

DO TRAIT-BASED GRADIENT PATTERNS PREDICT PLANT COMMUNITY RESPONSE TO CLIMATE CHANGE?

Keywords: Plant functional traits, climate change, community assembly, turf transplantation,
subalpine grasslands, community response

Elements included in this submission:

1. This manuscript
2. Online appendix A (included at the end of this document)
3. traitAnalysis_2015June17.Rmd: An R markdown file including the analysis and
simulation code used in this study. The file will not run without the raw data, which are
large in size and not included in this initial submission.
4. Traitdata.csv: a comma-separated value file including the list of species found in this
study and their accompanying trait data.

This submission is meant for consideration as an ‘article.’

ABSTRACT

Plant functional traits are explicitly connected to plant ecological performance and vary consistently along climate gradients. As such, current trait-climate associations are potential predictors of plant community response to climate change. However, trait-climate associations may fail as predictors if the processes driving short-term community response to rapid climate change differ from those governing longer-term community response. We test this idea using a combination of gradient analyses and whole-community turf transplantation along temperature and precipitation gradients in a network of 12 grassland sites in SW Norway. Turf transplantation differs from *in situ* approaches to climate manipulation by providing a maximum rate of immigration of individuals adapted to the local climate conditions, an important but often overlooked component to plant community response. Using trait data for 169 species and annual vegetation censuses of 235 turfs over four years, we show that species maximum height – the trait with the strongest association to temperature in our system – significantly influences species success in turfs transplanted to warmer climates. We test for the influence of individual traits on community dynamics by comparing our experimental observations to trait-neutral null model simulations. Our study provides rigorous experimental evidence connecting trait-climate correlations and trait-mediated community responses to rapid climate change.

INTRODUCTION

Plant functional traits, defined as measurable species characteristics with explicit connections to individual performance, reflect plant ecological strategy and exhibit consistent shifts along climatic gradients (Wright et al. 2005; McGill et al. 2006; Violle et al. 2007). As such, species-level functional traits ('traits' hereafter) have the potential to be predictors of community response to climate change. In addition, traits, unlike taxonomic definitions, are usually quantitative, taxon independent, and can be directly linked to the environment, making them particularly well suited for general insight and integration into mechanistic models of community response and community function (Suding et al. 2008; Webb et al. 2010).

Trait values associate with environmental factors at many spatial and ecological scales, supporting a general connection with species strategy (Reich et al. 2003; Silvertown 2004; Wright et al. 2005). Canopy height and seed mass, for example, show global and local patterns and are thought to represent fundamental tradeoffs relating to disturbance regime and dispersal ability, respectively (Thompson et al. 1998; Westoby 1998; Wright and Westoby 1999). SLA, leaf area, and leaf C/N ratio, three traits that covary strongly among species and reflect an axis of variation in plant 'economic' strategy, correlate to both soil moisture and temperature (Wright et al. 2004; Sterck et al. 2006; Ackerly and Cornwell 2007). Trait-environment data can be used to explain species turnover along environmental gradients (Shipley et al. 2006). Given the strong correlations linking plant traits, species strategies, and climate variables, it is reasonable to assume that trait patterns seem likely to track future changes in climate, leading to the maintenance of current trait-environment associations.

However, there are reasons why current trait-climate relationships could be poor predictors of community responses to climate changes, especially in the short term. First, given

the unprecedented rate of anthropogenic climate change (Solomon et al. 2007), it is not clear if species will adapt or migrate fast enough to maintain their current associations to climate, which developed over much longer time scales (Fox et al. 1999; Post and Pedersen 2008; Visser 2008). Instead, community compositions may be in continual flux as species show variable and inconsistent range limits as their populations adjust to shifting climate regimes or go extinct (Lande 1993; Neilson et al. 2005). Second, climate change could directly or indirectly disrupt biotic interaction networks, leading to idiosyncratic species responses that are inconsistent with expectations based on general trait-environment relationships. Indeed, climate change has already indirectly affected plant community compositions through disruptions of plant-herbivore dynamics (Fox et al. 1999; Post and Pedersen 2008) and plant-pollinator dynamics (Kudo et al. 2004). The variance in many trait-climate relationships at the species (Reich and Oleksyn 2004; Wright et al. 2004; Wright et al. 2005; Moles et al. 2007) and community levels (Cornwell and Ackerly 2009; Spasojevic and Suding 2012) is a reminder that factors other than climate influence trait-based community composition. Ultimately, if the processes that drive short-term community response are different from those that govern long-term community response, community dynamics could be neutral or even run counter to predictions derived from trait patterns along gradients.

Trait-based predictions of community response to climate change are conceptually appealing and potentially powerful, but evaluating their accuracy is difficult. One strategy is to use long-term monitoring (Soudzilovskaia et al. 2013) or reconstruction of past events using paleoecological data (Wolfe 1995; Peppe et al. 2011). These observation-based approaches have provided insight into how species and community compositions have responded to past climate change. However, experimental approaches are necessary to directly test how current plant

communities will respond to future climate change. Most experimental attempts to simulate climate change so far have modified climate *in situ* using equipment installations (Hobbie and Chapin III 1998; Shaw and Harte 2001; Liu et al. 2009; Hudson et al. 2011). *In situ* approaches have provided invaluable insights, but like all experimental methods they have their weaknesses. First, *in situ* plots are circumscribed by species and ecotypes adapted to pre-experiment conditions. As a result, the probability that propagules better suited to the new environmental conditions will reach the plot is less than would be true in real climate change scenarios, which would undergo more gradual change that allowed for some species to track climate. Indeed, *in situ* experiments could actually suppress community responses if propagule pressure from locally abundant species is high. This disregard for immigration is unfortunate as it is a central component of community response to climate change (Gottfried et al. 2012). Second, on-site climate manipulations suffer from undesirable side effects related to their experimental methods, which generally involve heat lamps, open top chambers, shade netting, or rain catches (Hobbie and Chapin III 1998; Shaw and Harte 2001; Liu et al. 2009). Open and closed-top chambers, for example, alter light intensity, light quality, seed dispersal, and wind speed, and can create non-uniform conditions within experimental treatments (Aronson and McNulty 2009). The difficulties in accounting for both the biotic and abiotic components of climate change impede progress in understanding the relationship between climate and plant community dynamics.

