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

3

4 Running head: Dispersal and filtering in grasslands

5

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24 ABSTRACT

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

47 these species arrived to new sites but did not establish locally-persistent adult populations. Our
48 study is the first to combine seed, seedling, and adult survey data across sites to rigorously
49 characterize how seed dispersal and local filtering govern community membership and shape
50 climate-associated vegetation patterns.

51

52 **Keywords:** Alpine grasslands, climate change, community assembly, dispersal dynamics, range
53 expansion, seedling survival, metacommunities, species sorting.

54

55 INTRODUCTION

56 Plant community assembly in a landscape or metacommunity context includes important roles
57 for seed dispersal among communities and local filtering (Leibold et al. 2004, Alexander et al.
58 2012). Despite empirical evidence illustrating how dispersal and filtering can shape community
59 membership on their own (Choler et al. 2001, Ehrlén et al. 2006, Armas et al. 2011, Laliberte et
60 al. 2014), there is a lack of data documenting how dispersal and filtering interact in natural plant
61 communities. This lack of data represents a missing link between our theoretical understanding
62 of how plant diversity patterns can form and how they actually form. Moreover, it hampers our
63 ability to predict community responses to climate change, because different species likely have
64 different dispersal abilities and/or different constraints to expansion, leading to variable
65 responses (Graae et al. 2017).

66 The absence of a clear empirical picture of how dispersal and filtering interactively shape
67 plant community membership and regional diversity patterns is due in large part to the logistical
68 challenges of connecting dispersed seeds to individual plant performance. Plant propagules are
69 often tiny, numerous, difficult to identify and track, capable of traveling great distances, and can

70 remain dormant in the soil for years prior to germination (Baskin and Baskin 1998, Vandvik et
71 al. 2016). Some researchers have tried to infer dispersal and filtering dynamics using indirect
72 methods (Alexander et al. 2012). The “nearest-neighbor” approach, for example, assumes
73 connectivity in a metacommunity to be proportional to inter-patch distance (Calabrese and Fagan
74 2004, Jacobson and Peres-Neto 2010). Other approaches infer dispersal patterns from historical
75 population range shifts over periods of climate change (Kelly and Goulден 2008, Bertrand et al.
76 2011) or by analyzing population genetic structure. These indirect methods are useful when
77 modeling species distributions phenomenologically, but fall far short of evaluating whether
78 species fail to arrive or fail to persist after arrival (Calabrese and Fagan 2004). The small number
79 of studies that have directly assessed dispersal patterns, either by manually marking seeds (e.g.,
80 Xiao et al. 2006) or connecting seeds to parents using parentage analyses (e.g., Cain et al. 2000),
81 are often conducted for single species and/or over short distances, and are of limited use when
82 considering responses of dozens of species at regional scales (Nathan and Muller-Landau 2000).

83 Here, we compare the seed rain, seed bank, seedlings, and adult plant communities at 12
84 sites falling along temperature and precipitation gradients in southern Norway to shed light on
85 how seed dispersal and filtering interact *in situ* to shape community membership and maintain
86 regional climate-associated vegetation patterns. Although our questions align with those of
87 metacommunity theory (Leibold et al. 2004), our sites exist within a broad and contiguous
88 patchwork of grassland habitat, making our system unsuitable to explicitly empirically evaluate
89 between-patch dispersal dynamics, and therefore motivating us to develop our own approach.
90 Specifically, we divide species at each site into two groups: “locally-transient” species, which
91 occur as seeds but are rare or absent as adults (i.e., they arrive from outside the site but are
92 filtered out), and “locally-persistent” species, which occur consistently as adults in annual

93 vegetation surveys. We use adult vegetation surveys to infer which species dispersed outside of
94 their realized climate niches (i.e., were found outside of the climate ranges where we found them
95 to persist as adults), and how their realized climate niches compared to local climate conditions
96 (i.e., if they have dispersed into warmer/wetter/cooler/drier climates). We then ask how and why
97 locally-transient species were selectively disfavored during community assembly at each site,
98 and how this process varied by climate. Our framework recalls the core-satellite framework of
99 Hanski (1982), but differs in that we allow species status to vary by site, enabling us to examine
100 how species performance varies by environment.

101 Our study takes place in a network of 12 alpine and subalpine grassland sites in southern
102 Norway, a region with unusually high spatial climate variability. The sites were selected
103 according to their mean summer temperatures and mean annual rainfalls such that they form an
104 orthogonal climate grid (Fig. 1), facilitating independent assessment of these two important
105 climate drivers in community assembly. Prior work in our system used subsets of the data used
106 in this study to compare diversity patterns in the seed bank and mature vegetation (Vandvik et al.
107 2016, Meineri et al. 2020), to understand how trait-based community composition varies with
108 climate (Guittar et al. 2016), and to evaluate the relative balance of competition and facilitation
109 in seedling recruitment (Klanderud et al. 2017). We combine these previously published data
110 with new data on seed rain and seedling survival to ask how dispersal and filtering interactively
111 govern community membership and regional vegetation patterns. After dividing species into
112 locally-transient and locally-persistent groups at each site, we ask the following questions:

- 113 1. How many seeds and species arrive to a site but fail to establish locally-persistent
114 adult populations, and how does this vary with climate?

- 115 2. At what life stages are locally-transient species disfavored? Are they less likely to
116 emerge as seedlings, establish as seedlings, compete as adults, or a combination of the
117 three?
- 118 3. Why do locally-transient species fail to persist? Is it because they dispersed from
119 outside of their realized climate niches and are disfavored due to their climate
120 preferences? Is it because they differ from locally-persistent species in their
121 functional traits, offering mechanistic hypotheses for their arrival and selective
122 removal?
- 123 4. What do our results mean for how these grasslands will respond to climate change?
124

125 MATERIALS AND METHODS

126 *Study area.* The study area comprises 12 semi-natural calcareous grassland sites in southern
127 Norway that host at least 144 non-woody vascular plant species at the adult life stage, and at
128 least 126 at the seed stage (Appendix S1: Table S1). Sites have similar bedrock, land use
129 histories, slopes of approximately 20°, and southwest aspects, but differ in mean summer
130 temperature, defined as the mean temperature of the four warmest months per year, and/or mean
131 annual precipitation, such that they form a grid with approximately orthogonal climate axes (Fig.
132 1). Interannual variation in mean summer temperature and annual precipitation at each site over
133 the sampling period (2008 – 2013) was modest, with standard deviations of 0.79 °C and 238 mm,
134 respectively, on average across sites. Each site has five blocks, placed in representative areas of
135 grassland vegetation within a 75 – 200 m² area, with individual positions that vary according to
136 local topography and accessibility. Each block has a variable number of 25 x 25 cm plots used
137 for the data sets described below, as well as other experiments and surveys. Blocks were

138 protected from grazers with electric fences and manually mowed once a year to evenly simulate
139 biomass loss due to grazing. Taxonomic identifications follow Lid & Lid (2007). Woody species
140 and bryophytes were not recorded in all datasets and therefore were excluded from analyses.

