

1 **Genetic differentiation and plasticity interact along temperature and precipitation**
2 **gradients to determine plant performance under climate change**

3
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10
11 **Summary**

12 1. Understanding species' abilities to cope with changing climate is a key prerequisite for
13 predicting the future fates of species and ecosystems. Despite considerable research on species
14 responses to changing climate, we still lack understanding of the role of specific climatic factors,
15 and their interactions, for species responses. We also lack understanding of the relative
16 importance of plasticity vs. adaptation in determining the observed responses.

17 2. As a model, we use a dominant clonal grass, *Festuca rubra*, originating from a natural
18 climatic grid of 12 localities in western Norway that allows factorial combinations of temperature
19 (mean growing season temperatures ranging from 6.5°C to 10.5°C) and precipitation (annual
20 precipitation ranging from 600 mm to 2700 mm). We grew clones from all populations in four
21 growth chambers representing the four climatic extremes in the climate grid (warm/cold ×
22 wet/dry).

23 3. Genetic differentiation and direction and magnitude of plastic responses vary
24 systematically among populations throughout the climatic grid. Growth-related plant traits are
25 highly plastic and their degree of plasticity depends on their origin. In contrast, the traits
26 reflecting species' foraging strategy are not plastic but vary with the climate of origin. Levels of
27 plasticity of growth-related traits and genetically differentiated foraging traits thus might
28 constrain local populations' ability to cope with novel climates.

29 4. *Synthesis:* Shifts in temperature and precipitation, at the scale and direction expected for
30 the region in the next century, are likely to dramatically affect plant performance. This study
31 illustrates how the interplay between genetic differentiation and plasticity in response to both

32 temperature and precipitation will affect the specific responses of species to climate change. Such
33 complex responses will affect how climate-change impacts scale up to the community and
34 ecosystem levels. Future studies thus need to specifically consider regionally relevant climate-
35 change projections, and also explore the role of genetic differentiation and plasticity and how this
36 varies within local floras. Our study also demonstrates that even widespread species with
37 seemingly broad climatic niches may strongly differ in their population performance and
38 plasticity. Climate-change studies should therefore not be limited to rare and restricted species.

39

40 **Keywords:**

41 Climate change, clonal growth, extravaginal ramets, foraging, genotype × environment
42 interaction, local adaptation, plant performance, reaction norm, reciprocal transplant
43 experiment, tillering.

44

45 **Running head: Drivers of plant growth under climate change**

46

47

48 **Introduction**

49 Understanding species' abilities to respond to climate change is important not only for the
50 prediction of future species and ecosystem distribution and loss, but also for effective investment in
51 biodiversity and ecosystem protection (Walther *et al.* 2002; Moss *et al.* 2010; Rands *et al.* 2010;
52 Blume-Werry *et al.* 2016). While migration to track suitable habitats is an obvious response to
53 changing climate (e.g., Kokko & Lopez-Sepulcre 2006; Nicotra *et al.* 2010), the slow migration
54 rates of most plant species imply that many species and populations will need to face climate
55 change *in situ* (e.g., Davis & Shaw 2001; Malcolm *et al.* 2002; Thomas *et al.* 2004; Loarie *et al.*
56 2009; Bullock *et al.* 2012; Ravenscroft, Fridley & Grime 2014).

57 An important mechanism that allows plants to cope with climate change is phenotypic
58 plasticity, i.e. the ability of a genotype to change phenotypic expression in response to different
59 environmental conditions (e.g., Pigliucci 2001; Valladares, Sanchez-Gomez & Zavala 2006;
60 Matesanz, Gianoli & Valladares 2010; Nicotra *et al.* 2010; Lazaro-Nogal *et al.* 2015). Phenotypic
61 plasticity allows populations to buffer detrimental effects of rapid climate change – at least in the
62 short term – thereby allowing time for evolutionary changes to occur (e.g., Ayrinhac *et al.* 2004,
63 Jump & Peñuelas 2005, Kim & Donohue 2011; Anderson *et al.* 2012; Kim & Donohue 2013;
64 Monty *et al.* 2013; Padilla *et al.* 2013). However, phenotypic plasticity is most likely to be
65 effective in coping with weak, short-term, undirected, random, and unpredictable fluctuations in
66 the environment (Gienapp *et al.* 2008, but see Matesanz, Gianoli & Valladares 2010). Surviving
67 more extensive and directional changes are more likely to require natural selection, favouring
68 genotypes able to grow and reproduce well under the new environmental conditions and resulting
69 in genetic change in the population (Ohsawa & Ide 2008; Matesanz, Gianoli & Valladares 2010;
70 Nicotra *et al.* 2010). In cases when the specific selection pressures lead to maximized fitness of
71 different local genotypes under different local conditions, this will result in population
72 differentiation and local adaptation (*sensu* Kawecki & Ebert 2004).

73 The selection pressures leading to genetic differentiation of populations may not only select
74 for differentiation in mean traits (i.e., genotype \times environment interactions), but may also result
75 in differentiation in the degree of phenotypic plasticity (Kawecki & Ebert 2004; Hamann *et al.*
76 2016). While plastic variation between populations, reflected by the genotype \times environment
77 interaction, has been repeatedly demonstrated (reviewed e.g. in Marais, Hernandez & Juenger
78 2013 and Franks, Weber & Aitken 2014), only a few studies have explicitly evaluated differences

79 in the degree of plasticity in plants of different origin (Eranen & Kozlov 2009; Frei, Ghazoul &
80 Pluess 2014). These studies suggest that plants from mesic lower-elevation climates tend to have
81 higher plasticity than plants from more extreme climates at higher elevations. They did not,
82 however, explore the effect of specific climatic drivers on the plasticity, and are thus not able to
83 predict species responses to specific climate changes. Assessment of the degree of genetic
84 differentiation vs. trait plasticity from populations across a range of well-defined environments is
85 thus crucial for understanding species potential to respond to novel climatic conditions. As the
86 degree of trait plasticity (and presumably population differentiation in plasticity) varies across
87 traits (e.g., Sultan & Bazzaz 1993; Sultan 2000; Griffith & Sultan 2006), multiple traits with
88 different functions need to be explored and compared to understand the relative importance of
89 these processes in populations of different origin and across a species' range.

90 One key methodology that has proved useful in studies of genetic differentiation vs.
91 phenotypic plasticity in relationship to changing climate and in assessing if genetic differentiation
92 led to local adaptation in the species, is using reciprocal transplant experiments in the field
93 (Hoffmann & Sgro 2011; Hargreaves, Samis & Eckert 2014; Franks, Weber & Aitken 2014). Most
94 reciprocal transplant experiments have been done by transplanting individuals upwards or
95 downwards along elevational or latitudinal gradients and then documenting their performance (e.g.,
96 Etterson 2004; Byars, Papst & Hoffmann 2007; De Frenne *et al.* 2011; Agren & Schemske 2012;
97 Kim & Donohue 2013; Scheepens & Stocklin 2013; Schreiber *et al.* 2013; Zhou *et al.* 2013;
98 Hamann *et al.* 2016). While all these studies allow us to understand the possible consequences of
99 the specific suites of climatic factors correlated to the particular spatial gradient, they do not allow a
100 more general understanding of how performance will be affected by interacting effects of
101 simultaneous change in multiple specific climatic factors. Nor can they be used to assess responses
102 to not yet realized novel climates. Experiments that make use of the reciprocal setup, augmented by
103 the strengths of controlled-condition experiments, e.g., by growing populations of known climatic
104 origin in multiple growth chambers simulating both home climates and specific climatic-change
105 scenarios, can provide mechanistic understanding of species performance in response to specific
106 climatic changes and to novel climates. While a range of previous studies used various alternatives
107 to reciprocal transplant experiments to assess the importance of genetic differentiation and plasticity
108 in response to climate (Hoffmann & Sgro 2011; Franks, Weber & Aitken 2014), we are not aware

109 of any study which would use such an approach to specifically study plant growth responses to
110 different types of well defined climates.

111 Climate change is not a unidirectional change in one climatic factor alone, but is predicted to
112 bring about novel combinations of precipitation, temperature and their fluctuations (IPCC 2014).
113 Understanding the interactive effects of specific climatic drivers on species performance, and the
114 specific mechanisms and processes underlying these responses, is thus important for predicting
115 species responses to future climatic changes (Elith & Leathwick 2009; Gotelli & Stanton-Geddes
116 2015; Meineri *et al.* 2015; Parmesan & Hanley 2015; Moran, Hartig & Bell 2016). Several studies
117 have assessed the interactive effect of CO₂ and temperature or precipitation on species performance
118 (e.g., Volk, Niklaus & Korner 2000; Shaw *et al.* 2002; Dieleman *et al.* 2012). To date only (Suseela
119 *et al.* 2012) and Meineri, Spindelbock & Vandvik (2013) have explored the interactive effects of
120 temperature and moisture - and demonstrated that such interactions can be important. Their studies,
121 however, dealt with soil respiration and seedling recruitment respectively, and we are not aware of
122 any such studies on plant-species performance.

123 The aim of this study is to understand the importance of genetic differentiation along
124 gradients of temperature and moisture and the degree of plastic response to shifts in the same
125 variables, by determining the performance of a widespread clonal grass, *Festuca rubra*. The species
126 grows across broad climatic gradients and is characterized by considerable genetic differentiation
127 even at the fine scale. It is also plastic in its response to environmental factors (Skálová *et al.* 1997;
128 Herben *et al.* 2001). We used plants originating from locations of different temperature and
129 precipitation from a unique natural grassland ‘climate grid’ spanning ~4°C in temperature and
130 ~2100 mm in precipitation established in western Norway (the SeedClim grid, see Meineri,
131 Skarpaas & Vandvik 2012; Meineri, Spindelbock & Vandvik 2013; Meineri *et al.* 2014; Klanderud,
132 Vandvik & Goldberg 2015). We set up a growth chamber experiment simulating different
133 combinations of temperature and moisture derived from the data on the conditions in the original
134 localities. In this way, we performed a controlled-climate equivalent of a reciprocal transplant
135 experiment, i.e., a ‘reciprocal climate common garden experiment’. This approach has the
136 advantage that it allows us to explore the effects of specific climate change drivers, alone as well as
137 in combination at pre-determined levels, and it ensures that climate is really the only driver of
138 species performance. The climatic prediction for Norway suggests increases in both precipitation
139 (by about 18%) and temperature (by about 1.5°C to 2.2°C) over the next century (Hanssen-Bauer *et*

140 *al.* 2005). Our experimental sites cover a climatic gradient larger than these expected changes and
141 the results of our study will thus allow us to predict species responses to the expected changes and
142 beyond.

143 In this study, we aim to answer the following questions: (1) *What is the relative importance of*
144 *genetic differentiation and plasticity in determining plant performance in response to different*
145 *temperature and precipitation?* We hypothesize that both genetic differences and plasticity will
146 contribute to variation in plant performance along the bioclimatic gradients and in response to
147 climate change, with interactions indicating that climate change responses vary across the species'
148 climatic niche. 2) *How does the degree of plasticity vary among populations across broad-scale*
149 *temperature and precipitation gradients?* We hypothesize that plants from warmer and wetter
150 conditions will be more plastic due to higher competition under these conditions (Olsen *et al.* 2016).
151 (3) *What is the effect of the specific climate-change scenario for the region on species performance,*
152 *and what is the relative importance of temperature and precipitation change in driving these*
153 *responses?* We hypothesize that all plants will strongly profit from transplantation to warmer and
154 wetter conditions, i.e. from the projected climate change in the region as such conditions are likely
155 more favourable for the species. Drought might, however, turn the positive effects of warmer
156 conditions to negative as plants in warm conditions will have increased moisture requirements. (4)
157 *How do these patterns differ between different plant traits?* We hypothesize that the degree of
158 plasticity and genetic differentiation will strongly vary between traits due to different
159 developmental constraints underlying different traits (Sharma *et al.* 2016). High between-trait
160 variation in response to local climate has already been shown in the same system at the community
161 level (Guittar *et al.* 2016).