In this study, we investigate the effects of climate change on plant communities using an alternative approach that mitigates the concerns of on-site climate manipulations described above: transplantation of entire, intact communities to warmer, wetter, and warmer and wetter 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. Indeed, it lies at the other extreme of *in situ* climate manipulations: it provides a liberal estimate of rate of community change because immigration of already-adapted species is higher than would be expected in communities subject to gradual environmental change. Unlike most gradient studies which focus on single environmental variables, we conduct our transplant experiment within a network of 12 sites that differ in both temperature and precipitation. Sites were selected so that temperature and precipitation varied independently, creating a ‘climate grid’. This layout enables us to separate the effects of two important climate drivers, thereby gauging their relative influence and identifying interactive effects. We monitor changes in the functional composition of 235 turf communities over five years using species-level averages of five commonly measured plant traits: leaf area, leaf C/N ratio, maximum vegetative height, seed mass, and specific leaf area (SLA). At its core, our study is a test whether traits with broad associations to the current climate can be used to predict community response to rapid climate change.

The inclusion of immigration in our experimental design is an important contribution to improving predictions of community response, but also requires an explicit reevaluation of our null expectations. Even under trait-neutral dynamics, natural turnover rates combined with the immigration and proliferation of locally-adapted species will result in experimental turf communities converging compositionally with local sites over time. Thus, tests for trait-mediated dynamics should evaluate turf responses only in comparison to null models that include stochastic replacement and immigration. Unfortunately, it is extremely difficult to measure these baseline rates in the field. We circumvent this challenge inferring the maximum possible rates of stochastic replacement and immigration that could have occurred in our experiment. We then compare simulations and observed data to identify when traits significantly influenced turf

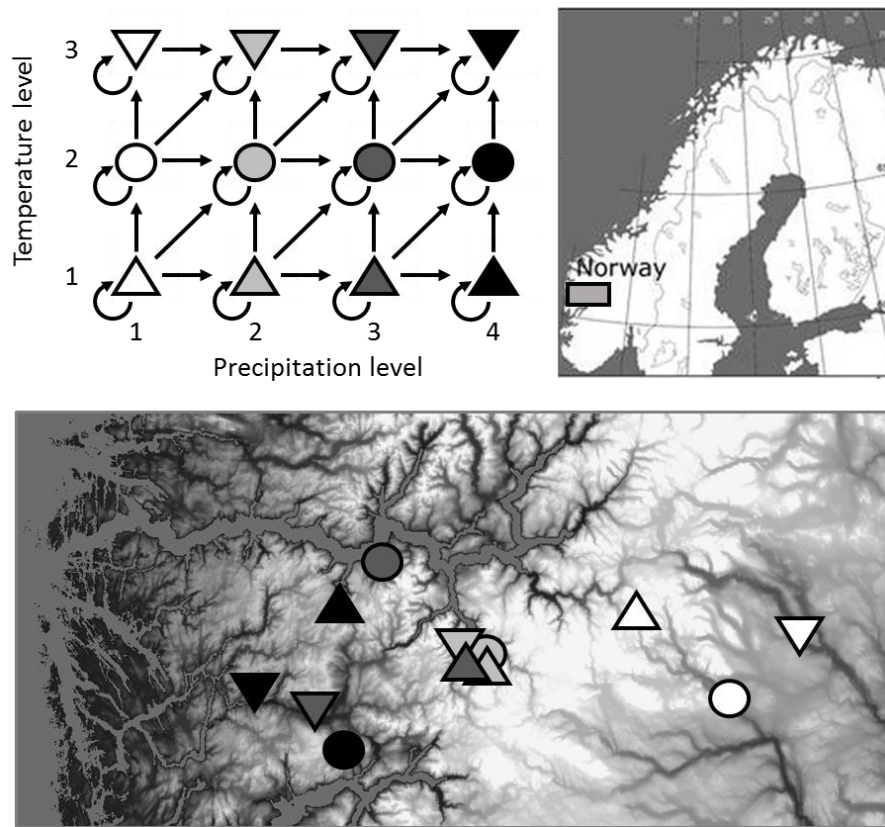
community response to transplantation. We use results from our gradient analysis, transplant experiment, and model simulations to address four questions: 1) Which traits vary with temperature and precipitation gradients? 2) Do temperature and precipitation affect trait patterns additively or interactively? 3) What is the rate and direction of trait-based community response to experimental increases in temperature and/or precipitation? 4) Do the same traits that correlate with climate gradients also drive community response to climate perturbations? We expect short species with conservative strategies (low SLA, low leaf area, high leaf C/N) to predominate in unproductive climates (the coldest and driest sites) and be outcompeted by tall species with exploitative strategies (high SLA, high leaf area, low leaf C/N) in productive climates (warmest and wettest sites). Our study is one of the first rigorous experimental examinations of the potential for commonly measured plant traits to predict community-level responses to environmental change.

METHODS

Study site description and turf transplantation experiment

The study area is located in an approximately 500 km x 500 km region in southern Norway (Figure 1). The region exhibits steep altitudinal gradients (0m – 2500m above sea level) which correlates with temperature, and a strong precipitation gradient from east to west (~380mm to ~3800mm, respectively). In this climatically heterogeneous area, twelve grassland sites were selected that differed in mean annual temperature and/or precipitation while other abiotic variables were relatively uniform (Klanderud et al. unpublished manuscript). Each site has one of three mean summer temperatures (7.5, 9.5, and 11.5°C) and one of four mean annual precipitations (600, 1200, 2000, and 2700mm), while all sites have calcareous soils, a southwest

150 aspect, slopes of about 20 degrees, similar grassland flora, and comparable grazing and land-use
151 history.



152

153 FIGURE 1. A map of the 12 study sites in southwest Norway. Sites are positioned in the upper
154 left panel according to their mean summer temperature level (shape) and mean annual
155 precipitation level (shading). Black arrows represent turf transplants in replicates of five. The
156 five undisturbed control turfs at each site are not shown.

The grasslands' short stature (usually $< 0.5\text{m}$ at peak biomass) and shallow but thickly interwoven root and rhizome mats allowed for the easy removal, transport, and replanting of soil 'turfs' and their attached flora to different hillsides. Each $0.25\text{m} \times 0.25\text{m}$ turf contained tens to hundreds of individual stems from 10-40 vascular plant species, as well as a bryophyte layer and the local soil and leaf litter biota (Klanderud et al. unpublished manuscript). In accordance with predictions that southern Norway will grow warmer and wetter as climate change proceeds (Hanssen-Bauer et al. 2009), 45 turfs were transplanted to warmer sites, 40 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. Thus, each turf has an origin site and a destination site; for controls, they are the same site. Vascular plant turf community censuses were undertaken in 2009 (before transplantation), 2011, 2012, and 2013, for a total of 928 community time points (12 community time points were discarded due to physical damage to the turf). For each turf census, percent cover of each species was estimated visually with the aid of a $5\text{cm} \times 5\text{cm}$ grid; to account for bare patches and/or overlapping individuals, net percent cover could fall below or above 100%. Environmental data were gathered continuously at all 12 sites (air temperature at 2m and 30cm, ground temperature at 0cm and 5cm depth, and soil moisture at 5cm depth).

