WILEY   ECOLOGY

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

| Abstract: | Plant functional traits vary consistently along climate gradients and are therefore potential predictors of plant community response to climate change. We test this space-for-time assumption by combining a spatial gradient study with whole-community turf transplantation along temperature and precipitation gradients in a network of twelve grassland sites in Southern Norway. Using data on eight traits for 169 species and annual vegetation censuses of 235 turfs over five years, we quantify trait-based responses to climate change by comparing observed community dynamics in transplanted turfs to field-parameterized null model simulations. Three traits related to species architecture (maximum height, number of dormant meristems, and ramet-ramet connection persistence) varied consistently along spatial temperature gradients and also correlated to changes in species abundances in turfs transplanted to warmer climates. Two traits associated with resource acquisition strategy (SLA, leaf area) increased along spatial temperature gradients but did not correlate to |

	changes in species abundances following warming. No traits correlated consistently with precipitation. Our study supports the hypothesis that spatial associations between plant traits and broad-scale climate variables can be predictive of community response to climate change, but illustrates that not all traits with clear patterns along climate gradients influence community response to an equal degree.

Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.

traitsTransplants.Rmd
bayesian_immigration_estimates.R
custom_functions.R
neutral_simulation.R
traitdataTable.csv

1   RUNNING HEAD: Community responses to warming

2

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

4

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13   Elements included in this submission:

14   1. This manuscript (*Guittar_etal_2016April.docx*).

15   2. Supporting information (*Guittar_etal_2016April_SupportingInformation.docx*).

16   3. Rmd/R Scripts: *TraitAnalysis_2016April.Rmd*: The R markdown document used to

17   process the data and generate the tables and figures in this study. The file will not run

18   without the raw data (not yet included). It sources code from seven other scripts

19   (*Guittar_etal_Rscripts.zip*).

20   4. *traitdataTable.csv*: a list of species found in this study and their accompanying trait data.

21

22   This submission is meant for consideration as an 'article.'

23   **Abstract:** Plant functional traits vary consistently along climate gradients and are therefore

24   potential predictors of plant community response to climate change. We test this space-for-time

25   assumption by combining a spatial gradient study with whole-community turf transplantation

26   along temperature and precipitation gradients in a network of twelve grassland sites in Southern

27   Norway. Using data on eight traits for 169 species and annual vegetation censuses of 235 turfs

28   over five years, we quantify trait-based responses to climate change by comparing observed

29   community dynamics in transplanted turfs to field-parameterized null model simulations. Three

30   traits related to species architecture (maximum height, number of dormant meristems, and ramet-

31   ramet connection persistence) varied consistently along spatial temperature gradients and also

32   correlated to changes in species abundances in turfs transplanted to warmer climates. Two traits

33   associated with resource acquisition strategy (SLA, leaf area) increased along spatial temperature

34   gradients but did not correlate to changes in species abundances following warming. No traits

35   correlated consistently with precipitation. Our study supports the hypothesis that spatial

36   associations between plant traits and broad-scale climate variables can be predictive of

37   community response to climate change, but illustrates that not all traits with clear patterns along

38   climate gradients influence community response to an equal degree.

39

42

43   INTRODUCTION

44   Plant functional traits, defined as measurable species characteristics with explicit

45   connections to individual performance, reflect plant ecological strategy and associate with

46 environmental factors at many spatial and ecological scales (Silvertown 2004, Wright et al. 2005,

47 McGill et al. 2006, Violle et al. 2007). The role that environmental variables play in structuring

48 community composition is often inferred from patterns of community-weighted mean trait values

49 along spatial gradients (De Bello et al. 2005, Shipley et al. 2006, Kraft et al. 2008, Cornwell and

50 Ackerly 2009). The consistency and prevalence of many trait-climate correlations over space

51 suggests they could be good predictors of community responses to climate change (Lavorel and

52 Garnier 2002, Enquist et al. 2015).

53 However, there are also reasons why spatial trait gradient patterns may be poor predictors

54 of community responses to climate change. First, it is not clear if species will migrate quickly

55 enough to maintain their current associations to climate (Post and Pedersen 2008, Visser 2008).

56 Instead, species assemblages may be in continual flux as species respond and adapt differentially

57 to changing climate conditions (Neilson et al. 2005). Second, rapid climate change could disrupt

58 biotic interaction networks, leading to idiosyncratic species responses that are inconsistent with

59 expectations based on broad-scale trait-environment relationships (Kudo et al. 2004, Post and

60 Pedersen 2008). Third, species may respond to finer-scale changes in environmental variables

61 that cannot be predicted using climate averages (Kimball et al. 2010, Graae et al. 2012).

62 One way to directly evaluate the potential for spatial trait patterns to predict community

63 responses to climate change is to experimentally manipulate climate *in situ* and observe

64 community response (e.g. Hobbie and Chapin III 1998, Hudson et al. 2011). *In situ* approaches

65 allow for precise manipulation of the desired climate variables but suffer from several

66 drawbacks. Most notably, the arrival and establishment of immigrants adapted to the new climate

67 conditions is sharply reduced, effectively removing an important driver of community response

68 to climate change (Gottfried et al. 2012). *In situ* experiments may even *suppress* community

69   responses if propagule pressure from locally abundant species is high enough to exert mass

70   effects on the community compositions of experimental plots. *In situ* climate manipulations also

71   often have undesirable side effects related to their experimental methods (Aronson and McNulty

72   2009).

73   Here, we investigate the effects of climate change on plant communities using an

74   alternative approach: transplantation of entire, intact communities to new climates. Whole-

75   community transplantation avoids the experimental artifacts of climate change manipulations,

76   while exposing the community to immigration from species adapted to the new environment. In

77   fact, transplantation lies at the other extreme of *in situ* climate manipulations: it provides a

78   scenario in which immigration of climate-adapted species is higher than would be expected in

79   communities subject to gradual environmental change. We monitored changes in the functional

80   composition of 235 control and transplanted turf communities over five years within a network

81   of twelve grassland sites in southern Norway. Our measures of functional composition rely on

82   species-level averages of four commonly measured plant traits: leaf area, maximum vegetative

83   height, seed mass, and specific leaf area (SLA), and four less commonly used traits relating to

84   clonal growth strategy: number of offspring per parent, persistence of plant-offspring connection,

85   rate of lateral spread, and bud number (i.e., the number of dormant meristems per ramet). Clonal

86   traits are often overlooked as indicators of plant performance, despite their widespread

87   prevalence and potential significance for community dynamics and ecosystem function,

88   especially in herbaceous plant biomes like grasslands, wetlands, and tundra (Zobel et al. 2010,

89   Cornelissen et al. 2014).

90   Our central goal was to test if traits with broad spatial associations to climate also drive

91   community responses to rapid climate change. To do this, we characterized baseline trait patterns

92 across temperature and precipitation gradients in our system, and then determined if these traits

93 correlated with species performance in turf communities transplanted to warmer and/or wetter

94 conditions. The fact that turf communities were open to immigration from the surrounding

95 vegetation necessitated a careful evaluation of our null expectations. Even under trait-neutral

96 dynamics, natural turnover combined with the immigration and proliferation of locally-abundant

97 species leads transplanted communities to converge compositionally with local sites over time.

