

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

JOHN GUITTAR <sup>1,10</sup>, DEBORAH GOLDBERG,<sup>2</sup> KARI KLANDERUD,<sup>3</sup> ASTRID BERGE,<sup>4</sup> MARTA RAMÍREZ BOIXADERAS,<sup>5</sup>  
 ERIC MEINERI <sup>6</sup>, JOACHIM TÖPPER <sup>7,8</sup> AND VIGDIS VANDVIK <sup>8,9</sup>

<sup>1</sup>*Kellogg Biological Station, Michigan State University, 3700 E Gull Lake Drive, Hickory Corners, Michigan 49060 USA*

<sup>2</sup>*Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109 USA*

<sup>3</sup>*Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway*

<sup>4</sup>*Species and Water Management Department, Norwegian Environment Agency, P.O. Box 5672, Torgarden, 7485 Trondheim, Norway*

<sup>5</sup>*CREAF, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain*

<sup>6</sup>*Aix Marseille Univ, Avignon Université, University of Avignon, CNRS, IRD, IMBE, Marseille, France*

<sup>7</sup>*Norwegian Institute for Nature Research, Thormøhlensgate 55, N-5008 Bergen, Norway*

<sup>8</sup>*Department of Biological Sciences, University of Bergen, P.O. Box 7803, N-5020 Bergen, Norway*

<sup>9</sup>*Bjerknes Centre for Climate Research, University of Bergen, P.O. Box 7803, N-5020 Bergen, Norway*

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**Abstract.** Seed dispersal and local filtering interactively govern community membership and scale up to shape regional vegetation patterns, but data revealing how and why particular species are excluded from specific communities in nature are scarce. This lack of data is a missing link between our theoretical understanding of how diversity patterns can form and how they actually form in nature, and it hampers our ability to predict community responses to climate change. Here, we compare seed, seedling, and adult plant communities at 12 grassland sites with different climates in southern Norway to examine how community membership is interactively shaped by seed dispersal and local filtering, and how this process varies with climate across sites. To do this, we divide 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), and *locally persistent* species, which occur consistently as adults in annual vegetation surveys. We then ask how and why locally transient species are disfavored during community assembly. Our results led to four main conclusions: (1) the total numbers of seeds and species that arrived, but failed to establish locally persistent populations, rose with temperature, indicating an increase in the realized effects of local filtering on community assembly, as well as an increase in the number of species poised to rapidly colonize those warmer sites if local conditions change in their favor, (2) locally transient species were selectively filtered out during seedling emergence, but not during seedling establishment, (3) selective filtering was partly driven by species climate preferences, exemplified by the poor performance of seeds dispersing outside of their realized climate niches into colder and drier foreign climates, and (4) locally transient species had traits that likely made them better dispersers (i.e., smaller seeds) but poorer competitors for light (i.e., shorter statures and less persistent clonal connections) than locally persistent species, potentially explaining why these species arrived to new sites but did not establish locally persistent adult populations. Our study is the first to combine seed, seedling, and adult survey data across sites to rigorously characterize how seed dispersal and local filtering govern community membership and shape climate-associated vegetation patterns.

**Key words:** *alpine grasslands; climate change; community assembly; dispersal dynamics; metacommunities; range expansion; seedling survival; species sorting*

## INTRODUCTION

Plant community assembly in a landscape or meta-community context includes important roles for seed

dispersal among communities and local filtering (Leibold et al. 2004, Alexander et al. 2012). Despite empirical evidence illustrating how dispersal and filtering can shape community membership on their own (Choler et al. 2001, Ehrlén et al. 2006, Armas et al. 2011, Laliberté et al. 2014), there is a lack of data documenting how dispersal and filtering interact in natural plant communities. This lack of data represents a missing link between our theoretical understanding of how plant

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<sup>10</sup>E-mail: guittarj@msu.edu

diversity patterns can form and how they actually form. Moreover, it hampers our ability to predict community responses to climate change, because different species likely have different dispersal abilities and/or different constraints to expansion, leading to variable responses (Graae et al. 2017).

The absence of a clear empirical picture of how dispersal and filtering interactively shape plant community membership and regional diversity patterns is due in large part to the logistical challenges of connecting dispersed seeds to individual plant performance. Plant propagules are often tiny, numerous, difficult to identify and track, 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 researchers have tried to infer dispersal and filtering dynamics 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 patterns from historical population range shifts over periods of climate change (Kelly and Goulden 2008, Bertrand et al. 2011) or by analyzing population genetic structure. These indirect methods are useful when modeling species distributions phenomenologically, but fall far short of evaluating whether species fail to arrive or fail to persist after arrival (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) or connecting seeds to parents using parentage analyses (e.g., Cain et al. 2000), are often conducted for single species and/or over short distances, and are of limited use when considering responses of dozens of species at regional scales (Nathan and Muller-Landau 2000).

