

1 **Running head:** Plant evolution in thermal soils

2 **The impact of microclimate and soil on the ecology and evolution of an arctic plant**

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20 plasticity, soil temperature

21

22 **Abstract**

23 The arctic and alpine regions are predicted to experience one of the highest rates of climate
24 change, and the arctic vegetation is expected to be especially sensitive to such changes.
25 Understanding the ecological and evolutionary responses of arctic plant species to changes in
26 climate is therefore a key objective. Geothermal areas, where temperature gradients naturally
27 occur over small spatial scales, and without many of the confounding environmental factors
28 present in latitudinal and other gradient studies, provide a natural experimental setting to
29 examine the impact of temperature on the response of arctic-alpine plants to increasing
30 temperatures. To test the ecological and evolutionary response of the circumpolar alpine
31 bistort (*Bistorta vivipara*) to temperature, we collected plant material and soil from areas with
32 low, intermediate, and high soil temperatures and grew them in all combinations at three
33 different temperatures. At higher experimental soil temperatures, sprouting was earlier, and
34 plants had more leaves. Sprouting was earlier in soil originating from intermediate
35 temperature and plants had more leaves when grown in soil originating from low
36 temperatures. We did not find evidence of local adaptation or genetic variation in reaction
37 norms among plants originating from areas with low, intermediate, and high soil temperature.
38 Our findings suggest that the alpine bistort has a strong plastic response to warming, but that
39 differences in soil temperature have not resulted in genetic differentiation. The lack of an
40 observed evolutionary response may, for example, be due to the absence of temperature-
41 mediated selection on *B. vivipara*, or high levels of gene flow balancing differences in
42 selection. When placed within the context of other studies, we conclude that arctic-alpine
43 plant species often show strong plastic responses to spring warming, while evidence of
44 evolutionary responses varies among species.

45

46 **Introduction**

47 Warming in the Arctic is predicted to be particularly strong (Pachauri et al. 2015). This
48 increase in temperature may have a major impact on the phenology, growth and reproduction
49 of arctic plants, whose life cycles are strongly influenced by seasonal shifts in temperature
50 (Henry and Molau 1997, Callaghan et al. 2004, Gornish and Prather 2014, Semenchuk et al.
51 2015). To predict the long-term effects of increasing temperatures on the arctic flora, it is
52 important to understand both immediate and evolutionary responses. For example, plant
53 individuals may respond plastically and advance development in response to increasing
54 spring temperatures (Anderson et al. 2012). At the same time, overall increases in
55 temperatures might lead to changes in how strong the optimal response of development to
56 temperature should be, and to evolutionary responses in reaction norms (Valdés et al. 2018).
57 To study the response of arctic plants to increasing temperature, studies commonly use
58 experiments with open-top climate chambers (Arft et al. 1999, Wolkovich et al. 2012), or
59 sample plants growing along altitudinal (Frei et al. 2014) and latitudinal gradients
60 (Toftegaard et al. 2016). Such methods have limitations, with the time-scale of experimental
61 work often too short to observe evolutionary responses, and changes in temperature along
62 altitudinal and latitudinal gradients often occurring alongside changes in other environmental
63 factors. Given these limitations, geothermal systems, where radiation heating causes small
64 scale variation in temperature but not in other environmental variables (O’Gorman et al.
65 2014, Sigurdsson et al. 2016), offer an alternative setting where plastic and evolutionary
66 responses to temperature can be explored (Gudmundsdottir et al., 2011; O’Gorman et al.,
67 2014; Sigurdsson et al., 2016; Valdés et al., 2018). For example, Iceland has many naturally
68 occurring geothermal areas, where volcanic activity close to the surface warms water and soil
69 through radiation heating (Gudmundsdottir et al. 2011, Zakharova and Spichak 2012). In

70 such geothermal areas, plants of the same species frequently grow side-by-side in heated and
71 non-heated soil.