98 Thus, any test for trait-mediated dynamics must measure community responses against null

99 expectations that account for stochastic replacement and immigration. We use shifts in species

100 abundances in control turfs to estimate stochastic replacement and immigration at each site, and

101 then use these estimates in model simulations to generate null expectations of turf response to

102 transplantation. Observed deviations from these null expectations are interpreted as evidence for

103 trait-mediated interactions.

104   The unusual topography of southern Norway allowed us to address an additional

105 shortcoming of most spatial gradient studies by methodologically separating temperature and

106 precipitation as potential climate drivers. Ecological studies along climate gradients often use

107 altitudinal transects that vary in both temperature and precipitation (Callaway et al. 2002, Djukic

108 et al. 2010), although not always in a consistent manner (Körner 2007). This covariation makes it

109 difficult to isolate the individual and interactive effects of temperature and precipitation and thus

110 project how vegetation will respond to novel climates. In southern Norway, a west-to-east

111 rainfall gradient interacts with a mosaic of fjords and mountain ridges to generate high climatic

112 heterogeneity over a small geographic area. We exploited this natural heterogeneity to establish a

113 "climate grid" in which temperature and precipitation vary orthogonally among the twelve field

114 sites, thereby allowing us to separate their effects and to identify potential interactions.

115   We use results from our gradient analysis, transplant experiment, and model simulations

116   to address three questions: 1) What is the relative influence of spatial variation in temperature

117   and precipitation on community trait composition? 2) Do the traits that respond to spatial climate

118   gradients also drive community temporal response to climate change? 3) What is the influence of

119   clonal traits relative to more commonly used leaf and canopy height traits in community

120   response to climate gradients and climate change? We expect short species with conservative

121   resource use strategies (low SLA, low leaf area, slow lateral spread) and/or high capacity for

122   resource integration (persistent ramet-ramet connections, more offspring per ramet, more buds

123   per ramet) to predominate in unproductive climates (the coldest and driest sites) relative to more

124   productive climates (the warmest and wettest sites). Our study is a rigorous experimental

125   evaluation of the assumption that trait patterns along climate gradients reflect, and can therefore

126   predict, how communities will respond to anthropogenic climate change.

127

128   METHODS

129   The study area is an approximately 500 km x 500 km region in southern Norway with

130   marked climatic heterogeneity (Figure 1). Twelve grassland sites were selected with one of three

131   mean summer temperatures (ca. 6.0, 9.0, and 10.5 °C) and one of four mean annual

132   precipitations (ca. 600, 1200, 1900, and 2800 mm), while other environmental variables were

133   relatively consistent (calcareous soil, southwest aspect, slope of about 20 degrees, and

134   comparable grazing and land-use history) (see Table S2 for precise climate data, and Klanderud

135   et al. 2015 for additional site details). The grasslands' short stature (usually < 0.3 m at peak

136   biomass) and shallow but thickly interwoven root and rhizome mats enabled the easy removal,

137   transport, and replanting of 'turfs' and their attached flora to different hillsides. Each 25 x 25 cm

138   turf contained tens to hundreds of individual stems, representing 10 - 40 vascular plant species,

139   with a mean canopy height of 9 ± 6 cm (1 SD). In accordance with predictions that climate

140   change will cause southern Norway to become warmer and wetter (Hanssen-Bauer et al. 2009),

141   40 turfs were transplanted to warmer sites, 45 turfs were transplanted to wetter sites, 30 turfs

142   were transplanted to warmer and wetter sites, 60 control turfs were replanted at the same site,

143   and 60 control turfs were delineated but left undisturbed. All non-local transplants were moved

144   one 'step' warmer and /or wetter in the climate grid. Turfs were transplanted between sites in

145   multiples of five; sample sizes differed by treatment because not all destination sites had cooler

146   and/or drier sites to serve as turf origins (Figure 1). For control turfs, origin and destination sites

147   are the same site. We refer to transplant destinations as 'target sites'; thus 'target controls' refers

148   to control turfs at transplant destination sites. Vascular plant turf community censuses were

149   conducted in 2009 (before transplantation), 2011, 2012, and 2013, for a total of 928 turf

150   community time points. Twelve turf community time points were discarded due to damaged

151   turfs. Percent cover of each species was estimated visually with the aid of a 5 x 5 cm grid. Total

152   percent cover was allowed to fall below or exceed 100% to account for bare patches and/or

153   overlapping species covers (mean cover in control plots across sites and years ranged from $87 \pm$

154   25% to $127 \pm 30\%$).

155

156   **Trait data:** We built a custom database containing values for up to eight traits for the 169

157   species present in our turf communities from across the climate grid. Woody seedlings and

158   unidentifiable individuals represented 1.1% total cover and were discarded. We used four

159   common traits: leaf area (mm^2), specific leaf area (SLA) ($m^2\ kg^{-1}$), maximum potential canopy

160   height (m), and seed mass (mg), and four traits relating to clonal growth: number of offspring per

161   parent per year (1 or $\geq$ 2), persistence of plant-offspring connection (< 2 years or $\geq$ 2 years), rate

162   of lateral spread ($\leq$ 1 cm year^{-1} or > 1 cm year^{-1}), and bud number, i.e., the prevalence of

163   aboveground and belowground dormant meristems. Leaf area and SLA were estimated using a

164   combination of field data and data from the LEDA online trait database (Kleyer et al. 2008). Our

165   field data derive from ~1200 leaves collected in the summer of 2012 for which SLA and leaf area

166   were calculated using established protocols (Cornelissen et al. 2003). We used Pearson

167   correlations to assess the extent to which LEDA species trait values matched field gathered trait

168   values (SLA: ρ = 0.69; leaf area: ρ = 0.73). Maximum potential height data were mined from Lid

169   and Lid (2007). We drew seed mass data from the Seed Information Database (Royal Botanic

170   Gardens Kew 2014). All continuous trait values were log-transformed. Clonal trait data were

171   extracted from the CLO-PLA database (Klimešová and Bello 2009) and, except for bud number,

172   transformed from categorical to binary metrics to simplify statistical analysis. For bud number,

173   species were assigned a score of 0 (no buds) to 8 (dozens of buds) based on estimates from

174   Klimešová and Bello (2009). Data on individual traits represented 140 - 164 species (84% - 99%

175   of total cover). Eight species (3.9% total cover) were identifiable only to genus but treated as

176   species in downstream analyses. For these species, trait values were either measured in the field

177   (SLA, leaf area), estimated by taking the median trait values of locally-present congeners (seed

178   mass, maximum height, clonal traits), or left blank. Species lists and trait values are available on

179   Dryad (*pending*). Only two of 28 pairwise comparisons of species trait values were significantly

180   correlated (SLA and bud number, SLA and connection persistence; see Table S1); apart from

181   these two exceptions, we consider trait responses to be statistically independent.

