

1 **Warming during maternal generations delays offspring germination in native and**
2 **nonnative species**

3

4 **ABSTRACT**

5 As environmental conditions shift due to global warming and other human-caused environmental
6 changes, plastic responses in phenological traits like germination or flowering time may become
7 increasingly important. While phenological plasticity is a common response to global warming,
8 with many populations exhibiting earlier germination or flowering in warmer years, warming
9 may also result in transgenerational plasticity, especially on early life stages. In other words,
10 seeds produced by mothers inhabiting warmer environments may germinate faster (or slower)
11 than seeds produced by mothers inhabiting ambient or cooler environments. Here, we use seeds
12 collected from a field warming experiment to examine how germination and early growth differ
13 in response to ambient vs. warmed (+3°C) temperatures experienced by both maternal and
14 offspring generations. Because nonnative species are often more phenotypically plastic than
15 native species and because a variety of life history traits and environmental factors affect the
16 evolution of both within- and transgenerational plasticity, we include multiple invasive and
17 native plant species in our study. On average, warming experienced during maternal generations
18 delayed germination by ~0.2 days/°C, although species varied in the magnitude of response. In
19 contrast, warming during the offspring generation tended to advance germination by ~0.1
20 days/°C. Nonnative species demonstrated higher germination success than native species, but we
21 detected no differences in germination timing between native and nonnative species or that
22 native and nonnative species differed in either within- or transgenerational plasticity, although
23 species (independent of native status) did exhibit differing degrees of within- and

24 transgenerational plasticity in germination timing and early growth. This study suggests that
25 temperatures experienced by maternal plants can influence their offspring's germination
26 phenology, potentially even more so than temperatures experienced in the offspring's immediate
27 environment.

28

29 **KEY WORDS:** biological invasions, climate change, germination, maternal effects, plasticity

30 INTRODUCTION

31 Phenotypic plasticity (i.e., the ability to vary in phenotype under different environmental
32 conditions; Pigliucci [2008]) may allow species to express advantageous phenotypes across a
33 broad range of environmental conditions (Baker 1965). Because phenotypic plasticity is a major
34 response to global warming, it potentially contributes to species success under future
35 environmental conditions (Matesanz et al. 2010, Merilä and Hendry 2014). For instance,
36 increased allocation to root mass increases water acquisition under drought (Sultan and Bazzaz
37 1993; Heschel et al. 2004), and advancing phenology under increasing temperature or nutrient
38 availability can help many plants escape stressful conditions or increase reproduction (Cohen
39 1976, Menzel et al. 2006, Power et al. 2006, Franks et al. 2007, Gugger et al. 2015,
40 Lustenhouwer et al. 2017). Thus, (within-generational) plastic responses may be beneficial for
41 plant performance under changing environments and reduce potential fitness consequences of
42 global change (Hendry et al. 2008, Nicotra et al. 2010, Lázaro-Nogal et al. 2015).

43 Transgenerational plasticity (i.e., the influence of the parental generation's environment
44 on offspring phenotypes), like within-generational plasticity, can affect fitness (survival and
45 fecundity) (Uller 2008, Snell-Rood 2013, Vayda et al. 2018) and population persistence
46 (Donelan et al. 2020). For example, transgenerational plasticity increases desiccation tolerance in
47 dog ticks (Yoder et al. 2006), drought tolerance in *Impatiens capensis* and *Polygonum persicaria*
48 (Riginos et al. 2007, Sultan et al. 2009, Herman and Sultan 2011, Herman et al. 2012), thermal
49 tolerance in minnows and sticklebacks (Salinas and Munch 2012, Shama and Wegner 2014),
50 dispersal in marine bryzoans (Burgess and Marshall 2011), and egg production in butterflies
51 (Steigenga and Fischer 2007). Transgenerational plasticity may provide a more rapid response to
52 novel environmental conditions than within-generational plasticity because maternal plants can

53 provision their offspring in a way that minimizes the stress their offspring experience (Donohue
54 and Schmitt 1998, Mousseau and Fox 1998, Dyer et al. 2010). In contrast, within-generational
55 plasticity is inherently delayed as species sense a cue and respond appropriately, so offspring still
56 experience stress (Weinig 2000, Chevin et al. 2010).

57 Both transgenerational plasticity and within-generational plasticity can affect the same
58 trait such that the offspring's phenotype depends on both the offspring environment and the
59 environment their parents experienced. In plants, for example, germination often demonstrates
60 both within- and transgenerational plasticity to temperature and light conditions experienced
61 during maternal and offspring generations in species including *Plantago lanceolata* (Lacey 1996,
62 Lacey and Herr 2000), *Leucanthemopsis alpina* (Bernareggi et al. 2016), *Brassica rapa*
63 (Wadgymar et al. 2018), and *Arabidopsis thaliana* (Blödner et al. 2007, Whittle et al. 2009,
64 Donohue 2009, Auge et al. 2017), and in *Campanula americana* seeds sown in light gaps had
65 greater germination and survival than seeds sown in shade, but only if their mother also grew in a
66 light gap (Galloway and Etterson 2007). Although transgenerational plasticity can be
67 maladaptive if environmental stress causes inferior offspring production or if parental and
68 offspring environments are not well-matched (Stearns 1992, Marshall and Uller 2007, Munday et
69 al. 2013, Munday 2014), adaptive transgenerational plasticity is predicted to evolve if the
70 parental environment is predictive of the offspring environment (Kingsolver and Huey 1998,
71 Herman et al. 2012, 2014, Burgess and Marshall 2014, Leimer and McNamara 2015, Colicchio
72 and Herman 2020). Transgenerational plasticity therefore might promote rapid responses (and
73 possible adaptation) to directional environmental change if parents can accurately convey
74 information about novel conditions to their offspring (Donelson et al. 2018, Bell and Hellmann
75 2019).