72 Plasticity allows plants to grow under variable conditions and to respond to changes
73 in the environment (Agrawal 2001). For example, plants often germinate earlier and grow
74 larger at higher temperatures (Anderson et al. 2012). The optimal plastic response of plants is
75 likely to differ depending on their local environmental conditions (Grether 2005). If there is
76 genetic variation in plasticity, we would thus expect selection to result in reaction norms that
77 are locally adapted (Valdés et al. 2018). For example, plants that have evolved in a low-
78 temperature environment may rapidly germinate, flush leaves or flower in response to
79 warming in spring, whereas plants from a high-temperature environment may respond more
80 slowly to spring warming. Indeed, previous studies have found that plants from geothermally
81 heated areas have an earlier spring phenology than plants from non-heated areas in the field,
82 while the pattern is reversed when grown in a common environment, a phenomenon referred
83 to as counter-gradient variation (Conover and Schultz 1995, Valdés et al. 2018).

84 The plastic responses and local adaptation of plants in geothermal landscapes may not
85 only be in response to the direct effect of warming, but also due to indirect effects of
86 warming on the local environment. One such potentially important indirect effect is the soil
87 environment (Wittenmayer and Merbach 2005, Bardgett and van der Putten 2014). There is
88 evidence for plant local adaptation to both abiotic (Bradshaw 1952, Joshi et al. 2001, Brady et
89 al. 2005) and biotic soil characteristics (Mursinoff and Tack 2017). Warmer soils often have
90 higher nutrient levels, which are frequently limited in the arctic environment (Sigurdsson et
91 al. 2016). Moreover, both beneficial and antagonistic soil biota, like fungi, bacteria and
92 archaea, might be more diverse in warmer soils (Tedersoo et al. 2014, Rasmussen et al. 2018,
93 2020).

94 The aim of this study was to investigate the effects of soil heating on plastic and
95 evolutionary responses of the plant *Bistorta vivipara*. For this, we carried out a three-way
96 multifactorial greenhouse experiment where we grew bulbils (i.e. asexually produced axillary
97 buds), collected from locations with low, intermediate and high temperatures, in soils from
98 the same three types of locations, under low, intermediate and high soil temperatures in a
99 climate chamber. We tested the following specific hypotheses:

- 100 1) Experimental heating of soil results in a higher probability of sprouting, earlier
101 sprouting, and increased size
- 102 2) The bulbils planted in soils originating from heated areas have a higher probability of
103 sprouting, sprout earlier, and grow larger due to higher availability of mineralized
104 nutrients
- 105 3) Selection has resulted in a counter-gradient pattern where bulbils originating from
106 heated sites show a weaker growth response to temperature than bulbils originating
107 from non-heated sites
- 108 4) Genetic differences among plants originating from different soil temperatures
109 correspond to local adaptation, i.e. plants perform better under environmental
110 conditions that correspond to conditions at their site of origin
- 111 5) Both the abiotic and biotic soil environment influence the ecological and evolutionary
112 response of plants to heating

113

114

115 **Material and methods**

116 *Study system*

117 Geothermal landscapes, where magma gets close to the surface and heats soils and ground
118 water, can act as hotspots of local adaptation (O’Gorman et al. 2014). Notably, within these
119 landscapes the temperature can vary strongly at small spatial scales, with temperatures
120 differing by several or tens of degrees Celsius between locations separated by only a few
121 meters (Gudmundsdottir et al. 2011). The plant and soil microbial communities in these
122 locations are frequently strongly affected by spatial variation in soil temperature (Friberg et
123 al. 2009, Zakharova and Spichak 2012). At the same time, variation in soil nutrient
124 concentrations across the temperature gradient is relatively limited, yet availability increases
125 with rising temperatures in arctic ecosystems through mineralization of locked nutrients
126 (Weintraub and Schimel 2003, O’Gorman et al. 2014, Semenchuk et al. 2015, Sigurdsson et
127 al. 2016).

