

Community assembly responses to warming and increased precipitation in an early successional forest

CHRISTINE R. ROLLINSON,^{1,†} MARGOT W. KAYE,^{1,2} AND LAURA P. LEITES²

¹*Intercollege graduate degree program in Ecology, The Pennsylvania State University, University Park, Pennsylvania 16802 USA*

²*Ecosystem Science and Management, The Pennsylvania State University, University Park, Pennsylvania 16802 USA*

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Abstract. Experimental climate manipulations provide the opportunity to link predicted changes in climate to the process of community assembly. We studied plant community assembly of a recently harvested forest exposed to three years of experimental 2°C warming and 20% increased precipitation. By the end of the experiment, trees were the only functional group that shifted composition in response to warming and precipitation treatments ($p = 0.03$), while the composition of the grass, forbs, and shrub/small tree/vine functional groups were unresponsive. Individual species within groups were associated with specific treatments, but did not result in a predictable community composition shift. Temporal dynamics of functional group cover were more sensitive to treatment effects than single, static measures of plant community responses such as biomass. Both static and dynamic plant analyses revealed interactive effects of warming and increased precipitation on cover and biomass of grass and all plants together (grass cover $p < 0.01$, grass biomass $p = 0.02$, total cover $p < 0.01$, total biomass $p = 0.05$). Short forb cover was negatively affected by increased precipitation throughout our experiment ($p = 0.03$). Grass, tree, and shrub/small tree/vine functional groups showed independent year effects on cover that can be attributed to successional development of the forest community (all $p \leq 0.01$). Random forest modeling indicated that cover of other plant functional groups and static plot-level variables such as plot location and components of soil texture were often the most important predictors of cover for a given functional group, while temperature and moisture availability measures were the least important. Importance of predictors of functional group cover varied greatly among random forest models from different treatments, suggesting that diverse environmental factors constrain functional group cover and may provide resilience of community assembly to climate change.

Key words: climate experiment; community ecology; forest succession; GAMM; random forest.

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† **E-mail:** crollinson@gmail.com

INTRODUCTION

Plant community composition is determined by species responses to both the biotic and abiotic environment. The role of climate in structuring communities and ecosystems is evident in paleobotanic records as well as modern

shifts in species distribution that correlate with warming temperatures (Bugmann 1996, Jackson and Overpeck 2000, Woodall et al. 2009). Recent research on climate-induced changes in species distribution focuses on ecotones such as alpine tree lines where climate restrictions of species survival and community assembly are clear (e.g.,

Beckage et al. 2008, Hudson and Henry 2010). In more temperate climates, such as in the eastern United States, plant responses to climate are mediated by many biotic and abiotic factors. Climate envelope models based on correlative species-climate relationships have been used to predict potential future species distributions in this region, but are unable to address the processes that influence species selection and community assembly (Iverson et al. 2011). Research on processes that impact tree species selection early in forest regeneration is necessary to understand temperate forest community assembly.

Community assembly immediately following disturbance is a critical phase in forest development and response to climate variability. Young tree regeneration is not only more sensitive to climate than its mature counterparts, but regeneration today is likely experiencing a climate significantly warmer than the previous generation (Jackson et al. 2009). Non-tree vegetation can be equally sensitive to climate variability and act as an ecological filter that indirectly affects climate-related shifts in tree species assembly (George and Bazzaz 1999). Patterns of survival and dominance early in succession can be used to infer the long-term tree community composition. Climate manipulation experiments can also be effectively implemented in this phase to understand how predicted climate change may alter future forest composition.

Field climate manipulation studies have been used in a variety of ecosystems over the past two decades to understand ecosystem and community responses to warming and altered precipitation regimes. Despite the generally short-term and small-scale nature of these experiments, they allow us to attribute changes in ecosystem structure or function to climate. Past studies of climate effects on community composition compared dominance of broad plant groups such as C3 and C4 grasses at key stages in the experiment (Hudson and Henry 2010, Kardol et al. 2010a, Yang et al. 2011). The use of plant functional groups allows comparison of climate treatment sensitivities in the face of varying species composition. However, differences in species composition within those functional groups may be a response to climate change that maintains the dominance of certain plant func-

tional groups and overall ecosystem structure. Consideration of both seasonal and annual changes in the plant community is essential to understanding how climate influences community dynamics in short term experiments within rapidly changing systems such as early successional forests.

Our study analyzes early successional forest community composition at species and functional group scales, considering both the community endpoint after three years of warming and increased precipitation as well as changes in the relative importance of biotic and abiotic drivers of community assembly through the course of the experiment. We address three hypotheses: (1) Climate treatments will result in unique community species assemblages because individual species are differentially favored by warming and increased precipitation. Furthermore, we predict that functional groups are also responsive to climate and the relative importance of individual functional groups will change with warming and precipitation treatments. (2) Functional group cover responses to warming and increased precipitation depend on community development at seasonal and annual time frames. (3) The cover of functional groups within the climate change experiment is moderated by other non-climate environmental factors such as soils, plot location within the harvested area, and biotic interactions within the plant community. We test these hypotheses using empirical plant community data and statistical models of the effects of field-based climate manipulations on temporal trends (generalized additive mixed models, GAMM) and relative importance of biotic, abiotic, and temporal variables in determining functional group cover (random forest, Breiman 2001).