76 Although phenotypic plasticity is a common response to global change, the extent of
77 plastic responses often varies across species (Henn et al. 2018). A variety of life-history traits
78 such as self-compatibility may affect the evolution of within- and transgenerational plasticity
79 (Dury and Wade 2019), and several hypotheses speculate that phenotypic plasticity may
80 facilitate biological invasions (Sultan 2001, Wolkovich and Cleland 2011), enabling them to
81 colonize and establish in novel climates (Schlichting and Levin 1986). Indeed, nonnative species
82 often demonstrate greater within-generational plasticity than native species (Richards et al. 2006;
83 Davidson et al. 2011; but see Godoy et al. 2011). For example, nonnative species show greater
84 increases in survival and growth than native species in response to nutrient addition and high
85 light (Milberg et al. 1999, Leishman and Thomson 2004, Gleason and Ares 2004, Brock et al.
86 2005) and stronger advances in leaf-out and flowering time in response to warming (Crawley et
87 al. 1996, DeFalco et al. 2007, Resasco et al. 2007, Xu et al. 2007, Godoy et al. 2009, Willis et al.
88 2010, Pearson et al. 2012, Wolkovich et al. 2013, Wilsey et al. 2015, 2018, Zettlemoyer et al.
89 2019). Such within-generational plasticity likely affects a species' establishment and spread, i.e.,
90 its "invasiveness" (van Kleunen and Richardson 2007), and could contribute to invasion success
91 under global warming.

92 Similar to the explanations for greater within-generational plasticity in nonnative species,
93 we hypothesize that nonnative species may also express greater transgenerational plasticity than
94 native species for two reasons. First, transgenerational plasticity can more rapidly increase stress
95 tolerance and fitness in offspring than within-generational plasticity. This could promote
96 establishment of nonnative species in stressful habitats or result in more rapid population spread
97 for widespread nonnatives (i.e., invasive species). For example, in nonnative *Cyperus esculentus*,
98 maternal responses to nutrient-poor soil conditions promoted greater propagule dispersal in the

99 next generation (Dyer et al. 2010). Second, nonnative species are more often self-compatible
100 than native species (Baker 1955, Razanajatovo et al. 2016), and selfing makes transgenerational
101 plasticity more likely to evolve (Dury and Wade 2019). Together, this suggests that nonnative
102 species may be particularly likely to have greater transgenerational plasticity.

103 Here, we use seeds collected from a field warming experiment at the W.K. Kellogg
104 Biological Station (KBS) to examine transgenerational and within-generation plasticity in
105 response to warming in a suite of grassland species. Although we use the general term
106 “transgenerational plasticity”, which includes non-genetic inheritance, parental effects, carry-
107 over effects, intergenerational effects, seed provisioning, and epigenetic transmission (Donelson
108 et al. 2018), we specifically test the effect of the maternal environment on offspring phenotypes,
109 or maternal effects (Roach and Wulff 1987). We focus on early phenological and growth traits
110 because both within- and transgenerational phenological plasticity (i.e., shifts in the timing of
111 life-history events like germination and flowering) may be especially important responses for
112 species success under climate change (Jump and Peñuelas 2005; Merilä and Hendry 2014;
113 Bonamour et al. 2019) and because germination timing can be plastic (see above) and is linked to
114 plant fitness (Kalisz 1986, Donohue 2002, Donohue et al. 2010, Cochrane et al. 2015, Leverett et
115 al. 2018). Similarly, offspring growth often demonstrates transgenerational plasticity (Agrawal
116 2001; Galloway and Etterson 2007; Sultan et al. 2009; Latzel et al. 2010), potentially providing
117 offspring an advantage in stressful conditions (Moles and Westoby 2006; Herman and Sultan
118 2011). Because nonnative species exhibit greater plasticity in flowering time than native species
119 in this (Zettlemyer et al. 2019) and other systems (Grman and Suding 2010, Wainwright and
120 Cleland 2013, Balshor et al. 2017, Wilsey et al. 2018) and to test whether patterns of within- and
121 transgenerational plasticity in germination and early growth are generalizable across native and

122 nonnative species, we include multiple native and nonnative species in this study. This work
123 extends studies investigating transgenerational plasticity in germination timing in response to
124 temperature, which has largely been tested in single species, by examining whether
125 transgenerational plasticity to warming is consistent across species and whether it differs
126 between native and nonnative taxa. We ask: Do germination and early growth demonstrate
127 within- or transgenerational plasticity and if so, do native and nonnative species differ in their
128 within- or transgenerational responses to warming temperatures?

129 **MATERIALS & METHODS**

130 To assess the roles of within- and transgenerational plasticity and their interaction on
131 germination and early growth of grassland species in response to warming, we planted seeds
132 from maternal plants that had been grown under an experimental warming simulation in the field
133 into warmed and ambient growth chamber conditions in a full factorial design (maternal
134 temperature environment \times offspring temperature environment). Although each generation
135 experienced different degrees of environmental control (i.e., maternal plants were grown in the
136 field while offspring were grown in potting soil in a growth chamber), this design is common for
137 testing maternal effects on germination (Galloway and Etterson 2007).