Here, we compare the seed rain, seed bank, seedlings, and adult plant communities at 12 sites falling along temperature and precipitation gradients in southern Norway to shed light on how seed dispersal and filtering interact in situ to shape community membership and maintain regional climate-associated vegetation patterns. Although our questions align with those of metacommunity theory (Leibold et al. 2004), our sites exist within a broad and contiguous patchwork of grassland habitat, making our system unsuitable to explicitly empirically evaluate between-patch dispersal dynamics, and therefore motivating us to develop our own approach. Specifically, we divide 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 from outside the site but are filtered out), and *locally persistent* species, which occur consistently as adults in annual vegetation surveys. We use adult vegetation surveys to infer which species dispersed outside of their realized climate niches (i.e., were found outside of the climate ranges where we found them to persist as adults), and how their realized climate niches compared to local climate conditions (i.e.,

if they have dispersed into warmer/wetter/cooler/drier climates). We then ask how and why locally transient species were selectively disfavored during community assembly at each site, and how this process varied by climate. Our framework recalls the core-satellite framework of Hanski (1982), but differs in that we allow species status to vary by site, enabling us to examine how species performance varies by environment.

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

1. How many seeds and species arrive to a site but fail to establish locally persistent adult populations, and how does this vary with climate?
2. At what life stages are locally transient species disfavored? Are they less likely to emerge as seedlings, establish as seedlings, compete as adults, or a combination of the three?
3. Why do locally transient species fail to persist? Is it because they dispersed from outside of their realized climate niches and are disfavored due to their climate preferences? Is it because they differ from locally persistent species in their functional traits, offering mechanistic hypotheses for their arrival and selective removal?
4. What do our results mean for how these grasslands will respond to climate change?

## MATERIALS AND METHODS

### *Study area*

The study area comprises 12 seminatural 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 (Appendix S1: 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