METHODS

Site and experiment description

Our climate manipulation experiment took place following a 2007 whole-tree clear-cut harvest of 2 hectares of a second-growth oak-hickory forest in central Pennsylvania (40°41' N, 77°54' W). Experimental plots were located on a 10% slope with a southeast aspect and Berk series soils. Mean annual temperature is 9°C and mean precipitation is approximately 100 cm per year.

Dominant tree species prior to harvest were *Quercus rubra* L., *Q. alba* L., *Q. velutina* Lam., *Carya alba* L., *Fraxinus americana* L., and *Acer rubrum* L. Harvesting resulted in a 34% decrease in the soil O horizon (48.0 ± 3.4 kg/ha [mean \pm SE] pre-harvest, 31.9 ± 5.0 kg/ha post-harvest) and a 20% increase in soil bulk density (0.61 ± 0.05 g/cm³ pre-harvest, 0.73 ± 0.02 g/cm³ post-harvest). However, harvesting increased the spatial heterogeneity of soils. The coefficient of variation for the O horizon increased 5.7 times while the coefficient of variation for bulk density more than doubled (2.2 times). Following harvest, a 2-m high large mammal exclosure fence was erected to deter deer browsing.

The factorial experimental design consisted of the following climate treatments: ambient, 2°C warming, 20% increase in precipitation, and warming plus increased precipitation. Treatments were randomly assigned to 2×2 m plots in a block design that was replicated four times within the site ($n = 4$ for each treatment) from May 2008 to August 2010. The experimental design of four blocks with randomly selected treatment plots accounts for potential differences in previous community composition across the site. Hourly mean surface temperatures in each plot were measured with infrared radiometers (IRR; model IRR-P Apogee Instruments Inc., Logan, UT, USA) and soil temperature and moisture with Decagon ECH₂O EC-TM sensors (Decagon Devices, Inc, Pullman, WA, USA). Plots were warmed with infrared lamps hung 1.5 m above the ground and controlled through a real-time proportional-integrative-derivative (PID) feedback programmed to maintain a 2°C surface temperature differential between warmed and not warmed plots (Kimball 2005, 2011). Warming only treatments received an effective $1.8^\circ \pm 0.0^\circ\text{C}$ increase in surface temperature above ambient, while temperatures in the warming + precipitation treatment were elevated $1.7^\circ \pm 0.0^\circ\text{C}$ relative to ambient (Rollinson and Kaye 2012). Soil temperature in warming only and warming + precipitation was increased above ambient by $2.5^\circ \pm 0.0^\circ\text{C}$ and $1.8^\circ \pm 0.0^\circ\text{C}$, respectively. Precipitation treatments consisted of a weekly application of 20% of the long-term (1882–2005) monthly mean record for State College, PA (Easterling et al. 1996). Even though plots receiving precipitation treatments received an

effective 23% increase in precipitation over the duration of the experiment, this did not translate into an overall increase in soil moisture (repeated measures ANOVA, $\alpha = 0.05$).

Community composition of all treatment plots was inventoried from March through November in 2009 and March through the end of the experiment in August in 2010. Vegetation inventories were conducted weekly during the spring green up period (March through June) and biweekly thereafter. A total of 22 vegetation inventories were conducted in 2009 and 14 were conducted in 2010. For each inventory, we visually estimated the percent cover of each species or genus if species identification was not possible. For some analyses, species were aggregated into functional groups based on general plant form based on descriptions in Rhoads and Block (2007): short forbs with maximum height <1 m, tall forbs with maximum height greater than 1m, trees that can occupy the canopy at maturity, grasses (not identified to genus or species), and a group that included shrubs, small trees, and vines (Appendix A). At the end of the experiment in August 2010, all above ground vegetation in each plot was harvested, separated by functional group, dried and weighed.

Analyses

We analyzed community composition at two temporal and three organizational scales. Time was treated as a single point in time at the end of the experiment as well as a time series over the course of two growing seasons. Vegetation was analyzed at the species, functional group, and whole-community levels.

The effects of warming and increased precipitation on species composition in the final year of the experiment in 2010 were evaluated with the following analyses: (1) treatment effects on species assembly, (2) treatment effects on individual species associations, (3) treatment effects on end-of-experiment biomass. Treatment effects on species assembly were evaluated using a permutation multiple analysis of variance (PERMANOVA, adonis function, vegan R package, R Development Core Team 2008, Oksanen et al. 2012). In this analysis, cover of each species was calculated as the sum of observed cover across all sample dates for 2010 to ensure

Table 1. Variables used in random forest modeling grouped in to five predictor classes. Predictor classes represent factors that help drive community assembly and success of a plant functional type. The randomized decision tree approach of random forest accommodates many variables that may or may not be interdependent. GDD5 indicates growing degree-days with a base temperature of 5°C. GDD5_year is the cumulative growing degree-days in the year, while GDD5_sum are the growing degree-days between vegetation inventories. SoilH2O indicates the average, maximum, and minimum soil moisture content.