138 *Maternal temperature environment*— The simulated warming array in the field uses
139 infrared heaters to elevate temperatures 3°C above ambient temperatures, matching regional
140 predictions for climate warming in this area by the end of the 21st century (0.3°C-4.8°C) (Stocker
141 et al. 2013). Warmed plots also have lower soil moisture (percent water content) than ambient
142 plots (warming $\chi^2_{1,6}=34.02$, $p<0.0001$; ambient = 16.2% vs. warmed = 9.31% water). The array
143 has run over the growing season (April-October) since 2008. In spring 2012, we planted 52
144 species (25 native and 27 nonnative) into the old field community in each plot ($n=3$

145 replicates/species/plot \times 4 plots/warming treatment), although only the 24 species (13 native and
146 11 nonnative) that successfully produced viable seeds in both warming treatments are used here
147 (see below). Study species were forb and grass species found in old fields or grasslands
148 (Schultheis et al. 2015). We define native species as species naturally occurring in Michigan
149 prior to European settlement and nonnative species as species introduced to Michigan from
150 outside the United States. For a full description of the simulated warming experiment, see
151 Zettlemoyer et al. (2019). In this system, nonnative species exhibit advanced flowering
152 phenology relative to native species and accelerate flowering in response to warming more so
153 than native species, although prior studies did not investigate other phenological stages like
154 germination timing (Zettlemoyer et al. 2019). However, because the study species are perennial,
155 we focused on early growth stages and did not grow plants to flowering for this experiment (see
156 below).

157 To determine which plants produced viable seeds, we conducted germination trials using
158 seeds from plants collected from the simulated warming experiment in the greenhouse (n=41
159 species; 21 native and 20 nonnative) (greenhouse conditions were 29°C with a 16-hour
160 photoperiod). Seeds were collected from the field in 2013 and stored in a cool, dark cabinet until
161 2019. However, we did not account for variable dormancy requirements among species (e.g.,
162 stratification), potentially limiting germination and restricting our experiment to those species
163 with lax germination requirements. We planted seeds in low-nutrient potting media (Sunshine
164 Mix LP5) and monitored daily seedling emergence over six weeks. 24 species (13 native and 11
165 nonnative) successfully germinated in the greenhouse. We included all species with at least 20%
166 germination in an attempt to boost the number of native species included in our study. For each
167 of those 24 species, we selected seeds from 3-5 individuals grown under ambient field maternal

168 conditions and another 3-5 individuals grown under warmed field maternal conditions. When
169 possible, we elected to use seeds from maternal plants from different field plots. We ended up
170 with 116 total maternal plants spanning the 24 species (3-5 individuals per maternal environment
171 per species).

172 *Offspring temperature environment*— To set growth chamber/offspring temperature
173 conditions, we collected daily maximum and minimum temperatures from 01-Apr-2013 thru 30-
174 June-2013 (approximately the time period when germination occurs in the field) from the
175 CLIMOD database (<http://climod2.nrcc.cornell.edu/>). We used these day and night temperature
176 extremes observed in the field dataset to program daily temperature curves for each growth
177 chamber (Percival Scientific, Perry, IA, USA), with the warmed chamber set to be consistently
178 3°C warmer than the ambient chamber. Day length was set at 14 hours, roughly matching
179 photoperiod in the field. This design allows us to separate effects of maternal temperatures (i.e.,
180 temperatures experienced during seed maturation in the field) vs. offspring temperatures (i.e.,
181 temperatures experienced post-dispersal in the growth chamber) (Burghardt et al. 2015).

182 We planted three seeds from each maternal plant into separate containers (SC10 Ray
183 Leach containers, Stuewe & Sons Inc., Tangent, OR, USA) filled with low-nutrient potting
184 media (Sunshine Mix LP5, BFG Supply, Kalamazoo, MI, USA) and placed them into ambient
185 and warmed growth chambers (n=3 replicates × 116 maternal plants × 2 chamber temperatures =
186 696 seedlings). We rotated trays between chambers every three days to minimize chamber
187 effects and watered as needed to maintain similar moisture levels between treatments.
188 Germination (indicated as cotyledon emergence) was recorded daily. We measured seedling
189 height (the longest leaf; cm) at the end of the experiment.

190 *Data analysis*

191 To examine whether native and nonnative species' germination and early growth
192 (seedling height) demonstrate within- or transgenerational plasticity in response to temperature,
193 we used generalized linear mixed models fit in the lme4 package in R v.3.0.2 (Bates et al. 2015,
194 R Core Development Team 2015). We conducted three models with three separate response
195 variables: (1) germination success (1=yes, 0=no; binomial distribution), (2) days to germination
196 (negative binomial distribution for overdispersed count data; Lindén and Mäntyniemi 2011),
197 excluding ungerminated seeds, and (3) seedling height (cm; Gaussian distribution). For
198 germination success, we included maternal temperature environment (E_M ; ambient vs. warmed
199 field conditions), offspring temperature environment (E_O ; ambient vs. warmed chamber
200 conditions), status (native vs. nonnative), and their interactions as predictor variables. We
201 included species (nested within status) and field plot (nested within maternal environment) as
202 random effects. For days to germination and seedling height, we only included species that
203 successfully germinated in all temperature combinations (n=3 native and 5 nonnative species).
204 Due to resulting low sample sizes, we could not test interactions between maternal and offspring
205 environments. We instead ran two models for each response variable, one for (i)
206 transgenerational plasticity and another for (ii) within-generational plasticity. Models for (i)
207 transgenerational plasticity included status, E_M , and status $\times E_M$ as predictor variables and
208 species (nested within status) and plot (nested within E_M) as random effects. Models for (ii)
209 within-generational plasticity were identical but included E_O instead of E_M . For seedling height
210 models, because seedling height depends on germination time, we first regressed height against
211 days to germination for each species. We subsequently used the residuals as the response
212 variable for the third model, thereby removing variation in height due to differences in

213 germination phenology. We provide the results of models using height as a response variable in
214 Appendix Table A1 (results are qualitatively similar).

