Trait-based community assembly in a changing climate: Dispersal dynamics and ecological filtering in a grassland metacommunity.

By

John Lee Guittar

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Doctoral Committee:

Professor Deborah E. Goldberg (Chair)
Associate Professor Ines Ibáñez
Associate Professor Annette Ostling
Professor Vigdis Vandvik, University of Bergen

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Abstract

Research on plant community assembly often focuses on single life stages, or transitions between two life stages, and rarely integrates multiple life stage transitions into a more complete picture of the community assembly process. This is unfortunate because it limits our ability to assess the relative influence of each life stage transition on community assembly outcomes, and hence, predict community response to perturbations such as climate change. In this dissertation, I use observational and experimental evidence at different points in the plant life cycle to improve short- and long-term predictions of community response to climate change. I work in twelve grassland sites in southern Norway that fall along orthogonal gradients of temperature and precipitation, allowing me to disentangle the influence of these climate drivers.

I first combine seed, seedling, and adult plant survey data at the twelve sites to infer regional patterns of seed dispersal and immigration among climate zones. On average, 5 to 10 percent of seeds at a site putatively originated from different climates, suggesting significant connectivity among climate zones. However, immigrant seedlings were less likely to emerge and establish in experimental gaps than seedlings with locally-present conspecific adults, suggesting that a climate-based filters are in part responsible for maintaining regional vegetation patterns at the seedling stage. Despite the evidence for site connectivity, 66 of the 163 species in our system were not observed as immigrants at any point in the study, highlighting the potential for dispersal to limit species ability to track rapid changes in climate.

Second, I examine changes in species diversity and community-weighted mean trait values over plant life stages to characterize the strength and nature of ecological filtering at each life stage transition. Each surveyed life stage had fewer species than expected by chance, indicating that species sorting processes restricted community membership at multiple points of plant community regeneration. Furthermore, shifts in community weighted trait means suggest that different life stage transitions are influenced by qualitatively different mechanisms. The strength of filtering varied little with temperature and precipitation, suggesting that these stage-specific assembly processes are of broad relevance.

Third, I evaluate whether traits associated with regional temperature and precipitation patterns can predict community responses to rapid experimental climate change. To avoid the artifacts of *in situ* climate manipulation, 25 x 25 cm turfs of standing vegetation were transplanted to warmer and wetter sites. Changes in transplanted turf community composition were monitored over five years and compared to a field-parameterized null model. Three of the six traits with spatial associations to temperature predicted species success following transplantation. My results underscore the importance of using ecologically relevant traits when making predictions of community response, and suggest that in our grassland system, architectural traits may exert more influence on initial species response to rapid warming than the more commonly used growth-related traits.

This dissertation offers a much-needed empirical exploration of how regional dispersal dynamics, seed and seedling performance, and adult community response interactively shape patterns of plant community diversity. In addition, it demonstrates how species traits, when chosen for their potential mechanistic relevance to community assembly processes, can be valuable hypothesis generators. Future work on plant community assembly should consider plant life stages and relevant traits to refine predictions of community response to climate change.

Chapter 1. Introduction

Understanding and predicting plant community assembly is a longtime goal in ecology (Gleason 1926, Clements 1936, Keddy 1992, Chase 2003, Weiher et al. 2011) that has become increasingly urgent as we seek to predict community responses to anthropogenic global change. Despite decades of progress, we still lack the ability to accurately predict how plant communities will respond to perturbations, and determine where and when specific ecological processes will influence assembly outcomes. One reason why predictions are so difficult is that plant community assembly occurs gradually over multiple organismal life stages, with individuals beginning as seeds, dispersing, germinating, emerging as seedlings, surviving to adulthood, and sometimes reproducing vegetatively. At each life stage, individuals have different phenotypes and are thus subject to potentially different assembly forces. For example, organismal characteristics that influence seed germination (e.g., dormancy ability, maternal subsidy) differ from those that influence soil-based resource acquisition (e.g., mycorrhizal associations, rooting depth). Approaches that focus on patterns of relative abundances of adults in a community to infer assembly processes (Hubbell 2001, Cavender-Bares et al. 2004, Kraft et al. 2007) therefore effectively lump multiple life stage transitions into a single step, making it difficult to identify the key assembly mechanism(s) (Mayfield and Levine 2010) and the life stages at which they operate (Larson and Funk 2016). As such, subdividing the assembly process into life stage-specific components and examining them individually is one promising approach to advancing our mechanistic understanding of the assembly process and our predictions of community response to specific perturbations.

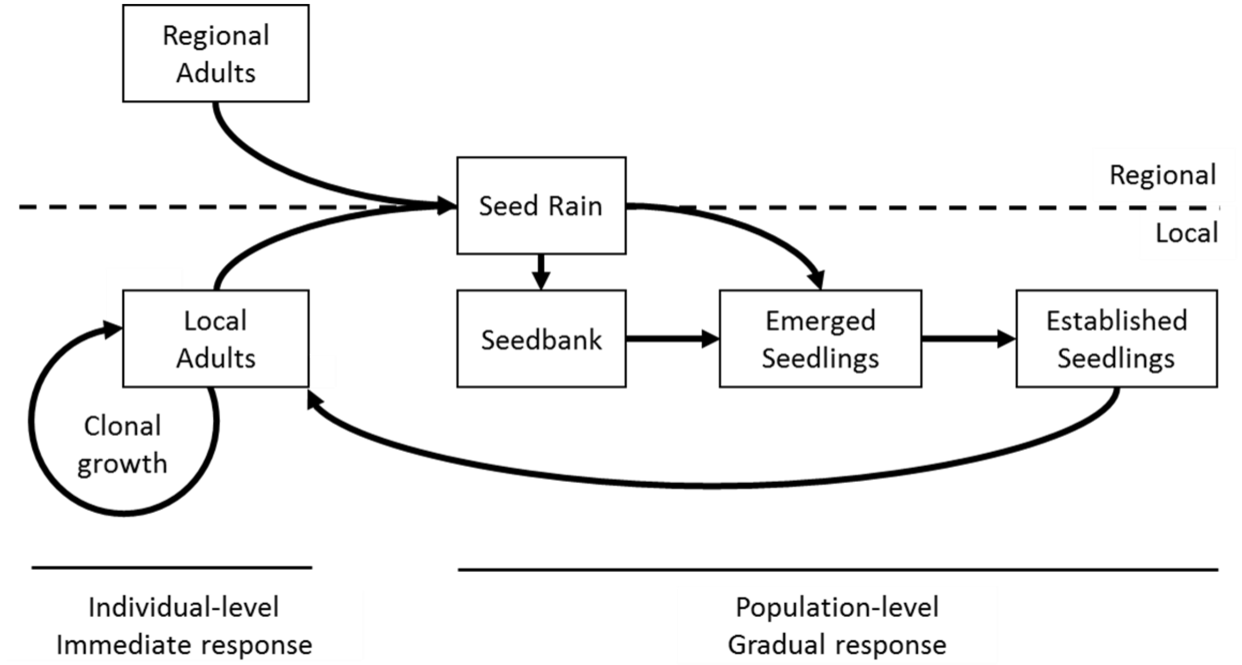

Figure 1.1. Conceptual diagram of plant life stage transitions and community assembly time scales.
A conceptual diagram showing transitions between the major plant life stages, and the time scales at which they are most likely to influence community assembly. Boxes above the dashed line denote transitions involving regional-scale dynamics, whereas boxes below the line denote transitions that occur primarily at local scales.

A second advantage to examining community assembly using individual plant life stages is that it allows for the consideration of different questions that may be relevant on different time scales (Figure 1.1). The initial effects of climate change on a grassland community, for example, will likely occur on the order of years and manifest primarily as shifts in the relative abundances of species already present in a community. In grasslands, new stems arise as vegetative growth from existing adults (i.e., are clonal offspring) far more often than as newly established seedlings (Herben et al. 2014), thus the near-term effects of climate change will likely from performance differences among adults. In other words, it is more pragmatic to focus on understanding the mechanisms underlying performance differences of adult plants – not seeds or seedlings –when modeling short-term community responses to climate change. Conversely, the long-term effects of climate change will include shifts in species ranges as populations track – or fail to track –

changes in climate. Seed dispersal and seedling establishment are prerequisites for successful immigration into new habitat, thus the analysis of regional dispersal patterns (seeds) and seedling performance are the most relevant life stages to focus on when trying to predict longer-term community responses to climate change.

In this dissertation, I use survey information on seed, seedling, and adult plant life stages to examine different components of the community assembly process, with an aim to improve predictions of vegetation responses to climate change at both short and mid-term timescales (Figure 1.1). I conduct my work in an experimental system of twelve diverse calcareous grasslands in southern Norway that is particularly well suited to disentangling multiple drivers of plant community assembly, especially climate. I frequently rely on the combination of plant community data and mean species trait values, as opposed to merely taxonomic identities, to better uncover the mechanisms underpinning plant community dynamics (McGill et al. 2006). The traits I use include four commonly measured plant traits and four less commonly used traits relating to clonal growth strategy. Clonal traits are often overlooked as indicators of plant performance, despite their widespread prevalence and potential significance for community dynamics and ecosystem function, especially in herbaceous plant biomes like grasslands (Zobel et al. 2010, Cornelissen et al. 2014). While I focus on plant communities, the methods I use and conclusions I draw should be applicable to other biological systems. I ask questions that can be grouped into four themes:

1. Patterns of seed production and seed dispersal (i.e., propagule connectivity) among climate zones as evidence for the potential for species to shift their ranges in response to climatic shifts over intermediate time scales (Chapter 2).
2. The relative strength and nature of ecological filtering (i.e., non-random species removal from the species pool) during seed dormancy (i.e., in the seed bank), seedling emergence, and seedling establishment (Chapter 3).

3. The short-term response of vegetation to rapid climate change primarily through changes in the relative abundances of locally present species via vegetative expansion (i.e., clonal growth of adults) or recession of individuals or genets (Chapter 4).
4. The use of species functional traits as proxies for plant performance to understand underlying mechanisms and predict community assembly outcomes. (Chapter 3, Chapter 4).

Each theme ties to different components of the plant life cycle (Figure 1.1), and is relevant to community dynamics operating on different temporal and spatial scales. Combined, this dissertation offers a much-needed empirical and *in situ* exploration of how regional dispersal dynamics, seed and seedling performance, and adult community response interactively shape patterns of plant community diversity.

Chapter 2. Habitat connectivity and immigrant persistence in a grassland metacommunity.[1]

Abstract

Despite well-established conceptual and experimental links between community assembly and dispersal, there are few *in situ* assessments of dispersal rates and immigrant performance at the community level, especially in plants. Here, we combine seed rain, seed bank, seedling emergence, and seedling establishment data from 12 grassland sites in southern Norway to characterize regional seed dispersal dynamics and evaluate the strength of local species sorting processes. The study sites fall orthogonally along temperature and precipitation gradients, enabling us to disentangle the effects of these important climate drivers on community assembly processes. We drew three significant conclusions from our seed dispersal analysis. First, immigrant seed numbers increased with temperature in the seed bank, but not in the seed rain, suggesting that immigrant seeds accumulated more readily under warmer conditions than seeds of local species. Second, immigrant species tended to be those with smaller leaves, smaller maximum height, and lighter seeds than local species, suggesting that species with these traits are favored for long-distance dispersal and/or persistence in the soil. Third, 66 of the 163 species in our system were never observed as immigrants, highlighting the potential for dispersal per se to limit species range shifts in response to changes in climate. In our analysis of seedling performance, we found

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immigrant species to be disfavored relative to local species at both seedling emergence and seedling establishment stages. The consistent disadvantage of immigrant species relative to local species illustrates how climate acts on community assembly processes by exerting direct or indirect species-specific effects on performance at multiple life stages; this implies that, as the rate and magnitude of climate change increase, climate-based filters could at some point favor immigrants over local species, hastening community response to climate change. Our study is a rare empirical examination of how regional seed dispersal dynamics and climate-mediated assembly processes interactively shape patterns of plant community diversity.

Introduction

Ecological communities assemble through the interaction of local and regional processes. Dispersal dynamics lie at the heart of this interaction because they are both a cause and consequence of community composition. Unsurprisingly, dispersal has been central to many important developments in ecological theory, including but not limited to the theory of island biogeography (MacArthur and Wilson 1967), metacommunity theory (Leibold et al. 2004), neutral theory (Hubbell 2001), succession theory and historical contingency (Gleason 1926, Chase 2003), and the competition-colonization life history tradeoff (Levins and Culver 1971, Tilman 1994). In conjunction with theoretical work on dispersal, experiments have validated the potential for dispersal to affect community composition. Propagule addition and exclusion experiments have, for example, illustrated that dispersal both limits diversity by not enabling species to reach suitable habitat, and enhances diversity by letting species persist in unsuitable habitat through source-sink dynamics (Vandvik and Goldberg 2005, Cadotte 2006).

Despite well-established conceptual and experimental links between community assembly and dispersal, there are few *in situ* assessments of dispersal rates and immigrant performance at the community level, especially in plants. 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 sidestep 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). The nearest-neighbor approach and its variations are valuable for their simplicity and minimal data requirements, but can be poor predictors of connectivity (Calabrese and Fagan 2004) and cannot distinguish between a lack of propagule arrival and a failure of propagule establishment.

The lack of quantitative *in situ* data on the arrival and performance of immigrants is unfortunate because it is critical to understand the extent to which communities are shaped by local ecological filters and/or regional dispersal dynamics (see Zobel 1997). Data on seed dispersal and immigrant dynamics would also improve our ability to accurately model and predict community dynamics, including community response to, e.g., habitat fragmentation and global climate change. Plant populations are already adapting and/or shifting their ranges in response to changing temperatures (Kudo et al. 2004, Post and Pedersen 2008), and will continue to do so as climate change proceeds. To predict species responses to climate change, we need to know the magnitudes and directions of dispersal over regional space, how local filters act on arriving propagules, and how that filtering process differs over environmental space. *In situ* data like these could also inform conservation strategies, including, for example, identifying when assisted migrations could be used to mitigate the risk of species extinctions.

Here, we determine the numbers, origins, and survival rates of seeds and seedlings across a network of 12 alpine grassland sites in southern Norway. The region is characterized by steep shifts in altitude and thus temperature, and a marked coast-to-inland rainfall gradient. This natural climate variability was used to establish a climate grid in which sites fall along orthogonal gradients of temperature and precipitation, enabling experiments that disentangle the influence of these climate drivers (Berge 2010, Boixaderas 2012, Meineri et al. 2014, Klanderud et al. 2015, Skarpaas et al. 2016, Olsen et al. 2016, Guittar et al. 2016). Our study has two main objectives. First, we infer immigration rates and hence dispersal patterns among communities and thereby assess the potential for species to shift their ranges to track future changes in climate. Second, we use seed and seedling data to explore how species pools and ecological filters interactively shape local community structure. Specifically, we ask:

1. In what directions and magnitudes does dispersal occur? Does immigration rate vary with climate? Do immigrant species differ from local species in their functional attributes, indicating the potential for dispersal-driven changes in community functional composition?
2. Can local species abundance, as a reflection of species suitability to the local environment, predict seedling emergence and establishment rates? Are seeds and seedlings of local species favored over immigrant species? If there is evidence of a filter acting differentially on immigrants, does the strength of filtering vary over plant life stages, or with climate?

To answer these questions, we combine seed rain, seed bank, seedling emergence, and seedling establishment data to identify patterns of dispersal and seedling performance. Like most perennial grasslands, seedling recruitment in our system is highly dependent on disturbances and occurs only rarely under the closed canopies of established clonal genets, presumably due to strong negative competitive effects from adult plants (Silvertown and Smith 1989, Eriksson 1989, Bullock et al. 1995, Berge 2010). As such, we monitor seedlings in experimental gaps where seedlings 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. Data were gathered over a two-year period and therefore offer a snapshot of community assembly dynamics.

Methods

Study area

The study area comprises 12 calcareous grassland sites in southern Norway that host at least 181 non-woody vascular plant species (169 species in this study; 62 ± 13 species per site). Sites have similar land use histories, slopes of ~20°, and southwest aspects, but differ in their mean summer temperature and/or mean annual precipitation such that they form a grid with orthogonal climate axes (Figure 2.1). See Klanderud et al. (2017) 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 (Astroturf) that were placed in vegetation gaps in each of the five blocks delineated at each site, for a total of 60 seed traps. The small synthetic filaments in artificial turfs are effective at catching and holding small particles like seeds, and are easy to clean and transport. 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, with help from the reference collection at the Biology Department at University of Bergen. We included fruits, bulbils (*Bistorta vivipara*) and viviparous seeds (*Festuca vivipara*), but not spores, in our working definition of 'seeds' or 'propagules', terms we use interchangeably. For additional details and analysis of seed rain, see Boixaderas (2012).

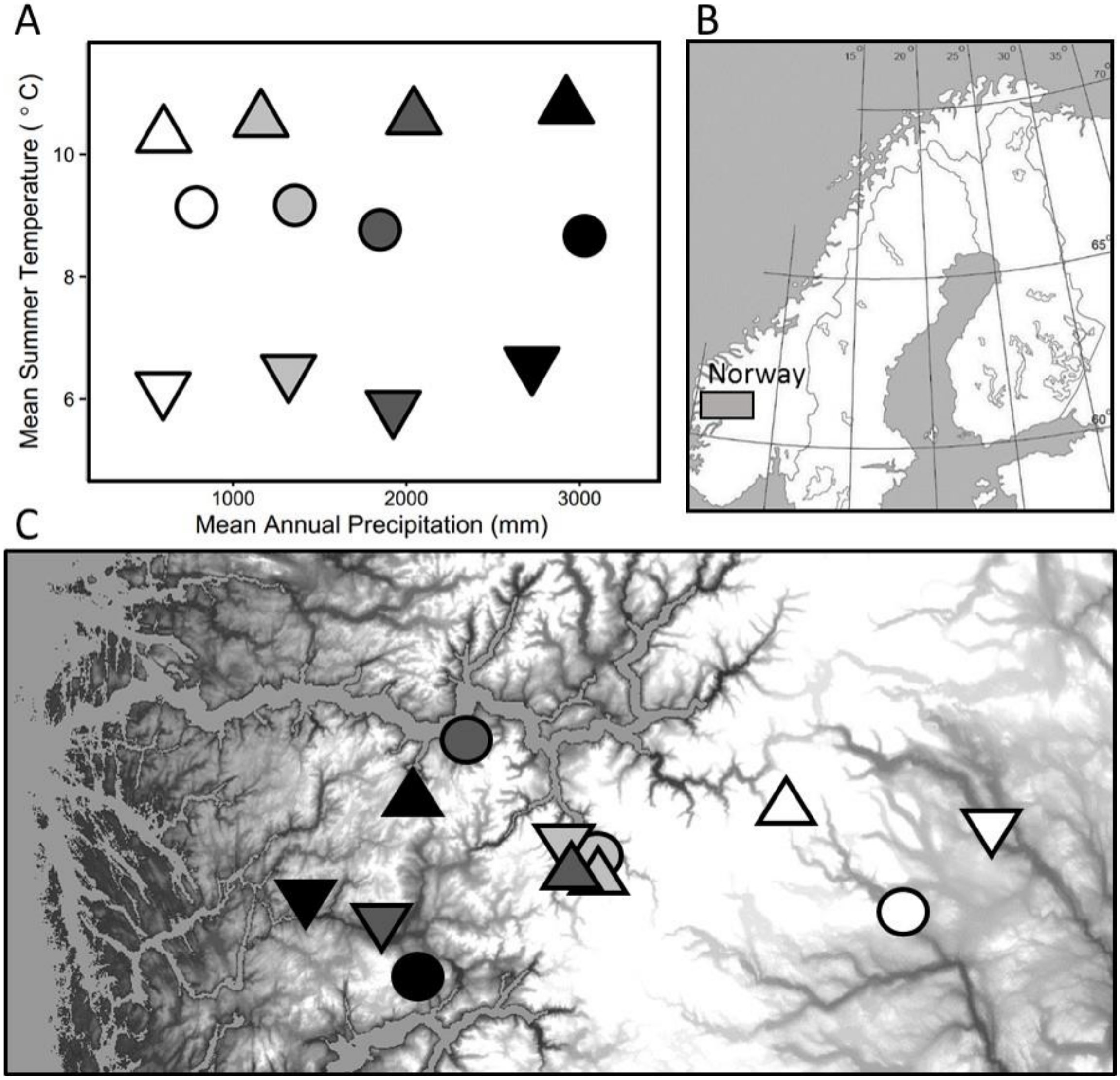

Figure 2.1. Site locations and mean climates, in greyscale.
Panel A shows mean summer temperature and mean annual precipitation values at the twelve sites. Panels B and C show the sites' locations in southern Norway.

Seed bank data

To characterize seed bank diversity we haphazardly selected one 64 x 64 cm plot at each site in 2008 and excavated soil to a depth of 3 cm. Because the sampled area (~0.41 m^2) was larger than the surveys for other plant life stages (five 25 x 25 cm plots; ~0.31 m^2), we divided all seed bank species abundances by ~1.31. To avoid sampling transient seeds and recent seed rain, we removed all aboveground vegetation, including the moss layer and the litter layer, before sampling in

September and October. We stored soil samples for three months at 2 – 4 °C and ambient moisture and then passed them through a 40-mm sieve to remove vegetation and debris. We 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. Bryophytes and woody species were discarded and excluded from analyses. For additional details and analysis of seed bank data, see Vandvik et al. (2015).

Seedling data

Five 25 x 25 cm gaps were created in each of the five blocks 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 % of seedlings, most of them graminoids, were either unidentifiable or died before they could be identified and were therefore lumped into a single generic group (“sp”), and were excluded from all analyses involving species identities. We carefully differentiated new seedlings from new clonal ramets originating from nearby adult plants, which were not recorded, by looking for cotyledons or signs of above- or below-ground connections. Seedling survival and establishment was recorded twice yearly from spring 2010 to spring 2012. Graminoid seedlings were considered established if they returned the following year at the same coordinate position, and forb seedlings were considered established when they had at least two non-cotyledon leaves and plant height exceeded 2 cm. We approximated seedling emergence rates by dividing the density (per m^2) of emerged seedlings by the sum of seed rain and seed bank densities at both site and species levels. Bryophytes and woody species were noted but excluded from this analysis. Nomenclature for seedlings and other taxonomic identifications follows Lid and Lid (2007). For additional details and analysis of seedling censuses see Berge (2010) and Klanderud et al. (2017)..

Mature vegetation data

We conducted community surveys of mature vegetation at peak biomass (July and August) in 2009. At each site, we visually estimated the percent cover of all species in five 25 x 25 cm plots with the aid of a 5 x 5 cm grid overlay. We conducted five censuses at each site for a total of 60 plot censuses. Bryophytes and woody species were noted but excluded from this analysis. Percent cover estimates were used in place of individual counts because identifying individuals in our primarily clonal system is difficult and not necessarily demographically meaningful. 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. Species leaf area and specific leaf area (SLA), 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 ~1200 leaves collected in summer 2012, for which SLA and leaf area were calculated using established protocols (Cornelissen et al. 2003). Seed mass, 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 potential canopy height data, a trait that is related to competitive ability for light and seed dispersal ability (Westoby 1998, Falster and Westoby 2003), were mined from Lid and Lid (2007). All traits were $\log_{10}$-transformed and are shown in Table B-1. See Guittar et al. (2016) for additional information on assembling the species trait data used here.

Assigning immigrant climate origins

We assumed seeds to be immigrants when adult conspecifics ("conspecifics" hereafter) were locally absent. While it is possible that some seeds were tagged as immigrants even though conspecifics were present at the site, but outside of the survey area and/or laying dormant during the surveys, this was probably rare, and thus it is less likely that these low abundance populations are the seed sources. We assigned immigrant origin based on where conspecifics were found relative to local conditions. Specifically, we assumed similar temperature and/or precipitation origins if conspecifics were observed elsewhere at those climates, or if conspecifics were recorded in both directions along climate gradients (i.e., same temperature and/or both warmer and cooler; same precipitation and/or both wetter and drier). If conspecifics were observed only at warmer, cooler, wetter, or drier sites, we assumed that these immigrants came from warmer, cooler, wetter, or drier conditions, respectively. Seeds without any recorded conspecifics were considered of "unknown" non-local origin. We used climate dissimilarity to define immigration "distance" rather than spatial distances between sites for two reasons. First, most species occur in many communities within the study region, so distances among study sites are not faithful proxies for dispersal distances. Second, we wanted to assess species' ability to move along climate gradients, and climate dissimilarity is a better measure of this than geographic distance.

Statistical approach

We initially test for baseline trends in total seed and seedling numbers, irrespective of species identity, along temperature and precipitation gradients using multiple linear regression. For all other statistical tests, we use species-level abundances at sites as the unit of analysis. We evaluate predictors of seedling emergence, i.e., the number of emerged seedlings offset by the number of conspecific seeds found at the site, with a two-component hurdle model. The 'hurdle' component uses a binomial regression to model zero counts, i.e., whether *any* seedlings of given species emerges or not at a site, and the second component uses a zero-truncated negative binomial regression with a log link to model non-zero numbers of emerged seedling number at a site. The same predictors are used for both model components. Because we were interested in modeling emergence as a proportion of available seeds, we removed instances when seedling number exceeded seed number. (We also tried treating these instances as emergence probabilities of 1; i.e. as if all present seeds emerged, but results were nearly identical, so the former method was used for simplicity.) We model emerged seedlings g for species i at site j as

$$g_{ij} \sim \text{offset}(\log(s_{ij})) + a_{ij} + \text{MAP}_j + \text{MST}_j + o_{ij},$$

where s_{ij} is the abundance of seeds (seed rain and seed bank) of species i at site j, a_{ij} is the relative abundance of adults of species i at site j (as a proxy for habitat suitability), o_{ij} is a factor indicating the putative origin of the seed (local, immigrant from a similar temperature/precipitation, or immigrant from a different temperature/precipitation), and MAP_j and MST_j are the mean annual precipitation and mean summer temperature at site j, respectively.

We model predictors of seedling establishment with a negative binomial GLM. The number of established seedlings e for species i at site j is modeled as

$$e_{ij} \sim \text{offset}(\log(g_{ij})) + a_{ij} + \text{MAP}_j + \text{MST}_j + o_{ij},$$

where the log of the number of emerged seedlings g of species i at site j serves as an offset, and a_{ij}, MAP_j, MST_j, and o_{ij} represent the same values as defined in the seedling emergence model.

