SPECIES RANGES ARE CONSTRAINED BY GERMINATION, NOT ESTABLISHMENT, IN A GRASSLAND METACOMMUNITY.

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ABSTRACT

1. Predicting plant community responses to climate change requires an understanding of how regional dispersal dynamics and local filtering processes interactively generate and maintain climate-associated vegetation patterns. Unfortunately, few empirical investigations have evaluated dispersal patterns and immigrant seed performance in the same system, hampering realistic predictions of community response to climate change.
2. We develop a new approach to evaluate the magnitudes and directions of dispersal among sites as well as immigrant performance upon arrival. First, we combine seed rain and seed bank surveys to characterize seed communities across 12 sites in southern Norway that differ in climate. Each seed species at each site is either “persistent,” if it has a local population of adults, or “transient,” if it does not (i.e., is putatively an immigrant dispersing outside of its range). We monitor a cohort of seedlings in experimental gaps at each site to determine the life stage(s) at which transient species are selectively removed – if at all – from the species pool. We also use regional vegetation patterns to assign putative climate origins to each transient seed at each site, and evaluate how it may affect performance.
3. About 10 % of the seeds recorded in our study were labeled locally transient, indicating that sites are generally well connected by dispersal. However, only a small minority of long-distance dispersal occurred among climate zones, raising concerns that species may be unable to track climate change to maintain their current climate associations. Contrary to conventional expectations, transient species were selectively disfavored during the transition from seed to emerged seedlings, rather than the transition from emerged to established seedlings. Locally transient species tended to have fewer clonal buds, faster rates of lateral spread, and smaller seeds than persistent species, offering some clues as to why they differ in performance during seedling emergence.
4. *Synthesis*. Our study combines survey data from seed rain, seed bank, emerged seedling, established seedling, and adult life stages across twelve grassland sites differing in temperature and precipitation to understand how climate-associated vegetation patterns are generated and maintained. Evidently, species ranges, and potential range expansions, are constrained through a combination of dispersal limitation and differential performance during seedling emergence, but not seedling establishment. Long-distance dispersal into cooler and drier sites was particularly uncommon, raising concerns that many species will be unable to track their preferred climates as the climate in the region grows warmer and wetter in the coming decades.

**Keywords:** Dispersal dynamics, community assembly, alpine grasslands, climate change, species sorting, seedling survival, range expansion, species distributions.

INTRODUCTION

Plant species ranges have shifted in response to anthropogenic climate change and will continue to do so in the coming decades (Post and Pedersen 2008, Morueta-Holme et al. 2015, Koide et al. 2017). Given the potential for significant and rapid changes to vegetation patterns, we need effective strategies to prevent local extinctions when possible, to assist population migrations when necessary, and to forecast changes in community functions and services. Yet, models of species responses to climate change still give inconsistent predictions (Pacifici et al. 2015), impeding our ability to make wise management decisions. One reason for our inability to make consistent predictions is an incomplete understanding of how regional dispersal dynamics and local filtering processes interact to govern species ranges, and how climate-associated vegetation patterns are maintained in general.

Species range limits can be explained by a lack of dispersal into new sites and/or an inability to persist in the local abiotic or biotic environment. Knowing the relative influence of these deterrents to range expansion is important because the first (dispersal limitation) is largely independent of climate, and the second (differential performance) may be strongly modulated by climate (Gilman et al. 2010, Olsen et al. 2016), resulting in fundamentally different predictions of species response in light of climate change. Yet, few studies separate these potential constraints on immigrant success; indeed, there are few *in situ* assessments of dispersal into plant communities level in general (Vandvik and Goldberg 2006). 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). Researchers have partially 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 work uses variability among species in their tracking of a changing climate to infer potential dispersal limitation, or lack thereof (Kelly and Goulden 2008, Bertrand et al. 2011). Such approaches are valuable for modeling species responses from a phenomenological standpoint, but fall short of uncovering true dispersal pathways (Calabrese and Fagan 2004).