215 We used similar models to examine variation in within- and transgenerational plasticity
216 in germination success, germination timing, and seedling height among species regardless of
217 status. For germination success, we included species, E_M , E_O , and their interactions as predictor
218 variables, with plot (nested in E_M) as a random effect. For days to germination and seedling
219 height (residuals), we again only included the eight species that successfully germinated in all
220 temperature combinations. Like above, we ran two models each for days to germination and
221 seedling height, one for (i) transgenerational and another for (ii) within-generational plasticity.
222 These models, respectively, included (i) species, E_M , and species $\times E_M$ and (ii) species, E_O , and
223 species $\times E_O$ as predictor variables. We included field plot (nested in E_M) as a random effect in
224 all models. Following significant interactions between species $\times E_M$ and species $\times E_O$ for days to
225 germination and seedling height (see Results), we conducted individual species models. For
226 species with sufficient sample sizes, we examined the effects of E_M , E_O , and the interaction of
227 $E_M \times E_O$ on days to germination and seedling height. For species with low sample sizes where
228 $E_M \times E_O$ could not be estimated, we removed the interaction and only tested the main effects of
229 maternal and offspring temperatures. Field plot (nested in E_M) was included as a random effect in
230 all individual species models. Individual species models were not conducted for germination
231 success because we detected no evidence for species-specific responses to temperature (see
232 Results).

233 Finally, to investigate whether and how plasticity in germination timing is associated
234 with plasticity in other phenological stages, we compared both within- and transgenerational
235 plasticity in germination timing found here to within-generational plasticity in flowering time

236 from Zettlemoyer et al. (2019) (again using only the eight species that germinated in every
237 temperature combination). Within-generational phenological plasticity was calculated as the
238 difference in mean offspring phenotype (\bar{X} ; i.e., germination timing or flowering time) when
239 offspring experienced warmed vs. ambient temperatures (Valladares et al. 2006):

$$240 \quad \textit{Within - generational phenological plasticity} = X_{\textit{offspring.warmed}} - X_{\textit{offspring.ambient}}$$

241 Transgenerational phenological plasticity was calculated as the difference in mean offspring
242 phenotype when maternal plants experienced warmed vs. ambient temperatures:

$$243 \quad \textit{Transgenerational phenological plasticity} = X_{\textit{maternal.warmed}} - X_{\textit{maternal.ambient}}$$

244 We used differences for phenological plasticity because proportional responses for
245 phenological estimates would cause later flowering individuals to appear to be less plastic when
246 they could in fact be advancing flowering time as much as early flowering individuals.

247 We calculated within-and transgenerational plasticity in early growth as the proportional
248 difference in mean offspring phenotype (seedling height) when offspring or maternal plants
249 (respectively) experienced warmed vs. ambient temperatures:

$$250 \quad \textit{Within - generational plasticity in early growth} = \frac{X_{\textit{offspring.warmed}} - X_{\textit{offspring.ambient}}}{X_{\textit{offspring.ambient}}}, \text{ and}$$

$$251 \quad \textit{Transgenerational plasticity in early growth} = \frac{X_{\textit{maternal.warmed}} - X_{\textit{maternal.ambient}}}{X_{\textit{maternal.ambient}}}$$

252 We averaged responses to temperature within generations because we detected no
253 interactions between maternal and offspring temperatures (see Results). We then estimated
254 Pearson's correlations among within-generational plasticity in flowering time, within-
255 generational plasticity in germination timing, transgenerational plasticity in germination timing,
256 within-generational plasticity in early growth (seedling height), transgenerational plasticity in
257 early growth, and mean early growth.

258 **RESULTS**

259 Nonnative species tended to be approximately twice as likely to germinate than native
260 species (status $\chi^2_{1,0.005}=3.30$, $p=0.06$; Table A2; Fig. 1). We detected no evidence that
261 temperatures experienced by either maternal or offspring generations affected germination
262 success in native or nonnative species or across species (all $E_M \times$ status {or species} and $E_O \times$
263 status {or species} interactions, $p>0.5$, Table A2-A3).

264 Species varied in their germination timing responses to warming during maternal
265 generations ($E_M \times$ species $\chi^2_{7,202}=17.56$, $p=0.02$; Table A3). On average, warmer temperatures
266 experienced during the maternal generation delayed germination by 0.20 ± 0.1 days/ $^{\circ}\text{C}$ relative
267 to ambient temperatures ($E_M \chi^2_{1,5.86}=3.58$, $p=0.05$; Fig. 2a). Three native species, *Achillea*
268 *millefolium*, *Panicum virgatum*, and *Coreopsis lanceolata*, and two nonnative species, *Dactylis*
269 *glomerata* and *Gaillardia pulchella*, demonstrated this pattern, with all other species not
270 responding significantly to maternal temperature environments (E_M : AM $\chi^2_{1,13}=3.09$, $p=0.07$; CL
271 $\chi^2_{1,3.24}=5.91$, $p=0.01$; PV $\chi^2_{1,5}=4.09$, $p=0.04$; DG $\chi^2_{1,16.81}=4.65$, $p=0.03$; GP $\chi^2_{1,3}=5.66$, $p=0.02$;
272 Table 1; Fig. 2b).