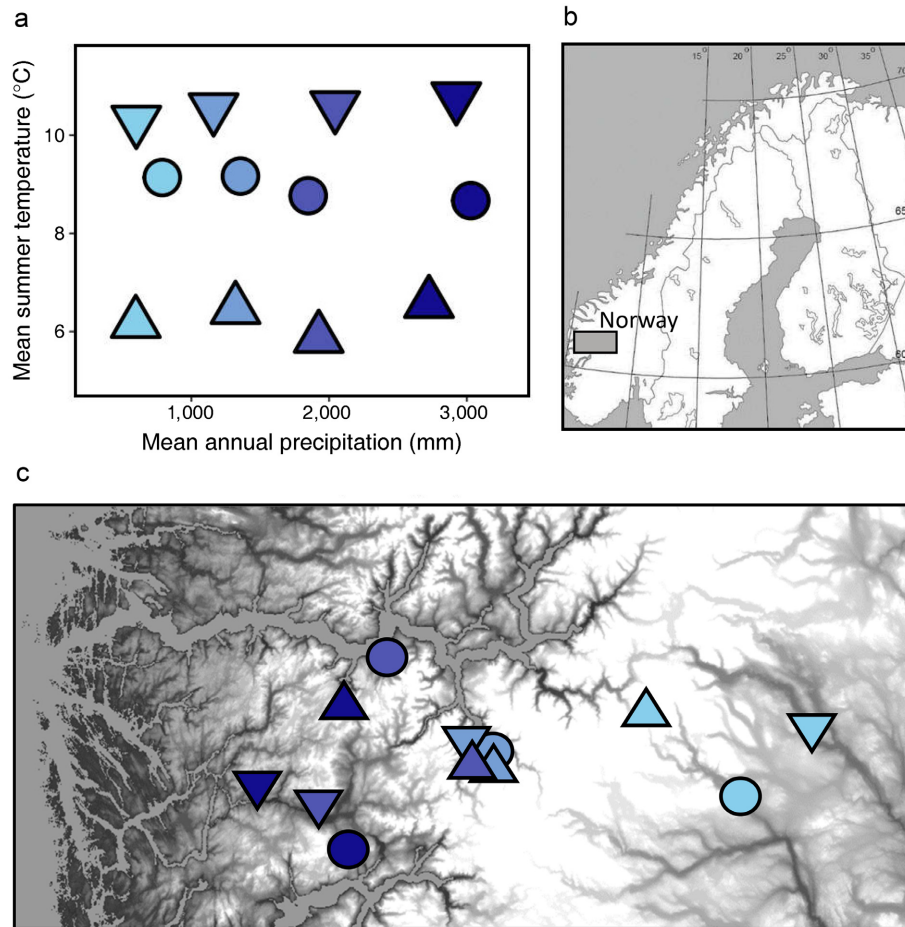


FIG. 1. (a) Climates (a) and (b and c) locations of the 12 field sites in southern Norway. Mean summer temperature is defined as the warmest four months at each site. Grayscale shading in panel c reflects altitude, which covaries closely with mean summer temperature.

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  $0.79^{\circ}\text{C}$  and 238 mm, respectively, on average across sites. Each site has five blocks, placed in representative areas of grassland vegetation within a  $75\text{--}200\text{ m}^2$  area, with individual positions that vary according to local topography and accessibility. Each block has a variable number of  $25 \times 25\text{ cm}$  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 and Lid (2007). Woody species and bryophytes were not recorded in all datasets and therefore were excluded from 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  $25 \times 25\text{ cm}$  artificial turfs placed in gaps about 50 cm from seedling monitoring gaps 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  $500\text{ }\mu\text{m}$  and  $125\text{ }\mu\text{m}$  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 on artificial turfs are likely similar to those on soil, thus seed predation should not bias our results.

### *Seed bank data*

To characterize seed bank diversity, we haphazardly selected one  $64 \times 64$  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 ( $0.41 \text{ m}^2$ ) was larger than the total areas used for seed rain and seedling surveys at each site (four  $25 \times 25$  cm plots,  $0.25 \text{ m}^2$ ), we randomly subsampled 61 % ( $0.25 \text{ m}^2/0.41 \text{ m}^2$ ) of the original seed bank community *in silico* and discarded the remainder to standardize sampling effort across plant life stages. To exclude the seeds from that year's seed rain from our seed bank surveys, we removed the aboveground vegetation, including moss and litter. Soil samples were stored for three months at  $2\text{--}4^\circ\text{C}$  and ambient moisture. Soil samples were then sowed into a standard mixture of sterile subsoil and placed in  $30 \times 60$  cm trays. The trays were incubated in a greenhouse with a diurnal cycle of 16 h light ( $25^\circ\text{C}$ ) and 8 h darkness ( $15^\circ\text{C}$ ). The diurnal cycle was continued for four months, followed by six months of cold stratification in darkness ( $4^\circ\text{C}$ ), followed by another four-month period of diurnal cycling. Emerging seedlings were counted and removed once identifiable to species. This method of characterizing the seed bank community effectively accounts for seed viability because non-viable seeds would not have emerged as seedlings.

### *Seedling data*

Like most perennial grasslands, seedling recruitment in our system is highly dependent on disturbances and occurs only rarely in intact vegetation due to strong competitive effects from adult plants (Eriksson 1989, Silvertown and Smith 1989, Bullock et al. 1995, Vandvik 2004, Berge 2010, Klanderud et al. 2017). We therefore monitored seedlings in experimental gaps where they were relatively free from competitive effects of adult plants, but still exposed to environmental stress and other biotic interactions, such as herbivory, disease, and potential resource competition among seedlings. One  $25 \times 25$  cm gap was created in each of four blocks at each site in spring 2009, for a total of four gaps per site and 48 gaps overall. The gaps were made by cutting along the inner edges of a metal frame mounted in metal pipes marking the corners of the plot, and peeling away the natural vegetation and its thickly interwoven root mat. Seeds and topsoil were returned to gaps by vigorously shaking excavated vegetation and passing it through a 4-mm sieve to remove plant remains. Emerged seedlings in the plots were ID-tagged in one of three censuses (late summer 2009, early summer 2010, 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 potential 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 as 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 were 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 (e.g., late spring frosts), and are distinct from the factors influencing seedling survival establishment (e.g., 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 or August) in 2009, 2011, 2012, and 2013. At each site, we used two  $25 \times 25$  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 turf 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 each species in each plot using a  $5 \times 5$  cm grid overlay, and then pooled the data by site. To ensure that site vegetation was not undergoing successional changes that could bias our conclusions, we used an NMDS ordination to confirm that site composition did not change substantively between years (Appendix S1: Fig. S1). Stage-specific species 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, an important facet of competitive ability in perennial grasslands. Each trait has hypothesized associations to dispersal ability and/or the ability to compete for resources. Seed mass (mg), a reflection of species regeneration strategy (Kraft et al. 2008, Cornwell and Ackerly 2009), was drawn from the Seed Information Database (Kew Royal Botanic Gardens 2008). Maximum canopy height (m) data,