Results

Baseline patterns

Our data comprised 16593 seeds (103 species) from seed rain traps, 29232 seeds (adjusted down from 37939 seeds due to a larger sampling area; 117 species) from seed bank samples, 2938 seedlings (84 species) from experimental gaps, 1049 (64 species) of which established successfully (Table 2.1, Table 2.2), and 5492 percent cover units (137 species) of adult vegetation from 60 plot surveys. Seedling densities, irrespective of species identities, correlated with seed rain densities ($\rho = 0.82$) but not seed bank densities ($\rho = 0.18$) (Table A-1). Mean seedling emergence rate among sites for the 2009 seedling cohort, based on the sum of seed rain and seed bank densities, was 10 ± 4 %. Mean seedling establishment rate across all sites was 30 ± 14 %. Thus, the mean probability of a seed germinating was 3 ± 2%. We found only two significant climate-based trends in our baseline survey data. First, seed rain density increased with temperature (Figure 2.2,Table A-2). Second, adult species richness decreased with temperature (Figure A-1). Species relative abundances at sites were weakly correlated among plant life stages, except for a correlation between emerged seedlings and established seedlings ($\rho = 0.77$) (Table A-3). Most notably, there was little correlation between species abundances in the seed bank and seed rain ($\rho = 0.16$), and seeds (seed rain and seed bank combined) and seedling number ($\rho = 0.32$) (Table A-3, Figure A-2).

Table 2.1. Numbers and putative origins of seeds and seedlings.

	Seed Rain		**Seed Bank**		**Emergents**		**Established**	
All Sources								
Local Site	16368	(99%)	26400	(90%)	2801	(95%)	1011	(96%)
Immigrant	249	(1%)	2832	(10%)	144	(5%)	39	(4%)
Immigrant Sources Only, by Temperature								
Same Temperature	171	(69%)	1586	(56%)	86	(60%)	35	(90%)
Cooler	10	(4%)	456	(16%)	41	(28%)	1	(3%)
Warmer	20	(8%)	216	(8%)	3	(2%)	1	(3%)
Unknown	48	(19%)	574	(20%)	14	(10%)	2	(5%)
Immigrant Sources Only, by Precipitation								
Same Precipitation	149	(60%)	2080	(73%)	116	(81%)	31	(79%)
Drier	33	(13%)	63	(2%)	6	(4%)	2	(5%)
Wetter	19	(8%)	115	(4%)	8	(6%)	4	(10%)
Unknown	48	(19%)	574	(20%)	14	(10%)	2	(5%)

Percentages are rounded to the nearest whole number and consequently do not always sum exactly to 100 within plant life stages. “Emergents” and “Established” refer to emerged seedlings and established seedlings, respectively.

Evidence for connectivity

We found evidence for widespread but modest connectivity among sites via seed dispersal. Immigrant seeds (i.e., seeds without local conspecifics) occurred in all 12 grassland sites, comprising 1 % of the seed rain and 9 % of the seed bank overall (Table 2.1, Figure 2.2). On average, sites had 3 ± 2 immigrant species in the seed rain (of 29 ± 6 total species) and 12 ± 4 immigrant species in the seed bank (of 40 ± 7 total species) (Table 2.2). Absolute and relative abundances of immigrant seeds increased with temperature in the seed bank but not in the seed rain (Figure 2.2).

Combining seed rain and seed bank data, about two thirds of immigrants originated from (i.e., had conspecifics at) sites with similar temperature or precipitation conditions (Table 2.1). Immigrant seeds originated from all directions along climate gradients (cooler, warmer, wetter, drier) in roughly similar numbers (Table 2.1), although there was considerable variation among sites (Table A-4). Usually, immigrant seed communities were dominated by one or a small handful of species, and then had a long tail of low-abundance species (Figure A-4). Immigrants represented 5 % (129 individuals) of emerged seedlings and 4 % (30 individuals) of established seedlings (Table 2.1), illustrating that seeds not only arrived from other sites but also successfully established, albeit in low numbers for individuals from other climates, and with considerable variation among sites (Table A-5). Trait values between immigrant and local species differed consistently across sites (Figure 2.3). In particular, immigrant species in the seed bank were shorter and had significantly smaller leaves than non-immigrant species. There was borderline statistical support ($P = 0.062$) for a lower mean seed mass among immigrants relative to local species.

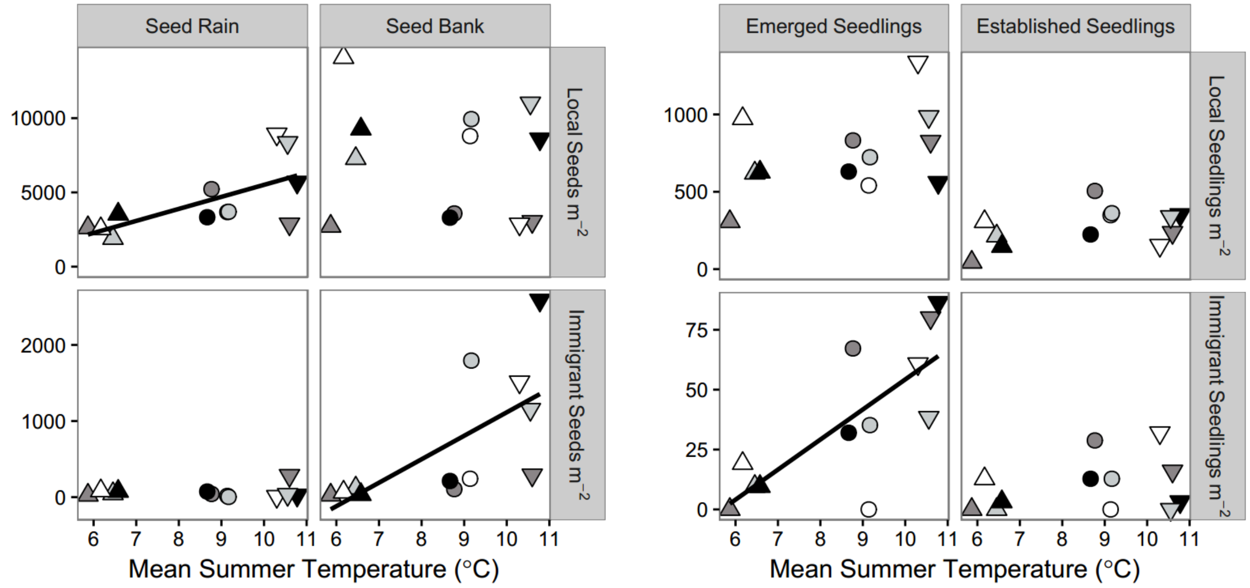

Figure 2.2. Seed and seedling abundances grouped by immigrant status.
Seed and seedling abundances per m^2, grouped by immigrant status. Each point represents data from one site. "Local" seeds have local conspecific adults, whereas "immigrant" seeds do not. Shapes and shadings are consistent with those shown in Figure 2.1, and reflect approximate mean summer temperatures of 6 °C (triangle), 9 °C (circle), and 10.5 °C (inverted triangle) and approximate annual precipitations of 650 mm (white), 1300 mm (light grey), 2000 mm (dark grey), and 2900 mm (black). Regression lines are shown when significant ($p < 0.05$). We detected no statistically significant relationships with precipitation.

Table 2.2. Seed and seedling densities and species richness values by stage.

***Group*, Life stage**	**Density**	**Site Richness**	**Regional Richness**
All Individuals			
Seed Rain	80485	28 ± 6	103
Seed Bank	93130	39 ± 6	117
All Seeds	173615	49 ± 8	143
Emerged Seedlings	24735	20 ± 5	84
Established Seedlings	8480	14 ± 4	64
Seeds and Seedlings	-	52 ± 8	145
Adults	-	47 ± 16	137
All Stages	-	63 ± 13	163
Immigrants Only			
Seed Rain	3048	3 ± 2	29
Seed Bank	8147	12 ± 4	73
All Seeds	11195	14 ± 4	89
Emerged Seedlings	3348	4 ± 2	29
Established Seedlings	677	2 ± 1	14
Seeds and Seedlings	-	16 ± 4	97

Values are site-level means ± 1.0 standard deviation. Densities reflect individuals per sq. m. Site N = 12. Adult vegetation was measured as percent cover units, rather than individuals, so adult density is omitted because it could not be determined.

Evidence for filtering

We found statistical support for non-random species sorting (i.e., selective removal) of immigrants, but no evidence that the magnitude of filtering differed consistently with climate. Immigrant species were less likely to emerge (i.e., had an emergence probability of zero), especially immigrants from other temperatures (Table 2.3, Figure 2.4 left panel) and precipitations (Table A-6). Among species with at least one emerged seedling at a site, immigrant species from other precipitations (Table A-6), but not immigrant species from other temperatures (Table 2.3, Figure 2.4 center panel), had significantly lower emergence rates than local species. Conversely, immigrant species from other temperatures (Table 2.3, Figure 2.4 right panel), but not immigrant species from other precipitations (Table A-6), had higher probabilities of establishment than local species. Overall, including species climate origins improved model performance (i.e., had higher AIC values) over null models without these predictors. Interaction terms involving immigrant status and climate variables were never significant and were dropped from the final models.

Discussion

Our study offers empirical evidence for the dispersal, emergence, and establishment of immigrants in small, but significant, numbers across grassland communities in southern Norway. We found the magnitude of seed immigration to increase with temperature, and that species with smaller leaves and lighter seeds disperse long-distance more often than expected by chance. In other words, habitat connectivity was evidently modulated by both climate and species traits in our grassland metacommunity system. While we found seedlings of immigrant species less likely to emerge and establish than seedlings of local species, immigrants nonetheless contributed to local site species richness, highlighting immigration as an important process for the maintenance of diversity.

Our study offers mixed prospects for grassland species responses to rapid climate change. On one hand, evidence for a non-random species-specific ecological filter implies that, following a large shift in climate, immigrant species could be favored over local species for survival. On the other hand, the wide range in observed species dispersal abilities indicates that many species could be limited by dispersal *per se* in their ability to track rapid changes in climate. Our study is a rare empirical examination of how regional seed dispersal dynamics and local climate-based ecological filters interactively shape patterns of plant community diversity.

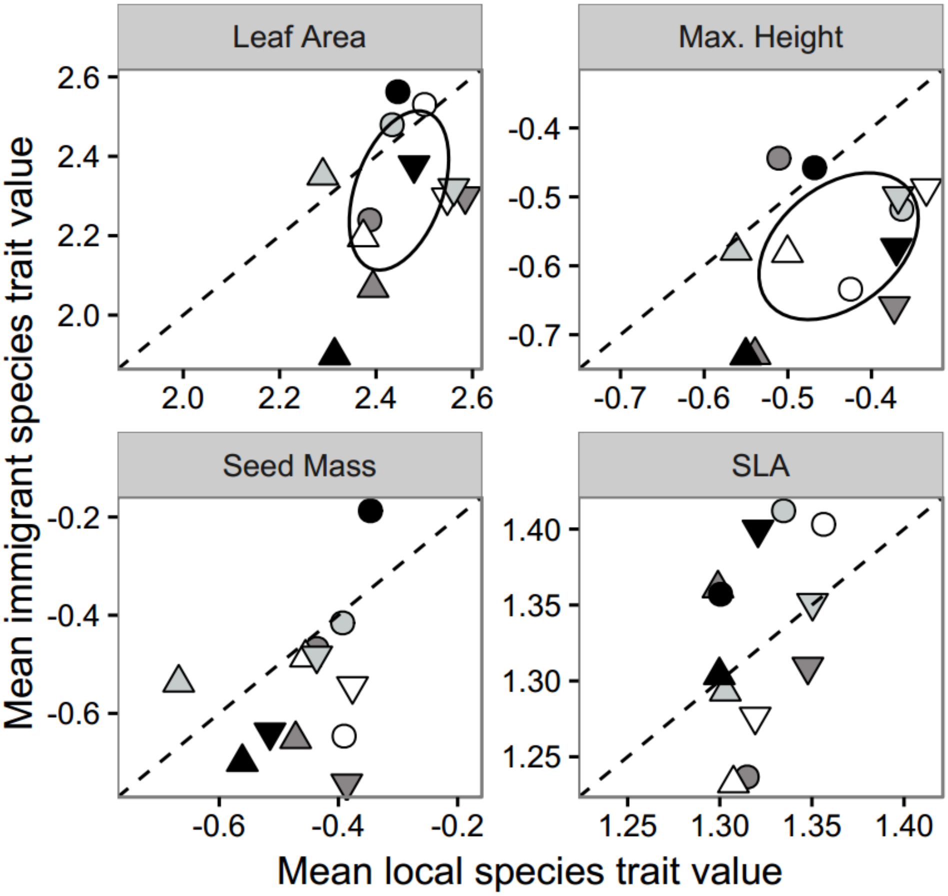

Figure 2.3. Mean trait values of local versus immigrant species in the seed bank. Mean trait values of local seed species vs. immigrant seed species at the 12 sites in this study. Shapes and shadings are consistent with those shown in Figure 2.1, and reflect approximate mean summer temperatures of 6 oC (triangle), 9 oC (circle), and 10.5 oC (inverted triangle) and approximate annual precipitations of 650 mm (white), 1300 mm (light grey), 2000 mm (dark grey), and 2900 mm (black). The dotted line denotes a 1:1 relationship. Ellipses with 50 % confidence intervals are shown when paired t-tests between immigrant status groups are statistically significant ($p < 0.05$). Immigrant N ranged from 6 - 20; local N ranged from 14 - 37. Similar analyses of seed rain and seedling communities were not possible due to low species richness (Table 2.2). Trait means were calculated irrespective of species abundances because we were interested in which immigrant species were arriving, not their relative rates of arrival. SLA refers to specific leaf area.

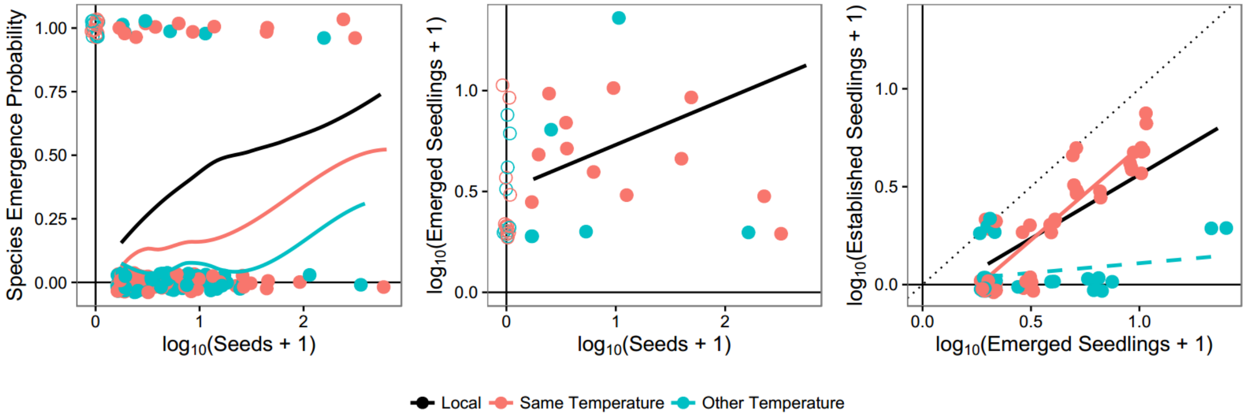

Figure 2.4. Probabilities of species emergence, seedling emergence, and seedling establishment, grouped by species and seed origin.

Numbers of emerged seedlings (left and center panels) plotted by seed number, and established seedlings (right panel) plotted by number of emerged seedlings. Each circle represents one species at one site, and seed number is equal to the sum of seeds in the seed rain and seed bank. Circles are jittered on both the x- and y-axes to improve visibility. All count data are increased by one to enable plotting zeroes on a log scale. Seeds are “Local” when adult conspecifics occur at the site. Non-local seeds originate from the “Same Temperature” when adult conspecifics occur at one or more of the sites with similar mean annual temperatures (see Figure 2.1), or from an “Other Temperature” when they do not. In the left panel, solid lines show a LOESS smoothing function reflecting the change in mean species emergence probability with seed density; species with no seed representatives were excluded from the calculation. In the center and right panels, solid lines reflect significant ($p < 0.05$) regression coefficients. Black regression lines were fitted to local species data, but local circles were removed to reduce clutter. See Figure A-3 for a version of this figure without local data omitted.

Table 2.3. Summary statistics for emergence and establishment models, using temperature-based origins.

Model, Variable	Estimate	St. Dev.	z-statistic	P-value
Emergence: Zero Hurdle (Offset by # Seeds)				
Local Abundance	0.004	0.011	0.365	0.715
Temperature	-0.024	0.075	-0.316	0.752
Precipitation	-0.252	0.151	-1.665	0.096
Immigrant (Same temp.)	**-1.376**	**0.557**	**-2.469**	**0.014**
Immigrant (Other temp.)	**-2.466**	**0.836**	**-2.949**	**0.003**
Emergence: Count (Offset by # Seeds)				
Local Abundance	0.002	0.007	0.282	0.778
Temperature	-0.109	0.071	-1.531	0.126
Precipitation	-0.007	0.160	-0.042	0.967
Immigrant (Same temp.)	-0.337	0.746	-0.451	0.652
Immigrant (Other temp.)	-12.688	107.984	-0.117	0.906
Establishment Count (Offset by # Emerged)				
Local Abundance	0.005	0.003	1.498	0.134
Temperature	0.033	0.038	0.881	0.379
Precipitation	-0.015	0.080	-0.189	0.850
Immigrant (Same temp.)	0.085	0.255	0.332	0.740
Immigrant (Other temp.)	**-1.770**	**0.634**	**-2.791**	**0.005**

Bold denotes variable significance. Emergence is modeled using a two-step zero inflated hurdle model (see Methods). Climate variables are centered at zero. Model intercepts are set to local species values.

Dispersal patterns and potential community responses to climate change

While most seeds in the seed rain and seed bank were of local origin, immigrants nonetheless arrived at all 12 of our sites, comprising about 6 % of all seeds. The magnitudes and directions of long-distance seed dispersal inferred from our study have implications for how this grassland system is likely to respond to climate change. Southern Norway is expected to become warmer and wetter as climate change proceeds (Hanssen-Bauer et al. 2009). As such, species will need to migrate to cooler (upslope) and drier (more inland) locations to maintain their current climate associations. Of the 163 species in our study, the 28 that dispersed to cooler and/or drier communities (data not shown) are the least likely to be limited by dispersal *per se* in their ability to track future climate changes. Conversely, 66 species were never observed as seeds or seedlings outside of the sites in which they occurred as adults, and 18 of those species had no seed or seedling representatives whatsoever (Table 2.2). Such species with low seed production, small dispersal ranges, or those that reproduce primarily through clonal outgrowth will be least able to shift their ranges to track environmental change (Hampe and Petit 2005). Seeds also dispersed into warmer and wetter communities (Table 2.1), illustrating that dispersal does not only occur in one direction due to prevailing winds or precipitation runoff, and that at least some species will be able to disperse into more climatically favorable communities regardless of how climate change proceeds.

For a species to shift its range, individuals must not only disperse to new communities but also emerge and establish there. Our analysis highlights some of the contingences facing seedling establishment. First, as in many other grasslands (Eriksson 1989, Bullock et al. 1995, Kalamees and Zobel 2002), seedling establishment in our system is highly dependent on disturbance. In a concurrent study in our experimental system, Berge (2010) found established seedling density to be 12 times greater in gaps than in undisturbed vegetation plots ((Klanderud et al. 2017). Traditionally, a common source of disturbance in southern Norwegian grasslands has been the hoof actions of browsing sheep, cows, and goats. These disturbances create microsites free from the competitive effects of established adults, and also provide opportunities for dormant seeds buried in deeper soil strata to germinate and emerge as seedlings (Olff and Ritchie 1998). Free-range domestic grazers have grown scarcer in southern Norway since the 1950s (Staaland et al. 1998), potentially lowering the disturbance rate and therefore the maintenance of grassland diversity and the ability for grasslands to change compositionally in response to environmental changes (Maarel and Sykes 1993, Bullock et al. 1994, 1995, Gross et al. 2005, Ejrnaes et al. 2006).

Mass effects from local populations can also limit immigrant seedling establishment. If local-origin seeds vastly outnumber immigrant seeds, and establishment is contingent on prior arrival rather than competitive ability, then local populations will preemptively occupy all suitable microsites (Leibold et al. 2004). However, if establishment is governed by niche-based competitive ability, and environmental conditions favor immigrants (e.g., due to a new climate regime), then species ranges will rapidly shift to track optimal climate conditions. We found several lines of evidence suggesting that recruitment was at least partially determined by climate-based niche differentiation rather than by a strictly species-neutral lottery model. First, seed density and seedling number were weakly correlated at the species level (Table A-3) which is inconsistent with a recruitment process that operates as random draws from the seed pool. Second, immigrant species had lower probabilities of emergence than local species and immigrant seedlings were less likely to establish than local seedlings (Table 2.3, Figure 2.4 left panel, Figure 2.4 right panel), both of which suggest climate-mediated niche-based performance differences. Third, broad-scale community trait values associate with climate (Guittar et al. 2016), supporting the existence and community-level influence of climate-based niches. On the other hand, seedling emergence and establishment rates varied within species (i.e., intraspecifically among sites), and among species (Figure A-2, Figure A-3), suggesting that climate-based niche differences may have been relatively weak (i.e., potentially overridden by species-neutral processes) and/or that community assembly was guided by other unexplored deterministic processes. Community dynamics in other grasslands are thought to arise from a balance of niche and neutral processes (Maarel and Sykes 1993, Hubbell 1997, Gravel et al. 2006, Weiher et al. 2011). A future direction of work could be to quantify the relative influence of niche and neutral processes at our sites, and how this relationship varies with climate and spatial scale (see Chase 2014).

Connectivity and diversity maintenance

Our results also bear on questions surrounding the role of dispersal in maintaining local and regional diversity. Intermediate levels of connectivity among communities are known to maximize local and regional diversity in a metacommunity framework (Cadotte and Fukami 2005, Cadotte 2006). We saw that immigrant seedlings emerged at ten sites (29 added species; 5 % of total seedlings) and established at eight sites (14 added species; 4 % of total established seedlings) (Table 2.1, Table 2.2), increasing site-level species richness in our study system.

True seed exchange rates among communities were no doubt higher than we estimated (~6 % of seeds) because seeds arriving from other sites that nonetheless have local conspecific adults are not identified as immigrants, making our dispersal estimates conservative. Community-weighted trait means of incoming propagules were significantly lower in leaf area, maximum height, and, to a lesser extent, seed mass (Figure 2.3), highlighting how immigration alters local species pools in terms of functional composition as well as taxonomic composition. Our results corroborate experiments showing local species richness to increase with seed pool diversity (Myers and Harms 2009), but go further by providing explicit *in situ* estimates of the contribution of natural immigrants to local diversity (also see Vandvik and Goldberg 2006).

Thinking of grasslands in southern Norway as a network of interconnected patches may not be the most appropriate conceptualization of regional diversity dynamics. Metacommunity theory is designed, in part, to understand and account for the effects of distance on local and regional diversity independent of environmental conditions. In our study, however, marked regional climatic heterogeneity allows us to focus on how environmental differences among sites structure diversity in addition to spatial distance. Moreover, grassland habitat in southern Norway, like in many other places, is not always divided into discrete patches separated by uninhabitable space, as is assumed by traditional metacommunity theory. As such, it may be more productive to think of connectivity as a system property that affects beta diversity patterns at the landscape scale. Likewise, environmental conditions like temperature and precipitation vary continuously along spatial gradients at different scales, affecting beta diversity by altering the strength and nature of abiotic filters in space. Considering dispersal dynamics within an overlapping mosaic of communities with variable levels of habitability may be a more realistic model of regional diversity than a traditional metacommunity model.

Seed bank versus seed rain

Despite the fact that seed banks comprise prior seed rain cohorts, considerable differences in their compositions are not unusual (Drake 1998, Edwards and Crawley 1999, Kalamees and Zobel 2002). Such discrepancies can offer insight into regional dispersal dynamics and variation in species dormancy characteristics. For example, our finding that immigrants in the seed bank significantly outnumber those in the seed rain (Figure 2.2) has at least three possible explanations. First, seed rain composition may vary over time, harboring in some years more immigrants than in others. In opposition to this, seed rain in other calcareous grasslands has exhibited little variability between years (Maarel and Sykes 1993, Willems and Bik 1998). Second, adult populations of seed species in the seed bank may have been locally extirpated in recent years, leading to the seeds being tagged as immigrants from other sites when in fact they are more appropriately thought of as immigrants in time (Harper 1977, Weiher et al. 1999). It seems unlikely that the combination of seed dormancy and local species turnover is responsible for all the immigrants we observed, especially given that most species in our study system are perennial and long-lived, but more work is needed to properly evaluate this hypothesis. Lastly, immigrant seeds may persist in the soil more often than local seeds, either through lower germination rates, higher survivorship, or increased dormancy capabilities. We found immigrant species to have consistently different trait values than local species (Figure 2.3), supporting the potential for functional differences to underlie performance differences between the two groups. Research has shown that smaller seeds disperse greater distances and are more likely to be buried (Thompson et al. 1993), supporting this hypothesis. Regardless of the mechanism, the seed bank clearly serves as an important reservoir of biodiversity in our system (Vandvik et al. 2016).

Curiously, the proportion of immigrants in the seed bank rose nearly twentyfold from the coldest (highest altitude) to warmest (lowest altitude) sites (Figure 2.2). This trend was not due to dispersal occurring primarily from colder to warmer communities (e.g., due to seeds traveling downslope due to gravity, wind, or water drainage), because most immigrants originated from communities with similar temperatures (Table 2.1). Likewise, the increase in immigrants at higher temperatures is not driven by shifts in mean seed mass values, which could influence dormancy dynamics, as seed mass does not vary along temperature gradients in our system (Guittar et al. 2016). Instead, as hypothesized above, seed bank immigrants could be more common at warmer temperatures because more local adult populations have been extirpated due to competitive exclusion, resulting in more seeds being tagged as immigrants. Local species richness dropped significantly with temperature among adult plants, but not in seeds or seedlings in gaps, supporting this hypothesis. Alternatively, species distributions may simply be patchier at the plot scale (e.g. due to patchier resources, larger individuals, and/or more pronounced niche-based competition), leading to more gradual species-area accumulation curves, a less complete list of local species, and therefore an overestimation of immigrants. A third possible explanation is that there is simply more seed exchange among grasslands at the warmest temperatures, although we see no obvious mechanism for such a trend.

Environmental filtering of seed species pools

Our analysis of seedling performance is a reminder of the importance of treating community assembly as a multi-stage process. More specifically, immigrant species were selectively removed at the seedling emergence stage regardless of their putative climate origin, while immigrant species were selectively removed at the seedling establishment phase only if they originated from communities with different temperatures (Figure 2.4). Tentatively, these results suggest that there is a more discerning ecological filter operating on emerging seedlings than establishing seedlings. However, we hesitate to draw conclusions on the relative strength and nature of filtering over life stages due to the low numbers of established seedlings. The high mortality rate of seedlings in our system (~70 %) makes it difficult to make strong statistical inferences at the seedling establishment stage.

