescue of part of our community. Evolution of phenological spread can in some
573 instances lead to increased competition and diversity losses. This result is consistent with
574 earlier results emphasizing that competition can alter evolutionary rescue. (Johansson 2008).

575 Note however that competition possibly facilitates evolutionary rescue when it sufficiently
576 increases selection in the direction of environmental changes (Osmond and de Mazancourt
577 2013).

578

579 Increasing competition through the evolution of the date or spread may decrease diversity.
580 Increases of overlap of phenologies can come from antagonistic forces selecting them.
581 Asymmetries in the evolutionary potential of the different species of the community may
582 increase phenology overlap as well, potentially leading to competitive exclusion
583 (THACKERAY et al. 2010; Visser, te Marvelde, and Lof 2012). Evolutionary potentials may
584 be related to variations in population size, generation time or mutation rates (Frankham 1996).
585 Changes in phenology overlap has been reported in Texas amphibian communities possibly
586 leading to increased competition (Carter, Saenz, and Rudolf 2018). In a changing
587 environment, when species adapt while competing, some often end up outcompeting the
588 other, partly by preventing its evolution as competition lowers population sizes and
589 corresponding evolutionary potentials (Johansson 2008; Norberg et al. 2012). While these
590 phenomena are well known in a spatial context (Norberg et al. 2012; Thompson and
591 Fronhofer 2019), we propose that they also likely happen for phenological shifts.
592
593 Whether rescue of biodiversity through niche tracking may happen through dispersal or
594 adaptation depends on geographical position as well as the ability to disperse. Our model
595 suggests that at high connectivity, dispersal plays a dominant role for niche tracking
596 compared to evolutionary contribution. Increasing dispersal allows a fast redistribution of pre-
597 adapted phenologies more quickly, consistent with observations of a more general model
598 (Thompson and Fronhofer 2019). On the other hand, if no pre-adapted phenotype exists,
599 dispersal has a negative contribution. In our simulations, this happens for the low
600 altitude/elevation patch, where the role of evolution is dominant. The dominant role of
601 evolution at low latitudes is consistent with another (non phenology) model (Norberg et al.
602 2012). Consistent with this view, empirical analyses of the role of evolution in extremely hot
603 environments have been undertaken. For instance, (Sinervo et al. 2010) particularly studied

604 Mexican lizard communities and proposed that by 2050 many areas could lose all their lizard
605 diversity and favor only extremophiles (Sinervo et al. 2010). This work also suggests that the
606 evolutionary potential of these populations may be too limited to allow evolutionary rescue.
607 Because in other latitudes a dominant role of dispersal is found, this raises the question of
608 connectivity. Habitat fragmentation could affect the ability of species to disperse, creating
609 genetic isolation and decreasing colonization potentials (Clark, Lewis, and Horvath 2001;
610 Jump and Penuelas 2005). Some places like islands or the high mountain floors cannot rely on
611 dispersal and can only count on adaptive evolution (Krajick 2004; Thuiller et al. 2005). The
612 ability of species to disperse is therefore likely to vary with habitat.
613 The model we propose here is very simple and therefore has many limitations. Particularly,
614 the diversification process is linked to species competition, so that it is necessary that
615 competition plays an important structuring role for the model to apply. While competition is
616 key here, many other mechanisms could of course allow the emergence and maintenance of
617 diversity, from the specialization on a precise set of conditions that would limit the temporal
618 presence of a species, to the evolution of bet-hedging strategies in a (within year) varying
619 environment. Our model is however an invitation to consider the possible role of interspecific
620 interactions (here competition) to better understand the effect of current changes on the eco-
621 evolutionary dynamics of natural communities.

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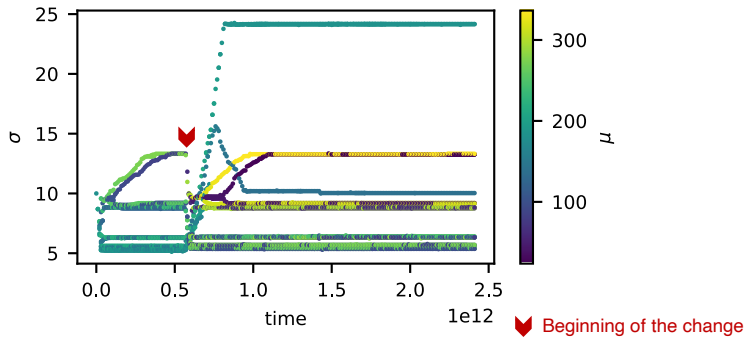
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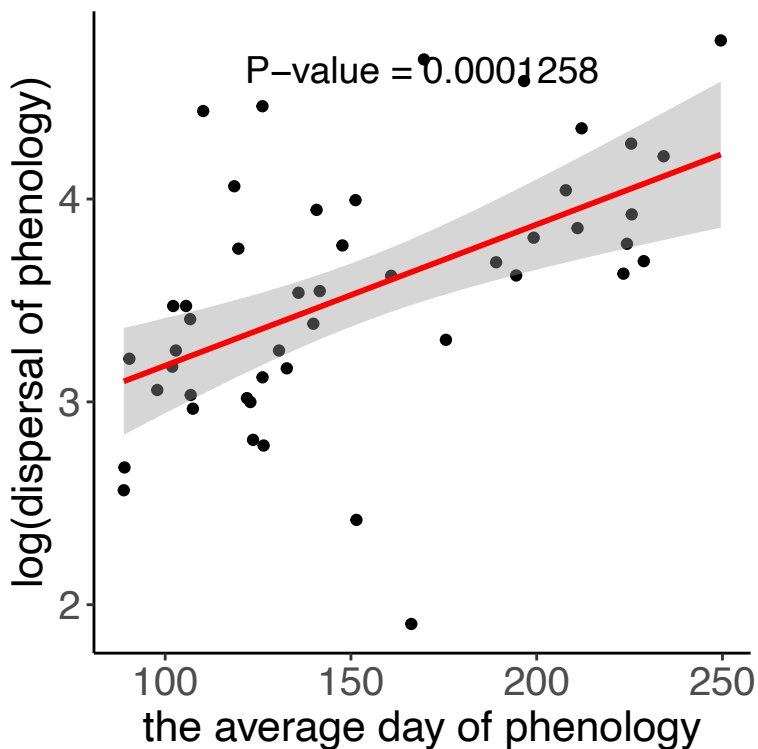
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808

809 Supplementary figure 1 : An example of coevolutionary dynamics of spread under

810 environmental changes. Variation of colors shows the associated mean date.



812 Supplementary figure 2 : Distribution of the mean date of phenology and their spread along

813 the year for pollinators of Corsica (Menegus 2018). The best fit is a linear regression model.

814 The methods used are the same that the one of figure 3c.

815

816 **Computation of the singularity for σ**

817 It is assumed that losses are minimal when the maximum of the Gaussian fits the

818 environmental window.

819 Let's take equation of the exploitation of the environment over time (2) :

820
$$g(x) = \frac{G}{\sigma 2\pi} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

821 The maximum of this function is for $x = \mu$: $g(\mu) = \frac{G}{\sigma 2\pi}$

822 At this date the richness of the environment is $P(\mu)$, under the assumption of relatively low

823 spread and not too close from the edge of the window:

824
$$g(\mu) = P(\mu)$$

825
$$\Leftrightarrow \frac{G}{2\pi\sigma} = P(\mu)$$

826
$$\Leftrightarrow \sigma = \frac{G}{2\pi P(\mu)}$$

827

828