Upon arrival, the probability that an immigrant species will establish at a new site depends on both the density of its seeds relative to local seeds (i.e., the probability of success assuming functional equivalence among seeds), and the degree to which it differs from local species in fitness. Conditions are optimal for immigrant establishment when it disperses to the new site in high numbers and strongly outperforms local species. An immigrant species will likely establish quickly under either of the above conditions; high propagule pressure (with weak fitness differences) or strong fitness differences (with low propagule pressure) are both likely to initiate a new local self-perpetuating population. However, an immigrant species will be slow to colonize a new site, and therefore slow to track climate change, if it disperses to new sites in low numbers and does not outperform local species upon arrival. Researchers have evaluated the relative influence of dispersal limitation and performance differences on species ranges by lifting dispersal limitation, either by manually sowing seeds or transplanting individual plants beyond their natural distributions, and then observing performance differences (Turnbull et al. 2000, Hargreaves et al. 2014, Katz and Ibáñez 2017). Overall, immigrants tended to perform poorly beyond their ranges. While such transplant studies implicate niche-based performance differences as *potential* mechanisms shaping species distributions, they do not show performance differences are operating *in situ*, nor do they explore how immigrant dispersal dynamics and species performance differences may interact to govern species range limits.

Here, we quantify seed dispersal outside of species’ current adult ranges, and directly assess the performance of these immigrant propagules. Rather than infer seed dispersal patterns from adult populations, seed communities are characterized directly using seed rain and seed bank surveys. Seed communities are compared to adult vegetation patterns across our study sites to infer potential seed origins. We then assess differences in the rates of seedling emergence and seedling establishment between individuals dispersing outside of their current adult ranges, and individuals falling within their current adult ranges. The former are designated as locally *transient* species – i.e., species that appear at a given site as seeds or seedlings but not as adults – and the latter as locally *persistent* species – i.e., species that appear at a given site as seeds or seedlings and as adults, according to site vegetation surveys. We consider an adult population to be persistent at a site if individuals are observed in at least three of the four annual vegetation surveys conducted from 2009 – 2013. Finally, species-level traits are used identify potential functional differences between transient and persistent species within sites that could explain any differences in dispersal and/or performance. Even if a species is mislabeled as transient at a site when in fact they are just locally rare, it should not affect the snapshot of regional dispersal dynamics and local species sorting that our analysis provides; the same processes that cause a species to be locally rare, such as being poorly adapted to local conditions, are likely to be similar to the processes that cause a species to be locally absent.

We apply this seed-based approach to assessing dispersal and immigrant performance at 12 alpine and subalpine grassland sites in southern Norway, a region with unusually high spatial climate variability due to a network of fjords extending into the interior. The sites were selected according to their summer temperature and annual rainfall such that they form an orthogonal climate grid, enabling independent assessment of the roles of these two climate drivers in community assembly (e.g., Meineri et al. 2014, Olsen et al. 2016). Climate preferences are defined for each species based on the sites where they persist as adults, and then these climate preferences are used to assign putative climate origins for each transient species at each site. This study has two parts: first, we use the grassland system and methodological approach to ask a fundamental ecological question; second, we discuss what the results mean for how the system will respond to climate change in the coming decades:

1. How do regional dispersal dynamics and local filtering processes interact to govern species ranges?
   1. To what extent are species ranges maintained because long-distance dispersal is rare, as opposed to because local species outperform arriving immigrant species?
   2. Are there systematic differences in performance between transient and persistent species? If so, at what life stages do these differences occur? Are locally-sourced seeds more likely than immigrant seeds to persist in the soil, to emerge as seedlings, to establish as seedlings, or to compete clonally among adults?
   3. Do transient species differ from persistent species in their functional traits, offering an explanation for their lack of a local population? If persistent species outperform transients during a specific life stage transition, can systematic differences in their functional traits explain why?
2. What implications do our results have for how these mountain grasslands will respond to climate change?
   1. How many seeds of how many species are dispersing into sites that will enable them to maintain their current climate associations, e.g., to cooler sites as the local climate warms?
   2. Are species performances strongly modulated by their climate preferences, such that species responses to climate change will be swift for any species with sufficient dispersal into new sites? Or, are species performances weakly modulated by their climate preferences, such that species responses to climate change will slow unless aided by high propagule pressure.

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 (Silvertown and Smith 1989, Eriksson 1989, Bullock et al. 1995, Vandvik 2004, Berge 2010, Klanderud et al. 2017). We therefore monitor seedlings in experimental gaps where they are free from competitive effects of adult plants, but are still exposed to environmental stress and other biotic interactions, such as herbivory, disease, and potential resource competition among seedlings.