182

183 **Community analyses:** We quantified differences in species composition using Bray-Curtis

184 dissimilarity. Community weighted means (CWMs) were used to quantify differences in

185 functional composition. We used species-level trait values in these calculations; thus, changes in

186 CWM reflect changes in species composition, not trait plasticity. A CWM is calculated by

187 averaging the values of a trait for all species in a community, weighted by their abundance (here,

188 percent cover). For lateral spread, connection persistence, and offspring per ramet, CWMs

189 reflected the proportion of the community with the higher value category ($\geq$ 2 offspring per

190 parent, $\geq$ 2 years connection persistence, or > 1cm $year^{-1}$ lateral spread). Pre-transplant (2009)

191 turf CWMs were regressed onto temperature and precipitation site means to assess community

192 trait patterns in environmental space. AIC values were used to determine when temperature,

193 precipitation, and/or their interaction were significant predictors ($p < 0.05$) in abundance-

194 weighted multiple linear regressions. For a deeper investigation of species-level variation in

195 community composition see Klanderud et al. (2015).

196   We quantified community change as shifts in dissimilarity over time between a turf and

197 its target site controls. Each site had five undisturbed controls and five controls replanted nearby

198 which enabled us to test for the effects of transplantation *per se*. Dissimilarity in species

199 composition among undisturbed controls was only statistically different ($p < 0.05$) from the

200 mean dissimilarity between undisturbed and replanted controls in 5 of 48 of turf community time

201 points, suggesting that transplantation *per se* did not noticeably affect species composition. Thus,

202 in some analyses, replanted controls and undisturbed controls are combined to increase the

203 control group sample size to ten per site.

204

205   **Null model rationale and process:** We used simulations to generate null expectations of turf

206   community responses to transplantation, and then determined when observed community

207   responses deviated from these null expectations. Our model is similar in principle to stochastic

208   models of species abundances using Hubbell's (2001) neutral local community model, but is

209   applied to a smaller spatial scale. For each step in the model, an individual is randomly removed

210   from the turf community and either replaced with a randomly selected offspring from the same

211   turf community (with probability $1 - m$), or replaced with a randomly selected offspring from the

212   site-level community (with probability m). Each step is a 'replacement event.' The site-level

213   community is conceptually equivalent to Hubbell's 'metacommunity', and is defined as the net

214   composition of the ten control turfs present at each site. The model has two parameters:

215   replacement rate (d), the number of replacement events that occur between consecutive years,

216   and immigration rate (m), the probability that replacements are drawn from the site-level

217   community pool as opposed to from within the turf-level community pool (see next section for

218   parameter estimation). Even though turfs are only 25 x 25 cm in size, we expected within-turf

219   recruitment to be high because most species in our system exhibit some degree of clonal growth

220   (Klimešová and Bello 2009), and nearly all new stems are vegetative outgrowths from extant

221   genets rather than seed germination events (Berge, Klanderud, Vandvik, unpublished data).

222   Our model differs from Hubbell's community model in three important ways. First, rather

223   than using births and deaths of individuals to quantify demographic changes, which would be

224   impractical to measure in our predominantly clonal system, we use increases and decreases in

225   percent cover units. Second, we relax the assumption of zero-sum replacement and instead force

226   simulated percent cover to match observed percent cover in each year of the experiment. Third,

227   we allow site-level communities, i.e., the source pools for migrants entering experimental turfs,

10

228   to vary by recalculating them after each census. The latter two modifications account for

229   temporal variability in the productivity or composition of site-level communities due to drift or

230   short-term climatic variability.

231   We simulated community dynamics from 2009 to 2013 on an individual turf basis,

232   calculating species and trait dissimilarities to target site controls each year. Compositional

233   changes in each turf were simulated 100 times and the resulting values were averaged.

234   Simulation data for 2010 were not presented because field observations do not exist for that year.

235   Paired t-tests were used to determine when observed and simulated null expectations differed

236   significantly.

237

238   **Estimating model parameters:** We used community census data from our control turfs to

239   estimate replacement rate (d) and immigration rate (m) at each site. We set d equal to half the

240   sum of differences in species covers in control turfs between years at each site. We divided by

241   two because each replacement event constitutes two shifts in species covers, one increase and

242   one decrease. Values of d ranged from 19.7 to 37.4. Our method of estimating d ignores self-

243   replacement and thus likely underestimates actual replacement rates; however, a visual

244   inspection of model fit under a broad range of parameter values illustrates that our results are

245   robust to moderate increases in replacement rate (Figure S3). Furthermore, it should be noted

246   that any potential underestimates in replacement rates do not affect estimates of immigration

247   rates.

248   We estimated m using a Bayesian approach based on shifts in species abundances in the

249   five replanted control turfs at each site over three consecutive years (2011-2013), assuming

250   neutral dynamics. The net composition of the five undisturbed control turfs at each site was used

11

251   as the site-level community. The expected cover λ of species i in a turf community at time t is

252   formally defined as

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

254   where J_{t-1} is the total cover of the turf community in the previous year, $C_{i,t-1}$ is the relative

255   abundance of species i in the turf community the previous year, $P_{i,t-1}$ is the relative abundance of

256   the species in the site-level community at time t, and m is the immigration parameter. The

257   percent cover y, rounded to the nearest whole number, of species i in turf community at time t

258   was modelled assuming

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

260   We gave m a uniform prior with a range from 0 to 1. We also explored using an informed prior

261   ($m < 0.5$) based on the expected predominance of clonal growth and within-turf recruitment, but

262   this led to identical results and was dropped. We fit the model using MCMC implemented in

263   JAGS 3.4.0 (Plummer 2003). We ran JAGS through the R package R2jags (Su and Yajima

264   2012). For each model fit, we ran three chains, used a burn-in of 1000 iterations, and chose

265   initial values in different regions of parameter space. We confirmed model convergence using

266   Gelman-Rubin diagnostics (Brooks and Gelman 1998). We assessed overall model fit by

267   regressing mean posterior estimates for percent cover on observed data ($R^2 = 0.63$). See Table S2

268   for parameter estimates. For a deeper exploration of how a Bayesian approach can be used to fit

269   a trait-neutral model of community change to time series data see Mutshinda et al. (2008).

270

271   RESULTS

272   　　　　Community weighted means (CWMs) of leaf area, SLA, maximum height and lateral

273   spread increased with temperature along spatial gradients, and CWM values of bud number and

274   connection persistence decreased with temperature along spatial gradients (Table 1, Figure 2). In

275   three of the eight traits, the best-fit weighted multiple linear regression model included

276   precipitation as a predictor variable, but the coefficient of the precipitation variable itself was

277   never significantly different from 0. The interaction of temperature and precipitation had a

278   significant effect on SLA. Exponential curves with increasing temperature fit bud number and

279   connection persistence patterns better than linear ones, reflecting stronger responses in the colder

280   part of the climate grid (Figure 2). Based on these associations, we limited our analysis of trait

281   convergence in transplanted turfs over time to the six traits with spatial associations to

282   temperature, and to turfs transplanted to warmer climates.

283   Species and trait compositions of transplanted turfs converged towards target site controls

284   over time, with the magnitude of convergence increasing with initial dissimilarity (Figure 3).

285   Rates of convergence in species composition only exceeded null model predictions that

286   accounted for random replacement by local immigrants in 2011 (Figure 4). In contrast, rates of

287   convergence in maximum height, bud number, and connection persistence consistently exceeded

288   null model predictions (Figure 4). These deviations from null expectations were driven by

289   responses across many species rather than responses in just a few of the most abundant taxa

290   (Figure S4). Site-level climate data confirm that transplanted turfs experienced consistently

291   warmer temperatures as intended (Figure S1, Figure S2).

