Dispersal limitation and stage-specific local filtering processes vary with climate across a network of alpine grasslands

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ABSTRACT

Dispersal dynamics and local filtering processes interact to generate regional vegetation patterns, but data on their relative importance in nature is scarce. Here, we compare seed and adult plant communities at twelve grassland sites with different climates in southern Norway to explore the degree to which community membership is shaped by dispersal limitation and local niche-based filtering, and how this varies with climate. To do this, we divide the species at each site into two groups: "locally-transient" species, which occur as seeds but are rare or absent as adults (i.e., they arrive but are filtered out), or "locally-persistent" species, which occur consistently as adults in annual vegetation surveys. We then ask four questions aimed to reveal where, when, why, and how locally-transient species are disfavored during community assembly. Overall, our results point to four main conclusions: (1) the influence of local filtering on community membership increases with temperature, (2) surprisingly, local filtering is stronger during seedling emergence than during seedling establishment, (3) climate-based niche differences drive differential performance among species, especially for seeds dispersing outside of their realized climate niches into colder and drier climates, and (4) locally-transient species have traits which may make them better dispersers (taller statures, smaller seeds) but poorer competitors for light (less persistent clonal connections) than locally-persistent species, which could explain their arrival to new sites and subsequent failure to establish persistent adult populations. Our study is one of the first to combine seed, seedling, and adult survey data across multiple sites with different climates to provide an empirically-grounded investigation into the influence of dispersal limitation and local filtering on the generation and maintenance of climate-associated vegetation patterns.

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

INTRODUCTION

Community membership necessarily arises through an interaction of regional dispersal dynamics and local filtering processes (Cottenie 2005, Gravel et al. 2006, Alexander et al. 2018). That is, a species will persist at a site only if it is locally competitive or if it arrives in high enough numbers to offset any competitive disadvantage (Leibold et al. 2004). While both dispersal limitation and niche-based performance differences can each preclude a species from colonizing a given site, their relative importance, and how their relative importance differs across species and communities, remains poorly studied from an empirical standpoint. This presents a challenge when trying to model species and community responses to disturbances like climate change, because populations with different dispersal abilities and/or different environmental constraints to expansion can have dramatically different responses (Graae et al. 2017).

While much work has evaluated performance differences among species in the field, it is unfortunately rare to also incorporate data on seed dispersal and dispersal patterns. The reasons for this are largely logistical: plant propagules are often tiny, numerous, difficult to identify, capable of traveling great distances, and can remain dormant in the soil for years prior to germination (Baskin and Baskin 1998, Vandvik et al. 2016). Some have sidestepped these difficulties by inferring dispersal patterns among communities using indirect methods (Alexander et al. 2012). The “nearest-neighbor” approach, for example, assumes connectivity in a metacommunity to be proportional to inter-patch distance (Calabrese and Fagan 2004, Jacobson and Peres-Neto 2010). Other approaches infer dispersal limitation from historical population shifts over periods of climate change (Kelly and Goulden 2008, Bertrand et al. 2011) or by analyzing population genetic structure. Such indirect methods are useful when modeling species distributions from a phenomenological standpoint, but fall far short of evaluating whether particular species arrive or not to a given site (Calabrese and Fagan 2004). The small number of studies that have directly assessed dispersal patterns, either by manually marking seeds (e.g., Xiao et al. 2006)

67 or connecting seeds to parents using parentage analyses (e.g., Cain et al. 2000), are often conducted at
68 single sites and/or over short distances, and are thus of limited use when considering potential
69 responses of dozens of species at regional scales (Nathan and Muller-Landau 2000).

70 Here, we compare the compositions of seed rain, seed bank, seedling, and adult plant
71 communities at sites along temperature and precipitation gradients to shed light on how seed dispersal
72 and local filtering interact to govern community membership and maintain regional vegetation patterns.
73 To do this, we divide the species at each site into two groups: "locally-transient" species, which occur as
74 seeds but are rare or absent as adults, or "locally-persistent" species, which occur consistently as adults
75 in annual vegetation surveys. We also use our adult vegetation surveys to infer which locally-transient
76 species are outside of their realized climate niches (i.e., have dispersed outside of the range of climates
77 where we know they persist as adults), and how their realized climate niches compare to local climate
78 conditions (i.e., if they have dispersed into warmer/wetter/cooler/drier climates). We then ask a series
79 of questions to elucidate where, when, why, and how locally-transient species are selectively removed
80 during community assembly.

81 We conduct our study in a network of 12 alpine and subalpine grassland sites in southern
82 Norway, a region with unusually high spatial climate variability. The sites were selected according to
83 their mean summer temperatures and mean annual rainfalls such that they form an orthogonal climate
84 grid, facilitating independent assessment of these two important climate drivers in community
85 assembly. Prior work used subsets of data from this study to compare diversity patterns in the seed
86 bank and mature vegetation (Vandvik et al. 2016), to understand how trait-based community
87 composition varies with climate (Guittar et al. 2016), and to evaluate the relative balance of competition
88 and facilitation in seedling recruitment (Klanderud et al. 2017). We combine these previously published
89 data with new data on seed rain and seedling survival to ask how interrelated ecological processes

interactively govern community membership and regional vegetation patterns. We ask the following specific questions:

1. How many locally-transient species occur as seeds at sites but lack locally-persistent adult populations, reflecting the degree to which local filtering shapes community membership? Does the strength of local filtering vary with climate?
2. At what life stage(s) are locally-transient species selectively disfavored? Do they lack locally-persistent adult populations because they fail to emerge as seedlings, fail to establish, fail to compete as adults, or a combination of the three?
3. Are locally-transient species disfavored because they have dispersed outside of their realized climate niches into particular climates, providing evidence for the role of climate-based niche filtering?
4. How are locally-transient species selectively disfavored? Do they differ systematically from locally-persistent species in their functional traits, offering mechanistic hypotheses for their selective removal?

Because our sites are located in a climate grid, we conclude by discussing the implications of our results for how these mountain grasslands will respond to climate change.