128 The alpine bistort (*Bistorta vivipara*) is a perennial herb that occurs in many parts of
129 the northern hemisphere (Jonsell and Karlsson 2000). In Iceland, *B. vivipara* can be found
130 growing naturally in a wide range of temperature conditions (Kristinsson 2001), including
131 geothermal areas. The herb primarily spreads clonally by bulbils, and only rarely produces
132 fertile seeds (Jonsell and Karlsson 2000). Bulbils are asexually produced bulb-like structures
133 that replace the lower inflorescence of *B. vivipara*. Bulbils have no specialized dispersal
134 structures, and often start growing within tens of centimeters from the mother plant (Bills et
135 al. 2015).

136

137 *Origin of plants and soil*

138 We collected plants and soil from Hengladalir, a geothermally active valley located a few
139 tens of kilometers east of Reykjavik, Iceland. Within this area, we identified three locations

140 with no heating (soil temperatures *c.* 13°C), three locations with slight heating (14-17°C) and
141 three locations with strong heating (25-30°C). From each location, we collected soil up to a
142 depth of *c.* 10 cm, which matches the average root depth of *B. vivipara*. From the soil, we
143 removed the litter layer and larger rocks and roots. From each location, we further collected
144 bulbils from one to three *B. vivipara* plants (henceforth referred to as ‘mother plants’),
145 resulting in seven mother plants from each temperature.

146

147 *Experimental design*

148 To investigate the effect of temperature and soil on plant performance, we designed a
149 multifactorial experiment where bulbils collected at different temperatures (3 levels) were
150 grown in soils collected at different temperatures (3 levels), and the soils were then
151 experimentally heated to low, intermediate and high temperatures, to simulate the natural
152 variation in soil temperature at the geothermal area. This resulted in 27 different treatment
153 combinations. For each treatment combination, we had seven 82 mm diameter pots (330 ml)
154 planted with two bulbils. We distributed bulbils from each mother plant equally across
155 treatment combinations. As maternal investment in bulbils may affect growth, we recorded
156 bulbil weight prior to planting.

157 We experimentally heated the plant pots in water baths. The water baths were
158 uniformly heated using a combination of aquarium heaters (Easyheater 75W, AQUAEL,
159 Poland) and water circulation pumps (Compact 300, EHEIM, Germany). In total there were
160 nine water baths, three at each temperature level: i) low temperature (13°C), ii) intermediate
161 (18°C) and iii) high (30°C). In each water bath, we placed 21 plant pots. Water baths were
162 placed in a climate chamber set to 13°C and a day length of 16 h.

163 To avoid microbial contamination, we sealed the plant pots, but filled the lower 2.5
164 cm with gravel and water-absorbing cloth to allow for drainage. To allow water to flow

165 below the plant pot, we glued three metal washers under each plant pot. To avoid positional
166 effects, the location of the plant pots was regularly randomized within the three water baths
167 belonging to the same temperature treatment.

168 To disentangle the effect of soil biota from that of the abiotic soil environment (e.g.
169 physical or chemical structure) on the probability and timing of bulbil sprouting, we set up a
170 complementary experiment using sterile soil. For this, we applied only the low and high
171 temperatures, resulting in eight treatment combinations and 56 plant pots. For sterilization,
172 soil was autoclaved for 1 h at 121°C.

173

174 *Plant performance measures*

175 Plants were monitored every other day for sprouting. The day of sprouting was determined as
176 the number of days from planting until the first sign of sprouting was observed. Plant height
177 and number of leaves were recorded on days 84 and 126, and the length and width of the
178 longest leaf were measured on days 97 and 159. Given the elliptical shape of the leaf, we
179 calculated leaf size using the formula for the area of an ellipse:

$$180 \text{ Leaf size} = \left(\frac{\text{leafwidth}}{2} * \frac{\text{leaflength}}{2} \right) * \pi$$

181

182 *Analysis*

183 Data were analyzed using the generalized linear mixed model framework as implemented in
184 R v. 3.6.1 (R Core Team 2019). We tested for significance using the *Anova* function in the
185 *car* package (Fox and Weisberg 2019).