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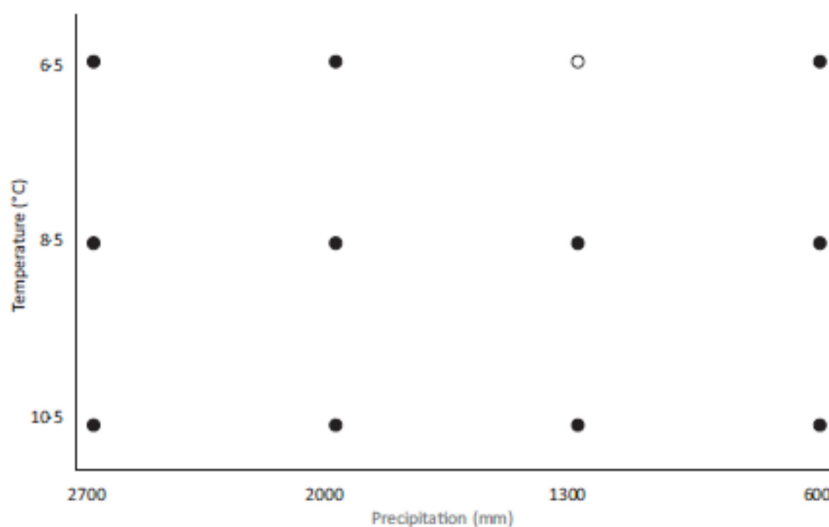
163 **Methods**

164 *Study species and localities*

165 *Festuca rubra* L. is a common perennial grass species of temperate grasslands in Europe.
166 In the experiment, we used *Festuca rubra* ssp. *rubra*, a widespread hexaploid type from the *F.*
167 *rubra* complex. It grows at different densities in grasslands, both as a dominant with only a few
168 other species and also as a subordinate of species-rich stands. It reproduces by seeds as well as
169 vegetatively, producing both intravaginal and extravaginal tillers on rhizomes. *Festuca rubra*

170 possesses considerable genetic variability and plasticity in growth and foraging-related traits
171 even within a single grassland locality (Skálová *et al.* 1997; Herben *et al.* 2001).

172 The experimental plants were collected along a natural climatic grid established in western
173 Norway (the SeedClim Grid, see Klanderud *et al.* 2015). It comprises 12 grassland localities
174 representing three levels of summer temperature [the experiment was set up to achieve means of
175 the four warmest months for individual locality types of ca. 6.5°C (alpine, ALP), 8.5°C (sub-
176 alpine, SUB) and 10.5°C (boreal, BOR) combined with each of four levels of mean annual
177 precipitation [ca. 600 (1), 1300 (2), 2000 (3) and 2700 (4) mm, Fig. 1, Meineri *et al.* 2014;
178 Klanderud *et al.* 2015]. The target communities are grazed intermediate-rich meadows
179 (Potentillo-Festucetum ovinae; G8 *sensu* Fremstad 1997) occurring on south-west facing (with
180 the exception of one site, (BOR 3), which was exposed to the east), shallow slopes (5–20°) with
181 relatively base-rich bedrock. Sites were selected specifically to ensure that grazing regime and
182 grazing history, bedrock, slope, aspect and vegetation types are as similar as possible.
183 Geographical distance between sites is on average 15 km and ranges from 0.65 km (BOR2 and
184 SUB2) to 175 km (BOR1 and BOR4) (Meineri *et al.* 2014).



185
186 **Figure 1.** Position of the studied localities along the temperature and precipitation gradient. The dots
187 represent all the localities in the SeedClim grid. The empty circle indicates the locality from which
188 *Festuca rubra* was not available for this study.

189
190

191 *Plant material*

192 At each locality, we laid out transects along which we collected at least 40 clones of *F.*
193 *rubra*, with at least 1 m between neighbour plants, in July 2014. The living plants were
194 transported to the experimental garden of the Institute of Botany, Czech Academy of Sciences,
195 Průhonice, Czech Republic (49°59'38.972"N, 14°33'57.637"E; means of the four warmest
196 months 16.5°C; and regular watering during the vegetation season) and immediately after the
197 transport they were planted into pots (16 × 16 × 16 cm, filled with a mixture of common garden
198 soil and sand at a 2:1 ratio). The common garden soil comprised compost from the experimental
199 garden containing approximately 0.135 % of nitrogen, 1.35% of carbon and 46.5 mg of
200 phosphorus in 1000 g of soil. The plants were allowed to recover from the transport. At the end
201 of August 2014 they were extracted from the pots and reduced to a single ramet. This was done to
202 ensure that there was only one clone per pot, preventing the possibility that we originally
203 collected multiple intermingled clones. At this stage, we also confirmed the identity of plants
204 using flow cytometry (see Castro *et al.* 2011 for methods) and selected only those with a genome
205 size ranging between 9.29 and 10.41 pg. This corresponds to the most widespread hexaploid
206 cytotype of *F. rubra* (Sampoux & Huyghe 2009). From each locality we selected 25 viable
207 genotypes fulfilling this condition. We use the term genotype throughout the subsequent text as
208 Šurinová *et al.* (unpubl.) confirmed that we worked with individuals that were genetically
209 differentiated from each other and therefore true independent genotypes. All the samples from the
210 ALP2 locality belonged to other *Festuca* species, so the study is based on 11 populations.

211 We continued cultivating the genotypes in the garden until November 2014 to remove
212 possible transgenerational effects. We then transferred the genotypes to the greenhouse. The
213 temperature in the greenhouse was set to be between 5°C and 10°C. At the beginning of February
214 2015, about 10 single ramets of similar size, each with three leaves and without visible signs of
215 initiating flower buds, were cut from the tussocks and placed into small plastic cups filled with
216 water, to set roots. At the end of February 2015, ramets with developed roots were individually
217 planted into 5 × 5 × 8.5 cm pots filled with a mixture of 1 part common garden soil and 2 parts
218 sand. While the pots may seem quite small, our model species is a tussock grass of small stature
219 and slow growth and the pots were not filled by the plant at the time of harvest. We are thus
220 confident that the results of the experiment are not affected by pot size. For each of the 25
221 genotypes from all of the 11 populations, we planted 4 ramets resulting in a total of 1100 ramets.

222 The pots were kept in the greenhouse and ramets that died within the next two weeks were
223 replaced. The plants in single pots will be referred to as individuals in the subsequent text (there
224 were 4 individuals per genotype, one in each growth chamber as described below).

225 In mid-March 2015, we measured the height of the tallest ramet and noted the number of
226 ramets of each individual providing us with a plant size value at the beginning of the experiment.
227 This was later used as a covariate in the analyses. Individuals were assigned to 4 groups, such
228 that one ramet of each genotype from each population was represented in each group, for
229 cultivation in growth chambers. In each group we had 11 populations \times 25 genotypes, i.e. 275
230 individuals in each growth chamber, comprising 1100 individuals in total. Pots assigned to each
231 growth chamber were fully randomized, placed into three metal trays and moved to the growth
232 chambers. The position of the pots in each growth chamber was randomized monthly. The
233 position of each genotype was always identical across the four growth chambers. For discussion
234 of using only four growth chambers in our study, please see *Methodological considerations* at the
235 end of the Methods section.

236 The plants were cultivated in climatic chambers (Vötsch 1014) under conditions simulating
237 four different scenarios for the spring to summer climate in the field (second half of April–second
238 half of June). The four scenarios were derived from climate data for the four extreme localities in
239 the SeedClim grid (wettest/driest combined with warmest/coldest), within the technical limits of
240 the climatic chambers and avoiding night frosts (minimum temperature during cultivation being
241 3°C). Note that this is in effect a controlled-climate equivalent to a reciprocal transplant
242 experiment, and we hence refer to it as a “reciprocal climate common garden experiment”. The
243 temperature in the growth chamber differed between the cold and warm treatments and changed
244 over the growing season following the course of temperature at the natural localities (for details
245 see Table 1). To set the correct moisture level in the growth chambers, we used TMS4 data-
246 loggers to continuously measure soil moisture in the pots (TOMST Co., Hemrová, Knappová &
247 Münzbergová 2016) and identified the correct level of watering to achieve soil moisture
248 comparable to that at the localities. As a result of this calibration, the dry regime plants were
249 watered with about 20 ml of tap water per plant applied to the trays if the soil moisture was lower
250 than 15%. In the wet regime, plants were cultivated under full soil saturation with about 1.5 cm
251 of water in the bottom of the tray. Soil moisture was monitored continuously during the whole
252 experiment and watering was modified to ensure constant moisture throughout the experiment.

253 Three data-loggers were placed in each growth chamber. Each data-logger was placed in a pot
254 with a growing *Festuca* plant, which was intermixed among the experimental plants and was of
255 the same size as the experimental plants, but was not a part of the experiment. For all the regimes,
256 the same day length and radiation were used, i.e. 16 hours of full light (6 am – 10 pm) and 4
257 hours of full dark with a gradual change of light availability in the transition between the light
258 and dark period over 2 hours. Over the full light period, the radiation was $360 \mu\text{mol.m}^{-2}.\text{s}^{-1}$, red
259 radiation (R, $\lambda=660 \text{ nm}$) of $26 \mu\text{mol.m}^{-2}.\text{s}^{-1}$, and far-red radiation (FR, $\lambda=730 \text{ nm}$) of $15 \mu\text{mol.m}^{-2}.\text{s}^{-1}$, R/FR = 1.73 (the radiation measured using a SPh 2020 photometer from Optické dílny
260 Turnov, Czech Republic).
261

262

263 *Plant performance*

264 Plant performance was recorded three times during the experiment. Specifically, we
265 counted the number of all ramets and of extravaginal ramets, and measured the length of the
266 longest ramet (hereafter referred to as plant height) of each individual at the beginning of May,
267 mid-June and end of August 2015. In mid-June and at the end of August 2015, we also cut all the
268 aboveground biomass at 3 cm, dried it to constant weight at 60°C and weighed it. The harvest
269 simulated biomass removal during regular management in the field sites. After the harvest at the
270 end of August, the remaining parts of the plants were removed from the pots, the belowground
271 parts were carefully washed and sorted into roots and rhizomes, dried to a constant mass at 60°C
272 and weighed. In addition, total length of rhizomes was measured before drying. As the total
273 rhizome length is strongly correlated with rhizome dry mass ($r = 0.95$), rhizome length is not
274 considered in the subsequent analyses. The number of extravaginal ramets divided by the total
275 number of ramets was calculated to give proportional data per plant. Production of extravaginal
276 ramets by the species indicates the species' ability to forage in space and thus to occupy areas
277 further away from the maternal ramet (Ye, Yu & Dong 2006). This may be an important
278 mechanism that allows species to cope with novel environments.

279

280 *Data analyses*

281 To study the effect of the conditions of the original sites as well as the target conditions
282 under cultivation on performance of the plants in the experiment, we coded the climatic
283 conditions each individual was subjected to relative to its climate of origin in the field. To do this,

284 temperature regimes of origin were coded with respect to the mean temperature of the four
285 warmest months for each locality type, i.e. as 6.5, 8.5 and 10.5°C. Similarly, moisture regimes of
286 origin were coded by mean annual precipitation at the localities, i.e. 600, 1300, 2000 and 2700
287 mm. We used the same codes to describe the conditions in the growth chambers, which simulated
288 the 4 climatic extremes at the sites, i.e. 6.5 and 10.5°C for low and high temperature and 600 and
289 2700 mm for low and high moisture. We tested the effects of the temperature and precipitation of
290 the origin and of the target and all their interactions on performance of the plants. We used results
291 of these tests to express the variation explained by environment of origin, target environment and
292 their interaction. A significant effect of target conditions will indicate plasticity of the plants, a
293 significant effect of origin will indicate genetic differentiation, and the interaction between target
294 and origin will indicate genetic differentiation in plasticity.

295 While significant interaction between target and origin will indicate genetic differentiation
296 in plasticity, it does not provide any information on whether these differences are due to a
297 different direction of the response to the environment, or whether there are any clear differences
298 in the magnitude of the response. To assess the degree of plasticity of the plants from the
299 different environments, we thus calculated the phenotypic plasticity index as the difference
300 between the maximum and minimum value of the trait for each clone (out of the four values
301 across the growth chambers) divided by the maximum value (Valladares *et al.* 2000). We use this
302 index as it is easy to use, robust, widely applied, and can be easily compared among traits
303 (Valladares, Sanchez-Gomez & Zavala 2006).

304 To assess whether characterization of populations by their original temperature and
305 precipitation and their interaction is sufficient, or where there is additional between-population
306 variation that cannot be explained by these characteristics, we performed tests in which the
307 temperature and precipitation of the original localities were replaced by locality code. The
308 original models and the models with the locality code were compared using Akaike information
309 criteria (AIC, Crawley 2012): models with the locality code were slightly better. The difference
310 in the AIC values, however, only range between 0.4 and 2.9% for the different dependent
311 variables suggesting that the two types of models are largely similar. The less parsimonious
312 locality code models are thus not presented further.