The emergence and establishment of 677 immigrant seedlings (14 species) further illustrates the temporal and spatial dynamism of community assembly in our grassland system. Specifically, it raises the question of why species capable of arriving and establishing in gaps – sometimes in significant numbers – have no local adult populations. One possibility is that these immigrant species exist in the seed bank but only emerge in gaps, and are quickly outcompeted as locally abundant, predominantly clonal species encroach on the disturbed area. In this case, immigrants could be considered representatives of the colonization side of the competition-colonization tradeoff (Levins and Culver 1971, Tilman 1994, Amarasekare and Nisbet 2001, Yu and Wilson 2001). A second possibility is that niche-based performance differences exist but are minor, and that high species turnover occurs through a combination of microsite dispersal limitation and effective functional equivalence (Maarel and Sykes 1993). Third, recent changes in the climate of southern Norway (Hanssen-Bauer et al. 2009) may have allowed immigrant species that were previously unable to persist in local conditions to arrive and establish. However, the latter hypothesis seems likely only to apply to immigrants originating from drier and warmer climates.

Conclusions and future directions

Community response to climate change will depend both on the degree to which species are capable of tracking environmental changes through dispersal to appropriate sites as their home sites grow less habitable, and on the degree to which species niche differences lead to performance differences in different environments. If niche differences are weak, i.e., if community dynamics are effectively neutral, then climate change will have minimal effects on species distributions regardless of species dispersal patterns. If niche differences are strong and linked to climate, then community responses to climate change will potentially be swift and strongly dependent on species dispersal ability. That is, species able to disperse to their optimal climate conditions will do so and thrive, whereas species that cannot (quickly enough) will be locally extirpated by more competitive species.

Our study provides evidence for non-random species sorting, but also suggests this filter is highly stochastic and thus may be of secondary importance in driving community assembly.

Two limitations of our study also highlight promising future directions of research. First, the method we use to identify immigrants was conservative because it only caught immigrants “in the act.” That is, because our operational definition of an immigrant was an individual without local conspecific adults, we missed immigrants with local conspecifics, including any with adult populations sustained by mass effects (Leibold et al. 2004). Characterizations of dispersal patterns for all species, including those with local adult populations, would greatly improve our understanding of potential community response to climate change. To this end, population genetic techniques should be used to build spatially explicit dispersal kernels for a handful of representative species, and the results of these used to parameterize models of regional vegetation dynamics (Broquet and Petit 2009).

A second limitation to our study was that we used emergence probabilities as a function of seed number to quantify species performance. Ideally, population-level measures of reproductive investment and return should be used as measures of species performance. For example, it is not necessarily meaningful to compare seedling emergence probability in a species that produces a large number of low-investment low-viability seeds with a species that produces a small number of high-investment seeds with large maternal subsidies. Unfortunately, assessing demographic rates of plant populations with long life spans, clonal reproduction (i.e., ambiguous population units), prolific seed production, and a wide range of dormancy capabilities is difficult. This is not to say that analyses of individual performance are not important; they shed light on community assembly processes, such as disturbance and colonization dynamics. However, additional work is needed to connect individual-level processes to their population-level consequences (Suding et al. 2003).

Our analysis is based on the assumption that the climate will change, and ignores the reality that the global climate has already changed and species have already shifted their ranges in response (Lenoir et al. 2008). That our results found immigrant species to be disfavored relative to local species suggests that climate change has not advanced to the point where immigrants are favored relative to local species. In other words, we find no evidence for a lag in community response to climate change, as has been hypothesized in other systems (Bertrand et al. 2011). Detailed studies such as ours are critical assessments of the state of systems vis-à-vis climate change, and important explorations of the processes underlying the vegetation shifts likely to occur in the coming decades.

Acknowledgements

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Chapter 3. Life stage matters: trait-based assembly of seeds and seedlings along climate gradients[2]

Abstract

Community assembly research often focuses on single life stages, or transitions between only two life stages, and rarely integrates multiple life stage transitions into a more complete picture of the community assembly process. This is unfortunate because it limits our ability to identify the relative influence of each life stage transition on community assembly outcomes, and hence, make accurate predictions of community response to perturbations. Here, we compare species- and trait-based community metrics across seed, emerged seedling, established seedling, and adult life stages in a montane grassland to gain a fuller picture of the seed-to-adult assembly process. We identify non-random transitions by comparing observed stage transitions to neutral predictions that assume all individuals are equally likely to survive to the subsequent stage. We found significantly fewer species than predicted for all life stage transitions, indicating that species are removed non-randomly throughout the community regeneration process. Community weighted mean trait values differed significantly from neutral model predictions in four of 16 trait-life stage comparisons, highlighting a role for trait-based abiotic filtering or competitive hierarchies in our system. Our results suggest that all life stages must be considered when modeling community assembly or forecasting community responses in our grassland system.

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[2] Will be submitted for publication as Guittar, J., D. Goldberg, K. Klanderud, A. Berge, M. R. Boixaderes, E. Meineri, J. Töpper, and V. Vandvik. Life stage matters: trait-based assembly of seeds and seedlings along climate gradients. *Journal TBD.*

Introduction

Understanding and quantifying the drivers of plant community assembly is an abiding challenge in ecology. Ideally, long-term demographic data would be used to test specific ideas relating to the maintenance of diversity or mechanisms of coexistence. However, many plants have long lifespans and offspring that are difficult to track and monitor, so ecologists instead often rely on patterns to infer process. As a result, a common approach to identifying non-random assembly processes is to compare the structure of observed communities with neutral models that simulate assembly by drawing from a regional species pool and assuming functional equivalence among species (Weiher and Keddy 1995, Hubbell 2001, Götzenberger et al. 2012, de Bello 2012). Hubbell (2001), for example, showed that tropical forest species abundance curves were similar to those predicted by neutral models assuming functional equivalence and dispersal limitation, although non-neutral explanations for the pattern were later discussed (Alonso et al. 2006). Additional insight into the mechanisms of assembly can be gained by comparing the distribution of individuals' trait values in observed and simulated communities, assuming that individual performance and therefore community dynamics are functions of species traits (Violle et al. 2007). Generally, abiotic filtering is thought to constrain the range of potential trait values in a community, leading to trait patterns that are more clustered than expected by chance. Biotic filters are thought to then remove any species from the resulting pool that are inferior competitors, causing trait patterns to become less clustered (overdispersed) than expected by chance due to limiting similarity and resource partitioning (MacArthur and Levins 1967, Cornwell et al. 2006, Petchey and Gaston 2006, Kraft et al. 2007, Kraft and Ackerly 2010, Weiher et al. 2011).

This basic conceptual framework seems to hold true in some cases (Weiher et al. 2011), but theoretical and empirical work shows it can also sometimes lead to erroneous conclusions. For example, trait values can be clustered in a community when individuals compete for a limiting resource that cannot be partitioned (e.g., heights of plants in competition for light, as would result from "competitive hierarchies" *sensu* Herben and Goldberg 2014) and in response to classical abiotic filtering (e.g., the filtering out of species with thin, tender leaves in drought-prone habitats) (Mayfield and Levine 2010, Herben and Goldberg 2014). Conversely, trait overdispersion can result both from classical limiting similarity processes (e.g., beak size for Darwin's finches; Grant and Grant 2006)) and abiotic filtering if multiple microenvironment conditions filter for disparate trait optima within a single community. Interpretation of community trait patterns can also be difficult if a single trait is implicated in multiple assembly processes. For example, the distribution of specific root length (SRL) values in a community is influenced both by interspecific competition for a shared resource (e.g., water) and plant anchorage (Comas et al. 2013, Kramer-Walter et al. 2016). These potential pitfalls are why it is advisable to validate tentative conclusions about assembly mechanisms with targeted experiments (McGill et al. 2006, Weiher et al. 2011).

While experiments are the best way to unambiguously connect process with pattern, they are not always possible. A strategy to mitigate the risk of misinterpreting community trait patterns is to subdivide assembly into components and examine each component individually (Larson and Funk 2016). Treating assembly as a dynamic sequence of processes that unfolds over individuals' lives rather than as a single process with a single outcome (e.g., clustered traits implies abiotic filtering) reduces the probability that a trait pattern was shaped by multiple processes over prior life stages and therefore the probability that it is difficult to interpret. In addition, examining assembly over individual life stage transitions is one way to integrate research on the formation of species pools (i.e., dispersal dynamics) with research on the roles of ecological filters in structuring local biodiversity (Myers and Harms 2009). Furthermore, life-stage specific analyses can also inform when and where community composition is most susceptible to perturbations or changes in assembly drivers. Plant communities are good study systems for such an approach because they have well-defined life stages, transitioning consistently from seeds, to emerged seedlings, to established seedlings, to adults. Even though many individual studies have characterized ecological filtering (i.e., biotic and/or abiotic filtering) between pairs of plant life stages, few studies have combined more than two life stage transitions with the aim of characterizing assembly as a sequence of processes (Welling et al. 2004, Vandvik and Goldberg 2006, Aicher et al. 2011, Myers and Harms 2011), and none to our knowledge have used traits to quantitatively characterize changes in functional community composition over life stages.

Here, we compare the compositions and structures of montane grassland communities over seed, emerged seedling, established seedling, and adult life stages to gain a fuller picture of the seed-to-adult assembly process. We compare observed community metrics to neutral model expectations derived from data on the immediately prior life stages. In doing so, we look for non-random trait-mediated assembly processes at each stage, rather than simply comparing adult community composition to neutral model simulations built from local and/or regional species pools, as is commonly done. For our study system, we use survey data from twelve montane grasslands in southern Norway. The natural climate variability in the region was used previously to establish a climate grid in which sites fall along orthogonal gradients of temperature and precipitation, enabling experiments that disentangle the influence of these climate drivers (Berge 2010, Boixaderas 2012, Meineri et al. 2014, Klanderud et al. 2015, Skarpaas et al. 2016, Olsen et al. 2016, Guittar et al. 2016). Therefore, we are also able to evaluate how the strengths of non-random assembly processes change with climate. Specifically, we ask:

1. To what extent are species being filtered non-randomly during community assembly? How does strength of filtering vary over plant life stages?
2. Are there differences in community trait patterns over plant life stages, and can these differences help us identify the mechanisms driving community assembly?
3. How does the strength and nature of filtering vary with climate? How will climate change affect the community assembly process?

To identify the strength of and nature of transitions between each pair of life stages, we compare species- and trait-based metrics to neutral expectations. To generate our neutral models, we use adult communities to predict seed rain and seed bank communities, seed communities to predict emerged seedling communities, and emerged seedling communities to predict established seedling communities. A trait-based approach is particularly advantageous when exploring life stage transitions because it reduces the risk of incomplete sampling. That is, because species can be functionally redundant and/or because traits reduce the dimensionality of diversity, less sampling depth is required to characterize the functional structure of a community than to characterize the taxonomic structure of a community. We use four commonly used traits known to influence grassland dynamics (Kalamees and Zobel 2002, Newton et al. 2012, Jung et al. 2014, Guittar et al. 2016). Namely, two traits indicative of resource use strategy (leaf area, specific leaf area), one trait related to competition for light and dispersal ability (maximum height), and one trait correlated to seedling survival and seedling growth rate (seed mass).

We hypothesize that abiotic filters will increase the similarity (i.e., increase the degree of clustering in trait values) of species as communities transition from seeds to emergent seedlings, as those that cannot survive the local abiotic environment die off. We predict that high seed mass, low SLA species will be less abundant in the seed bank and seed rain, but more likely to emerge and establish as seedlings. To conclude, we frame our results in the context of a changing climate, and speculate how our system is likely to respond as the climate in the region grows warmer and wetter in the coming decades.

Methods

Study area

The study area comprises 12 calcareous grassland sites in southern Norway home to at least 163 non-woody vascular plant species (62 ± 13 species per site). Sites have similar land use histories, slopes of ~20°, and southwest aspects, but differ in their mean summer temperature and/or mean annual precipitation such that they form a grid with orthogonal climate axes (Figure 3.1). See Klanderud et al. (2015) for additional on site selection and site characteristics.

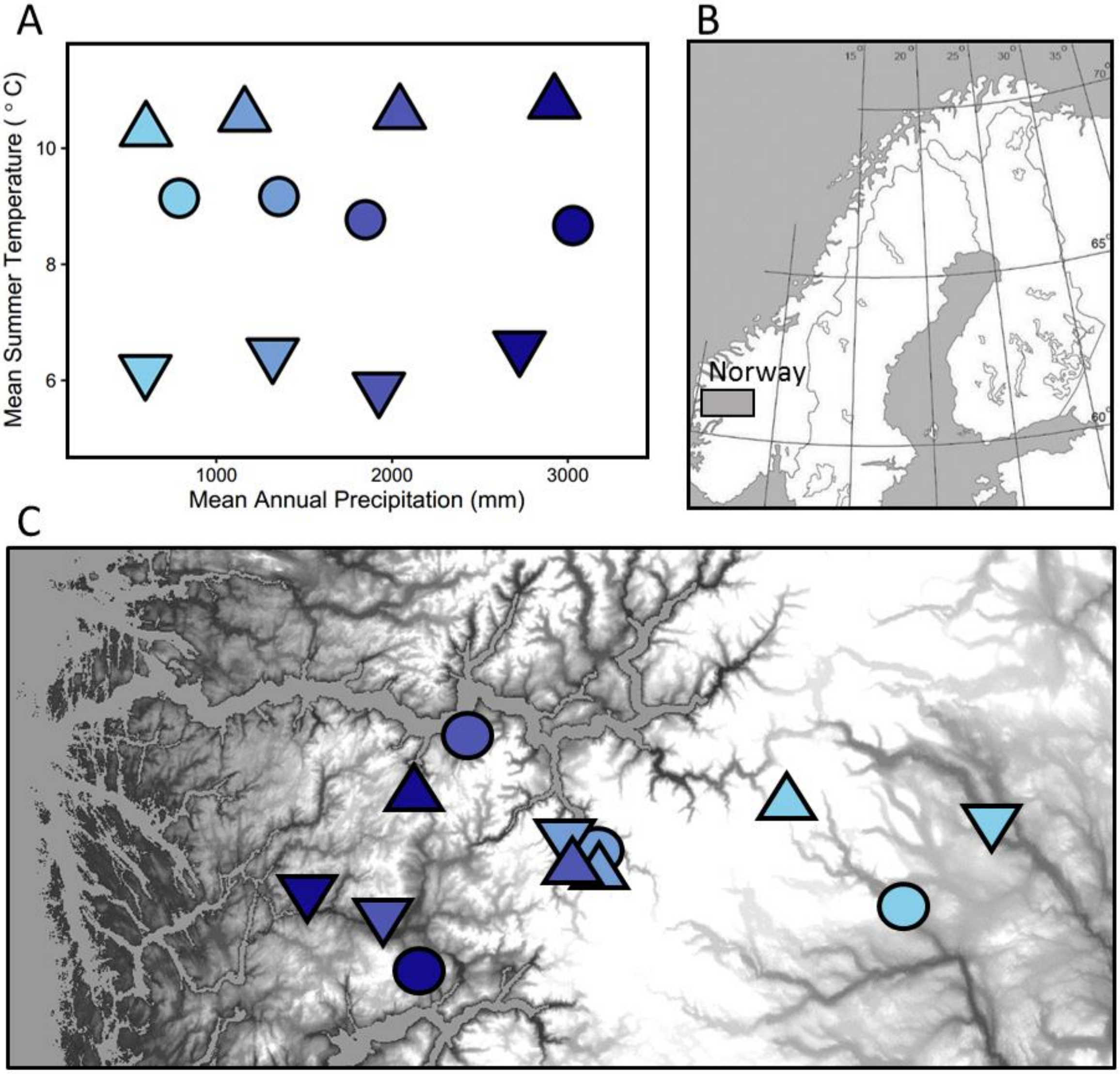

Figure 3.1. Site locations and mean climates, in color.
Panel A shows mean summer temperature (shape) and mean annual precipitation (color) values at the twelve sites. Panels B and C show site locations in southern Norway.

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 (Astroturf) that were placed in vegetation gaps in each of the five blocks delineated at each site, for a total of 60 seed traps. The small synthetic filaments in artificial turfs are effective at catching and holding small particles like seeds, and are easy to clean and transport. 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, with help from the reference collection at the Biology Department at University of Bergen. We included fruits, bulbils (*Bistorta vivipara*) and viviparous seeds (*Festuca vivipara*), but not spores, in our working definition of 'seeds' or 'propagules', terms we use interchangeably. Nomenclature for seeds, seedlings, and adults follows Lid and Lid (2007). For additional details and analysis of seed rain see Boixaderas (2012).

Seed bank data

To characterize seed bank diversity we haphazardly selected one 64 x 64 cm plot at each site in 2008 and excavated soil to a depth of 3 cm. Because the sampled area (0.41 m2) was larger than the surveys for other plant life stages (five 25 x 25 cm plots; 0.31 m2), we divided all seed bank species abundances by 1.31. To avoid sampling transient seeds and recent seed rain, we removed all aboveground vegetation before sampling and sampled in August, a period after seed germination but before most dispersal. We stored soil samples for three months at 2 – 4 °C and ambient moisture and then passed them through a 40 mm sieve to remove vegetation and debris. We 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 with 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. (2015).

Seedling data

Five 25 x 25 cm gaps were created in each of the five blocks 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 % of seedlings, most of them graminoids, were not considered for any species or trait-based analyses. We carefully differentiated new seedlings from new clonal ramets originating from nearby adult plants, which were not recorded. Seedling status was updated twice yearly through spring 2012 to record survival and establishment rates. Graminoid seedlings were considered established if they returned the following year at the same coordinate position, and forb seedlings were considered established when they had at least two non-cotyledon leaves and plant height exceeded 2 cm. We approximated seedling emergence rates by dividing the density of emerged seedlings by the sum of seed rain and seed bank densities at both site and species levels. For additional details and analysis of seedling censuses see Berge (2010) and Klanderud et al. (2017).

Mature vegetation data

We conducted community surveys of mature vegetation at peak biomass (July and August) in 2009. At each site, we visually estimated the percent cover of all species in five 25 x 25 cm plots with the aid of a 5 x 5 cm grid overlay. We conducted five censuses at each site for a total of 60 plot censuses. Percent cover estimates were used in place of individual counts because identifying individuals in our primarily clonal system is difficult and not necessarily demographically meaningful. For additional details and analysis of mature vegetation patterns see Klanderud et al. (2015) and Guittar et al. (2016).

Trait data

We used a previously compiled custom database (Guittar et al. 2016) with values for up to four commonly measured plant traits (leaf area, mm^2; specific leaf area (SLA), m^2/kg^{-1}; maximum potential canopy height, m; seed mass, mg) for the 163 identifiable species in our experimental system. Data for woody species, non-vascular plant species, and unidentifiable individuals were excluded from all analyses. Six groups of difficult-to-distinguish (at any life stage) congeners were lumped into single categories (*Epilobium spp.*, *Euphrasia spp.*, *Hieracium spp.*, *Pyrola spp.*, *Sagina spp.*, *Taraxacum spp.*), and the average trait values of their constituent species were calculated and used. Leaf area and SLA were estimated using a combination of field data and data from the LEDA online trait database (Kleyer et al. 2008). Maximum potential height data were mined from Lid and Lid (2007). We drew seed mass data from the Seed Information Database (SID) (Royal Botanic Gardens Kew 2014). All trait values were log-transformed. Data on traits represented 125 – 144 of the 163 species in our study system and 93% to 99% of individuals, depending on the trait and life stage (Table 3.1). For the species list and trait values see Appendix B. While some species-level traits were significantly correlated, Pearson correlations were never greater than 0.50 (Figure B-1), thus traits were analyzed individually.

Table 3.1. Numbers of species and proportions of individuals for which there is trait data, by life stage.

Stage	Leaf Area	SLA	Max. Height	Seed Mass	Species	Individuals
Mature	119 (0.97)	125 (0.97)	132 (0.99)	124 (0.96)	137	5637
Seed Rain	96 (0.97)	98 (0.97)	100 (0.99)	96 (0.93)	103	16593
Seed Bank	91 (0.98)	98 (0.98)	101 (0.99)	97 (0.98)	117	21569
Seeds	114 (0.97)	122 (0.98)	126 (0.99)	120 (0.96)	143	38162
Emergent	79 (0.94)	79 (0.94)	82 (0.99)	78 (0.94)	84	2938
Established	59 (0.94)	59 (0.94)	62 (0.99)	59 (0.94)	64	1049

The numbers of species with trait data, with the proportion of individuals with trait data in parentheses. The species and individuals columns show the total species richness and abundance by stage across sites.

Community metrics and statistical approach

We characterize community diversity using species richness and the Shannon index (Spellerberg and Fedor 2003). Community weighted means (CWMs) were used to quantify differences in functional composition (Ricotta and Moretti 2011). A CWM is calculated by averaging the values of a trait for all species in a community, weighted by species abundances; percent cover was used as a measure of abundance when calculating CWMs for mature vegetation; numbers of individuals were used as the measure for abundance for other stages. We use the Rao coefficient to characterize the spread of trait values around the mean, i.e., as a coarse measure of over-dispersion or clustering (Ricotta and Moretti 2011). Rao reflects the mean pairwise trait difference between individuals in a community. We use multiple linear regression to identify and quantify significant relationships with mean summer temperature and mean annual precipitation.

We test for non-neutral community assembly by comparing the diversity and functional compositions of observed communities to those of neutral model simulations. Neutral models work by randomly drawing individuals from a pool built using survey data from prior life stages, where the number of draws is equal to the size of the community being simulated. In other words, the neutral expectation is that all individuals are equally likely to transition to subsequent life stage (i.e., are functionally equivalent). For seed rain and seed bank simulations, we draw from a pool built using mature vegetation survey data (percent cover units were treated as individuals); for emerged seedling simulations, we draw from a pool built using combined seed rain and seed bank survey data; for established seedling simulations, we draw from a pool built using emerged seedling survey data. We stop short of completing the life stage cycle (i.e., building a neutral expectation of adult community composition) because the diversity of established seedlings in our two-year snapshot is far below the local diversity of adults. We perform 100 neutral model simulations per life stage per site.

Previous work with these data estimated immigrants to comprise 10% of seeds in the seed bank and 1% of the seeds in the seed rain (Guittar et al., Chapter

2). It was thus necessary to account for immigration in our neutral model simulations of seed bank and seed rain communities. To do this, we drew a fraction of individuals from an immigrant pool reflecting the net community compositions of adult plants at the other three sites in our study system with similar mean summer temperatures (Figure 3.1). We restricted immigrant origins to communities with similar temperatures because more than 60% of immigrants are likely to originate from these conditions (Figure 2.2). The numbers of individuals drawn from local and immigrant pools varied by site according to the putative numbers of local and immigrant individuals observed in seed bank and seed rain communities Table A-4. To assess whether our inclusion of immigration influenced our results, we removed immigrants from seed bank and seed rain communities and repeated the analyses. We found no qualitative differences and therefore report analyses that account for immigration.

Results

Diversity measures

We observed significantly fewer species than predicted by our neutral model at all life stages suggesting strong species sorting processes at work across our study system (Figure 3.2). Averaged across sites, there were 19 ± 10 (1 S.D.) fewer species than predicted in seed rain and seed bank communities, 24 ± 7 fewer species than predicted in emerged seedling communities, and 5 ± 3 species fewer than predicted in established seedling communities. However, when seed rain and seed bank data were pooled, deviations from neutral expectations were less. Differences between observed and predicted species richness varied considerably across sites. The magnitude by which species richness was below predictions in seed bank, seed rain, and emerged seedling communities decreased with increasing temperature (Figure 3.3). Shannon diversity was significantly lower than predictions in seed bank, seed rain, and emerged seedling communities, but not different in established seedling communities (Figure 3.2) and did not trend with temperature or precipitation (Figure 3.3).

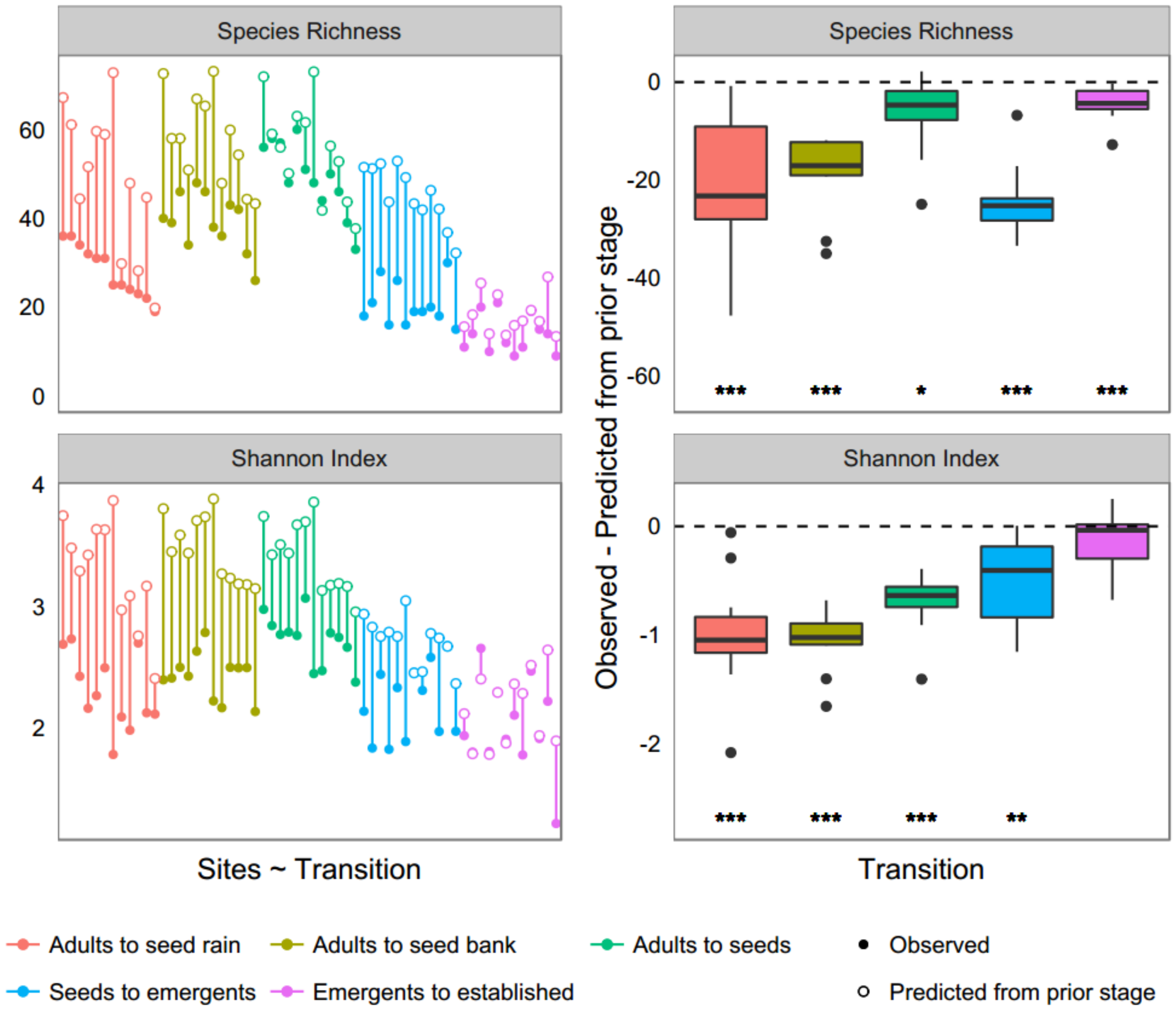

Figure 3.2. Stage-specific diversity metrics versus neutral expectations. *At left*, differences between predicted (open circles) and observed (closed circles) species richness (top) and Shannon Index values (bottom) plotted at the site level over four plant life stages transitions. Sites are ordered by decreasing observed species richness in the leftmost 'Adults to seed rain' life stage transition. *At right*, boxplots of the differences between observed species richness (top) and Shannon Index values (bottom) and those predicted by neutral models assuming equal transition probabilities for individuals in the prior stage. Seed rain, seed bank, and overall seed predictions assume equal seed production and dispersal from adults; seedling emergence predictions assume equal probability among all seeds in the seed bank and seed rain; seedling establishment predictions assume equal probability among emerged seedlings. Community diversity metrics are calculated at the site level (N = 12). Dashed lines show where observed and predicted values would be equal. Asterisks denote significance (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The lower and upper limits of the colored boxes correspond to the first and third quartiles, respectively, and whiskers extend to the highest and lowest values within 1.5 times the first and third quartiles, respectively. Data beyond the whiskers are outliers and plotted as filled circles.

