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7 RUNNING HEAD: Community responses to warming

8

9 TITLE: Can trait patterns along gradients predict plant community responses to climate change?

10

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18

19 Elements included in this submission:

- 20 1. This manuscript (*traits_transplants_2016-06-04.docx*).
- 21 2. AppendixS1 (*AppendixS1.docx*).
- 22 3. Supplementary files: The metadata file (*supplementary_file_metadata.docx*) lists and
23 describes the supplementary files, which include the central R Markdown file used in the
24 analysis (*traits_transplants.Rmd*), the scripts that it sources (*custom_functions.R*,
25 *bayesian_immigration_estimates.R*, *neutral_simulation.R*, *simdat_processing_veg.R*,
26 *simdat_processing_traits.R*, *simdat_spp.R*), and a table of the species found in this study
27 and their associated trait data (*species_data.csv*).

28

29 This submission is meant for consideration as an ‘article.’

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30 **Abstract:** Plant functional traits vary consistently along climate gradients and are therefore
31 potential predictors of plant community response to climate change. We test this space-for-time
32 assumption by combining a spatial gradient study with whole-community turf transplantation
33 along temperature and precipitation gradients in a network of twelve grassland sites in Southern
34 Norway. Using data on eight traits for 169 species and annual vegetation censuses of 235 turfs
35 over five years, we quantify trait-based responses to climate change by comparing observed
36 community dynamics in transplanted turfs to field-parameterized null model simulations. Three
37 traits related to species architecture (maximum height, number of dormant meristems, and ramet-
38 ramet connection persistence) varied consistently along spatial temperature gradients and also
39 correlated to changes in species abundances in turfs transplanted to warmer climates. Two traits
40 associated with resource acquisition strategy (SLA, leaf area) increased along spatial temperature
41 gradients but did not correlate to changes in species abundances following warming. No traits
42 correlated consistently with precipitation. Our study supports the hypothesis that spatial
43 associations between plant traits and broad-scale climate variables can be predictive of
44 community response to climate change, but illustrates that not all traits with clear patterns along
45 climate gradients influence community response to an equal degree.

46
47 **Keywords:** Plant functional traits, clonal traits, environmental gradient analysis, turf
48 transplantation, grasslands, alpine plant communities, community response.

50 INTRODUCTION

51 Plant functional traits, defined as measurable species characteristics with explicit
52 connections to individual performance, reflect plant ecological strategy and associate with
53 environmental factors at many spatial and ecological scales (Silvertown 2004, Wright et al. 2005,
54 McGill et al. 2006, Violle et al. 2007). The roles that environmental variables play in structuring
55 community composition are often inferred from patterns of community-weighted mean trait
56 values along spatial gradients (De Bello et al. 2005, Shipley et al. 2006, Kraft et al. 2008,
57 Cornwell and Ackerly 2009). The consistency and prevalence of many trait-climate correlations
58 over space suggests they could be good predictors of community responses to climate change
59 (Lavorel and Garnier 2002, Enquist et al. 2015).

60 However, there are also reasons why spatial trait gradient patterns may be poor predictors
61 of community responses to climate change. First, it is not clear if species will migrate quickly
62 enough to maintain their current associations to climate (Post and Pedersen 2008, Visser 2008).
63 Instead, species assemblages may be in continual flux as species respond and adapt differentially
64 to changing climate conditions (Neilson et al. 2005). Second, rapid climate change could disrupt
65 biotic interaction networks, leading to idiosyncratic species responses that are inconsistent with
66 expectations based on broad-scale trait-environment relationships (Kudo et al. 2004, Post and
67 Pedersen 2008). Third, species may respond to finer-scale changes in environmental variables
68 that cannot be predicted using climate averages (Kimball et al. 2010, Graae et al. 2012).

69 One way to directly evaluate the potential for spatial trait patterns to predict community
70 responses to climate change is to experimentally manipulate climate *in situ* and observe
71 community response (e.g. Hobbie and Chapin III 1998, Hudson et al. 2011). *In situ* approaches
72 allow for precise manipulation of the desired climate variables but suffer from several
73 drawbacks. Most notably, the arrival and establishment of immigrants adapted to the new climate
74 conditions is sharply reduced, effectively removing an important driver of community response
75 to climate change (Gottfried et al. 2012). *In situ* experiments may even *suppress* community
76 responses if propagule pressure from locally abundant species is high enough to exert mass
77 effects on the community compositions of experimental plots. *In situ* climate manipulations also
78 often have undesirable side effects related to their experimental methods (Aronson and McNulty
79 2009).