141

142 **Seed rain data.** We collected seed rain over two periods to target winter (September 2009 to
143 June 2010) and summer (June 2010 to September 2010) seed deposition. We trapped seeds in 25
144 x 25 cm artificial turfs placed in gaps about 50 cm from seedling monitoring gaps (see below) in
145 four blocks at each site, for a total of 48 traps across all sites. The small synthetic filaments in
146 artificial turfs effectively catch and retain small particles like seeds. Turfs were gathered and
147 flushed with water to free collected seeds. The rinse water was passed through 500 μm and 125
148 μm diameter sieves to discriminate seeds by size and remove debris. Seeds were counted and
149 identified taxonomically using a stereomicroscope. We included fruits, bulbils, and viviparous
150 seeds in our working definition of “seeds.” Rates of seed predation on artificial turfs are likely
151 similar to those on soil, thus seed predation should not bias our results.

152

153 **Seed bank data.** To characterize seed bank diversity we haphazardly selected one 64 x 64 cm
154 plot at each site and excavated soil to a depth of 3 cm in October 2008. Because the seed bank
155 survey area at each site (0.41 m^2) was larger than the total areas used for seed rain and seedling
156 surveys at each site (four 25 x 25 cm plots, 0.25 m^2), we randomly subsampled 61 % (0.25 m^2 /
157 0.41 m^2) of the original seed bank community *in silico* and discarded the remainder to
158 standardize sampling effort across plant life stages. To exclude the seeds from that year’s seed
159 rain from our seed bank surveys, we removed the aboveground vegetation, including moss and
160 litter. Soil samples were stored for three months at 2 – 4 °C and ambient moisture. Soil samples

161 were then sowed into a standard mixture of sterile subsoil and placed in 30 x 60 cm trays. The
162 trays were incubated in a greenhouse with a diurnal cycle of 16 hours light (25 °C) and 8 hours
163 darkness (15 °C). The diurnal cycle was continued for four months, followed by six months of
164 cold stratification in darkness (4 °C), followed by another four-month period of diurnal cycling.
165 Emerging seedlings were counted and removed once identifiable to species. This method of
166 characterizing the seed bank community effectively accounts for seed viability because non-
167 viable seeds would not have emerged as seedlings.

168

169 ***Seedling data.*** Like most perennial grasslands, seedling recruitment in our system is highly
170 dependent on disturbances and occurs only rarely in intact vegetation due to strong competitive
171 effects from adult plants (Silvertown and Smith 1989, Eriksson 1989, Bullock et al. 1995,
172 Vandvik 2004, Berge 2010, Klanderud et al. 2017). We therefore monitored seedlings in
173 experimental gaps where they were relatively free from competitive effects of adult plants, but
174 still exposed to environmental stress and other biotic interactions, such as herbivory, disease, and
175 potential resource competition among seedlings. One 25 x 25 cm gap was created in each of four
176 blocks at each site in spring 2009, for a total of four gaps per site and 48 gaps overall. The gaps
177 were made by cutting along the inner edges of a metal frame mounted in metal pipes marking the
178 corners of the plot, and peeling away the natural vegetation and its thickly interwoven root mat.
179 Seeds and topsoil were returned to gaps by vigorously shaking excavated vegetation and passing
180 it through a 4 mm sieve to remove plant remains. Emerged seedlings in the plots were ID-tagged
181 in one of three censuses (late summer 2009, early summer 2010, late summer 2010) using
182 numbered plastic toothpicks and plot coordinates. About 70 % of seedlings were identifiable to
183 species; the remaining 30 % were unidentifiable or died before they could be identified and were

184 lumped into two generic groups for graminoids and forbs. Seedlings were differentiated from
185 emergent clonal ramets by looking for cotyledons or signs of above- or below-ground
186 connections. Seedling survival and potential establishment were recorded twice yearly from
187 spring 2010 to spring 2012. We approximated seedling emergence rates by dividing the density
188 of emerged seedlings by the sum of seed rain and seed bank densities. We marked seedlings
189 established when they had grown to a size greater than what could be derived exclusively from
190 their maternal subsidies, which we estimated to be when stems were longer than 2 cm, and if a
191 forb, also when they had grown their first non-cotyledonous leaves. Although we took pains to
192 census each site at times of peak seedling emergence, some seedlings may have emerged, died,
193 and disappeared before ever being recorded; even if this were the case, however, we contend
194 that it is unlikely to influence our overall conclusions because the factors discouraging seedling
195 survival during the earliest stages of establishment are likely the same as those discouraging
196 seedling emergence (e.g., late spring frosts), and are distinct from the factors influencing
197 seedling survival establishment (e.g., drought, competition for light, predation, early fall frosts,
198 and late spring frosts in the year after seedling emergence).

199

200 ***Mature vegetation data.*** We surveyed mature vegetation at peak biomass (July or August) in
201 2009, 2011, 2012, and 2013. At each site, we used two 25 x 25 cm plots in each of five blocks at
202 each site, for a total of 10 plots per site (except for the third-wettest second-warmest site, which
203 only had nine plots), and 119 plots overall. These plots were controls for a turf transplant
204 experiment and included five undisturbed controls and five transplant controls (i.e., turfs dug up
205 and replaced in the same location). The two types of controls did not differ in species
206 composition or any other aspect of community structure at any of the survey periods (Guittar et

207 al. 2016). We visually estimated the percent cover of each species in each plot using a 5 x 5 cm
208 grid overlay, and then pooled the data by site. To ensure that site vegetation was not undergoing
209 successional changes that could bias our conclusions, we used an NMDS ordination to confirm
210 that site composition did not change substantively between years (Appendix S1: Fig. S1). Stage-
211 specific species abundance data are provided as a supplementary file.