Plot	Time	Plant cover	Temperature	Moisture
Block	GDD5_year	Short forbs	GDD5_sum	Precipitation
Soil density	Julian Day	Tall forbs	Tsoil_Avg	SoilH2O_Avg
Soil pH	Year	Grasses	Tsoil_Max	SoilH2O_Max
Soil clay content		Trees	Tsoil_Min	SoilH2O_Min
Soil sand content		Shrubs/small trees/vines	Tsurface_Avg	
Soil silt content			Tsurface_Max	
			Tsurface_Min	

representation of spring ephemerals while allowing greater weight to be assigned to dominant species that persisted throughout the growing season. PERMANOVA analysis included a block effect to account for spatially related variation in composition as well as an interaction term between warming and precipitation. Treatment effects on individual species associations were evaluated using the Defrene-Legendre indicator species analysis (*labdsv*, R package, Roberts 2012). Grasses were excluded from the PERMANOVA and indicator species analyses because we did not identify them beyond the functional group level. All results presented for these and another analyses are significant at $\alpha = 0.05$ unless otherwise noted. Treatment effects on final biomass of individual functional groups were evaluated by modeling final biomass as a function of warming, precipitation and block effects using linear mixed effects model techniques (LMM, *lme4* R package, Bates and Maechler 2012). Warming, precipitation, and an interaction term between the two were included as fixed effects while block was included as a random effect.

A second set of analyses evaluated the effects of warming and precipitation over the 2009 and 2010 growing seasons. First, we modeled the trend of functional group cover during the growing seasons and evaluated the effects of warming and precipitation on these trends using a generalized additive mixed modeling (GAMM) framework. The functional group cover trend through time (Julian day) was modeled with a cubic smoothing spline, whereas the year, warming, precipitation, and interaction effects were

included as fixed effects. Block and plot nested within block were incorporated as random effects adjusting the intercept. Autocorrelation among observations within the same plot were modeled using a continuous autoregressive correlation structure. GAMMs were fit using the *mgcv* R package (Wood 2012).

Second, we evaluated the treatment effects on the relative importance of potential biotic and abiotic drivers of functional group cover using the regression tree-based approach, random forest (Breiman 2001). We used 25 predictor variables classified into the following five groups, herein referred to as “predictor classes”, to predict functional group cover in each plot at each of the inventory dates: (1) soil characteristics, (2) plant cover, (3) time, (4) temperature, and (5) moisture availability (Table 1). Plot characteristics are static through time and included soil texture, density, and pH as well as a block effect to represent relative plot locations. Soil properties were determined by analyzing samples taken at the beginning of the experiment. Plant cover included the estimated cover of each functional group at each survey and represents the influence of competition or other potential biotic interactions among plant functional groups. Time included year, Julian day, and cumulative growing degree-days with a base temperature of 5°C (GDD5_sum) within a growing season. The temperature class variables were measured at the plot level and included mean, maximum, and minimum surface (Tsurface) and soil temperatures (Tsoil) between vegetation surveys. Measures of moisture availability included the recorded mean, maximum, and minimum soil

moisture (SoilH₂O) from each plot as well as received precipitation between vegetation surveys. Received precipitation included the ambient precipitation recorded on-site and weekly experimental precipitation additions.

We assessed the effects of treatments on functional group cover by running each treatment and functional group combination independently so that four plots with 36 observations each were used in each model. Random forest is a robust statistical technique particularly suited for characterization of drivers of ecological patterns because it uses numerous iterations of randomized subsets of both predictors and observations to reach a stable solution (De'ath and Fabricius 2000, De'ath 2002). This approach is also less sensitive to correlation among predictor variables (Cutler et al. 2007). Modeling each treatment independently is a similar conceptual framework as modeling changes in vegetation distribution with predicted climate changes (Miller and Franklin 2002, Prasad et al. 2006). Model fit is assessed through the mean square error (MSE) and the pseudo-R² statistic that is calculated by: $1 - \text{MSE}/\text{variance}(y)$, where y is the response variable. We assessed the relative importance of potential drivers of functional group cover by comparing the improvement in model accuracy attributed to a predictor variable. This is quantified through the percent increase in MSE if a variable is excluded from the model and is reported as variable "importance" in the results.

RESULTS

Plant community composition

Of the four functional groups that we used to analyze community composition, only tree species assemblages were affected by the interaction of warming and increased precipitation, although all functional groups had individual species with specific treatment associations. Tree species associations were influenced by interactions of heat and water (PERMANOVA, $p = 0.03$), but also varied spatially, as indicated by the block effect (PERMANOVA, $p = 0.05$). Community compositions of the remaining functional groups, as well as the entire community in aggregate (all species analyzed together), were not affected by treatments or block (Appendix B). Trees had a

higher proportion of species associated with specific treatments, with the following three of 16 species showing significant associations: *Carya ovata* (Mill.) K. Koch (warming+precipitation, $p = 0.03$), *Prunus serotina* Ehrh. (warming only, $p = 0.048$), and *Populus tremuloides* Michx. (precipitation only, $p < 0.01$). Short forbs that showed treatment associations (3 of 35 species) were *Gallium triflorum* Mich. (ambient, $p = 0.01$), *Potentilla canadensis* L. (ambient, $p = 0.046$), and *Taraxacum officinale* F.H. Wigg (precipitation only, $p = 0.04$). Only one vine (of six species), *Vitis* spp. (warming, $p < 0.01$), and one tall forb (of 18 species) *Symphotrichum laeve* (no precipitation, $p = 0.03$) showed non-interactive treatment associations.