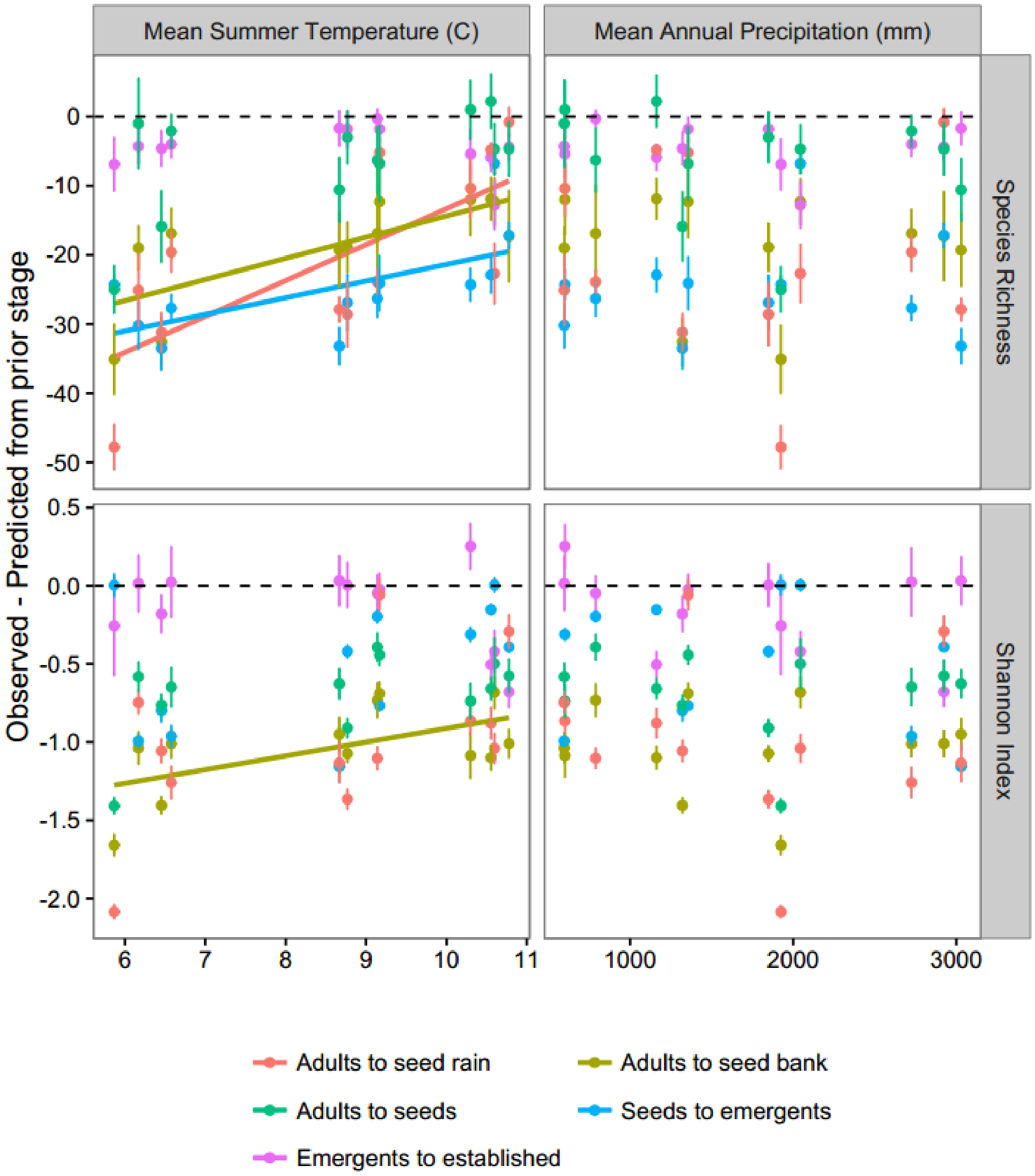

Figure 3.3. Differences between observed diversity metrics and neutral expectations, plotted by temperature.

Scatter plots showing the differences between observed species richness (top) and Shannon index values (bottom) and those predicted by neutral models assuming equal transition probabilities for individuals in the prior stage. Filled circles show data for four plant life stages transitions, plotted by mean summer temperature (left) and mean annual precipitation (right). Seed rain, seed bank, and overall seed predictions assume equal seed production and dispersal from adults; seedling emergence predictions assume equal probability among all seeds in the seed bank and seed rain; seedling establishment predictions assume equal probability among emerged seedlings. Neutral models were run 100 times per site per transition per trait (N = 100). Error bars reflect ± 2.0 S.D. of neutral model predictions for that site. Dashed lines show where observed and predicted values would be equal. Colored lines show when regressions with site mean summer temperature are significant ($P < 0.05$).

CWMs and trait distributions

Community weighted mean (CWM) trait values differed significantly from neutral model predictions in four of 16 trait-life stage comparisons (Figure 3.4), highlighting a role for trait-based abiotic filtering or competitive hierarchies in our system. Differences in the strength and direction of these deviations stands as empirical evidence for the sequential nature of community assembly over plant life stages. Specifically, species with smaller leaves were more common in seed rain communities than predicted, species with smaller leaves and smaller seeds were more abundant in seed bank communities than predicted, and species with lower maximum height were more common in emerged seedling communities than predicted. CWMs of established seedlings did not differ consistently from neutral model predictions, suggesting that the traits we measured played a minor or inconsistent role in mediating the transition from emerged seedlings to seedling establishment. Differences in observed and predicted CWMs trended with temperature in only a few cases (Figure B-2), the most significant of which was a decrease in the degree to which leaf area was smaller than neutral expectations. Trends in the difference of observed and predicted CWMs with precipitation were modest to absent.

The dispersions of community trait values, as measured by the Rao coefficient, differed consistently and significantly from neutral model predictions in four of 16 trait-life stage comparisons (Figure B-3). Seed mass values were more clustered (less dispersed) than expected by chance in the seed rain, but less clustered (more dispersed) than expected by chance in the seed bank. Clustering in SLA among emerged seedlings was greater than expected by chance. Less dramatic but still significant was a decrease in clustering of maximum height values relative to neutral model predictions. We saw three trends in the deviation of clustering relative to neutral expectations with temperature (Figure B-4). These included a less clustering (i.e., more overdispersion) in leaf area in the seed rain at the coldest temperatures than expected by chance, and more clustering (i.e., less overdispersion) in leaf area among emerged seedlings at the coldest temperatures.

In both cases, the degree of clustering was similar to neutral expectations at intermediate and warm temperatures. Clustering in SLA increased among emerged seedlings with precipitation, relative to neutral expectations.

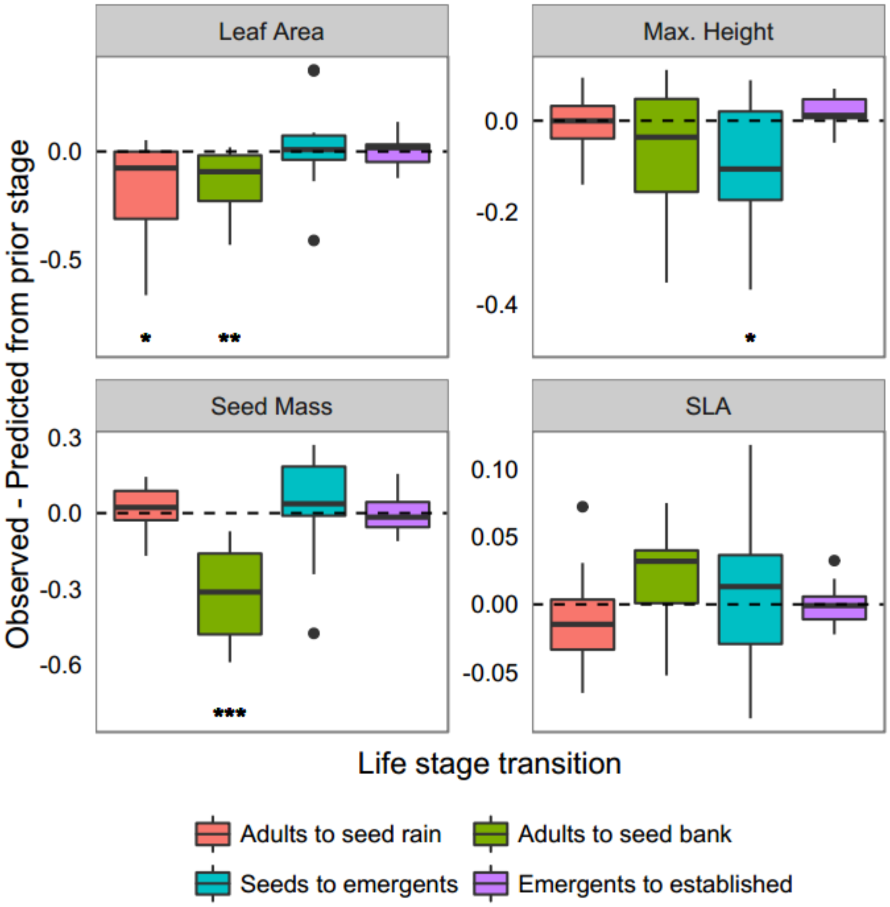

Figure 3.4. Stage-specific community trait means versus neutral expectations. Boxplots of the differences between observed abundance-weighted trait means and those predicted by neutral models assuming equal transition probabilities for individuals in the prior stage. Seed rain and seed bank predictions assume equal seed production and dispersal from adults; seedling emergence predictions assume equal probability among all seeds in the seed bank and seed rain; seedling establishment predictions assume equal probability among emerged seedlings. Community trait metrics are calculated at the site level (N = 12). Dashed lines show where observed and predicted values would be equal. Asterisks at bottom of panels denote significance *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The lower and upper limits of the colored boxes correspond to the first and third quartiles, respectively, and whiskers extend to the highest and lowest values within 1.5 times the first and third quartiles, respectively. Data beyond the whiskers are outliers and plotted as filled circles.

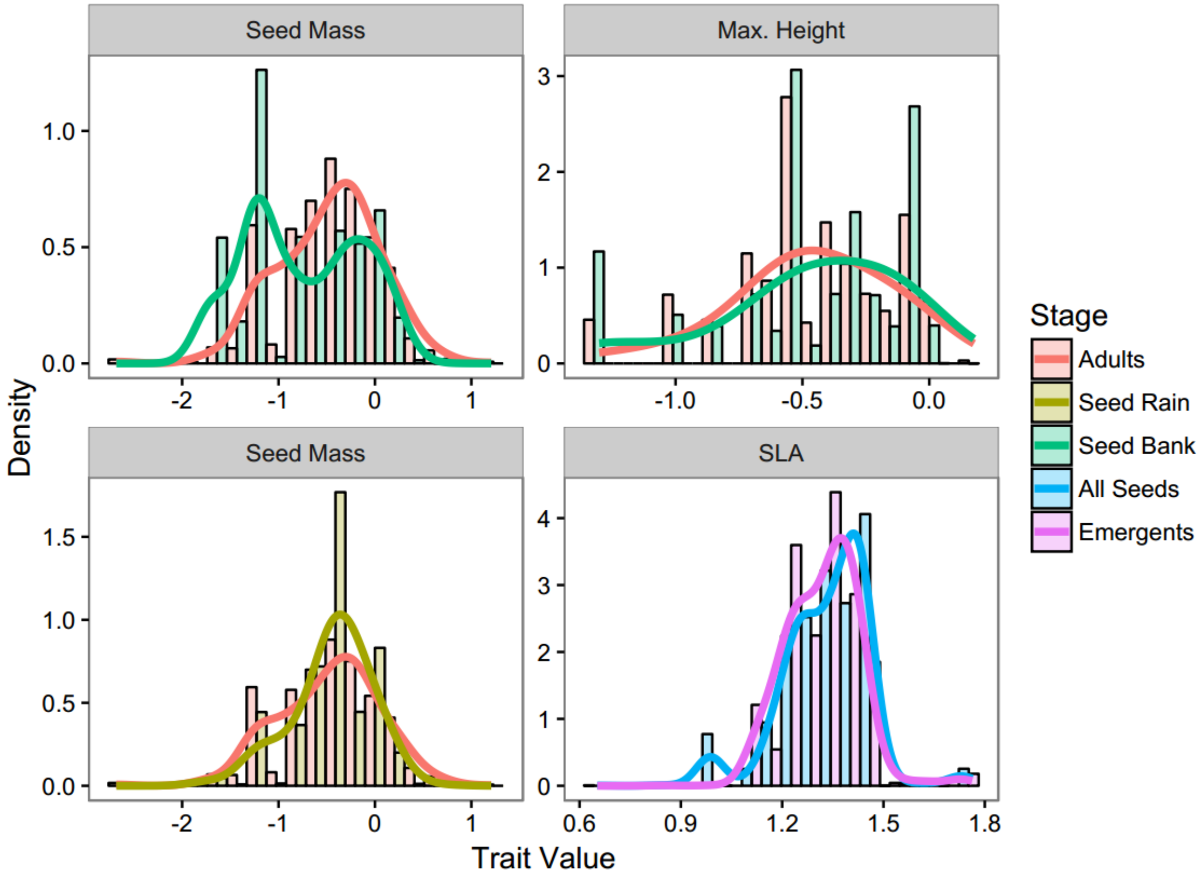

Figure 3.5. Comparisons of community trait distributions before and after four life stage transitions.

Density histograms of trait distributions before and after four life stage transitions. The specific transitions were chosen because they were the only instances for which the Rao coefficient differed significantly across all sites relative to what was expected by chance (Figure B-3). Density histograms reflect the relative abundances of individuals of given trait values, centered to zero at each site (but not scaled), grouped into 20 bins. Density polygons are smoothed trait distributions of the same data. The 'All Seeds' category is the sum of seed rain and seed bank data at the same spatial scale. At top left and top right, trait values of adults (red) are more clustered than trait values of seeds in the seed bank (green), both in terms of seed mass (left) and max. height (right). At bottom left, seed mass values of adults (red) are less clustered than seed mass values of seeds in the seed rain (gold). At bottom right, SLA values of seeds are less clustered than SLA values of emerging seedlings.

Discussion

Our analysis revealed step-wise non-random elimination of species at each life stage transition, suggesting the existence of multiple processes operating sequentially on the community assembly timeline. In addition, the observed shifts in mean trait values at each life stage suggest that species with smaller leaves and seeds are more abundant than expected in the seed rain and seed bank, perhaps due to higher seed production or dormancy capability, and shorter species are more likely to emerge; trait values were uncorrelated with seedling establishment rates. As such, our results corroborate the notion that traits are useful correlates to species performance. However, the lack of major trends in the strength of trait-mediated filtering with climate suggest that the traits used in this study may be of limited use for predicting community responses to climate change mediated through life stage transitions. Our approach and results are an important step towards integrating information about life stage transitions in community assembly models.

Seed pool assembly

Propagule arrival is the first critical step to community membership. The consistently lower levels of species richness and – even more pronounced – diversity in seed life stages (i.e., seed rain plus seed bank) relative to neutral expectations (Figure 3.2) illustrates how dispersal limitation affects the numbers and abundances of species from the local species pool. In other words, we find evidence that non-random assembly processes shape the local species pool during this 'first' plant life stage transition in our study system. This result is unsurprising as propagule limitation has been noted in many other systems (Howe and Miriti 2004, Vandvik and Goldberg 2005, Aicher et al. 2011). One clue to determining the nature of this dispersal-related filter could lie in the significantly lower leaf areas of species in seed communities relative to neutral expectations. Species with smaller leaves are thought to fall on the slower end of the fast-slow resource-use efficiency continuum (Franco and Silvertown 1996); thus, this pattern could arise if "slow" species are producing more seeds than "fast" species, although how this tradeoff translates to differences in population-level seed abundances is unclear. Contrary to our expectations, smaller seeded species were not more common in the seed rain than expected by chance, illustrating that seed size per se is not a good predictor of per capita seed production in a community. We did, however, observe a much lower mean seed mass in the seed bank, although this is likely due to post-dispersal seed mortality rather than differential seed production (see next paragraph). The predominance of clonal reproduction in grassland systems like ours is another potential explanation for the difference in diversity between adult and seed stages, if clonal-growth specialist species are forgoing seed production in lieu of vegetative reproduction (Halassy et al. 2005).

Analyzing seed rain and seed bank components of the total seed pool separately offers additional insights into the community assembly process. First, while species richness of the species pool was modestly lower than expected by chance, species richness of the seed rain and seed bank site pools were far lower than expected by chance (Figure 3.2). One explanation for the discrepancy between the two seed pools could be the existence of species in the seed rain that are either less capable of dormancy (Baskin and Baskin 1998), or are disproportionately removed by granivores or decomposers (Dalling et al. 2011). Conversely, species in the seed bank that are absent in the seed rain could arise via temporal variation in seed production, e.g., as predicted by the storage effect (Chesson 2000). The dramatically lower mean seed mass values for species in the seed bank (Figure 3.4) supports both hypotheses, as smaller seeds are less appealing to granivores, and some evidence suggests that they have greater capacity for dormancy (Thompson et al. 1993). Regardless of the particular mechanism, the fact that we observe less clustering than expected in seed mass values in the seed bank but more clustering than expected in the seed mass values in the seed rain provides unambiguous evidence of two qualitatively different assembly processes operating independently.

Seedling emergence and establishment

Species were affected non-randomly as individuals transitioned from seeds to emerged seedlings, and again as individuals transitioned from emerged seedlings to established seedlings (Figure 3.2). Importantly, the nature of these filters differed qualitatively, underscoring the value of a stage-specific approach when using patterns to infer community assembly processes. Specifically, shorter species emerged as seedlings more often than expected by chance (Figure 3.4). In addition, we found marginal statistical support ($P = 0.058$) for taller species being more likely to establish as seedlings than expected by chance. If this contrasting pattern between the optimal maximum height values of emerged and established seedlings is validated by future work, it could be indicative of a tradeoff in which short species emerge more readily but are less likely to establish. As a stepwise process it would result in a more clustered distribution of maximum trait values when moving from seeds to established seedlings; in tentative support of this, clustering in maximum height was much greater than expected by chance in seven of the 12 sites (Figure B-4). Species maximum height is known to vary consistently with climate in this system and elsewhere (Westoby 1998, Guittar et al. 2016), and thus may be an important determinant of species success under certain environmental conditions. For example, maximum height may become increasingly important as experimental gaps are filled by seedlings and individuals must compete for light (Falster and Westoby 2003). We also saw an increase in clustering in SLA values relative to neutral expectations when transitioning from seeds to seedlings (Figure B-4), although the magnitude of the difference was slight (Figure 3.5), but nonetheless provides another instance where successful species have trait values closer to the community mean than expected by chance, indicative of abiotic filtering or competitive hierarchies (Herben and Goldberg 2014).

Conclusion and future directions

This study, unlike much community assembly research, integrates multiple life stage transitions to offer a more complete picture of the community assembly process. An advantage of this approach is that it lowers the risk of encountering difficult-to-interpret patterns arising from multiple interacting processes. Life stage-specific data allowed us to divide the assembly process into smaller, more digestible parts, that could be studied independently. Our use of seed bank and seed rain data as explicit species pools, for example, as opposed to ones inferred from regional adult abundance data, meant that we could distinguish species that never arrived to a site from those that were filtered from the seed community in a subsequent life stage.

However, care was necessary when interpreting the trait-based shifts between life stages because the costs and benefits of a given life history tradeoff may be present at different points of community regeneration. Our observation of smaller seeds in the seed bank, for example, does not necessarily indicate that smaller seeded species were more successful than larger seeded species. Instead, a reduction in mean seed mass compared to neutral expectations could have resulted from a life history tradeoff between fecundity, which would be evident in seed stages, and survival probability, which would be evident at seedling stages (i.e., smaller seeds being more common than larger seeds, but reaching adulthood less frequently).

A potential criticism of this study is that it is based on only two years of data, and therefore may reflect ephemeral dynamics that are unrepresentative of long-term trends. However, this criticism is unfounded because our results (e.g. Figure 3.2, Figure 3.4) showed statistically significant trends over twelve sites with different climate conditions. Our sites, because they have different environmental characteristics, offer a space for time substitution and thus serve as replicates that enable more confident conclusions to be drawn.

Future work should move beyond observations of life-stage specific data, and conduct experiments which alter the composition of specific life stages and predict changes in assembly outcomes. For example, it would be interesting to vary the size and composition of the seed pool and follow community shifts in the trait-based composition of subsequent stages, e.g., to determine the extent to which a tradeoff between fecundity and survival shapes the community assembly process.

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Chapter 4. Can trait patterns along gradients predict plant community responses to climate change?[3]

Abstract

Plant functional traits vary consistently along climate gradients and are therefore potential predictors of plant community response to climate change. We test this space-for-time assumption by combining a spatial gradient study with whole-community turf transplantation along temperature and precipitation gradients in a network of twelve grassland sites in Southern Norway. Using data on eight traits for 169 species and annual vegetation censuses of 235 turfs over five years, we quantify trait-based responses to climate change by comparing observed community dynamics in transplanted turfs to field-parameterized null model simulations. Three traits related to species architecture (maximum height, number of dormant meristems, and ramet-ramet connection persistence) varied consistently along spatial temperature gradients and also correlated to changes in species abundances in turfs transplanted to warmer climates. Two traits associated with resource acquisition strategy (SLA, leaf area) increased along spatial temperature gradients but did not correlate to changes in species abundances following warming. No traits correlated consistently with precipitation. Our study supports the hypothesis that spatial associations between plant traits and broad-scale climate variables can be predictive of community response to climate change, but illustrates that not all traits with clear patterns along climate gradients influence community response to an equal degree.

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[3] Published as Guittar, J., D. Goldberg, K. Klanderud, R. J. Telford, and V. Vandvik. 2016. Can trait patterns along gradients predict plant community responses to climate change? Ecology 97:2791–2801.

Introduction

Plant functional traits, defined as measurable species characteristics with explicit connections to individual performance, reflect plant ecological strategy and associate with environmental factors at many spatial and ecological scales (Silvertown 2004, Wright et al. 2005, McGill et al. 2006, Violle et al. 2007). The roles that environmental variables play in structuring community composition are often inferred from patterns of community-weighted mean trait values along spatial gradients (De Bello et al. 2005, Shipley et al. 2006, Kraft et al. 2008, Cornwell and Ackerly 2009). The consistency and prevalence of many trait-climate correlations over space suggests they could be good predictors of community responses to climate change (Lavorel and Garnier 2002, Enquist et al. 2015).

However, there are also reasons why spatial trait gradient patterns may be poor predictors of community responses to climate change. First, it is not clear if species will migrate quickly enough to maintain their current associations to climate (Post and Pedersen 2008, Visser 2008). Instead, species assemblages may be in continual flux as species respond and adapt differentially to changing climate conditions (Neilson et al. 2005). Second, rapid climate change could disrupt biotic interaction networks, leading to idiosyncratic species responses that are inconsistent with expectations based on broad-scale trait-environment relationships (Kudo et al. 2004, Post and Pedersen 2008). Third, species may respond to finer-scale changes in environmental variables that cannot be predicted using climate averages (Kimball et al. 2010, Graae et al. 2012).

One way to directly evaluate the potential for spatial trait patterns to predict community responses to climate change is to experimentally manipulate climate *in situ* and observe community response (e.g. Hobbie and Chapin III 1998, Hudson et al. 2011). *In situ* approaches allow for precise manipulation of the desired climate variables but suffer from several drawbacks. Most notably, the arrival and establishment of immigrants adapted to the new climate conditions is sharply reduced, effectively removing an important driver of community response to climate change (Gottfried et al. 2012). *In situ* experiments may even *suppress* community responses if propagule pressure from locally abundant species is high enough to exert mass effects on the community compositions of experimental plots. *In situ* climate manipulations also often have undesirable side effects related to their experimental methods (Aronson and McNulty 2009).

Here, we investigate the effects of climate change on plant communities using an alternative approach: transplantation of entire, intact communities to new climates. Whole-community transplantation avoids the experimental artifacts of climate change manipulations, while exposing the community to immigration from species adapted to the new environment. In fact, transplantation lies at the other extreme of *in situ* climate manipulations: it provides a scenario in which immigration of climate-adapted species is higher than would be expected in communities subject to gradual environmental change. We monitored changes in the functional composition of 235 control and transplanted turf communities over five years within a network of twelve grassland sites in southern Norway. Our measures of functional composition rely on species-level averages of four commonly measured plant traits: leaf area, maximum vegetative height, seed mass, and specific leaf area (SLA), and four less commonly used traits relating to clonal growth strategy: number of offspring per parent, persistence of plant-offspring connection, rate of lateral spread, and bud number (i.e., the number of dormant meristems per ramet). Clonal traits are often overlooked as indicators of plant performance, despite their widespread prevalence and potential significance for community dynamics and ecosystem function, especially in herbaceous plant biomes like grasslands, wetlands, and tundra (Zobel et al. 2010, Cornelissen et al. 2014).

Our central goal was to test if traits with broad spatial associations to climate also drive community responses to rapid climate change. To do this, we characterized baseline trait patterns across temperature and precipitation gradients in our system, and then determined if these traits correlated with species performance in turf communities transplanted to warmer and/or wetter conditions. The fact that turf communities were open to immigration from the surrounding vegetation necessitated a careful evaluation of our null expectations. Even under trait-neutral dynamics, natural turnover combined with the immigration and proliferation of locally-abundant species leads transplanted communities to converge compositionally with local sites over time. Thus, any test for trait-mediated dynamics must measure community responses against null expectations that account for stochastic replacement and immigration. We use shifts in species abundances in control turfs to estimate stochastic replacement and immigration at each site, and then use these estimates in model simulations to generate null expectations of turf response to transplantation. Observed deviations from these null expectations are interpreted as evidence for trait-mediated interactions.