which relates to both dispersal ability and light competition (Westoby 1998, Falster and Westoby 2003, D'Andrea et al. 2020), were mined from Lid and Lid (2007). Leaf area ( $\text{mm}^2$ ) and specific leaf area (SLA;  $\text{m}^2/\text{kg}$ ), two traits indicative of where species fall along a continuum of slow-to-fast resource use strategies (Reich et al. 1997, Ackerly and Reich 1999, Reich 2014), 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,  $\geq 2$  offspring), persistence of plant-offspring connections (0,  $< 2$  yr; 1,  $\geq 2$  yr), rate of lateral spread (0,  $\leq 1$  cm/yr; 1,  $> 1$  cm/yr), 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.

#### *Assigning local species status*

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

#### *Assigning putative climate origins*

For each locally transient species at each site, we identified the sites and climates where we knew it had persistent adult populations, and then used these to infer whether it was dispersing outside of its realized climate niche. If a locally transient species at a given site had persistent adult populations at other sites with similar temperatures and/or precipitations, we assumed it

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

#### *Statistical approach*

We used linear regressions to test for baseline trends in the total abundance and richness of locally transient and locally persistent species in the seed rain, the seed bank, and the two combined along temperature and precipitation gradients. Unlike other data in this study, seed bank data were not collected in replicate across blocks within a site, thus we performed regressions on data aggregated by site ( $N = 12$ ). Each linear regression model assumes normally distributed errors and takes the form of  $y_j \sim \text{MAP}_j$  or  $y_j \sim \text{MST}_j$ , where  $y_j$  is the response variable being examined at site  $j$ , and  $\text{MAP}_j$  and  $\text{MST}_j$  are the mean annual precipitation (centered to zero) and mean summer temperature (centered to zero) at site  $j$ . We also used linear regressions to test for baseline trends in species richness in the mature vegetation with temperature and precipitation.

We used four sets of generalized linear models (GLMs) to test potential predictors of species performance during seedling emergence and seedling establishment. The dependent variable for seedling emergence GLMs was the number of emerged seedlings of each species at each site ( $N = 692$ , the number of unique seed and/or seedling species-by-site combinations), and the dependent variable for seedling establishment GLMs was the number of established seedlings of each species at each site ( $N = 279$ , the number of unique seedling species-by-site combinations). The GLMs used negative binomial error distributions and log link functions. Because each site has a unique combination of temperature and precipitation values (i.e., there is no nestedness), it was not appropriate to include site as a random effect while also testing for the effects of climate. When using seed and seedling numbers as predictors of emergence and establishment, respectively, we normalized their highly skewed abundance distributions with Yeo-Johnson transformations, which are similar to Box-Cox transformations but can be used with zeros. The lambda values used for the Yeo-Johnson transformations were those that maximized normality, as quantified by Shapiro-Wilk normality tests; specifically, the lambda used

to transform seed abundance data was  $-0.204$  and the lambda used to transform emerged seedling data was  $-0.35$ .

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

$$g_{ij} \sim s\_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \times p_{ij}) + (MST_j \times p_{ij})$$

where  $p_{ij}$  is the factor indicating local species status, and the other variables as described above. Likewise, we modeled the number of established seedlings  $e$  for species  $i$  at site  $j$  as

$$e_{ij} \sim g\_trans_{ij} + MAP_j + MST_j + p_{ij} + (MAP_j \times p_{ij}) + (MST_j \times p_{ij})$$

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

In the fourth and final set of GLMs (“site climate + species status + species climate origin” models), we dropped  $p_{ij}$ , the model term for locally transient/locally persistent species status, and replaced it with  $o_{ij}$ , a new term denoting the putative temperature/precipitation origins of each locally transient species  $i$  at site  $j$ . Specifically, the  $o_{ij}$  term tags 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), or (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 reduce excessive model complexity. Formally, we modelled the number of emerged seedlings  $g$  as

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

and the number of established seedlings  $e$  as

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

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 the two 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 the traits with significant differences between the two groups, we performed linear regressions to see whether the magnitude of the difference 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 confidence in calculations of within-site trait means (only  $3 \pm 4$  [mean  $\pm$  SD] locally transient species occurred on average as emerged seedlings at each site; Appendix S1: Table S1). All scripts in this study were written in R and are available online (see *Data Availability*).