273 In contrast, germination timing responses to offspring warming were much weaker and
274 did not vary substantially across species (E_O : effect size = -0.11 ± -0.10 days/ $^{\circ}\text{C}$ earlier under
275 warmed relative to ambient temperatures; $\chi^2_{1,190.37}=1.14$, $p=0.2$; Table A2; Fig. 2c; species $\times E_O$
276 $\chi^2_{7,202}=7.31$, $p=0.4$; Table A3). Native *Coreopsis lanceolata* and nonnative *Dactylis glomerata*,
277 *Hypericum perforatum*, and *Phleum pratense* germinated earlier under warmed relative to
278 ambient offspring temperatures, but no other species responded significantly to offspring
279 temperatures (E_O : CL $\chi^2_{1,2.01}=11.17$, $p=0.0008$; DG $\chi^2_{1,47.74}=2.15$, $p=0.1$; HP $\chi^2_{1,18.27}=4.15$,
280 $p=0.04$; PP $\chi^2_{1,44.73}=2.44$, $p=0.1$; Table 1; Fig. 2d). We detected no consistent differences in

281 germination phenology between native vs. nonnative species in response to temperatures
282 experienced by either generation (Table A2).

283 Warming during both maternal and offspring generations affected plant height, although
284 the direction of effects varied across species (species \times E_M: $\chi^2_{7,184.68}=32.82$, $p<0.0001$; species \times
285 E_O: $\chi^2_{7,184.22}=13.57$, $p=0.05$; Table A3; Fig. 3). On average, seedlings tended to grow more
286 rapidly than expected under warmed relative to ambient offspring environments (E_O:
287 $\chi^2_{1,192.93}=3.23$, $p=0.07$; Fig. 3c; Table A2), with three nonnative species, *Dactylis glomerata*,
288 *Gaillardia pulchella*, and *Poa compressa*, growing significantly more rapidly under warmed
289 offspring conditions (DG: $\chi^2_{1,53}=6.41$, $p=0.01$; GP $\chi^2_{1,3}=6.35$, $p=0.01$; PC $\chi^2_{1,41.09}=5.55$, $p=0.02$;
290 Table 1; Fig. 3d). However, native *C. lanceolata* and nonnative *Hypericum perforatum* grew
291 more slowly under warmed temperatures (CL $\chi^2_{1,2.10}=22.59$, $p<0.0001$; HP $\chi^2_{1,18.72}=7.29$,
292 $p=0.007$). Seedling height responses to maternal temperature conditions were weaker, with only
293 native *Coreopsis lanceolata* responding significantly to the maternal temperature environment. It
294 grew more slowly than expected (i.e., seedlings were shorter than expected after controlling for
295 differences in height due to variation in germination phenology) under ambient relative to
296 warmed maternal environments ($\chi^2_{1,3.40}=78.65$, $p<0.0001$). As with germination timing, we
297 detected no evidence that native and nonnative taxa differed in within- or transgenerational
298 plasticity in height.

299 *Correlations among plasticity in germination and flowering phenology*

300 Within-generational plasticity in germination timing, transgenerational plasticity in
301 germination timing, and plasticity in flowering time were not correlated (Fig. A2), with one
302 possible exception. Within-generational plasticity in germination timing was negatively
303 correlated with within-generational plasticity in early-growth ($r=-0.84$, $p=0.006$; Fig A2f),

304 suggesting that species that are more plastic in their germination timing in response to
305 temperatures experienced as offspring are less plastic in their growth rates.

306 **DISCUSSION**

307 *Effects of warming temperatures on germination phenology*

308 Consistent with the few prior investigations of maternal warming, we found that warming
309 experienced during the maternal generation, on average, delayed germination in the offspring
310 generation. For example, warming during maternal generations results in delayed bud burst in
311 *Populus nigra* (Dewan et al. 2018), and shorter winters as a result of warming temperatures can
312 also delay offspring germination (Walck et al. 2011). Similarly, stressful or unfavorable
313 conditions during maternal generations delay germination in species such as *Arabidopsis*
314 *thaliana* (Donohue et al. 2005), *Pinus pinaster* (Cendán et al. 2013), and *Banksia* species
315 (Cochrane et al. 2014) (but see Moriuchi et al. 2016, Walter et al. 2016). If warmed
316 environments are similarly stressful, then delayed germination in response to warming
317 temperatures experienced by maternal plants may reflect this stress response. Such responses
318 could be adaptive and a strategy to avoid future stressful conditions (i.e., predictive plasticity or
319 predictive germination) (Cohen 1967, Gremer et al. 2016), if delayed germination reduces the
320 likelihood of experiencing conditions with catastrophic fitness effects (e.g., frost; Milbau et al.
321 2009). Delaying germination in stressful environments is also predicted to reduce the risk of all
322 seeds germinating into an unfavorable environment, thereby reducing temporal variation in
323 fitness (Clauss and Venable 2000, Simons 2011, Gremer and Venable 2014, Gremer et al. 2016).
324 However, these hypotheses require future work investigating whether delayed germination in
325 response to warming parental environments corresponds with higher fitness under warming
326 temperatures.