313 To assess whether the possible genetic differentiation of the populations lead to local
314 adaptation, we used the local vs. foreign criterion, as suggested by Kawecki & Ebert (2004). To

315 do this, we included an additional code distinguishing plants grown in their home temperature or
316 home moisture (i.e. plants grown in conditions simulating conditions of their site of origin) from
317 plants grown in a foreign environment (i.e. plants grown in all other conditions than the
318 conditions of their site of origin). We included the effect of home temperature and home moisture
319 and their interaction with temperature and moisture of origin in the models. The effect of these
320 factors was tested against original climate \times target climate interaction as in previous studies (e.g.,
321 Raabová, Münzbergová & Fischer 2007). While there are many significant effects in these tests,
322 most of the patterns detected are also clear from the tests presented below. These results are
323 therefore only briefly mentioned in the results section and are mainly presented in the
324 supplementary material Text S1 and Fig. S2.

325 Finally, we also explored impacts of the directionality of the climate change by subtracting
326 the above described values of temperature and moisture of the growth chambers from the values
327 of temperature and moisture at the original localities. In this way we obtained codes ranging from
328 -4°C to 4°C for temperature and -2100 mm to 2100 mm for moisture with negative values
329 indicating transplantations to colder or drier conditions and positive values indicating
330 transplantations to warmer or wetter conditions. Zero indicates plants growing under their home
331 conditions. We then tested the effect of these differences and their interaction on plant
332 performance using the models described below. Significant effects detected in this test will
333 indicate that species performance will be affected by the specific type of climate change to occur.

334 All of the above described tests were done for each measurement period and the following
335 dependent variables were used – plant height, number of ramets, and proportion of extravaginal
336 ramets. In addition, the following variables were tested based on the results at the time of final
337 harvest of the experiment: total aboveground biomass, total belowground biomass, ratio between
338 belowground and aboveground biomass, and rhizome biomass. Because the data from the first
339 and second censuses did not bring any additional insights to data from the third final census, we
340 only present the latter.

341 For plant height and number of ramets, we used the same characteristics measured at the
342 beginning of the experiment as a covariate. We used plant height \times number of ramets as a proxy
343 of plant biomass, and as a covariate when using aboveground, belowground and rhizome biomass
344 as dependent variables. There was no need for a covariate for number of extravaginal ramets as
345 there were no extravaginal ramets at the beginning of the experiment. Plant height, number of

346 ramets and aboveground and belowground biomass were tested assuming a normal distribution of
347 the data. Data on rhizome biomass and belowground to aboveground ratio were log transformed
348 to fit assumptions of normality and homogeneity of variance. The proportion of extravaginal
349 ramets was tested assuming a binomial distribution (number of extra- and intravaginal ramets
350 were linked using cbind function and tested as binary data, (Crawley 2012). All tests were done
351 using mixed effect models as implemented in the lme4 package in R (Bates *et al.* 2015) with
352 genotype as a random factor.

353 In this study, we performed each test independently for 7 different traits measured on the
354 same experimental plants. Theoretically, we should apply the Bonferroni correction and reduce
355 the conventional p-level from 0.05 to 0.0071 (Dunn 1961). We decided to use a modification of
356 this approach, the sequential Bonferroni correction (Holm-Bonferroni correction, Rice 1989) as it
357 is considered as less conservative. Still any such correction is considered as too conservative by
358 some authors (e.g., Moran 2003; Garcia 2004; Gotelli & Ellison 2004) and many studies have not
359 applied any correction, for this reason (e.g., Münzbergová 2007; Bowman *et al.* 2008; Scheepens
360 & Stocklin 2013). Here, we report and illustrate results both with and without this correction (see
361 also Husáková & Münzbergová 2016).

362

363 *Methodological considerations*

364 It may be argued that our experiment is pseudoreplicated as the growth chambers may
365 theoretically differ in a range of other variables (e.g. light intensity) leading to possible spurious
366 treatment effects (Hurlbert 1984). The conclusions of Hurlbert (1984) on pseudoreplication in
367 growth chamber experiments have, however, been extensively criticized (e.g., Oksanen 2001;
368 Johnson *et al.* 2016). Later, Hurlbert (2004) concluded that such experiments can be analysed
369 with standard statistical approaches as long as the interaction term is used as an estimate of the
370 error term to test the main effect. In our experiment, the effect manipulated at the growth
371 chamber level, i.e. the target environment, is not the effect of primary interest. Rather, we were
372 primarily interested in the effect of original environment, which is well replicated and the
373 interaction between the original and target environment. In such a case, using the standard error
374 terms is well justified. Thus in line with a range of other studies using similar settings for
375 unreplicated gardens at different elevations (Scheepens & Stocklin 2013; Gugger *et al.* 2015) or
376 growth chambers (Bezemer, Thompson & Jones 1998; Cavieres & Arroyo 2000; Souther,

377 Lechowicz & McGraw 2012; Matias & Jump 2014; Zhang *et al.* 2014), we suggest that such
378 studies are useful by allowing the separation of genetic differentiation of plants from their
379 phenotypic plasticity and provide insights into the effect of specific climatic variables without the
380 confounding effects of other naturally varying factors. For an extended discussion of this issue,
381 see Text S3.

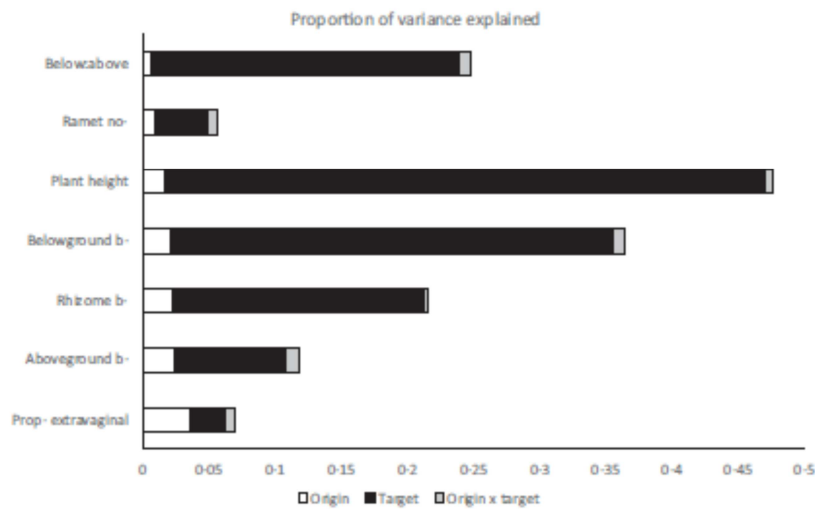
382

383 **Results**

384

385 *Target climate*

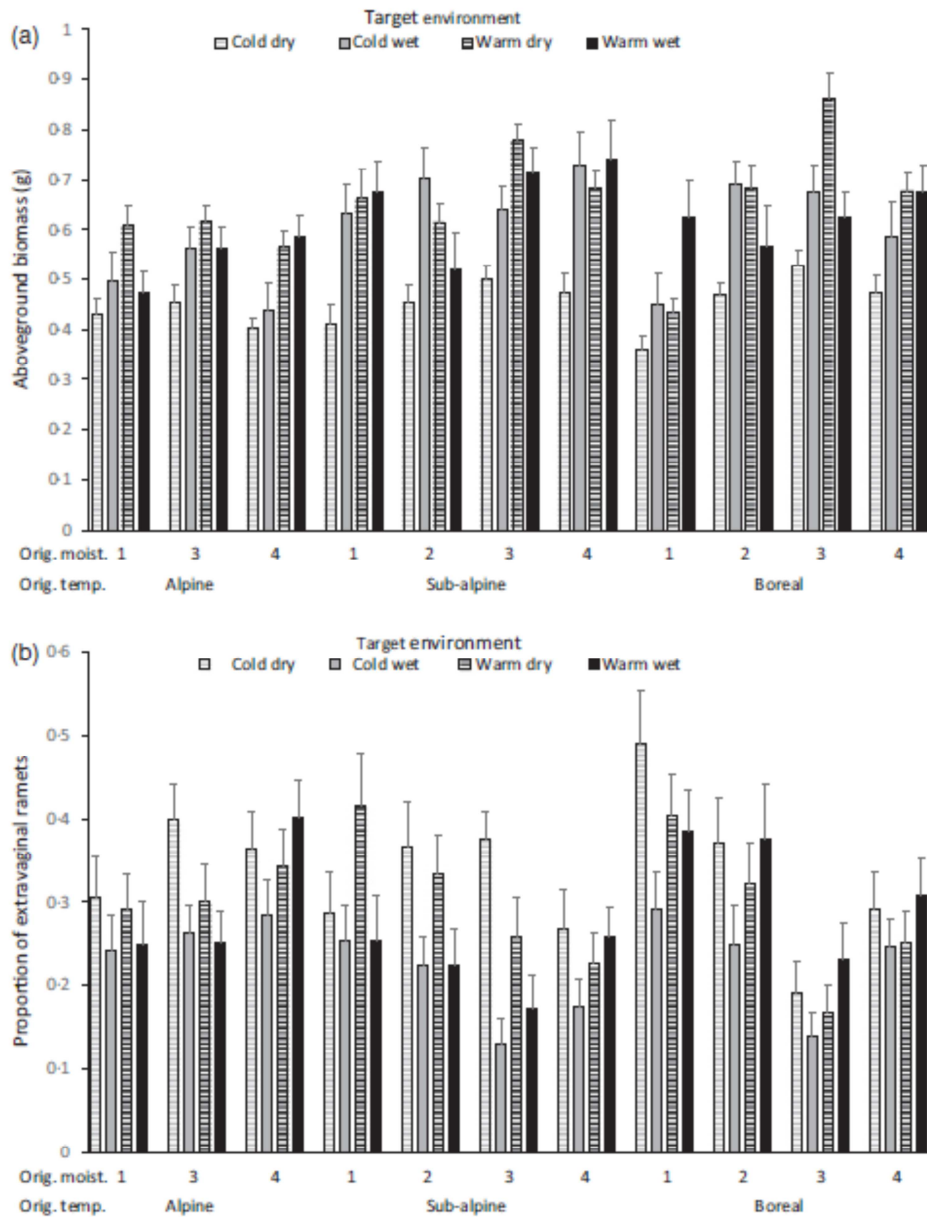
386 All of the observed plant characteristics were significantly affected by target moisture and
387 temperature, except for proportion of extravaginal ramets and rhizome biomass, suggesting that
388 the plants respond plastically to the environment (Fig. 2, Table 2). Plants in warm growth
389 chambers were significantly taller (Fig. S4A), produced more ramets (Fig. S4B), had more
390 aboveground biomass (Fig. 3A), but had lower belowground biomass (Fig. S4C) and lower below
391 to aboveground biomass ratio (Fig. S4D) than plants grown in cold conditions. The plants in the
392 dry growth chambers were also taller, produced more ramets, had greater belowground biomass
393 and rhizome biomass, and had higher below to aboveground biomass ratio (Fig. S4A-E) and
394 proportion of extravaginal ramets (Fig 3B). The effect of temperature interacted with the effect of
395 moisture in several cases (Table 2). Specifically, the negative effect of moisture on plant height
396 was stronger in the cold growth chamber with plants in the cold-wet growth chamber being the
397 shortest (Table 2, Fig. S4A). Low temperature in the dry growth chambers led to an increased
398 proportion of extravaginal ramets, while low temperature in the wet growth chamber led to a
399 decrease in the proportion of extravaginal ramets (Fig. 3B). Aboveground biomass increased with
400 temperature in dry but not in wet growth chambers (Fig. 3A). Belowground biomass decreased
401 with temperature in the wet growth chambers but not in the dry ones (Fig. S4C). All the effects of
402 target temperature, target moisture as well as their interaction are significant after applying the
403 Bonferroni correction (Table 2).



404
 405 **Figure 2.** Proportion of variation explained by the target environment, the environment of origin and their
 406 interaction. The remaining variation is unexplained.