## RESULTS

### *Mature vegetation rarefactions*

Rarefactions indicated that the numbers of plots of mature vegetation surveyed at each site were more than sufficient to stabilize the compositions of locally persistent species (Appendix S1: Fig. S2), 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 (Appendix S1: Fig. S3), illustrating the minor overall contribution of locally transient species to local community structure.

### *Evidence of dispersal and 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 seed rain and seed bank, the number of locally transient species and their total abundances increased significantly with temperature (Fig. 2; species richness:  $P = 0.045$ ,  $R^2 = 0.34$ ; total abundance:  $P = 0.016$ ,

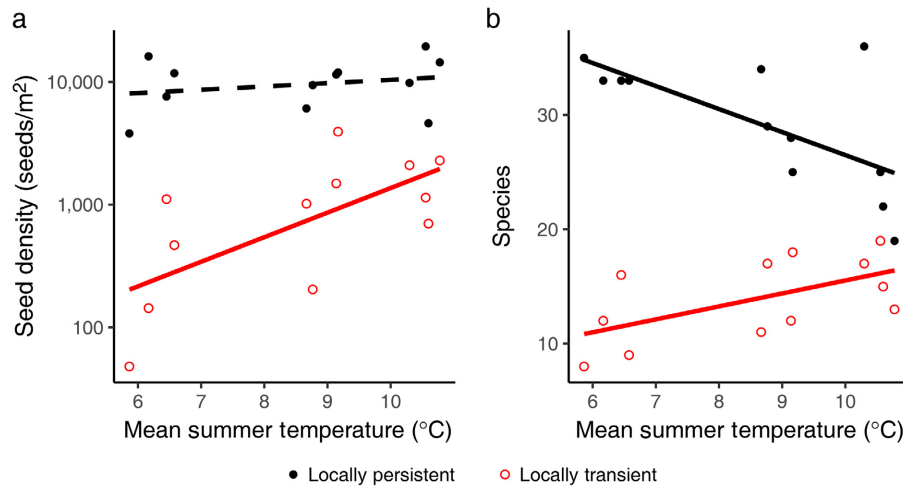


FIG. 2. (a) Seed density and (b) species richness in the combined seed rain and seed bank, grouped by locally transient/locally persistent species status and plotted by mean summer temperature. Summer is defined as the four warmest months at each site. Regression trendlines are solid when temperature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

$R^2 = 0.46$ ). These trends were driven primarily by increases of local-transients in the seed bank (species richness:  $P = 0.031$ ,  $R^2 = 0.39$ ; total abundance  $P = 0.035$ ,  $R^2 = 0.37$ ), not the seed rain (Appendix S1: Fig. S4), underscoring the fact that the composition of the seed rain likely differs between years, and that the seed bank likely serves as an important reservoir of local plant diversity. The strength at which locally transient species were disfavored during seedling emergence did not change with temperature (Table 1; refer to the lack of significance for the transient  $\times$  local temperature interaction term). There were no significant trends in species richness or total abundance with precipitation in either the seed rain, the seed bank, or the two combined. Species richness in the adult vegetation rose significantly with temperature ( $P = 0.0063$ ,  $R^2 = 0.54$ ) but not with precipitation ( $P = 0.871$ ).

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

To determine how sensitive our conclusions were to changes in our operational definition of locally

transient/locally persistent species status, we explored how results changed under each of the four possible cut-off scenarios offered by our data. That is, we looked at how results changed as the definition of locally persistent species shifted from those species present in at least one, at least two, at least three, or all four annual surveys of mature vegetation at each given site. As the cutoff for locally persistent became more stringent, and the cutoff for locally transient (by definition) relaxed, the total number of locally transient species-by-site combinations in the combined seed rain and seed bank rose from 119 (1,989 seeds), to 149 (2,549 seeds), to 167 (3,665 seeds), to 205 (5,007 seeds). However, these differences did not alter our main conclusions that (1) the realized effect of local filtering on community membership increases with temperature, and that (2) grassland sites in southern Norway are connected by dispersal, albeit primarily among sites with similar climates.

