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Running head: Dispersal and filtering in grasslands

Quantifying the roles of seed dispersal, filtering, and climate on regional patterns of grassland biodiversity

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31   ABSTRACT

32   Seed dispersal and local filtering interactively govern community membership and scale up to
33   shape regional vegetation patterns, but data revealing how and why particular species are
34   excluded from specific communities in nature are scarce. This lack of data is a missing link
35   between our theoretical understanding of how diversity patterns can form and how they actually
36   form in nature, and it hampers our ability to predict community responses to climate change.
37   Here, we compare seed, seedling, and adult plant communities at twelve grassland sites with
38   different climates in southern Norway to examine how community membership is interactively
39   shaped by seed dispersal and local filtering, and how this process varies with climate across sites.
40   To do this, we divide species at each site into two groups: "locally-transient" species, which
41   occur as seeds but are rare or absent as adults (i.e., they arrive but are filtered out), and "locally-
42   persistent" species, which occur consistently as adults in annual vegetation surveys. We then ask
43   how and why locally-transient species are disfavored during community assembly. Our results
44   led to four main conclusions: (1) the total numbers of seeds and species that arrived, but failed to
45   establish locally-persistent populations, rose with temperature, indicating an increase in the
46   realized effects of local filtering on community assembly, as well as an increase in the number of
47   species poised to rapidly colonize those warmer sites if local conditions change in their favor, (2)
48   locally-transient species were selectively filtered out during seedling emergence, but not during
49   seedling establishment, (3) selective filtering was partly driven by species climate preferences,
50   exemplified by the poor performance of seeds dispersing outside of their realized climate niches
51   into colder and drier foreign climates, and (4) locally-transient species had traits that likely made
52   them better dispersers (i.e., smaller seeds) but poorer competitors for light (i.e., shorter statures
53   and less persistent clonal connections) than locally-persistent species, potentially explaining why
54   these species arrived to new sites but did not establish locally-persistent adult populations. Our
55   study is the first to combine seed, seedling, and adult survey data across sites to rigorously
56   characterize how seed dispersal and local filtering govern community membership and shape
57   climate-associated vegetation patterns.

58

61

62 INTRODUCTION

63 Plant community assembly in a landscape or metacommunity context includes important roles

64 for seed dispersal among communities and local filtering (Leibold et al. 2004, Alexander et al.

65 2012). Despite empirical evidence illustrating how dispersal and filtering can shape community

66 membership on their own (Choler et al. 2001, Ehrlén et al. 2006, Armas et al. 2011, Laliberte et

67 al. 2014), there is a lack of data documenting how dispersal and filtering interact in natural plant

68 communities. This lack of data represents a missing link between our theoretical understanding

69 of how plant diversity patterns can form and how they actually form. Moreover, it hampers our

70 ability to predict community responses to climate change, because different species likely have

71 different dispersal abilities and/or different constraints to expansion, leading to variable

72 responses (Graae et al. 2017).

73   The absence of a clear empirical picture of how dispersal and filtering interactively shape

74 plant community membership and regional diversity patterns is due in large part to the logistical

75 challenges of connecting dispersed seeds to individual plant performance. Plant propagules are

76 often tiny, numerous, difficult to identify and track, capable of traveling great distances, and can

77 remain dormant in the soil for years prior to germination (Baskin and Baskin 1998, Vandvik et

78 al. 2016). Some researchers have tried to infer dispersal and filtering dynamics using indirect

79 methods (Alexander et al. 2012). The "nearest-neighbor" approach, for example, assumes

80 connectivity in a metacommunity to be proportional to inter-patch distance (Calabrese and Fagan

81 2004, Jacobson and Peres-Neto 2010). Other approaches infer dispersal patterns from historical

82 population range shifts over periods of climate change (Kelly and Goulden 2008, Bertrand et al.

83 2011) or by analyzing population genetic structure. These indirect methods are useful when

84 modeling species distributions phenomenologically, but fall far short of evaluating whether

85 species fail to arrive or fail to persist after arrival (Calabrese and Fagan 2004). The small number

86 of studies that have directly assessed dispersal patterns, either by manually marking seeds (e.g.,

87 Xiao et al. 2006) or connecting seeds to parents using parentage analyses (e.g., Cain et al. 2000),

88 are often conducted for single species and/or over short distances, and are of limited use when

89 considering responses of dozens of species at regional scales (Nathan and Muller-Landau 2000).

90   Here, we compare the seed rain, seed bank, seedlings, and adult plant communities at 12

91 sites falling along temperature and precipitation gradients in southern Norway to shed light on

92   how seed dispersal and filtering interact *in situ* to shape community membership and maintain

93   regional climate-associated vegetation patterns. Although our questions align with those of

94   metacommunity theory (Leibold et al. 2004), our sites exist within a broad and contiguous

95   patchwork of grassland habitat, making our system unsuitable to explicitly empirically evaluate

96   between-patch dispersal dynamics, and therefore motivating us to develop our own approach.

97   Specifically, we divide species at each site into two groups: "locally-transient" species, which

98   occur as seeds but are rare or absent as adults (i.e., they arrive from outside the site but are

99   filtered out), and "locally-persistent" species, which occur consistently as adults in annual

100   vegetation surveys. We use adult vegetation surveys to infer which species dispersed outside of

101   their realized climate niches (i.e., were found outside of the climate ranges where we found them

102   to persist as adults), and how their realized climate niches compared to local climate conditions

103   (i.e., if they have dispersed into warmer/wetter/cooler/drier climates). We then ask how and why

104   locally-transient species were selectively disfavored during community assembly at each site,

105   and how this process varied by climate. Our framework recalls the core-satellite framework of

106   Hanski (1982), but differs in that we allow species status to vary by site, enabling us to examine

107   how species performance varies by environment.

108   Our study takes place in a network of 12 alpine and subalpine grassland sites in southern

109   Norway, a region with unusually high spatial climate variability. The sites were selected

110   according to their mean summer temperatures and mean annual rainfalls such that they form an

111   orthogonal climate grid (Fig. 1), facilitating independent assessment of these two important

112   climate drivers in community assembly. Prior work in our system used subsets of the data used

113   in this study to compare diversity patterns in the seed bank and mature vegetation (Vandvik et al.

114   2016, Meineri et al. 2020), to understand how trait-based community composition varies with

115   climate (Guittar et al. 2016), and to evaluate the relative balance of competition and facilitation

116   in seedling recruitment (Klanderud et al. 2017). We combine these previously published data

117   with new data on seed rain and seedling survival to ask how dispersal and filtering interactively

118   govern community membership and regional vegetation patterns. After dividing species into

119   locally-transient and locally-persistent groups at each site, we ask the following questions:

120   1. How many seeds and species arrive to a site but fail to establish locally-persistent

121   adult populations, and how does this vary with climate?