212

213 **Trait data.** We used four commonly used plant traits, and four traits related to clonal growth
214 strategy, an important facet of competitive ability in perennial grasslands. Each trait has
215 hypothesized associations to dispersal ability and/or the ability to compete for resources. Seed
216 mass (mg), a reflection of species regeneration strategy (Kraft et al. 2008, Cornwell and Ackerly
217 2009), was drawn from the Seed Information Database (Kew Royal Botanic Gardens 2008).
218 Maximum canopy height (m) data, which relates to both dispersal ability and light competition
219 (Westoby 1998, Falster and Westoby 2003, D'Andrea et al. 2020), were mined from Lid and Lid
220 (2007). Leaf area (mm²) and specific leaf area (SLA; m²/kg), two traits indicative of where
221 species fall along a continuum of slow-to-fast resource use strategies (Reich et al. 1997, Ackerly
222 and Reich 1999, Reich 2014), were estimated using a combination of field data (Guittar et al.
223 2016) and data from the LEDA online trait database (Kleyer et al. 2008). Leaf area, SLA,
224 maximum height, and seed mass values were log-transformed. Clonal traits included the number
225 of offspring per parent per year (“0” = 1 offspring; “1” = ≥ 2 offspring), persistence of plant–
226 offspring connections (“0” = < 2 years; “1” = ≥ 2 years), rate of lateral spread (“0” = ≤ 1
227 cm/year; “1” = > 1 cm/year), and number of buds per ramet (an integer score ranging from “1” =
228 few buds either belowground or aboveground, to “8” = many buds both below and
229 aboveground). Clonal attributes are thought to help plants integrate over spatially heterogeneous

230 resources (Eilts et al. 2011), recover from disturbances (Klimešová and Klimeš 2007), and
231 provide sustained maternal subsidies to new ramets as they grow horizontally and vie for local
232 establishment (Herben and Wildová 2012). Clonal trait data were drawn from Klimeš and
233 Klimešová (1999) and converted from categorical to quantitative formats to enable calculations
234 of community means. Trait data are provided as a supplementary file.

235

236 ***Assigning local species status.*** Each species observed at each site at any life stage was labeled as
237 “locally-persistent” if adults were recorded in more than half (i.e., at least three of four) of the
238 site vegetation surveys conducted from 2009 to 2013, or otherwise labeled “locally-transient.” In
239 using this cutoff, we distinguish species that are consistent community members from those that
240 are not. Because locally-transient/locally-persistent species status assignments were potentially
241 sensitive to the depth at which we characterized local site community composition, we used
242 rarefaction to ensure that we had sufficiently surveyed the mature vegetation such that the
243 number of locally-persistent species observed at each site had stabilized (Appendix S1: Fig. S2).
244 We also re-ran our analysis with all possible locally-transient/locally-persistent cutoffs to assess
245 the sensitivity of our conclusions to our methodology.

246

247 ***Assigning putative climate origins.*** For each locally-transient species at each site, we identified
248 the sites and climates where we knew it had persistent adult populations, and then used these to
249 infer whether it was dispersing outside of its realized climate niche. If a locally-transient species
250 at a given site had persistent adult populations at other sites with similar temperatures and/or
251 precipitations, we assumed it dispersed from a site with approximately the same temperature
252 and/or the same precipitation, such as from a neighboring site with a similar climate but with

253 potentially different topographical, edaphic, or biotic characteristics. If a locally-transient species
254 at a given site had persistent adult populations only at sites with warmer/cooler or wetter/drier
255 conditions, we then assumed it dispersed from a warmer/cooler or wetter/drier site (i.e., it
256 dispersed *into* a cooler/warmer or drier/wetter site). Again, we are not assuming that a given seed
257 of a locally-transient species literally dispersed from a given climate, but that the seed is
258 occurring outside of the climate range at which it is a common and persistent community
259 member, and is presumably on the cusp of being locally excluded.

260

261 ***Statistical approach.*** We used linear regressions to test for baseline trends in the total abundance
262 and richness of locally-transient and locally-persistent species in the seed rain, the seed bank, and
263 the two combined along temperature and precipitation gradients. Unlike other data in this study,
264 seed bank data were not collected in replicate across blocks within a site, thus we performed
265 regressions on data aggregated by site ($N = 12$). Each linear regression model assumes normally
266 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
267 being examined at site j , and MAP_j and MST_j are the mean annual precipitation (centered to
268 zero) and mean summer temperature (centered to zero) at site j . We also used linear regressions
269 to test for baseline trends in species richness in the mature vegetation with temperature and
270 precipitation.

271 We used four sets of generalized linear models (GLMs) to test potential predictors of
272 species performance during seedling emergence and seedling establishment. The dependent
273 variable for seedling emergence GLMs was the number of emerged seedlings of each species at
274 each site ($N = 692$, the number of unique seed and/or seedling species-by-site combinations), and
275 the dependent variable for seedling establishment GLMs was the number of established seedlings

276 of each species at each site ($N = 279$, the number of unique seedling species-by-site
277 combinations). The GLMs used negative binomial error distributions and log link functions.
278 Because each site has a unique combination of temperature and precipitation values (i.e., there is
279 no nestedness), it was not appropriate to include site as a random effect while also testing for the
280 effects of climate. When using seed and seedling numbers as predictors of emergence and
281 establishment, respectively, we normalized their highly skewed abundance distributions with
282 Yeo-Johnson transformations, which are similar to Box-Cox transformations but can be used
283 with zeros. The lambda values used for the Yeo-Johnson transformations were those which
284 maximized normality, as quantified by Shapiro-Wilk normality tests; specifically, the lambda
285 used to transform seed abundance data was -0.204 and the lambda used to transform emerged
286 seedling data was -0.35.

287 In the first, baseline set of GLMs (“null” models), local species abundances in the
288 combined seed rain and seed bank were used as predictors of local species abundances of
289 emerged seedlings, and local species abundances of emerged seedlings were used as predictors
290 of local species abundances of established seedlings. Formally, we modeled the number of
291 emerged seedlings g for species i at site j as $g_{ij} \sim s_trans_{ij}$, where s_trans_{ij} is the Yeo-Johnson
292 transformed abundance of seeds (seed rain + seed bank) of species i at site j . In other words, our
293 null expectation was that all seeds were equally likely to emerge, and all seedlings were equally
294 likely to establish. In the second set of GLMs (“site climate” models), we added model terms
295 MAP_j and MST_j for local site mean summer temperature and mean annual precipitation at site j
296 to evaluate how these climate variables improved predictions of seedling emergence and seedling
297 establishment rates.