80 Here, we investigate the effects of climate change on plant communities using an
81 alternative approach: transplantation of entire, intact communities to new climates. Whole-
82 community transplantation avoids the experimental artifacts of climate change manipulations,
83 while exposing the community to immigration from species adapted to the new environment. In
84 fact, transplantation lies at the other extreme of *in situ* climate manipulations: it provides a
85 scenario in which immigration of climate-adapted species is higher than would be expected in
86 communities subject to gradual environmental change. We monitored changes in the functional
87 composition of 235 control and transplanted turf communities over five years within a network
88 of twelve grassland sites in southern Norway. Our measures of functional composition rely on
89 species-level averages of four commonly measured plant traits: leaf area, maximum vegetative
90 height, seed mass, and specific leaf area (SLA), and four less commonly used traits relating to

91 clonal growth strategy: number of offspring per parent, persistence of plant-offspring connection,
92 rate of lateral spread, and bud number (i.e., the number of dormant meristems per ramet). Clonal
93 traits are often overlooked as indicators of plant performance, despite their widespread
94 prevalence and potential significance for community dynamics and ecosystem function,
95 especially in herbaceous plant biomes like grasslands, wetlands, and tundra (Zobel et al. 2010,
96 Cornelissen et al. 2014).

97 Our central goal was to test if traits with broad spatial associations to climate also drive
98 community responses to rapid climate change. To do this, we characterized baseline trait patterns
99 across temperature and precipitation gradients in our system, and then determined if these traits
100 correlated with species performance in turf communities transplanted to warmer and/or wetter
101 conditions. The fact that turf communities were open to immigration from the surrounding
102 vegetation necessitated a careful evaluation of our null expectations. Even under trait-neutral
103 dynamics, natural turnover combined with the immigration and proliferation of locally-abundant
104 species leads transplanted communities to converge compositionally with local sites over time.
105 Thus, any test for trait-mediated dynamics must measure community responses against null
106 expectations that account for stochastic replacement and immigration. We use shifts in species
107 abundances in control turfs to estimate stochastic replacement and immigration at each site, and
108 then use these estimates in model simulations to generate null expectations of turf response to
109 transplantation. Observed deviations from these null expectations are interpreted as evidence for
110 trait-mediated interactions.

111 The unusual topography of southern Norway allowed us to address an additional
112 shortcoming of most spatial gradient studies by methodologically separating temperature and
113 precipitation as potential climate drivers. Ecological studies along climate gradients often use
114 altitudinal transects that vary in both temperature and precipitation (Callaway et al. 2002, Djukic
115 et al. 2010), although not always in a consistent manner (Körner 2007). This covariation makes it
116 difficult to isolate the individual and interactive effects of temperature and precipitation and thus
117 project how vegetation will respond to novel climates. In southern Norway, a west-to-east
118 rainfall gradient interacts with a mosaic of fjords and mountain ridges to generate high climatic
119 heterogeneity over a small geographic area. We exploited this natural heterogeneity to establish a
120 “climate grid” in which temperature and precipitation vary orthogonally among the twelve field
121 sites, thereby allowing us to separate their effects and to identify potential interactions.

122 We use results from our gradient analysis, transplant experiment, and model simulations
123 to address three questions: 1) What is the relative influence of spatial variation in temperature
124 and precipitation on community trait composition? 2) Do the traits that respond to spatial climate
125 gradients also drive community temporal response to climate change? 3) What is the influence of
126 clonal traits relative to more commonly used leaf, seed, and canopy height traits in community
127 response to climate gradients and climate change? We expect short species with conservative
128 resource use strategies (low SLA, low leaf area, slow lateral spread) and/or high capacity for
129 resource integration (persistent ramet-ramet connections, more offspring per ramet, more buds
130 per ramet) to predominate in unproductive climates (the coldest and driest sites) relative to more
131 productive climates (the warmest and wettest sites). Our study is a rigorous experimental
132 evaluation of the assumption that trait patterns along climate gradients reflect, and can therefore
133 predict, how communities will respond to anthropogenic climate change.