MATERIALS AND METHODS

*Study area*

The study area comprises 12 calcareous grassland sites in southern Norway that host at least 151 non-woody vascular plant species at the adult life stage, and at least 141 at the seed stage (Table S1). Sites have similar land use histories, slopes of approximately 20°, and southwest aspects, but differ in their mean summer temperature and/or mean annual precipitation such that they form a grid with approximately orthogonal climate axes (Fig. 1). See Klanderud et al. (2015) for additional site details.

*Seed rain data*

We collected seed rain at each site during two periods aimed to target winter (September 2009 to June 2010) and summer (June 2010 to September 2010) seed deposition. We trapped seeds in artificial turf mats placed in vegetation gaps in each of the four blocks delineated at each site, for a total of 48 seed traps. The small synthetic filaments in artificial turfs are effective at catching and holding small particles like seeds. We gathered the turfs and flushed them with water to free collected seeds. We passed the rinse water through 500µm and 125µm diameter sieves to discriminate seeds by size and remove debris. Seeds were counted and identified taxonomically using a stereomicroscope. We included fruits, bulbils (e.g., *Bistorta vivipara*) and viviparous seeds (e.g., *Festuca vivipara*), but not spores (e.g., *Polytrichum spp.*), in our working definition of “seed” or “propagule,” terms we use interchangeably. For additional details and analysis of seed rain, see Boixaderas (2012). Taxonomic identifications for seeds, seedlings, and adults follow Lid & Lid (2007). Woody species were also excluded from all analyses.

*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 (0.41 m2) was larger than the areas used for seed rain and seedling surveys (four 25 x 25 cm plots = 0.25 m2), we randomly selected a subset of 61 % (0.25 / 0.41) of seeds and discarded the remainder, to reflect equaling sampling effort of each data type at each site. To avoid sampling seed rain, we removed aboveground vegetation, including moss and litter, before storing soil samples for three months at 2 – 4 °C and ambient moisture. We then passed soil samples through a 40 mm sieve to remove vegetation and debris and sowed the resulting seed samples into a standard mixture of sterile subsoil and placed them in 30 x 60 cm trays. The trays were incubated in a greenhouse with a diurnal cycle of 16 hours light (25 °C) and 8 hours darkness (15 °C). The diurnal cycle was continued for four months, followed by six months of cold stratification in darkness (4 °C), followed by another four-month period of diurnal cycling. Emerging seedlings were counted and removed when identifiable to species. For additional details and analysis of seed bank data, see Vandvik et al. (2016).

*Seedling data*

Four 25 x 25 cm gaps were created at each site in spring 2009. The gaps were made by cutting along the inner edges of a square 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 ensure the separation of soil and plant remains. Emerged seedlings were ID-tagged in one of three censuses (late summer 2009, early summer 2010, late summer 2010) using numbered plastic toothpicks and assigned plot coordinates. About 70 % of seedlings were identifiable to species; the remaining 30 %, most of them graminoids, were either unidentifiable or died before they could be identified and were therefore lumped into a single generic group (“spp.”) and excluded from all analyses that required species identities. We differentiated seedlings from newly emerged 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. Graminoids were considered established if they were present the following year at the same coordinate position, and forb seedlings were considered established when they had at least two non-cotyledon leaves (or, in the case of species with opposite leaves, pairs of non-cotyledon leaves) and plant height exceeded 2 cm. We approximated seedling emergence rates by dividing the density per m2 of emerged seedlings by the sum of seed rain and seed bank densities. For additional details and analysis of seedling censuses see Berge (2010) and Klanderud et al. (2017).

We recorded a total of 4383 emerged seedlings in experimental gaps, 1245 of which established, yielding an estimated 3 % rate of seed-to-established seedlings (i.e., of 40115 seeds) and a 28 % rate of emerged seedling-to-established seedling. Of these, only 3045 emerged seedlings and 1080 established seedlings were identifiable to species. Unidentifiable seedlings were excluded from all analyses that required species identities.

*Mature vegetation data*

We surveyed mature vegetation at peak biomass (July and August) in 2009, 2011, 2012, and 2013. At each site, we visually estimated the percent cover of individual species in five 25 x 25 cm plots using a 5 x 5 cm grid overlay, and then summed the data by site for this analysis. For additional details and analysis of mature vegetation patterns, see Klanderud et al. (2015) and Guittar et al. (2016).