MATERIALS AND METHODS

Study area. The study area comprises 12 semi-natural calcareous grassland sites in southern Norway that host at least 144 non-woody vascular plant species at the adult life stage, and at least 126 at the seed stage (Table S1). Sites have similar bedrock, land use histories, slopes of approximately 20°, and southwest aspects, but differ in mean summer temperature, defined as the mean temperature of the four warmest months per year, and/or mean annual precipitation, such that they form a grid with approximately orthogonal climate axes (Fig. 1). Interannual variation in mean summer temperature and

annual precipitation at each site over the sampling period (2008 – 2013) was modest, with standard deviations of 0.79 °C and 238 mm, respectively, on average across sites. Each site has five blocks, placed in representative areas of grassland vegetation within a 75 – 200 m^2 area that varies due to local topography and accessibility. Each block has a variable number of 25 x 25 cm plots used for the data sets described below, as well as other experiments and surveys. Blocks were protected from grazers with electric fences and manually mowed once a year to evenly simulate biomass loss due to grazing. Taxonomic identifications follow Lid & Lid (2007). Woody species and bryophytes were excluded from all analyses.

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

Seed bank data. To characterize seed bank diversity we haphazardly selected one 64 x 64 cm plot at each site and excavated soil to a depth of 3 cm in October 2008. Because the seed bank survey area at each site (0.41 m^2) was larger than the total areas used for seed rain and seedling surveys at each site (four 25 x 25 cm plots, 0.25 m^2), we randomly subsampled 61 % (0.25 m^2 / 0.41 m^2) of the original seed

138 bank community *in silico* and discarded the remainder to standardize sampling effort across data types
139 at each site. To exclude the seeds from that year's seed rain from our seed bank surveys, we removed
140 aboveground vegetation, including moss and litter. Soil samples were stored for three months at 2 – 4 °C
141 and ambient moisture. Soil samples were then sowed into a standard mixture of sterile subsoil and
142 placed in 30 x 60 cm trays. The trays were incubated in a greenhouse with a diurnal cycle of 16 hours
143 light (25 °C) and 8 hours darkness (15 °C). The diurnal cycle was continued for four months, followed by
144 six months of cold stratification in darkness (4 °C), followed by another four-month period of diurnal
145 cycling. Emerging seedlings were counted and removed once identifiable to species. This method of
146 characterizing the seed bank community effectively accounts for seed viability because non-viable seeds
147 would not have emerged as seedlings.
148
149 ***Seedling data.*** Like most perennial grasslands, seedling recruitment in our system is highly dependent
150 on disturbances and occurs only rarely in intact vegetation due to strong competitive effects from adult
151 plants (Silvertown and Smith 1989, Eriksson 1989, Bullock et al. 1995, Vandvik 2004, Berge 2010,
152 Klanderud et al. 2017). We therefore monitored seedlings in experimental gaps where they were
153 relatively free from competitive effects of adult plants, but still exposed to environmental stress and
154 other biotic interactions, such as herbivory, disease, and potential resource competition among
155 seedlings. One 25 x 25 cm gap was created in each of four blocks at each site in spring 2009, for a total
156 of four gaps per site and 48 gaps overall. The gaps were made by cutting along the inner edges of a
157 metal frame mounted in metal pipes marking the corners of the plot, and peeling away the natural
158 vegetation and its thickly interwoven root mat. Seeds and topsoil were returned to gaps by vigorously
159 shaking excavated vegetation and passing it through a 4 mm sieve to remove plant remains. Emerged
160 seedlings in the plots were ID-tagged in one of three censuses (late summer 2009, early summer 2010,
161 late summer 2010) using numbered plastic toothpicks and plot coordinates. About 70 % of seedlings

were identifiable to species; the remaining 30 % were unidentifiable or died before they could be identified and were lumped into two generic groups for graminoids and forbs. Seedlings were differentiated from emergent clonal ramets by looking for cotyledons or signs of above- or below-ground connections. Seedling survival and establishment were recorded twice yearly from spring 2010 to spring 2012. We approximated seedling emergence rates by dividing the density of emerged seedlings by the sum of seed rain and seed bank densities. We marked seedlings established when they had grown to a size greater than what could be derived exclusively from their maternal subsidies, which we estimated to be when stems were longer than 2 cm, and if a forb, also when they had grown their first non-cotyledonous leaves. Although we took pains to census each site at times of peak seedling emergence, some seedlings may have emerged, died, and disappeared before ever being recorded; even if this where the case, however, we contend that it is unlikely to influence our overall conclusions because the factors discouraging seedling survival during the earliest stages of establishment are likely the same as those discouraging seedling emergence (i.e., late spring frosts), and are distinct from the factors influencing seedling survival establishment (i.e., drought, competition for light, predation, early fall frosts, and late spring frosts in the year after seedling emergence).

Mature vegetation data. We surveyed mature vegetation at peak biomass (July and August) in 2009, 2011, 2012, and 2013. At each site, we used two 25 x 25 cm plots in each of five blocks at each site, for a total of 10 plots per site (except for the third-wettest second-warmest site, which only had nine plots), and 119 plots overall. These plots were controls for a transplant experiment and included five undisturbed controls and five transplant controls, i.e., turfs dug up and replaced in the same location. The two types of controls did not differ in species composition or any other aspect of community structure at any of the survey periods (Guittar et al. 2016). We visually estimated the percent cover of

individual species in each plot using a 5 x 5 cm grid overlay, and then pooled the data by site. Stage-specific species abundance or relative abundance data are provided as a supplementary file.