134

135 METHODS

136 The study area is an approximately 500 km x 500 km region in southern Norway with
137 marked climatic heterogeneity (Figure 1). Twelve grassland sites were selected with one of three
138 mean summer temperatures (ca. 6.0, 9.0, and 10.5 °C) and one of four mean annual
139 precipitations (ca. 600, 1200, 1900, and 2800 mm), while other environmental variables were
140 relatively consistent (calcareous soil, southwest aspect, slope of about 20 degrees, and
141 comparable grazing and land-use history) (see Table S2 for precise climate data, and Klanderud
142 et al. 2015 for additional site details). The grasslands' short stature (usually < 0.3 m at peak
143 biomass) and shallow but thickly interwoven root and rhizome mats enabled the easy removal,
144 transport, and replanting of 'turfs' and their attached flora to different hillsides. Each 25 x 25 cm
145 turf contained tens to hundreds of individual stems, representing 10 - 40 vascular plant species,
146 with a mean canopy height of 9 ± 6 cm (1 SD). In accordance with predictions that climate
147 change will cause southern Norway to become warmer and wetter (Hanssen-Bauer et al. 2009),
148 40 turfs were transplanted to warmer sites, 45 turfs were transplanted to wetter sites, 30 turfs
149 were transplanted to warmer and wetter sites, 60 control turfs were replanted at the same site,
150 and 60 control turfs were delineated but left undisturbed. All non-local transplants were moved
151 one 'step' warmer and /or wetter in the climate grid. Turfs were transplanted between sites in
152 multiples of five; sample sizes differed by treatment because not all destination sites had cooler

153 and/or drier sites to serve as turf origins (Figure 1). For control turfs, origin and destination sites
154 are the same site. We refer to transplant destinations as 'target sites'; thus 'target controls' refers
155 to control turfs at transplant destination sites. Vascular plant turf community censuses were
156 conducted in 2009 (before transplantation), 2011, 2012, and 2013, for a total of 928 turf
157 community time points. Twelve turf community time points were discarded due to damaged
158 turfs. Percent cover of each species was estimated visually with the aid of a 5 x 5 cm grid. Total
159 percent cover was allowed to fall below or exceed 100% to account for bare patches and/or
160 overlapping species covers (mean cover in control plots across sites and years ranged from $87 \pm$
161 25% to $127 \pm 30\%$).

162
163 **Trait data:** We built a custom database containing values for up to eight traits for the 169
164 species present in our turf communities from across the climate grid. Woody seedlings and
165 unidentifiable individuals represented 1.1% total cover and were discarded. We used four
166 common traits: leaf area (mm^2), specific leaf area (SLA) ($\text{m}^2 \text{kg}^{-1}$), maximum potential canopy
167 height (m), and seed mass (mg), and four traits relating to clonal growth: number of offspring per
168 parent per year (1 or ≥ 2), persistence of plant-offspring connection (< 2 years or ≥ 2 years), rate
169 of lateral spread ($\leq 1 \text{ cm year}^{-1}$ or $> 1 \text{ cm year}^{-1}$), and bud number, i.e., the prevalence of
170 aboveground and belowground dormant meristems. Leaf area and SLA were estimated using a
171 combination of field data and data from the LEDA online trait database (Kleyer et al. 2008). Our
172 field data derive from ~1200 leaves collected in the summer of 2012 for which SLA and leaf area
173 were calculated using established protocols (Cornelissen et al. 2003). We used Pearson
174 correlations to assess the extent to which LEDA species trait values matched field gathered trait
175 values (SLA: $\rho = 0.69$; leaf area: $\rho = 0.73$). Maximum potential height data were mined from Lid
176 and Lid (2007). We drew seed mass data from the Seed Information Database (Royal Botanic
177 Gardens Kew 2014). All continuous trait values were log-transformed. Clonal trait data were
178 extracted from the CLO-PLA database (Klimešová and Bello 2009) and, except for bud number,
179 transformed from categorical to binary metrics to simplify statistical analysis. For bud number,
180 species were assigned a score of 0 (no buds) to 8 (dozens of buds) based on estimates from
181 Klimešová and Bello (2009). Data on individual traits represented 140 - 164 species (84% - 99%
182 of total cover). Eight species (3.9% total cover) were identifiable only to genus but treated as
183 species in downstream analyses. For these species, trait values were either measured in the field

184 (SLA, leaf area), estimated by taking the median trait values of locally-present congeners (seed
185 mass, maximum height, clonal traits), or left blank. Species names and their trait values are
186 provided as a supplementary table (*species_data.csv*). Only two of 28 pairwise comparisons of
187 species trait values were significantly correlated (SLA and bud number, SLA and connection
188 persistence; see Table S1); apart from these two exceptions, we consider trait responses to be
189 statistically independent.