#### *The stage-wise removal of locally transient species*

Locally transient species were outperformed by locally persistent species during seedling emergence (Fig. 3, Table 1), but not seedling establishment (Fig. 3, Appendix S1: Table S3). The lower emergence rates of locally transient species appeared to be driven primarily by the species that had putatively dispersed outside of their realized climate niches into cooler climates, drier climates, or those that had dispersed from unknown climates (see “Origin-based predictors” in Table 1). In addition, after accounting for local seed abundances, warmer sites tended to have higher rates of seedling emergence than cooler sites (“General predictors” in Table 1), linking climate and overall seedling performance. No GLM of seedling establishment

TABLE 1. Standardized coefficients ( $z$  scores) from different GLM models (columns) predicting numbers of emerged seedlings by species and site.

Predictors	Null model	Site climate	Site climate + Sp. status	Site climate + Sp. pref. temp.	Site climate + Sp. pref. precip.
$\Delta$ 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 temperature	-	2.79*	2.24*	2.98*	3.15*
Local precipitation	-	-1.09	-1.30	-1.52	-1.65
Transient/persistent predictors					
Transient	-	-	-4.65**	-	-
Transient $\times$ Local temperature	-	-	1.79	-	-
Transient $\times$ Local precipitation	-	-	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**

Notes: In column headers, "Sp. status" refers to whether the species is locally transient or locally persistent, and "Sp. pref. temp./precip." refers to the nearest temperatures/precipitations at which we found the species to have a persistent adult population, which we used to infer the climate from which they likely dispersed. The predictor "Seed no. (transformed)" refers to the numbers of seeds of each species at each site, normalized with Yeo-Johnson transformations (refer to *Methods*).  $\Delta$ AIC refers to the difference in the Akaike information criterion relative to the null model. Data consisted of all recorded seeds and seedlings that could be identified to species.  $N$  is equal to 692, the number of unique emerged seedling and/or seed species-by-site combinations. Dashes denote predictors that were not included in a given model.

\* $P < 0.05$ , \*\* $P < 0.001$ .

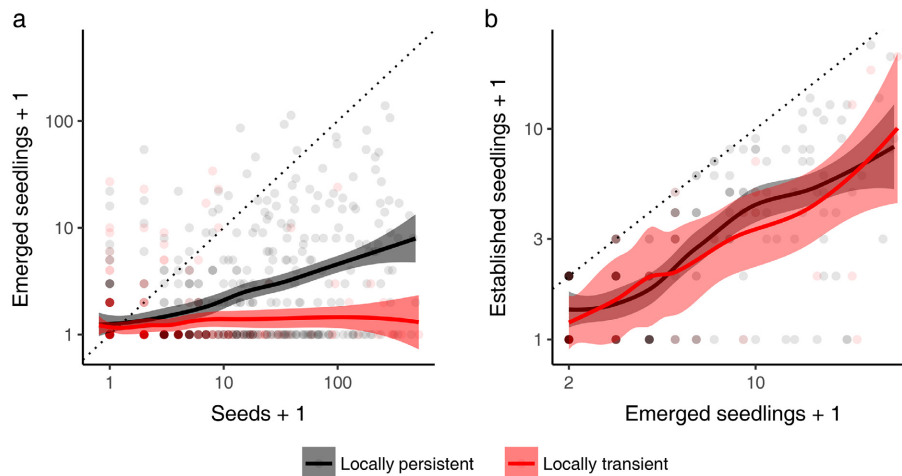


FIG. 3. Life-stage transition probabilities, grouped by locally transient/locally persistent species status. Specifically, (a) numbers of emerged seedlings of each species at each site are plotted by their corresponding number of seeds at each site and (b) numbers of established seedlings of each species at each site are plotted by their corresponding number of emerged seedlings at each site. As such, 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 abundances equal the total number of seeds in the seed rain and seed bank. Seedling abundances equal the total number of individuals in four  $25 \times 25$  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.