122   2. At what life stages are locally-transient species disfavored? Are they less likely to

123   emerge as seedlings, establish as seedlings, compete as adults, or a combination of the

124   three?

125   3. Why do locally-transient species fail to persist? Is it because they dispersed from

126   outside of their realized climate niches and are disfavored due to their climate

127   preferences? Is it because they differ from locally-persistent species in their

128   functional traits, offering mechanistic hypotheses for their arrival and selective

129   removal?

130   4. What do our results mean for how these grasslands will respond to climate change?

131

132 MATERIALS AND METHODS

133 ***Study area.*** The study area comprises 12 semi-natural calcareous grassland sites in southern

134 Norway that host at least 144 non-woody vascular plant species at the adult life stage, and at

135 least 126 at the seed stage (Appendix S1: Table S1). Sites have similar bedrock, land use

136 histories, slopes of approximately 20°, and southwest aspects, but differ in mean summer

137 temperature, defined as the mean temperature of the four warmest months per year, and/or mean

138 annual precipitation, such that they form a grid with approximately orthogonal climate axes (Fig.

139 1). Interannual variation in mean summer temperature and annual precipitation at each site over

140 the sampling period (2008 – 2013) was modest, with standard deviations of 0.79 °C and 238 mm,

141 respectively, on average across sites. Each site has five blocks, placed in representative areas of

142 grassland vegetation within a 75 – 200 m^2 area, with individual positions that vary according to

143 local topography and accessibility. Each block has a variable number of 25 x 25 cm plots used

144 for the data sets described below, as well as other experiments and surveys. Blocks were

145 protected from grazers with electric fences and manually mowed once a year to evenly simulate

146 biomass loss due to grazing. Taxonomic identifications follow Lid & Lid (2007). Woody species

147 and bryophytes were not recorded in all datasets and therefore were excluded from analyses.

148

149 ***Seed rain data.*** We collected seed rain over two periods to target winter (September 2009 to

150 June 2010) and summer (June 2010 to September 2010) seed deposition. We trapped seeds in 25

151 x 25 cm artificial turfs placed in gaps about 50 cm from seedling monitoring gaps (see below) in

152 four blocks at each site, for a total of 48 traps across all sites. The small synthetic filaments in

153   artificial turfs effectively catch and retain small particles like seeds. Turfs were gathered and

154   flushed with water to free collected seeds. The rinse water was passed through 500 μm and 125

155   μm diameter sieves to discriminate seeds by size and remove debris. Seeds were counted and

156   identified taxonomically using a stereomicroscope. We included fruits, bulbils, and viviparous

157   seeds in our working definition of "seeds." Rates of seed predation on artificial turfs are likely

158   similar to those on soil, thus seed predation should not bias our results.

159

160   ***Seed bank data.*** To characterize seed bank diversity we haphazardly selected one 64 x 64 cm

161   plot at each site and excavated soil to a depth of 3 cm in October 2008. Because the seed bank

162   survey area at each site (0.41 m^2) was larger than the total areas used for seed rain and seedling

163   surveys at each site (four 25 x 25 cm plots, 0.25 m^2), we randomly subsampled 61 % (0.25 m^2 /

164   0.41 m^2) of the original seed bank community *in silico* and discarded the remainder to

165   standardize sampling effort across plant life stages. To exclude the seeds from that year's seed

166   rain from our seed bank surveys, we removed the aboveground vegetation, including moss and

167   litter. Soil samples were stored for three months at 2 – 4 °C and ambient moisture. Soil samples

168   were then sowed into a standard mixture of sterile subsoil and placed in 30 x 60 cm trays. The

169   trays were incubated in a greenhouse with a diurnal cycle of 16 hours light (25 °C) and 8 hours

170   darkness (15 °C). The diurnal cycle was continued for four months, followed by six months of

171   cold stratification in darkness (4 °C), followed by another four-month period of diurnal cycling.

172   Emerging seedlings were counted and removed once identifiable to species. This method of

173   characterizing the seed bank community effectively accounts for seed viability because non-

174   viable seeds would not have emerged as seedlings.

175

176   ***Seedling data.*** Like most perennial grasslands, seedling recruitment in our system is highly

177   dependent on disturbances and occurs only rarely in intact vegetation due to strong competitive

178   effects from adult plants (Silvertown and Smith 1989, Eriksson 1989, Bullock et al. 1995,

179   Vandvik 2004, Berge 2010, Klanderud et al. 2017). We therefore monitored seedlings in

180   experimental gaps where they were relatively free from competitive effects of adult plants, but

181   still exposed to environmental stress and other biotic interactions, such as herbivory, disease, and

182   potential resource competition among seedlings. One 25 x 25 cm gap was created in each of four

183   blocks at each site in spring 2009, for a total of four gaps per site and 48 gaps overall. The gaps

184   were made by cutting along the inner edges of a metal frame mounted in metal pipes marking the
185   corners of the plot, and peeling away the natural vegetation and its thickly interwoven root mat.
186   Seeds and topsoil were returned to gaps by vigorously shaking excavated vegetation and passing
187   it through a 4 mm sieve to remove plant remains. Emerged seedlings in the plots were ID-tagged
188   in one of three censuses (late summer 2009, early summer 2010, late summer 2010) using
189   numbered plastic toothpicks and plot coordinates. About 70 % of seedlings were identifiable to
190   species; the remaining 30 % were unidentifiable or died before they could be identified and were
191   lumped into two generic groups for graminoids and forbs. Seedlings were differentiated from
192   emergent clonal ramets by looking for cotyledons or signs of above- or below-ground
193   connections. Seedling survival and potential establishment were recorded twice yearly from
194   spring 2010 to spring 2012. We approximated seedling emergence rates by dividing the density
195   of emerged seedlings by the sum of seed rain and seed bank densities. We marked seedlings
196   established when they had grown to a size greater than what could be derived exclusively from
197   their maternal subsidies, which we estimated to be when stems were longer than 2 cm, and if a
198   forb, also when they had grown their first non-cotyledonous leaves. Although we took pains to
199   census each site at times of peak seedling emergence, some seedlings may have emerged, died,
200   and disappeared before ever being recorded; even if this where the case, however, we contend
201   that it is unlikely to influence our overall conclusions because the factors discouraging seedling
202   survival during the earliest stages of establishment are likely the same as those discouraging
203   seedling emergence (e.g., late spring frosts), and are distinct from the factors influencing
204   seedling survival establishment (e.g., drought, competition for light, predation, early fall frosts,
205   and late spring frosts in the year after seedling emergence).
206
207   *Mature vegetation data.* We surveyed mature vegetation at peak biomass (July or August) in
208   2009, 2011, 2012, and 2013. At each site, we used two 25 x 25 cm plots in each of five blocks at
209   each site, for a total of 10 plots per site (except for the third-wettest second-warmest site, which
210   only had nine plots), and 119 plots overall. These plots were controls for a turf transplant
211   experiment and included five undisturbed controls and five transplant controls (i.e., turfs dug up
212   and replaced in the same location). The two types of controls did not differ in species
213   composition or any other aspect of community structure at any of the survey periods (Guittar et
214   al. 2016). We visually estimated the percent cover of each species in each plot using a 5 x 5 cm

215   grid overlay, and then pooled the data by site. To ensure that site vegetation was not undergoing

216   successional changes that could bias our conclusions, we used an NMDS ordination to confirm

217   that site composition did not change substantively between years (Appendix S1: Fig. S1). Stage-

218   specific species abundance data are provided as a supplementary file.