190
191 **Community analyses:** We quantified differences in species composition using Bray-Curtis
192 dissimilarity. Community weighted means (CWMs) were used to quantify differences in
193 functional composition. We used species-level trait values in these calculations; thus, changes in
194 CWM reflect changes in species composition, not trait plasticity. A CWM is calculated by
195 averaging the values of a trait for all species in a community, weighted by their abundance (here,
196 percent cover). For lateral spread, connection persistence, and offspring per ramet, CWMs
197 reflected the proportion of the community with the higher value category (≥ 2 offspring per
198 parent, ≥ 2 years connection persistence, or $> 1\text{ cm year}^{-1}$ lateral spread). Pre-transplant (2009)
199 turf CWMs were regressed onto temperature and precipitation site means to assess community
200 trait patterns in environmental space. AIC values were used to determine when temperature,
201 precipitation, and/or their interaction were significant predictors ($p < 0.05$) in abundance-
202 weighted multiple linear regressions. For a deeper investigation of species-level variation in
203 community composition see Klanderud et al. (2015).

204 We quantified community change as shifts in dissimilarity over time between a turf and
205 its target site controls. Each site had five undisturbed controls and five controls replanted nearby
206 which enabled us to test for the effects of transplantation *per se*. Dissimilarity in species
207 composition among undisturbed controls was only statistically different ($p < 0.05$) from the
208 mean dissimilarity between undisturbed and replanted controls in 5 of 48 of turf community time
209 points, suggesting that transplantation *per se* did not noticeably affect species composition. Thus,
210 in some analyses, replanted controls and undisturbed controls are combined to increase the
211 control group sample size to ten per site.

212
213 **Null model rationale and process:** We used simulations to generate null expectations of turf
214 community responses to transplantation, and then determined when observed community

215 responses deviated from these null expectations. Our model is similar in principle to stochastic
216 models of species abundances using Hubbell's (2001) neutral local community model, but is
217 applied to a smaller spatial scale. For each step in the model, an individual is randomly removed
218 from the turf community and either replaced with a randomly selected offspring from the same
219 turf community (with probability $1 - m$), or replaced with a randomly selected offspring from the
220 site-level community (with probability m). Each step is a 'replacement event.' The site-level
221 community is conceptually equivalent to Hubbell's 'metacommunity', and is defined as the net
222 composition of the ten control turfs present at each site. The model has two parameters:
223 replacement rate (d), the number of replacement events that occur between consecutive years,
224 and immigration rate (m), the probability that replacements are drawn from the site-level
225 community pool as opposed to from within the turf-level community pool (see next section for
226 parameter estimation). Even though turfs are only 25 x 25 cm in size, we expected within-turf
227 recruitment to be high because most species in our system exhibit some degree of clonal growth
228 (Klimešová and Bello 2009), and nearly all new stems are vegetative outgrowths from extant
229 genets rather than seed germination events (Berge, Klanderud, Vandvik, unpublished data).

230 Our model differs from Hubbell's community model in three important ways. First, rather
231 than using births and deaths of individuals to quantify demographic changes, which would be
232 impractical to measure in our predominantly clonal system, we use increases and decreases in
233 percent cover units. Second, we relax the assumption of zero-sum replacement and instead force
234 simulated percent cover to match observed percent cover in each year of the experiment. Third,
235 we allow site-level communities, i.e., the source pools for migrants entering experimental turfs,
236 to vary by recalculating them after each census. The latter two modifications account for
237 temporal variability in the productivity or composition of site-level communities due to drift or
238 short-term climatic variability.

239 We simulated community dynamics from 2009 to 2013 on an individual turf basis,
240 calculating species and trait dissimilarities to target site controls each year. Compositional
241 changes in each turf were simulated 100 times and the resulting values were averaged.
242 Simulation data for 2010 were not presented because field observations do not exist for that year.
243 Paired t-tests were used to determine when observed and simulated null expectations differed
244 significantly.

245

246 **Estimating model parameters:** We used community census data from our control turfs to
247 estimate replacement rate (d) and immigration rate (m) at each site. We set d equal to half the
248 sum of differences in species covers in control turfs between years at each site. We divided by
249 two because each replacement event constitutes two shifts in species covers, one increase and
250 one decrease. Values of d ranged from 19.7 to 37.4. Our method of estimating d ignores self-
251 replacement and thus likely underestimates actual replacement rates; however, a visual
252 inspection of model fit under a broad range of parameter values illustrates that our results are
253 robust to moderate increases in replacement rate (Figure S3). Furthermore, it should be noted
254 that any potential underestimates in replacement rates do not affect estimates of immigration
255 rates.