The unusual topography of southern Norway allowed us to address an additional shortcoming of most spatial gradient studies by methodologically separating temperature and precipitation as potential climate drivers. Ecological studies along climate gradients often use altitudinal transects that vary in both temperature and precipitation (Callaway et al. 2002, Djukic et al. 2010), although not always in a consistent manner (Körner 2007). This covariation makes it difficult to isolate the individual and interactive effects of temperature and precipitation and thus project how vegetation will respond to novel climates. In southern Norway, a west-to-east rainfall gradient interacts with a mosaic of fjords and mountain ridges to generate high climatic heterogeneity over a small geographic area. We exploited this natural heterogeneity to establish a "climate grid" in which temperature and precipitation vary orthogonally among the twelve field sites, thereby allowing us to separate their effects and to identify potential interactions.

We use results from our gradient analysis, transplant experiment, and model simulations to address three questions: 1) What is the relative influence of spatial variation in temperature and precipitation on community trait composition? 2) Do the traits that respond to spatial climate gradients also drive community temporal response to climate change? 3) What is the influence of clonal traits relative to more commonly used leaf, seed, and canopy height traits in community response to climate gradients and climate change? We expect short species with conservative resource use strategies (low SLA, low leaf area, slow lateral spread) and/or high capacity for resource integration (persistent ramet-ramet connections, more offspring per ramet, more buds per ramet) to predominate in unproductive climates (the coldest and driest sites) relative to more productive climates (the warmest and wettest sites). Our study is a rigorous experimental evaluation of the assumption that trait patterns along climate gradients reflect, and can therefore predict, how communities will respond to anthropogenic climate change.

Methods

The study area is an approximately 500 km x 500 km region in southern Norway with marked climatic heterogeneity (Figure 4.1). Twelve grassland sites were selected with one of three mean summer temperatures (ca. 6.0, 9.0, and 10.5 °C) and one of four mean annual precipitations (ca. 600, 1200, 1900, and 2800 mm), while other environmental variables were relatively consistent (calcareous soil, southwest aspect, slope of about 20 degrees, and comparable grazing and land-use history) (see Klanderud et al. 2015 for additional site details). The grasslands' short stature (usually < 0.3 m at peak biomass) and shallow but thickly interwoven root and rhizome mats enabled the easy removal, transport, and replanting of 'turfs' and their attached flora to different hillsides. Each 25 x 25 cm turf contained tens to hundreds of individual stems, representing 10 - 40 vascular plant species, with a mean canopy height of 9 ± 6 cm (1 SD). In accordance with predictions that climate change will cause southern Norway to become warmer and wetter (Hanssen-Bauer et al. 2009), 40 turfs were transplanted to warmer sites, 45 turfs were transplanted to wetter sites, 30 turfs were transplanted to warmer and wetter sites, 60 control turfs were replanted at the same site, and 60 control turfs were delineated but left undisturbed. All non-local transplants were moved one 'step' warmer and /or wetter in the climate grid. Turfs were transplanted between sites in multiples of five; sample sizes differed by treatment because not all destination sites had cooler and/or drier sites to serve as turf origins (Figure 4.1). For control turfs, origin and destination sites are the same site. We refer to transplant destinations as 'target sites'; thus 'target controls' refers to control turfs at transplant destination sites.

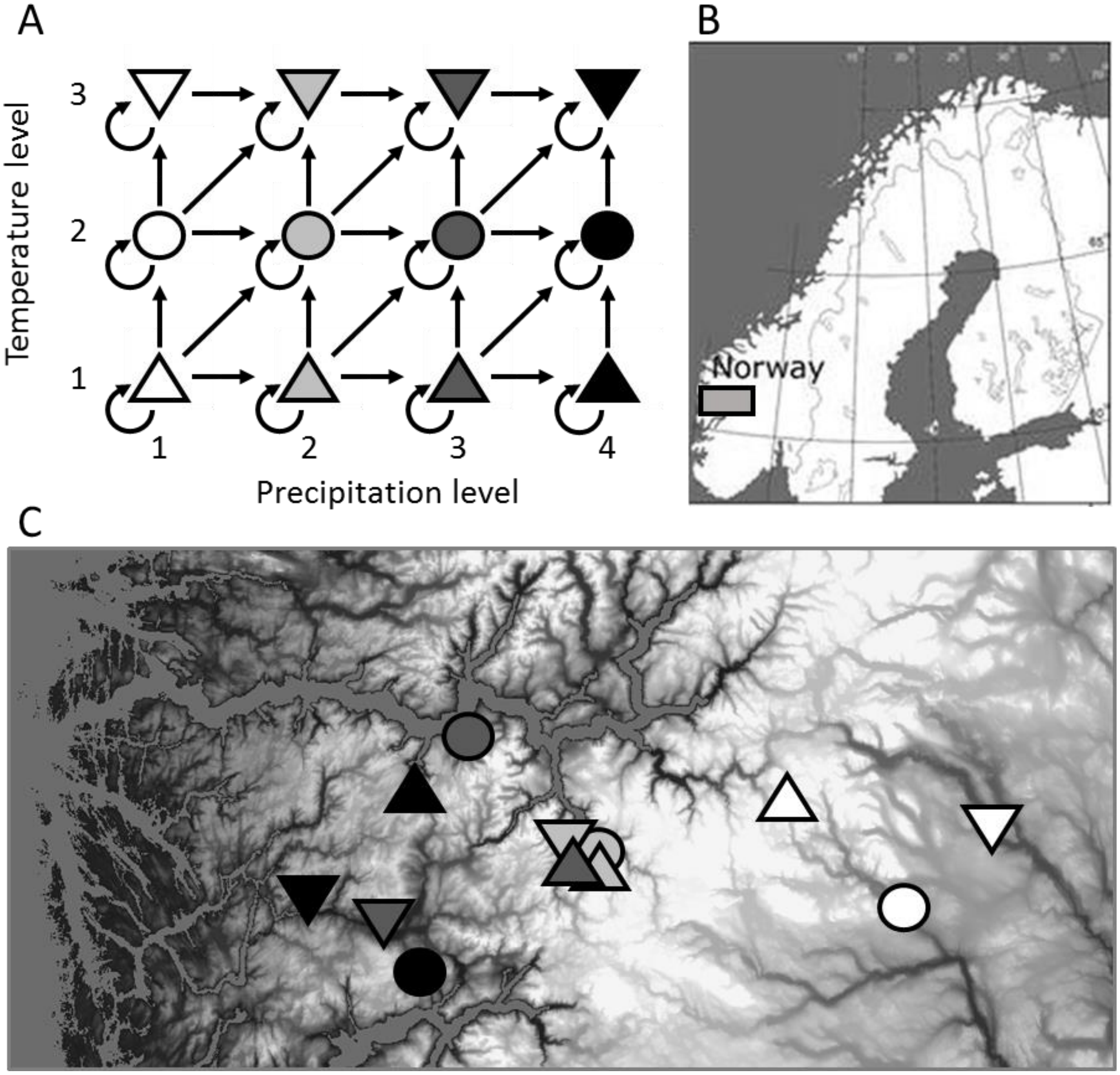

Figure 4.1. Study system and turf transplant schema.
Panel A: a schematic illustration of the orthogonal nature of climate variables across experimental sites, with black arrows representing the directions of turf transplants in replicates of five. Panels B and C show the geographical locations of experimental sites in southern Norway. Symbol shapes and shadings reflect mean summer temperature levels and mean annual precipitation levels, respectively, in accordance with panel A.

Vascular plant turf community censuses were conducted in 2009 (before transplantation), 2011, 2012, and 2013, for a total of 928 turf community time points. Twelve turf community time points were discarded due to damaged turfs. Percent cover of each species was estimated visually with the aid of a 5 x 5 cm grid. Total percent cover was allowed to fall below or exceed 100% to account for bare patches and/or overlapping species covers (mean cover in control plots across sites and years ranged from 87 ± 25% to 127 ± 30%).

Trait data

We built a custom database containing values for up to eight traits for the 169 species present in our turf communities from across the climate grid. Woody seedlings and unidentifiable individuals represented 1.1% total cover and were discarded. We used four common traits: leaf area (mm^2), specific leaf area (SLA) (m^2 kg^{-1}), maximum potential canopy height (m), and seed mass (mg), and four traits relating to clonal growth: number of offspring per parent per year (1 or ≥ 2), persistence of plant-offspring connection (< 2 years or ≥ 2 years), rate of lateral spread (≤ 1 cm $year^{-1}$ or > 1 cm $year^{-1}$), and bud number, i.e., the prevalence of aboveground and belowground dormant meristems. Leaf area and SLA were estimated using a combination of field data and data from the LEDA online trait database (Kleyer et al. 2008). Our field data derive from ~1200 leaves collected in the summer of 2012 for which SLA and leaf area were calculated using established protocols (Cornelissen et al. 2003). We used Pearson correlations to assess the extent to which LEDA species trait values matched field gathered trait values (SLA: $\rho = 0.69$; leaf area: $\rho = 0.73$). Maximum potential height data were mined from Lid and Lid (2007). We drew seed mass data from the Seed Information Database (Royal Botanic Gardens Kew 2014). All continuous trait values were log-transformed. Clonal trait data were extracted from the CLO-PLA database (Klimešová and Bello 2009) and, except for bud number, transformed from categorical to binary metrics to simplify statistical analysis. For bud number, species were assigned a score of 0 (no buds) to 8 (dozens of buds) based on estimates from Klimešová and Bello (2009). Data on individual traits represented 140 - 164 species (84% - 99% of total cover). Eight species (3.9% total cover) were identifiable only to genus but treated as species in downstream analyses. For these species, trait values were either measured in the field (SLA, leaf area), estimated by taking the median trait values of locally-present congeners (seed mass, maximum height, clonal traits), or left blank. Species names and their trait values are listed in Table B-1; only species with adult present were used in this chapter. Pearson correlations among traits were always below 0.51 (Table 4.1), thus we consider trait responses to be statistically independent.

Table 4.1. Pearson correlations of species trait values.

	MXH	SM	SLA	BN	LAT	OFF	PER
LFA	0.46	0.51	0.34	-0.13	-0.12	-0.11	-0.03
MXH		0.33	0.17	0.15	-0.02	-0.01	0.18
SM			0.16	0.06	-0.12	0.05	0.16
SLA				-0.36	-0.14	0.11	-0.40
BN					0.30	0.00	0.30
LAT						0.16	-0.08
OFF							-0.12

Pearson correlations of species trait values in the species pool. N ranges from 140 - 152. Abbreviations: LFA: leaf area; MXH: maximum potential canopy height; SM: seed mass; SLA: specific leaf area; BN: bud number; LAT: rate of lateral spread; OFF: number of new ramets per mother ramet per year; PER: persistence of plant-offspring connection.

Community analyses

We quantified differences in species composition using Bray-Curtis dissimilarity. Community weighted means (CWMs) were used to quantify differences in functional composition. We used species-level trait values in these calculations; thus, changes in CWM reflect changes in species composition, not trait plasticity. A CWM is calculated by averaging the values of a trait for all species in a community, weighted by their abundance (here, percent cover). For lateral spread, connection persistence, and offspring per ramet, CWMs reflected the proportion of the community with the higher value category (≥ 2 offspring per parent, ≥ 2 years connection persistence, or > 1cm year^{-1} lateral spread). Pre-transplant (2009) turf CWMs were regressed onto temperature and precipitation site means to assess community trait patterns in environmental space. AIC values were used to determine when temperature, precipitation, and/or their interaction were significant predictors ($p < 0.05$) in abundance-weighted multiple linear regressions.

For a deeper investigation of species-level variation in community composition see Klanderud et al. (2015).

We quantified community change as shifts in dissimilarity over time between a turf and its target site controls. Each site had five undisturbed controls and five controls replanted nearby which enabled us to test for the effects of transplantation *per se*. Dissimilarity in species composition among undisturbed controls was only statistically different ($p < 0.05$) from the mean dissimilarity between undisturbed and replanted controls in 5 of 48 of turf community time points, suggesting that transplantation *per se* did not noticeably affect species composition. Thus, in some analyses, replanted controls and undisturbed controls are combined to increase the control group sample size to ten per site.

Null model rationale and process

We used simulations to generate null expectations of turf community responses to transplantation, and then determined when observed community responses deviated from these null expectations. Our model is similar in principle to stochastic models of species abundances using Hubbell's (2001) neutral local community model, but is applied to a smaller spatial scale. For each step in the model, an individual is randomly removed from the turf community and either replaced with a randomly selected offspring from the same turf community (with probability $1 - m$), or replaced with a randomly selected offspring from the site-level community (with probability m). Each step is a 'replacement event.' The site-level community is conceptually equivalent to Hubbell's 'metacommunity', and is defined as the net composition of the ten control turfs present at each site. The model has two parameters: replacement rate (d), the number of replacement events that occur between consecutive years, and immigration rate (m), the probability that replacements are drawn from the site-level community pool as opposed to from within the turf-level community pool (see next section for parameter estimation). Even though turfs are only 25 x 25 cm in size, we expected within-turf recruitment to be high because most species in our system exhibit some degree of clonal growth

(Klimešová and Bello 2009), and nearly all new stems are vegetative outgrowths from extant genets rather than seed germination events (Berge, Klanderud, Vandvik, unpublished data).

Our model differs from Hubbell's community model in three important ways. First, rather than using births and deaths of individuals to quantify demographic changes, which would be impractical to measure in our predominantly clonal system, we use increases and decreases in percent cover units. Second, we relax the assumption of zero-sum replacement and instead force simulated percent cover to match observed percent cover in each year of the experiment. Third, we allow site-level communities, i.e., the source pools for migrants entering experimental turfs, to vary by recalculating them after each census. The latter two modifications account for temporal variability in the productivity or composition of site-level communities due to drift or short-term climatic variability.

We simulated community dynamics from 2009 to 2013 on an individual turf basis, calculating species and trait dissimilarities to target site controls each year. Compositional changes in each turf were simulated 100 times and the resulting values were averaged. Simulation data for 2010 were not presented because field observations do not exist for that year. Paired t-tests were used to determine when observed and simulated null expectations differed significantly.

Estimating model parameters

We used community census data from our control turfs to estimate replacement rate (*d*) and immigration rate (*m*) at each site. We set *d* equal to half the sum of differences in species covers in control turfs between years at each site. We divided by two because each replacement event constitutes two shifts in species covers, one increase and one decrease. Values of *d* ranged from 19.7 to 37.4. Our method of estimating *d* ignores self-replacement and thus likely underestimates actual replacement rates; however, a visual inspection of model fit under a broad range of parameter values illustrates that our results are robust to moderate increases in replacement rate (Figure C-3). Furthermore, it should be noted that any potential underestimates in replacement rates do not affect estimates of immigration rates.

We estimated m using a Bayesian approach based on shifts in species abundances in the five replanted control turfs at each site over three consecutive years (2011-2013), assuming neutral dynamics. The net composition of the five undisturbed control turfs at each site was used as the site-level community. The expected cover λ of species i in a turf community at time t is formally defined as

$$\lambda_{i,t} = J_{t-1}[(1 - m) \times C_{i,t-1} + m \times P_{i,t-1}]$$

where J_{t-1} is the total cover of the turf community in the previous year, $C_{i,t-1}$ is the relative abundance of species i in the turf community the previous year, $P_{i,t-1}$ is the relative abundance of the species in the site-level community at time t, and m is the immigration parameter. The percent cover y, rounded to the nearest whole number, of species i in turf community at time t was modelled assuming

$$y_{i,t} \sim \text{Poisson}(\lambda_{i,t}).$$

We gave m a uniform prior with a range from 0 to 1. We also explored using an informed prior ($m < 0.5$) based on the expected predominance of clonal growth and within-turf recruitment, but this led to identical results and was dropped. We fit the model using MCMC implemented in JAGS 3.4.0 (Plummer 2003). We ran JAGS through the R package R2jags (Su and Yajima 2012). For each model fit, we ran three chains, used a burn-in of 1000 iterations, and chose initial values in different regions of parameter space. We confirmed model convergence using Gelman-Rubin diagnostics (Brooks and Gelman 1998). We assessed overall model fit by regressing mean posterior estimates for percent cover on observed data ($R^2 = 0.63$). See (Table 4.2) for parameter estimates. For a deeper exploration of how a Bayesian approach can be used to fit a trait-neutral model of community change to time series data see Mutshinda et al. (2008).

Table 4.2. Site-level neutral model parameter estimates.

Site	Summer Temp. (C°)	Precipitation (mm)	d	m
Ulvhaugen	6.2	596	31	0.06
Låvisdalen	6.5	1321	23	0.17
Gudmedalen	5.9	1925	26	0.28
Skjellingahaugen	6.6	2725	20	0.32
Ålrust	9.1	789	34	0.26
Høgsete	9.2	1356	31	0.36
Rambæra	8.8	1848	24	0.29
Veskre	8.7	3029	32	0.39
Fauske	10.3	600	37	0.18
Vikesland	10.6	1161	36	0.17
Arhelleren	10.6	2044	33	0.16
Øvstedal	10.8	2923	22	0.17

Site-level simulation parameters, sorted by temperature level (ca. 6.0, 9.0, and 10.5 C°) then precipitation level (ca. 600, 1200, 1900, and 2800 mm year-1). Summer temperature is the mean of the four warmest months. Replacement rate (d) was estimated based on observed changes in cover between years. Immigration rate (m) was estimated in control turfs at each site using a Bayesian approach that assumed control turf dynamics were species-neutral. Parameter estimates are shown graphically in the top right panel of Figure C-3.

Results

Community weighted means (CWMs) of leaf area, SLA, maximum height and lateral spread increased with temperature along spatial gradients, and CWM values of bud number and connection persistence decreased with temperature along spatial gradients (Table 4.3, Figure 4.2). In three of the eight traits, the best-fit weighted multiple linear regression model included precipitation as a predictor variable, but the coefficient of the precipitation variable itself was never significantly different from 0. The interaction of temperature and precipitation had a significant effect on SLA. Exponential curves with increasing temperature fit bud number and connection persistence patterns better than linear ones, reflecting stronger responses in the colder part of the climate grid (Figure 4.2). Based on these associations, we limited our analysis of trait convergence in transplanted turfs over time to the six traits with spatial associations to temperature, and to turfs transplanted to warmer climates.

Species and trait compositions of transplanted turfs converged towards target site controls over time, with the magnitude of convergence increasing with initial dissimilarity (Figure 4.3). Rates of convergence in species composition only exceeded null model predictions that accounted for random replacement by local immigrants in 2011 (Figure 4.4). In contrast, rates of convergence in maximum height, bud number, and connection persistence consistently exceeded null model predictions (Figure 4.4).These deviations from null expectations were driven by responses across many species rather than responses in just a few of the most abundant taxa (Figure C-4). Site-level climate data confirm that transplanted turfs experienced consistently warmer temperatures as intended (Figure C-1, Figure C-2).

Table 4.3. Summary statistics for best-fit weighted linear models.

Trait	Variable	Estimate	SE	t-statistic	p-value
Bud Number	exp(-Temp)	118.15	52.83	2.24	0.049
Lat. Spread	Temp	0.04	0.01	2.5	0.031
Leaf Area	Temp	0.05	0.01	3.83	0.004
	Precip	< 0.01	< 0.01	-1.5	0.167
Max. Height	Temp	0.05	0.01	4.26	0.002
Offspring	(none)				
Persistence	exp(-Temp)	109.14	19.28	5.66	< 0.001
Seed Mass	(none)				
SLA	Temp	0.02	0	5.35	< 0.001
	Precip	< 0.01	< 0.01	-1.24	0.251
	Temp x Precip	< 0.01	< 0.01	2.48	0.038

Summary statistics for best-fit weighted multiple linear regression models for each trait using mean summer temperature, annual precipitation, and their interaction as potential predictor variables, weighted by the sample size at each site (N ranges from 10 to 25). Model fit was determined using AIC values. For bud number and connection persistence, exponentially transforming the temperature axis resulted in better model fit. Turf-level community weighted trait means and significant regressions are shown in Figure 4.2.

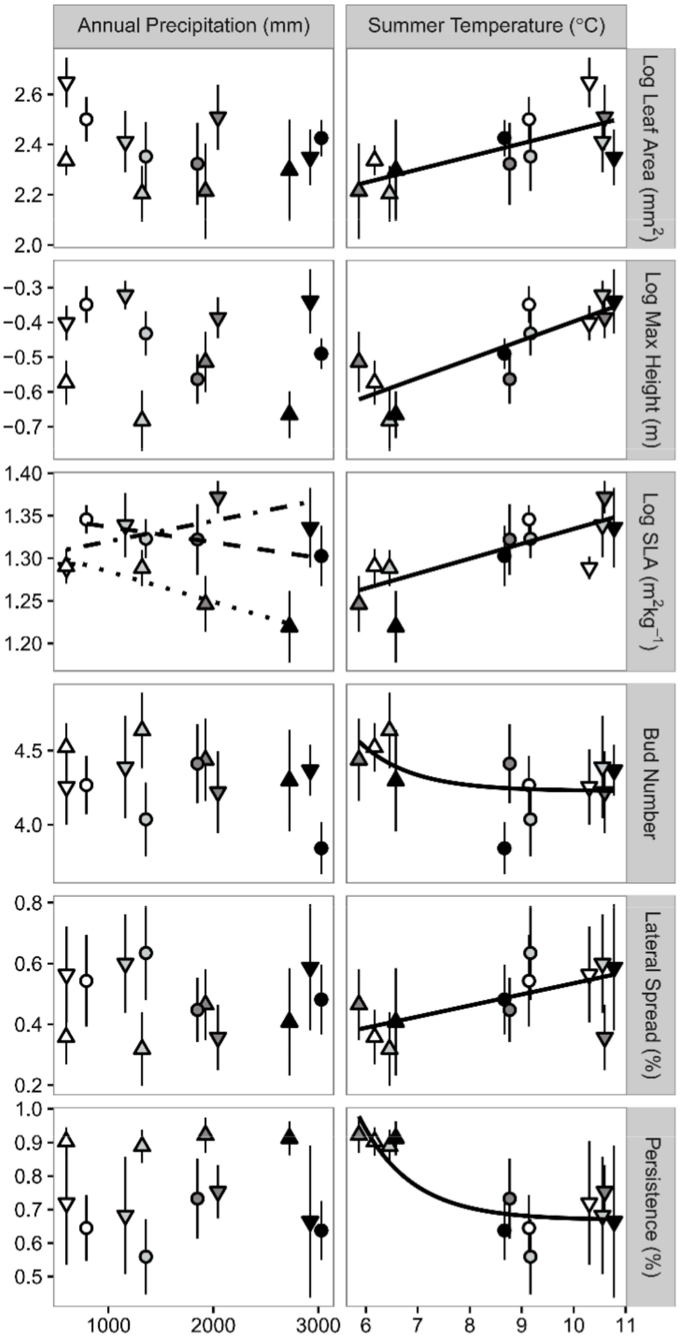

Figure 4.2. Community-weighted trait means plotted by climate.
Community weighted trait means (CWMs) of turfs before transplantation along natural gradients of mean summer temperature (left) and mean annual precipitation (right). CWMs are aggregated by site (N ranges from 10 to 25). Vertical lines show ± 1 S.D. Symbol shapes and shadings reflect temperature and precipitation levels, respectively, in accordance with Figure 4.1, panel A. Best-fit lines are shown as solid lines when trait-gradient relationships are significant; for simplicity, trend lines represent univariate regressions, even if multivariate regressions led to higher AIC values. The interactive effects of temperature and precipitation on SLA is shown using three trend lines (~3°C: dotted, ~6°C: dashed, ~9°C: dot-dashed). CWMs in seed mass and offspring per ramet did not exhibit significant trends along temperature or precipitation gradients and are therefore omitted. See Table 4.3 for model summary statistics.

Discussion

Our study uses observational and experimental data to test the assumption that traits with broad-scale associations to climate in space are predictive of plant community response to climate change in time. This space-for-time assumption is supported when using three traits related to species architecture, but not supported when using three traits related to species resource use strategy. Our results underscore the importance of using ecologically relevant traits when making predictions of community response, and suggest that in our grassland system, architectural traits may exert more influence on initial species response to rapid warming than the more commonly used growth-related traits.

Trait patterns along climate gradients

Despite the large range in both mean summer temperature and annual precipitation across sites, CWMs trended only with temperature. The lack of functional turnover over a nearly 2500 mm year^{-1} increase in precipitation is surprising given the consistent directional turnover in species composition along both temperature and precipitation gradients in our system (Klanderud et al. 2015), underscoring the fact that species turnover does not always beget functional turnover (Hooper et al. 2002). This finding contrasts with vegetation trait patterns found elsewhere over narrower ranges of precipitation (Fonseca et al. 2000, Wright et al. 2005). A lack of precipitation effects could occur if soil moisture is similar at all sites and/or not limiting at any sites, however this seems unlikely given the large range in mean annual precipitation and the otherwise similar site abiotic conditions. Regardless of the mechanism, the implication is that functional shifts in these grasslands are likely to occur in response to changes in temperature, not precipitation.