219

220   ***Trait data.*** We used four commonly used plant traits, and four traits related to clonal growth

221   strategy, an important facet of competitive ability in perennial grasslands. Each trait has

222   hypothesized associations to dispersal ability and/or the ability to compete for resources. Seed

223   mass (mg), a reflection of species regeneration strategy (Kraft et al. 2008, Cornwell and Ackerly

224   2009), was drawn from the Seed Information Database (Kew Royal Botanic Gardens 2008).

225   Maximum canopy height (m) data, which relates to both dispersal ability and light competition

226   (Westoby 1998, Falster and Westoby 2003, D'Andrea et al. 2020), were mined from Lid and Lid

227   (2007). Leaf area (mm^2) and specific leaf area (SLA; m^2/kg), two traits indicative of where

228   species fall along a continuum of slow-to-fast resource use strategies (Reich et al. 1997, Ackerly

229   and Reich 1999, Reich 2014), were estimated using a combination of field data (Guittar et al.

230   2016) and data from the LEDA online trait database (Kleyer et al. 2008). Leaf area, SLA,

231   maximum height, and seed mass values were log-transformed. Clonal traits included the number

232   of offspring per parent per year ("0" = 1 offspring; "1" = ≥ 2 offspring), persistence of plant–

233   offspring connections ("0" = < 2 years; "1" = ≥ 2 years), rate of lateral spread ("0" = ≤ 1

234   cm/year; "1" = > 1 cm/year), and number of buds per ramet (an integer score ranging from "1" =

235   few buds either belowground or aboveground, to "8" = many buds both below and

236   aboveground). Clonal attributes are thought to help plants integrate over spatially heterogeneous

237   resources (Eilts et al. 2011), recover from disturbances (Klimešová and Klimeš 2007), and

238   provide sustained maternal subsidies to new ramets as they grow horizontally and vie for local

239   establishment (Herben and Wildová 2012). Clonal trait data were drawn from Klimeš and

240   Klimešová (1999) and converted from categorical to quantitative formats to enable calculations

241   of community means. Trait data are provided as a supplementary file.

242

243   ***Assigning local species status.*** Each species observed at each site at any life stage was labeled as

244   "locally-persistent" if adults were recorded in more than half (i.e., at least three of four) of the

245   site vegetation surveys conducted from 2009 to 2013, or otherwise labeled "locally-transient." In

246 using this cutoff, we distinguish species that are consistent community members from those that

247 are not. Because locally-transient/locally-persistent species status assignments were potentially

248 sensitive to the depth at which we characterized local site community composition, we used

249 rarefaction to ensure that we had sufficiently surveyed the mature vegetation such that the

250 number of locally-persistent species observed at each site had stabilized (Appendix S1: Fig. S2).

251 We also re-ran our analysis with all possible locally-transient/locally-persistent cutoffs to assess

252 the sensitivity of our conclusions to our methodology.

253

254 ***Assigning putative climate origins.*** For each locally-transient species at each site, we identified

255 the sites and climates where we knew it had persistent adult populations, and then used these to

256 infer whether it was dispersing outside of its realized climate niche. If a locally-transient species

257 at a given site had persistent adult populations at other sites with similar temperatures and/or

258 precipitations, we assumed it dispersed from a site with approximately the same temperature

259 and/or the same precipitation, such as from a neighboring site with a similar climate but with

260 potentially different topographical, edaphic, or biotic characteristics. If a locally-transient species

261 at a given site had persistent adult populations only at sites with warmer/cooler or wetter/drier

262 conditions, we then assumed it dispersed from a warmer/cooler or wetter/drier site (i.e., it

263 dispersed *into* a cooler/warmer or drier/wetter site). Again, we are not assuming that a given seed

264 of a locally-transient species literally dispersed from a given climate, but that the seed is

265 occurring outside of the climate range at which it is a common and persistent community

266 member, and is presumably on the cusp of being locally excluded.

267

268 ***Statistical approach.*** We used linear regressions to test for baseline trends in the total abundance

269 and richness of locally-transient and locally-persistent species in the seed rain, the seed bank, and

270 the two combined along temperature and precipitation gradients. Unlike other data in this study,

271 seed bank data were not collected in replicate across blocks within a site, thus we performed

272 regressions on data aggregated by site (N = 12). Each linear regression model assumes normally

273 distributed errors and takes the form of $y_j \sim MAP_j$ or $y_j \sim MST_j$, where y_j is the response variable

274 being examined at site j, and MAP_j and MST_j are the mean annual precipitation (centered to

275 zero) and mean summer temperature (centered to zero) at site j. We also used linear regressions

276   to test for baseline trends in species richness in the mature vegetation with temperature and

277   precipitation.

278   We used four sets of generalized linear models (GLMs) to test potential predictors of

279   species performance during seedling emergence and seedling establishment. The dependent

280   variable for seedling emergence GLMs was the number of emerged seedlings of each species at

281   each site (N = 692, the number of unique seed and/or seedling species-by-site combinations), and

282   the dependent variable for seedling establishment GLMs was the number of established seedlings

283   of each species at each site (N = 279, the number of unique seedling species-by-site

284   combinations). The GLMs used negative binomial error distributions and log link functions.

285   Because each site has a unique combination of temperature and precipitation values (i.e., there is

286   no nestedness), it was not appropriate to include site as a random effect while also testing for the

287   effects of climate. When using seed and seedling numbers as predictors of emergence and

288   establishment, respectively, we normalized their highly skewed abundance distributions with

289   Yeo-Johnson transformations, which are similar to Box-Cox transformations but can be used

290   with zeros. The lambda values used for the Yeo-Johnson transformations were those which

291   maximized normality, as quantified by Shapiro-Wilk normality tests; specifically, the lambda

292   used to transform seed abundance data was -0.204 and the lambda used to transform emerged

293   seedling data was -0.35.