*Trait data*

We used four commonly used plant traits with known associations to performance, and four traits related to clonal growth strategy. Leaf area (mm2) and specific leaf area (SLA; m2/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 and data from the LEDA online trait database (Kleyer et al. 2008). The field data derive from approximately 1200 leaves collected in summer 2012 (Guittar et al. 2016), for which SLA and leaf area were calculated using established protocols (Cornelissen et al. 2003). Seed mass (mg), which reflects 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 (m2) data, a trait related to competitive ability for light and dispersal ability (Westoby 1998, Falster and Westoby 2003), were mined from Lid and Lid (2007). Leaf area, SLA, maximum height, and seed mass values were log10-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), and were drawn from Klimeš and Klimešová (1999) and subsequently converted from categorical to quantitative formats to enable calculations of community means. Trait data are available in Appendix C. For additional details on trait data collection and curation see (Guittar et al. 2016).

*Assigning putative climate origins*

Each species found as a seed or seedling at a given site was labeled as “persistent” if adults were recorded in two or more of the four site vegetation surveys conducted from 2009 to 2013, or “transient” if adults were recorded in one or none of the site vegetation surveys. We assigned putative climate origins to transient seeds based on the climate of their most climatically-similar persistent adult population. That is, we assumed transient individuals were from sites with similar temperature and/or precipitation if conspecific adult populations persisted in such climates, or in both climatic directions (i.e., warmer and cooler climates, or wetter and drier climates). If adult conspecifics were observed only at warmer, cooler, wetter, or drier sites, we assumed the transient seeds came from those climates. Seeds without any recorded adult conspecifics in our vegetation surveys were labeled as coming from an “unknown origin.” We used climate dissimilarity rather than spatial distances between sites to define immigration “distance” for two reasons. First, species occured in many more sites than those that we surveyed, so spatial distances among study sites are not faithful proxies for dispersal distances. Second, we wanted to assess species’ ability to disperse along climate gradients, and climate dissimilarity is a better measure of this than geographic distance in this topographically complex landscape.

*Statistical approach*

We use multiple linear regressions to test for baseline trends (i.e., site-level; N = 12) in abundance and species richness along temperature and precipitation gradients. Specifically, we look for trends in (1) the abundances and richness of seeds in the seed rain and seed bank, (2) the abundances and richness of transient species in the seed rain and seed bank, and (3) the proportional contributions of transient species to the abundances and richness of seeds in the seed rain and seed bank. Each model takes the form of *y*­*j* ~ MAP*j* + MST*j,* where *y­j* is the response variable being examined at site *j*, andMAP*j* and MST*j* are the mean annual precipitation (centered to zero) and mean summer temperature (centered to zero) at site *j*.

We use four sets of generalized linear models (GLMs) to evaluate potential predictors of species performance during seedling emergence and seedling establishment. All GLM sets used negative binomial error distributions and log link functions. In the null models, species abundances in the seed community (i.e., the combined seed rain and seed bank) predict species abundances of emerged seedlings, and species abundances of emerged seedlings predict species abundances of established seedlings. In other words, null expectations are that each seed is equally likely to emerge, and each emerged seedling is equally likely to establish. In the second set of GLMs, we add model terms for local (i.e., site-level) mean summer temperature and mean annual precipitation to evaluate how these climate variables affect seedling emergence and seedling establishment rates. Note that it was inappropriate to use generalized linear mixed-effects models because each site had a unique combination of temperature and precipitation values, which would have eliminated the possibility of using climate to predict performance.

In the third set of GLMs, we asked whether species transient/persistent status predicts performance differences during seedling emergence and seedling establishment. Specifically, we added an additional model term specifying whether species were transient or persistent at each site, as well as terms for potential interactions between species status and site temperature and precipitation. That is, we formally modeled the number of emerged seedlings *g* for species *i* at site *j* as

*gij* ~ log(*sij*) + MAP*j* + MST*j* + *pij* + (MAP*j* ∙ *pij*) + (MST*j* ∙ *pij*),

where *sij* is the abundance of seeds (seed rain + seed bank) of species *i* at site *j*, *pij* is a factor indicating local species status (i.e., either transient or persistent), 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

*eij* ~ log(*gij*) + MAP*j* + MST*j* + *pij* + (MAP*j* ∙ *pij*)+ (MST*j* ∙ *pij*).