186 To test for the impact of soil temperature and origin of plants and soil on bulbil
187 sprouting and plant growth, we modelled sprouting (0/1), day of sprouting, plant height,
188 number of leaves and leaf size as a function of original soil temperature, original bulbil
189 temperature, experimental soil temperature and their two- and three-way interactions. Bulbil

190 weight was included as a covariate. To account for variation among mother plants, we
191 included the random factor ‘*Mother plant*’. As we planted two bulbils in each plant pot, we
192 further included the random factor ‘*Plant pot*’ which was nested under ‘*Mother plant*’. For
193 probability of sprouting, we used a binomial distribution with a logit link; for day of
194 sprouting, plant height and leaf size, we used a normal distribution with an identity link; and
195 for the number of leaves, we used a Poisson distribution with a log link.

196 We *a priori* planned to test for local adaptation in those cases where we found an
197 interaction between original bulbil temperature and original soil temperature, or between
198 original bulbil temperature and experimental soil temperature (Kawecki and Ebert 2004,
199 Blanquart et al. 2013), using a contrast statement as implemented with the function *emmeans*
200 in the R-package *emmeans* (Lenth 2019).

201 An effect of temperature of the soil at the collection site on the probability of
202 sprouting and the date of sprouting could be due to either the abiotic or biotic soil
203 characteristics. To disentangle the role of the soil abiotic and biotic environment, we first
204 created a data set with data from both field and sterile soil experiment, where we only
205 retained those treatment combinations present in both experiments (i.e. only ‘low’ and ‘high’
206 temperatures). We then modelled the affected plant traits as a function of original soil
207 temperature, original bulbil temperature, experimental soil temperature and soil sterilization,
208 including all two- and three-way interactions. As above, we included the random factors
209 ‘*Mother plant*’ and ‘*Plant pot*’ (nested under ‘*Mother plant*’). Given the many terms in the
210 full model, we then identified the minimum adequate model using backward selection, using
211 a p-value of 0.05 as a threshold (Crawley 2013).

212

213 **Results**

214 Bulbils were more likely to sprout and sprouted earlier when grown at higher soil
215 temperatures (Fig 1AB, Table 1). Plants had the smallest leaves when grown at intermediate
216 soil temperature when measured 97 days after planting, whereas plants grown at higher soil
217 temperatures had more leaves when plants were measured 126 days after planting (Fig. 1CD,
218 Table 1). Bulbils sprouted earlier in soil originating from areas with intermediate temperature
219 than in soil originating from low or high temperatures (Table 1, Fig. 2A). Plants had a higher
220 number of leaves at 126 days after planting when grown in soil from a low temperature origin
221 (Fig. 2B, Table 1). At day 159, the end of the experiment, leaf size was interactively affected
222 by experimental soil temperature and original soil temperature: plants had larger leaves when
223 grown in soil originating from intermediate temperature, but only when the experimental soil
224 temperature was either low or high (Fig. S1). Plant height increased with bulbil weight, but
225 was not affected by any of the experimental factors (Table 1).

226 Plants originating from areas with low, intermediate, and high soil temperature did not
227 differ in probability of sprouting, day of sprouting or growth traits (Table 1). We also did not
228 detect any evidence of local adaptation in terms of an effect of the interaction between
229 original bulbil temperature and original or experimental soil temperature on sprouting
230 probability, day of sprouting or plant growth (Table 1).

231 Bulbil sprouting was later in the sterile soil than in the field soil, and sprouting was
232 earlier with experimental soil heating (Fig. S2, Table S1). We further detected a weak
233 interactive effect between original bulbil temperature, experimental soil temperature and soil
234 sterilization, suggesting that bulbils of a high temperature origin sprouted later than expected
235 when growing in soil originating from an area with low temperature, but only when the soil
236 was sterilized.