294   In the first, baseline set of GLMs ("null" models), local species abundances in the

295   combined seed rain and seed bank were used as predictors of local species abundances of

296   emerged seedlings, and local species abundances of emerged seedlings were used as predictors

297   of local species abundances of established seedlings. Formally, we modeled the number of

298   emerged seedlings g for species i at site j as $g_{ij} \sim s\_trans_{ij}$, where s_trans_{ij} is the Yeo-Johnson

299   transformed abundance of seeds (seed rain + seed bank) of species i at site j. In other words, our

300   null expectation was that all seeds were equally likely to emerge, and all seedlings were equally

301   likely to establish. In the second set of GLMs ("site climate" models), we added model terms

302   MAP_j and MST_j for local site mean summer temperature and mean annual precipitation at site j

303   to evaluate how these climate variables improved predictions of seedling emergence and seedling

304   establishment rates.

305   In the third set of GLMs ("site climate + species status" models), we evaluated how well

306   locally-transient/locally-persistent species status predicted performance differences during

307   seedling emergence and seedling establishment. Specifically, we added model terms specifying

308   the status of each species at each site, and interactions between species status and local climate.

309   Formally, this is

310 $$g_{ij} \sim s\_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \cdot p_{ij}) + (MST_j \cdot p_{ij}),$$

311   where p_{ij} is the factor indicating local species status, and the other variables as described above.

312   Likewise, we modeled the number of established seedlings e for species i at site j as

313 $$e_{ij} \sim g\_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \cdot p_{ij}) + (MST_j \cdot p_{ij}),$$

314   where g_trans_{ij} is the Yeo-Johnson transformed abundance of emerged seedlings of species i at

315   site j, and the other variables are as described above.

316   In the fourth and final set of GLMs ("site climate + species status + species climate

317   origin" models), we dropped p_{ij}, the model term for locally-transient/locally-persistent species

318   status, and replaced it with o_{ij}, a new term denoting the putative temperature/precipitation origins

319   of each locally-transient species i at site j. Specifically, the o_{ij} term tags each species at each site

320   with one of five labels: (1) locally-persistent, (2) locally-transient but likely dispersed from an

321   adjacent site with similar temperature/precipitation, (3) locally-transient and likely dispersed

322   from a cooler/drier site (i.e., into a warmer/wetter site), (4) locally-transient and likely dispersed

323   from a warmer/wetter site (i.e., into a cooler/drier site), (5) locally-transient with no locally-

324   persistent populations at any of our grassland sites (i.e., an 'unknown' climate preference). We

325   dropped the interaction terms from these GLMs to reduce excessive model complexity.

326   Formally, we modelled the number of emerged seedlings g as

327 $$g_{ij} \sim s\_trans_{ij} + MAP_j + MST_j + o_{ij},$$

328   and the number of established seedlings e as

329 $$e_{ij} \sim g\_trans_{ij} + MAP_j + MST_j + o_{ij},$$

330   Finally, we asked if systematic differences in the traits of locally-transient and locally-

331   persistent species at each site offered mechanistic explanations for performance differences

332   between the two groups. To do this, we averaged the trait values of all species (not weighted by

333   their relative abundances) in the combined seed rain and seed bank at each site, grouped by

334   local-transient/locally-persistent species status. We used paired t-tests, paired by site, to identify

335   which traits, if any, differed consistently between locally-transient and locally-persistent species

336   across all sites. For the traits with significant differences between the two groups, we performed

337 linear regressions to see whether the magnitude of the difference trended with site temperature or

338 precipitation. We did not test for trait-based differences by species status in seedling

339 communities because the number of locally-transient species was too low to provide confidence

340 in calculations of within-site trait means (only 4 ± 3 locally-transient species occurred on average

341 as emerged seedlings at each site; Appendix S1: Table S1). All scripts in this study were written

342 in R and are available online (see Data Availability statement).

343

344 RESULTS

345 *Mature vegetation rarefactions.* Rarefactions indicated that the numbers of plots of mature

346 vegetation surveyed at each site were more than sufficient to stabilize the compositions of

347 locally-persistent species (Appendix S1: Fig. S2), lending confidence to our locally-

348 transient/locally-persistent species status assignments. Furthermore, no locally-transient species

349 by itself ever represented more than 0.4% of total cover at any site (Appendix S1: Fig. S3),

350 illustrating the minor overall contribution of locally-transient species to local community

351 structure.

352

353 *Evidence of dispersal and filtering.* Seeds of locally-transient species occurred at all 12 of our

354 grassland sites, representing, on average, 4 of 42 species in the combined seed rain and seed

355 bank. In the combined seed rain and seed bank, the number of locally-transient species and their

356 total abundances increased significantly with temperature (Fig. 2; species richness: p = 0.045, R^2

357 = 0.34; total abundance: p = 0.016, R^2 = 0.46). These trends were driven primarily by increases

358 of local-transients in the seed bank (species richness: p = 0.031, R^2 = 0.39; total abundance p =

359 0.035, R^2 = 0.37), not the seed rain (Appendix S1: Fig. S4), underscoring the fact that the

360 composition of the seed rain likely differs between years, and that the seed bank likely serves as

361 an important reservoir of local plant diversity. The strength at which locally-transient species

362 were disfavored during seedling emergence did not change with temperature (Table 1; refer to

363 the lack of significance for the transient*local temperature interaction term). There were no

364 significant trends in species richness or total abundance with precipitation in either the seed rain,

365 the seed bank, or the two combined. Species richness in the adult vegetation rose significantly

366 with temperature (p = 0.0063, R^2 = 0.54) but not with precipitation (p = 0.871).

367   About 10% of all seeds were from locally-transient species, with more transients
368 represented in the seed bank (ca. 14% of total seed bank) than in the seed rain (ca. 4% of total
369 seed rain) (Appendix S1: Table S2). Not all locally-transient populations had locally-persistent
370 adult populations at sites with similar climates (Appendix S1: Table S2), pointing to an exchange
371 of seeds among climate zones. Operating on the assumption that locally-transient species
372 dispersed from the most-climatically similar sites at which they persist as adults, seeds of
373 locally-transient species were about four times more likely to have dispersed outside of their
374 realized climate niches into warmer sites (i.e., from cooler climates) and slightly more likely to
375 have dispersed outside of their realized climate niches into drier sites (i.e., from wetter climates)
376 (Appendix S1: Table S2).