Final above ground biomass of most functional groups was not affected by warming or increased precipitation (Fig. 1). Across all treatments, the shrub/small tree/vine functional group accounted for the majority of the biomass ($44\% \pm 5\%$ [mean \pm SE] of the total). Within this functional group, *Rubus* spp. accounted for most of the biomass ($66\% \pm 6\%$ across all treatments). However, grass was the only functional group to have a statistically significant treatment effect: the interaction between warming and precipitation (GLMM, $p = 0.02$). Increased total biomass from an interaction of warming and precipitation was of questionable significance ($p = 0.05$).

Temporal community dynamics

While GAMM analyses detected effects of warming and increased precipitation on functional group cover over the course of the growing seasons, random forest models indicated that these effects were often indirect (Fig. 2, Appendices C, D). The treatment-specific random forest models were able to explain a large portion of the variance with an average pseudo-R² of 0.81 ± 0.03 (Table 2). However, when variables were grouped by predictor class, temperature and moisture availability, the two predictor classes altered by our experimental treatments, were generally the least important predictors of functional group cover, as indicated by the low importance values when removed from the model (importance [mean \pm SE] across all models: 17.9 ± 0.9 temperature, 13.8 ± 0.9 moisture; Fig. 3). In contrast, cover of co-occurring functional groups, an indicator of

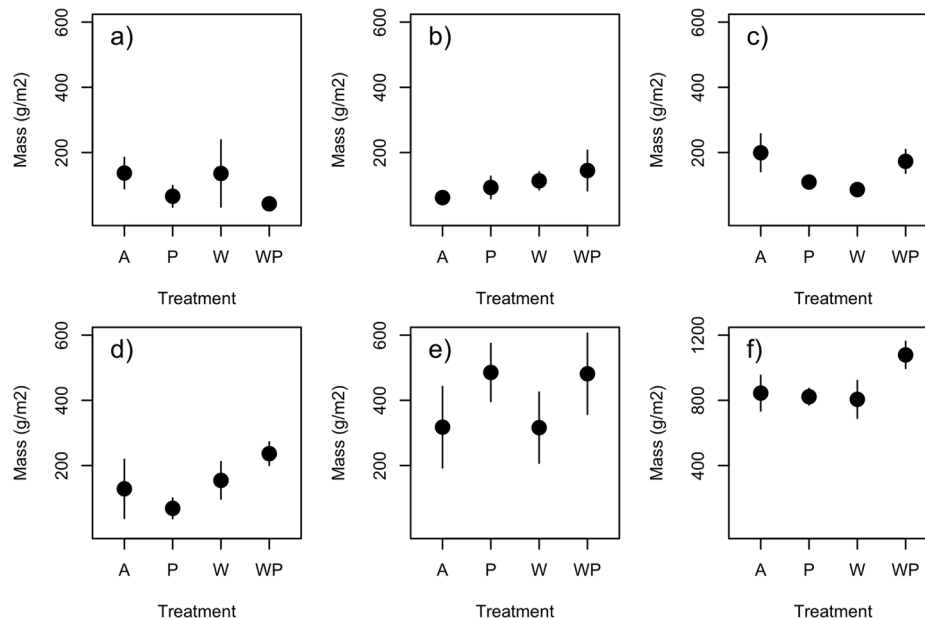


Fig. 1. Final dried above ground biomass for each plant functional group: (a) short forbs, (b) tall forbs, (c) grasses, (d) trees, (e) shrubs/small trees/vines, as well as (f) total live biomass in each treatment ($n = 4$ plots for each treatment). Grass and total biomass showed significant warming \times precipitation effects (ANOVA, $p = 0.02$ and $p = 0.05$, respectively). Treatment codes are as follows: A = ambient, P = precipitation only, W = warming only, WP = warming + precipitation. Values presented are mean \pm SE and $n = 4$ for each treatment. Note the different scale for total biomass (f).

competition dynamics, had relatively high importance for most models (importance: 37.8 ± 2.8). The interaction of warming and precipitation affected total cover (GAMM, $p < 0.01$) and appears to be driven by changes in the balance of functional group cover. Mean importance value of the functional group cover predictor class was of greater importance for explaining total cover than in other random forest models 60.6 ± 6.5 and was much higher than the next highest class (time, importance: 26.3 ± 5.1). However minimum surface temperatures had a higher influence on the ambient (82.8), warming only (65.2), and warming + precipitation (49.5) total cover models relative to functional group-specific models (24.3 ± 2.4). Surprisingly, plot-based predictor variables had little effect on total cover models (importance: 7.0 ± 0.8).

Precipitation decreased cover of short forbs during the course of our experiment (GAMM, -49.3 ± 21.9 , $p = 0.03$). The significant precipitation effect coincided with decreased influence of plot predictors, and in particular block, in

precipitation treatment random forest models. In these models, block importance dropped from 133.2 in ambient to 43.8 in precipitation only and 93.1 warming only to 15.9 in warming + precipitation. At the same time, variables in the time predictor class appeared to gain in mean importance with precipitation, going from 25.1 ± 6.0 in ambient to 29.6 ± 8.4 in precipitation only and 16.8 ± 1.7 to 32.0 ± 20.5 in warming + precipitation. In the warming + precipitation treatment, year is of particularly strong influence with an importance value of 72.9.