237 **Discussion**

238 We used a multi-factorial experiment to investigate the impact of microclimate and soil on
239 the immediate and evolutionary response of the alpine bistort. As expected, higher
240 experimental soil temperature advanced bulbil sprouting and led to plants with more leaves.
241 In contrast to our prediction, sprouting was earliest in soil originating from locations with
242 intermediate temperature, and the number of leaves was highest when plants were grown in
243 soil from a low temperature origin. We found no evidence for either genetic variation in
244 phenotypic plasticity or local adaptation. The microbial community in the soil advanced
245 bulbil sprouting, with some weak evidence for delayed sprouting of plants originating from
246 high temperature soils when they were grown at low soil temperature in the absence of soil
247 biota.

248 Plants sprouted earlier and had more leaves with higher experimental soil
249 temperature. This is consistent with previous studies that have shown an advance of spring
250 phenology and flowering, as well as increased plant growth, with increasing temperature
251 (Arft et al. 1999, Valdés et al. 2018). For example, flowering phenology has been shown to
252 advance with heating in geothermal areas (Anderson et al. 2012, Valdés et al. 2018), and
253 plant biomass is higher in *Arctagrostis latifolia* and *Carex bigelowii* when grown at higher
254 soil temperature (Marchand et al. 2005). Taken together, these findings suggest that the
255 circumpolar *B. vivipara* will start growing earlier, and grow larger, with climate change.

256 Surprisingly, the bulbils sprouted earliest in soil from the intermediate temperature
257 origins, and plants had the highest number of leaves when grown in soil from low
258 temperature origins. This did not match our expectation that the higher mineralization rates,
259 and associated higher availability of nutrients, in soils from high temperature would result in
260 earlier sprouting and increased performance. Previous studies have shown that nutrients are
261 frequently a limiting factor in arctic ecosystems and increased temperatures enhance nutrient

262 availability for plants and increase growth (Henry and Molau 1997, Weintraub and Schimel
263 2003, Semenchuk et al. 2015). Moreover, warmer soil is often associated with a more diverse
264 soil community and higher soil biotic activity (Friberg et al. 2009, Zakharova and Spichak
265 2012). One explanation for the lack of the expected pattern is that nutrient variation across
266 temperature gradients is limited in geothermal areas (O’Gorman et al. 2014, Sigurdsson et al.
267 2016), and even if mineralization is higher in soils in heated areas, this may not result in
268 higher availability of nutrients when the soil is exposed to lower temperatures. Importantly,
269 our findings illustrate that warming-mediated changes in the soil environment can have
270 idiosyncratic effects on plant phenology and plant traits.

271 We found no evidence for genetic variation in phenotypic plasticity or local
272 adaptation of plants to spatial variation in soil temperature. This contrasts to previous studies,
273 which found adaptive patterns of phenotypic plasticity by comparing plants grown in the field
274 and common garden (Valdés et al. 2018), and local adaptation using reciprocal transplant
275 experiments (Conover and Schultz 1995, Joshi et al. 2001, Anderson et al. 2012). For
276 example, Valdés et al. (2018) found that the arctic plant *Cerastium fontanum* flowered earlier
277 when growing in heated areas than in non-heated areas in the field, but that individuals from
278 heated areas flowered later than individuals from non-heated areas when growing in a
279 common garden. The lack of counter-gradient variation and local adaptation in *B. vivipara*
280 might have three non-mutually exclusive explanations. First, selection on the investigated
281 traits may be weak or absent. Second, *B. vivipara* mostly reproduces clonally, and the lack of
282 recombination may slow down the rate of local adaptation compared to sexually reproducing
283 plant species. Indeed, sexually reproducing species used in other studies showed adaptive
284 patterns of counter-gradient variation (Anderson et al. 2012, Valdés et al. 2018). Finally, gene
285 flow may swamp the effect of natural selection, but as dispersal distances are low in *B.*
286 *vivipara*, this appears less likely to explain the absence of an evolutionary response to

287 temperature in this species. To tease apart these explanations, future studies could use
288 quantitative genetic approaches to assess additive genetic variation for the investigated traits,
289 as combined with a genetic or experimental assessment of gene flow.