377   To determine how sensitive our conclusions were to changes in our operational definition
378 of locally-transient/locally-persistent species status, we explored how results changed under each
379 of the four possible cutoff scenarios offered by our data. That is, we looked at how results
380 changed as the definition of locally-persistent species shifted from those species present in at
381 least one, at least two, at least three, or all four annual surveys of mature vegetation at each given
382 site. As the cutoff for locally-persistent became more stringent, and the cutoff for locally-
383 transient (by definition) relaxed, the total number of locally-transient species-by-site
384 combinations in the combined seed rain and seed bank rose from 119 (1989 seeds), to 149 (2549
385 seeds), to 167 (3665 seeds), to 205 (5007 seeds). However, these differences did not alter our
386 main conclusions that (1) the realized effect of local filtering on community membership
387 increases with temperature, and that (2) grassland sites in southern Norway are connected by
388 dispersal, albeit primarily among sites with similar climates.

389

390 ***The stage-wise removal of locally-transient species.*** Locally-transient species were
391 outperformed by locally-persistent species during seedling emergence (Fig. 3, Table 1), but not
392 seedling establishment (Fig. 3, Appendix S1: Table S3). The lower emergence rates of locally-
393 transient species appeared to be driven primarily by the species that had putatively dispersed
394 outside of their realized climate niches into cooler climates, drier climates, or those that had
395 dispersed from unknown climates (see "Origin-based predictors" in Table 1). In addition, after
396 accounting for local seed abundances, warmer sites tended to have higher rates of seedling
397 emergence than cooler sites ("General predictors" in Table 1), linking climate and overall

398 seedling performance. No GLM of seedling establishment outperformed null expectations

399 (Appendix S1: Table S3), suggesting that neither climate, species status, nor putative seed

400 origins were meaningful predictors of seedling establishment rates.

401   To confirm that these results were not artifacts of how we combined seed rain and seed

402 bank data (e.g., if seeds of locally-transient species emerged at lower rates because most were

403 from the seed bank, and the seed bank had overall lower rates of emergence), we re-ran GLMs

404 with only seed rain data and observed qualitatively similar results (data not shown). To

405 determine how sensitive our conclusions involving seedling performance were to changes in the

406 operational definition of locally-transient/locally-persistent species status, we re-ran the GLMs

407 for emergence and establishment using each of the four possible locally-transient/locally-

408 persistent cutoff scenarios offered by our data. Changes to the locally-transient/locally-persistent

409 cutoff did not alter our overall conclusion that locally-transient species are disfavored during

410 emergence but not establishment (Appendix S1: Fig. S5).

411

412 ***Trait-based mechanisms of local filtering.*** Locally-transient and locally-persistent species in the

413 combined seed rain and seed bank differed significantly in three functional traits (Fig. 4).

414 Specifically, when averaged across species at the site level, locally-transient species were

415 significantly shorter, had smaller seeds, and had less persistent vegetative connections among

416 ramets than locally-persistent species. Of the three traits that differed consistently between

417 locally-transient and locally-persistent species, the only instance where those differences varied

418 significantly with site climate was an increase in the magnitude by which locally-transient

419 species had less persistent connections than locally-persistent species with increasing

420 temperature.

421

422 DISCUSSION

423 In this study, we compared the composition of seed rain, seed bank, seedlings, and adult plant

424 communities along temperature and precipitation gradients to shed light on how dispersal and

425 filtering interactively shape community membership, and how this process varies across a

426 landscape. Overall, our results point to four main conclusions: (1) the total numbers of seeds and

427 species that arrived, but failed to establish locally-persistent populations, rose with temperature,

428 indicating an increase in the realized effects of local filtering on community assembly, as well as

429   an increase in the number of species poised to rapidly colonize those warmer sites if local

430   conditions change in their favor, (2) locally-transient species were selectively filtered out during

431   seedling emergence, but not during seedling establishment, (3) selective filtering was partly

432   driven by species climate preferences, exemplified by the poor performance of seeds dispersing

433   outside of their realized climate niches into foreign climates that were more stressful (colder and

434   drier), and (4) locally-transient species had traits that may have made them better dispersers (i.e.,

435   smaller seeds) but poorer competitors for light (i.e., shorter statures and less persistent clonal

436   connections) than locally-persistent species, potentially explaining why these species arrived to

437   new sites but failed to establish locally-persistent adult populations. We elaborate on these

438   conclusions below, and end with a discussion of what our results mean for how these alpine

439   grasslands will likely respond to climate change.

440

441   ***Community assembly and the determinants of species' ranges***

442   Community membership and the potential for compositional change over time are influenced by

443   the numbers and identities of seeds dispersing, or not dispersing, into a given site. We found

444   relatively few species to be dispersing outside of their realized climate niches, emphasizing the

445   important limiting role that dispersal plays in shaping population distributions, at least on shorter

446   time scales. At the same time, the seeds of the few species that did disperse outside of their

447   realized climate niches were the ones most strongly disfavored by filtering processes (Table 1),

448   highlighting the role that filtering also plays in shaping community composition in our system.

449   These results empirically demonstrate how dispersal and filtering interactively drive community

450   assembly.

451   Within the general detection of filtering across all communities and climates (Table 1),

452   we observed the numbers of locally-transient seeds and species to increase from the coldest

453   (highest altitude) to warmest (lowest altitude) sites (Fig. 2), suggesting that the realized effect of

454   local filtering on community membership (i.e., the numbers of seeds and species that arrive but

455   are filtered out) increases with temperature. Such a temperature-based trend could arise for at

456   least three non-exclusive reasons. First, warm-adapted species could have spatially larger seed

457   dispersal shadows than cold-adapted species, resulting in more seeds traveling to unsuitable

458   patches, such as those with undesirable topographic, edaphic, or biotic conditions. Factors

459   affecting seed dispersal distances include wind speed and plant height (Thomson et al. 2011),

460 although neither are likely to be important in our experimental system: the colder, alpine sites are

461 consistently windier than the warmer, lowland sites, due to their more exposed topography and

462 less protective tree-cover, and the variation in mean maximum plant height among our sites is

463 minor (< 30 cm) (Guittar et al. 2016) compared to the differences in plant height known to affect

464 dispersal distance (Thomson et al. 2011). A second explanation could be that seeds are simply

465 more likely to disperse downhill (i.e., from colder high-altitude sites to warmer low-altitude

466 sites) than the reverse, again leading to more seeds arriving at unsuitably warm patches than

467 unsuitably cold patches. A third explanation could be that competition for resources is fiercer at

468 warmer temperatures, resulting in more local extirpations in the adult plant communities at

469 warmer sites, although, importantly, this explanation presumes that similar numbers of seeds and

470 species are dispersing to all sites, which may not be the case. Nevertheless, other studies have

471 found support for such an explanation: competition for light is hypothesized to be stronger at

472 warmer sites due to higher productivity, more developed soils, and overall less stressful growth

473 conditions (Grime 1973, Olsen et al. 2016). In our study, species richness fell steeply with

474 temperature in the adult vegetation (from an average of 64 species at the coldest sites to 42

475 species at the warmest sites), but only slightly in the seed rain and not in the seed bank (Fig. S4),

476 consistent with a scenario in which similar numbers of species arrive to all sites, but more

477 species are competitively excluded by adulthood at warmer sites. Future work could track

478 individuals after establishment but before mature adulthood to determine if the degree to which

479 locally-transient taxa are disfavored increases with temperature, substantiating this hypothesis.