Trait data

We built a custom database containing values for up to five traits for the 181 species present in our turf communities from across the climate grid. Fourteen of the 169 species could only be identified to the genus level, but are treated as species in downstream analyses. Traits included: leaf area (mm^2), Specific Leaf Area (SLA) ($\text{m}^2/\text{kg}^{-1}$), leaf C/N ratio, maximum

potential height (m), and seed mass (mg). 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. We gathered five healthy mature leaves from five different individuals at each site for each available species (representing 80 species and 94% of total cover). We took digital pictures of flattened freshly-sampled leaves beside a scale bar for reference and calculated leaf area using the imaging processing program, ImageJ (Abràmoff et al. 2004). The leaves were transported back to the lab, dried in an oven at 60C for 72 hours, and weighed on a digital scale in accordance with established protocol (Cornelissen et al. 2003). Before merging our field data with LEDA data, we ensured that the two datasets were compatible by comparing values from shared species (SLA $R^2 = 0.47$, leaf area $R^2 = 0.63$). The combined leaf area data set represents 149 species and 98.6% of total cover; the combined SLA data set represents 162 species and 99.32% of total cover. Maximum potential height data were mined from Lid and Lid (2007) and represent 164 species and 90.8% of total cover. We drew seed mass data from the Seed Information Database (SID) (Royal Botanic Gardens Kew 2014), representing 144 species and 87.8% of total cover. All trait values were log-transformed. The species list and trait values are publically available on Dryad (pending). Species-level and community-level trait correlations were relatively low (Table A1 and Table A2) and were thus treated univariately throughout this study.

Community analysis

Bray-Curtis dissimilarity was used to describe patterns in species composition. Community weighted means (CWMs) were used to represent functional composition of continuous traits (leaf area, leaf C/N, maximum height, seed mass, SLA). CWMs are calculated

by averaging the trait values for all species in a community, weighted by their abundance and thus represent the expected trait value of a random community sample.

Natural patterns of community variation along temperature and precipitation gradients were assessed using pre-transplant (2009) turf communities. We used linear regressions to test for significant relationships between continuous traits (CWMs) and climate gradients. Species-level gradient patterns and responses to transplantation are explored in depth by (Klanderud et al. unpublished manuscript) and Vandvik et al. (unpublished manuscript) so are not reported on in detail here.

We quantify community change as the difference in species or trait dissimilarity between turfs and their local controls over time. Local controls comprise the ten control turfs at each site. Dissimilarity is measured in Bray-Curtis distance or difference in CWMs (i.e. Euclidian distance). Each turf begins with a mean dissimilarity to its local controls in 2009 (its ‘initial dissimilarity’). Control turfs have mean initial dissimilarities to the remaining nine control turfs at each site. This method of measuring community change factors out environmental stochasticity because dissimilarity is recalculated each year (i.e. we treat control communities as moving targets).

Simulation

Community dynamics in our neutral simulation are driven by two interacting processes: replacement and immigration. The model has two parameters: replacement rate (d), which determines the number of replacement events between time points, and immigration rate (m), the probability that replacements are immigrants from the surrounding site flora (i.e. the site species pool), as opposed to the current turf community (i.e. the turf species pool). The site species pool

is defined as the net composition of the ten control turfs present at that site; we recalculate floras each year to account for any environmental stochasticity that may have shifted species relative abundances at a site. Rather than using births and deaths of individuals to simulate demographic changes, which would be meaningless and difficult to measure in our predominantly clonal system, we use increases and decreases in species percent cover units. Our model is conceptually similar to Hubbell's neutral local community model (Hubbell 2001), only that replacement is done using percent cover units rather than individuals, and we account for environmental stochasticity.

We simulated community dynamics from 2009 to 2013 on an individual turf basis, generating annual community time points. The simulation process proceeds as follows: First, d replacement events are executed on each of the 2009 turf communities. For each replacement event, one species decreases in cover by one percent and one species increases in cover by one percent. The decreasing species is selected by simple random sample (i.e. probabilistically), based on the relative abundances of species in the turf community at that time step. The increasing species is selected randomly based on the relative abundance of species in one of two species pools: the turf pool (i.e. from within the turf), or the site pool (i.e. from outside of the turf); the m parameter (immigration rate) is used to weight the selection of the appropriate pool for each replacement event. Additional single-percent increases or decreases are performed until total cover matches the total cover measured for that turf in the field that year. Dissimilarity between the turf and local controls is calculated using species-based and trait-based measures of community composition. This process is repeated for each simulated year until reaching 2013. The entire simulation is repeated 25 times, and the resulting dissimilarity values are averaged by year. Simulation data for 2010 were discarded because field data do not exist for that year.

Exploring and estimating model parameters ' d ' and ' m '

Our goal was to find values for d and m that explained the greatest amount of variation in observed rates of species-based change. Our exploration of parameter space revealed that there was likely a suite of multiple best-fit solutions (Figure A1). To resolve this, we set replacement rate equal to the mean observed differences in species covers in control turfs between years at each site, and then determined immigration rates that led to the best fit. Thus, the rates of replacement and immigration in our simulations varied by site (d from 25 to 45, m from 0.1 to 0.475) (Table A3).

Testing for trait-mediated dynamics

We used model simulations to generate scenarios of turf community dynamics under strictly trait-neutral processes. As detailed above, we parameterized our models to explain as much variation in species-based responses as possible, and then used these models to generate null expectations of trait-neutral responses to transplantation. Our analysis is thus a very conservative test for evidence of trait-mediated dynamics. Paired t-tests were used to determine when observed and neutral expectations differed significantly.

RESULTS

Of the five traits investigated, maximum height, SLA, and leaf area values correlated positively with temperature ($R^2 = 0.49, 0.28, 0.23$, respectively) and leaf CN values correlated negatively with precipitation (Figure 2). A few other trait-gradient correlations were significant but very weak ($R^2 < 0.1$) and thus disregarded (Table 1). The only notable interactive effect of

temperature and precipitation was on SLA; the percent variance explained in SLA increased from 30% to 45% when the interaction coefficient was included in the multiple regression. Rates of species turnover were consistent and of comparable magnitude along temperature and precipitation gradients (Vandvik et al. unpublished manuscript).