In our fourth and final set of GLMs, we dropped the transient/persistent model term, *pij*, and added a new term, *oij*, denoting the putative temperature or precipitation from which each transient species *i* at each site *j* immigrated. These terms contained five temperature-based categories and five precipitation-based categories. Specifically, when considering putative temperature origins, species were either (1) locally persistent, (2) from a non-local site with a similar temperature (but different precipitation), (3) from a cooler site, (4) from a warmer site, or (5) from a site with unknown temperature (and unknown precipitation). When considering putative precipitation origins, species were either (1) locally persistent, (2) from a non-local site with a similar precipitation (but different temperature), (3) from a drier site, (4) from a wetter site, or (5) from a site with an unknown temperature (and unknown precipitation). We dropped the interaction terms to avoid excessive complexity. Formally, we modelled the number of emerged seedlings *g* for species *i* at site *j* as

*gij* ~ log(*sij*) + MAP*j* + MST*j* + *pij*,

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

*eij* ~ log(*gij*) + MAP*j* + MST*j* + *pij*.

In addition to using GLMs to model the numbers of emerged and established seedlings, we use a parallel set of GLMs to model the probability that species have *any* seedlings emerge or establish at a given site. These presence/absence models used binomial error distributions and logit links. This analysis explored the possibility that model predictors (i.e., local temperature, local precipitation, and putative climate origins of transient species) act as binary environmental filters, either allowing or preventing the emergence or establishment of a species at a given site altogether. Results from our presence/absence analysis were qualitatively similar to results from the abundance-based analysis and were relegated to Appendix A.

Finally, we ask if systematic differences between the traits of transient and persistent species within sites offer potential mechanisms driving performance differences between these groups. Differences were calculated by averaging the trait values of all species present within each species group at each site for each life stage (i.e., combined seed rain and seed bank, emerged seedling, and established seedling). Abundance-weighted community trait means were not used in this analysis in order to focus on differences between transient and persistent species *per se*, rather than potential shifts in relative abundances.

RESULTS

*To what degree are species ranges limited by long-distance dispersal?*

Transient seeds occurred at all 12 grassland sites, comprising 4 % of all seeds in the seed rain and 14 % of all seeds in the seed bank (Fig. 2, left panel), illustrating a moderate degree of long-distance dispersal across sites. Transients contributed even more to seed communities when considering species: 14 % of the species in the seed rain (i.e., 4 of 28 on average by site), and 33 % of the species in the seed bank (i.e., 12 of 36 on average by site) were transient (Table S1). Both transient seeds and transient species in the seed bank increased with temperature (Fig. 3, Table S3), whereas transient seeds in the seed rain showed no trends with temperature (Fig. 3, Table S3).

Seeds of transient species comprised 9.6 % of the combined seed rain and seed bank communities, with most seeds putatively originating from sites with similar temperature and/or precipitation (Table S4). Specifically, 66 % of transient seeds originated from sites with similar temperatures, and 47 % of transient seeds originated from sites with similar precipitations (Fig. 4, Table S4). Transient seeds were four times more likely to originate from cooler climates than warmer climates, and slightly less likely to originate from drier climates than wetter climates (Fig 4, Table S4). Seeds of transient species tended to have less even abundance distributions at sites than persistent species, with only five to 10 abundant species and many rare species (Fig. S1).

*To what degree are transient species selective removed after arrival?*

Correlations in species abundances between life stages are coarse measures of how equally-likely species are to survive life stage transitions. Species abundances correlated weakly between seed rain and seed bank communities (r = 0.16; N = 564, excluding double zeroes; Table S5) and weakly between the combined seed rain and seed bank and emerged seedlings (r = 0.39; N = 600, excluding double zeroes; Table S5), suggesting marked performance differences among species during these life stage transitions. Conversely, species abundances correlated more strongly between emerged and established seedlings (r = 0.77; N = 243, excluding double zeroes; Table S5), suggesting a less discerning ecological filter during this life stage transition.