298 In the third set of GLMs (“site climate + species status” models), we evaluated how well
 299 locally-transient/locally-persistent species status predicted performance differences during
 300 seedling emergence and seedling establishment. Specifically, we added model terms specifying
 301 the status of each species at each site, and interactions between species status and local climate.
 302 Formally, this is

$$303 \quad g_{ij} \sim s_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \cdot p_{ij}) + (MST_j \cdot p_{ij}),$$

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

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

$$306 \quad e_{ij} \sim g_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \cdot p_{ij}) + (MST_j \cdot p_{ij}),$$

307 where g_trans_{ij} is the Yeo-Johnson transformed abundance of emerged seedlings of species i at
 308 site j , and the other variables are as described above.

309 In the fourth and final set of GLMs (“site climate + species status + species climate
 310 origin” models), we dropped p_{ij} , the model term for locally-transient/locally-persistent species
 311 status, and replaced it with o_{ij} , a new term denoting the putative temperature/precipitation
 312 origins of each locally-transient species i at site j . Specifically, the o_{ij} term tags each species at
 313 each site with one of five labels: (1) locally-persistent, (2) locally-transient but likely dispersed
 314 from an adjacent site with similar temperature/precipitation, (3) locally-transient and likely
 315 dispersed from a cooler/drier site (i.e., into a warmer/wetter site), (4) locally-transient and likely
 316 dispersed from a warmer/wetter site (i.e., into a cooler/drier site), (5) locally-transient with no
 317 locally-persistent populations at any of our grassland sites (i.e., an ‘unknown’ climate
 318 preference). We dropped the interaction terms from these GLMs to reduce excessive model
 319 complexity. Formally, we modelled the number of emerged seedlings g as

$$320 \quad g_{ij} \sim s_trans_{ij} + MAP_j + MST_j + o_{ij},$$

321 and the number of established seedlings e as

$$322 \quad e_{ij} \sim g_{trans_{ij}} + MAP_j + MST_j + o_{ij},$$

323 Finally, we asked if systematic differences in the traits of locally-transient and locally-
324 persistent species at each site offered mechanistic explanations for performance differences
325 between the two groups. To do this, we averaged the trait values of all species (not weighted by
326 their relative abundances) in the combined seed rain and seed bank at each site, grouped by
327 local-transient/locally-persistent species status. We used paired t-tests, paired by site, to identify
328 which traits, if any, differed consistently between locally-transient and locally-persistent species
329 across all sites. For the traits with significant differences between the two groups, we performed
330 linear regressions to see whether the magnitude of the difference trended with site temperature or
331 precipitation. We did not test for trait-based differences by species status in seedling
332 communities because the number of locally-transient species was too low to provide confidence
333 in calculations of within-site trait means (only 4 ± 3 locally-transient species occurred on average
334 as emerged seedlings at each site; Appendix S1: Table S1). All scripts in this study were written
335 in R.

336

337 RESULTS

338 ***Mature vegetation rarefactions.*** Rarefactions indicated that the numbers of plots of mature
339 vegetation surveyed at each site were more than sufficient to stabilize the compositions of
340 locally-persistent species (Appendix S1: Fig. S2), lending confidence to our locally-
341 transient/locally-persistent species status assignments. Furthermore, no locally-transient species
342 by itself ever represented more than 0.4% of total cover at any site (Appendix S1: Fig. S3),

343 illustrating the minor overall contribution of locally-transient species to local community
344 structure.

345
346 ***Evidence of dispersal and filtering.*** Seeds of locally-transient species occurred at all 12 of our
347 grassland sites, representing, on average, 4 of 42 species in the combined seed rain and seed
348 bank. In the combined seed rain and seed bank, the number of locally-transient species and their
349 total abundances increased significantly with temperature (Fig. 2; species richness: $p = 0.045$, R^2
350 $= 0.34$; total abundance: $p = 0.016$, $R^2 = 0.46$). These trends were driven primarily by increases
351 of local-transients in the seed bank (species richness: $p = 0.031$, $R^2 = 0.39$; total abundance $p =$
352 0.035 , $R^2 = 0.37$), not the seed rain (Appendix S1: Fig. S4), underscoring the fact that the
353 composition of the seed rain likely differs between years, and that the seed bank likely serves as
354 an important reservoir of local plant diversity. The strength at which locally-transient species
355 were disfavored during seedling emergence did not change with temperature (Table 1; refer to
356 the lack of significance for the transient*local temperature interaction term). There were no
357 significant trends in species richness or total abundance with precipitation in either the seed rain,
358 the seed bank, or the two combined. Species richness in the adult vegetation rose significantly
359 with temperature ($p = 0.0063$, $R^2 = 0.54$) but not with precipitation ($p = 0.871$).

360 About 10% of all seeds were from locally-transient species, with more transients
361 represented in the seed bank (ca. 14% of total seed bank) than in the seed rain (ca. 4% of total
362 seed rain) (Appendix S1: Table S2). Not all locally-transient populations had locally-persistent
363 adult populations at sites with similar climates (Appendix S1: Table S2), pointing to an exchange
364 of seeds among climate zones. Operating on the assumption that locally-transient species
365 dispersed from the most-climatically similar sites at which they persist as adults, seeds of

366 locally-transient species were about four times more likely to have dispersed outside of their
367 realized climate niches into warmer sites (i.e., from cooler climates) and slightly more likely to
368 have dispersed outside of their realized climate niches into drier sites (i.e., from wetter climates)
369 (Appendix S1: Table S2).

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

382

383 ***The stage-wise removal of locally-transient species.*** Locally-transient species were
384 outperformed by locally-persistent species during seedling emergence (Fig. 3, Table 1), but not
385 seedling establishment (Fig. 3, Appendix S1: Table S3). The lower emergence rates of locally-
386 transient species appeared to be driven primarily by the species that had putatively dispersed
387 outside of their realized climate niches into cooler climates, drier climates, or those that had
388 dispersed from unknown climates (see “Origin-based predictors” in Table 1). In addition, after

389 accounting for local seed abundances, warmer sites tended to have higher rates of seedling
390 emergence than cooler sites (“General predictors” in Table 1), linking climate and overall
391 seedling performance. No GLM of seedling establishment outperformed null expectations
392 (Appendix S1: Table S3), suggesting that neither climate, species status, nor putative seed
393 origins were meaningful predictors of seedling establishment rates.