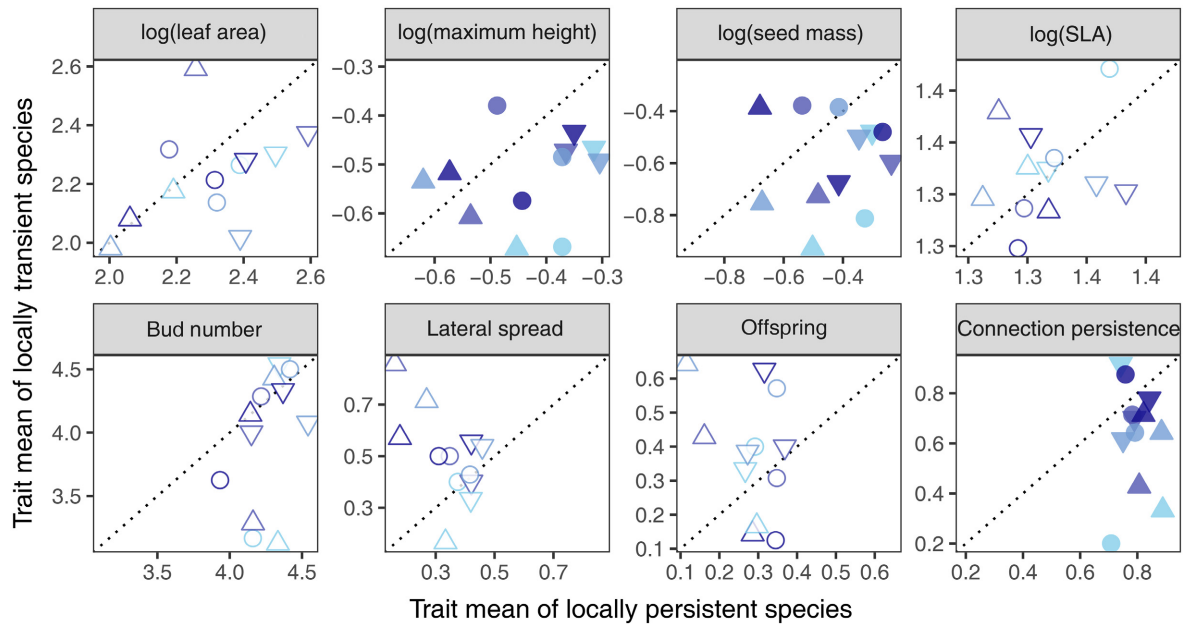


FIG. 4. Mean trait values of locally transient species relative to locally persistent species at each site. Panels show data for four commonly used traits (top row) and four clonal traits (bottom row). Shapes and shadings are consistent with Fig. 1 and reflect approximate mean summer temperatures of 6 °C (triangle), 9 °C (circle), and 10.5 °C (inverted triangle) and annual precipitations of 650 mm, 1,300 mm, 2,000 mm, and 2,900 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 ( $\text{m}^2/\text{kg}$ ). Bud number is an integer score that ranges from 1 (few buds either belowground or aboveground) to 8 (many buds both below and aboveground); lateral spread refers to the proportion of species with rates of lateral spread greater than 1 cm/yr; offspring refers to the proportion of species that commonly produce two or more vegetative offshoots per parent per year; connection persistence refers to the proportion of species with inter-ramet connections that persist for 2 or more yr. Leaf area was measured as  $\text{m}^2$ ; maximum height was measured in m; seed mass was measured in mg.

outperformed null expectations (Appendix S1: Table S3), suggesting that neither climate, species status, nor putative seed origins were meaningful predictors of seedling establishment rates.

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

#### *Trait-based mechanisms of local filtering*

Locally transient and locally persistent species in the combined seed rain and seed bank differed significantly

in three functional traits (Fig. 4). Specifically, when averaged across species at the site level, locally transient species were significantly shorter, had smaller seeds, and had less persistent vegetative connections among ramets than locally persistent species. Of the three traits that differed consistently between locally transient and locally persistent species, the only instance where those differences varied significantly with site climate was an increase in the magnitude by which locally transient species had less persistent connections than locally persistent species with increasing temperature.

#### DISCUSSION

In this study, we compared the composition of seed rain, seed bank, seedlings, and adult plant communities along temperature and precipitation gradients to shed light on how dispersal and filtering interactively shape community membership and how this process varies across a landscape. Overall, our results point to four main conclusions: (1) the total numbers of seeds and species that arrived, but failed to establish locally persistent populations, rose with temperature, indicating an increase in the realized effects of local filtering on community assembly, as well as an increase in the number of species poised to rapidly colonize those warmer sites if

local conditions change in their favor, (2) locally transient species were selectively filtered out during seedling emergence, but not during seedling establishment, (3) selective filtering was partly driven by species climate preferences, exemplified by the poor performance of seeds dispersing outside of their realized climate niches into foreign climates that were more stressful (colder and drier), and (4) locally transient species had traits that may have made them better dispersers (i.e., smaller seeds) but poorer competitors for light (i.e., shorter statures and less persistent clonal connections) than locally persistent species, potentially explaining why these species arrived to new sites but failed to establish locally persistent adult populations. We elaborate on these conclusions below, and end with a discussion of what our results mean for how these alpine grasslands will likely respond to climate change.