Results from GLMs provided more rigorous statistical support for species sorting during the transition from seed to emerged seedling (Fig. 5, Table 1). First, after accounting for local seed abundance, warmer sites tended to have higher rates of seedling emergence than cooler sites, drawing a general connection between climate and performance (Table 1). Second, transient species tended to emerge at lower rates than persistent species (Fig. 5, Table 1). Third, we found a significant, albeit modest, interaction between site temperature and species transient/persistent status, such that differences in emergence rates were greater at higher temperatures (Fig. S2, Table 1). Fourth, lower emergence rates of transient species relative to persistent species was driven primarily by the poor performance of species immigrating from warmer climates (i.e., seeds dispersing into colder climates), from wetter climates (i.e., seeds dispersing into drier climates), and from unknown climates (Table 1).

In contrast to seedling emergence, GLMs offered no evidence for species sorting during seedling establishment. The null model of seedling establishment, in which all emerged seedlings were equally likely to establish, had a lower AIC score than models with site temperature, site precipitation, species transient/persistent status, and species’ putative climate origins (Table S6). To confirm that the results were not an artifact of how we combined seed rain and seed bank data (e.g., if transient seeds had emerged at lower rates because most transients were in 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).

*Are there systematic trait-based differences between transient and persistent species?*

Functional traits of transient and persistent species differed consistently in both emerged and established seedlings (Fig. 6). In the combined seed community, transient species had fewer clonal buds, less persistent connections among clonal ramets, faster rates of lateral spread, and smaller seeds than persistent species, illustrating how long-distance dispersal brings species into sites that are functionally different, on average, than local species. However, the present absence of these transient species in the local adult vegetation suggests that their trait differences have thus far proven disadvantageous. Overall, trait values of transient and persistent species converged over sequential plant life stages, consistent with a gradual winnowing of maladapted species from the regional species pool (Fig. 6).

Shifts in trait-based differences between transient and persistent species during emergence and establishment can offer clues why transient species are selectively removed during these life stage transitions. However, any trait-based differences must be interpreted differently than trait-based differences among seeds. Specifically, differences must be compared to the null expectation that each species from the prior stage was equally likely to survive, i.e., that any trait-based differences from the prior life stage will persist. With this in mind, trait-based differences between transient and persistent species changed considerably during the transition from seeds to emerged seedlings, indicating that species sorting was significantly non-random with respect to species traits. Specifically, transient and persistent species became more similar on average in terms of bud number, rate of lateral spread, and seed mass over seedling emergence, suggesting that transient species that differed in these traits were less likely to emerge. However, emerged seedlings of transient species had higher SLAs (thinner leaves) and less persistent clonal connections than expected, suggesting that these two traits may confer an advantage to immigrants during emergence. There were no notable shifts in trait-based differences between transients and persistent species during establishment, consistent with the absence of a discerning ecological filter at this life stage transition.

DISCUSSION

In this study, we examine the dispersal and performance of seeds beyond the ranges of their adult populations across a network of twelve grassland sites in southern Norway. We find that instances of long-distance dispersal are not uncommon (Fig. 2), particularly at warmer (i.e., lowland) sites (Fig. 3), but that they occur primarily among sites with similar climates (Fig. 4). The seeds that dispersed outside of their adult ranges (i.e., seeds of locally transient species) emerged at lower rates than locally persistent species (Fig. 5), perhaps due to physiological adaptation to their source climates (Table 1) and/or systematic differences in their functional traits (Fig. 6). Together, these results suggest that species will be limited in their ability to shift their ranges to track future changes in climate. Below, we elaborate on these findings in two ways. First, we discuss how regional dispersal pathways and local filtering interactively influence the assembly process, leading to the generation and maintenance of climate-associated vegetation patterns. Second, we ask what our results mean for how our system – and grassland systems in general – will respond to climate change in the coming decades.

*Community assembly and the limits to species ranges*

To thrive at a new site, prospective grassland immigrants must arrive, emerge, establish, and persist, or in the case of obligate annuals, repeatedly re-colonize the local site from seed. Results from dispersal analysis suggest that most species in the regional pool are absent from particular sites, at least in the short term, because they fail to arrive. Of the 129 species with persistent adult populations, 66 were not observed as seed or seedlings outside of the sites at which they persisted as adults. While not unexpected, these results lend quantitative support to the role of dispersal limitation in constraining species ranges and maintaining regional vegetation patterns. Indeed, 14 species with persistent adult populations were never observed as seeds or seedlings at any site, suggesting that their adult populations are either maintained exclusively through vegetative reproduction (i.e., clonal growth), or are in a state of local decline. These species included *Coeloglossum viride*, an orchid, and *Minuartia biflora*, a short mat-forming perennial. The evident lack of viable seed production effectively confines these species to their current ranges, at least on short to medium time scales, regardless of how well or poorly adapted they are to local environmental conditions.