Trait data. We used four commonly used plant traits, and four traits related to clonal growth strategy, each with hypothesized associations to dispersal ability and/or resource competition. Seed mass (mg), a reflection of species regeneration strategy (Kraft et al. 2008, Cornwell and Ackerly 2009), was drawn from the Seed Information Database (Royal Botanic Gardens Kew 2014). Maximum canopy height (m) data, which relates to both dispersal ability and light competition (Westoby 1998, Falster and Westoby 2003), were mined from Lid and Lid (2007). Leaf area (mm^2) and specific leaf area (SLA; m^2/kg), two traits indicative of where species fall along a continuum of slow-to-fast resource use strategies (Sterck et al. 2006, Rusch et al. 2011), were estimated using a combination of field data (Guittar et al. 2016) and data from the LEDA online trait database (Kleyer et al. 2008). Leaf area, SLA, maximum height, and seed mass values were log-transformed. Clonal traits included the number of offspring per parent per year ("0" = 1 offspring; "1" = ≥ 2 offspring), persistence of plant–offspring connections ("0" = < 2 years; "1" = ≥ 2 years), rate of lateral spread ("0" = ≤ 1 cm/year; "1" = > 1 cm/year), and number of buds per ramet (an integer score ranging from "1" = few buds either belowground or aboveground, to "8" = many buds both below and aboveground). Clonal attributes are thought to help plants integrate over spatially heterogeneous resources (Eilts et al. 2011), recover from disturbances (Klimešová and Klimeš 2007), and provide sustained maternal subsidies to new ramets as they grow horizontally and vie for local establishment (Herben and Wildová 2012). Clonal trait data were drawn from Klimeš and Klimešová (1999) and converted from categorical to quantitative formats to enable calculations of community means. Trait data are provided as a supplementary file.

208 ***Assigning local species status.*** Each species observed at each site at any life stage was labeled as
209 "locally-persistent" if adults were recorded in more than half (i.e., at least three of four) of the site
210 vegetation surveys conducted from 2009 to 2013, or otherwise labeled "locally-transient." In using this
211 cutoff, we aim to understand the mechanisms leading a species to be a consistent member of a given
212 community, not whether it can occur there at all. That is, an individual of a locally-transient species need
213 not be a first generation immigrant, but could be a second-or-more generation immigrant, so long as it
214 has evidently unable to establish a locally-persistent adult population. Because locally-transient/locally-
215 persistent species status assignments were potentially sensitive to the depth at which we characterized
216 local site community composition, we used rarefaction to verify that we had sufficiently surveyed the
217 mature vegetation such that the number of locally-persistent species observed at each site had
218 stabilized (Fig. S1). In addition, we re-ran our analysis with all possible locally-transient/locally-persistent
219 cutoffs to assess the sensitivity of our conclusions to our methodology.
220
221 ***Assigning putative climate origins.*** For each locally-transient species at each site, we identified the sites
222 and climates where we knew it had persistent adult populations, and then used these to infer whether it
223 was dispersing outside of its realized climate niche. If a locally-transient species at a given site had
224 persistent adult populations at other sites with similar temperatures or precipitations, we assumed it
225 dispersed from a site with the "same temperature" or the "same precipitation," such as from a
226 neighboring site, e.g.., one with similar climate but with potentially different topographical, edaphic, or
227 biotic characteristics. If a locally-transient species at a given site had persistent adult populations only at
228 sites with warmer/cooler or wetter/drier conditions, we then assumed it dispersed from a
229 warmer/cooler or wetter/drier site (i.e., it dispersed *into* a cooler/warmer or drier/wetter site). Again,
230 we are not assuming that a given seed of a locally-transient species literally dispersed from a given

231 climate, but that the seed is occurring outside of the climate range at which it is a common and
232 persistent community member, and is presumably on the edge of being locally excluded.
233
234 ***Statistical approach.*** We used linear regressions to test for baseline trends in the total abundance and
235 richness of locally-transient and locally-persistent species in the seed rain, the seed bank, and the two
236 combined along temperature and precipitation gradients. Unlike other data in this study, seed bank data
237 were not collected in replicate across blocks within a site, thus our analyses were performed at a site-
238 level resolution (hence, N = 12). Each linear regression model assumes normally distributed errors and
239 takes the form of $y_j \sim MAP_j$ or $y_j \sim + MST_j$, where y_j is the response variable being examined at site *j*, and
240 MAP_j and MST_j are the mean annual precipitation (centered to zero) and mean summer temperature
241 (centered to zero) at site *j*. We also used linear regressions to test for baseline trends in species richness
242 in the mature vegetation with temperature and precipitation.
243 We used four sets of generalized linear models (GLMs) to test predictors of differential species
244 performance during seedling emergence and seedling establishment. These GLMs used negative
245 binomial error distributions and log link functions. We log-transformed seed and seedling numbers to
246 account for their highly skewed abundance distributions, and added one to their abundances to avoid
247 having to omit zeroes as predictors. In the first set of GLMs ("null" models), local species abundances in
248 the combined seed rain and seed bank are used to predict local species abundances of emerged
249 seedlings, and local species abundances of emerged seedlings predict local species abundances of
250 established seedlings. In other words, our null expectation was that all seeds were equally likely to
251 emerge, and all seedlings were equally likely to establish. In the second set of GLMs ("site climate"
252 models), we added model terms for local site mean summer temperature and mean annual
253 precipitation to evaluate how these climate variables affected seedling emergence and seedling
254 establishment rates.

In the third set of GLMs ("site climate + species status" models), we evaluated how well locally-transient/locally-persistent species status predicted performance differences during seedling emergence and seedling establishment. Specifically, we added model terms specifying the status of each species at each site, and interactions between species status and local climate. We formally modeled the number of emerged seedlings *g* for species *i* at site *j* as

$$g_{ij} \sim \log(s_{ij} + 1) + \mathrm{MAP}_j + \mathrm{MST}_j + p_{ij} + (\mathrm{MAP}_j \cdot p_{ij}) + (\mathrm{MST}_j \cdot p_{ij}),$$

where s_{ij} is the abundance of seeds (seed rain + seed bank) of species *i* at site *j*, p_{ij} is a factor indicating species status, and MAP_j and MST_j are as described above. Likewise, we modeled the number of established seedlings *e* for species *i* at site *j* as

$$e_{ij} \sim \log(g_{ij} + 1) + \mathrm{MAP}_j + \mathrm{MST}_j + p_{ij} + (\mathrm{MAP}_j \cdot p_{ij}) + (\mathrm{MST}_j \cdot p_{ij}).$$