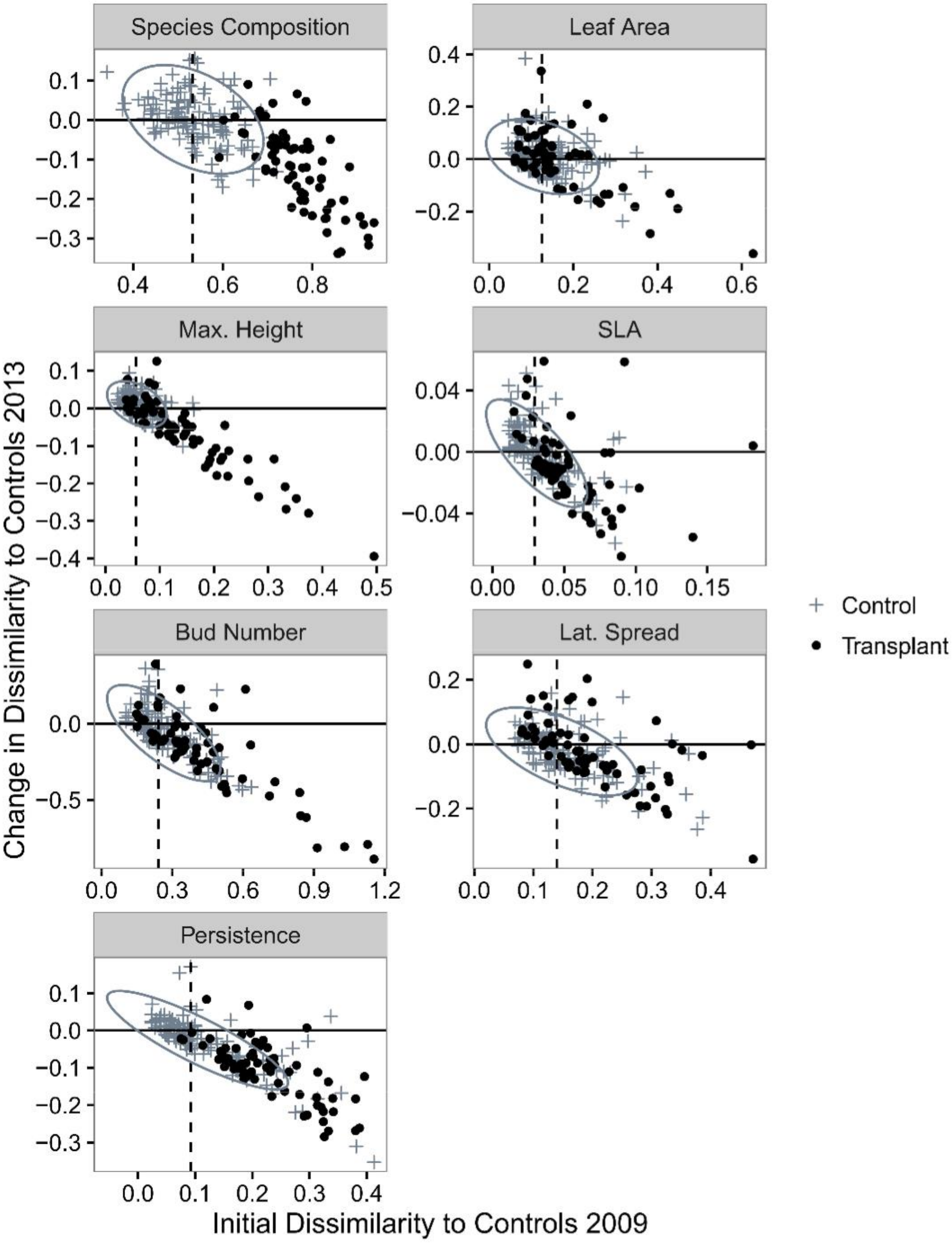

Figure 4.3. Trait-based turf responses to transplantation to warmer climates. Changes in dissimilarity of turfs transplanted to warmer climates and target site controls from 2009 to 2013. The x-axis shows Bray-Curtis dissimilarity between turfs and the centroids of their control turfs in 2009; the y-axis shows how that dissimilarity changed by 2013. Each symbol represents a turf community. Grey crosses represent control turfs; black circles represent transplanted turfs. Dissimilarity was calculated using Bray-Curtis distance for species composition (top left panel) or Euclidian distance of community weighted means (all remaining panels). Symbols below zero on the y-axis reflect turf communities that converged compositionally towards target controls, whereas communities above zero on the y-axis diverged compositionally. Dashed vertical lines are placed at 50% of mean dissimilarity among controls as an approximation of natural community stochasticity. Grey ellipses represent 95% confidence intervals of the centroids of control turf dissimilarities.

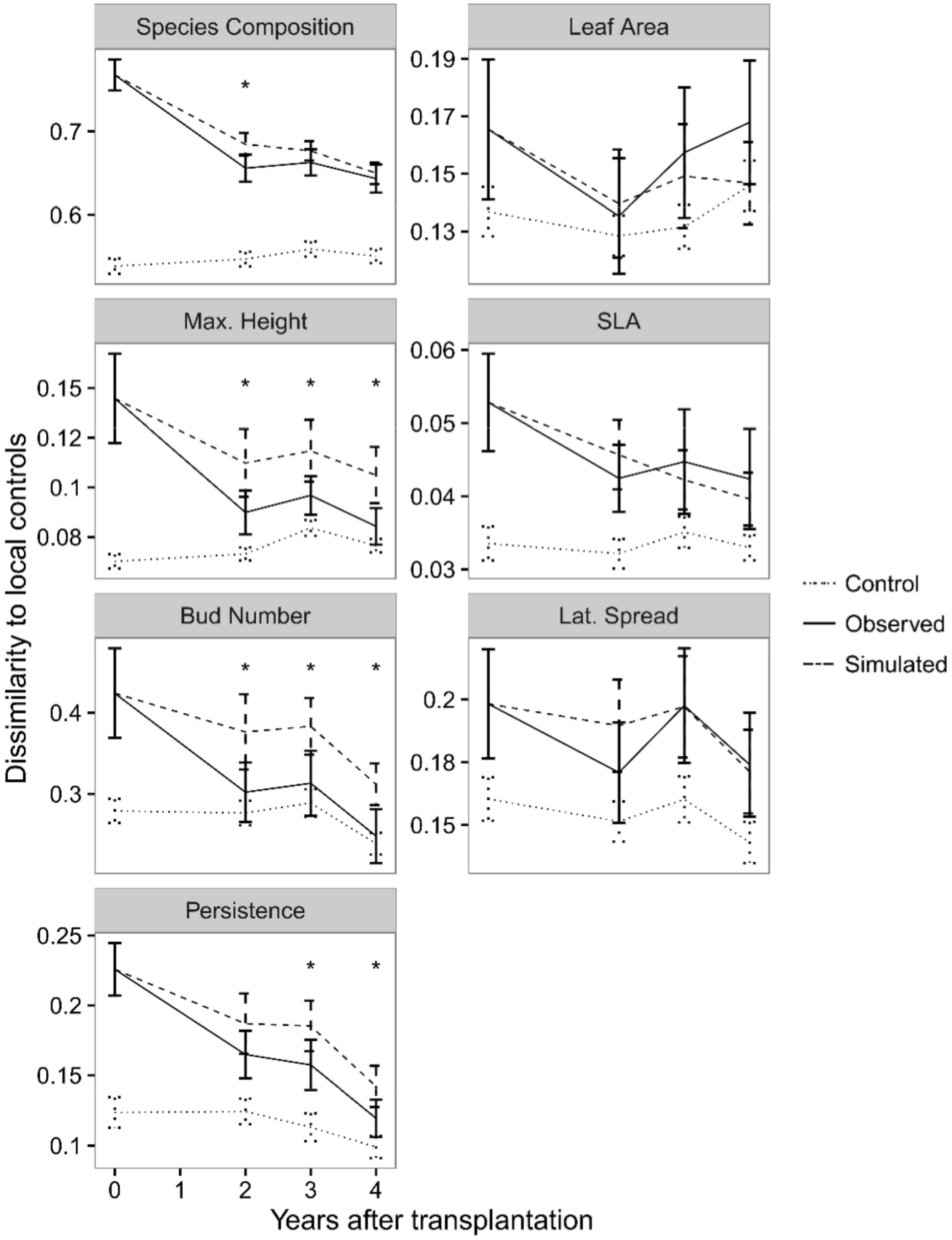

Figure 4.4. Turf responses to transplantation relative to neutral expectations. Mean trait dissimilarities of transplanted turf communities and target controls from 2009 to 2013. Solid lines represent observed field data. Dashed lines represent simulated null expectations based on the means of 100 null model simulation runs. Dotted lines represent mean dissimilarity among control turfs within sites. Null model simulations use estimates of replacement and immigration rates derived from our field data (see Methods). Error bars show 95% confidence intervals. Statistical differences between observed and simulated community weighted means are shown when $p < 0.05$ (*).

The consistent shifts in CWMs with increasing temperature in our system signify shifts in plant ecological strategy. Increases in leaf area, SLA, and the rate of lateral spread with temperature suggest a shift from slow-growing stress-tolerant species to fast-growing species with acquisitive resource use strategies (Sterck et al. 2006, Rusch et al. 2011). Also increasing with temperature are maximum height, duration of connection persistence, and bud number, three traits related to plant architecture. The increase in CWMs of maximum height may reflect a tradeoff in the ability to compete for light at warm sites amenable to growth and the ability to tolerate wind stress and freezing temperatures at the coldest sites (Westoby 1998, Falster and Westoby 2003). Higher CWMs of bud number and connection persistence at the coldest sites may reflect an increased importance of resource integration and/or recovery from disturbances (Klimešová and Klimeš 2007), although we see no obvious reasons why resources would be patchier and/or disturbances more common at the coldest sites. More work is needed to confirm the functional roles of these understudied clonal traits and their role in organizing grassland species along gradients.

Community responses to warming

The central goal of this study was to test the hypothesis that trait-climate relationships over space are predictive of temporal community response to climate change in time, a common assumption in climate change research. Of the six traits with significant trends with temperature in space, maximum height, bud number, and connection persistence - three traits related to species architecture - associated consistently with turf community response to warming in time. The large deviation in maximum height from neutral expectations may be have resulted from competition for light being more intense in more productive, warmer conditions, and taller species preempting access to light, shading out competitors, and earning disproportionate returns due to size-asymmetric competition (Schwinning and Weiner 1998). Species with fewer buds and reduced connection persistence succeeded disproportionately following warming, suggesting that the development and maintenance of these clonal traits, which are believed to support new ramets under stressful conditions (Klimešová and Klimeš 2007), comes at a cost when conditions are more amenable to growth. That CWMs of architectural traits deviated from neutral expectations of community response while CWMs of growth-related traits (SLA, leaf area, lateral spread) did not, despite showing strong trends along spatial temperature gradients, is unexpected and interesting. Perhaps, the capacity for rapid growth is not useful to new ramets vying for resources in grassland communities already packed with established individuals (but see: Wildová et al. 2007). Alternatively, SLA and leaf area may be poor predictors of growth in herbaceous species with photosynthetic stems. The strong responses of clonal traits to changes in temperature highlight the need for more emphasis on clonal traits in studies of community response to climate change and herbaceous community assembly in general.

Defining null expectations was challenging given the lack of standard practices of how to model demographic stochasticity in predominantly clonal systems (Eriksson 1994). Traditionally, demographic analyses rely on population numbers and vital rates, but the concepts of individuals, populations, births, and deaths break down in clonal, modular organisms. For instance, ramet number is impractical to measure and may not be demographically meaningful for graminoids that form hummocks with clumps of stems (e.g. *Festuca ovina*), nor is it possible to distinguish individuals in forbs with sprawling aboveground stems with adventitious roots (e.g. *Veronica biflora*), or species that divide via root splitting which results in fragmentation just below the litter layer (e.g. *Cerastium alpinum*). Our decision to simulate demographic changes using percent cover units therefore has both practical and conceptual appeal. The drawback, however, is that percent cover is sensitive to factors that are not demographically significant, such as variation in phenological stage among individuals, species, and sampling times, and thus may inaccurately reflect shifts in abundance between years. Nevertheless, our approach accounts for demographic stochasticity, annual variation in community-level composition, and the realities of dispersal limitation in a predominantly clonal system to generate explicit null expectations of community response to perturbation.

Conclusions and future directions

Using patterns in CWMs along environmental gradients to forecast community response to climate change is an intuitively appealing approach. Our study provides qualified support for such an approach: three of the six traits with spatial associations to temperature in our system associated significantly with species success following transplantation to warmer climates. Evidently, spatial associations between plant traits and broad-scale climate variables can be predictive of community response to climate change, but are not always so.

Our results shed some light on how our system could respond to climate change in the coming decades. Despite high rates of annual turnover, without gaps created by disturbances, virtually all replacement stems are clonal outgrowths of extant genets rather than new seedlings (Bullock et al. 1995; Berge, Klanderud, Vandvik, unpublished data). Thus, the potential for community change is largely limited by the prevalence of gaps and the proportion of species in the seed rain that are immigrants rather than local species. Once established, warmer-adapted immigrants will likely proliferate vegetatively, outcompeting species adapted to cooler temperatures (Olsen et al. 2016). Our approach and conclusions underscore the importance of accounting for stochasticity and immigration when making predictions of community response (Tilman 2004, Shipley et al. 2011). Future studies should consider the effects of dispersal limitation on short-term transient responses, and how disturbances and dispersal limitation will affect long-term equilibrium responses. Predictions of 'extinction debts' and 'immigration credits' in the field of habitat distribution modeling are an important step in the right direction (Dirnböck and Dullinger 2004), but could be developed further by considering how and when traits modulate species interactions.

Acknowledgments

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Chapter 5. Conclusions and synthesis

In this dissertation, I use observational and experimental data from a network of grasslands in southern Norway to advance different aspects of our understanding of community assembly and improve our ability to predict community responses to climate change. Three general results rise from my analysis. First, community structure of this alpine grassland was dynamic –more dynamic than expected – suggesting the potential for rapid community responses should environmental conditions change dramatically. Second, species trait values correlated with species performance on multiple levels, underscoring their potential utility as ways to understand community assembly and predict community response, although more work is needed to determine when and where specific traits are most influential. Third, conclusions from each chapter reveal community structure and community response to arise from several qualitatively different processes that occur at multiple life history stages, many of which appear to be closely influenced by climate-mediated filters.

In Chapter 2, I combined data from seed rain, seedbank, and adult plant surveys at the twelve sites to infer regional patterns of seed dispersal and immigration among climate zones. I found empirical evidence for the dispersal, emergence, and establishment of immigrants in small, but significant, numbers across grassland communities in southern Norway, with habitat connectivity being modulated by both climate and species traits. My results offer mixed prospects for grassland species responses to rapid climate change. On one hand, evidence for non-random species-specific ecological filters implies that, following a large shift in climate, immigrant species could be favored over local species for survival. On the other hand, the wide range in observed species dispersal abilities indicates that many species could be limited by dispersal *per se* in their ability to track rapid changes in climate.

In Chapter 3, I characterize a step-wise non-random elimination of species at each life stage transition, suggesting the existence of multiple processes operating sequentially on the community assembly timeline. I also show shifts in the mean community-weighted trait values at each life stage, supporting the notion that traits are useful correlates to species performance, and indicating that focusing merely on a single life stage will make inferences from trait-based patterns difficult or even impossible. In addition, the lack of major trends in the strength of trait-mediated filtering with climate suggest that the traits used in my study may be of limited use for predicting community responses to climate change mediated through life stage transitions. The approach demonstrated of how life stage-specific information can be integrated into community assembly models.

In Chapter 4, I use data to test the assumption that traits with broad-scale associations to climate in space are predictive of plant community response to climate change in time, and find this space-for-time assumption is supported when using three traits related to species architecture, but not supported when using three traits related to species resource use strategy. My results underscore the importance of using ecologically relevant traits when making predictions of community response, and suggest that in our grassland system, architectural traits may exert more influence on initial species response to rapid warming than the more commonly used growth-related traits.

Community dynamics are governed interactively by local and regional processes, which can apply to different organismal life stages and operate over different timescales. As such, processes related to seeds, seedlings, and adults should be considered when forecasting, and potentially mitigating, the effects of climate change. For one, assisted migration could stave off local extirpation of those species that exhibited little seed production and no long-distance dispersal. Manual disturbances that allow seedlings to emerge from the seed bank may also be a way to accelerate community adaptation to novel climates, if desired. Combined, this dissertation offers a much-needed empirical and *in situ* exploration of how regional dispersal dynamics, seed and seedling performance, and adult community response interactively shape patterns of plant community diversity.

Appendices

Appendix A. Supplementary Tables and Figures for Chapter 2

Tables

Table A-1. Pearson correlations of site abundances among stages.

	Seed Bank	Emergents	Established	Adults
Seed Rain	0.04	0.52	0.82	0.16
Seed Bank		0.87	0.18	0.42
All Seeds			0.55	0.44
Emergents				0.30

Correlations are calculated using the abundances of individuals at each stage at each site, ignoring species identity.

Table A-2. Summary statistics for trends in site-level abundances with climate.

***Model,* Variable**	**Estimate**	**St. Dev.**	**t-statistic**	**P-value**
Seed Rain				
Temperature	**259.00**	**84.00**	**3.08**	**0.02**
Precipitation	-0.18	0.18	-0.99	0.35
Temperature x Precipitation	-0.17	0.10	-1.58	0.15
Seed Bank				
Temperature	4.73	281.00	0.02	0.99
Precipitation	-0.60	0.61	-0.99	0.35
Temperature x Precipitation	0.40	0.35	1.14	0.29
Emerged Seedlings				
Temperature	47.30	16.90	2.79	0.22
Precipitation	-0.05	0.04	-1.32	0.83
Temperature x Precipitation	0.00	0.02	-0.22	0.81
% Established				
Temperature	0.01	0.03	0.25	0.81
Precipitation	0.00	0.00	-0.30	0.77
Temperature x Precipitation	0.00	0.00	0.43	0.68

Bold denotes variable significance. Climate variables show mean summer temperature (°C) and mean annual precipitation (mm), both centered at zero. Multiple linear regression models were used on site-aggregated abundance data (n = 12).

Table A-3. Pearson correlations of species abundances by stage.

	Seed Bank	Emergents	Established	Adults
Seed Rain	0.16	0.28	0.19	0.34
Seed Bank		0.30	0.28	0.18
All Seeds		0.37	0.32	0.30
Emergents			0.77	0.36
				0.37

Correlations are calculated using the abundances of individuals of each species at each stage at each site.

Table A-4. Abundances and site percentages of seeds, by climate origin.

MST	MAP	Local		Same MST		Cooler		Warmer		Unk. MST	
6.0	650	5199	(99%)	21	(0.4%)			3	(0.1%)	23	(0.4%)
6.0	1300	2870	(98%)	4	(0.1%)			20	(0.7%)	27	(0.9%)
6.0	2000	1671	(99%)	9	(0.5%)			6	(0.4%)	2	(0.1%)
6.0	2900	4001	(99%)	10	(0.2%)			19	(0.5%)	6	(0.1%)
9.0	650	3895	(98%)	52	(1.3%)	0	(0.0%)	5	(0.1%)	24	(0.6%)
9.0	1300	4260	(88%)	379	(7.9%)	0	(0.0%)	175	(3.6%)	7	(0.1%)
9.0	2000	2751	(98%)	34	(1.2%)	1	(0.0%)	5	(0.2%)	7	(0.3%)
9.0	2900	2071	(96%)	56	(2.6%)	0	(0.0%)	4	(0.2%)	30	(1.4%)
10.5	650	3686	(89%)	62	(1.5%)	395	(9.5%)			19	(0.5%)
10.5	1300	6052	(94%)	335	(5.2%)	23	(0.4%)			13	(0.2%)
10.5	2000	1847	(91%)	132	(6.5%)	19	(0.9%)			28	(1.4%)
10.5	2900	4465	(85%)	663	(12.6%)	28	(0.5%)			126	(2.4%)
				Same MAP		**Drier**		**Wetter**		**Unk. MAP**	
6.0	650	5199	(99%)	4	(0.1%)			20	(0.4%)	23	(0.4%)
6.0	1300	2870	(98%)	4	(0.1%)	1	(0.0%)	20	(0.7%)	27	(0.9%)
6.0	2000	1671	(99%)	7	(0.4%)	8	(0.5%)	0	(0.0%)	2	(0.1%)
6.0	2900	4001	(99%)	5	(0.1%)	24	(0.6%)			6	(0.1%)
9.0	650	3895	(98%)	52	(1.3%)			5	(0.1%)	24	(0.6%)
9.0	1300	4260	(88%)	534	(11.1%)	5	(0.1%)	16	(0.3%)	7	(0.1%)
9.0	2000	2751	(98%)	21	(0.8%)	1	(0.0%)	17	(0.6%)	7	(0.3%)
9.0	2900	2071	(96%)	50	(2.3%)	10	(0.5%)			30	(1.4%)
10.5	650	3686	(89%)	410	(9.9%)			47	(1.1%)	19	(0.5%)
10.5	1300	6052	(94%)	328	(5.1%)	28	(0.4%)	2	(0.0%)	13	(0.2%)
10.5	2000	1847	(91%)	144	(7.1%)	0	(0.0%)	8	(0.4%)	28	(1.4%)
10.5	2900	4465	(85%)	671	(12.7%)	20	(0.4%)			126	(2.4%)

Abundances are equal to the sum of seed rain and seed bank seed abundances at each site. MST and MAP refer to mean summer temperatures (°C) and mean annual precipitations (mm), respectively, and were rounded so sites fell into three temperature levels and four precipitation levels. For precise climate values refer to Figure 2.1.

Table A-5. Abundances and site percentages of seedlings, by climate origin.

MST	MAP	Local	Same MST	Cooler	Warmer	Unk. MST
6.0	650	400 (98%)	10 (2.4%)		0 (0.0%)	0 (0.0%)
6.0	1300	261 (99%)	2 (0.8%)		1 (0.4%)	0 (0.0%)
6.0	2000	110 (100%)	0 (0.0%)		0 (0.0%)	0 (0.0%)
6.0	2900	242 (98%)	4 (1.6%)		0 (0.0%)	0 (0.0%)
9.0	650	278 (100%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
9.0	1300	339 (96%)	14 (4.0%)	0 (0.0%)	1 (0.3%)	0 (0.0%)
9.0	2000	418 (93%)	26 (5.8%)	0 (0.0%)	2 (0.4%)	2 (0.4%)
9.0	2900	267 (95%)	14 (5.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
10.5	650	466 (94%)	29 (5.9%)	0 (0.0%)		0 (0.0%)
10.5	1300	414 (97%)	4 (0.9%)	8 (1.9%)		0 (0.0%)
10.5	2000	332 (92%)	16 (4.4%)	8 (2.2%)		6 (1.7%)
10.5	2900	285 (91%)	2 (0.6%)	26 (8.3%)		0 (0.0%)
			Same MAP	**Drier**	**Wetter**	**Unk. MAP**
6.0	650	400 (98%)	0 (0.0%)		10 (2.4%)	0 (0.0%)
6.0	1300	261 (99%)	2 (0.8%)	0 (0.0%)	1 (0.4%)	0 (0.0%)
6.0	2000	110 (100%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
6.0	2900	242 (98%)	1 (0.4%)	3 (1.2%)		0 (0.0%)
9.0	650	278 (100%)	0 (0.0%)		0 (0.0%)	0 (0.0%)
9.0	1300	339 (96%)	15 (4.2%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
9.0	2000	418 (93%)	28 (6.3%)	0 (0.0%)	0 (0.0%)	2 (0.4%)
9.0	2900	267 (95%)	10 (3.6%)	4 (1.4%)		0 (0.0%)
10.5	650	466 (94%)	29 (5.9%)		0 (0.0%)	0 (0.0%)
10.5	1300	414 (97%)	12 (2.8%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
10.5	2000	332 (92%)	22 (6.1%)	1 (0.3%)	1 (0.3%)	6 (1.7%)
10.5	2900	285 (91%)	28 (8.9%)	0 (0.0%)		0 (0.0%)

Abundances are equal to the number of emerged seedlings at each site. Unidentified seedlings were not considered. MST and MAP refer to mean summer temperatures (°C) and mean annual precipitations (mm), respectively, and were rounded so sites fell into three temperature levels and four precipitation levels. For precise climate values refer to Figure 2.1.

Table A-6. Summary statistics for emergence and establishment models using precipitation-based origins.

Model, Variable	Estimate	St. Dev.	z-statistic	P-value
Emergence: Zero Hurdle (Offset by # Seeds)				
Local Abundance	0.004	0.011	0.365	0.715
Temperature	-0.023	0.075	-0.307	0.759
Precipitation	-0.252	0.151	-1.667	0.096
Immigrant (Same precip.)	**-1.416**	**0.624**	**-2.268**	**0.023**
Immigrant (Other precip.)	**-2.119**	**0.675**	**-3.140**	**0.002**
Emergence: Count (Offset by # Seeds)				
Local Abundance	0.002	0.007	0.237	0.812
Temperature	-0.120	0.071	-1.686	0.092
Precipitation	-0.034	0.160	-0.212	0.832
Immigrant (Same precip.)	-0.159	0.803	-0.199	0.843
Immigrant (Other precip.)	**-2.687**	**1.321**	**-2.034**	**0.042**
Establishment Count (Offset by # Emerged)				
Local Abundance	0.005	0.003	1.465	0.143
Temperature	0.021	0.038	0.534	0.593
Precipitation	-0.036	0.082	-0.434	0.665
Immigrant (Same precip.)	-0.163	0.284	-0.575	0.565
Immigrant (Other precip.)	-0.365	0.383	-0.954	0.340

Bold denotes variable significance. Emergence is modeled using a two-step zero inflated hurdle model (see Methods). Climate variables are centered at zero.

Table A-7. Species list and abundances by life stage.