Differences in seed bank and seed rain community compositions provide additional insight into regional dispersal dynamics. Notably, the total seed bank had about five times as many transient seeds as the total seed rain (Fig. 3), which harbored three times as many transient species on average across sites (Table S1). This large discrepancy might be due to one or both of the following phenomena: 1) Contrary to studies in other calcareous grasslands (Maarel and Sykes 1993, Willems and Bik 1998), seed rain compositions (i.e., local dispersal dynamics) in our system may differ markedly from year to year; 2) Transient seeds may have been more abundant in prior years and/or persisted in the soil longer than locally persistent species. In partial support of the latter, locally transient species emerged at lower rates than locally persistent species (Fig. 5, Table 1), which could lead to a faster accumulation of transient seeds than persistent seeds in the soil over time. Such differences could also result if seeds of transient species were less likely to be targeted by decomposers, to lose viability, or to be eaten by granivores (Dalling et al. 2011). In line with this, transient species had smaller seeds than persistent species (Fig. 6), a trait thought to increase dispersal range, persistence in the soil, and the likelihood of being buried (Thompson et al. 1993). Regardless of the mechanism underlying the increased abundance of transient seeds in the seed community, seed connectivity among sites combined with dormancy in the soil clearly provide an important reservoir of biodiversity in our system (Mouquet and Loreau 2003, Cadotte and Fukami 2005, Cadotte 2006, Olsen et al. 2016), enabling immigrant seeds to lay in wait until a gap appears and/or local environmental conditions become amenable to growth.

Curiously, the number of transient seeds, the proportion of transient seeds, and the species richness of transients in the seed bank all rose steeply from the coldest (highest altitude) to warmest (lowest altitude) sites (Fig. 3), although the trend was sometimes only marginally significant (Table S3). Such patterns could result if dispersal occurred primarily from colder to warmer communities (e.g., due to seeds traveling downslope due to gravity, wind, or water drainage), yet we found most immigrants to putatively originate from communities with similar temperatures (Fig. 4). Alternatively, an increase in transient seeds and transient species at higher temperatures could have arisen if warm-adapted species had smaller, wind-dispersed seeds better suited to traveling long distances (Moles et al. 2007). However, seed mass does not trend with temperature in our system (Guittar et al. 2016), and we found no systematic difference in seed mass between transient and persistent species within sites, ruling out this possible explanation as well. Instead, the increase in transients at warmer temperatures may be the result of a concomitant decrease in species richness in the adult vegetation (Table S2), possibly due to higher rates of competitive exclusion due to longer growing seasons and less stressful growth conditions (Grime 1973, Olsen et al. 2016). Species richness in adult plants fell precipitously with temperature, but only slightly in the seed rain and not at all in the seed bank (Table S2), supporting this interpretation.

Transient species were selectively removed during seedling emergence (Fig. 5, Table 1), but not selectively removed during seedling establishment (Fig. 5, Table S6). This was the opposite of our expectation of weak filtering during seedling emergence over the relatively warmer growing season months, and strong filtering during seedling establishment as emergents faced the chill and snowpack of winter. To investigate why this might be the case, we subdivided transient species by their putative climate origins at each site and examined seedling emergence rates of each group. We found that transient seeds from warmer, wetter, and unknown climates were driving the low emergence rates among transient species (Table 1). One possible explanation is that seeds from warmer and wetter conditions germinated prematurely, before conditions were amenable to survival. In support of this hypothesis, temperature is known to play a pivotal role in the release of 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). Likewise, a delayed spring in wetter places due to larger snowpack could also reduce the risk of early germination due to frost. Thus, immigrants from wetter and warmer sites may have been genetically predisposed to emerging before spring was safely underway. A complementary explanation for the observed differences in emergence rates between transient and persistent species is reflected in the systematic differences in their traits (Fig. 6). Most notably, seeds of transient species had smaller seeds than persistent species, a characteristic often associated with lower germination rates (Dalling et al. 2011, but see Shipley and Parent 1991, Bu et al. 2007).