In the fourth and final set of GLMs ("site climate + species status + species climate origin" models), we dropped the model term for locally-transient/locally-persistent species status, p_{ij}, and replaced it with a new term, o_{ij}, denoting the putative temperature/precipitation origins of each locally-transient species *i* at site *j*. Specifically, the o_{ij} term was used to tag each species at each site with one of five labels: (1) locally-persistent, (2) locally-transient but likely dispersed from an adjacent site with similar temperature/precipitation, (3) locally-transient and likely dispersed from a cooler/drier site (i.e., into a warmer/wetter site), (4) locally-transient and likely dispersed from a warmer/wetter site (i.e., into a cooler/drier site), (5) locally-transient with no locally-persistent populations at any of our grassland sites (i.e., an 'unknown' climate preference). We dropped the interaction terms from these GLMs to avoid excessive model complexity. Formally, we modelled the number of emerged seedlings *g* for species *i* at site *j* as

$$g_{ij} \sim \log(s_{ij} + 1) + \mathrm{MAP}_j + \mathrm{MST}_j + o_{ij},$$

and the number of established seedlings *e* for species *i* at site *j* as

$$e_{ij} \sim \log(g_{ij} + 1) + \mathrm{MAP}_j + \mathrm{MST}_j + o_{ij}.$$

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

RESULTS

Mature vegetation rarefactions. Rarefaction analysis indicated that the numbers of plots of mature vegetation surveyed at each site were more than sufficient to stabilize the local composition of locally-persistent species (Fig. S1), lending confidence to our locally-transient/locally-persistent species status assignments. Furthermore, no locally-transient species by itself ever represented more than 0.4% of total cover at any site (Fig. S2), illustrating the minor overall contribution of locally-transient species to local community structure.

Evidence for local filtering. Seeds of locally-transient species occurred at all 12 of our grassland sites, representing, on average, 4 of 42 species in the combined seed rain and seed bank. In the combined

303 seed rain and seed bank, the number of locally-transient species and their total abundances increased
304 significantly with temperature (Fig. 2; species richness: $p = 0.045$; total abundance: $p = 0.017$). These
305 trends were driven primarily by increases in the seed bank (species richness: $p = 0.031$; total abundance
306 $p = 0.035$), not the seed rain (Fig. S3), underscoring the fact that the composition of the seed rain likely
307 differs between years, and that the seed bank likely serves as an important reservoir of local plant
308 diversity. There were no significant trends in species richness or total abundance with precipitation in
309 either the seed rain, the seed bank, or the two combined. Species richness in the adult vegetation rose
310 significantly with temperature ($p = 0.0063$) but not with precipitation ($p = 0.871$).

311 About 10% of all seeds were from locally-transient species, with more transients represented in
312 the seed bank (ca. 13% of total seed bank) than in the seed rain (ca. 4% of total seed rain) (Table S2).
313 While most locally-transient populations had locally-persistent adult populations at sites with similar
314 climates (67% with similar temperatures, 49% with similar precipitations), some did not (Table S2).
315 Operating on the assumption that locally-transient species dispersed from the most-climatically similar
316 sites at which they persist as adults, seeds of locally-transient species were about four times more likely
317 to have dispersed outside of their realized climate niches into warmer sites (i.e., from cooler climates)
318 and slightly more likely to have dispersed outside of their realized climate niches into drier sites (i.e.,
319 from wetter climates) (Table S2).

320 To determine how sensitive our conclusions were to changes in our operational definition of
321 locally-transient/locally-persistent species status, we explored how results changed under each of the
322 four possible cutoff scenarios offered by our data. Specifically, we looked at how results changed as the
323 definition of locally-persistent species shifted from those species present in at least one, at least two, at
324 least three, or all four annual surveys of mature vegetation at each given site. As the cutoff for locally-
325 persistent became more stringent, and the cutoff for locally-transient (by definition) relaxed, the total
326 number of locally-transient populations (i.e., unique species*site combinations) in the combined seed

327 rain and seed bank at our sites rose from 119 (1989 seeds), to 149 (2549 seeds), to 167 (3665 seeds), to
328 205 (5007 seeds). However, these differences in the estimated numbers of locally-transient/locally-
329 persistent species by site did not alter our main conclusions that (1) the influence of local filtering
330 increases with temperature, and that (2) grassland sites in southern Norway are connected by dispersal,
331 albeit primarily among nearby sites with similar climates.
332
333 ***The stage-wise removal of locally-transient species.*** Locally-transient species were outperformed by
334 locally-persistent species during seedling emergence (Fig. 3, Table 1), but not seedling establishment
335 (Fig. 3, Table S3). The lower emergence rates of locally-transient species appeared to be driven primarily
336 by species which had putatively dispersed outside of their realized climate niches into cooler climates,
337 drier climates, or those that had dispersed from unknown climates (see "Origin-based predictors" in
338 Table 1). In addition, after accounting for local seed abundances, warmer sites tended to have higher
339 rates of seedling emergence than cooler sites ("General predictors" in Table 1), linking climate and
340 overall seedling performance. No GLM of seedling establishment outperformed null expectations (Table
341 S3), suggesting that neither climate, species status, nor putative seed origins were meaningful predictors
342 of seedling establishment rates.
343 To confirm that these results were not artifacts of how we combined seed rain and seed bank
344 data (e.g., if seeds of locally-transient species emerged at lower rates because most were from the seed
345 bank, and the seed bank had overall lower rates of emergence), we re-ran GLMs with only seed rain
346 data and observed qualitatively similar results (data not shown). To determine how sensitive our
347 conclusions involving seedling performance were to changes in the operational definition of locally-
348 transient/locally-persistent species status, we re-ran the GLMs for emergence and establishment using
349 each of the four possible locally-transient/locally-persistent cutoff scenarios offered by our data.