480   Surprisingly, locally-transient species were disfavored more strongly during the first life-

481 history transition, seedling emergence (Fig. 3, Table 1), than later, during seedling establishment

482 (Fig. 3, Appendix S1: Table S3). This suggests that germination and early seedling survival are

483 more important for success than seedling establishment, at least in our system. This result

484 contradicts conventional expectations of weak filtering during seedling emergence but strong

485 filtering during seedling establishment (Moles and Westoby 2004). Differential germination rates

486 among species could be driven by species preferences for soil (Evans and Etherington 1990,

487 Benvenuti 2003) or climate conditions. It should be noted that while some individuals could have

488 been filtered out after meeting our operational definition of establishment (i.e., had stems at least

489 2 cm long and, if a forb, also had non-cotyledonous leaves), but before becoming reproductively

490 active (i.e., before establishment *sensu stricto*), this does not appear to be the case. Across sites,

491   the mean proportion of species that were classified as locally-transient among established

492   seedlings was only slightly higher than that found in the adult vegetation data (~14.6 % vs. ~13.6

493   %, respectively), indicating that any locally-transient species which successfully emerged were

494   essentially just as likely as locally-persistent species to survive long enough to be captured by

495   our mature vegetation surveys, although these species were not present consistently enough to be

496   classified locally-persistent. In other words, locally-transient species evidently failed to persist

497   not because they failed to establish, but because they failed to arrive in high enough numbers,

498   because their seeds failed to germinate, and/or because their post-establishment juveniles failed

499   to reach sexual maturity.

500   The lower emergence rates among locally-transient species were largely driven by seeds

501   that had putatively dispersed outside their realized climate niches into cooler climates (i.e., from

502   warmer climates), into drier climates (i.e., from wetter climates), and those from unknown

503   climates (Table 1), illustrating how climate-based niche preferences can influence community

504   membership and limit range expansion. Climate is known to play a pivotal role in the release of

505   seed dormancy in plants (Probert 2000), and variation in germination timing is known to occur

506   even among populations of the same species at different climates (Shimono and Kudo 2003,

507   Bischoff et al. 2006, Spindelböck et al. 2013). If the seeds of locally-transient species dispersing

508   outside of their realized climate niches into colder and/or drier climates were predisposed to

509   emerging before spring is safely underway, this could explain their particularly low emergence

510   rates. A second, complementary explanation could be that seeds dispersing outside of their

511   realized climate niches into colder and/or drier climates simply find these conditions more

512   stressful and are thus less likely (i.e., not adapted) to successfully emerge as seedlings.

513   Locally-transient species differed consistently from locally-persistent species in their

514   functional traits, offering some mechanistic hypotheses for why they dispersed into new sites but

515   failed to persist as adults (Fig. 4). First, locally-transient species had consistently smaller seeds

516   than locally-persistent species, which is thought to increase dispersal distance (Greene and

517   Johnson 1993, Westoby 1998), and may also decrease performance upon arrival due to their

518   smaller maternal subsidies (Moles and Westoby 2006). Second, locally-transient species were

519   shorter in stature and had less long-lasting ramet-ramet connections, on average, than locally-

520   persistent species, suggesting that the latter species' ability to grow both vertically and exchange

521   resources horizontally confer important advantages for long-term survival in mature vegetation.

522 Maximum potential height and the capacity for clonal growth are associated with the ability to

523 compete for light (Falster and Westoby 2003) and soil resources in spatially heterogenous

524 systems (Oborny and Kun 2003, Eilts et al. 2011), respectively, and can work synergistically to

525 confer competitive ability in herbaceous communities (Gough et al. 2012). These two traits

526 predicted competitive ability in a turf transplant experiment in the same system (Guittar et al.

527 2016), offering additional support for the importance of architectural traits in driving grassland

528 species performance. Equally noteworthy were the generally weak correlations between locally-

529 transient and locally-persistent species in the remaining functional traits. The weak correlations

530 in these traits does not imply that they have no influence on the selective removal of locally-

531 transient species, but that their influence may not be consistent or predictable across sites.

532   The trait-based differences between locally-transient species and locally-persistent

533 species align with a general tradeoff between colonization and competitive ability (Levins and

534 Culver 1971, Tilman 1994, Amarasekare and Nisbet 2001, Yu and Wilson 2001), and thus

535 suggest that such a tradeoff, when combined with disturbance, is an important driver of

536 succession and community assembly dynamics. That is, the smaller seeds of locally-transient

537 species may promote their probability of arriving to fresh openings in the canopy, while their

538 lower statures and decreased capacity for clonal growth may decrease their chances of

539 establishing locally-persistent populations. The same trade-off underlies the core-satellite

540 hypothesis (Hanski 1982), and likely operates alongside climate-based performance differences

541 among species to shape regional diversity patterns. While our trait-based analysis offers no

542 obvious mechanistic explanation for why locally-transient species were disfavored during

543 seedling emergence, the trait-based differences may correlate with other unmeasured traits that

544 do influence species performance during seedling emergence, and thus may serve as important

545 proxies.

546

547 ***Implications for community responses to climate and climate change.***

548 Community response to climate change will depend both on species' abilities to track

549 environmental changes via dispersal, and on niche-based performance differences among species

550 in different environments (Graae et al. 2017). Southern Norway is expected to grow warmer and

551 wetter as climate change progresses (Hanssen-Bauer et al. 2009), so species will have to disperse

552 into cooler (upslope) and drier (more inland) sites to maintain their current climate conditions.

553   However, of the 122 species with persistent adult populations at one or more of our sites, only 10

554   species (representing 0.3 % of total seeds) dispersed outside of their realized climate niches into

555   cooler sites, and 13 species (representing 1.9 % of total seeds) into drier sites (Appendix S1: Fig.

556   S4, Appendix S1: Table S2), suggesting that many if not most species will likely fail to rapidly

557   shift their populations into cooler and drier climates, and are at risk of being extirpated as

558   competitively-superior species arrive to their communities (Alexander et al. 2015). Yet, our

559   finding that immigrant seeds from other climates were strongly disfavored provides a potential

560   silver lining: if a species can disperse into a site with a newly suitable climate, it should be

561   strongly favored over local residents, and thus be able to quickly establish a locally-persistent

562   population. Overall, our results provide insight into the dynamic way in which communities will

563   respond to climate change, and emphasize the need for further work on how species will vary in

564   their ability to disperse and compete in different community contexts.