*Predicting 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. If niche differences are weak, i.e., if species are effectively functionally equivalent, then climate change will not affect species distributions regardless of dispersal patterns. If niche differences are strong and linked to climate, then community responses to climate change could be swift, depending on species dispersal ability. That is, species able to disperse to optimal climate conditions will do so and thrive, and species that cannot – quickly enough – will be extirpated by more competitive species. Predicting community responses to climate change requires consideration both of dispersal patterns and climate-driven performance differences among species.

Although most seeds in the seed rain and seed bank were of putative local origin, transient species nonetheless occurred at all 12 of our sites (Fig. 3). The magnitudes and directions of these long-distance dispersal events shed light on how this grassland system is likely to respond to climate change. Southern Norway is expected to grow warmer and wetter as climate change progresses (Hanssen-Bauer et al. 2009). Maintenance of current climate conditions will require migration to cooler (upslope) and drier (more inland) locations. Our results suggest that few species disperse outside of their current climate ranges, and fewer still disperse outside of their current ranges towards cooler and drier sites. Of the 129 species with persistent adult populations at our sites, only 12 species (0.2 % of total seeds) dispersed into cooler ranges, and 18 species (1.8 % of total seeds) dispersed into drier ranges (Fig. 4, Table S4). Species with low seed production and/or small dispersal ranges – especially those that tend to reproduce vegetatively – will be the slowest to shift their ranges to track environmental change (Hampe and Petit 2005), and are most at risk of being extirpated should better-adapted species disperse into their local communities. Dispersal into cooler ranges was far less common than dispersal into warmer ranges, perhaps because seeds disperse more easily downslope than upslope, e.g., due to rainfall wash (Mermut et al. 1997) or seasonal variations in animal migrations, suggesting that range expansion into cooler sites may be particularly slow.

The observation that transient seeds from warmer and wetter climates emerged at lower rates than their locally-sourced counterparts (Table 1) illustrates how species climate preferences can modulate performance on local and regional scales. Although this result is not surprising given the broad-scale associations between plant species traits and climate (Wright et al. 2004, Reich 2014, Guittar et al. 2016), it is nonetheless instructive because it points to emerged seedlings as the life stage at which climate-vegetation associations are generated. Our results suggest that efforts to mitigate the negative effects of climate change through facilitating range shifts should focus on interventions that would increase the probability of successful emergence, rather than on facilitating seedling survival and establishment. A second, related result is the observation that seeds of transient species were disfavored more strongly at warmer temperatures than colder temperatures, illustrating how the process of local filtering itself varies with climate, and underscoring the need to consider climatic context when forecasting species responses to climate change.

A remaining question is why 96 transient seedlings, representing 24 locally-new species, had no locally persistent adult populations in the study sites. One possibility is that recent changes in the climate of southern Norway (Hanssen-Bauer et al. 2009) have already eroded performance differences between persistent and transient species, and these species will soon establish locally persistent adult populations, but this seems unlikely as it would only apply to transients from drier and warmer climates. Instead, transient species may arrive and establish in gaps, but be outcompeted by locally abundant, predominantly clonal species that encroach in on the disturbed area and smother any new seedlings. These transient species could be colonization specialists in a community mostly driven by competition (Levins and Culver 1971, Tilman 1994, Amarasekare and Nisbet 2001, Yu and Wilson 2001), and therefore only occur rarely and ephemerally. Regardless, the absence of these species in the adult vegetation highlights the potential importance of clonality and clonal traits when trying to understand grassland community dynamics. To this end, transient species had fewer buds, less persistent clonal connections, and a faster rate of lateral spread than persistent species, suggesting that these traits may put transients at a competitive disadvantage as vegetative adults.

Evidently, potential range expansions are constrained through a combination of dispersal limitation and differential performance during seedling emergence, but not differential performance during seedling establishment. Dispersal is limited among sites with different climates, especially into colder sites. Taken together, these findings point to the importance of processes operating in the very early plant life-history for species range dynamics, and also raise concerns that many species will be unable to track their preferred climates as climate change proceeds.

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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 on 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.

DATA ACCESSIBILITY

All raw data will be available on Dryad following publication.

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