256 We estimated m using a Bayesian approach based on shifts in species abundances in the
257 five replanted control turfs at each site over three consecutive years (2011-2013), assuming
258 neutral dynamics. The net composition of the five undisturbed control turfs at each site was used
259 as the site-level community. The expected cover λ of species i in a turf community at time t is
260 formally defined as

$$261 \quad \lambda_{i,t} = J_{t-1}[(1 - m) \times C_{i,t-1} + m \times P_{i,t-1}]$$

262 where J_{t-1} is the total cover of the turf community in the previous year, $C_{i,t-1}$ is the relative
263 abundance of species i in the turf community the previous year, $P_{i,t-1}$ is the relative abundance of
264 the species in the site-level community at time t , and m is the immigration parameter. The
265 percent cover y , rounded to the nearest whole number, of species i in turf community at time t
266 was modelled assuming

$$267 \quad y_{i,t} \sim \text{Poisson}(\lambda_{i,t}).$$

268 We gave m a uniform prior with a range from 0 to 1. We also explored using an informed prior
269 ($m < 0.5$) based on the expected predominance of clonal growth and within-turf recruitment, but
270 this led to identical results and was dropped. We fit the model using MCMC implemented in
271 JAGS 3.4.0 (Plummer 2003). We ran JAGS through the R package R2jags (Su and Yajima
272 2012). For each model fit, we ran three chains, used a burn-in of 1000 iterations, and chose
273 initial values in different regions of parameter space. We confirmed model convergence using
274 Gelman-Rubin diagnostics (Brooks and Gelman 1998). We assessed overall model fit by
275 regressing mean posterior estimates for percent cover on observed data ($R^2 = 0.63$). See Table S2

276 for parameter estimates. For a deeper exploration of how a Bayesian approach can be used to fit
277 a trait-neutral model of community change to time series data see Mutshinda et al. (2008).

278

279 RESULTS

280 Community weighted means (CWMs) of leaf area, SLA, maximum height and lateral
281 spread increased with temperature along spatial gradients, and CWM values of bud number and
282 connection persistence decreased with temperature along spatial gradients (Table 1, Figure 2). In
283 three of the eight traits, the best-fit weighted multiple linear regression model included
284 precipitation as a predictor variable, but the coefficient of the precipitation variable itself was
285 never significantly different from 0. The interaction of temperature and precipitation had a
286 significant effect on SLA. Exponential curves with increasing temperature fit bud number and
287 connection persistence patterns better than linear ones, reflecting stronger responses in the colder
288 part of the climate grid (Figure 2). Based on these associations, we limited our analysis of trait
289 convergence in transplanted turfs over time to the six traits with spatial associations to
290 temperature, and to turfs transplanted to warmer climates.

291 Species and trait compositions of transplanted turfs converged towards target site controls
292 over time, with the magnitude of convergence increasing with initial dissimilarity (Figure 3).
293 Rates of convergence in species composition only exceeded null model predictions that
294 accounted for random replacement by local immigrants in 2011 (Figure 4). In contrast, rates of
295 convergence in maximum height, bud number, and connection persistence consistently exceeded
296 null model predictions (Figure 4). These deviations from null expectations were driven by
297 responses across many species rather than responses in just a few of the most abundant taxa
298 (Figure S4). Site-level climate data confirm that transplanted turfs experienced consistently
299 warmer temperatures as intended (Figure S1, Figure S2).

300

301 DISCUSSION

302 Our study uses observational and experimental data to test the assumption that traits with
303 broad-scale associations to climate in space are predictive of plant community response to
304 climate change in time. This space-for-time assumption is supported when using three traits
305 related to species architecture, but not supported when using three traits related to species
306 resource use strategy. Our results underscore the importance of using ecologically relevant traits

307 when making predictions of community response, and suggest that in our grassland system,
308 architectural traits may exert more influence on initial species response to rapid warming than
309 the more commonly used growth-related traits.

310
311 **Trait patterns along climate gradients:** Despite the large range in both mean summer
312 temperature and annual precipitation across sites, CWMs trended only with temperature. The
313 lack of functional turnover over a nearly 2500 mm year⁻¹ increase in precipitation is surprising
314 given the consistent directional turnover in species composition along both temperature and
315 precipitation gradients in our system (Klanderud et al. 2015), underscoring the fact that species
316 turnover does not always beget functional turnover (Hooper et al. 2002). This finding contrasts
317 with vegetation trait patterns found elsewhere over narrower ranges of precipitation (Fonseca et
318 al. 2000, Wright et al. 2005). A lack of precipitation effects could occur if soil moisture is similar
319 at all sites and/or not limiting at any sites, however this seems unlikely given the large range in
320 mean annual precipitation and the otherwise similar site abiotic conditions. Regardless of the
321 mechanism, the implication is that functional shifts in these grasslands are likely to occur in
322 response to changes in temperature, not precipitation.