350 Changes to the locally-transient/locally-persistent cutoff did not alter our overall conclusion that locally-
351 transient species are disfavored during emergence but not establishment (Fig. S4).
352
353 ***Trait-based mechanisms of local filtering.*** Locally-transient and locally-persistent species in the
354 combined seed rain and seed bank differed significantly in three functional traits (Fig. 4). Specifically,
355 when averaged across species at the site level, locally-transient species were significantly shorter, had
356 smaller seeds, and had longer-lasting vegetative connections among ramets than locally-persistent
357 species. Of the three traits that differed consistently between locally-transient and locally-persistent
358 species, the only instance where those differences varied significantly with site climate was an increase
359 in the magnitude by which locally-transient species had longer-lasting connections than locally-
360 persistent species with increasing site temperature.
361
362 DISCUSSION
363 In this study, we compared the compositions of seed, seedling, and adult plant communities along
364 temperature and precipitation gradients to shed light on how seed dispersal and local filtering interact
365 to generate and maintain regional vegetation patterns. Overall, our results point to four main
366 conclusions: (1) the influence of local filtering on community membership increases with temperature,
367 (2) local filtering is stronger during seedling emergence than during seedling establishment, (3) climate-
368 based niche differences drive differential performance among species, especially for seeds dispersing
369 outside of their realized climate niches into colder and drier climates (i.e., dispersing from warmer and
370 wetter climates), and (4) locally-transient species have traits which may make them better dispersers
371 (taller statures, smaller seeds) but poorer competitors for light (less persistent clonal connections),
372 which could explain their arrival to new sites and subsequent failure to establish persistent adult

373 populations. We elaborate on these results below, and conclude with a discussion of the implications for
374 how these alpine grasslands will respond to climate change.
375
376 ***Community assembly and the determinants of species ranges***
377 The number of seeds and species of local-transients in the seed bank rose from the coldest
378 (highest altitude) to warmest (lowest altitude) sites (Fig. 2), suggesting that the influence of local
379 filtering on community membership increases with temperature. Such a pattern with temperature could
380 arise from at least two non-exclusive explanations. First, warm-adapted species may simply have larger
381 seed shadows than cold-adapted species, resulting in more seeds traveling to unsuitable patches, such
382 as those with undesirable topographic, edaphic, or biotic conditions. Maximum plant height correlates
383 positively with temperature in our system (Guittar et al. 2016), and is also thought to increase dispersal
384 distance (Thomson et al. 2011), offering one mechanistic hypothesis for why seed shadows increase in
385 size with temperature. Alternatively, it may simply be that seeds are more likely to disperse downhill
386 (i.e., from colder high-altitude sites to warmer low-altitude sites) than the reverse. A third,
387 complementary, explanation for why there are more locally-transient species at warmer sites could be
388 because competition for resources is fiercer and competitive exclusion is more common in the adult
389 vegetation at these sites. Indeed, competition has been hypothesized to be stronger at warmer sites due
390 to longer growing seasons and less stressful growth conditions (Grime 1973, Olsen et al. 2016). Species
391 richness fell steeply with temperature in the adult vegetation (from an average of 42 species at the
392 warmest sites to 64 species at the coldest sites), but only slightly in the seed rain and not in the seed
393 bank (Fig. 2), consistent with higher rates of competitive exclusion of mature plants at warmer sites.
394 Surprisingly, locally-transient species were significantly disfavored during seedling emergence
395 (Fig. 3, Table 1), but not during seedling establishment (Fig. 3, Table S3), suggesting that germination
396 and early survival is a more important determinant of seedling success than successful establishment.

397 This result contradicts conventional expectations of weak filtering during seedling emergence but strong
398 filtering during seedling establishment (Moles and Westoby 2004). It should be noted that while some
399 individuals could in theory have been selectively filtered after meeting our operational definition of
400 establishment (i.e., had stems at least 2 cm long and, if a forb, also had non-cotyledonous leaves), but
401 before becoming reproductively active (i.e., before establishment *sensu stricto*), this does not appear to
402 be the case. Across sites, the mean proportion of species that were locally-transient among established
403 seedlings was only slightly higher than that found in the adult vegetation data (~14.6 % vs. ~13.6 %,
404 respectively), indicating that any locally-transient species which successfully emerged were essentially
405 just as likely as locally-persistent species to survive long enough to be captured by our mature
406 vegetation surveys, but not long enough to be considered locally-persistent. In other words, locally-
407 transient species evidently failed to persist as adults not because they failed to establish, but either
408 because they failed to germinate or because they failed to compete as post-establishment juveniles,
409 resulting in local population growth rates below maintenance levels.

410 The low emergence rates among locally-transient species were largely driven by seeds that had
411 putatively dispersed outside their realized climate niches into cooler climates (i.e., from warmer
412 climates), into drier climates (i.e., from wetter climates), and those from unknown climates (Table 1),
413 illustrating how climate-based niche preferences can influence community membership and thus range
414 expansion. Climate is known to play a pivotal role in the release of seed dormancy in plants (Probert
415 2000), and variation in germination timing is known to occur even among populations of the same
416 species at different climates (Shimono and Kudo 2003, Bischoff et al. 2006, Spindelböck et al. 2013). If
417 the seeds of locally-transient species dispersing outside of their realized climate niches into colder
418 and/or drier climates were predisposed to emerging before spring is safely underway, this could explain
419 their particularly low emergence rates. A second, complementary explanation could be that seeds