Grass cover was also affected by the interaction of warming and increased precipitation (GAMM, 33.5 ± 11.5 , $p < 0.01$), with warming alone associated with decreased cover and warming + precipitation associated with an increase. Random forest models showed relatively little influence of the cover of other functional groups (importance: 27.7 ± 2.4). Instead, time, and particularly year, were of higher influence in the warming models (year importance: 92.5 warming only, 69.4 warming + precipitation

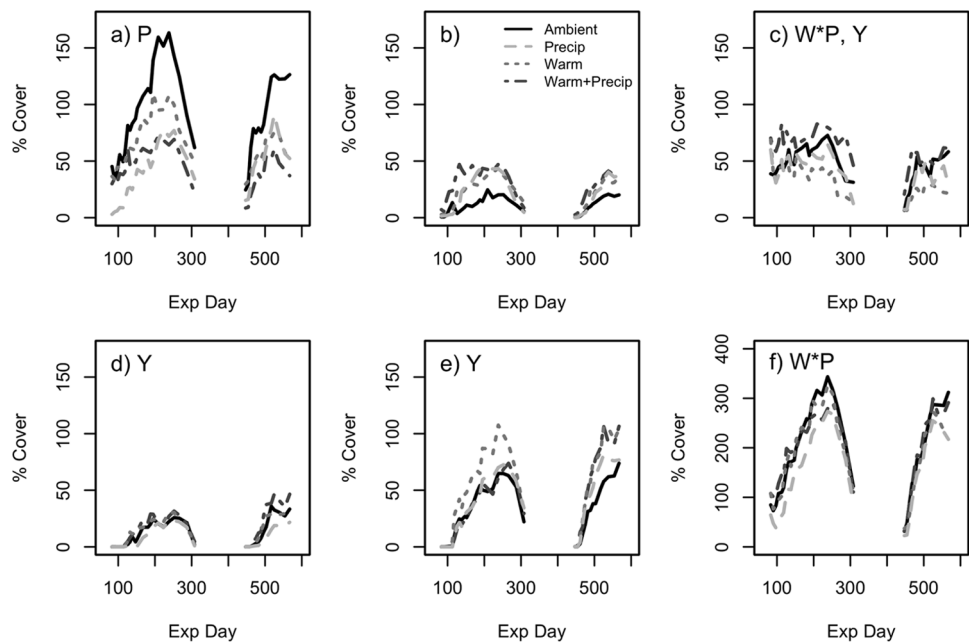


Fig. 2. Average cover of the five plant functional groups and total cover used for time series mixed modeling and random forest modeling: (a) short forbs, (b) tall forbs, (c) grasses, (d) trees, (e) shrubs/small trees/vines, and (f) total cover. Time is in experimental day where day 1 = Jan 1 2009 and cover is summed percent cover of all species belonging to a functional group. Significant fixed effects ($\alpha = 0.05$) from GAMM time series analysis are denoted using the following code: P = precipitation only, W = warming only, W*P = interaction of warming precipitation, Y = year. $n = 4$ for each treatment and error bars were not included to improve graph clarity. Note the different scale of the y-axis for total cover (f).

versus 34.6 in ambient and 45.8 in precipitation only), which coincides with a significant year effect in the GAMM model ($p < 0.01$). Moisture availability had slightly higher influence in the warming models (importance: 23.9 ± 3.5) relative to other treatments (importance: 13.7 ± 2.3) and may have contributed to the significant warming by precipitation interaction effect in

the time series. Both the tree and shrub/small tree/vine functional groups only had significant year effects in the GAMM models (tree cover: $p = 0.01$; shrub/small tree/vine: $p < 0.01$). In both of these models, cover of other functional groups and time were the predictor classes with the highest importance across models from different treat-

Table 2. Measure of random forest (RF) model fit for each treatment and functional group. R2 is the pseudo-R2 measure and MSE is mean square error for the model. Separate models for each functional group-treatment combination were developed from cover estimates from 36 vegetation inventories from 2009 and 2010 in each of 4 plots per treatment.

Functional group	Ambient		Warm		Precip		Warm + Precip	
	R2	MSE	R2	MSE	R2	MSE	R2	MSE
Short forbs	0.91	353.3	0.84	326.4	0.80	267.6	0.87	268.3
Tall forbs	0.66	44.7	0.83	46.8	0.85	69.6	0.80	89.3
Grasses	0.74	184.6	0.43	210.3	0.43	199.1	0.66	208.8
Trees	0.81	63.6	0.89	89.1	0.83	82.3	0.88	31.9
Shrubs/small trees/vines	0.91	127.3	0.90	199.4	0.90	101.7	0.89	164.3
Total	0.92	700.9	0.91	647.0	0.93	450.3	0.89	685.2