565

571

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720

721   **Data Availability**
722   All data and scripts are available on Zenodo: https://doi.org/10.5281/zenodo.3695773
723

724 **Table 1.** Standardized coefficients (z-scores) from different GLM models (columns) predicting numbers of emerged seedlings by
725 species and site. In column headers, "Sp. status" refers to whether the species is locally-transient or locally-persistent, and "Sp. pref.
726 temp./precip." refers to the nearest temperatures/precipitations at which we found the species to have a persistent adult population,
727 which we used to infer the climate from which they likely dispersed. The predictor "Seed no. (transformed)" refers to the numbers of
728 seeds of each species at each site, normalized with Yeo-Johnson transformations (refer to Methods). Data consisted of all recorded
729 seeds and seedlings that could be identified to species. N is equal to 692, the number of unique emerged seedling and/or seed species-
730 by-site combinations. Asterisks denote significance (*: p < 0.05, **: p < 0.001). Dashes denote predictors that were not included in a
731 given model.

732

	Null model	Site climate	Site climate + Sp. status	Site climate + Sp. pref. temp.	Site climate + Sp. pref. precip.
ΔAIC	0.00	-5.14	-16.28	-28.18	-35.11
General predictors					
Seed no. (transformed)	**6.84	**7.19	**5.15	**5.98	**6.30
Local temp.	-	*2.79	*2.24	*2.98	*3.15
Local precip.	-	-1.09	-1.30	-1.52	-1.65
Transient/Persistent predictors					
Transient	-	-	**-4.65	-	-
Transient * Local temp.	-	-	1.79	-	-
Transient * Local precip.	-	-	1.29	-	-
Origin-based predictors					

Transients from similar temp.	-	-	-	-1.34	-
Transients from cooler into warmer	-	-	-	-1.78	-
Transients from warmer into cooler	-	-	-	*-2.86	-
Transients from similar precip.	-	-	-	-	-1.54
Transients from drier into wetter	-	-	-	-	-0.06
Transients from wetter into drier	-	-	-	-	**-4.45
Transients from unknown climates	-	-	-	**-5.58	**-5.60

734   **Figure 1.** Climates (a) and locations (b and c) of the twelve field sites in southern Norway. Mean

735   summer temperature is defined as the warmest four months at each site. Grayscale shading in c

736   reflects altitude, which covaries closely with mean summer temperature.

737

738   **Figure 2.** Seed density (a) and species richness (b) in the combined seed rain and seed bank,

739   grouped by locally-transient/locally-persistent species status and plotted by mean summer

740   temperature. Summer is defined as the four warmest months at each site. Regression trendlines

741   are solid when temperature is a significant predictor ($p < 0.05$) of $\log_{10}$-transformed seed density

742   or species richness in a linear regression. A parallel set of regressions was performed using mean

743   annual precipitation as the sole predictor, but no trends were even marginally significant (p-

744   values always > 0.1).

745

746   **Figure 3.** Life-stage transition probabilities, grouped by locally-transient/locally-persistent

747   species status. Specifically, numbers of emerged seedlings of each species at each site are plotted

748   by their corresponding number of seeds at each site (a), and numbers of established seedlings of

749   each species at each site are plotted by their corresponding number of emerged seedlings at each

750   site (b). As such, each circle represents the presence/absence of one species at one site, and

751   colored lines and shadings show LOESS smoothing functions and 95 % confidence intervals.

752   Seed abundances equal the total number of seeds in the seed rain and seed bank. Seedling

753   abundances equal the total number of individuals in four 25 x 25 cm subplots at each site. Count

754   data are increased by one to allow for plotting zeroes on a log scale. Panels only show data

755   falling within the observed window of locally-transient seed abundances (< 400 seeds) and

756   locally-transient seedling abundances (< 33 seedlings) in order to focus on the comparison of

757   locally-transient and locally-persistent species.

758

759   **Figure 4.** Mean trait values of locally-transient species relative to locally-persistent species at

760   each site. Panels show data for four commonly used traits (top row) and four clonal traits

761   (bottom row). Shapes and shadings are consistent with Fig. 1 and reflect approximate mean

762   summer temperatures of 6 °C (triangle), 9 °C (circle), and 10.5 °C (inverted triangle) and annual

763   precipitations of 650 mm, 1300 mm, 2000 mm, and 2900 mm, from light blue to dark blue.
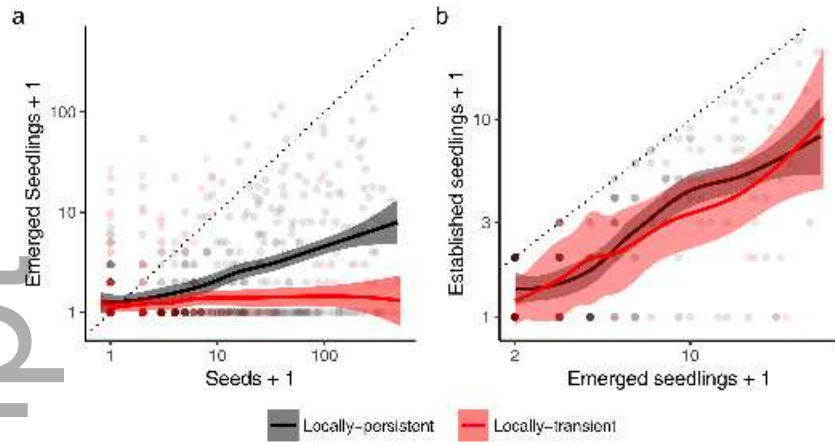
764   Shapes are filled with color only when values differ significantly between locally-transient and

765   locally-persistent species across all sites (paired t-test; $p < 0.05$). SLA: specific leaf area. Bud

766   number is an integer score that ranges from 1 (few buds either belowground or aboveground) to

767   8 (many buds both below and aboveground); percent lateral spread refers to the proportion of

768   species with rates of lateral spread greater than 1 cm/year; percent offspring refers to the

769   proportion of species that commonly produce two or more vegetative offshoots per parent per