292

293   DISCUSSION

294   Our study uses observational and experimental data to test the assumption that traits with

295   broad-scale associations to climate in space are predictive of plant community response to

296   climate change in time. This space-for-time assumption is supported when using three traits

297   related to species architecture, but not supported when using three traits related to species

298   resource use strategy. Our results underscore the importance of using ecologically relevant traits

299   when making predictions of community response, and suggest that in our grassland system,

300   architectural traits may exert more influence on initial species response to rapid warming than

301   the more commonly used growth-related traits.

302

303   **Trait patterns along climate gradients:** Despite the large range in both mean summer

304   temperature and annual precipitation across sites, CWMs trended only with temperature. The

305   lack of functional turnover over a nearly 2500 mm year^{-1} increase in precipitation is surprising

306   given the consistent directional turnover in species composition along both temperature and

307   precipitation gradients in our system (Klanderud et al. 2015), underscoring the fact that species

308   turnover does not always beget functional turnover (Hooper et al. 2002). This finding contrasts

309   with vegetation trait patterns found elsewhere over narrower ranges of precipitation (Fonseca et

310   al. 2000, Wright et al. 2005). The reason for a lack of precipitation effects in our sites is unclear,

311   but, regardless of mechanisms, implies that functional shifts in these grasslands are likely to

312   occur in response to changes in temperature, not precipitation.

313   The consistent shifts in CWMs with increasing temperature in our system signify shifts in

314   plant ecological strategy. Increases in leaf area, SLA, and the rate of lateral spread with

315   temperature suggest a shift from slow-growing stress-tolerant species to fast-growing species

316   with acquisitive resource use strategies (Sterck et al. 2006, Rusch et al. 2011). Also increasing

317   with temperature are maximum height, duration of connection persistence, and bud number,

318   three traits related to plant architecture. The increase in CWMs of maximum height may reflect a

319   tradeoff in the ability to compete for light at warm sites amenable to growth and the ability to

14

320   tolerate wind stress and freezing temperatures at the coldest sites (Westoby 1998, Falster and

321   Westoby 2003). Higher CWMs of bud number and connection persistence at the coldest sites

322   may reflect an increased importance of resource integration and/or recovery from disturbances

323   (Klimešová and Klimes 2007), although we see no obvious reasons why resources would be

324   patchier and/or disturbances more common at the coldest sites. More work is needed to confirm

325   the functional roles of these understudied clonal traits and their role in organizing grassland

326   species along gradients.

327

328   **Community responses to warming:** The central goal of this study was to test the hypothesis

329   that trait-climate relationships over space are predictive of temporal community response to

330   climate change in time, a common assumption in climate change research. Of the six traits with

331   significant trends with temperature in space, maximum height, bud number, and connection

332   persistence - three traits related to species architecture - associated consistently with turf

333   community response to warming in time. The large deviation in maximum height from neutral

334   expectations may be have resulted from competition for light being more intense in more

335   productive, warmer conditions, and taller species preempting access to light, shading out

336   competitors, and earning disproportionate returns due to size-asymmetric competition

337   (Schwinning and Weiner 1998). Species with fewer buds and reduced connection persistence

338   succeeded disproportionately following warming, suggesting that the development and

339   maintenance of these clonal traits, which are believed to support new ramets under stressful

340   conditions (Klimešová and Klimes 2007), comes at a cost when conditions are more amenable to

341   growth. That CWMs of architectural traits deviated from neutral expectations of community

342   response while CWMs of growth-related traits (SLA, leaf area, lateral spread) did not, despite

15

343   showing strong trends along spatial temperature gradients, is unexpected and interesting.

344   Perhaps, the capacity for rapid growth is not useful to new ramets vying for resources in

345   grassland communities already packed with established individuals (but see: Wildová et al.

346   2007). Alternatively, SLA and leaf area may be poor predictors of growth in herbaceous species

347   with photosynthetic stems. The strong responses of clonal traits to changes in temperature

348   highlight the need for more emphasis on clonal traits in studies of community response to

349   climate change and herbaceous community assembly in general.

350   Modeling null model expectations was challenging given the lack of standard practices of

351   how to model demographic stochasticity in predominantly clonal systems (Eriksson 1994).

352   Traditionally, demographic analyses rely on population numbers and vital rates, but the concepts

353   of individuals, populations, births, and deaths break down in clonal, modular organisms. For

354   instance, ramet number is impractical to measure and may not be demographically meaningful

355   for graminoids that form hummocks with clumps of stems (e.g. *Festuca ovina*), nor is it possible

356   to distinguish individuals in forbs with sprawling aboveground stems with adventitious roots

357   (e.g. *Veronica biflora*), or species that divide via root splitting which results in fragmentation just

358   below the litter layer (e.g. *Cerastium alpinum*). Our decision to simulate demographic changes

359   using percent cover units therefore has both practical and conceptual appeal. The drawback,

360   however, is that percent cover is sensitive to factors that are not demographically significant,

361   such as variation in phenological stage among individuals, species, and sampling times, and thus

362   may inaccurately reflect shifts in abundance between years. Nevertheless, our approach accounts

363   for demographic stochasticity, annual variation in community-level composition, and the realities

364   of dispersal limitation in a predominantly clonal system to generate explicit null expectations of

365   community response to perturbation.

16

366

367 **Conclusions and future directions:** Using patterns in CWMs along environmental gradients to

368 forecast community response to climate change is an intuitively appealing approach. Our study

369 provides qualified support for such an approach: three of the six traits with spatial associations to

370 temperature in our system associated significantly with species success following transplantation

371 to warmer climates. Evidently, spatial associations between plant traits and broad-scale climate

372 variables can be predictive of community response to climate change, but are not always so.

373   Our results shed some light on how our system could respond to climate change in the

374 coming decades. Despite high rates of annual turnover, without gaps created by disturbances,

375 virtually all replacement stems are clonal outgrowths of extant genets rather than new seedlings

376 (Bullock et al. 1995; Berge, Klanderud, Vandvik, unpublished data). Thus, the potential for

377 community change is largely limited by the prevalence of gaps and the proportion of species in

378 the seed rain that are immigrants rather than local species. Once established, warmer-adapted

379 immigrants will likely proliferate vegetatively, outcompeting species adapted to cooler

380 temperatures (Olsen et al. 2016). Our approach and conclusions underscore the importance of

381 accounting for stochasticity and immigration when making predictions of community response

382 (Tilman 2004, Shipley et al. 2011). Future studies should consider the effects of dispersal

383 limitation on short-term transient responses, and how disturbances and dispersal limitation will

384 affect long-term equilibrium responses. Predictions of 'extinction debts' and 'immigration

385 credits' in the field of habitat distribution modeling are an important step in the right direction

386 (Dirnböck and Dullinger 2004), but could be developed further by considering how and when

387 traits modulate species interactions.