Species	Seed Rain	Seed Bank	Emerged	Established	Adults
Achillea millefolium	101	34	1	0	217
Aconitum septentrionale	0	0	0	0	3
Agrostis capillaris	1079	4554	108	103	480
Agrostis mertensii	9	0	0	0	25
Ajuga pyramidalis	0	15	0	0	0
Alchemilla alpina	198	351	189	68	183
Alopecurus pratensis	0	1	0	0	0
Anemone nemorosa	0	35	6	0	0
Antennaria dioica	45	1	0	0	78
Anthoxanthum odoratum	1783	398	20	17	184
Arabis alpina	0	13	0	0	0
Arabis hirsuta	0	5	0	0	0
Arctous alpinus	3	0	0	0	4
Astragalus alpinus	7	4	0	0	40
Avenella flexuosa	84	30	2	1	66
Bartsia alpina	0	0	0	0	2
Bistorta vivipara	179	455	76	16	194
Botrychium lunaria	0	0	0	0	5
Calluna vulgaris	0	468	2	0	17
Campanula rotundifolia	271	1966	113	28	69
Carex atrata	0	1	0	0	6
Carex bigelowii	59	22	0	0	51
Carex capillaris	55	45	0	0	56
Carex dioica	0	3	0	0	0
Carex echinata	31	3	0	0	4
Carex flava	0	1	0	0	5
Carex leporina	744	776	16	5	31
Carex nigra	6	34	1	0	14
Carex norvegica	6	139	0	0	24
Carex pallescens	229	1501	16	7	32
Carex panicea	1	13	0	0	11
Carex pilulifera	222	321	13	4	30
Carex pulicaris	12	3	0	0	8
Carex saxatilis	0	0	0	0	1
Carex vaginata	2	17	1	0	55
Carum carvi	2	0	4	3	5
Cerastium alpinum	0	2	1	0	4
Cerastium cerastoides	7	7	2	1	25
Cerastium fontanum	60	225	34	9	15
Cirsium palustre	0	3	0	0	12
Comastoma tenellum	1	0	0	0	3

Dactylis glomerata	1	0	0	0	1
Danthonia decumbens	6	0	0	0	0
Deschampsia alpina	0	0	1	1	0
Deschampsia cespitosa	616	520	1	1	145
Dianthus deltoides	30	137	26	7	13
Dryas octopetala	0	1	0	0	0
Empetrum hermaphroditum	35	3	2	0	12
Epilobium sp	1	545	14	3	21
Erigeron uniflorus	0	1	0	0	0
Euphrasia sp	276	14	128	38	47
Festuca ovina	236	3	1	0	66
Festuca rubra	126	87	5	3	95
Festuca vivipara	0	1	0	0	6
Filipendula ulmaria	0	1	0	0	0
Fragaria vesca	0	7	0	0	0
Galium boreale	0	8	0	0	2
Galium saxatile	9	10	4	0	4
Galium uliginosum	0	8	5	3	8
Galium verum	3	0	3	2	35
Gentiana nivalis	30	0	0	0	8
Gentiana purpurea	0	0	0	0	1
Gentianella amarella	2	0	4	4	2
Gentianella campestris	1	0	0	0	0
Geranium sylvaticum	20	3	1	0	15
Geum rivale	0	4	0	0	11
Hieracium alpinum	0	0	0	0	3
Hieracium pilosella	1060	419	157	5	182
Hieracium sp	0	0	0	0	2
Hieracium vulgatum	15	2	1	0	25
Hypericum maculatum	0	239	90	6	41
Hypochaeris maculata	4	0	0	0	8
Juncus alpinoarticulatus	0	18	0	0	4
Juncus bufonius	0	5	0	0	0
Juncus bulbosus	0	1	0	0	0
Juncus filiformis	0	183	0	0	0
Juncus trifidus	37	0	0	0	4
Knautia arvensis	24	3	7	3	59
Kobresia simpliciuscula	0	0	0	0	11
Leontodon autumnalis	813	66	127	33	119
Leucanthemum vulgare	460	116	18	2	13
Loiseleuria procumbens	16	0	0	0	0
Lotus corniculatus	3	8	6	3	52
Luzula multiflora	464	318	7	7	31
Luzula pilosa	2	130	2	2	4

Luzula spicata	3	1	0	0	21
Melampyrum pratense	1	0	10	6	7
Myosotis decumbens	0	0	0	0	3
Nardus stricta	1144	180	0	0	141
Noccaea caerulescens	1	0	53	2	11
Omalotheca norvegica	8	24	31	5	7
Omalotheca supina	10	58	9	4	29
Omalotheca sylvatica	2	167	0	0	2
Oxalis acetosella	6	4	0	0	9
Oxyria digyna	0	0	0	0	11
Parnassia palustris	5	85	0	0	28
Phleum alpinum	20	0	0	0	23
Phleum pratense	77	0	0	0	8
Phyllodoce caerulea	4	0	0	0	3
Pimpinella saxifraga	422	7	5	1	17
Pinguicula vulgaris	1	69	12	2	29
Plantago lanceolata	57	25	9	7	23
Plantago major	0	5	0	0	2
Plantago media	39	22	0	0	23
Poa alpina	62	81	10	3	52
Poa pratensis	330	86	1	0	45
Polygonum aviculare	0	1	0	0	0
Potentilla agrentea	0	33	17	2	3
Potentilla crantzii	4	10	7	2	21
Potentilla erecta	503	1197	102	27	158
Primula skandinavica	0	1	0	0	0
Prunella vulgaris	236	282	70	34	80
Pyrola sp	0	0	2	0	19
Ranunculus acris	139	577	46	18	53
Ranunculus auricomus	0	3	1	0	2
Ranunculus repens	0	0	0	0	8
Rhinanthus minor	19	2	5	1	17
Rhodiola rosea	0	0	0	0	1
Rubus idaeus	12	0	0	0	13
Rumex acetosa	683	1248	25	4	82
Rumex acetosella	529	0	158	117	54
Sagina sp	148	11134	258	108	27
Salix herbacea	11	1	2	0	97
Salix reticulata	20	0	0	0	7
Saussurea alpina	0	2	0	0	16
Saxifraga aizoides	0	94	7	3	9
Saxifraga cespitosa	0	2	0	0	0
Saxifraga oppositifolia	0	1	0	0	0
Saxifraga rivularis	0	2	0	0	0

Saxifraga stellaris	1	3	0	0	0
Schedonorus pratensis	0	18	0	0	0
Sedum acre	0	0	0	0	5
Sedum annuum	0	23	0	0	0
Selaginella selaginoides	762	0	1	0	46
Sibbaldia procumbens	3	300	213	64	67
Silene acaulis	49	0	26	2	62
Silene vulgaris	1	11	1	1	10
Solidago virgaurea	2	0	0	0	40
Stellaria graminea	163	6	40	21	23
Stellaria media	0	699	28	0	5
Succisa pratensis	0	0	0	0	10
Taraxacum sp	191	17	25	12	59
Thalictrum alpinum	29	63	1	0	105
Tofieldia pusilla	20	0	0	0	13
Trichophorum cespitosum	0	0	0	0	13
Trifolium medium	0	0	0	0	9
Trifolium pratense	229	15	6	3	78
Trifolium repens	20	98	50	4	158
Urtica diocia	0	54	0	0	0
Vaccinium myrtillus	2	10	3	1	22
Vaccinium uliginosum	2	1	1	0	6
Vaccinium vitis-idaea	0	0	0	0	16
Veronica alpina	26	36	6	1	51
Veronica chamaedrys	6	572	13	6	37
Veronica fruticans	4	0	4	1	10
Veronica officinalis	910	2571	152	62	293
Veronica serpyllifolia	0	2111	116	48	24
Vicia cracca	0	0	0	0	8
Viola biflora	30	92	16	0	78
Viola palustris	110	779	27	13	145
Viola riviniana	42	266	62	27	63
Viola tricolor	9	432	86	47	8
Viscaria vulgaris	0	51	6	5	3

Figures

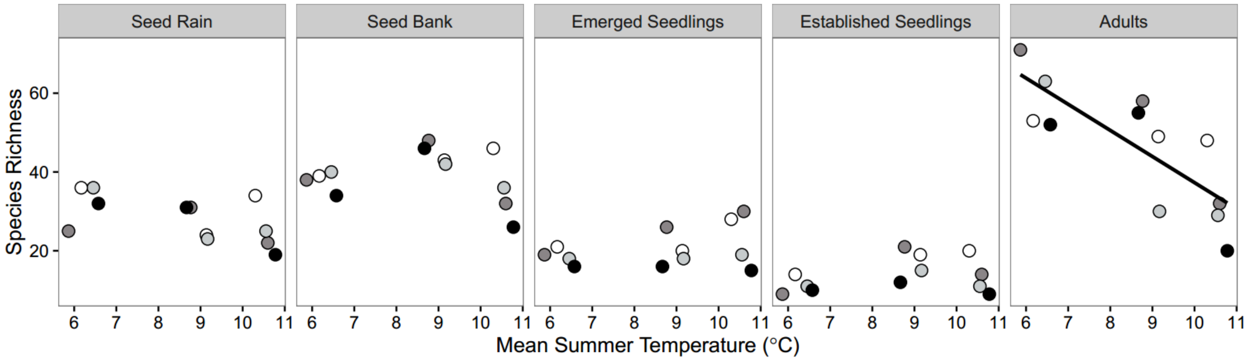

Figure A-1. Site-level species richness by life stage.
Site-level species richness values for each type of data used in this study, plotted by mean summer temperature. Regression lines are solid when significant ($p < 0.05$). Shapes and shadings are consistent with those shown in Figure 2.1, and reflect approximate mean summer temperatures of 6 ˚C (triangle), 9 ˚C (circle), and 10.5 ˚C (inverted triangle) and approximate annual precipitations of 650 mm (white), 1300 mm (light grey), 2000 mm (dark grey), and 2900 mm (black). There were no significant relationships between site-level richness and mean annual precipitation.

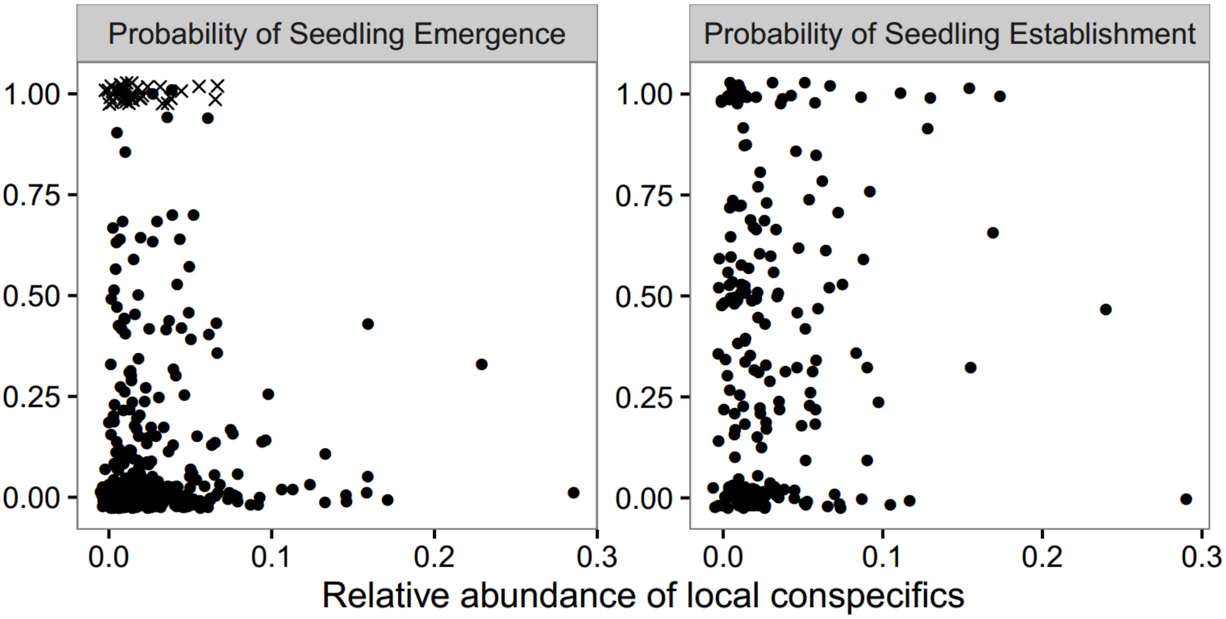

Figure A-2. Seedling emergence and establishment rates plotted by local adult abundance.

Seedling emergence and establishment rates, plotted by the relative abundances of local conspecifics. In the left panel, each filled circle represents the number of emerged seedlings divided by the number of seeds of one species at one site; crosses represent species for which there were fewer seeds than seedlings at that site, in which case seed number was increased such that the probability of seedling emergence was 100 %. In the right panel, each filled circle represents the number of established seedlings divided by the number of emerged seedlings of one species at one site. Circles are jittered along the y-axis to improve visibility. Linear regressions were not significant (i.e., $P > 0.05$) in either panel.

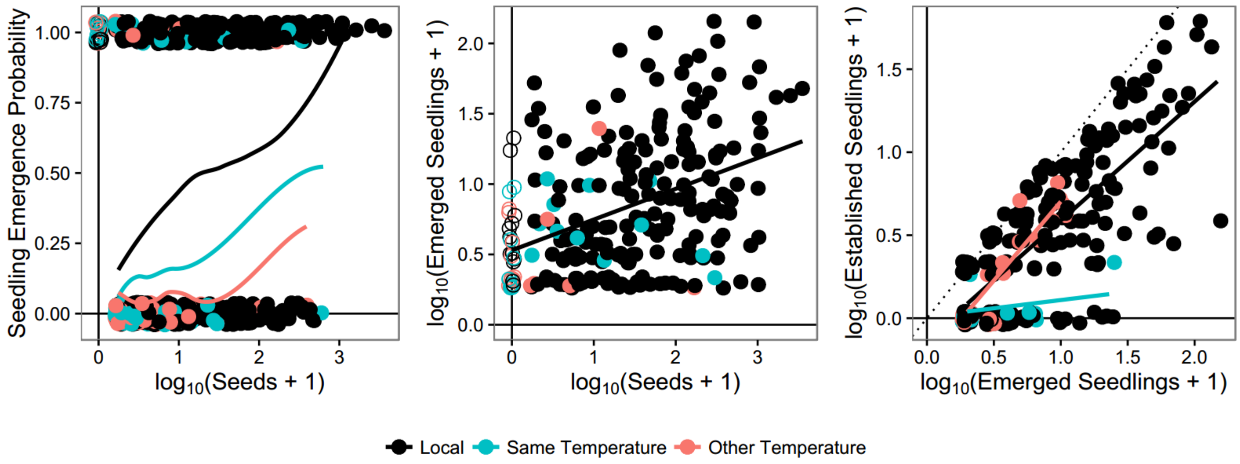

Figure A-3. Probabilities of species emergence, seedling emergence, and seedling establishment, grouped by species and seed origin, and including locals.
Numbers of emerged seedlings (left and center panels) plotted by seed number, and established seedlings (right panel) plotted by number of emerged seedlings. Each circle represents one species at one site, and seed number is equal to the sum of seeds in the seed rain and seed bank. Circles are jittered on both the x- and y-axes to improve visibility. All count data are increased by one to enable plotting zeroes on a log scale. Seeds are "Local" when adult conspecifics occur at the site. Non-local seeds originate from the "Same Temperature" when adult conspecifics occur at one or more of the sites with similar mean annual temperatures (see Figure 2.1), or from an "Other Temperature" when they do not. In the left panel, solid lines show a LOESS smoothing function reflecting the change in mean species emergence probability with seed density; species with no seed representatives were excluded from the calculation. In the center and right panels, solid lines reflect significant ($p < 0.05$) regression coefficients. Black regression lines were fitted to local species data. See Figure 2.4 for a version with local circles removed.

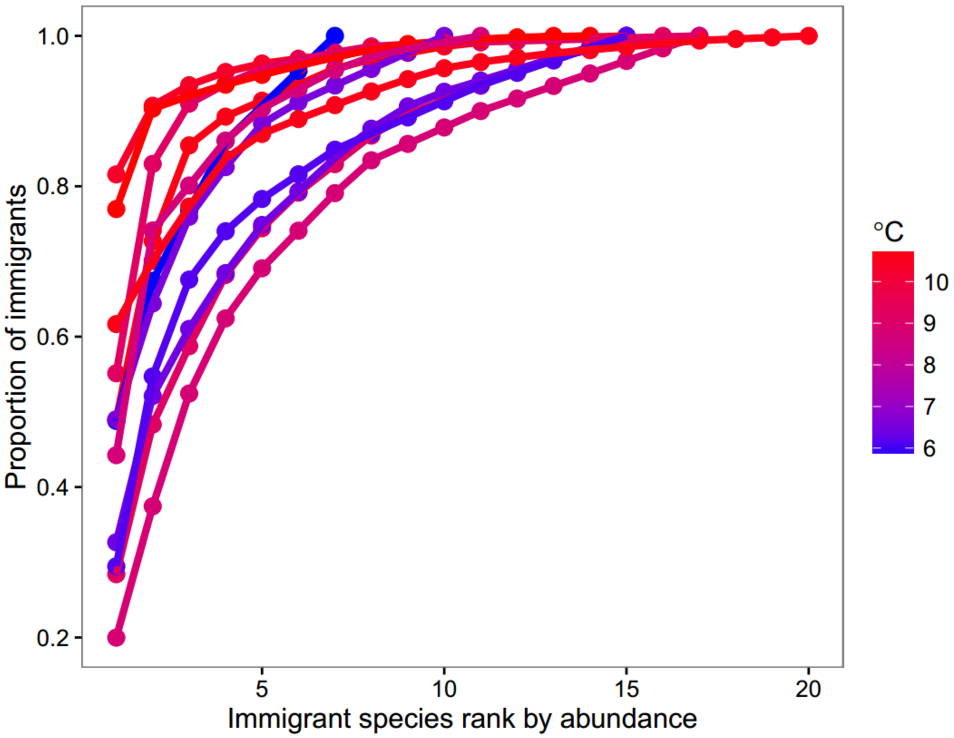

Figure A-4. Immigrant species accumulation curves.
Cumulative abundances of immigrant seeds plotted by species abundance rank by site. Each line reflects a site and is colored according to its mean annual temperature.

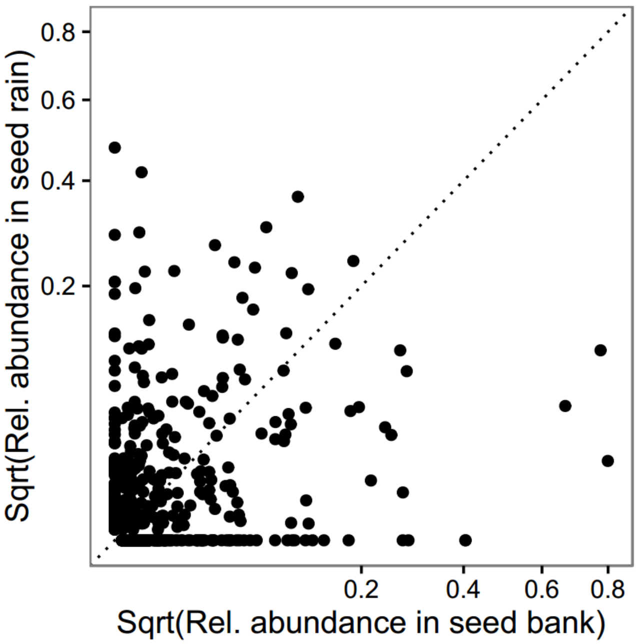

Figure A-5. Relative abundances of species in the seed rain and seed bank.
Relative abundances of species in the seed rain at the site level plotted by their relative abundances in the seed bank. Axes are plotted on square-root scales. The dotted line shows the 1:1 relationship. There is a significant linear relationship between the two variables ($p < 0.001$), but the R-squared value is only 0.02, so the trendline is not shown as it not meaningful.

Appendix B. Supplementary Tables and Figures for Chapter 3

Tables

Table B-1. Species list and trait values.

Species	Adults	Leaf Area	Max. Height	Seed Mass	SLA
Achillea millefolium	Y	2.674	-0.222	-0.889	1.223
Aconitum septentrionale	Y			0.559	
Agrostis capillaris	Y	2.378	-0.097	-1.222	1.439
Agrostis mertensii	Y	1.720	-0.523	-0.900	1.312
Ajuga pyramidalis	N	2.877	-0.602	0.186	1.239
Alchemilla alpina	Y	2.579	-0.699	-0.541	1.131
Anemone nemorosa	N	3.253	-0.523	0.331	1.367
Antennaria dioica	Y	1.873	-0.602	-1.301	1.254
Anthoxanthum odoratum	Y	2.093	-0.500	-0.311	1.410
Arctous alpinus	Y	2.140	-1.301	0.380	1.064
Astragalus alpinus	Y	2.389	-0.699		1.376
Avenella flexuosa	Y	2.393	-0.155	-0.508	1.196
Bartsia alpina	Y	2.424	-0.523	-0.481	1.244
Bistorta vivipara	Y	2.388	-0.523	0.262	1.193
Botrychium lunaria	Y	2.624	-0.824		1.326
Calluna vulgaris	Y	2.090	-0.301	-1.612	0.987
Campanula rotundifolia	Y	2.181	-0.301	-1.207	1.317
Carex atrata	Y	2.677	-0.222	-0.208	1.318
Carex bigelowii	Y	2.542	-0.398	-0.207	1.321
Carex capillaris	Y	1.783	-0.602	-0.249	1.225
Carex dioica	N	1.534	-0.523	-0.262	1.096
Carex echinata	Y	2.241	-0.523	-0.129	1.178
Carex flava	Y	2.454	-0.301	-0.067	1.397
Carex leporina	Y	2.214	-0.301	-0.208	1.224
Carex nigra	Y	2.202	-0.301	-0.132	1.250
Carex norvegica	Y	2.159	-0.398	-0.455	1.191
Carex pallescens	Y	2.591	-0.222	0.096	1.439
Carex panicea	Y	2.629	-0.301	0.369	1.228
Carex pilulifera	Y	2.362	-0.398	0.089	1.341
Carex pulicaris	Y	2.138	-0.699	0.168	0.969
Carex saxatilis	Y	2.551	-0.398	-0.102	1.075
Carex vaginata	Y	2.440	-0.301	0.481	1.334
Cerastium alpinum	Y	1.610	-0.699	-0.563	1.507
Cerastium cerastoides	Y	1.151	-1.000	-0.830	1.395
Cerastium fontanum	Y	2.261	-0.398	-0.848	1.438
Cirsium palustre	Y			0.193	1.258
Comastoma tenellum	Y		-1.000		
Dactylis glomerata	Y	3.161	0.079	-0.043	1.393
Danthonia decumbens	N	2.577	-0.398	0.163	1.229
Deschampsia alpina	N		-0.301		
Deschampsia cespitosa	Y	2.446	0.000	-0.678	1.175

Dianthus deltoides	Y	1.380	-0.602	-0.703	1.205
Dryas octopetala	N	2.339	-1.000	-0.135	1.009
Empetrum hermaphroditum	Y	1.801	-0.699	0.015	0.849
Epilobium sp	Y	1.966	-0.824	-1.213	1.344
Erigeron uniflorus	N		-0.824	-0.645	1.272
Euphrasia sp	Y		-0.602		
Festuca ovina	Y	2.397	-0.398	-0.362	1.155
Festuca rubra	Y	2.395	-0.155	-0.043	1.276
Festuca vivipara	Y	1.624	-0.523		1.041
Filipendula ulmaria	N		0.176	-0.127	1.386
Galium boreale	Y	1.690	-0.398	-0.152	1.288
Galium saxatile	Y	0.699	-0.699	-0.216	1.384
Galium uliginosum	Y	1.114	-0.398	-0.403	1.519
Galium verum	Y	1.503	-0.222	-0.298	1.246
Gentiana nivalis	Y	0.998	-0.699	-1.824	1.598
Gentiana purpurea	Y		-0.097	-0.319	
Gentianella amarella	Y	3.544	-0.602	-0.854	1.447
Gentianella campestris	N		-0.523	-0.706	1.468
Geranium sylvaticum	Y	3.244	-0.097	0.779	1.325
Geum rivale	Y		-0.398	0.009	1.314
Hieracium alpinum	Y		-0.699	0.004	1.495
Hieracium pilosella	Y	2.287	-0.523	-0.616	1.311
Hieracium vulgatum	Y	3.565	-0.097	-0.355	1.763
Hypericum maculatum	Y	2.686	0.000	-0.781	1.372
Hypochaeris maculata	Y	3.337	-0.222	0.215	1.298
Juncus alpinoarticulatus	Y		-0.398		
Juncus trifidus	Y	2.179	-0.602	-0.879	1.203
Knautia arvensis	Y	3.367	-0.097	0.616	1.261
Kobresia simpliciuscula	Y		-0.523	-0.319	
Leontodon autumnalis	Y	2.458	-0.398	-0.098	1.400
Leucanthemum vulgare	Y	2.826	-0.155	-0.419	1.285
Loiseleuria procumbens	N	0.951	-1.000	-1.773	0.653
Lotus corniculatus	Y	2.135	-0.523	0.146	1.319
Luzula multiflora	Y	2.555	-0.398	-0.398	1.366
Luzula pilosa	Y	2.822	-0.602	-0.014	1.400
Luzula spicata	Y	1.788	-0.602	-0.514	1.086
Melampyrum pratense	Y	2.380	-0.398	0.753	1.384
Myosotis decumbens	Y		-0.398		
Nardus stricta	Y	2.734	-0.523	-0.448	0.988
Noccaea caerulescens	Y	2.546	-0.412	-0.189	1.366
Omalotheca norvegica	Y	2.538	-0.523	-1.046	1.319
Omalotheca supina	Y	1.936	-0.824	-1.081	1.391
Omalotheca sylvatica	Y		-0.398	-1.337	1.379
Oxalis acetosella	Y	2.779	-1.000	-0.019	1.693

Oxyria digyna	Y	2.906	-0.523	-0.143	1.424
Parnassia palustris	Y	2.535	-0.602	-1.481	1.407
Phleum alpinum	Y	2.374	-0.523	-0.415	1.285
Phleum pratense	Y	2.580	0.000	-0.233	1.386
Phyllodoce caerulea	Y	0.925	-0.824	-1.684	1.010
Pimpinella saxifraga	Y	3.417	-0.301	0.058	1.199
Pinguicula vulgaris	Y	2.334	-0.699	-1.737	1.553
Plantago lanceolata	Y	3.357	-0.301	0.208	1.283
Plantago major	Y		-0.523	-0.576	1.324
Plantago media	Y	3.645	-0.301	-0.422	1.285
Poa alpina	Y	2.032	-0.398	-0.367	1.209
Poa pratensis	Y	2.777	0.000	-0.571	1.345
Potentilla agrentea	Y	2.722	-0.301	-1.008	1.223
Potentilla crantzii	Y	2.285	-0.602	-0.197	1.180
Potentilla erecta	Y	2.324	-0.523	-0.319	1.362
Prunella vulgaris	Y	2.691	-0.602	-0.164	1.406
Pyrola sp	Y	2.622	-0.641	-2.682	1.230
Ranunculus acris	Y	2.709	-0.125	0.237	1.354
Ranunculus auricomus	Y	3.106	-0.301	0.365	1.504
Ranunculus repens	Y	3.270	-0.398	0.350	1.414
Rhinanthus minor	Y	2.557	-0.398	0.428	1.297
Rhodiola rosea	Y	2.057	-0.523	-0.509	1.376
Rubus idaeus	Y	3.118	0.176	0.310	1.322
Rumex acetosa	Y	3.143	-0.097	-0.026	1.439
Rumex acetosella	Y	2.243	-0.301	-0.449	1.349
Sagina sp	Y	1.300	-1.301	-1.699	1.255
Salix herbacea	Y	2.155	-1.301	-0.707	1.271
Salix reticulata	Y	2.323	-1.301	-0.818	0.982
Saussurea alpina	Y	2.888	-0.301	0.243	1.256
Saxifraga aizoides	Y	1.807	-0.824	-1.312	1.111
Saxifraga cespitosa	N		-0.824	-1.301	
Saxifraga oppositifolia	N		-1.301	-0.963	1.170
Sedum acre	Y		-1.000	-1.469	1.037
Selaginella selaginoides	Y	0.086	-1.000		1.389
Sibbaldia procumbens	Y	2.396	-1.000	-0.298	1.204
Silene acaulis	Y	1.546	-1.301	-0.510	1.241
Silene vulgaris	Y	3.072	-0.155	-0.029	1.328
Solidago virgaurea	Y	3.362	0.000	-0.220	1.336
Stellaria graminea	Y	1.898	-0.523	-0.479	1.374
Stellaria media	Y	2.688	-0.523	-0.420	1.730
Succisa pratensis	Y	3.144	-0.222	0.135	1.254
Thalictrum alpinum	Y	2.214	-0.699	-0.071	1.211
Tofieldia pusilla	Y	1.737	-0.699	-1.444	1.218
Trichophorum cespitosum	Y		-0.398		
Trifolium medium	Y	3.157	-0.301	0.327	1.314

Trifolium pratense	Y	2.787	-0.301	0.198	1.258
Trifolium repens	Y	2.679	-0.398	-0.233	1.421
Vaccinium myrtillus	Y	2.215	-0.301	-0.571	1.280
Vaccinium uliginosum	Y	2.069	-0.222	-0.636	1.161
Vaccinium vitis-idaea	Y	1.803	-0.523	-0.549	0.884
Veronica alpina	Y	2.172	-0.824	-1.093	1.365
Veronica chamaedrys	Y	2.488	-0.523	-0.690	1.384
Veronica fruticans	Y	2.020	-1.000	-0.864	1.241
Veronica officinalis	Y	2.231	-0.523	-0.918	1.259
Veronica serpyllifolia	Y	2.127	-0.699	-1.347	1.407
Vicia cracca	Y	2.987	-0.097	1.206	1.405
Viola biflora	Y	2.430	-0.824	-0.131	1.627
Viola palustris	Y	3.069	-1.000	-0.165	1.488
Viola riviniana	Y	2.691	-0.699	0.079	1.372
Viola tricolor	Y	2.644	-0.523	-0.102	1.432
Viscaria vulgaris	Y		-0.398		

The adult column refers to whether there were adult representatives of this species in the study system dataset. If not (N), the species were only observed as seeds or seedlings.