770   year; percent connection persistence refers to the proportion of species with inter-ramet
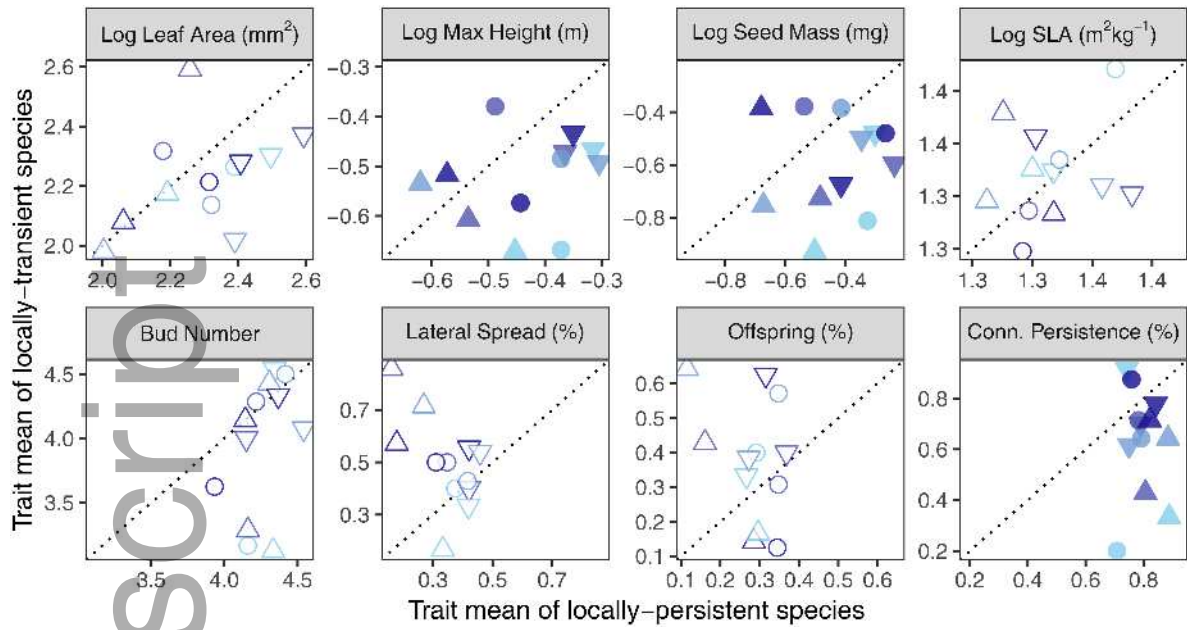
771   connections that persist for two or more years.

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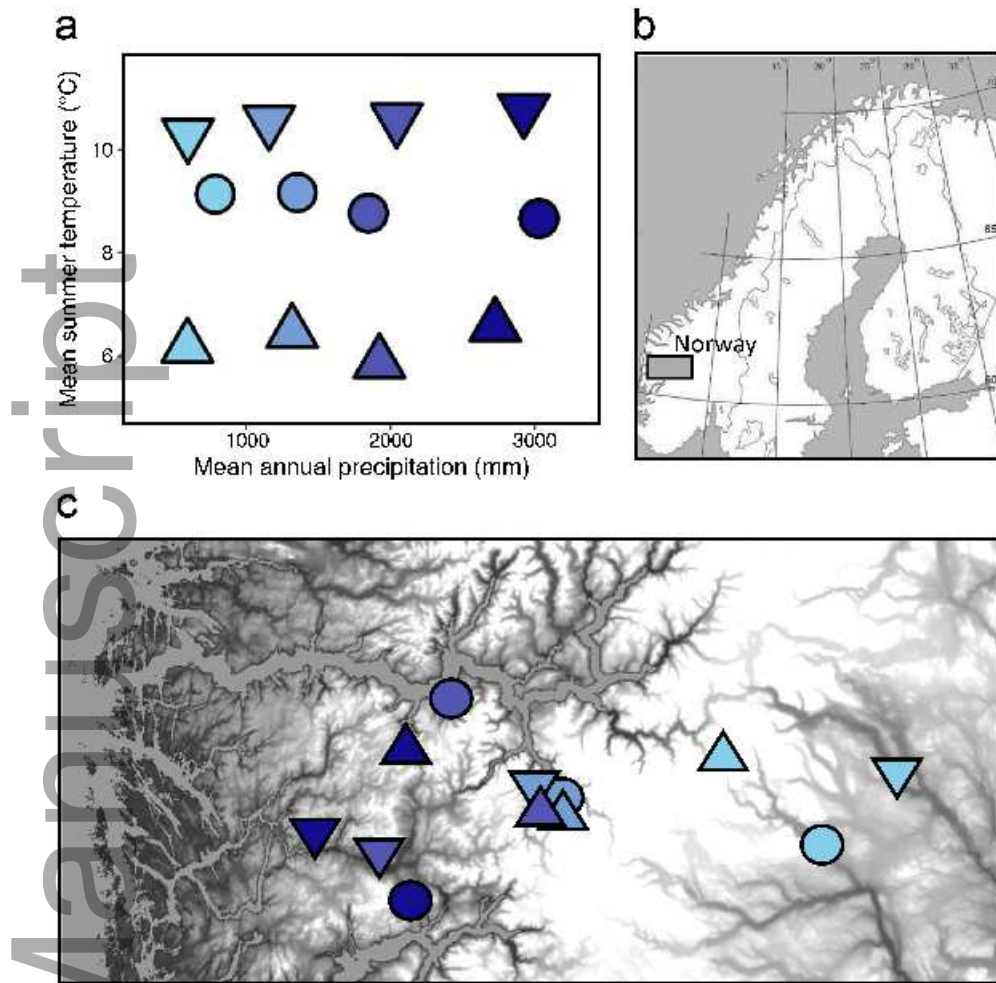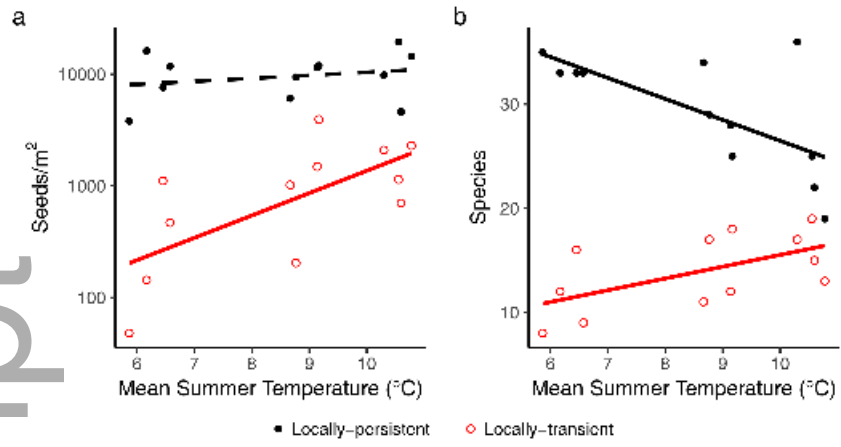
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