407
 408 ***Original climate***

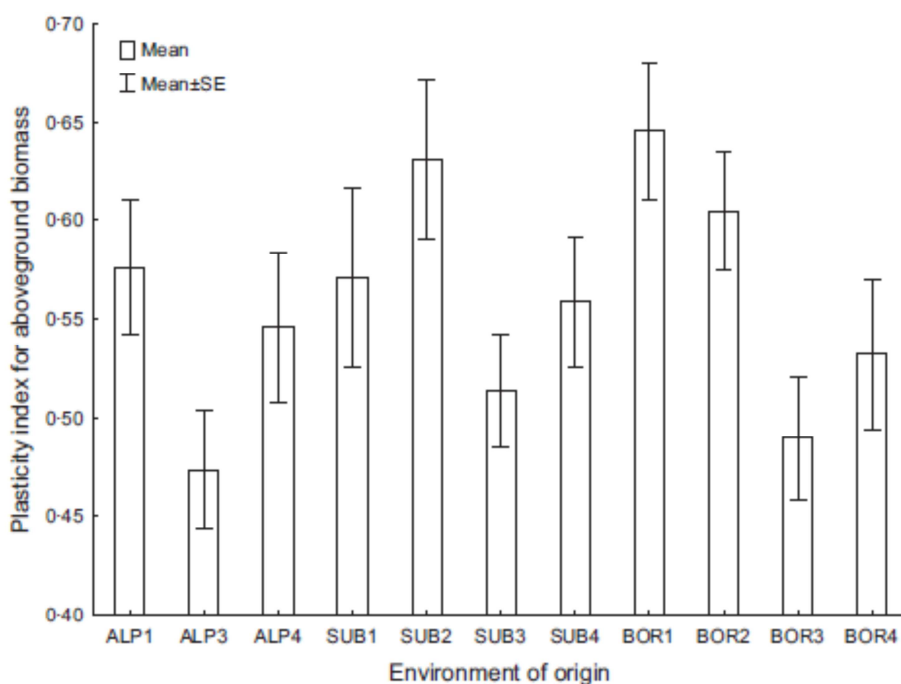
409 Plant height, aboveground biomass and belowground biomass are significantly affected by
 410 temperature of origin and aboveground and belowground biomass also by moisture of origin (Fig.
 411 2, Table 2), suggesting genetic differences between the plants originating from different
 412 environments. Plants originating from warmer sites were significantly taller and had more
 413 aboveground (Fig. 3A) and belowground biomass (Fig. S4C) than those from colder sites. Plants
 414 from wetter sites had more aboveground biomass (Fig. 3A) and belowground biomass (Fig. S4C).
 415 Temperature and moisture of origin also interacted in their effects (Table 2). Specifically, plants
 416 produced less aboveground biomass (Fig. 3A), were shorter and had more rhizomes when
 417 originating from wetter colder sites, while the values were opposite when they were from wetter
 418 warmer sites (Fig. S4). For proportion of extravaginal ramets, the effect of moisture is more
 419 pronounced in plants originating from warmer conditions and thus plants from warm and wet
 420 sites produced the lowest proportion of extravaginal ramets (Fig. 3B). The effects of original
 421 temperature, original moisture, as well as their interaction are still significant after applying the
 422 Bonferroni correction, with one exception: the interactive effect of original moisture and
 423 temperature on aboveground biomass (Table 2).



424
 425 **Figure 3.** The effect of original environment and target environment on plant performance measured as A)
 426 aboveground biomass and B) proportion of extravaginal ramets. ALP denotes the cold alpine sites, SUB
 427 denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4 indicates moisture at the original
 428 localities with 1 indicating the driest and 4 the wettest sites; for the test of significance see Table 2. The
 429 graphs show mean \pm SE.

430 Original environment also affects trait plasticity. Specifically, the plasticity index for
 431 aboveground (Fig. 4) and belowground biomass (Fig. S5), number of ramets and plant height are

432 significantly affected by moisture of origin (Table 3) with plants from drier sites being more
 433 plastic in all the traits. In addition, plasticity in belowground biomass and plant height is also
 434 affected by temperature of origin with plants from the colder sites being more plastic (Table 3,
 435 Fig. S5). Three out of six of these significant effects are non-significant after applying the
 436 Bonferroni correction (Table 3). Plants from the colder sites are still significantly more plastic in
 437 plant height, and plants from drier sites are significantly more plastic in aboveground and
 438 belowground biomass after the correction (Table 3).

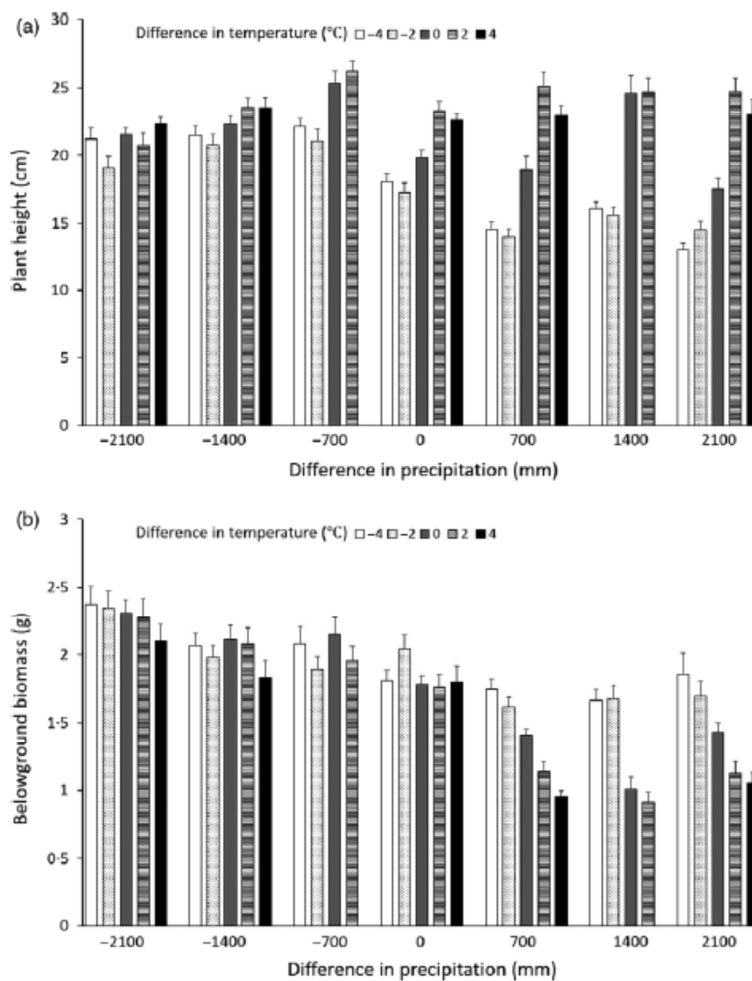


439
 440 **Figure 4.** Plasticity index of aboveground biomass of plants of different origin. ALP denotes the cold
 441 alpine sites, SUB denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4 indicates moisture at
 442 the original localities with 1 indicating the driest and 4 the wettest sites.

443
 444 ***Interaction between target and original climate***

445 There are also a few significant interactions between plant origin and responses in the target
 446 growth chambers (Fig. 2, Table 2, Table S6). Two out of the three significant double interactions
 447 are non-significant with the Bonferroni correction. As the important interactive patterns are seen
 448 from the exploration of the difference between target and original environment presented below,
 449 the results are not described in detail here, but only in Text S7.

450 The tests of the effect of local vs. foreign conditions on species performance exploring
 451 local adaptation in the system are shown in detail in Text S1, Fig. S2 and Table S8. There is a
 452 number of significant differences indicating that plants grown in their local conditions perform
 453 better than plants grown in foreign conditions on average. However, as seen in Fig. 5 and Fig. S9,
 454 there is also quite high variation and the effect of local and foreign conditions interacts with plant
 455 origin (Table S8). Thus, clear evidence for local adaptation is available only for ramet number
 456 (Fig. S9A) and, in some populations, for proportion of extravaginal ramets (Fig. S9B).



457
 458 **Figure 5.** The effect of difference in temperature and moisture between target and original environment
 459 (target-origin) on A) plant height and B) belowground biomass. The colour scale indicates difference in
 460 temperature, the sets of columns indicate differences in moisture. Negative values indicate plants grown in
 461 colder and drier conditions, positive values indicate plants grown in warmer and wetter conditions and 0
 462 indicates plants grown in conditions corresponding to the conditions from which they originate. The
 463 graphs show mean \pm SE.

464 ***Directionality in environmental change responses***

465 Plants subjected to warming were taller (Fig. 5A), had more ramets, higher aboveground
466 biomass and proportion of extravaginal ramets than plants subjected to cooling (Fig. S9, Table 4).
467 Under warming, plants also had lower belowground biomass (Fig. 5B) and ratio of below to
468 aboveground biomass (Fig. S9, Table 4). The effect for number of ramets and proportion of
469 extravaginal ramets is non-significant when applying the Bonferroni correction, while the rest are
470 still significant (Table 4).

471 Plants subjected to a wetter environment were shorter (Fig. 5A), had fewer ramets (Fig.
472 S9A), a lower proportion of extravaginal ramets (Fig. S9B), lower rhizome biomass (Fig. S9E),
473 less belowground biomass (Fig. 5B) and a lower below to aboveground ratio (Fig. S9D) than
474 plants grown in drier conditions (Table 4). All these patterns are significant even with the
475 sequential Bonferroni correction (Table 4).

476 For plant height (Fig. 5A), aboveground (Fig. S9C) and belowground biomass (Fig. 5B)
477 and rhizome biomass there is also a significant interaction between difference in temperature and
478 moisture (Table 4). Plant size increased much more with increasing temperature when the plants
479 were grown in wetter conditions, while warming did not have any effect in drier conditions (Fig.
480 5A). All these patterns are significant even with the sequential Bonferroni correction (Table 4).

481

482 **Discussion**

483 Performance of our model species, *Festuca rubra*, depends strongly on plant origin, suggesting
484 genetic differences between populations, with some signs of local adaptation. At the same time,
485 the plants also show a high degree of phenotypic plasticity and populations from different
486 climates also differ markedly in their degree of plasticity. Such combined genetic and plastic
487 responses to climate seem to be a common pattern. Indeed, the review by Franks, Weber &
488 Aitken (2014) conclude that all studies that explicitly study both of these processes find both to
489 be important. In line with our study, this review also demonstrates that the importance of
490 plasticity vs. genetic differentiation strongly varies among traits. Our results, however, add
491 unique insights into the specific mechanisms behind the differentiation by demonstrating that
492 both temperature and moisture of cultivation and of origin affect plant performance, and that
493 these effects strongly interact.

494

495 *Plasticity and genetic differentiation*

496 High plasticity in relation to temperature as well as moisture and high variation in
497 plasticity between different traits is in line with a range of previous studies demonstrating that
498 target conditions impact plant performance (e.g., Raabová, Münzbergová & Fischer 2011; Couso
499 & Fernandez 2012; Černá & Münzbergová 2015; Lazaro-Nogal *et al.* 2015; Malyshev *et al.*
500 2016). Specifically, target conditions explain most of the variation in the growth-related traits
501 (plant height, number of ramets, aboveground and belowground biomass) in our study, although
502 the plasticity of these traits strongly varies with origin. In contrast, the traits reflecting species
503 ability to forage for resources (proportion of extravaginal ramets, rhizome biomass) are primarily
504 explained by the environment of origin. Traits related to foraging are also found to drive
505 community responses to climate change in a community-wide field study in the same study
506 system (Guittar *et al.* 2016). Plasticity of the foraging-related traits is low and constant across
507 origins. Our results thus suggest that size is highly plastic, and that the species has an ability to
508 take advantage of suitable conditions through increased growth (number of ramets, plant height
509 and biomass). In contrast, the foraging behaviour is a more fixed trait under changing climatic
510 factors, which nevertheless varies between populations. The fact that the foraging traits do not
511 vary may suggest presence of strong stabilizing selection working on these traits (Pelabon *et al.*
512 2010). These traits therefore seem to be the primary drivers of a species' ability to respond to
513 climate (see also Guittar *et al.* 2016). However, Herben *et al.* (2001) and Skálová (2010)
514 demonstrated that the proportion of extravaginal ramets is highly plastic in *Festuca rubra* in
515 relation to neighbour density and light availability. Plasticity in foraging traits could thus still
516 occur in our system, and even vary with climate, as the changing climate is expected to be linked
517 to increased competition and reduced light availability under natural conditions (Olsen *et al.*
518 2016).

519 The interaction between origin and target climate always explains the lowest proportion
520 of the variation in our models, suggesting relatively low genetic differentiation in plasticity
521 between environments (*sensu* Pigliucci 2001). This is in line with other studies testing
522 interactions between genotype (represented by origin in our study) and environment (represented
523 by target in our study, e.g., Gugger *et al.* 2015).