394 To confirm that these results were not artifacts of how we combined seed rain and seed
395 bank data (e.g., if seeds of locally-transient species emerged at lower rates because most were
396 from the seed bank, and the seed bank had overall lower rates of emergence), we re-ran GLMs
397 with only seed rain data and observed qualitatively similar results (data not shown). To
398 determine how sensitive our conclusions involving seedling performance were to changes in the
399 operational definition of locally-transient/locally-persistent species status, we re-ran the GLMs
400 for emergence and establishment using each of the four possible locally-transient/locally-
401 persistent cutoff scenarios offered by our data. Changes to the locally-transient/locally-persistent
402 cutoff did not alter our overall conclusion that locally-transient species are disfavored during
403 emergence but not establishment (Appendix S1: Fig. S5).

404
405 ***Trait-based mechanisms of local filtering.*** Locally-transient and locally-persistent species in the
406 combined seed rain and seed bank differed significantly in three functional traits (Fig. 4).
407 Specifically, when averaged across species at the site level, locally-transient species were
408 significantly shorter, had smaller seeds, and had less persistent vegetative connections among
409 ramets than locally-persistent species. Of the three traits that differed consistently between
410 locally-transient and locally-persistent species, the only instance where those differences varied
411 significantly with site climate was an increase in the magnitude by which locally-transient

412 species had less persistent connections than locally-persistent species with increasing
413 temperature.

414

415 DISCUSSION

416 In this study, we compared the composition of seed rain, seed bank, seedlings, and adult plant
417 communities along temperature and precipitation gradients to shed light on how dispersal and
418 filtering interactively shape community membership, and how this process varies across a
419 landscape. Overall, our results point to four main conclusions: (1) the total numbers of seeds and
420 species that arrived, but failed to establish locally-persistent populations, rose with temperature,
421 indicating an increase in the realized effects of local filtering on community assembly, as well as
422 an increase in the number of species poised to rapidly colonize those warmer sites if local
423 conditions change in their favor, (2) locally-transient species were selectively filtered out during
424 seedling emergence, but not during seedling establishment, (3) selective filtering was partly
425 driven by species climate preferences, exemplified by the poor performance of seeds dispersing
426 outside of their realized climate niches into foreign climates that were more stressful (colder and
427 drier), and (4) locally-transient species had traits that may have made them better dispersers (i.e.,
428 smaller seeds) but poorer competitors for light (i.e., shorter statures and less persistent clonal
429 connections) than locally-persistent species, potentially explaining why these species arrived to
430 new sites but failed to establish locally-persistent adult populations. We elaborate on these
431 conclusions below, and end with a discussion of what our results mean for how these alpine
432 grasslands will likely respond to climate change.

433

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

435 Community membership and the potential for compositional change over time are influenced by
436 the numbers and identities of seeds dispersing, or not dispersing, into a given site. We found
437 relatively few species to be dispersing outside of their realized climate niches, emphasizing the
438 important limiting role that dispersal plays in shaping population distributions, at least on shorter
439 time scales. At the same time, the seeds of the few species that did disperse outside of their
440 realized climate niches were the ones most strongly disfavored by filtering processes (Table 1),
441 highlighting the role that filtering also plays in shaping community composition in our system.
442 These results empirically demonstrate how dispersal and filtering interactively drive community
443 assembly.

444 Within the general detection of filtering across all communities and climates (Table 1),
445 we observed the numbers of locally-transient seeds and species to increase from the coldest
446 (highest altitude) to warmest (lowest altitude) sites (Fig. 2), suggesting that the realized effect of
447 local filtering on community membership (i.e., the numbers of seeds and species that arrive but
448 are filtered out) increases with temperature. Such a temperature-based trend could arise for at
449 least three non-exclusive reasons. First, warm-adapted species could have spatially larger seed
450 dispersal shadows than cold-adapted species, resulting in more seeds traveling to unsuitable
451 patches, such as those with undesirable topographic, edaphic, or biotic conditions. Factors
452 affecting seed dispersal distances include wind speed and plant height (Thomson et al. 2011),
453 although neither are likely to be important in our experimental system: the colder, alpine sites are
454 consistently windier than the warmer, lowland sites, due to their more exposed topography and
455 less protective tree-cover, and the variation in mean maximum plant height among our sites is
456 minor (< 30 cm) (Guittar et al. 2016) compared to the differences in plant height known to affect
457 dispersal distance (Thomson et al. 2011). A second explanation could be that seeds are simply

458 more likely to disperse downhill (i.e., from colder high-altitude sites to warmer low-altitude
459 sites) than the reverse, again leading to more seeds arriving at unsuitably warm patches than
460 unsuitably cold patches. A third explanation could be that competition for resources is fiercer at
461 warmer temperatures, resulting in more local extirpations in the adult plant communities at
462 warmer sites, although, importantly, this explanation presumes that similar numbers of seeds and
463 species are dispersing to all sites, which may not be the case. Nevertheless, other studies have
464 found support for such an explanation: competition for light is hypothesized to be stronger at
465 warmer sites due to higher productivity, more developed soils, and overall less stressful growth
466 conditions (Grime 1973, Olsen et al. 2016). In our study, species richness fell steeply with
467 temperature in the adult vegetation (from an average of 64 species at the coldest sites to 42
468 species at the warmest sites), but only slightly in the seed rain and not in the seed bank (Fig. S4),
469 consistent with a scenario in which similar numbers of species arrive to all sites, but more
470 species are competitively excluded by adulthood at warmer sites. Future work could track
471 individuals after establishment but before mature adulthood to determine if the degree to which
472 locally-transient taxa are disfavored increases with temperature, substantiating this hypothesis.

473 Surprisingly, locally-transient species were disfavored more strongly during the first life-
474 history transition, seedling emergence (Fig. 3, Table 1), than later, during seedling establishment
475 (Fig. 3, Appendix S1: Table S3). This suggests that germination and early seedling survival are
476 more important for success than seedling establishment, at least in our system. This result
477 contradicts conventional expectations of weak filtering during seedling emergence but strong
478 filtering during seedling establishment (Moles and Westoby 2004). Differential germination rates
479 among species could be driven by species preferences for soil (Evans and Etherington 1990,
480 Benvenuti 2003) or climate conditions. It should be noted that while some individuals could have

481 been filtered out after meeting our operational definition of establishment (i.e., had stems at least
482 2 cm long and, if a forb, also had non-cotyledonous leaves), but before becoming reproductively
483 active (i.e., before establishment *sensu stricto*), this does not appear to be the case. Across sites,
484 the mean proportion of species that were classified as locally-transient among established
485 seedlings was only slightly higher than that found in the adult vegetation data (~14.6 % vs. ~13.6
486 %, respectively), indicating that any locally-transient species which successfully emerged were
487 essentially just as likely as locally-persistent species to survive long enough to be captured by
488 our mature vegetation surveys, although these species were not present consistently enough to be
489 classified locally-persistent. In other words, locally-transient species evidently failed to persist
490 not because they failed to establish, but because they failed to arrive in high enough numbers,
491 because their seeds failed to germinate, and/or because their post-establishment juveniles failed
492 to reach sexual maturity.