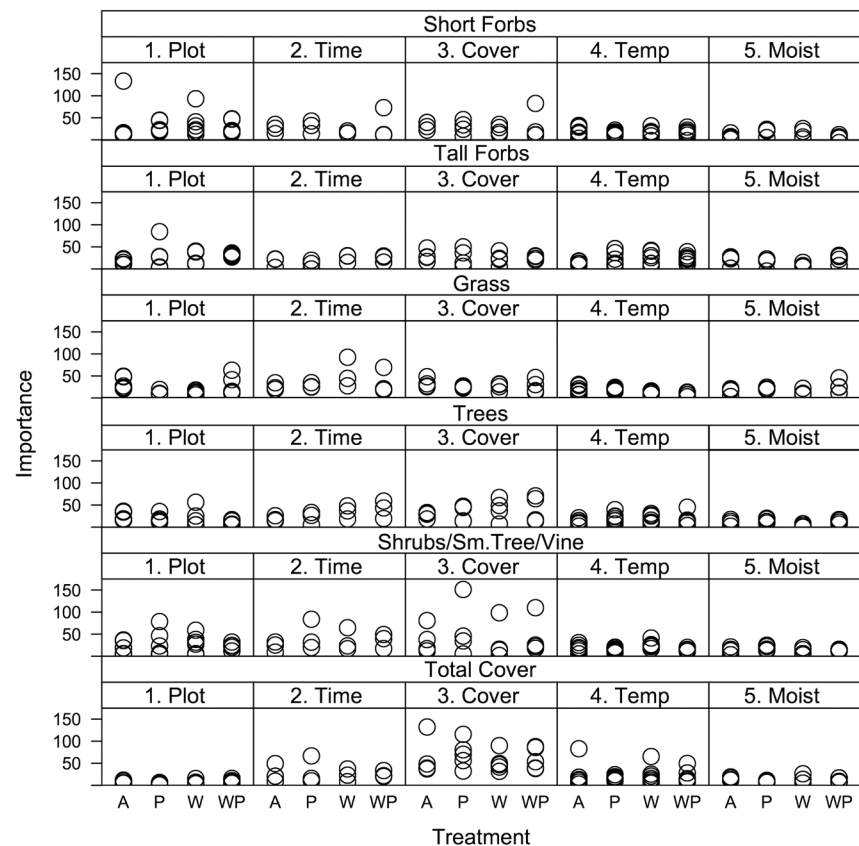


Fig. 3. Predictor variable importance in random forest models of functional group cover as measured by improvement in model accuracy attributed to predictor variables for each plant functional type and treatment combination. Each functional group-treatment combination was modeled separately based on 36 observations from 4 replicate plots between 2009 and 2010. Individual predictor variable (Table 1) scores are represented by circles that are grouped by climate treatment (columns of circles), class (boxed columns), and functional group (rows). Raw importance scores for each predictor variable and model combination can be found in Appendix D. Treatment codes for climate models are as follows: A = ambient, P = precipitation only, W = warming only, WP = warming + precipitation.

ments (tree model: cover = 34.8 ± 5.2 , time = 29.0 ± 4.5 ; shrub/small tree/vine: cover = 43.1 ± 10.9 , time = 34.4 ± 6.3). Within these two classes, cumulative growing degree-days (importance: 55.1 ± 11.8) and cover of large trees (99.3 ± 23.5) had particularly high predictor importance in the shrub/small tree/vine models. For trees, no functional group predictor variable consistently had the highest importance value across models, but year increased in model influence in warmed treatments (importance: 14.4 ambient, 5.3 precipitation only, 48.2 warming only, 43.4 warming + precipitation).

Tall forbs were the only group to show no

treatment effects in the GAMM models. In random forest modeling, predictor classes were relatively similar among models with plant cover and plot having the highest average importance value across models (26.0 ± 3.3 and 24.8 ± 3.6 , respectively).

DISCUSSION

Changes in both species assembly and functional group cover demonstrate that warming and increased precipitation can alter the composition of an early successional temperate forest community. Our experiment had higher diversity

than many previous studies (e.g., Hudson and Henry 2010, Kardol et al. 2010a, Hoeppe and Dukes 2012), but the treatment associations of individual species and an overall shift in tree community composition demonstrates that changes in climate can lead to detectable shifts in the early successional plant community of eastern forests. The available species pools as well as the biotic and abiotic soil properties were not directly manipulated in our experiment, which allowed natural plant-soil feedbacks to mediate community responses to warming and increased precipitation. For example, direct effects of temperature can alter plant composition, which in turn affects soil nutrient availability and soil biotic communities (Lovett et al. 2004, Kardol et al. 2010b, Heil 2011). These changes in below-ground dynamics can reinforce shifts in the above ground plant community (Bezemer et al. 2010, Eisenhauer et al. 2010).

Sensitivity of tree species regeneration to direct and indirect effects of climate perturbation highlights the importance of regeneration dynamics in determining long-term forest composition. Adult tree species distribution is often constrained by abiotic and biotic pressure during the regeneration phase (Poorter 2007, Jackson et al. 2009). Two explanations exist for why we did not observe similar climate sensitivity of other plant functional groups. First, high diversity and scattered distribution of non-tree species among plots makes it hard to detect both shifts in community composition or associations of individual species with treatments. Higher replication would allow us to better detect treatment effects but was not possible in our experiment. Second, many of the herbaceous species and shrubs in our community are considered early successional generalists. These species are unlikely to persist following canopy closure and are likely adapted to grow in a wide variety of climates as long as there is an abundance of light. In this case, the degree of warming or increased precipitation in our experiment is of less influence on these species than other factors such as canopy closure and competition for resources from other species and functional groups.