388

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393

394   WORKS CITED

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521

522   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

523

524   Summary statistics for best-fit weighted multiple linear regression models for each trait using

525   mean summer temperature, annual precipitation, and their interaction as potential predictor

526   variables, weighted by the sample size at each site (N ranges from 10 to 25). Model fit was

527   determined using AIC values. For bud number and connection persistence, exponentially

528   transforming the temperature axis resulted in better model fit. Turf-level community weighted

529   trait means and significant regressions are shown in Figure 2.

530

531   **Figure 1:** Panel A: a schematic illustration of the orthogonal nature of climate variables across

532   experimental sites, with black arrows representing the directions of turf transplants in replicates

533   of five. Panels B and C show the geographical locations of experimental sites in southern

534   Norway. Symbol shapes and shadings reflect mean summer temperature levels and mean annual

535   precipitation levels, respectively, in accordance with panel A.

536

537   **Figure 2:** Community weighted trait means (CWMs) of turfs before transplantation along natural

538   gradients of mean summer temperature (left) and mean annual precipitation (right). CWMs are

539   aggregated by site (N ranges from 10 to 25). Vertical lines show ± 1 S.D. Symbol shapes and

540   shadings reflect temperature and precipitation levels, respectively, in accordance with Figure 1A.

541   Best-fit lines are shown as solid lines when trait-gradient relationships are significant; for

542   simplicity, trend lines represent univariate regressions, even if multivariate regressions led to

543   higher AIC values. The interactive effects of temperature and precipitation on SLA is shown

544   using three trend lines (~3°C: dotted, ~6°C: dashed, ~9°C: dot-dashed). CWMs in seed mass and

545   offspring per ramet did not exhibit significant trends along temperature or precipitation gradients

546   and are therefore omitted. See Table 1 for model summary statistics.

547

548   **Figure 3:** Changes in dissimilarity of turfs transplanted to warmer climates and target site

549   controls from 2009 to 2013. The x-axis shows Bray-Curtis dissimilarity between turfs and the

550   centroids of their control turfs in 2009; the y-axis shows how that dissimilarity changed by 2013.

551   Each symbol represents a turf community. Grey crosses represent control turfs; black circles

552   represent transplanted turfs. Dissimilarity was calculated using Bray-Curtis distance for species

553   composition (top left panel) or Euclidian distance of community weighted means (all remaining

554   panels). Symbols below zero on the y-axis reflect turf communities that converged

555   compositionally towards target controls, whereas communities above zero on the y-axis diverged

556   compositionally. Dashed vertical lines are placed at 50% of mean dissimilarity among controls as

557   an approximation of natural community stochasticity. Grey ellipses represent 95% confidence

558   intervals of the centroids of control turf dissimilarities.

559

560   **Figure 4:** Mean trait dissimilarities of transplanted turf communities and target controls from

561   2009 to 2013. Solid lines represent observed field data. Dashed lines represent simulated null

562   expectations based on the means of 100 null model simulation runs. Dotted lines represent mean

563   dissimilarity among control turfs within sites. Null model simulations use estimates of

564   replacement and immigration rates derived from our field data (see Methods). Error bars show

565   95% confidence intervals. Statistical differences between observed and simulated community

566   weighted means are shown when p < 0.05 (*).