493 The lower emergence rates among locally-transient species were largely driven by seeds
494 that had putatively dispersed outside their realized climate niches into cooler climates (i.e., from
495 warmer climates), into drier climates (i.e., from wetter climates), and those from unknown
496 climates (Table 1), illustrating how climate-based niche preferences can influence community
497 membership and limit range expansion. Climate is known to play a pivotal role in the release of
498 seed dormancy in plants (Probert 2000), and variation in germination timing is known to occur
499 even among populations of the same species at different climates (Shimono and Kudo 2003,
500 Bischoff et al. 2006, Spindelböck et al. 2013). If the seeds of locally-transient species dispersing
501 outside of their realized climate niches into colder and/or drier climates were predisposed to
502 emerging before spring is safely underway, this could explain their particularly low emergence
503 rates. A second, complementary explanation could be that seeds dispersing outside of their

504 realized climate niches into colder and/or drier climates simply find these conditions more
505 stressful and are thus less likely (i.e., not adapted) to successfully emerge as seedlings.

506 Locally-transient species differed consistently from locally-persistent species in their
507 functional traits, offering some mechanistic hypotheses for why they dispersed into new sites but
508 failed to persist as adults (Fig. 4). First, locally-transient species had consistently smaller seeds
509 than locally-persistent species, which is thought to increase dispersal distance (Greene and
510 Johnson 1993, Westoby 1998), and may also decrease performance upon arrival due to their
511 smaller maternal subsidies (Moles and Westoby 2006). Second, locally-transient species were
512 shorter in stature and had less long-lasting ramet-ramet connections, on average, than locally-
513 persistent species, suggesting that the latter species' ability to grow both vertically and exchange
514 resources horizontally confer important advantages for long-term survival in mature vegetation.
515 Maximum potential height and the capacity for clonal growth are associated with the ability to
516 compete for light (Falster and Westoby 2003) and soil resources in spatially heterogenous
517 systems (Oborny and Kun 2003, Eilts et al. 2011), respectively, and can work synergistically to
518 confer competitive ability in herbaceous communities (Gough et al. 2012). These two traits
519 predicted competitive ability in a turf transplant experiment in the same system (Guittar et al.
520 2016), offering additional support for the importance of architectural traits in driving grassland
521 species performance. Equally noteworthy were the generally weak correlations between locally-
522 transient and locally-persistent species in the remaining functional traits. The weak correlations
523 in these traits does not imply that they have no influence on the selective removal of locally-
524 transient species, but that their influence may not be consistent or predictable across sites.

525 The trait-based differences between locally-transient species and locally-persistent
526 species align with a general tradeoff between colonization and competitive ability (Levins and

527 Culver 1971, Tilman 1994, Amarasekare and Nisbet 2001, Yu and Wilson 2001), and thus
528 suggest that such a tradeoff, when combined with disturbance, is an important driver of
529 succession and community assembly dynamics. That is, the smaller seeds of locally-transient
530 species may promote their probability of arriving to fresh openings in the canopy, while their
531 lower statures and decreased capacity for clonal growth may decrease their chances of
532 establishing locally-persistent populations. The same trade-off underlies the core-satellite
533 hypothesis (Hanski 1982), and likely operates alongside climate-based performance differences
534 among species to shape regional diversity patterns. While our trait-based analysis offers no
535 obvious mechanistic explanation for why locally-transient species were disfavored during
536 seedling emergence, the trait-based differences may correlate with other unmeasured traits that
537 do influence species performance during seedling emergence, and thus may serve as important
538 proxies.

539

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

541 Community response to climate change will depend both on species' abilities to track
542 environmental changes via dispersal, and on niche-based performance differences among species
543 in different environments (Graae et al. 2017). Southern Norway is expected to grow warmer and
544 wetter as climate change progresses (Hanssen-Bauer et al. 2009), so species will have to disperse
545 into cooler (upslope) and drier (more inland) sites to maintain their current climate conditions.
546 However, of the 122 species with persistent adult populations at one or more of our sites, only 10
547 species (representing 0.3 % of total seeds) dispersed outside of their realized climate niches into
548 cooler sites, and 13 species (representing 1.9 % of total seeds) into drier sites (Appendix S1: Fig.
549 S4, Appendix S1: Table S2), suggesting that many if not most species will likely fail to rapidly

550 shift their populations into cooler and drier climates, and are at risk of being extirpated as
551 competitively-superior species arrive to their communities (Alexander et al. 2015). Yet, our
552 finding that immigrant seeds from other climates were strongly disfavored provides a potential
553 silver lining: if a species can disperse into a site with a newly suitable climate, it should be
554 strongly favored over local residents, and thus be able to quickly establish a locally-persistent
555 population. Overall, our results provide insight into the dynamic way in which communities will
556 respond to climate change, and emphasize the need for further work on how species will vary in
557 their ability to disperse and compete in different community contexts.