Transplanted turfs exhibited large directional shifts in traits and species, especially in the first two years after transplantation. Neither replanted controls nor undisturbed controls showed any directional changes, and were thus combined to increase the control group sample size to ten per site. In all turfs, the magnitude of observed directional change varied proportionally with initial dissimilarity to controls (Figure 3). For example, turfs transplanted to wetter sites with smaller initial differences in composition underwent less change than turfs transplanted to warmer sites with larger initial differences in composition. As detailed above, stochastic replacement by local species alone can drive compositional changes in transplanted turfs. To determine if trait-mediated interactions influenced turf response rather than just stochastic replacement, i.e. if traits actually influenced species success, we compared observed responses to null expectations based on trait-neutral model simulations.

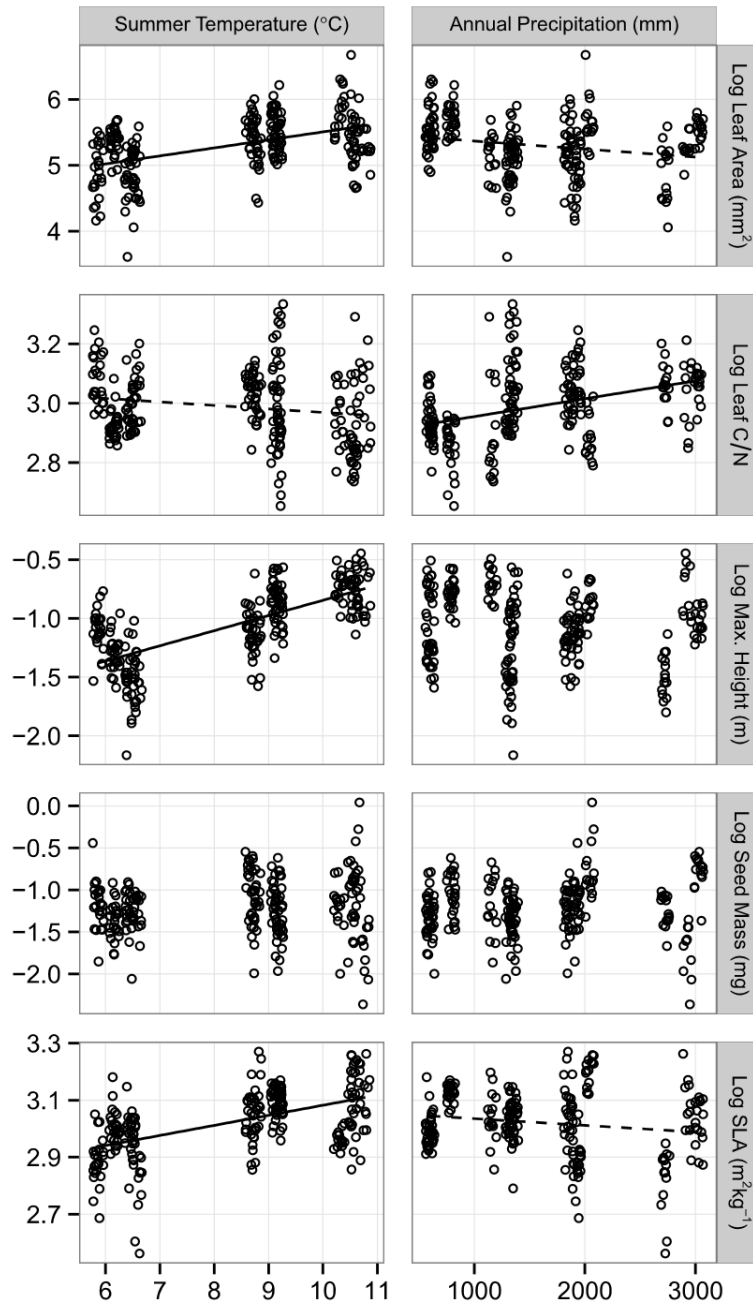


FIGURE 2. Community weighted mean trait values plotted by mean annual summer temperature (left) and precipitation (right). Points show community weighted means of all 232 turfs before transplantation, and thus reflect natural trait patterns. Points are horizontally jittered to reduce over-plotting. Statistically significant regressions ($p < 0.05$) are shown as solid lines when $R^2 > 0.1$ or as dashed lines when $R^2 < 0.1$. See Table 1 for linear model summary statistics.

294 Table 1: Linear model summary statistics

Trait	~Temperature		~Precipitation		Interaction	
	P	R ²	P	R ²	P	R ² (Total)
Leaf Area	<0.001*	0.23	0.0013*	0.044	0.19	0.28
Leaf CN	0.0097*	0.029	<0.001*	0.14	0.027*	0.2
Max. Height	<0.001*	0.49	0.062	0.015	0.088	0.52
Seed Mass	0.12	0.011	0.087	0.013	0.0044*	0.057
SLA	<0.001*	0.28	0.017*	0.024	<0.001*	0.45

295 P-values and R² values for linear regressions of community weighted trait means along mean
 296 summer temperature and mean annual precipitation gradients as shown in Figure 2. The
 297 ‘Interaction’ column shows the p-value of the interaction coefficient that was included in the
 298 multiple linear regression alongside temperature and precipitation; in this case, the R² refers to
 299 the total variance explained.