567   FIGURE 1
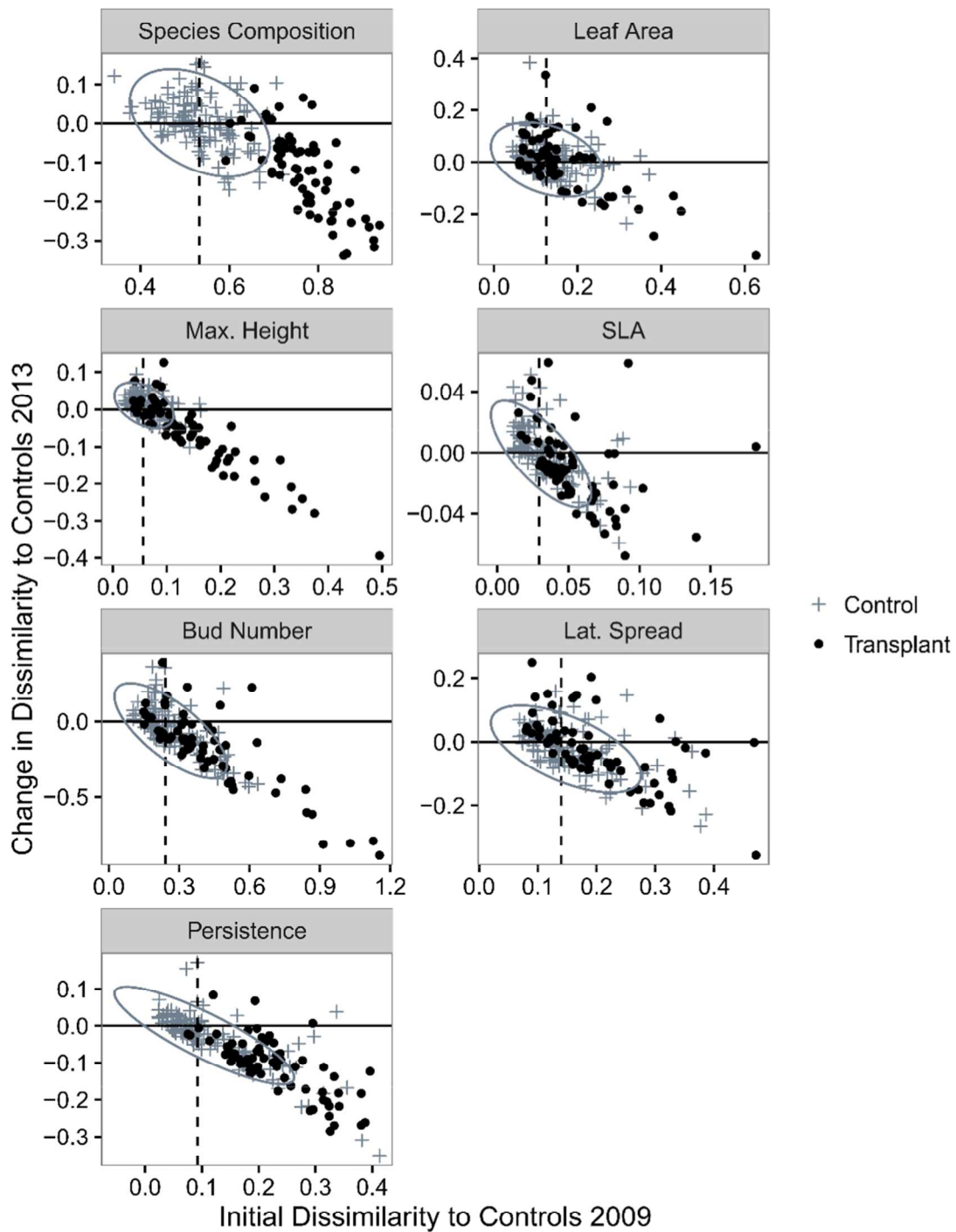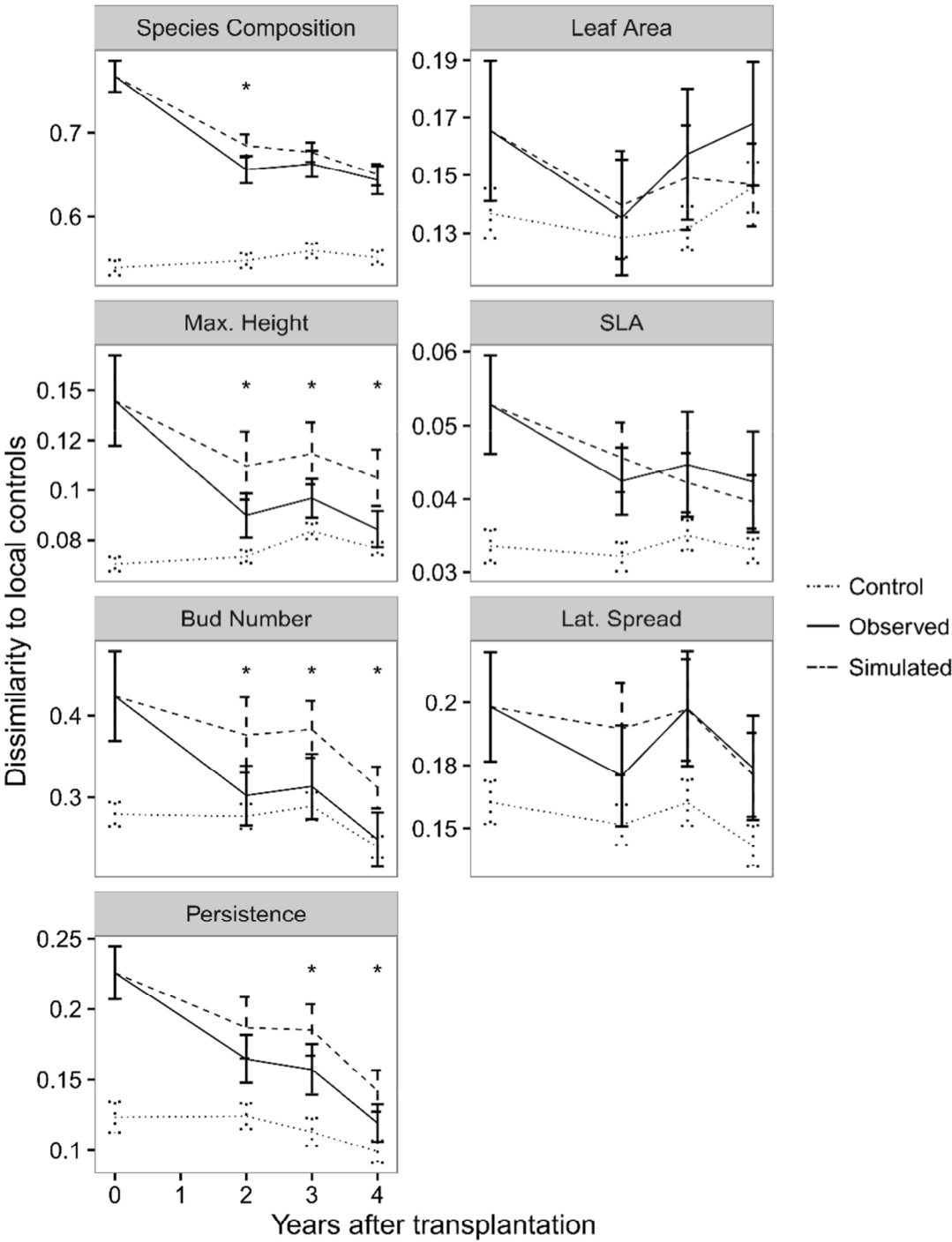
A

B

C
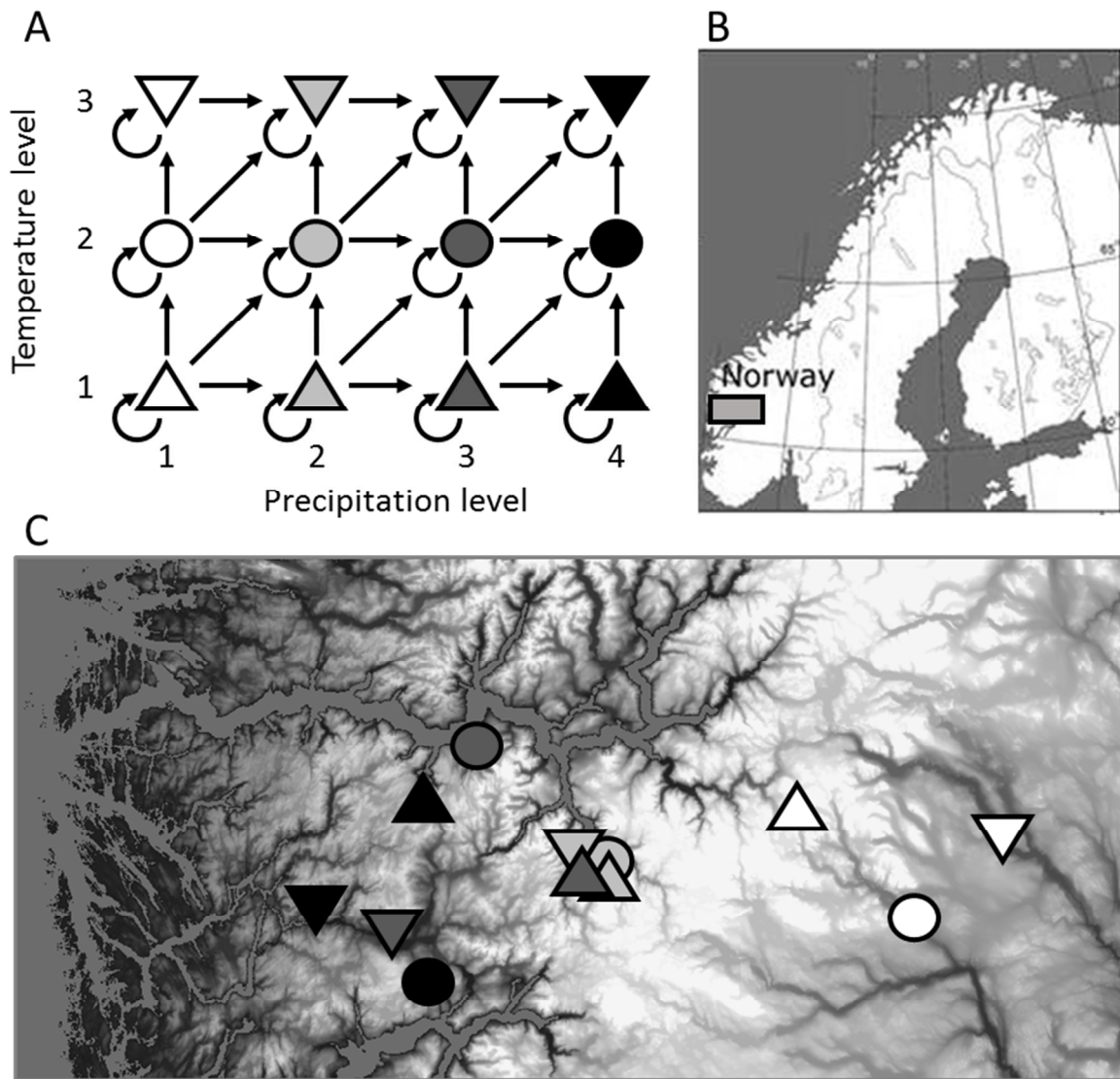
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569   FIGURE 2
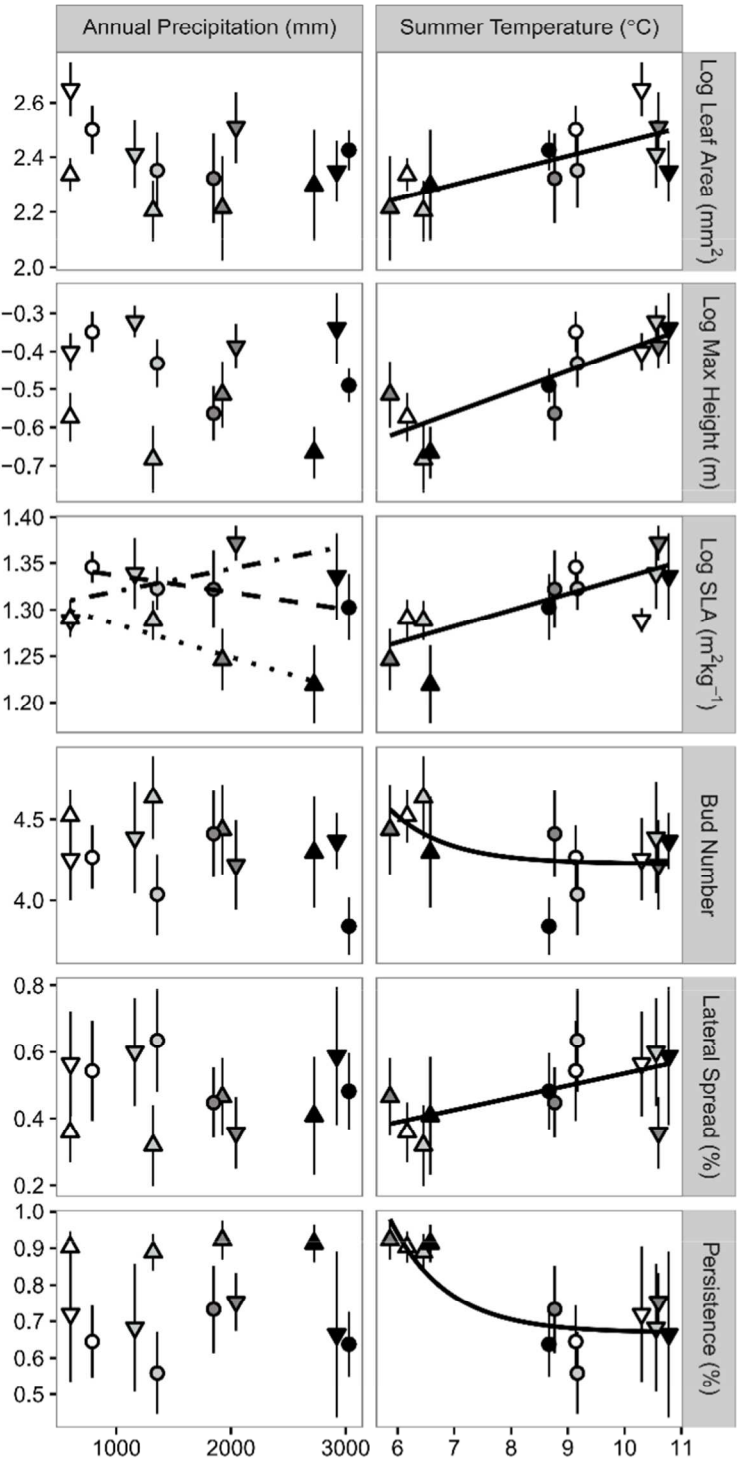
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571

572   FIGURE 3

573

574   FIGURE 4

575

1   TABLE S1

	Max. Height	Seed Mass	SLA	Bud Number	Lat. Spread	Offspring	Persistence
Leaf Area	0.46	0.51	0.34	-0.13	-0.12	-0.11	-0.03
Max. Height		0.33	0.17	0.15	-0.02	-0.01	0.18
Seed Mass			0.16	0.06	-0.12	0.05	0.16
SLA				**-0.36**	-0.14	0.11	**-0.40**
Bud Number					0.30	0.00	0.30
Lat. Spread						0.16	-0.08
Offspring							-0.12

2   Pearson correlations of species trait values in the species pool. Bold indicates significance ($p <$

3   0.05). N ranges from 140 - 152.

4

5   TABLE S2

Site	Summer Temp. (C°)	Precipitation (mm)	d	m
Ulvhaugen	6.17	596	31	0.064
Låvisdalen	6.45	1321	23	0.165
Gudmedalen	5.87	1925	26	0.280
Skjellingahaugen	6.58	2725	20	0.322
Ålrust	9.14	789	34	0.263
Høgsete	9.17	1356	31	0.356
Rambæra	8.77	1848	24	0.293
Veskre	8.67	3029	32	0.391
Fauske	10.30	600	37	0.175
Vikesland	10.55	1161	36	0.170
Arhelleren	10.60	2044	33	0.159
Øvstedal	10.78	2923	22	0.170

6   Site-level simulation parameters, sorted by temperature level (ca. 6.0, 9.0, and 10.5 C°) then