420 dispersing outside of their realized climate niches into colder and/or drier climates simply find these
421 conditions more stressful and are thus less likely (i.e., not adapted) to successfully emerge as seedlings.
422 Locally-transient species differed consistently from locally-persistent species in their functional
423 traits, offering some mechanistic hypotheses for why they can disperse into new sites but fail to persist
424 as adults (Fig. 4). First, locally-transient species had consistently smaller seeds than locally-persistent
425 species, which is thought to increase dispersal distance (Greene and Johnson 1993, Westoby 1998), and
426 may also decrease performance upon arrival due to their smaller maternal subsidies. Second, locally-
427 transient species were shorter and had less long-lasting ramet-ramet connections, on average, than
428 locally-persistent species, suggesting that the ability to grow both vertically and exchange resources
429 horizontally confer important advantages for long-term survival in mature vegetation. Maximum
430 potential height and the capacity for clonal growth are associated with the ability to compete for light
431 (Falster and Westoby 2003) and soil resources in spatially heterogenous systems (Oborny and Kun 2003,
432 Eilts et al. 2011), respectively, and can work synergistically to confer competitive ability in herbaceous
433 communities (Gough et al. 2012). Interestingly, these two traits were also significantly associated with
434 competitive ability in a turf transplant experiment in the same system (Guittar et al. 2016), offering
435 additional support for the importance of architectural traits in driving grassland species performance.
436 Together, the trait-based differences between locally-transient species and locally-persistent species
437 align with a general tradeoff between colonization and competitive ability (Levins and Culver 1971,
438 Tilman 1994, Amarasekare and Nisbet 2001, Yu and Wilson 2001). That is, the smaller seeds of locally-
439 transient species may promote their probability of arriving to fresh openings in the canopy (like our
440 experimental gaps), while their lower statures and decreased capacity for clonal growth may decrease
441 their chances of establishing locally-persistent populations. Although the trait-based differences
442 between locally-transient and locally-persistent species do not offer an obvious mechanistic explanation
443 for why locally-transient species were disfavored during seedling emergence, they may correlate with

differences in life history strategies and/or unmeasured traits that do impact species performance during seedling emergence.

Implications for community responses to climate change. Community response to climate change will depend both on species' abilities to track environmental changes via dispersal, and on the degree to which niche differences lead to performance differences in different environments (Graae et al. 2017). Southern Norway is expected to grow warmer and wetter as climate change progresses (Hanssen-Bauer et al. 2009), so maintenance of current climate conditions will require dispersal into cooler (upslope) and drier (more inland) sites. However, we found that of the 122 species with persistent adult populations at one or more of our sites, only 10 species (representing 0.3 % of total seeds) dispersed outside of their realized climate niches into cooler sites, and 13 species (representing 1.9 % of total seeds) into drier sites (Fig. S3, Table S2), suggesting that many if not most species will likely be unable to be rapidly shift their populations into cooler and drier climates, and are at risk of being extirpated as competitively-superior species arrive to their communities (Alexander et al. 2015).

Acknowledgements. We thank the landowners for allowing us to set up the experiments on their land, the Norwegian Research Council (KLIMAFORSK project 184912/S30), NSF GRFP (JLG; Grant Number: 1256260), and Norge-Amerika Foreningen for funding. We thank Siri L. Olsen, Mari Jokerud, Pascale Michel, Hilary H. Birks and Berhe Luel for contributions to the data collection.

Authors' contributions. JG wrote the manuscript and analyzed data with conceptual and editorial help from all authors. VV, KK, and DG conceived of the experimental study system and the experiments upon which this paper is based. VV, KK, and AB gathered seedling and mature vegetation data, MB gathered seed rain data, and KK, EM, JT, AB, and VV gathered seed bank data. VV and JG secured funding.

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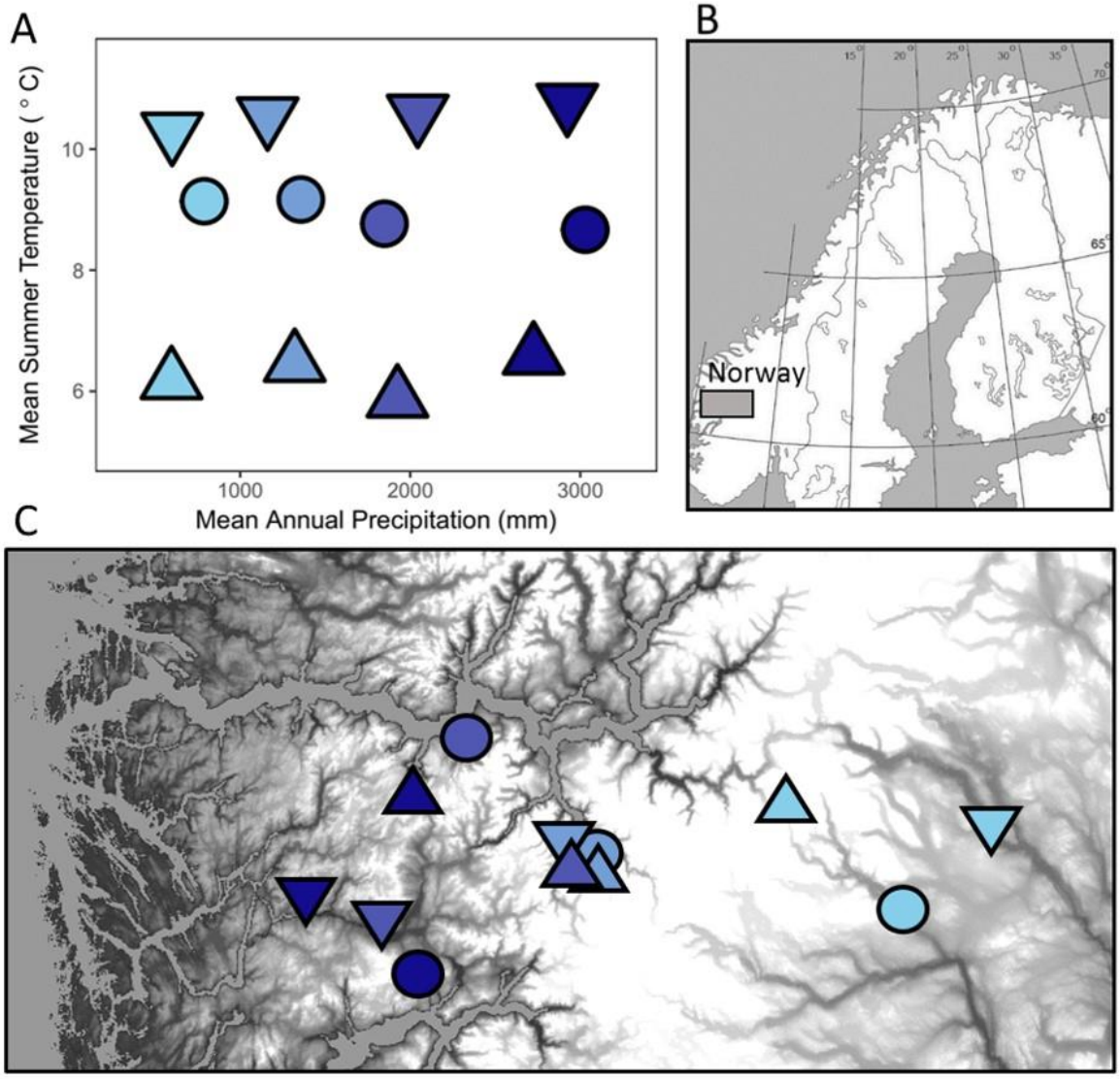
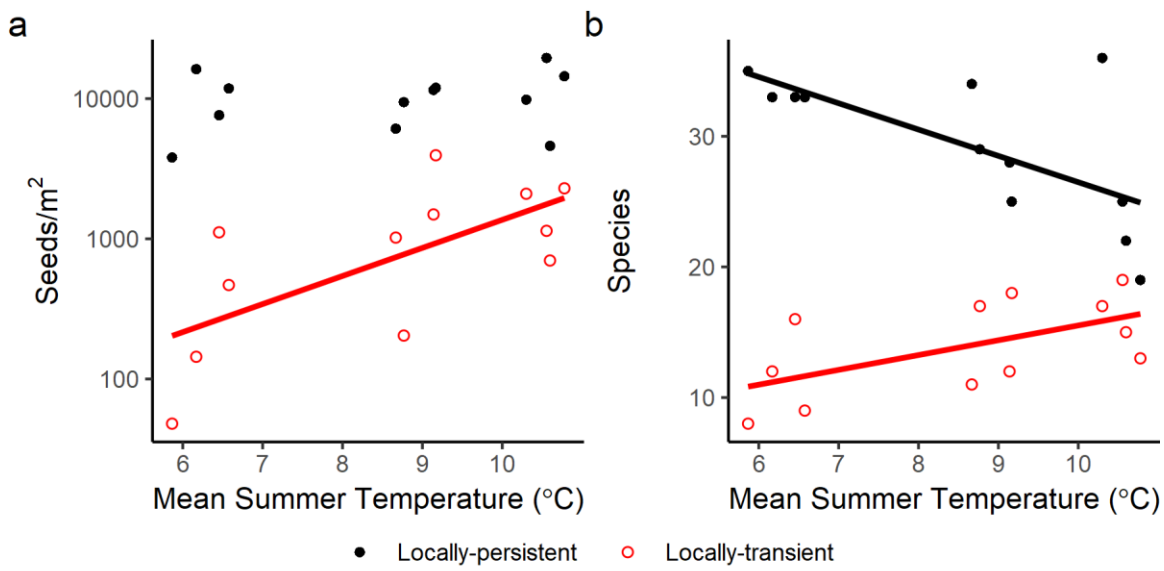