323 The consistent shifts in CWMs with increasing temperature in our system signify shifts in
324 plant ecological strategy. Increases in leaf area, SLA, and the rate of lateral spread with
325 temperature suggest a shift from slow-growing stress-tolerant species to fast-growing species
326 with acquisitive resource use strategies (Sterck et al. 2006, Rusch et al. 2011). Also increasing
327 with temperature are maximum height, duration of connection persistence, and bud number,
328 three traits related to plant architecture. The increase in CWMs of maximum height may reflect a
329 tradeoff in the ability to compete for light at warm sites amenable to growth and the ability to
330 tolerate wind stress and freezing temperatures at the coldest sites (Westoby 1998, Falster and
331 Westoby 2003). Higher CWMs of bud number and connection persistence at the coldest sites
332 may reflect an increased importance of resource integration and/or recovery from disturbances
333 (Klimešová and Klimes 2007), although we see no obvious reasons why resources would be
334 patchier and/or disturbances more common at the coldest sites. More work is needed to confirm
335 the functional roles of these understudied clonal traits and their role in organizing grassland
336 species along gradients.

337

338 **Community responses to warming:** The central goal of this study was to test the hypothesis
339 that trait-climate relationships over space are predictive of temporal community response to
340 climate change in time, a common assumption in climate change research. Of the six traits with
341 significant trends with temperature in space, maximum height, bud number, and connection
342 persistence - three traits related to species architecture - associated consistently with turf
343 community response to warming in time. The large deviation in maximum height from neutral
344 expectations may be have resulted from competition for light being more intense in more
345 productive, warmer conditions, and taller species preempting access to light, shading out
346 competitors, and earning disproportionate returns due to size-asymmetric competition
347 (Schwinning and Weiner 1998). Species with fewer buds and reduced connection persistence
348 succeeded disproportionately following warming, suggesting that the development and
349 maintenance of these clonal traits, which are believed to support new ramets under stressful
350 conditions (Klimešová and Klimes 2007), comes at a cost when conditions are more amenable to
351 growth. That CWMs of architectural traits deviated from neutral expectations of community
352 response while CWMs of growth-related traits (SLA, leaf area, lateral spread) did not, despite
353 showing strong trends along spatial temperature gradients, is unexpected and interesting.
354 Perhaps, the capacity for rapid growth is not useful to new ramets vying for resources in
355 grassland communities already packed with established individuals (but see: Wildová et al.
356 2007). Alternatively, SLA and leaf area may be poor predictors of growth in herbaceous species
357 with photosynthetic stems. The strong responses of clonal traits to changes in temperature
358 highlight the need for more emphasis on clonal traits in studies of community response to
359 climate change and herbaceous community assembly in general.

360 Defining null expectations was challenging given the lack of standard practices of how to
361 model demographic stochasticity in predominantly clonal systems (Eriksson 1994).
362 Traditionally, demographic analyses rely on population numbers and vital rates, but the concepts
363 of individuals, populations, births, and deaths break down in clonal, modular organisms. For
364 instance, ramet number is impractical to measure and may not be demographically meaningful
365 for graminoids that form hummocks with clumps of stems (e.g. *Festuca ovina*), nor is it possible
366 to distinguish individuals in forbs with sprawling aboveground stems with adventitious roots
367 (e.g. *Veronica biflora*), or species that divide via root splitting which results in fragmentation just
368 below the litter layer (e.g. *Cerastium alpinum*). Our decision to simulate demographic changes

369 using percent cover units therefore has both practical and conceptual appeal. The drawback,
370 however, is that percent cover is sensitive to factors that are not demographically significant,
371 such as variation in phenological stage among individuals, species, and sampling times, and thus
372 may inaccurately reflect shifts in abundance between years. Nevertheless, our approach accounts
373 for demographic stochasticity, annual variation in community-level composition, and the realities
374 of dispersal limitation in a predominantly clonal system to generate explicit null expectations of
375 community response to perturbation.

376

377 **Conclusions and future directions:** Using patterns in CWMs along environmental gradients to
378 forecast community response to climate change is an intuitively appealing approach. Our study
379 provides qualified support for such an approach: three of the six traits with spatial associations to
380 temperature in our system associated significantly with species success following transplantation
381 to warmer climates. Evidently, spatial associations between plant traits and broad-scale climate
382 variables can be predictive of community response to climate change, but are not always so.