558

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564

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712

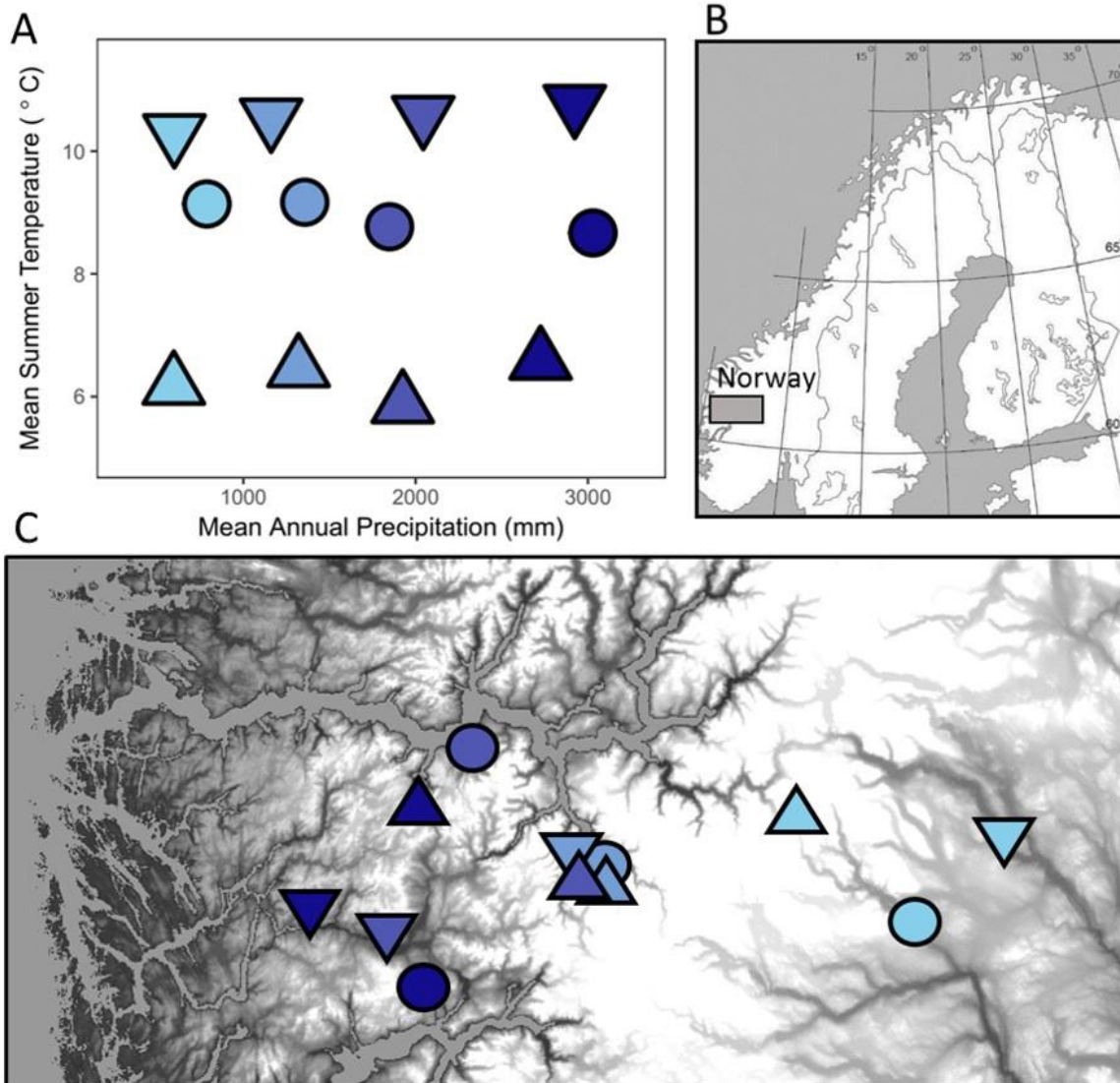
713 **Data Availability.** All data and scripts are available as a single repository at

714 https://github.com/guittarj/Guittar_2020_Ecology (doi: 10.5281/zenodo.3695969).

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

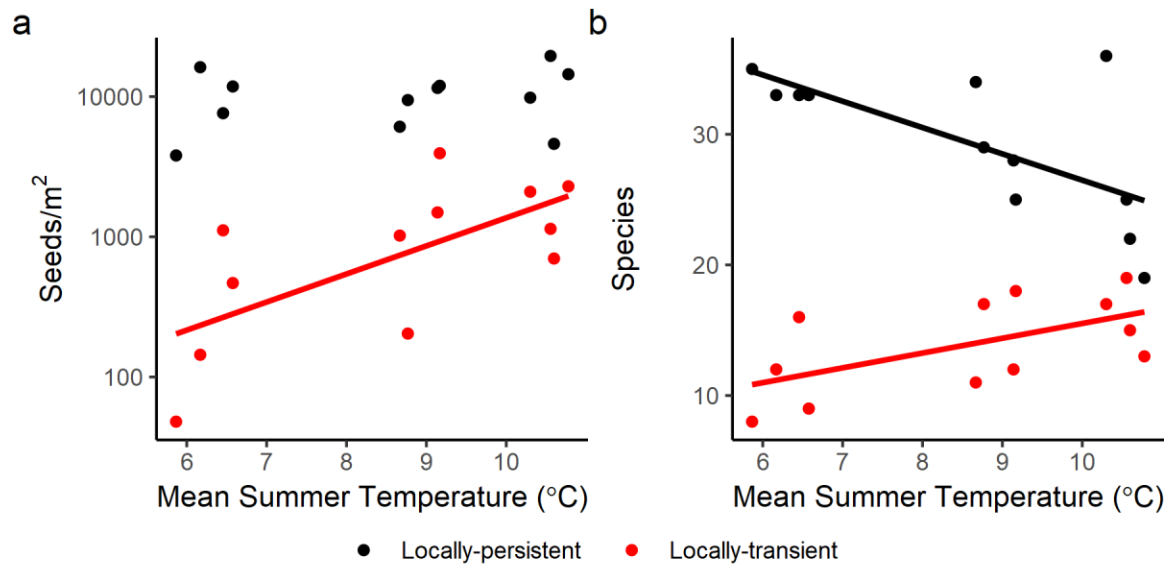
723

	Null model	Site climate	Site climate + Sp. status	Site climate + Sp. pref. temp.	Site climate + Sp. pref. precip.
Δ AIC	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