Figure 1. Panel A shows mean summer temperature and mean annual precipitation values at the twelve sites. Summer is defined as the warmest four months at each site. Panels B and C show site locations in southern Norway. The grayscale shading in panel C denotes altitude, which covaries closely with mean summer temperature. The transition in shape color from dark blue to light blue in panel C reflects the east-to-west gradient in annual precipitation.



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

595 locally-transient/locally-persistent species status and plotted by mean summer temperature. Summer is

596 defined as the four warmest months at each site. Solid lines are present when temperature was a

597 significant predictor ($p < 0.05$) of $\log_{10}$-transformed seed density or species richness in a linear

598 regression. A parallel set of regressions was performed using mean annual precipitation as the sole

599 predictor, but no trends were even marginally significant (p-value was always > 0.1).

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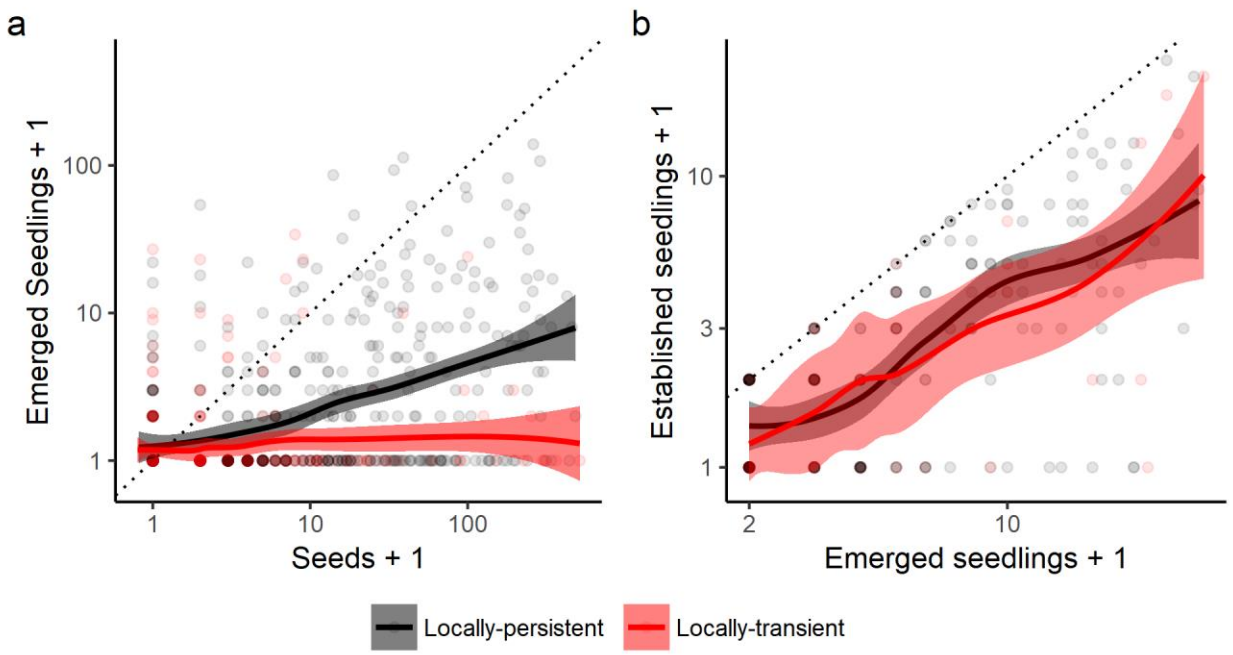