383 Our results shed some light on how our system could respond to climate change in the
384 coming decades. Despite high rates of annual turnover, without gaps created by disturbances,
385 virtually all replacement stems are clonal outgrowths of extant genets rather than new seedlings
386 (Bullock et al. 1995; Berge, Klanderud, Vandvik, unpublished data). Thus, the potential for
387 community change is largely limited by the prevalence of gaps and the proportion of species in
388 the seed rain that are immigrants rather than local species. Once established, warmer-adapted
389 immigrants will likely proliferate vegetatively, outcompeting species adapted to cooler
390 temperatures (Olsen et al. 2016). Our approach and conclusions underscore the importance of
391 accounting for stochasticity and immigration when making predictions of community response
392 (Tilman 2004, Shipley et al. 2011). Future studies should consider the effects of dispersal
393 limitation on short-term transient responses, and how disturbances and dispersal limitation will
394 affect long-term equilibrium responses. Predictions of ‘extinction debts’ and ‘immigration
395 credits’ in the field of habitat distribution modeling are an important step in the right direction
396 (Dirnböck and Dullinger 2004), but could be developed further by considering how and when
397 traits modulate species interactions.

398

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403

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531

532 TABLE 1: Summary statistics for best-fit weighted linear models for each trait

Trait	Variable	Estimate	SE	t-statistic	p-value
Bud Number	exp(-Temp)	118.15	52.83	2.24	0.049
Lat. Spread	Temp	0.04	0.01	2.50	0.031
Leaf Area	Temp	0.05	0.01	3.83	0.004
	Precip	< 0.01	< 0.01	-1.50	0.167
Max. Height	Temp	0.05	0.01	4.26	0.002
Offspring	(none)				
Persistence	exp(-Temp)	109.14	19.28	5.66	< 0.001
Seed Mass	(none)				
SLA	Temp	0.02	0.00	5.35	< 0.001
	Precip	< 0.01	< 0.01	-1.24	0.251
	Temp x Precip	< 0.01	< 0.01	2.48	0.038

533

534 Summary statistics for best-fit weighted multiple linear regression models for each trait using
 535 mean summer temperature, annual precipitation, and their interaction as potential predictor
 536 variables, weighted by the sample size at each site (N ranges from 10 to 25). Model fit was
 537 determined using AIC values. For bud number and connection persistence, exponentially
 538 transforming the temperature axis resulted in better model fit. Turf-level community weighted
 539 trait means and significant regressions are shown in Figure 2.

540

541 **Figure 1:** Panel A: a schematic illustration of the orthogonal nature of climate variables across
542 experimental sites, with black arrows representing the directions of turf transplants in replicates
543 of five. Panels B and C show the geographical locations of experimental sites in southern
544 Norway. Symbol shapes and shadings reflect mean summer temperature levels and mean annual
545 precipitation levels, respectively, in accordance with panel A.

546

547 **Figure 2:** Community weighted trait means (CWMs) of turfs before transplantation along natural
548 gradients of mean summer temperature (left) and mean annual precipitation (right). CWMs are
549 aggregated by site (N ranges from 10 to 25). Vertical lines show ± 1 S.D. Symbol shapes and
550 shadings reflect temperature and precipitation levels, respectively, in accordance with Figure 1A.
551 Best-fit lines are shown as solid lines when trait-gradient relationships are significant; for
552 simplicity, trend lines represent univariate regressions, even if multivariate regressions led to
553 higher AIC values. The interactive effects of temperature and precipitation on SLA is shown
554 using three trend lines ($\sim 3^{\circ}\text{C}$: dotted, $\sim 6^{\circ}\text{C}$: dashed, $\sim 9^{\circ}\text{C}$: dot-dashed). CWMs in seed mass and
555 offspring per ramet did not exhibit significant trends along temperature or precipitation gradients
556 and are therefore omitted. See Table 1 for model summary statistics.