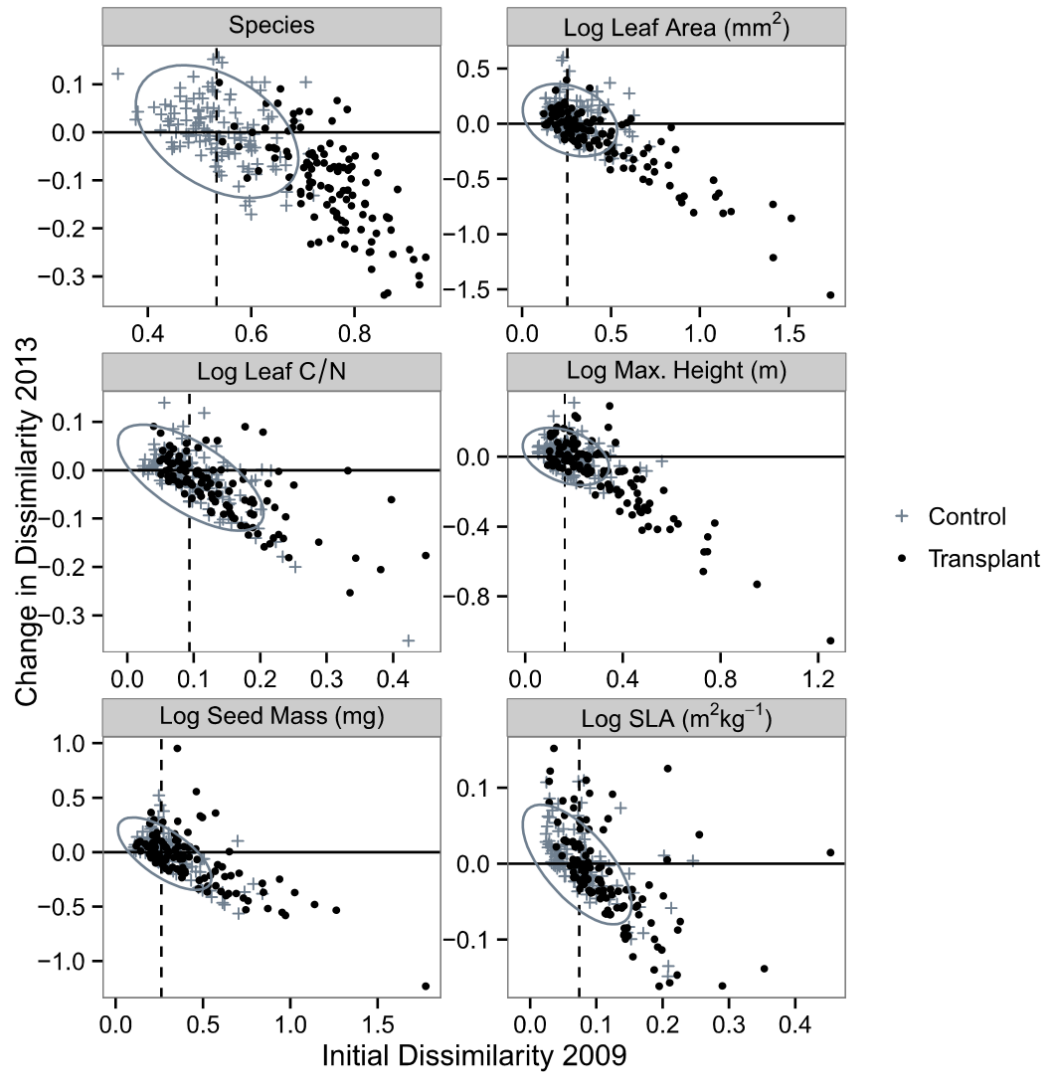
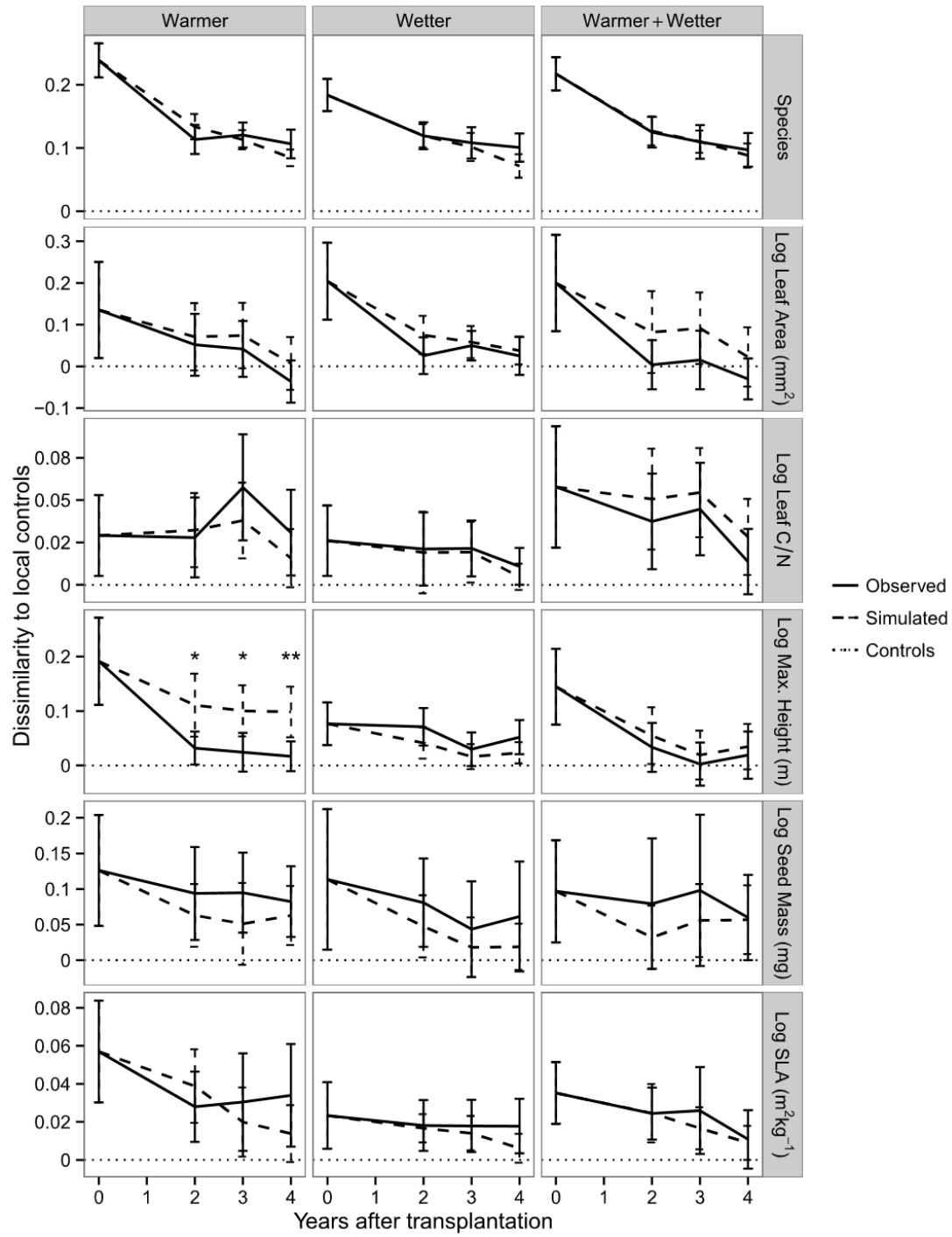


FIGURE 3. Change in dissimilarity of turfs to local controls from 2009 to 2013. Each shape represents a single turf community. Grey crosses represent control turfs; black points represent transplanted turfs. Dissimilarity was calculated using Bray-Curtis distance for species composition (top left) or Euclidian distance of community weighted means (all remaining). Communities below the x-axis converged compositionally with local controls, whereas communities above the x-axis diverged. 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 centroid of control turfs.