Figure 3. The abundances of emerged seedlings (a) and established seedlings (b) of species at individual sites, colored by locally-transient/locally-persistent species status. Each circle represents the presence/absence of one species at one site, and colored lines and shadings show LOESS smoothing functions and 95 % confidence intervals. Seed number is equal to the sum of seeds in the seed rain and seed bank. Abundances reflect the total number of individuals in four 25 x 25 cm subplots at each site. Count data are increased by one to allow for plotting zeroes on a log scale. Panels only show data falling within the observed window of locally-transient seed abundances (< 400 seeds) and locally-transient seedling abundances (< 33 seedlings) in order to focus on the comparison of locally-transient and locally-persistent species.

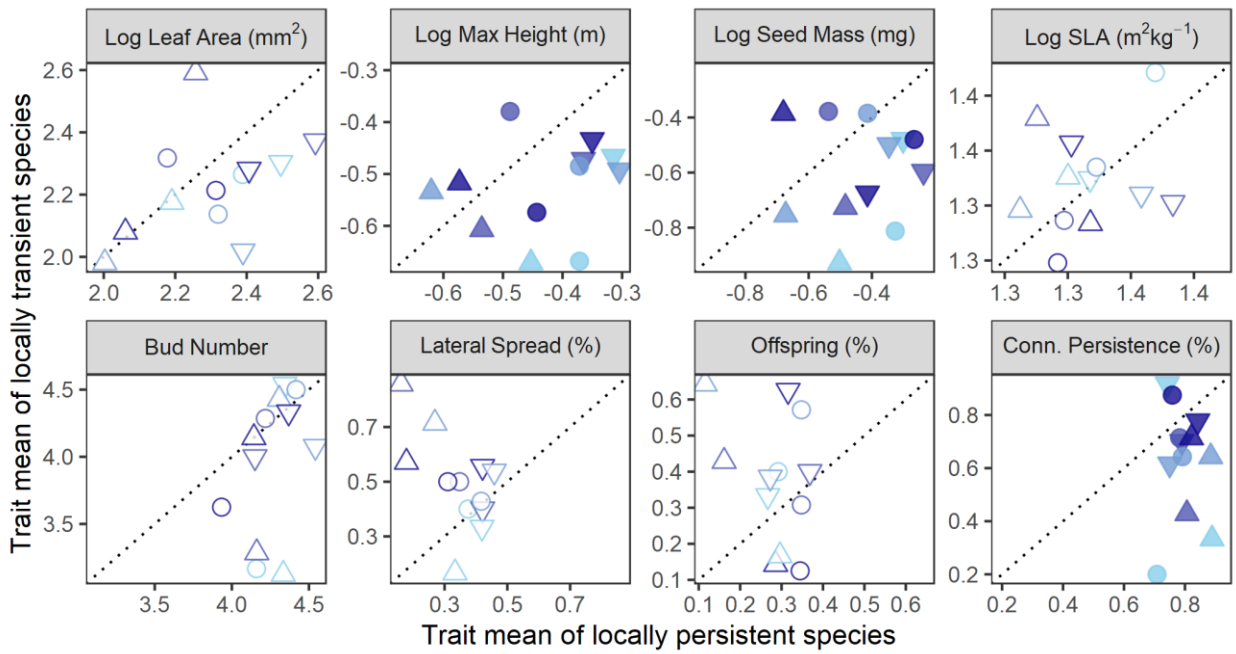

Figure 4. Mean trait values of locally-transient species relative to locally-persistent species at each site. Shapes and shadings are consistent with Fig. 1 and reflect approximate mean summer temperatures of 6 °C (triangle), 9 °C (circle), and 10.5 °C (inverted triangle) and annual precipitations of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

	Null model	Site climate	Site climate + Sp. status	Site climate + Sp. pref. temp.	Site climate + Sp. pref. precip
ΔAIC	0.00	-3.78	-14.37	-25.76	-32.02
General predictors					
Log(seed no.)	**7.68	**7.96	**5.95	**6.73	**7.00
Local temp.	-	*2.56	*2.04	*2.77	*2.92
Local precip.	-	-0.93	-1.19	-1.36	-1.48
Transient/Persistent predictors					
Transient	-	-	**-4.47	-	-
Transient * Local temp.	-	-	1.90	-	-
Transient * Local precip.	-	-	1.22	-	-
Origin-based predictors					
Transients from similar temp.	-	-	-	-1.29	-
Transients from cooler into warmer	-	-	-	-1.67	-
Transients from warmer into cooler	-	-	-	*-2.76	-
Transients from similar precip.	-	-	-	-	-1.45
Transients from drier into wetter	-	-	-	-	-0.16
Transients from wetter into drier	-	-	-	-	**-4.28
Transients from unknown climates	-	-	-	**-5.44	**-5.46

Table 1.
Standardized coefficients (z-scores) from different GLM models (columns) predicting numbers of emerged seedlings by species and site. In column headers (i.e., model descriptions), "Species status" refers to whether the species is locally-transient or locally-persistent, and "Species preferred temp/precip" refers to the nearest climates at which the species has a persistent adult population, which we use to infer the climate from which they likely dispersed. Data include all recorded seeds and seedlings that could be identified to species. N is equal to the number of unique species-by-site combinations for each category/predictor. Asterisks denote significance (*: $p < 0.05$, **: $p < 0.001$). Dashes indicate predictors that were not included in a given model. Including model terms for locally-transient/locally-persistent species status and then preferred temperature and precipitation progressively improved model performance, as reflected in the reduction of AIC values relative to the null model that uses only local seed numbers as a predictor.