327 In contrast to our finding of delayed germination in response to maternal warming,
328 warming during the offspring generation has minimal effects, but tended to act in the opposite
329 direction by advancing germination phenology as might be expected given many species'
330 temperature cues for germination. The three species responding significantly to warming during
331 the offspring generation all responded by advancing germination. Other studies frequently detect
332 advancing germination (Milbau et al. 2009, Zettlemyer et al. 2017), leaf-out (Basler & Körner
333 2014, Geng et al. 2020) and flowering under warmer conditions (Fitter and Fitter 2002,
334 Parmesan and Yohe 2003, Thackeray et al. 2016). Earlier germination can provide earlier access
335 to resources like space, water, and light via priority effects (Wolkovich and Cleland 2011,
336 Wainwright et al. 2012), allows for earlier growth relative to other species in the community
337 (Dickson et al. 2012, Fridley 2012, Wilsey et al. 2015), and can increase chances of surviving to
338 reproduction (Leverett et al. 2018) and enhance plant fitness (Verdú and Traveset 2005).
339 However, as climate change continues to alter local environmental conditions in a directional
340 manner, mismatched responses between maternal and offspring generations, as detected here,
341 could reduce plant fitness by counteracting one another and minimizing the phenological
342 response.

343 *Correlations among plasticity in germination and flowering phenology*

344 Overall, our results suggest that plasticity in one life-history stage does not predict
345 plasticity in another. If plasticity in germination timing and flowering time are truly not
346 correlated, these traits could evolve separately in response to local environmental conditions as
347 opposed to representing a correlated response to warming temperatures (Burgess et al. 2007).
348 However, multiple species demonstrated consistent patterns in phenological plasticity across life-
349 history stages; *Coreopsis lanceolata*, *Hypericum perforatum*, *Dactylis glomerata*, and *Phleum*

350 *pratense* all tended to advance flowering under warming (Zettlemoyer et al. 2019) and also
351 tended to advance germination timing under warmed offspring environments. Some of these
352 species also demonstrated transgenerational plasticity. For one species (*P. virgatum*),
353 germination responses to maternal warming were in the same direction as flowering responses to
354 warming temperatures (i.e., a tendency for delayed flowering and germination in response to
355 warming in both generations), but for the other (*C. lanceolata*), the transgenerational response
356 opposed both within-generational germination plasticity and flowering plasticity to warming
357 (i.e., maternal warming delayed germination while offspring warming accelerated both
358 germination and flowering).

359 *Differences between native and nonnative species*

360 In contrast to previous studies detecting earlier and more plastic germination phenology
361 in nonnative species than natives in response to rising temperatures (Gerlach and Rice 2003,
362 Seabloom et al. 2003, Resasco et al. 2007, Xu et al. 2007, Abraham et al. 2009, Grman and
363 Suding 2010, Wainwright and Cleland 2013, Balshor et al. 2017, Wilsey et al. 2018; reviewed in
364 Gioria and Pyšek 2017), we detected no differences in germination phenology between the native
365 and nonnative species studied here in response to either maternal or offspring temperatures,
366 although we had limited power (eight species) to detect such effects. Similar germination
367 phenology between native and nonnative species has been observed in *Impatiens* species (Laube
368 et al. 2015) and between native vs. nonnative populations of *Hieracium pilosella* and *Hypericum*
369 *perforatum* (Beckmann et al. 2011). Other species characteristics beyond native or invasive
370 status are also predicted to influence the evolution of transgenerational plasticity. For example,
371 theory predicts that self-incompatibility should correlate with lower transgenerational plasticity
372 (Dury and Wade 2019). Counter to this prediction, all four species that demonstrated

373 transgenerational plasticity in our study by delaying germination under maternal warming are
374 self-incompatible (Table A4). While a greater complement of species would be needed to
375 rigorously test the association between mating system and transgenerational plasticity, it is
376 possible that the transgenerational plasticity observed here is a maladaptive stress response,
377 rather than the adaptive transgenerational plasticity modeled in Dury and Wade (2019).

378 Similar to the germination timing results, we also detected no evidence that nonnative
379 species exhibited more plastic growth responses to warming. However, three of the six nonnative
380 species studied here (*Dactylis glomerata*, *Gaillardia pulchella*, and *Poa compressa*)
381 demonstrated within-generational plasticity to warming temperatures via greater early growth.
382 While this result in part supports previous findings suggesting that invasive species' growth and
383 fitness increase under warming conditions (Parker-Allie et al. 2009; Verlinden and Nijs 2010;
384 Compagnoni and Adler 2014) potentially providing invasive species with an advantage under
385 climate change (Hellmann et al. 2008), it also suggests that these growth benefits are not
386 pervasive and that warming may lead to increased success of some, but certainly not all,
387 invasives.

388 Nonnative species had a higher probability of germination than native species regardless
389 of temperature, consistent with other studies comparing germination success in native vs.
390 nonnative species (Colautti et al. 2006, Beckmann et al. 2011, Wainwright and Cleland 2013,
391 Balshor et al. 2017). On one hand, this could be due to harvesting time: native species flower
392 later in this system, and some of the latest flowering species (e.g., *Aster pilosis* and *Solidago*
393 *canadensis*) likely had less-ripe seeds at collection. We checked for seed viability using
394 tetrazolium assays; similar percentages of seeds were viable in native vs. nonnative species
395 (although nonnative species tended to have more viable seeds; Table A4; status $\chi^2_{1,34}=2.25$,