7   precipitation level (ca. 600, 1200, 1900, and 2800 mm year^{-1}). Summer temperature is the mean

8   of the four warmest months. Replacement rate (*d*) was estimated based on observed changes in

9   cover between years. Immigration rate (*m*) was estimated in control turfs at each site using a

10   Bayesian approach that assumed control turf dynamics were species-neutral. Parameter estimates

11   are shown graphically in the top right panel of Figure S3.

2

12   **Figure S1:** Mean summer temperature values measured over the duration of the experiment at

13   two heights above ground (2 m and 30 cm). Summer temperatures reflect the mean of the four

14   warmest months, calculated individually by site. Four site values are included in each

15   temperature level; error bars reflect ± 1.0 SD.

16

17   **Figure S2:** A boxplot diagram depicting the mean increase in temperature experienced by turfs

18   transplanted to warmer sites over the duration of the experiment. Measurements occurred at two

19   heights (2 m and 30 cm). Temperature increase was determined by subtracting the mean

20   temperature of the turf origin site from the mean summer temperature at the destination site each

21   year. Summer temperatures reflect the mean of the four warmest months, calculated individually
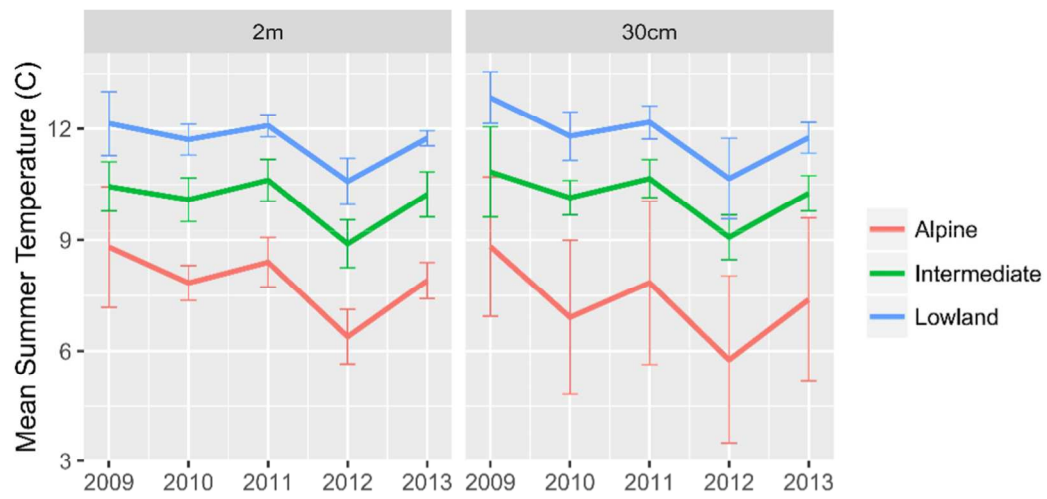
22   by site.