Plant communities are influenced by both seasonal and annual cycles of climate and community development. Species establishment can be highly influenced by both the climate and

competitive environment during the year of germination (Noe and Zedler 2001). Even though seedling survival constrains future community composition, effects of climate on seedling growth are often age-dependent (Pérez-Ramos et al. 2010). Spring phenology of trees and tall forbs was advanced by warming in our study (Rollinson and Kaye 2012). Earlier leaf out of these two functional groups did not cause increased biomass or cover during our experiment but may have been a mechanism influencing changes in species composition associated with warming treatments. Species with greater advance in leaf out in response to warming may have been able to out-compete less phenologically plastic species early in the growing season during the initial establishment phase. This competitive advantage could lead to shifts in species composition. However, because we were unable to compare species phenology across treatments, we cannot determine if phenology is directly linked to shifts in community composition.

Short forbs, tall forbs, trees, and shrubs/small trees/vines in our early successional temperate forest community all appear resilient to climate perturbation. There are three potential sources of this resilience within the plant community. The first is that changes in species composition may confer resilience at the functional group level (Hector et al. 2010). Documented treatment-based changes in species composition of our tree community may explain lack of treatment effects in final biomass or time series analysis of cover. However, this explanation does not apply to functional groups without shifts in species composition. Furthermore, the lack of control in species composition prevents us from separating direct influences of warming or increased precipitation on functional group biomass from those related to variation in species composition.

Functional group resilience may also be the product of lack of climate sensitivity of the many generalist species that dominate our non-tree functional groups. Many of the woody and herbaceous species found in our study are known to have a broad distribution that encompasses the degree of warming and increased precipitation used in our study (Rhoads and Block 2007). These species are likely greater affected by the competitive environment, particularly light avail-

ability. The high importance of cover of competing functional groups for predicting cover of the forb and shrub/small tree/vine functional groups supports this explanation.

Finally, community resilience to warming and increased precipitation may be the result of ecosystem- and community-level feedbacks that constrain functional group cover (Myers and Harms 2011). Both species interactions and soil properties can constrain functional group cover and sensitivity to warming and increased precipitation (Menge et al. 2011, Fridley et al. 2011). Our random forest approach to analysis of co-dependent variables such as time, temperature, and functional group cover allows us to determine that all of these predictor classes are important for determining plant community dynamics. However, a key limitation of this approach is that we cannot determine how these variables are mechanistically related to each other or to functional group cover.

Climate influences on community composition early in succession can have long-lasting impacts on forest development. Both shifts in tree community composition and individual species treatment associations correspond to climate-envelope model predictions of changes in suitable habitat for our study area (Prasad et al. 2007). Our research illustrates that direct effects of predicted climate change can cause these shifts, but functional group level responses are mediated by environmental constraints as well as plant community feedbacks. Even though many processes can affect species survival past the time scale of our study, the changes in community composition that we observed may persist into the future.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Species distribution among treatments. Total annual cover of all species observed in 2009 and 2010. Values presented are mean \pm SE (n = 4).