524 In spite of the limited magnitude of the interaction between origin and target climate
525 impacts, the degree of trait plasticity described by the plasticity index (expressing the

526 proportional change of a trait across different environments) is affected by conditions of origin,
527 suggesting that phenotypic plasticity itself is a trait under selection (Thompson 1991) and that
528 selection can change the degree of plasticity depending on the conditions (e.g., Emery,
529 Chinnappa & Chmielewski 1994; Springate *et al.* 2011; Gugger *et al.* 2015). Specifically, plants
530 coming from drier and colder environments are most plastic in growth-related traits (mainly in
531 production of aboveground and belowground biomass). The link between dry conditions and
532 plasticity is in line with previous studies demonstrating that drought is a key factor exerting
533 selection on trait plasticity (Couso & Fernandez 2012, Lazaro-Nogal *et al.* 2015). While those
534 two studies come from much drier environments and suggest that the plasticity may be caused by
535 high variation in water availability, our results suggest that greater plasticity can also be found in
536 plants from mesic conditions compared to sites which are very wet.

537 The higher plasticity in growth-related traits in plants from colder climates may reflect
538 that plants from cold environments need to be able to make use of short ‘windows of opportunity’
539 when favourable conditions occur in the harsh alpine environment to rapidly increase their
540 growth. This pattern contrasts with expectations of previous studies, predicting and, in some
541 cases, confirming that plants from extreme environments at higher elevations tend to be less
542 plastic (e.g., Emery, Chinnappa & Chmielewski 1994; Eranen & Kozlov 2009; Frei, Ghazoul &
543 Pluess 2014). All these studies only worked along elevational gradients, and did not explicitly
544 test the effect of different climatic variables. We are not aware of any previous study that
545 explicitly isolated and compared plasticity of plants across different temperatures while
546 controlling for precipitation differences and vice versa. While Lemke *et al.* (2015) attempted to
547 separate effects of temperature and precipitation along a wide transect across Europe and
548 suggested a contrary pattern, i.e. higher phenotypic plasticity under warm and wet conditions,
549 their study did not separate phenotypic plasticity from genetic differentiation. Our study is thus
550 the first study demonstrating higher growth plasticity of plants from colder conditions. More
551 studies using other species and systems using controlled designs similar to ours are now needed
552 to confirm the generality of our conclusions.

553 In addition to high plasticity, this study demonstrates that both temperature and moisture of
554 origin play an important role in plant performance, with plants from warmer and drier sites
555 growing larger, indicating genetic differentiation between populations. Reduced plant size in
556 plants from colder conditions is in line with studies showing similar patterns from localities at

557 higher elevations or latitudes (e.g., Nunez-Farfan & Schlichting 2001; Kollmann & Banuelos
558 2004; Byars, Papst & Hoffmann 2007; Gonzalo-Turpin & Hazard 2009; Monty & Mahy 2009;
559 Fischer *et al.* 2011; Scheepens & Stocklin 2013; Dostálek *et al.* 2016). In addition, Guittar *et al.*
560 (2016) indicate that plants from warmer sites tend to be larger in a community-wide study and
561 Meineri *et al.* (2014) show an increased size at flowering for *Veronica officinalis*, both working
562 in the same model system as us.

563 Decreased plant stature is usually expected to be maladaptive (van Kleunen & Fischer
564 2005). We, however, suggest that reduced stature of plants in extreme conditions at high
565 elevation may in fact be seen as an adaptation allowing plants to withstand the extreme weather
566 conditions, such as low temperature, high snow cover and shorter growing season (Kollmann &
567 Banuelos 2004). It may also be an adaptation to higher wind speed and higher light exposure as
568 these might be more important stress factors at higher elevations than temperature (McIntire,
569 Piper & Fajardo 2016). In addition, increased plant size might be viewed as a result of selection
570 pressure for increased ability to compete for light in a warmer climate while there is no need to
571 invest excessively in aboveground biomass in a colder climate with much lower competition
572 (Olsen *et al.* 2016). While we attempted to select our sites to be as similar as possible, differences
573 in these factors cannot be fully excluded and have to be considered as an alternative explanation
574 for the effect of temperature of origin on plant size. In general, our results are in line with
575 previous studies suggesting the importance of climate for performance of various rare as well as
576 widespread species (e.g., Fournier-Level *et al.* 2011; Bennington *et al.* 2012; Kim & Donohue
577 2013; Mendola *et al.* 2015; Malyshev *et al.* 2016) and reviews of older studies in Hereford (2009)
578 and Alberto *et al.* (2013).

579 The effect of climate of origin might suggest that the plants are locally adapted. Despite our
580 data showing a significant effect of local vs. foreign environment for a range of traits, the
581 indication of local adaptation in our data is only convincing for number of ramets. This is due to
582 strong interactions between foreign vs. local contrast for moisture and temperature and also the
583 interaction of the foreign vs. local contrast with population origin. This result contrasts with
584 conclusions of previous studies suggesting that local adaptation to climate is one of the key
585 factors limiting species ability to cope with climate variation and thus to adapt to changing
586 climates even for widespread species with apparently wide climatic niches (e.g., De Frenne *et al.*
587 2011; Aitken & Whitlock 2013; Mendola *et al.* 2015).

588 The contrasting results might be caused by the numerous interactions described above and
589 the fact that we study adaptation to two different factors. This makes our results very complex.
590 The absence of a clear indication of local adaptation in the majority of the traits we study may be
591 attributed also to the lack of a clear link between the traits and life-time fitness. While it is clear
592 that having data on life-time seed production would indeed be better (see e.g., Volis *et al.* 2015),
593 our species is a long-lived clonal species and measuring life-time fitness is definitely not
594 straightforward. It has been estimated that a single genet of *Festuca rubra* can live for several
595 hundred years (Harberd 1961; de Witte & Stocklin 2010). In addition, our experimental plants
596 flowered very rarely and early flowering in long-lived perennials may not be an indication of
597 high fitness, but a response to stress (Ahmad & Prasad 2012). The trait showing local adaptation
598 most clearly—the number of ramets—is a trait that might be most closely linked to fitness in the
599 clonal species (note that number of ramets is a growth-related trait, while proportion of
600 extravaginal ramets is a foraging-related trait, so these two traits have very different biological
601 meaning).

602 Previous studies specifically exploring local adaptation of species (*sensu* Kawecki & Ebert
603 2004) in relation to climate mainly assessed adaptation to temperature (Williams & Black 1993;
604 Mimura & Aitken 2010; De Frenne *et al.* 2011; Souther, Lechowicz & McGraw 2012) and
605 demonstrate that temperature is an important factor driving local adaptation of species. For
606 moisture, Gimenez-Benavides, Escudero & Iriondo (2007) demonstrate that soil moisture may
607 also be an important factor affecting species adaptation and Garcia-Fernandez *et al.* (2013)
608 confirm that the ability to cope with drought is a key factor driving performance of their model
609 species. The only study comparing the effects of precipitation of origin to the effect of
610 temperature of origin on plant performance concludes that elevation and temperature of origin,
611 but not precipitation of origin, affect species performance (Scheepens & Stocklin 2013).
612 Compared to our system, their precipitation gradient is much shorter and precipitation partly
613 correlated with elevation and temperature (Scheepens & Stocklin 2013). In contrast, precipitation
614 of origin, and, importantly, also its predictability, has been shown to be an important determinant
615 of performance of species coming from semi-arid environments, with plants from wetter sites
616 being larger (Couso & Fernandez 2012; Lazaro-Nogal *et al.* 2015). In our system, there is an
617 opposite trend with plants from wetter climates tending to be smaller, likely due to the negative
618 effect of high snow cover resulting in shorter growing seasons at the wetter sites.

619 Interestingly, there is a strong interaction between precipitation and temperature in our
620 system, such that plants originating from cold and wet sites were the smallest. This is likely due
621 to persistent snow cover at these locations and linked to the strongly reduced growing-season
622 length. While a range of previous studies have demonstrated the effect of length of the growing
623 season on plant size (e.g., Natali, Schuur & Rubin 2012; Liu *et al.* 2016), most of the patterns
624 previously reported are just a matter of plastic response and not linked to genetic differences
625 between the genotypes. The different genotypes of *F. rubra* are thus clearly adapted to their local
626 conditions and any shift in the environment may at least partly restrict their growth. Few previous
627 studies have simultaneously explored adaptation to moisture and temperature. One of these
628 studies, Allan & Pannell (2009), conclude that moisture but not temperature plays a role for plant
629 performance. In contrast, Andalo, Beaulieu & Bousquet (2005) demonstrate that adaptation to
630 temperature but not to moisture is important for performance of white spruce. Neither of these,
631 however, explicitly study interactions between the two factors. Thus our study is unique in
632 demonstrating that temperature and moisture may interact to determine plant adaptations and
633 suggest that both of these factors need to be studied simultaneously when attempting to
634 understand the consequences of climate change.

635

636 *Effects of changing climate*

637 The general climatic prediction for Norway suggests increases in both precipitation and
638 temperature over the next century (Hanssen-Bauer *et al.* 2005). The expected change in mean
639 annual temperature ranges from 1.5°C to 2.2°C, with the change being stronger in winter and
640 spring than in summer. In addition, precipitation is expected to increase by about 18%, with the
641 change being stronger in winter than in summer (Hanssen-Bauer *et al.* 2005). We find that plant
642 performance is generally higher under warmer and wetter conditions, suggesting that our model
643 species is likely able to take advantage of climate change. Increased performance of plants
644 exposed to warmer and wetter climates suggests that even though the plants show certain levels
645 of genetic differentiation and local adaptation, they will still be able to profit from more favourable
646 growth conditions under future climate change in the region. This is in line with our finding that
647 plants from the environments most endangered by climate change, i.e. the coldest and driest sites,
648 are the most plastic.

649 As the species is dominant in the studied systems, it may be expected that it will increase its
650 dominance in the sites in the future, leading to a potential loss in subordinate species and thus a
651 reduction in the diversity of the plant communities (Olsen *et al.* 2016). Other scenarios, such as
652 its suppression due to even higher profit of other native or invasive plant species or increased
653 negative interactions with other trophic levels, are, however, also possible (e.g., Plowman &
654 Richards 1997; Robinson, Ryan & Newman 2012). Importantly, the results demonstrate that the
655 change in temperature interacts with the change in moisture, suggesting that these two factors
656 should be studied in combination.

657 Most previous studies looking at the interacting effect of changed moisture and temperature
658 are field climate-change experiments that also modified the level of CO₂. While several of these
659 studies demonstrate the interactive effects of moisture and temperature on various aspects of soils
660 (e.g., Wan *et al.* 2007; Larsen *et al.* 2011; Selsted *et al.* 2012), the only study that investigates
661 plant biomass and plant community composition concludes that the effect of moisture and
662 temperature are largely additive (Kardol *et al.* 2010). Our study is thus the first to demonstrate a
663 strong interaction between changes in temperature and changes in precipitation on species
664 performance in response to changing climate. It suggests that future studies aiming to understand
665 species responses to changing climate need to consider carefully the specific changes expected
666 and attempt to understand the effect of all the potentially changing factors, separately as well as
667 in combination.

668

669 *Conclusions*

670 A key result of our study is that both temperature and moisture of cultivation and of origin
671 affect plant performance, and that these effects strongly interact. This allows us to make
672 predictions about the species' response to future climate change. Specifically, our results imply
673 that our target species, *Festuca rubra*, will profit from warming provided the climate gets wetter
674 at the same time, while the species will not show any significant response to climate warming
675 under simultaneous climatic drying. As the plants have the ability to compensate for increased
676 drought by investing more in belowground structures independent of temperature, they are able to
677 perform equally well under drought as under warm and wet conditions. Cold and wet conditions
678 thus seem to be the most stressful for this species.

679 Species response to climate change necessarily also depends on response of the remaining
680 species in the community. *F. rubra* tends to be more abundant in lower elevations as long as the
681 productivity of the stands is not too high. We thus expect that climate change in the nutrient poor
682 alpine environment, as was studied here, will lead to increased dominance of the species. This
683 general prediction is, however, constrained by the fact species' response to climate change is
684 strongly modified by the plasticity of plants from different origins, with plants from the extreme
685 cold and dry conditions being the most plastic. This may allow the plants from cold and dry
686 conditions, i.e. from the environments most endangered by climate change, to profit from the
687 future climate change more than plants from the other environments. In contrast, the specific
688 genotypes from cold and wet environments are likely to be lost in the course of climate change.
689 The response of the species as a whole, commonly predicted by species distribution models, may
690 thus be overly optimistic in some parts of the range and too pessimistic in others. Global response
691 of the species will thus also crucially depend on the specific structure of the landscape and the
692 specific genotypes available to occupy the novel environments in the landscape. Present day
693 species distribution can thus not be easily used to predict how the specific populations and thus
694 the species as a whole will behave under climate change.