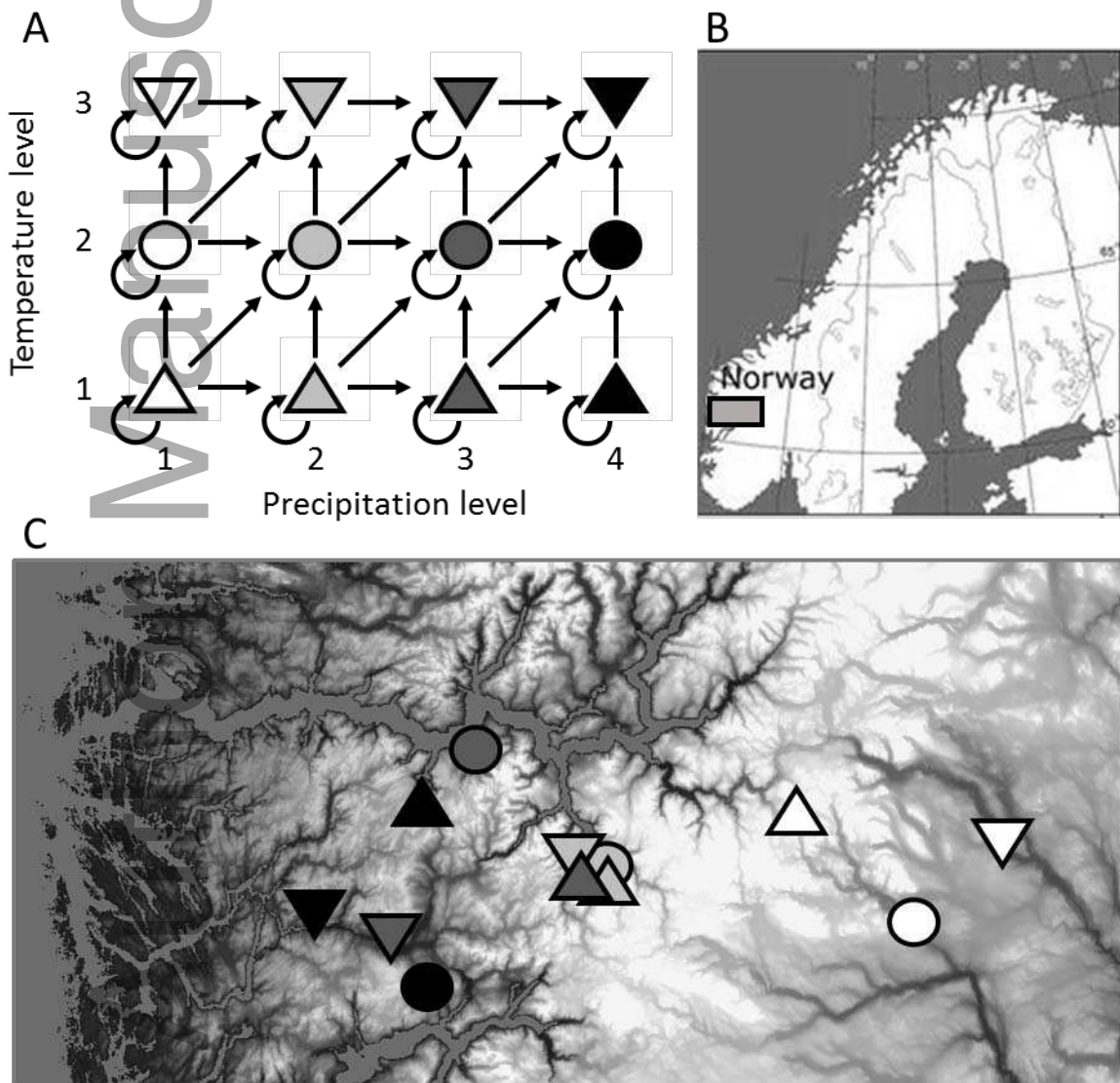
557

558 **Figure 3:** Changes in dissimilarity of turfs transplanted to warmer climates and target site
559 controls from 2009 to 2013. The x-axis shows Bray-Curtis dissimilarity between turfs and the
560 centroids of their control turfs in 2009; the y-axis shows how that dissimilarity changed by 2013.
561 Each symbol represents a turf community. Grey crosses represent control turfs; black circles
562 represent transplanted turfs. Dissimilarity was calculated using Bray-Curtis distance for species
563 composition (top left panel) or Euclidian distance of community weighted means (all remaining
564 panels). Symbols below zero on the y-axis reflect turf communities that converged
565 compositionally towards target controls, whereas communities above zero on the y-axis diverged
566 compositionally. Dashed vertical lines are placed at 50% of mean dissimilarity among controls as
567 an approximation of natural community stochasticity. Grey ellipses represent 95% confidence
568 intervals of the centroids of control turf dissimilarities.

569

570 **Figure 4:** Mean trait dissimilarities of transplanted turf communities and target controls from
 571 2009 to 2013. Solid lines represent observed field data. Dashed lines represent simulated null
 572 expectations based on the means of 100 null model simulation runs. Dotted lines represent mean
 573 dissimilarity among control turfs within sites. Null model simulations use estimates of
 574 replacement and immigration rates derived from our field data (see Methods). Error bars show
 575 95% confidence intervals. Statistical differences between observed and simulated community
 576 weighted means are shown when $p < 0.05$ (*).

577 FIGURE 1



578