23

24   **Figure S3**: A contoured heat map showing the alignment of model simulations to field data in

25   terms of species composition under a broad survey of replacement rates (*d*) and immigration

26   rates (*m*). The heat map depicts the mean difference ("Mean Deviation") in Bray-Curtis

27   dissimilarity of species-level composition between observed field data and 100 simulation reps

28   for each set of parameters. In the top right panel, solid circles show the combinations of site-level

29   immigration and replacement rates used in null model simulations.

30

31   **Figure S4:** Differences between predicted and observed species abundances in 2013, plotted by

32   trait value using scatterplots (continuous traits) or boxplots (binary traits). Red lines and 95%

33   confidence intervals are shown when there are significant (solid red line) or nearly significant

34   (dashed red line) relationships. The diameter of each solid circle is proportional to its abundance
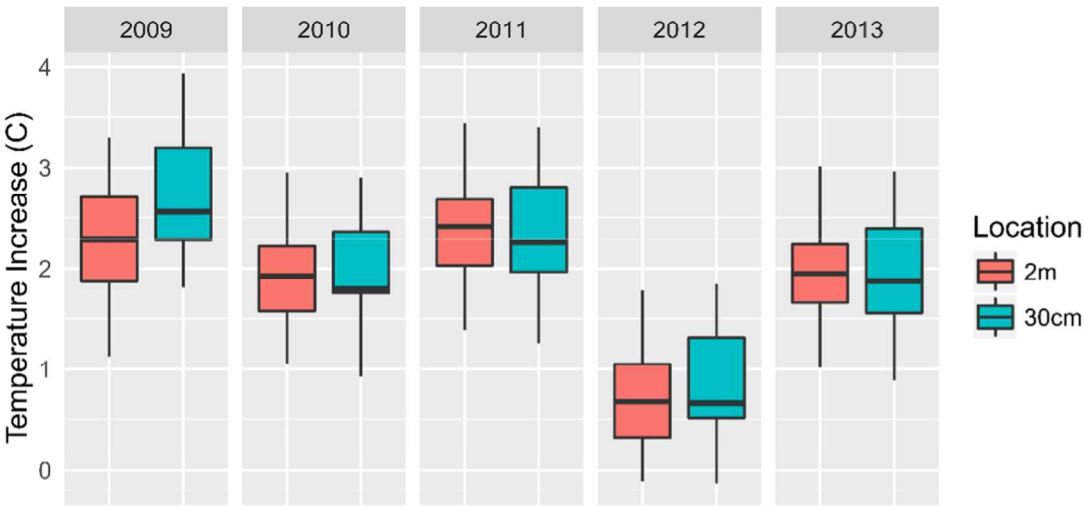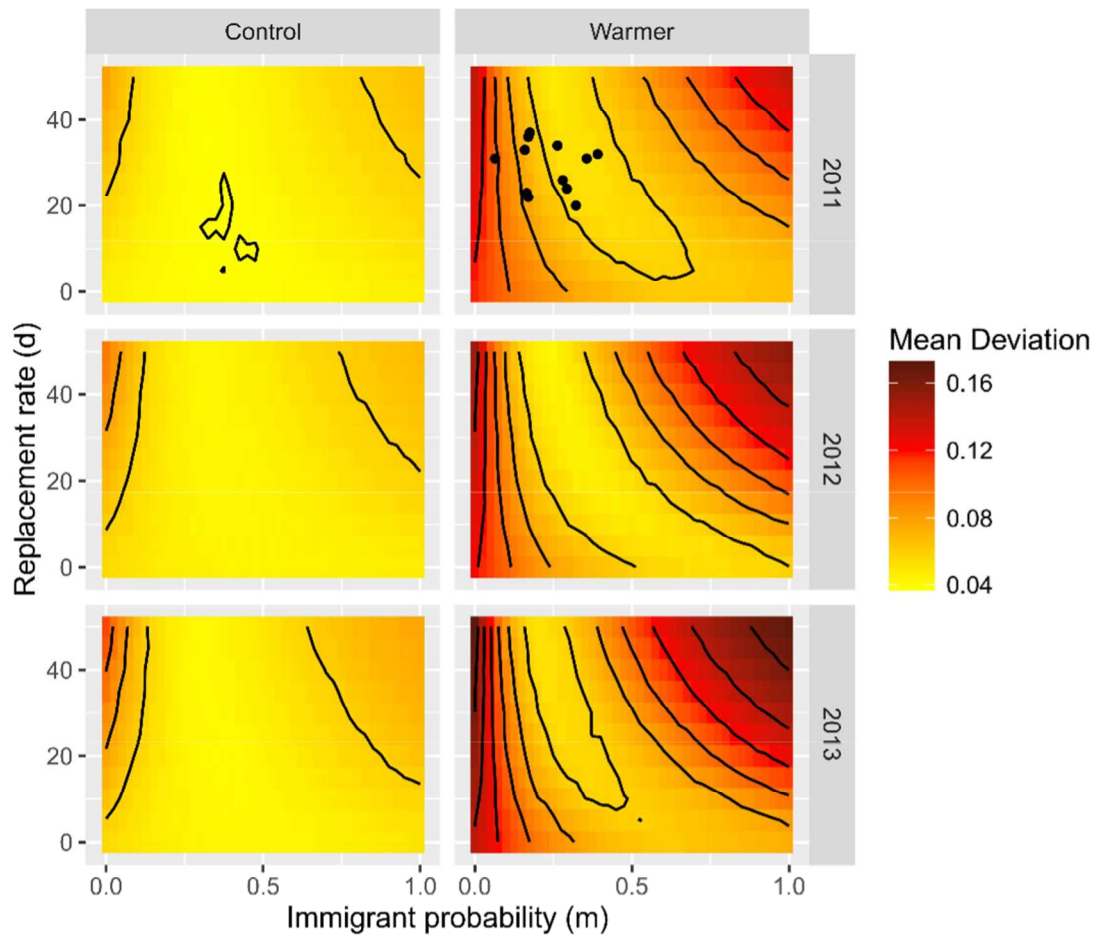
35   in the region.

36   FIGURE S1

37

38   FIGURE S2

39

6

40   FIGURE S3

41

42   FIGURE S4