695

696 *Author contributions*

697 Planning the project ZM, VH, VV, HS; Executing the experiment VH, ZM, HS; Analysing the
698 data ZM; Writing the manuscript ZM; Commenting on the manuscript VV, VH, HS.

699

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712

713 **Table 1.** The specific regime settings in the growth chambers providing information on minimum
 714 (min), maximum (max) and average (av.) temperature in the growth chamber each day. The
 715 regimes mimic the course of temperatures at the localities during the day as well as over the
 716 course of the growing season.

Time (day)	Cold regime			Warm regime		
	Min	Max	Av	Min	Max	Av
1-4	5°C	15°C	9.8°C	5°C	16°C	10.1°C
5-25	3°C	12.5°C	7.5°C	3°C	16°C	9.2°C
26-46	3°C	12.5°C	7.5°C	3°C	18.5°C	10.2°C
47-67	3°C	12.5°C	7.5°C	3°C	24.3°C	12.5°C
68-88	3°C	14.5°C	8.4°C	3.4°C	25°C	12.9°C
89-176	3°C	14.7°C	8.5°C	5°C	23.8°C	14.8°C

717

718

719

720 **Table 2.** The effect of original (O) and target (T) temperature (temp) and moisture (mois) and their two-way interactions on plant
721 performance in the growth chambers. Higher-order interactions are shown in Table S6. Plant size at the beginning of the
722 experiment was used as a covariate and genotype as a random factor. Df Error = 1078. Significant values ($p \leq 0.05$) are in bold.
723 Results marked with * are significant after correcting for multiple testing. Dev. indicates deviance explained by the given
724 variable.

	Plant height		Ramet no.		Prop. extravag.		Aboveg. b.		Belowg. b.		Below : above		Rhizome b.	
	dev.	p	dev.	p	dev.	p	dev.	p	dev.	p	dev.	p	dev.	p
Ttemp	541.24	<0.001*	21.70	<0.001*	2.99	0.083	63.03	<0.001*	41.87	<0.001*	172.29	<0.001*	0.24	0.62
Tmois	187.10	<0.001*	37.62	<0.001*	132.52	<0.001*	17.47	<0.001*	344.30	<0.001*	196.28	<0.001*	298.91	<0.001*
Otemp	9.03	0.003*	2.45	0.118	0.17	0.678	7.97	0.005*	12.09	<0.001*	0.03	0.86	0.01	0.923
Omois	2.32	0.127	2.13	0.144	3.39	0.066	8.12	0.004*	11.08	<0.001*	1.85	0.17	1.10	0.295
Otemp:Omois	8.20	0.004*	1.39	0.238	244.52	<0.001*	5.36	0.02	3.36	0.07	2.16	0.142	10.93	<0.001*
Otemp:Ttemp	1.71	0.196	2.86	0.09	3.03	0.082	0.25	0.677	0.36	0.548	1.21	0.27	0.01	0.927
Otemp:Tmois	4.61	0.032	0.89	0.346	5.78	0.016	1.68	0.196	0.20	0.655	0.05	0.824	1.68	0.195
Omois:Ttemp	7.79	0.005*	0.11	0.739	2.23	0.136	1.75	0.185	1.63	0.202	1.14	0.285	0.02	0.891
Omois:Tmois	3.00	0.08	0.73	0.392	27.30	<0.001*	0.07	0.79	0.14	0.711	0.28	0.596	1.65	0.201
Ttemp:Tmois	206.62	<0.001*	0.21	0.65	119.59	<0.001*	44.33	<0.001*	116.81	<0.001*	2.35	0.125	0.70	0.404

726 Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass; Belowg. b. = belowground biomass

727

728 **Table 3.** The effect of temperature (Otemp) and moisture (Omois) of origin on plasticity index
 729 based on the single traits. Most of the tests were done using linear regressions and the reported
 730 values are F-values. The tests for proportion of extravaginal ramets were done using GLM
 731 assuming a binomial distribution of the dependent variable and the reported values represent
 732 explained deviance. Df Error = 269. Significant values ($p \leq 0.05$) are in bold. Results marked
 733 with * are significant after correcting for multiple testing.

734

Response:		Plant height	Ramet no.	Prop. extravag.	Aboveg. b.	Belowg. b.	Below : above	Rhizome biomass
Otemp	F/Dev.	9.42	0.23	21.98	1.20	4.48	0.41	7.76
	p	0.002*	0.634	0.093	0.274	0.035	0.522	0.981
Omois	F/Dev.	5.70	5.38	22.15	8.26	7.26	1.58	7.74
	p	0.018	0.021	0.844	0.004*	0.008*	0.210	0.076
Otemp. × Omois.	F/Dev.	0.61	0.07	21.82	1.62	0.20	1.77	7.73
	p	0.437	0.799	0.110	0.204	0.656	0.185	0.279

735 Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass;

736 Belowg. b. = belowground biomass

737

738

739

740 **Table 4.** The effect of difference in temperature and moisture between localities of origin and
741 target conditions and their interaction on plant performance. Significant values ($p \leq 0.05$) are in
742 bold. Results marked with * are significant after correcting for multiple testing. Df Error = 1094.
743

		Plant height	Ramet no.	Prop. extravag.	Aboveg. b.	Belowg. b.	Below : above	Rhizome biomass
Diff. temp	dev.	209.04	4.86	5.62	12.79	48.07	87.97	0.01
	p	<0.001*	0.028	0.018	<0.001*	<0.001*	<0.001*	0.944
Diff. mois	dev.	54.18	29.52	6.91	1.07	300.22	83.66	164.73
	p	<0.001*	<0.001*	0.009*	0.302	<0.001*	<0.001*	<0.001*
Diff. temp × diff. mois	dev.	66.54	0.71	0.26	13.88	21.44	1.31	7.02
	p	<0.001*	0.398	0.61	<0.001*	<0.001*	0.253	0.008*

744 Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass;

745 Belowg. b. = belowground biomass

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748 **References**

- 749 Agren, J. & Schemske, D.W. (2012) Reciprocal transplants demonstrate strong adaptive differentiation of
750 the model organism *Arabidopsis thaliana* in its native range. *New Phytologist*, **194**, 1112-1122.
- 751 Ahmad, P. & Prasad, M. (2012) *Abiotic stress responses in plants. Metabolism, productivity and*
752 *sustainability*. Springer, New York.
- 753 Aitken, S.N. & Whitlock, M.C. (2013) Assisted gene flow to facilitate local adaptation to climate change.
754 *Annual Review of Ecology, Evolution, and Systematics, Vol 44*, **44**, 367-+.
- 755 Alberto, F.J., Aitken, S.N., Alia, R., Gonzalez-Martinez, S.C., Hanninen, H., Kremer, A., Lefevre, F.,
756 Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O. (2013) Potential for evolutionary
757 responses to climate change evidence from tree populations. *Global Change Biology*, **19**, 1645-
758 1661.
- 759 Allan, E. & Pannell, J.R. (2009) Rapid divergence in physiological and life-history traits between northern
760 and southern populations of the British introduced neo-species, *Senecio squalidus*. *Oikos*, **118**,
761 1053-1061.
- 762 Andalo, C., Beaulieu, J. & Bousquet, J. (2005) The impact of climate change on growth of local white
763 spruce populations in Quebec, Canada. *Forest Ecology and Management*, **205**, 169-182.
- 764 Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I. & Mitchell-Olds, T. (2012) Phenotypic
765 plasticity and adaptive evolution contribute to advancing flowering phenology in response to
766 climate change. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 3843-3852.
- 767 Ayrinhac, A., Debat, V., Gibert, P., Kister, A.G., Legout, H., Moreteau, B., Vergilino, R. & David, J.R. (2004)
768 Cold adaptation in geographical populations of *Drosophila melanogaster*: phenotypic plasticity is
769 more important than genetic variability. *Functional Ecology*, **18**, 700-706.
- 770 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4.
771 *Journal of Statistical Software*, **67**, 1-48.
- 772 Bennington, C.C., Fetcher, N., Vavrek, M.C., Shaver, G.R., Cummings, K.J. & McGraw, J.B. (2012) Home
773 site advantage in two long-lived arctic plant species: results from two 30-year reciprocal
774 transplant studies. *Journal of Ecology*, **100**, 841-851.
- 775 Bezemer, T.M., Thompson, L.J. & Jones, T.H. (1998) *Poa annua* shows inter-generational differences in
776 response to elevated CO₂. *Global Change Biology*, **4**, 687-691.
- 777 Blume-Werry, G., Kreyling, J., Laudon, H. & Milbau, A. (2016) Short-term climate change manipulation
778 effects do not scale up to long-term legacies: effects of an absent snow cover on boreal forest
779 plants. *Journal of Ecology*, **104**, 1638-1648.
- 780 Bowman, G., Perret, C., Hoehn, S., Galeuchet, D.J. & Fischer, M. (2008) Habitat fragmentation and
781 adaptation: a reciprocal replant-transplant experiment among 15 populations of *Lychnis flos-*
782 *cuculi*. *Journal of Ecology*, **96**, 1056-1064.
- 783 Bullock, J.M., White, S.M., Prudhomme, C., Tansey, C., Perea, R. & Hooftman, D.A.P. (2012) Modelling
784 spread of British wind-dispersed plants under future wind speeds in a changing climate. *Journal*
785 *of Ecology*, **100**, 104-115.
- 786 Byars, S.G., Papst, W. & Hoffmann, A.A. (2007) Local adaptation and cogradient selection in the alpine
787 plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution*, **61**, 2925-2941.
- 788 Castro, S., Münzbergová, Z., Raabová, J. & Loureiro, J. (2011) Breeding barriers at a diploid-hexaploid
789 contact zone in *Aster amellus*. *Evolutionary Ecology*, **25**, 795-814.
- 790 Cavieres, L.A. & Arroyo, M.T.K. (2000) Seed germination response to cold stratification period and
791 thermal regime in *Phacelia secunda* (Hydrophyllaceae) - Altitudinal variation in the
792 mediterranean Andes of central Chile. *Plant Ecology*, **149**, 1-8.
- 793 Černá, L. & Münzbergová, Z. (2015) Conditions in home and transplant soils have differential effects on
794 the performance of diploid and allotetraploid *Anthericum* species. *Plos One*, **10**.