Our null model simulations show that rates of turf compositional change are interactively affected by replacement rate and immigration rate (Figure A1). If either replacement or immigration rate is zero, simulated communities change little. If replacement or immigration rates increase, so does the rate of compositional change. We identified replacement and immigration rates for each site that led to simulations that most closely resembled observed species-based changes (Table A3), and used these rates to create null expectations of trait-neutral turf responses. Rates of change in maximum height were much faster than model predictions in turfs transplanted to warmer temperatures (Figure 4). SLA, leaf area, and leaf CN, which exhibited clear shifts along environmental gradients, did not deviate from null model predictions.



319 FIGURE 4. Mean dissimilarity of transplanted turfs to local controls over time. Solid lines
320 represent observed field data; dashed lines represent simulated data based on a model of
321 community change with strictly trait-neutral processes, averaged over 25 model simulation runs.
322 The model was parameterized such that simulated community change aligned with observed
323 community change in terms of species composition, i.e. to align observed and simulated lines in
324 the top row (refer to Table A3 for parameter values). Y-axis values equal the mean dissimilarity
325 of transplanted turfs minus the mean dissimilarity of local controls each year. Error bars show
326 95% confidence intervals. Statistical differences between observed and simulated community
327 weighted means are shown when $p < 0.05$ (*) and $p < 0.01$ (**).

DISCUSSION

Our study provides experimental evidence that some but not all trait-based gradient patterns can predict community responses to climate change. In particular, species maximum height correlated strongly with temperature as well as species success following experimental warming. Leaf area, SLA, and leaf CN, correlated with climate gradients but did not measurably affect species response to climate change. Our results suggest that the traits involved in community assembly processes along gradients may not always be the same traits and processes that govern short-term community dynamics or community response to perturbation. Below, we elaborate on our findings and discuss the importance of accounting for demographic stochasticity, the vulnerability of temperate grasslands to climate change, and the work needed before we can satisfactorily predict the effect of climate change on ecosystem functions and services.

Trait patterns along climate gradients

Species turnover does not necessarily beget functional turnover (Hooper et al. 2002). Despite consistent rates of species turnover along temperature and precipitation gradients in our system (Vandvik et al. unpublished manuscript), community weighted trait means trended strongly with temperature but weakly with precipitation (Figure 2). This discrepancy supports the notion that species turnover can be functionally redundant. It also suggests that moderate increases in mean summer temperature, but not mean annual precipitation, could alter the functional composition of our grassland. Interestingly, precipitation had a significant effect on SLA but only at the coldest temperatures, a finding inconsistent with the general evidence that SLA increases with precipitation (Wright et al. 2004). We hypothesize that water may not be a

limiting resource at the wettest ends of our gradients (> 2500 ml / year). Instead, decreased solar radiation due to increased cloud cover may favor species that better persist under colder and darker growing conditions.

The temperature-associated trait patterns in our system suggest shifts in two aspects of plant ecological strategy. First, the increase in maximum height with temperature points to an increase in the ability of species to compete for light at warmer sites. This hypothesis is further supported by a smaller range of maximum height values in turfs at warmer sites (data not shown), indicating that shorter species that do not prioritize access to light fail to establish. Second, increases in leaf area and SLA with temperature suggest an increase in species with the ability to preempt resources from competitors when conditions are amenable to growth, as seen on the ‘growth’ side of the growth-tolerance tradeoff (Sterck et al. 2006), or the ‘fast’ side of the fast-slow continuum of plant strategy (Franco and Silvertown 1996). Conversely, low leaf area and SLA values common at the cooler ends of our gradients suggest an increase in species with the ability to survive when conditions are harsh or resources are limited. Similar correlations in leaf area and SLA values to temperature have been found in other sub-alpine and alpine systems (Choler et al. 2001; Callaway et al. 2002). Again, we observe marked decreases in the ranges of leaf area and SLA at warmer sites (data not shown), indicating that species with small leaves and low SLA values are unable to establish. Based on the trait-environment patterns in our system, we anticipated that tall species with large leaves and high SLA values would thrive disproportionately in turfs transplanted to warmer climates.

Accounting for trait-neutral processes

Demographic and environmental stochasticity are important processes in the structuring of ecological communities but are frequently ignored in interpretations of experimental results (Durrett and Levin 1994; Alonso et al. 2006). In this system, on average, there was a net 30% change in species covers between years in control turfs, providing a rough approximation of demographic stochasticity. This high rate of demographic stochasticity may act to maintain compositional differences among control turfs within sites, as has been speculated in other grasslands (Herben et al. 1993; Maarel and Sykes 1993). Although species percent covers fluctuated dramatically over time in control turfs, which we interpret as demographic stochasticity, the abundance-weighted mean trait values at the site level did not fluctuate over time.

The high level of stochasticity we observed at the turf level in controls is central to our interpretation of turf responses to transplantation. In general, species and trait compositions of transplanted turfs converged with local controls over time. The magnitude of convergence (i.e. the decrease in dissimilarity) correlated with initial dissimilarity (Figure 3), a relationship consistent across all turfs, years, and treatments, including controls. While striking, our simulations show that similar outcomes can result from purely stochastic processes (Figure A2). Specifically, compositional convergence occurs as randomly selected immigrants from local species pools replaces randomly selected individuals from original turf communities. Because the probability of selecting an individual from the original turf community decreases as they are replaced, the rate of convergence intrinsically decreases over time. The initially high rates of compositional convergence in our experiment appear to be driven more by the arrival of local immigrants than by turf extinctions (Vandvik et al. unpublished manuscript). This finding is also not inconsistent with stochastic or neutral processes which can result in the prolonged

persistence of rare species (Borggreffe et al. 2002; Alonso et al. 2006). Due to the potentially large role that stochasticity may have played in shaping turf responses to transplantation, our test for trait-mediated dynamics relies on the comparison of observed and simulated data, rather than direct evaluations of turf community performance.