290 Interestingly, bulbil sprouting was slower in the sterile soil than in the field soil,
291 indicating that the soil microbial community stimulates bulbil sprouting. The effect of soil
292 biota matches previous studies, which found that soil organisms can advance phenology and
293 influence plant growth (Wagner et al. 2014, Rasmussen et al. 2017, 2020). The delayed
294 sprouting of bulbils originating from high temperature when grown at low soil temperature,
295 but only when the soil was sterilized, may indicate that soil biota plays a role in the
296 evolutionary response of plants to soil heating. However, we have no insights into the
297 putative adaptive nature of this pattern.

298

299 *Conclusions*

300 Our findings highlight that the circumpolar alpine bistort has a strong plastic response to
301 temperature. We did not find an evolutionary response in the form of counter-gradient
302 variation or local adaptation. This contrasts with previous reports from other plant species in
303 geothermal areas, and along latitudinal and altitudinal gradients, and may imply that the
304 relative importance of plastic vs genetic responses is highly variable among plant species.
305 Such variable responses, in combination with underlying mechanisms, have profound
306 implications for our understanding of how the arctic vegetation will respond to a changing
307 climate. For example, some plant species may lack genetic variation for selection to act on,
308 and thereby show maladaptive plastic responses to changes in temperature. Other plant
309 species may have additive genetic variation, but not show an evolutionary response in the
310 current context due to high rates of gene flow. Still other plant species may have a relatively
311 weak plastic response but show local adaptation across small spatial scales. Overall, we hope

312 that future studies will test for the ecological and evolutionary response of plants to changes
313 in temperature across a broad range of plant species and environmental clines, and unravel
314 the underlying mechanisms, which will allow for the development of eco-evolutionary
315 models to predict the response of the arctic vegetation to changes in climate. This will give
316 insights in the threats posed by climate change to the arctic vegetation and help inform about
317 potential mitigation actions.

318

319 **Declarations**

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326 manuscript, with contributions from all authors.

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416 **Table 1** The impact of original soil temperature (OST), original bulbil temperature (OBT) and experimental soil temperature (EST), as well as
 417 bulbil weight, on the performance of *Bistorta vivipara* in field soil. Shown are P-values, with significant values in bold. The number of replicates
 418 for each response variable is given within parentheses.

	Original soil temperature (OST)	Original bulbil temperature (OBT)	Experimental soil temperature (EST)	Bulbil weight	OST × OBT	OST × EST	OBT × EST	OST × OBT × EST
Sprouting success (n = 378)	0.856	0.849	<0.001	0.164	0.121	0.212	0.276	0.313
Day of sprouting (n = 240)	<0.001	0.094	<0.001	0.072	0.935	0.080	0.456	0.445
Plant height on day 84 (n = 217)	0.792	0.088	0.338	<0.001	0.790	0.106	0.753	0.468
Plant height on day 126 (n = 77)	0.401	0.648	0.529	0.030	0.561	0.337	0.623	0.102
Leaf number on day 84 (n = 217)	0.291	0.514	0.177	0.561	0.874	0.785	0.816	0.992
Leaf number on day 126 (n = 77)	0.012	0.118	0.004	0.984	0.939	0.772	0.559	0.999
Leaf size on day 97 (n = 162)	0.066	0.296	0.043	0.067	0.538	0.652	0.050	0.571
Leaf size on day 159 (n = 48)	0.162	0.924	0.055	0.521	0.296	0.025	0.074	-

419

420 **Figure legends**

421

422 **Figure 1.** The impact of experimental soil temperature on bulbil sprouting and performance
423 of *Bistorta vivipara*. Shown are the impact of experimental soil temperature on A) probability
424 of sprouting, B) day of sprouting, C) leaf size at 97 days after planting (DAP) and D) number
425 of leaves at 126 days after planting. Shown are means \pm standard errors.