- 795 Couso, L.L. & Fernandez, R.J. (2012) Phenotypic plasticity as an index of drought tolerance in three
796 Patagonian steppe grasses. *Annals of Botany*, **110**, 849-857.
- 797 Crawley, M. (2012) *The R Book*, 2nd Edition edn. John Wiley & Sons, Chichester, United Kingdom.
- 798 Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change.
799 *Science*, **292**, 673-679.
- 800 De Frenne, P., Brunet, J., Shevtsova, A., Kolb, A., Graae, B.J., Chabrierie, O., Cousins, S.A., Decocq, G., De
801 Schrijver, A., Diekmann, M., Gruwez, R., Heinken, T., Hermy, M., Nilsson, C., Stanton, S., Tack, W.,
802 Willaert, J. & Verheyen, K. (2011) Temperature effects on forest herbs assessed by warming and
803 transplant experiments along a latitudinal gradient. *Global Change Biology*, **17**, 3240-3253.
- 804 de Witte, L.C. & Stocklin, J. (2010) Longevity of clonal plants: why it matters and how to measure it.
805 *Annals of Botany*, **106**, 859-870.
- 806 Dieleman, W.I.J., Vicca, S., Dijkstra, F.A., Hagedorn, F., Hovenden, M.J., Larsen, K.S., Morgan, J.A., Volder,
807 A., Beier, C., Dukes, J.S., King, J., Leuzinger, S., Linder, S., Luo, Y.Q., Oren, R., de Angelis, P.,
808 Tingey, D., Hoosbeek, M.R. & Janssens, I.A. (2012) Simple additive effects are rare: a quantitative
809 review of plant biomass and soil process responses to combined manipulations of CO₂ and
810 temperature. *Global Change Biology*, **18**, 2681-2693.
- 811 Dostálek, T., Rokaya, M., Maršík, P., Rezek, J., Skuhrovec, J., Pavela, R. & Münzbergová, Z. (2016) Trade-
812 off among different anti-herbivore defence strategies along an altitudinal gradient. *AoB Plants*.
- 813 Dunn, O. (1961) Comparisons Among Means. *Journal of the American Statistical Association*, **56**, 52-64.
- 814 Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction
815 Across Space and Time. *Annual Review of Ecology Evolution and Systematics*, **40**, 677-697.
- 816 Emery, R.J.N., Chinnappa, C.C. & Chmielewski, J.G. (1994) Specialization, plant strategies, and phenotypic
817 plasticity in populations of *Stellaria longipes* along an elevational gradient. *International Journal*
818 *of Plant Sciences*, **155**, 203-219.
- 819 Eranen, J.K. & Kozlov, M.V. (2009) Interactions between mountain birch seedlings from differentiated
820 populations in contrasting environments of subarctic Russia. *Plant Ecology*, **200**, 167-177.
- 821 Etterson, J.R. (2004) Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. 1.
822 Clinal patterns of selection along an environmental gradient in the great plains. *Evolution*, **58**,
823 1446-1458.
- 824 Fischer, M., Weyand, A., Rudmann-Maurer, K. & Stoecklin, J. (2011) Adaptation of *Poa alpina* to altitude
825 and land use in the Swiss Alps. *Alpine Botany*, **121**, 91-105.
- 826 Fournier-Level, A., Korte, A., Cooper, M.D., Nordborg, M., Schmitt, J. & Wilczek, A.M. (2011) A Map of
827 Local Adaptation in *Arabidopsis thaliana*. *Science*, **334**, 86-89.
- 828 Franks, S.J., Weber, J.J. & Aitken, S.N. (2014) Evolutionary and plastic responses to climate change in
829 terrestrial plant populations. *Evolutionary Applications*, **7**, 123-139.
- 830 Frei, E.R., Ghazoul, J. & Pluess, A.R. (2014) Plastic responses to elevated temperature in low and high
831 elevation populations of three grassland species. *Plos One*, **9**.
- 832 Garcia, L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos*, **105**, 657-663.
- 833 Garcia-Fernandez, A., Iriondo, J.M., Bartels, D. & Escudero, A. (2013) Response to artificial drying until
834 drought-induced death in different elevation populations of a high-mountain plant. *Plant*
835 *Biology*, **15**, 93-100.
- 836 Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. & Merila, J. (2008) Climate change and evolution:
837 disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167-178.
- 838 Gimenez-Benavides, L., Escudero, A. & Iriondo, J.M. (2007) Local adaptation enhances seedling
839 recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of*
840 *Botany*, **99**, 723-734.
- 841 Gonzalo-Turpin, H. & Hazard, L. (2009) Local adaptation occurs along altitudinal gradient despite the
842 existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, **97**, 742-751.

843 Gotelli, N. & Ellison, A. (2004) A Primer of ecological statistics. Sinauer Associates, Sunderland, USA.
844 Gotelli, N.J. & Stanton-Geddes, J. (2015) Climate change, genetic markers and species distribution
845 modelling. *Journal of Biogeography*, **42**, 1577-1585.
846 Griffith, T.M. & Sultan, S.E. (2006) Plastic and constant developmental traits contribute to adaptive
847 differences in co-occurring *Polygonum* species. *Oikos*, **114**, 5-14.
848 Gugger, S., Kesselring, H., Stoecklin, J. & Hamann, E. (2015) Lower plasticity exhibited by high- versus
849 mid-elevation species in their phenological responses to manipulated temperature and drought.
850 *Annals of Botany*, **116**, 953-962.
851 Guittar, J., Goldberg, D., Klanderud, K., Telford, R.J. & Vandvik, V. (2016) Can trait patterns along
852 gradients predict plant community responses to climate change? *Ecology*, **97**, 2791-2801.
853 Hamann, E., Kesselring, H., Armbruster, G.F.J., Scheepens, J.F. & Stocklin, J. (2016) Evidence of local
854 adaptation to fine- and coarse-grained environmental variability in *Poa alpina* in the Swiss Alps.
855 *Journal of Ecology*, **104**, 1627-1637.
856 Hanssen-Bauer, I., Achberger, C., Benestad, R.E., Chen, D. & Forland, E.J. (2005) Statistical downscaling of
857 climate scenarios over Scandinavia. *Climate Research*, **29**, 255-268.
858 Harberd, D. (1961) Observations on population structure and longevity of *Festuca rubra* L. *New*
859 *Phytologist*, **60**, 184-206.
860 Hargreaves, A.L., Samis, K.E. & Eckert, C.G. (2014) Are species' range limits simply niche limits writ large?
861 a review of transplant experiments beyond the range. *American Naturalist*, **183**, 157-173.
862 Hemrová, L., Knappová, J. & Münzbergová, Z. (2016) Assessment of habitat suitability is affected by
863 plant-soil feedback: comparison of field and garden experiment. *Plos One*, **11**.
864 Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. (2001) Clone-specific response of *Festuca rubra*
865 to natural variation in biomass and species composition of neighbours. *Oikos*, **95**, 43-52.
866 Hereford, J. (2009) A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*,
867 **173**, 579-588.
868 Hoffmann, A.A. & Sgro, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479-485.
869 Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological*
870 *Monographs*, **54**, 187-211.
871 Hurlbert, S.H. (2004) On misinterpretations of pseudoreplication and related matters: a reply to
872 Oksanen. *Oikos*, **104**, 591-597.
873 Husáková, I. & Münzbergová, Z. (2016) The effect of current and historical landscape structure and
874 species life-history traits on species distribution in dry grassland-like forest openings. *Journal of*
875 *Vegetation Science*, **27**, 545-556.
876 IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of working groups I, II and III to the
877 fifth assessment report of the intergovernmental panel on climate change [core writing team,
878 R.K. Pachauri and L.A. Meyer (eds.)], 151 pp. IPCC, Geneva, Switzerland.
879 Johnson, S.N., Gherlenda, A.N., Frew, A. & Ryalls, J.M.W. (2016) The importance of testing multiple
880 environmental factors in legume-insect research: replication, reviewers, and rebuttal. *Frontiers*
881 *in Plant Science*, **7**.
882 Jump, A.S. & Penuelas, J. (2005) Running to stand still: adaptation and the response of plants to rapid
883 climate change. *Ecology Letters*, **8**, 1010-1020.
884 Kardol, P., Company, C.E., Souza, L., Norby, R.J., Weltzin, J.F. & Classen, A.T. (2010) Climate change
885 effects on plant biomass alter dominance patterns and community evenness in an experimental
886 old-field ecosystem. *Global Change Biology*, **16**, 2676-2687.
887 Kawecki, T.J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225-1241.
888 Kim, E. & Donohue, K. (2011) Population differentiation and plasticity in vegetative ontogeny: effects on
889 life-history expression in *Erysimum capitatum* (Brassicaceae). *American Journal of Botany*, **98**,
890 1752-1761.

891 Kim, E. & Donohue, K. (2013) Local adaptation and plasticity of *Erysimum capitatum* to altitude: its
892 implications for responses to climate change. *Journal of Ecology*, **101**, 796-805.

893 Klanderud, K., Vandvik, V. & Goldberg, D. (2015) The importance of biotic vs. abiotic drivers of local plant
894 community composition along regional bioclimatic gradients. *Plos One*, **10**.

895 Kokko, H. & Lopez-Sepulcre, A. (2006) From individual dispersal to species ranges: Perspectives for a
896 changing world. *Science*, **313**, 789-791.

897 Kollmann, J. & Banuelos, M.J. (2004) Latitudinal trends in growth and phenology of the invasive alien
898 plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions*, **10**, 377-385.

899 Larsen, K.S., Andresen, L.C., Beier, C., Jonasson, S., Albert, K.R., Ambus, P., Arndal, M.F., Carter, M.S.,
900 Christensen, S., Holmstrup, M., Ibrom, A., Kongstad, J., van der Linden, L., Maraldo, K.,
901 Michelsen, A., Mikkelsen, T.N., Pilegaard, K., Prieme, A., Ro-Poulsen, H., Schmidt, I.K., Selsted,
902 M.B. & Stevnbak, K. (2011) Reduced N cycling in response to elevated CO₂, warming, and
903 drought in a Danish heathland: Synthesizing results of the CLIMAITE project after two years of
904 treatments. *Global Change Biology*, **17**, 1884-1899.

905 Lazaro-Nogal, A., Matesanz, S., Godoy, A., Perez-Trautman, F., Gianoli, E. & Valladares, F. (2015)
906 Environmental heterogeneity leads to higher plasticity in dry-edge populations of a semi-arid
907 Chilean shrub: insights into climate change responses. *Journal of Ecology*, **103**, 338-350.

908 Lemke, I.H., Kolb, A., Graae, B.J., De Frenne, P., Acharya, K.P., Blandino, C., Brunet, J., Chabrierie, O.,
909 Cousins, S.A.O., Decocq, G., Heinken, T., Hermy, M., Liira, J., Schmucki, R., Shevtsova, A.,
910 Verheyen, K. & Diekmann, M. (2015) Patterns of phenotypic trait variation in two temperate
911 forest herbs along a broad climatic gradient. *Plant Ecology*, **216**, 1523-1536.

912 Liu, W., Maung-Douglass, K., Strong, D.R., Pennings, S.C. & Zhang, Y. (2016) Geographical variation in
913 vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. *Journal*
914 *of Ecology*, **104**, 173-181.

915 Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of
916 climate change. *Nature*, **462**, 1052-U1111.

917 Malcolm, J.R., Markham, A., Neilson, R.P. & Garaci, M. (2002) Estimated migration rates under scenarios
918 of global climate change. *Journal of Biogeography*, **29**, 835-849.

919 Malyshev, A.V., Khan, M., Beierkuhnlein, C., Steinbauer, M.J., Henry, H.A.L., Jentsch, A., Dengler, J.,
920 Willner, E. & Kreyling, J. (2016) Plant responses to climatic extremes: within-species variation
921 equals among-species variation. *Global Change Biology*, **22**, 449-464.

922 Marais, D.L.D., Hernandez, K.M. & Juenger, T.E. (2013) Genotype-by-environment interaction and
923 plasticity: exploring genomic responses of plants to the abiotic environment. *Annual Review of*
924 *Ecology, Evolution, and Systematics*, Vol 44 (ed. D.J. Futuyma), pp. 5-+. Annual Reviews, Palo
925 Alto.

926 Matesanz, S., Gianoli, E. & Valladares, F. (2010) Global change and the evolution of phenotypic plasticity
927 in plants. *Year in Evolutionary Biology* (eds C.D. Schlichting & T.A. Mousseau), pp. 35-55. Wiley-
928 Blackwell, Malden.

929 Matias, L. & Jump, A.S. (2014) Impacts of predicted climate change on recruitment at the geographical
930 limits of Scots pine. *Journal of Experimental Botany*, **65**, 299-310.

931 McIntire, E.J.B., Piper, F.I. & Fajardo, A. (2016) Wind exposure and light exposure, more than elevation-
932 related temperature, limit tree line seedling abundance on three continents. *Journal of Ecology*,
933 **104**, 1379-1390.

934 Meineri, E., Deville, A.S., Gremillet, D., Gauthier-Clerc, M. & Bechet, A. (2015) Combining correlative and
935 mechanistic habitat suitability models to improve ecological compensation. *Biological Reviews*,
936 **90**, 314-329.