Evidence for trait-mediated dynamics

If a trait influences species response to experimental climate change, then species with optimal values of that trait should succeed more often than expected by random chance. We compared observed and simulated turf responses to transplantation to discern when traits were associated with disproportionate species success (Figure 4). Of the traits we tested, maximum height, a trait strongly associated to temperature in our system, conferred strong advantages to species following climate warming. The advantage was most pronounced when initial dissimilarity in maximum height was highest (Figure A2), suggesting a relationship between the influence that traits have on community dynamics and the degree to which a community is in trait-based disequilibrium with the environment. There were also large shifts in the mean leaf area of transplanted turfs, which nearly converged with controls after only two years and exceeded null expectations on average. However, due to high variance in responses, we cannot conclude that leaf area had any consistent influence on community dynamics in our experiment.

Additional evidence for trait-mediated dynamics in our experiment may be concealed by the conservative nature of our analysis. Our simulations determine replacement and immigration rates maximizing fit with observed species-based changes; this method thus assumes that the magnitude of species-based changes is unaffected by trait mediated interactions. This assumption is unlikely to be true as trait-mediated interactions would likely increase rates of replacement and

immigration. Nonetheless, even with this conservative approach, our study shows that traits can influence community response to climate change even on very short time scales.

Conclusions and future directions

A trait-based framework for predicting plant community response to climate change is intuitively appealing. Unfortunately, short-term transient responses to perturbations may not necessarily reflect predicted long-term equilibrium responses, and instead be driven by unpredictable context-dependent biotic relationships, multi-trait interactions, or morphological plasticity at individual or species levels. Our analysis supports the notion that commonly measured plant traits can sometimes be used to predict community response, but also illustrates the important role that demographic stochasticity likely plays at the turf level. We conclude that any predictions of community response to climate change should include the combined influence of stochasticity and trait-mediated competitive interactions, as has been proposed elsewhere (Tilman 2004, Alonso et al. 2006, Gravel et al. 2006, Shipley et al. 2011). In addition to accounting for stochasticity, we suggest two research directions that may help in reducing the percentage of unexplained variation in species response.

First, there should be more in-depth explorations into how to best model demographic stochasticity in primarily clonal systems like grasslands (see: Eriksson 1994, Winkler and Klotz 1997, Mandujano et al. 2001). In the sub-alpine/alpine grasslands of our system, like most grasslands, annual changes in percent cover are often the result of differences in sizes of returning perennial plants, or the result of clonal propagation, not seedling germination. In a concurrent study in our system, Michel et al. (unpublished manuscript) found an average of only ~ 0.6 seedlings established per turf community per year. Of the 191 species present in this study,

175 are known to be able to propagate vegetatively (Klimešová and Bello 2009), and the actual number is probably higher. A consideration of how clonality affects community dynamics will lead to improved models of community change.

Second, models need a better understanding of how dispersal limitation will affect the relationship, or lack thereof, between short-term transient responses and long-term equilibrium responses. Discussions about ‘extinction debts’ and ‘immigration credits’ in the field of habitat distribution modeling are a step in the right direction (Dirnböck and Dullinger 2004), but these approaches are still based on the notion that present day species distributions will reflect future species-climate relationships. This premise is dubious as current plant communities are already showing unpredictable responses to climatic changes in the last 50 years (Elmendorf et al. 2012; Gottfried et al. 2012).

Our study is an exploration of the potential for plant trait patterns to forecast community response to climate change. We begin by showing the suitability of our system, i.e. that traits vary significantly over the gradients in our system. We then compare experimental observations to a neutral model with maximum rates of stochastic replacement and immigration, highlighting the presence of trait-mediated interactions in our transplant communities, particularly related to maximum height. Ultimately, community response to climate change will likely result from the interaction of local trait-neutral processes and broader trait-based climate-driven processes.

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601

602 ONLINE APPENDIX A: Supplementary analyses

603 Table A1. Species trait correlations.

	Leaf CN	Max. Height	Seed Mass	SLA
Leaf area	-0.13	0.4	0.42	0.28
Leaf CN		-0.22	-0.35	-0.14
Max. Height			0.33	-0.073
Seed Mass				0.039

604

605 Table A2. Community-level trait correlations.

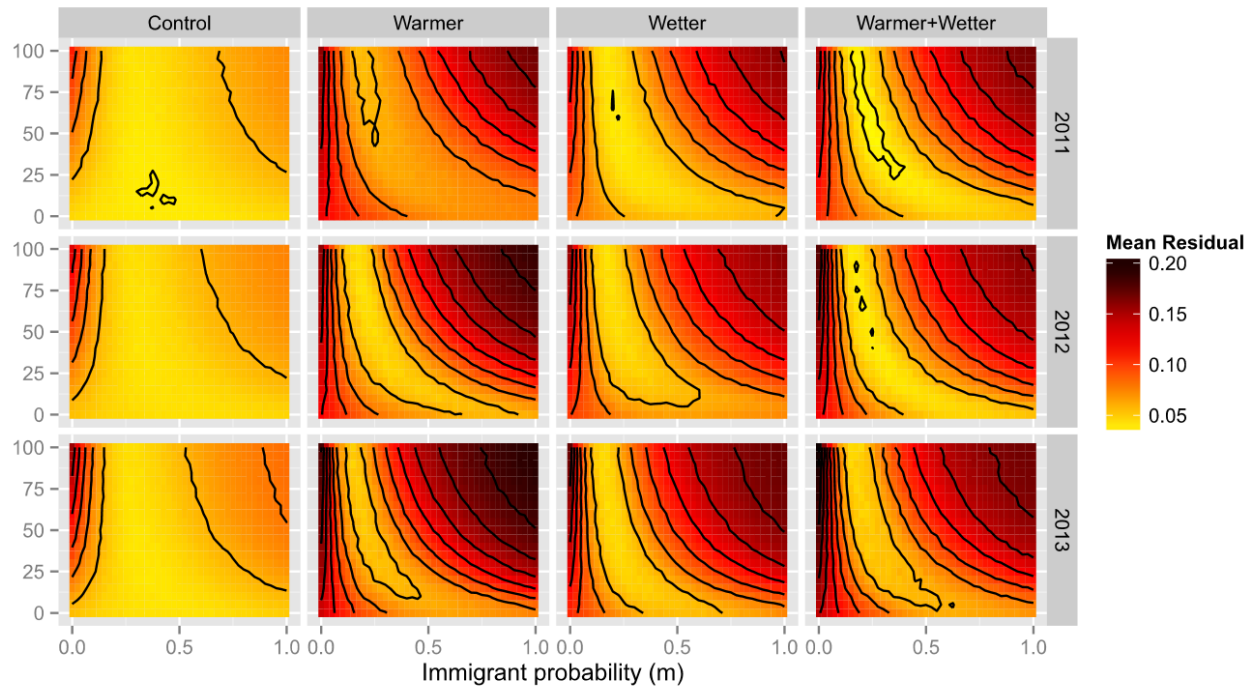
	Leaf CN	Max. Height	Seed Mass	SLA
Leaf area	-0.41	0.52	0.4	0.44
Leaf CN		-0.22	-0.33	-0.45
Max. Height			0.065	0.36
Seed Mass				0.11