396 $p=0.14$), suggesting that differences in seed viability did not influence our results. Alternatively,
397 this could be due to higher thresholds for breaking dormancy in native species, wherein seeds
398 require a cold period (i.e., vernalization) and an environmental cue that conditions are suitable
399 for germination and growth (Fenner and Thompson 2005, Baskin and Baskin 2014). Future
400 studies should account for species differences in requirements to break dormancy (e.g.,
401 stratification, diurnal vs. nocturnal temperatures, photoperiod). We did not include a
402 stratification treatment in this study, which could limit germination success (Munir et al. 2001).
403 However, as temperatures warm, native species may be less likely to experience sufficient
404 vernalization (Murray et al. 1989, Schwartz and Hanes 2010, Cook et al. 2012, Fu et al. 2015).
405 Additionally, nonnative species may have broader germination requirements than native species
406 (Gioria and Pyšek 2017), so future work should test whether the invasive species have similarly
407 high germination success in field conditions. Ultimately, higher germination success in
408 nonnative species suggests that germination could increase nonnative species' population growth
409 rates relative to native species because germination plays an important role in determining
410 population growth rates (Picó 2012, Leverett et al. 2018).

411 *Conclusions*

412 We find that maternal warming delays germination and that warmed temperatures
413 experienced during the offspring generation tend to advance germination, although this latter
414 pattern is weaker and not statistically significant. Our results indicate that temperatures
415 experienced by maternal plants can impact their offspring's germination phenology, potentially
416 even more so than temperatures experienced by the offspring themselves. This study furthers our
417 understanding of both within- and transgenerational plasticity to temperature during early life-

418 history stages, but future work is needed to understand potential benefits or consequences of
419 delayed germination under maternal warming.

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429 **Data accessibility** – Upon publication, all data for this study will be available as .csv files in the
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746

747 **TABLES**

748 **Table 1. Species-specific models for the effect of maternal and offspring temperatures on**
749 **germination and early growth.** Results of generalized linear mixed models (GLMMs) for
750 individual species' germination success (1=yes, 0=no; binomial distribution), (B) germination
751 timing (days to germination; negative binomial distribution), and (C) height (residuals after
752 controlling for germination timing; Gaussian distribution). We included offspring environment
753 (E_O ; ambient vs. warmed chamber conditions), maternal environment (E_M ; ambient vs. warmed
754 field conditions), and their interaction as fixed predictor variables (where possible). Plot (nested
755 in maternal environment) was included as a random effect in each model. "--" indicates that a
756 parameter was not estimated due to low power. *** $p \leq 0.0001$, ** $p \leq 0.01$, * $p \leq 0.05$, · $p \leq 0.1$ (bold
757 indicates $p \leq 0.1$).

Species	Germination timing χ^2			Height (residuals) χ^2		
	E_O	E_M	$E_M \times E_O$	E_O	E_M	$E_M \times E_O$
<i>Natives</i>						
<i>Arabis glabra (AG)</i>	2e ⁻⁰⁴	3e ⁻⁰⁴	2e ⁻⁰⁴	0.00	3e ⁻⁰⁴	2e ⁻⁰⁴
<i>Achillea millefolium (AM)</i>	0.18	3.09 ·	1.44	0.00	0.00	0.25
<i>Coreopsis lanceolata (CL)</i>	11.18 ***	5.91 *	NA	22.59 ***	78.66 ***	NA
<i>Penstemon hirsutus (PH)</i>	--	--	--	--	--	--
<i>Panicum virgatum (PV)</i>	0.03	4.09 *	--	0.00	0.79	--
<i>Nonnatives</i>						
<i>Bromus inermis (BI)</i>	--	--	--	--	--	--
<i>Leucanthemum vulgare (LV)</i>	--	--	--	--	--	--
<i>Centaurea maculosa (CM)</i>	--	--	--	--	--	--
<i>Dianthus armeria (DA)</i>	0.62	0.06	0.21	0.09	0.29	1.02
<i>Dactylis glomerata (DG)</i>	0.28	4.65 *	2.15	6.41 *	1.08	0.03
<i>Gaillardia pulchella (GP)</i>	0.32	5.66 *	--	6.35 *	0.45	--

<i>Hypericum perforatum (HP)</i>	4.15 *	1.51	--	7.29 **	0.05	--
<i>Melilotus officinalis (MO)</i>	--	--	--	--	--	--
<i>Poa compressa (PC)</i>	0.25	0.03	0.11	5.55 *	0.19	0.01
<i>Phleum pratense (PP)</i>	2.44 ·	0.47	0.02	0.00	0.00	0.98

758

759 **FIGURE LEGENDS**

760 **Figure 1.** Germination success (proportion of seeds germinated; least square means \pm standard
761 error) under ambient vs. warmed ($+3^{\circ}\text{C}$) maternal environments (x-axis) and ambient (blue) vs.
762 warmed (orange) offspring environments in native (left) vs. nonnative (right) species.

763 **Figure 2.** Days to germination under ambient (blue) vs. warmed ($+3^{\circ}\text{C}$; orange) (a) maternal
764 environments or (c) offspring environments. (b) and (d) show species-specific response to
765 maternal and offspring temperatures, respectively. Native species are indicated with asterisks and
766 green lines while nonnative species are indicated with purple lines. An asterisk within a bracket
767 indicates that species differed in germination timing between ambient vs. warmed temperatures
768 (Tukey tests, $\alpha=0.05$), where $***p<0.0001$, $*p<0.05$, $\S p<0.1$. We provide sample sizes in the top
769 species panels.