Figures

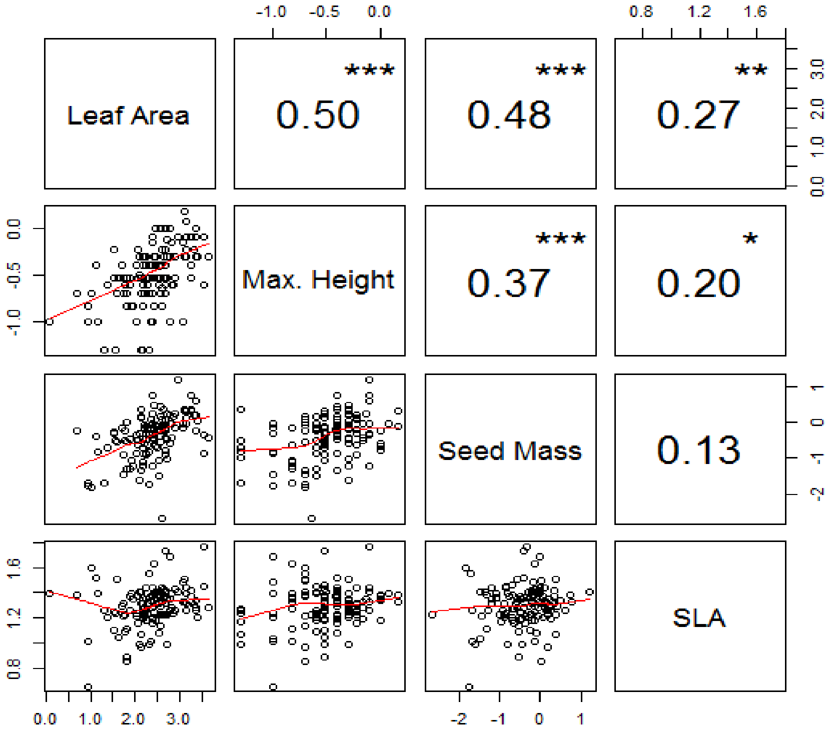

Figure B-1. Pairwise trait correlations among species.
Scatter plots (below the diagonal) and Pearson correlations (above the diagonal) illustrating pairwise relationships between trait values at the species level. Red lines show a locally weighted polynomial regression (LOWESS). Asterisks denote significance (., $P < 0.1$, *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

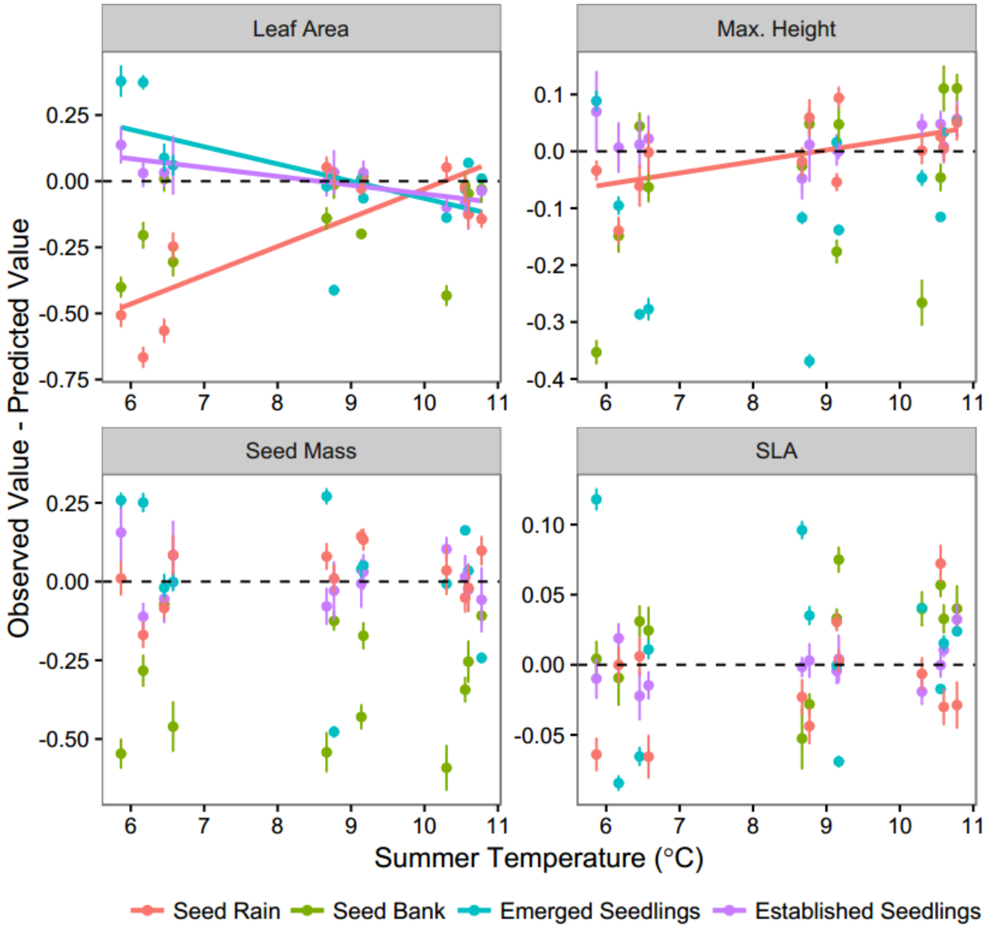

Figure B-2. Stage-specific community trait means versus neutral expectations, plotted by site temperature.

Scatter plot showing the differences between observed community metrics and those predicted by a null model assuming equal transition probabilities among individuals in the prior stage, over four plant life stages. Null model predictions (N = 100 null simulations) are calculated as described in Figure 2; error bars reflect ± 2.0 S.D. of null model predictions for that site. Panels show community weighted mean trait values. Dashed lines show where observed and predicted values would be equal. Colored lines show when regressions with site mean summer temperature are significant ($p < 0.05$).

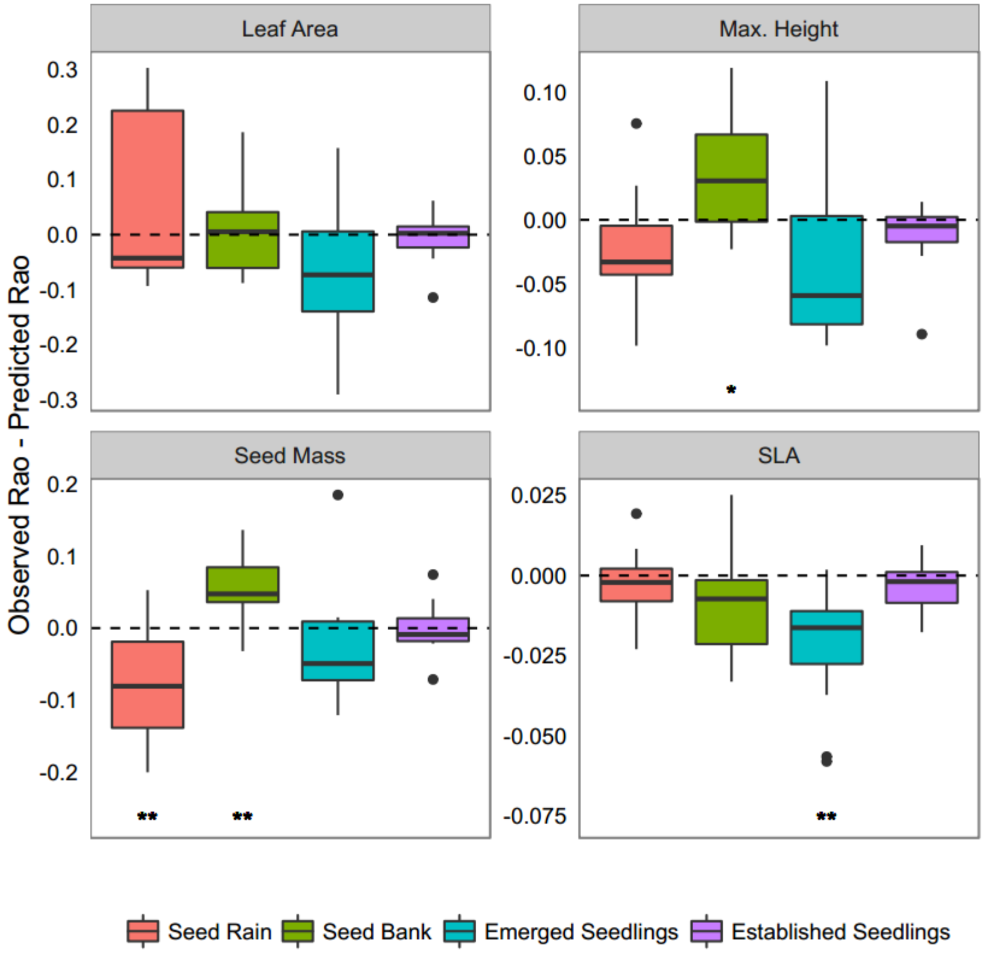

Figure B-3. Stage-specific community Rao coefficients versus neutral expectations.

Boxplots of the differences between observed and predicted community Rao coefficients of trait distributions at sites. Data above the dashed line indicates that communities had Rao coefficients that were greater (i.e., more overdispersed) than expected by chance, whereas data below the dashed line indicates that communities had Rao coefficients smaller than expected by chance. Predictions were generated by neutral models assuming equal transition probabilities for individuals in the prior stage. Seed rain and seed bank predictions assume equal seed production and dispersal from adults; seedling emergence predictions assume equal probability among all seeds in the seed bank and seed rain; seedling establishment predictions assume equal probability among emerged seedlings. Community trait metrics are calculated at the site level (N = 12). Asterisks denote significance *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The lower and upper limits of the colored boxes correspond to the first and third quartiles, respectively, and whiskers extend to the highest and lowest values within 1.5 times the first and third quartiles, respectively. Data beyond the whiskers are outliers and plotted as filled circles.

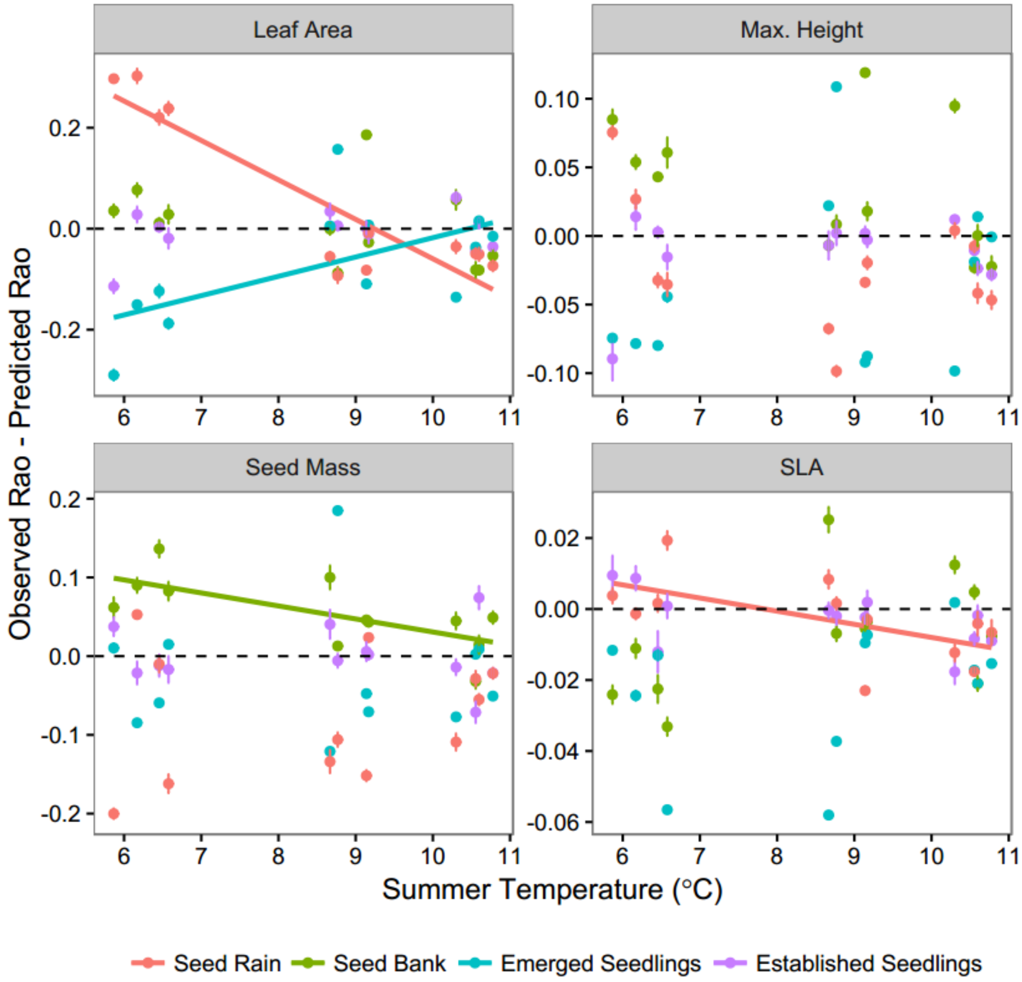

Figure B-4. Stage-specific community Rao coefficients versus neutral expectations, plotted by site temperature.

Scatter plot showing the differences between observed and predicted community Rao coefficients of trait distributions at sites. Data above the dashed line indicates that communities had Rao coefficients that were greater (i.e., more overdispersed) than expected by chance, whereas data below the dashed line indicates that communities had Rao coefficients smaller than expected by chance. Predictions were generated by neutral models (N = 100 null simulations) assuming equal transition probabilities for individuals in the prior stage. Seed rain and seed bank predictions assume equal seed production and dispersal from adults; seedling emergence predictions assume equal probability among all seeds in the seed bank and seed rain; seedling establishment predictions assume equal probability among emerged seedlings. Error bars reflect ± 2.0 S.D. of null model predictions for that site. Dashed lines show where observed and predicted values would be equal. Colored lines show when regressions with site mean summer temperature are significant ($p < 0.05$).

Appendix C. Supplementary Tables and Figures for Chapter 4

Figures

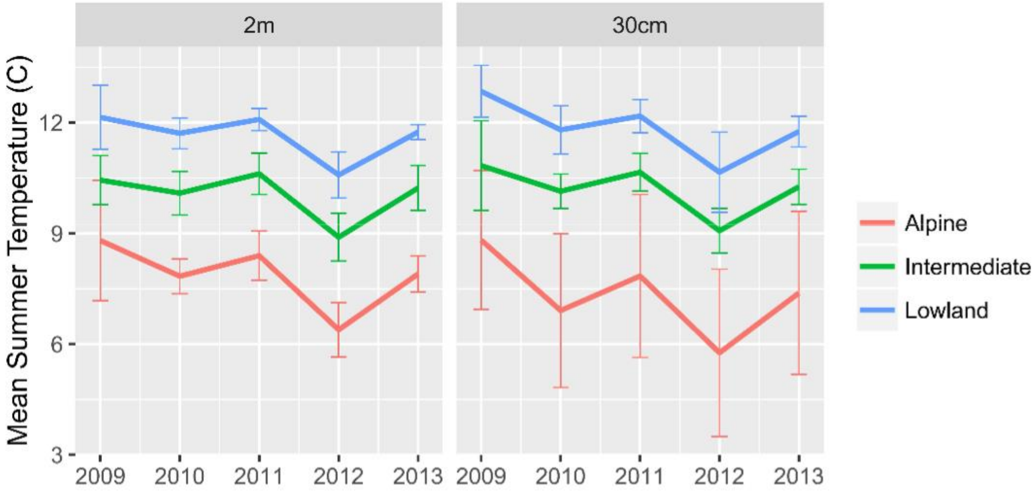

Figure C-1. Mean summer temperatures at 2m and 30cm above ground level. Mean summer temperature values measured over the duration of the experiment at two heights above ground (2 m and 30 cm). Summer temperatures reflect the mean of the four warmest months, calculated individually by site. Four site values are included in each temperature level; error bars reflect ± 1.0 SD.

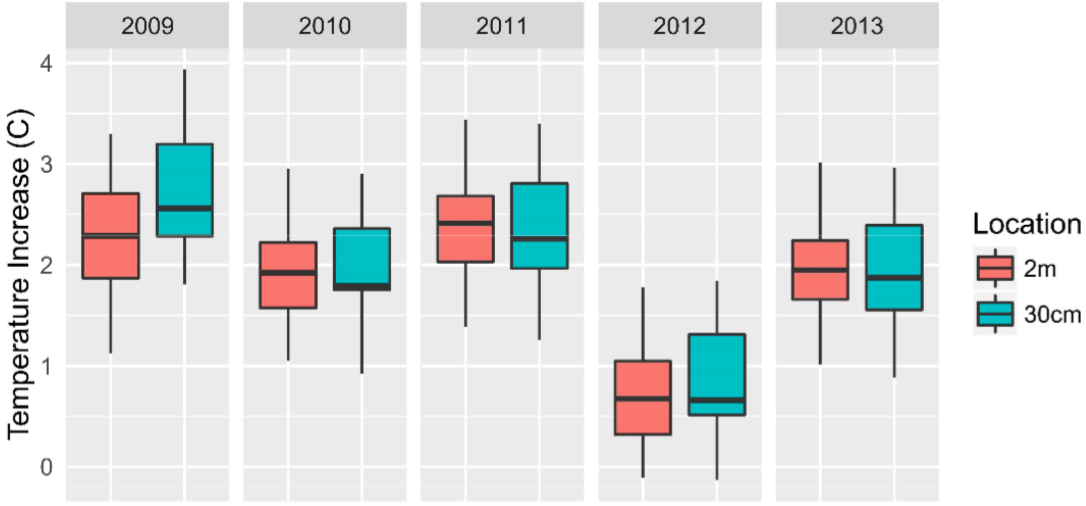

Figure C-2. Mean increases in temperature experienced by turf transplants. A boxplot diagram depicting the mean increase in temperature experienced by turfs transplanted to warmer sites over the duration of the experiment. Measurements occurred at two heights (2 m and 30 cm). Temperature increase was determined by subtracting the mean temperature of the turf origin site from the mean summer temperature at the destination site each year. Summer temperatures reflect the mean of the four warmest months, calculated individually by site.

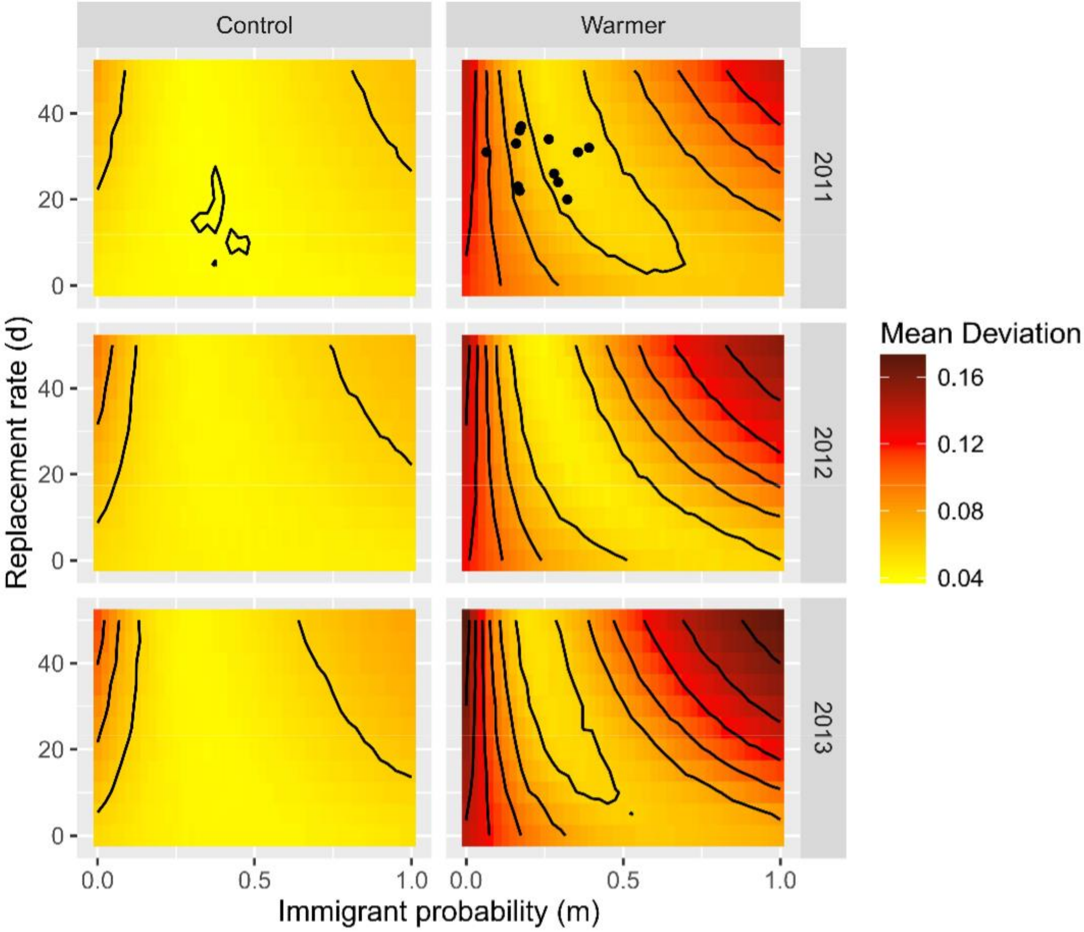

Figure C-3. Heat map comparing neutral simulations to transplant observations. A contoured heat map showing the alignment of model simulations to field data in terms of species composition under a broad survey of replacement rates (d) and immigration rates (m). The heat map depicts the mean difference ("Mean Deviation") in Bray-Curtis dissimilarity of species-level composition between observed field data and 100 simulation reps for each set of parameters. In the top right panel, solid circles show the combinations of site-level immigration and replacement rates used in null model simulations.

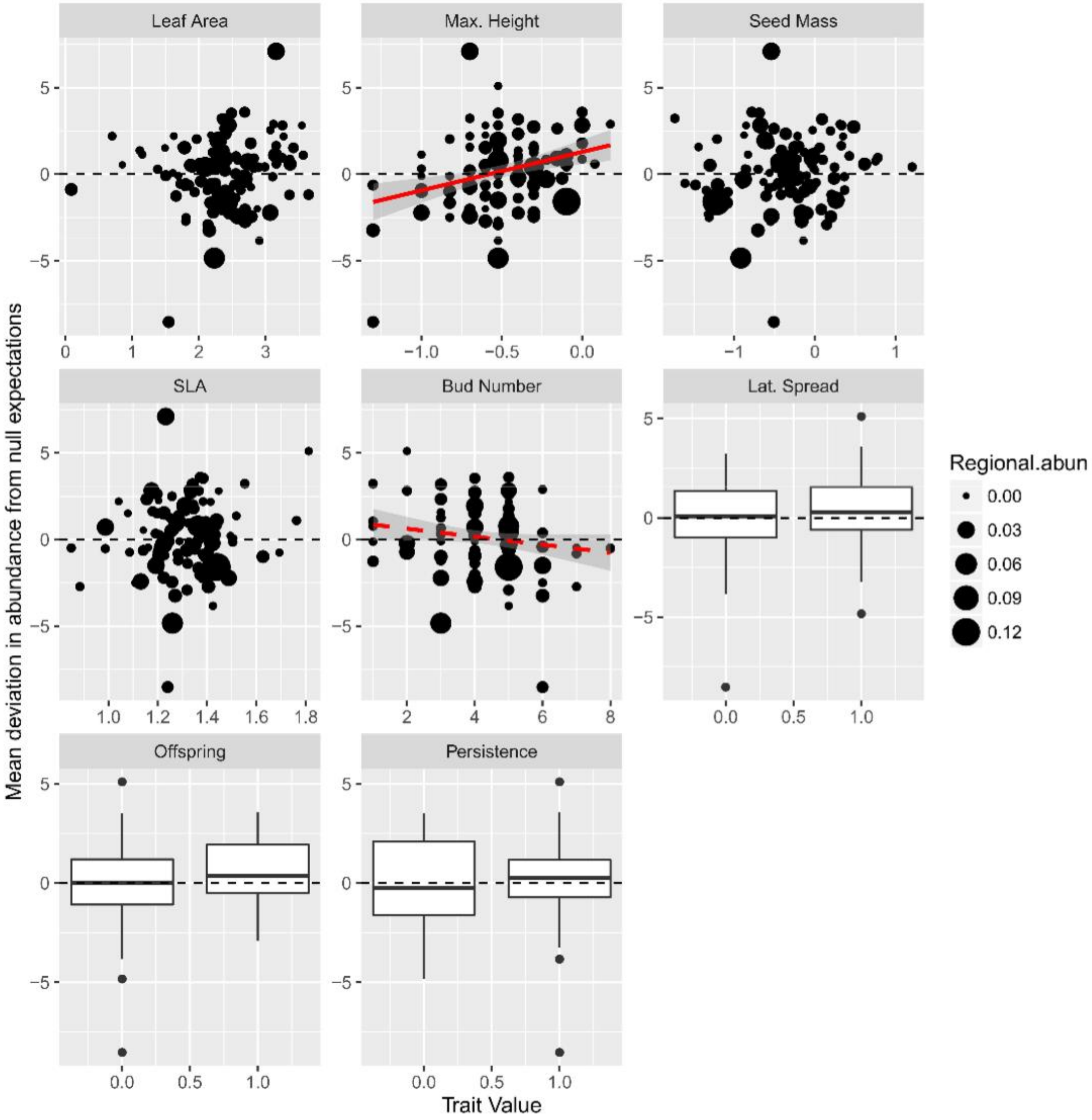

Figure C-4. Differences between observed and predicted species abundances. Differences between predicted and observed species abundances in 2013, plotted by trait value using scatterplots (continuous traits) or boxplots (binary traits). Red lines and 95% confidence intervals are shown when there are significant (solid red line) or nearly significant (dashed red line) relationships. The diameter of each solid circle is proportional to its abundance in the region.

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