606 Correlations in community weighted means.

607 Table A3: Simulation parameters and closeness of fit.

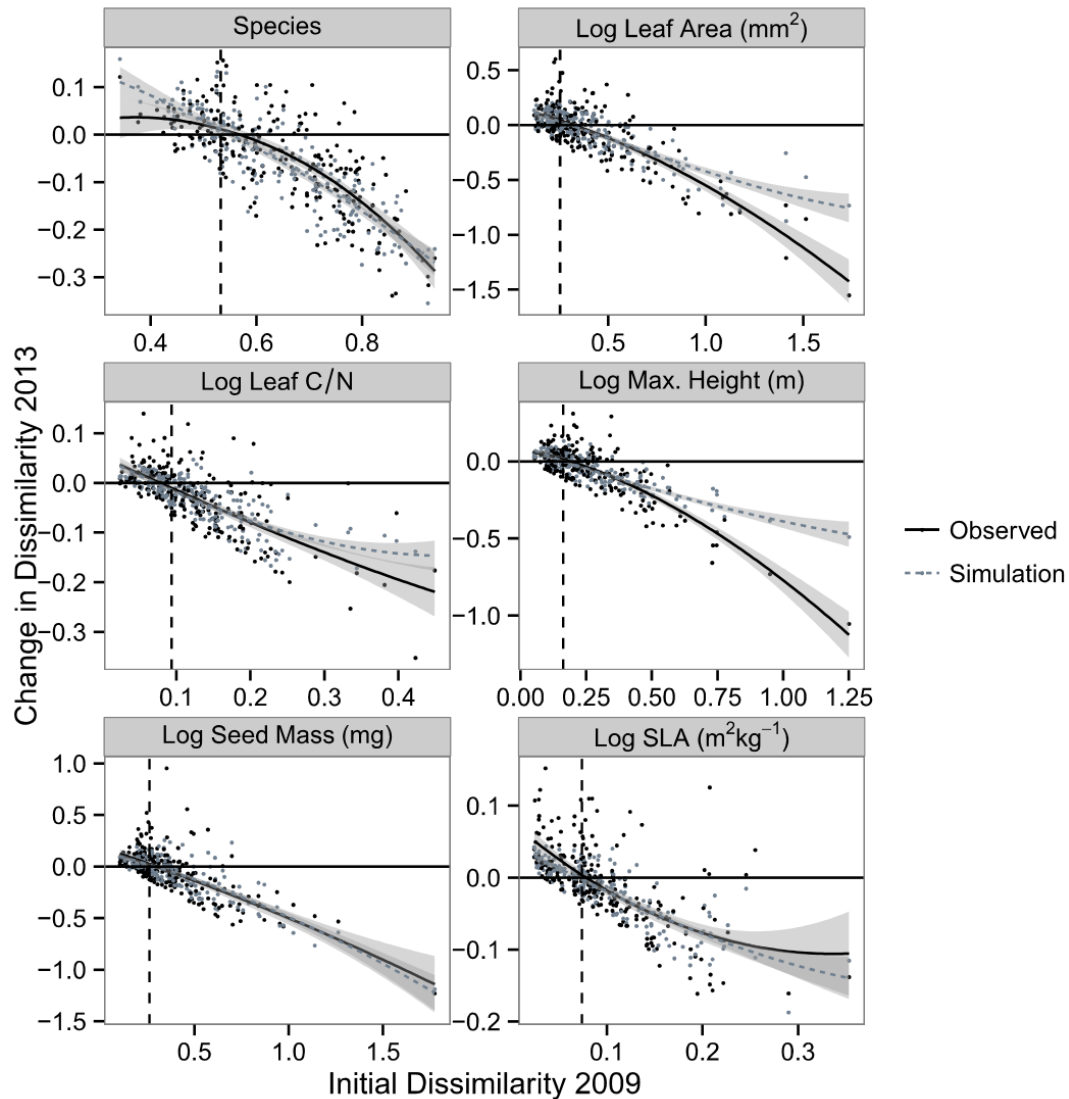
Site	Temperature (°C)	Precipitation (mm/year)	d	m	Mean Residual
Alrust	9.14	789	45	0.35	0.048
Arhelleren	10.6	2040	40	0.275	0.044
Fauske	10.3	600	45	0.175	0.039
Gudmedalen	5.87	1920	30	0.275	0.033
Hogsete	9.17	1360	40	0.25	0.046
Lavidalen	6.45	1320	30	0.325	0.043
Ovstedal	10.8	2920	25	0.075	0.027
Rambera	8.77	1850	30	0.25	0.036
Skjellingahaugen	6.58	2720	25	0.3	0.035
Ulvhaugen	6.17	596	40	0.3	0.043
Veskre	8.67	3030	40	0.25	0.044
Vikesland	10.6	1160	45	0.475	0.052

608 Temperature refers to mean annual summer temperature. Replacement rate (d) and immigration
609 rate (m) were selected to maximize closeness of fit with observed turf data, determined by
610 Bray-Curtis dissimilarity in species-based community composition ('Mean Residuals').



611

612 FIGURE A1. A contoured heat map showing how well model simulations aligned to field data
 613 under a range of replacement rates (d) and immigration rates (m). The heat map depicts the
 614 absolute difference (“Mean Residual”) in Bray-Curtis dissimilarity between field data and
 615 simulated data.



617

618 Figure A2. Change in dissimilarity of turfs to local controls from 2009 to 2013 in observed

619 (black, solid line) and simulated (grey, dashed line) data. Each point is a turf community.

620 Dissimilarity was calculated using Bray-Curtis distance for species composition (top left) or

621 Euclidian distance of community weighted means (all remaining). Lines are calculated for each

622 data type using the loess smoothing function from the R {stats} package. Grey bands represent

623 95% confidence intervals.