770 **Figure 3.** Residuals of seedling height (cm; after removing variation due to days to germination)
771 under ambient (blue) vs. warmed ($+3^{\circ}\text{C}$; orange) temperatures experienced during (a) maternal
772 or (c) offspring generations. (b) and (d) show species-specific response to maternal and offspring
773 temperatures, respectively. Positive residual values indicate more rapid growth (i.e., taller
774 seedlings) than expected based on germination timing. Native species are indicated with asterisks
775 and green lines while nonnative species are indicated with purple lines. An asterisk within a
776 bracket indicates that species differed in early growth between ambient vs. warmed temperatures
777 (Tukey tests, $\alpha=0.05$), where $***p<0.0001$, $*p<0.05$, $\S p<0.1$.

FIGURES

Figure 1.

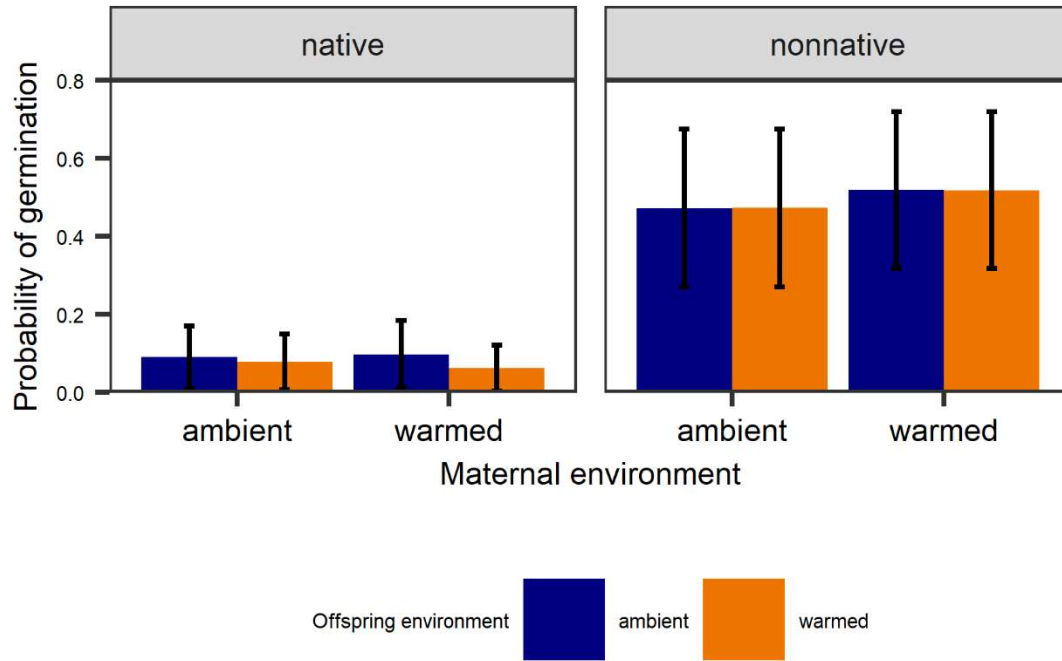


Figure 2.

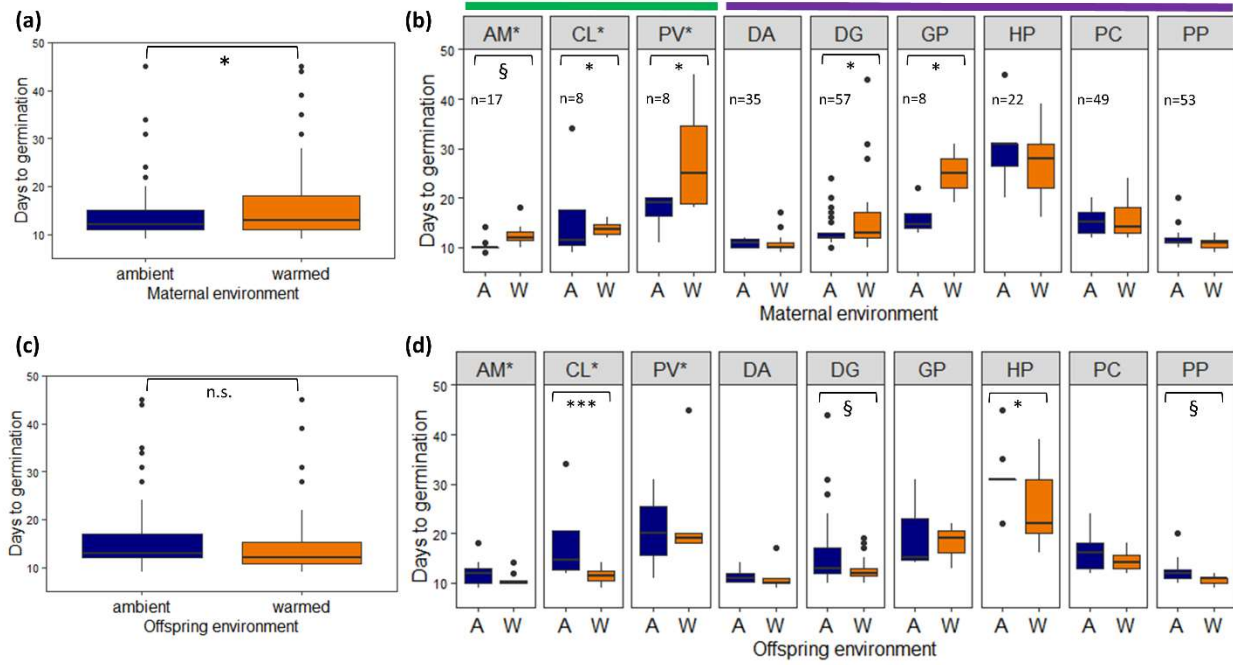


Figure 3.