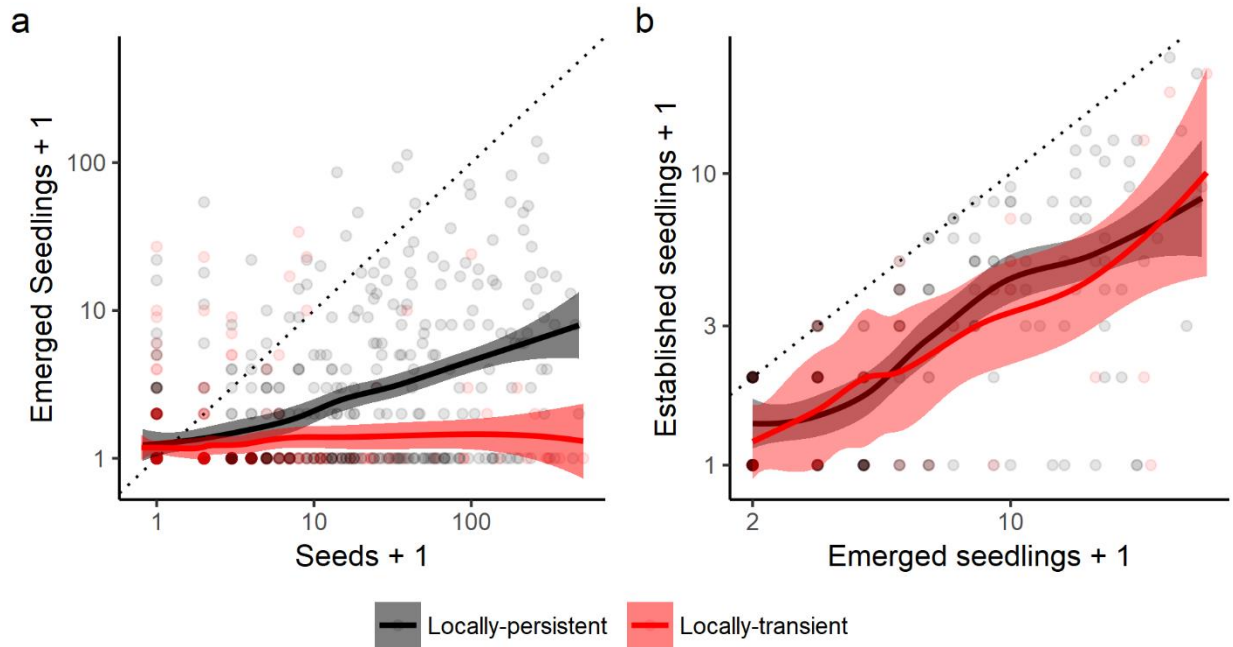


725
 726 **Figure 1.** Climates (a) and locations (b and c) of the twelve field sites in southern Norway. Mean
 727 summer temperature is defined as the warmest four months at each site. Grayscale shading in c
 728 reflects altitude, which covaries closely with mean summer temperature.

729



730
 731 **Figure 2.** Seed density (a) and species richness (b) in the combined seed rain and seed bank,
 732 grouped by locally-transient/locally-persistent species status and plotted by mean summer
 733 temperature. Summer is defined as the four warmest months at each site. Regression trendlines
 734 are solid when temperature is a significant predictor ($p < 0.05$) of \log_{10} -transformed seed density
 735 or species richness in a linear regression. A parallel set of regressions was performed using mean
 736 annual precipitation as the sole predictor, but no trends were even marginally significant (p -
 737 values always > 0.1).



738

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

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

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

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

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

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

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

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

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

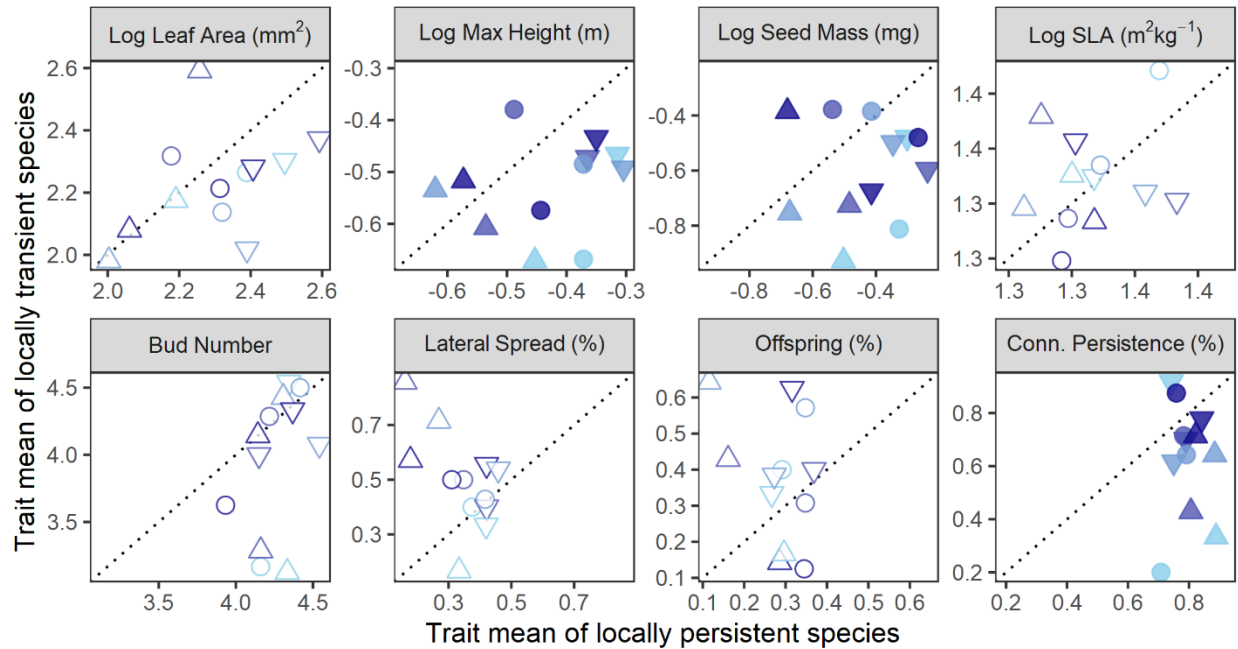
748 falling within the observed window of locally-transient seed abundances (< 400 seeds) and

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

750 locally-transient and locally-persistent species.

751

752



753

754 **Figure 4.** Mean trait values of locally-transient species relative to locally-persistent species at
 755 each site. Panels show data for four commonly used traits (top row) and four clonal traits
 756 (bottom row). Shapes and shadings are consistent with Fig. 1 and reflect approximate mean
 757 summer temperatures of 6 °C (triangle), 9 °C (circle), and 10.5 °C (inverted triangle) and annual
 758 precipitations of 650 mm, 1300 mm, 2000 mm, and 2900 mm, from light blue to dark blue.
 759 Shapes are filled with color only when values differ significantly between locally-transient and
 760 locally-persistent species across all sites (paired t-test; $p < 0.05$). SLA: specific leaf area. Bud
 761 number is an integer score that ranges from 1 (few buds either belowground or aboveground) to
 762 8 (many buds both below and aboveground); percent lateral spread refers to the proportion of
 763 species with rates of lateral spread greater than 1 cm/year; percent offspring refers to the
 764 proportion of species that commonly produce two or more vegetative offshoots per parent per
 765 year; percent connection persistence refers to the proportion of species with inter-ramet
 766 connections that persist for two or more years.

767