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

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

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

2011). A second explanation could be that seeds are simply more likely to disperse downhill (i.e., from colder high-altitude sites to warmer low-altitude sites) than the reverse, again leading to more seeds arriving at unsuitably warm patches than unsuitably cold patches. A third explanation could be that competition for resources is fiercer at warmer temperatures, resulting in more local extirpations in the adult plant communities at warmer sites, although, importantly, this explanation presumes that similar numbers of seeds and species are dispersing to all sites, which may not be the case. Nevertheless, other studies have found support for such an explanation: competition for light is hypothesized to be stronger at warmer sites due to higher productivity, more developed soils, and overall less stressful growth conditions (Grime 1973, Olsen et al. 2016). In our study, species richness fell steeply with temperature in the adult vegetation (from an average of 64 species at the coldest sites to 42 species at the warmest sites), but only slightly in the seed rain and not in the seed bank (Appendix S1: Fig. S4), consistent with a scenario in which similar numbers of species arrive to all sites, but more species are competitively excluded by adulthood at warmer sites. Future work could track individuals after establishment but before mature adulthood to determine if the degree to which locally transient taxa are disfavored increases with temperature, substantiating this hypothesis.

Surprisingly, locally transient species were disfavored more strongly during the first life-history transition, seedling emergence (Fig. 3, Table 1), than later, during seedling establishment (Fig. 3, Appendix S1: Table S3). This suggests that germination and early seedling survival are more important for success than seedling establishment, at least in our system. This result contradicts conventional expectations of weak filtering during seedling emergence but strong filtering during seedling establishment (Moles and Westoby 2004). Differential germination rates among species could be driven by species preferences for soil (Evans and Etherington 1990, Benvenuti 2003) or climate conditions. It should be noted that while some individuals could have been filtered out after meeting our operational definition of establishment (i.e., had stems at least 2 cm long and, if a forb, also had non-cotyledonous leaves), but before becoming reproductively active (i.e., before establishment *sensu stricto*), this does not appear to be the case. Across sites, the mean proportion of species that were classified as locally transient among established seedlings was only slightly higher than that found in the adult vegetation data (~14.6% vs. ~13.6%, respectively), indicating that any locally transient species that successfully emerged were essentially just as likely as locally persistent species to survive long enough to be captured by our mature vegetation surveys, although these species were not present consistently enough to be classified locally persistent. In other words, locally transient species evidently failed to persist not because they failed to establish, but because they failed to arrive in high

enough numbers, because their seeds failed to germinate, and/or because their post-establishment juveniles failed to reach sexual maturity.

The lower emergence rates among locally transient species were largely driven by seeds that had putatively dispersed outside their realized climate niches into cooler climates (i.e., from warmer climates), into drier climates (i.e., from wetter climates), and those from unknown climates (Table 1), illustrating how climate-based niche preferences can influence community membership and limit range expansion. Climate is known to play a pivotal role in the release of seed dormancy in plants (Probert 2000), and variation in germination timing is known to occur even among populations of the same species at different climates (Shimono and Kudo 2003, Bischoff et al. 2006, Spindelböck et al. 2013). If the seeds of locally transient species dispersing outside of their realized climate niches into colder and/or drier climates were predisposed to emerging before spring is safely underway, this could explain their particularly low emergence rates. A second, complementary explanation could be that seeds dispersing outside of their realized climate niches into colder and/or drier climates simply find these conditions more stressful and are thus less likely (i.e., not adapted) to successfully emerge as seedlings.

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

but that their influence may not be consistent or predictable across sites.

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

#### *Implications for community responses to climate and climate change*

Community response to climate change will depend both on species' abilities to track environmental changes via dispersal, and on niche-based performance differences among species in different environments (Graae et al. 2017). Southern Norway is expected to grow warmer and wetter as climate change progresses (Hanssen-Bauer et al. 2017), so species will have to disperse into cooler (upslope) and drier (more inland) sites to maintain their current climate conditions. However, 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 (Appendix S1: Fig. S4, Appendix S1: Table S2), suggesting that many if not most species will likely fail to 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). Yet, our finding that immigrant seeds from other climates were strongly disfavored provides a potential silver lining: if a species can disperse into a site with a newly suitable climate, it should be strongly favored over local residents, and thus be able to quickly establish a locally persistent population. Overall, our results provide insight into the dynamic way in which communities will respond to climate change, and emphasize the need for further work on how species will vary in their ability to disperse and compete in different community contexts.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3061/supinfo>

## DATA AVAILABILITY

All data and scripts are available on Zenodo: <https://doi.org/10.5281/zenodo.3695969>