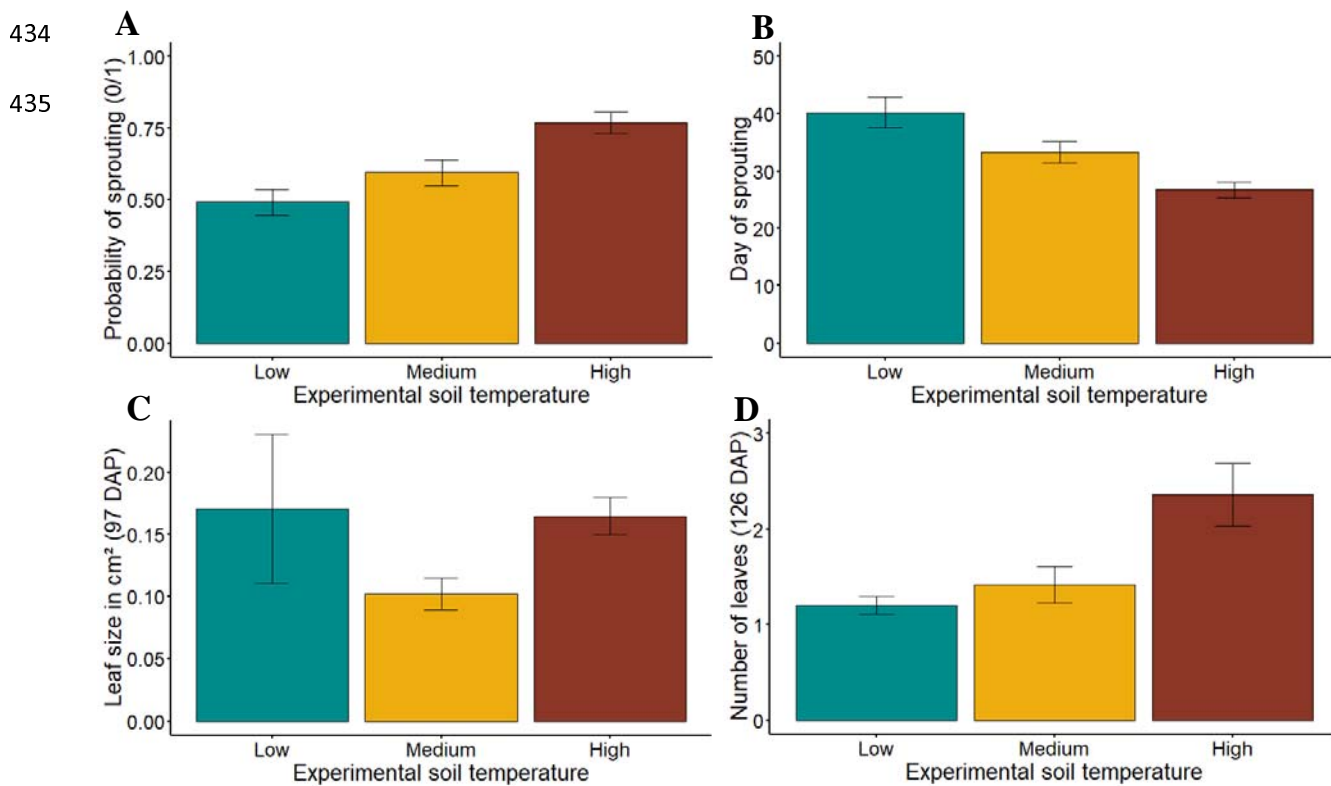
426

427 **Figure 2.** The impact of original soil temperature on bulbil sprouting and performance of
428 *Bistorta vivipara*. Shown are the impact of experimental soil temperature on A) day of
429 sprouting and B) the number of leaves at 126 days after planting (DAP). Shown are means \pm
430 standard errors.

431

432

433 **Figure 1.**



436 **Figure 2.**

437