- 937 Meineri, E., Skarpaas, O., Spindelbock, J., Bargmann, T. & Vandvik, V. (2014) Direct and size-dependent
938 effects of climate on flowering performance in alpine and lowland herbaceous species. *Journal of*
939 *Vegetation Science*, **25**, 275-286.
- 940 Meineri, E., Skarpaas, O. & Vandvik, V. (2012) Modeling alpine plant distributions at the landscape scale:
941 Do biotic interactions matter? *Ecological Modelling*, **231**, 1-10.
- 942 Meineri, E., Spindelbock, J. & Vandvik, V. (2013) Seedling emergence responds to both seed source and
943 recruitment site climates: a climate change experiment combining transplant and gradient
944 approaches. *Plant Ecology*, **214**, 607-619.
- 945 Mendola, M.L., Baer, S.G., Johnson, L.C. & Maricle, B.R. (2015) The role of ecotypic variation and the
946 environment on biomass and nitrogen in a dominant prairie grass. *Ecology*, **96**, 2433-2445.
- 947 Mimura, M. & Aitken, S.N. (2010) Local adaptation at the range peripheries of Sitka spruce. *Journal of*
948 *Evolutionary Biology*, **23**, 249-258.
- 949 Monty, A., Bizoux, J.P., Escarre, J. & Mahy, G. (2013) Rapid plant invasion in distinct climates involves
950 different sources of phenotypic variation. *Plos One*, **8**, 10.
- 951 Monty, A. & Mahy, G. (2009) Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae)
952 along altitudinal gradients in Europe. *Oecologia*, **159**, 305-315.
- 953 Moran, E.V., Hartig, F. & Bell, D.M. (2016) Intraspecific trait variation across scales: implications for
954 understanding global change responses. *Global Change Biology*, **22**, 137-150.
- 955 Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**,
956 403-405.
- 957 Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori,
958 S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J.,
959 Stouffer, R.J., Thomson, A.M., Weyant, J.P. & Wilbanks, T.J. (2010) The next generation of
960 scenarios for climate change research and assessment. *Nature*, **463**, 747-756.
- 961 Münzbergová, Z. (2007) Population dynamics of diploid and hexaploid populations of a perennial herb.
962 *Annals of Botany*, **100**, 1259-1270.
- 963 Natali, S.M., Schuur, E.A.G. & Rubin, R.L. (2012) Increased plant productivity in Alaskan tundra as a result
964 of experimental warming of soil and permafrost. *Journal of Ecology*, **100**, 488-498.
- 965 Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P.,
966 Purugganan, M.D., Richards, C.L., Valladares, F. & van Kleunen, M. (2010) Plant phenotypic
967 plasticity in a changing climate. *Trends in Plant Science*, **15**, 684-692.
- 968 Nunez-Farfan, J. & Schlichting, C.D. (2001) Evolution in changing environments: The "synthetic" work of
969 Clausen, Keck, and Hiesey. *Quarterly Review of Biology*, **76**, 433-457.
- 970 Ohsawa, T. & Ide, Y. (2008) Global patterns of genetic variation in plant species along vertical and
971 horizontal gradients on mountains. *Global Ecology and Biogeography*, **17**, 152-163.
- 972 Oksanen, L. (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, **94**, 27-38.
- 973 Olsen, S.L., Topper, J.P., Skarpaas, O., Vandvik, V. & Klanderud, K. (2016) From facilitation to competition:
974 temperature-driven shift in dominant plant interactions affects population dynamics in
975 seminatural grasslands. *Global Change Biology*, **22**, 1915-1926.
- 976 Padilla, F.M., Aarts, B.H.J., Roijendijk, Y.O.A., de Caluwe, H., Mommer, L., Visser, E.J.W. & de Kroon, H.
977 (2013) Root plasticity maintains growth of temperate grassland species under pulsed water
978 supply. *Plant and Soil*, **369**, 377-386.
- 979 Parmesan, C. & Hanley, M.E. (2015) Plants and climate change: complexities and surprises. *Annals of*
980 *Botany*, **116**, 849-864.
- 981 Pelabon, C., Hansen, T.F., Carter, A.J.R. & Houle, D. (2010) Evolution of variation and variability under
982 fluctuating, stabilizing, and disruptive selection. *Evolution*, **64**, 1912-1925.

- 983 Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. The Johns Hopkins University
984 Press, Baltimore, Maryland, USA.
- 985 Plowman, A.B. & Richards, A.J. (1997) The effect of light and temperature on competition between
986 atrazine susceptible and resistant *Brassica rapa*. *Annals of Botany*, **80**, 583-590.
- 987 Raabová, J., Münzbergová, Z. & Fischer, M. (2007) Ecological rather than geographic or genetic distance
988 affects local adaptation of the rare perennial herb, *Aster amellus*. *Biological Conservation*, **139**,
989 348-357.
- 990 Raabová, J., Münzbergová, Z. & Fischer, M. (2011) The role of spatial scale and soil for local adaptation in
991 *Inula hirta*. *Basic and Applied Ecology*, **12**, 152-160.
- 992 Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A.,
993 Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J. & Vira, B. (2010) Biodiversity
994 conservation: challenges beyond 2010. *Science*, **329**, 1298-1303.
- 995 Ravenscroft, C.H., Fridley, J.D. & Grime, J.P. (2014) Intraspecific functional differentiation suggests local
996 adaptation to long-term climate change in a calcareous grassland. *Journal of Ecology*, **102**, 65-73.
- 997 Rice, W.R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.
- 998 Robinson, E.A., Ryan, G.D. & Newman, J.A. (2012) A meta-analytical review of the effects of elevated CO₂
999 on plant-arthropod interactions highlights the importance of interacting environmental and
1000 biological variables. *New Phytologist*, **194**, 321-336.
- 1001 Sampoux, J.P. & Huyghe, C. (2009) Contribution of ploidy-level variation and adaptive trait diversity to
1002 the environmental distribution of taxa in the 'fine-leaved fescue' lineage (genus *Festuca* subg.
1003 *Festuca*). *Journal of Biogeography*, **36**, 1978-1993.
- 1004 Scheepens, J.F. & Stocklin, J. (2013) Flowering phenology and reproductive fitness along a mountain
1005 slope: maladaptive responses to transplantation to a warmer climate in *Campanula thyrsoides*.
1006 *Oecologia*, **171**, 679-691.
- 1007 Schreiber, S.G., Ding, C., Hamann, A., Hacke, U.G., Thomas, B.R. & Brouard, J.S. (2013) Frost hardiness vs.
1008 growth performance in trembling aspen: an experimental test of assisted migration. *Journal of*
1009 *Applied Ecology*, **50**, 939-949.
- 1010 Selsted, M.B., van der Linden, L., Ibrom, A., Michelsen, A., Larsen, K.S., Pedersen, J.K., Mikkelsen, T.N.,
1011 Pilegaard, K., Beier, C. & Ambus, P. (2012) Soil respiration is stimulated by elevated CO₂ and
1012 reduced by summer drought: three years of measurements in a multifactor ecosystem
1013 manipulation experiment in a temperate heathland (CLIMAITE). *Global Change Biology*, **18**,
1014 1216-1230.
- 1015 Sharma, A.I., Yanes, K.O., Jin, L.Y., Garvey, S.L., Taha, S.M. & Suzuki, Y. (2016) The phenotypic plasticity of
1016 developmental modules. *Evodevo*, **7**, 14.
- 1017 Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A. & Field, C.B. (2002) Grassland
1018 responses to global environmental changes suppressed by elevated CO₂. *Science*, **298**, 1987-
1019 1990.
- 1020 Skálová, H. (2010) Potential and constraints for grasses to cope with spatially heterogeneous radiation
1021 environments. *Plant Ecology*, **206**, 115-125.
- 1022 Skálová, H., Pecháčková, S., Suzuki, J., Herben, T., Hara, T., Hadincová, V. & Krahulec, F. (1997) Within
1023 population genetic differentiation in traits affecting clonal growth: *Festuca rubra* in a mountain
1024 grassland. *Journal of Evolutionary Biology*, **10**, 383-406.
- 1025 Souther, S., Lechowicz, M.J. & McGraw, J.B. (2012) Experimental test for adaptive differentiation of
1026 ginseng populations reveals complex response to temperature. *Annals of Botany*, **110**, 829-837.
- 1027 Springate, D.A., Scarcelli, N., Rowntree, J. & Kover, P.X. (2011) Correlated response in plasticity to
1028 selection for early flowering in *Arabidopsis thaliana*. *Journal of Evolutionary Biology*, **24**, 2280-
1029 2288.

- 1030 Sultan, S.E. (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant*
1031 *Science*, **5**, 537-542.
- 1032 Sultan, S.E. & Bazzaz, F.A. (1993) Phenotypic plasticity in *Polygonum persicaria*. 1. Diversity
1033 and uniformity in genotypic norms of reaction to light. *Evolution*, **47**, 1009-1031.
- 1034 Suseela, V., Conant, R.T., Wallenstein, M.D. & Dukes, J.S. (2012) Effects of soil moisture on the
1035 temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate
1036 change experiment. *Global Change Biology*, **18**, 336-348.
- 1037 Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N.,
1038 de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley,
1039 G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction
1040 risk from climate change. *Nature*, **427**, 145-148.
- 1041 Thompson, J.D. (1991) Phenotypic plasticity as a component of evolutionary change. *Trends in Ecology &*
1042 *Evolution*, **6**, 246-249.
- 1043 Valladares, F., Sanchez-Gomez, D. & Zavala, M.A. (2006) Quantitative estimation of phenotypic plasticity:
1044 bridging the gap between the evolutionary concept and its ecological applications. *Journal of*
1045 *Ecology*, **94**, 1103-1116.
- 1046 Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. & Pearcy, R.W. (2000) Plastic phenotypic response to
1047 light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, **81**, 1925-1936.
- 1048 van Kleunen, M. & Fischer, M. (2005) Constraints on the evolution of adaptive phenotypic plasticity in
1049 plants. *New Phytologist*, **166**, 49-60.
- 1050 Volis, S., Ormanbekova, D., Yermekbayev, K., Song, M.S. & Shulgina, I. (2015) Multi-approaches analysis
1051 reveals local adaptation in the emmer wheat (*Triticum dicoccoides*) at macro- but not micro-
1052 geographical scale. *Plos One*, **10**, 19.
- 1053 Volk, M., Niklaus, P.A. & Korner, C. (2000) Soil moisture effects determine CO₂ responses of grassland
1054 species. *Oecologia*, **125**, 380-388.
- 1055 Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-
1056 Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**,
1057 389-395.
- 1058 Wan, S., Norby, R.J., Ledford, J. & Weltzin, J.F. (2007) Responses of soil respiration to elevated CO₂, air
1059 warming, and changing soil water availability in a model old-field grassland. *Global Change*
1060 *Biology*, **13**, 2411-2424.
- 1061 Williams, D.G. & Black, R.A. (1993) Phenotypic variation in contrasting temperature environments -
1062 growth and photosynthesis in *Pennisetum setaceum* from different altitudes on Hawaii.
1063 *Functional Ecology*, **7**, 623-633.
- 1064 Ye, X.H., Yu, F.H. & Dong, M. (2006) A trade-off between guerrilla and phalanx growth forms in *Leymus*
1065 *secalinus* under different nutrient supplies. *Annals of Botany*, **98**, 187-191.
- 1066 Zhang, H.X., Yu, Q., Huang, Y.X., Zheng, W., Tian, Y., Song, Y.T., Li, G.D. & Zhou, D.W. (2014) Germination
1067 shifts of C-3 and C-4 species under simulated global warming scenario. *Plos One*, **9**.
- 1068 Zhou, W., Wang, Z.X., Davy, A.J. & Liu, G.H. (2013) Geographic variation and local adaptation in *Oryza*
1069 *rufipogon* across its climatic range in China. *Journal of Ecology*, **101**, 1498-1508.

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1072 <http://onlinelibrary.wiley.com/doi/10.1111/1365-2745.12762/supinfo>

1073 **Supporting Information captions**

1074 Text S1. Detailed description of the results comparing plant performance in local vs. foreign
1075 conditions

1076 Figure S2. The effect of cultivation in local vs. foreign moisture and temperature on proportion of
1077 extravaginal ramets created by the plants.

1078 Text S3. Detailed consideration of the possible pseudoreplication issue in the experiment.

1079 Figure S4. The effect of original environment and target environment on plant performance
1080 measured as A) plant height, B) ramet number, C) belowground biomass, D) proportion of
1081 aboveground and belowground biomass and E) rhizome biomass.

1082 Figure S5. Plasticity index of belowground biomass of plants of different origin. ALP denotes the
1083 cold alpine sites, SUB denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4
1084 indicates moisture at the original localities with 1 indicating the driest and 4 the wettest
1085 sites.

1086 Table S6. The effect of original and target temperature and moisture and all their interactions on
1087 plant performance in the growth chambers.

1088 Text S7. Detailed description of the results testing target and origin interaction

1089 Table S8. The effect of foreign vs. local temperature and moisture and their interactions with
1090 temperature and moisture of origin on plant performance in the growth chambers.

1091 Figure S9. The effect of difference in temperature and moisture between target and original
1092 environment (target-origin) on A) number of ramets, B) proportion of extravaginal ramets,
1093 C) aboveground biomass, D) proportion of aboveground and belowground biomass and E)
1094 rhizome biomass.

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