Species	Ambient	Precip	Warm	Warm + Precip
Short forbs				
<i>Allium vineale</i>	0.6 \pm 0.6	1.8 \pm 1.8	1.7 \pm 1.3	0.0 \pm 0.0
<i>Anemone americana</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0
<i>Asclepias quadrifolia</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0
<i>Circaea canadensis</i>	1.7 \pm 1.7	1.1 \pm 1.1	0.0 \pm 0.0	32.6 \pm 19.4
<i>Clinopodium vulgare</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	28.3 \pm 28.3
<i>Desmodium nudiflorum</i>	0.0 \pm 0.0	0.0 \pm 0.0	1.1 \pm 1.1	0.0 \pm 0.0
<i>Desmodium paniculatum</i>	0.0 \pm 0.0	2.9 \pm 2.9	0.0 \pm 0.0	1.6 \pm 1.6
<i>Dianthus ameria</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	3.0 \pm 3.0
<i>Fragaria virginiana</i>	0.0 \pm 0.0	6.3 \pm 3.8	31.4 \pm 31.4	27.3 \pm 25.9
<i>Galium circaezans</i>	0.8 \pm 0.8	0.2 \pm 0.2	13.6 \pm 6.7	6.9 \pm 6.9
<i>Galium triflorum</i>	136.1 \pm 60.0	31.7 \pm 9.3	28.1 \pm 7.9	37.8 \pm 15.4
<i>Geum canadense</i>	19.5 \pm 13.2	16.8 \pm 10.3	31.1 \pm 17.0	43.6 \pm 15.2
<i>Geranium maculatum</i>	22.9 \pm 22.9	1.6 \pm 1.6	14.8 \pm 8.7	29.4 \pm 29.4
<i>Hieracium caepitosum</i>	1.0 \pm 1.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Hypericum punctatum</i>	16.8 \pm 5.9	1.9 \pm 1.9	8.7 \pm 6.9	6.1 \pm 6.1
<i>Lysimachia quadrifolia</i>	0.4 \pm 0.4	8.5 \pm 6.8	7.4 \pm 2.8	11.7 \pm 7.8
<i>Maianthemum canadense</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.7 \pm 0.7	0.0 \pm 0.0
<i>Maianthemum racemosum</i>	0.0 \pm 0.0	1.0 \pm 1.0	0.0 \pm 0.0	21.9 \pm 12.7
<i>Melampyrum lineare</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.2 \pm 0.2
<i>Oxalis stricta</i>	10.1 \pm 4.5	10.2 \pm 9.8	15.8 \pm 13.4	9.2 \pm 9.2
<i>Plantago major</i>	0.4 \pm 0.4	0.7 \pm 0.7	2.7 \pm 1.6	1.9 \pm 1.9
<i>Potentilla canadensis</i>	625.8 \pm 194.5	272.1 \pm 136.4	128.0 \pm 81.9	154.4 \pm 112.9
<i>Potentilla norvegica</i>	0.0 \pm 0.0	7.4 \pm 7.4	0.0 \pm 0.0	0.0 \pm 0.0
<i>Podophyllum peltatum</i>	5.4 \pm 3.7	9.2 \pm 9.2	7.6 \pm 5.2	3.6 \pm 3.6
<i>Ranunculus abortivus</i>	0.2 \pm 0.2	1.8 \pm 1.8	0.0 \pm 0.0	0.0 \pm 0.0
<i>Sisyrinchium mucronatum</i>	3.8 \pm 3.8	0.0 \pm 0.0	1.6 \pm 1.6	7.1 \pm 7.1
<i>Solidago nemoralis</i>	1.5 \pm 1.0	4.8 \pm 2.4	5.4 \pm 2.9	0.0 \pm 0.0
<i>Taraxacum officinale</i>	10.2 \pm 7.1	39.2 \pm 11.1	9.7 \pm 7.5	11.7 \pm 7.1
<i>Thalictrum thalictroides</i>	3.1 \pm 2.0	2.9 \pm 2.9	3.9 \pm 2.3	0.7 \pm 0.7
<i>Trifolium aureum</i>	1.2 \pm 1.2	1.9 \pm 1.6	0.0 \pm 0.0	12.6 \pm 12.6
<i>Uvularia perfoliata</i>	0.0 \pm 0.0	0.0 \pm 0.0	2.6 \pm 2.6	0.0 \pm 0.0
<i>Veronica officinalis</i>	349.7 \pm 135.7	238.1 \pm 95.3	414.0 \pm 326.4	40.8 \pm 26.8
<i>Viola blanda</i>	0.0 \pm 0.0	10.6 \pm 10.6	0.0 \pm 0.0	0.0 \pm 0.0
<i>Viola hirsutula</i>	0.0 \pm 0.0	7.7 \pm 4.7	0.0 \pm 0.0	0.1 \pm 0.1
<i>Viola spp.</i>	10.4 \pm 4.5	35.6 \pm 13.2	35.3 \pm 14.2	10.5 \pm 7.3
Tall forbs				
<i>Actea racemosa</i>	18.0 \pm 16.1	51.3 \pm 51.3	24.7 \pm 12.5	31.0 \pm 31.0
<i>Arctium minus</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.5 \pm 0.5	0.0 \pm 0.0
<i>Cirsium arvense</i>	10.7 \pm 9.5	22.0 \pm 11.5	8.4 \pm 5.0	56.6 \pm 53.2
<i>Cirsium vulgare</i>	14.8 \pm 14.8	0.0 \pm 0.0	0.0 \pm 0.0	18.6 \pm 18.6
<i>Epilobium ciliatum</i>	0.1 \pm 0.1	2.0 \pm 1.9	0.0 \pm 0.0	0.5 \pm 0.5
<i>Erigeron annuus</i>	1.1 \pm 1.0	0.0 \pm 0.0	0.8 \pm 0.8	0.4 \pm 0.4
<i>Euthamia graminifolia</i>	11.2 \pm 7.8	21.7 \pm 11.1	29.4 \pm 21.0	16.1 \pm 9.0
<i>Galium aparine</i>	1.1 \pm 0.6	2.8 \pm 1.4	3.2 \pm 1.9	27.4 \pm 19.5
<i>Oenothera biennis</i>	0.0 \pm 0.0	2.4 \pm 2.4	0.0 \pm 0.0	0.0 \pm 0.0
<i>Phytolacca americana</i>	5.3 \pm 5.3	30.9 \pm 13.9	29.3 \pm 22.9	42.8 \pm 16.7
<i>Solidago canadensis</i>	52.2 \pm 19.1	37.9 \pm 22.7	67.4 \pm 13.8	80.7 \pm 36.2
<i>Solidago caesia</i>	0.0 \pm 0.0	5.0 \pm 5.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Solidago rugosa</i>	0.0 \pm 0.0	45.1 \pm 36.9	40.7 \pm 21.6	44.2 \pm 39.4
<i>Symphytotrichum lateriflorum</i>	14.6 \pm 8.5	20.4 \pm 8.8	11.8 \pm 11.8	9.1 \pm 8.0
<i>Symphytotrichum laeve</i>	12.6 \pm 7.5	0.0 \pm 0.0	32.1 \pm 17.4	1.6 \pm 1.6
<i>Symphytotrichum pilosum</i>	5.3 \pm 5.3	0.0 \pm 0.0	7.8 \pm 7.8	5.8 \pm 5.8
<i>Verbascum thapsus</i>	0.0 \pm 0.0	0.0 \pm 0.0	2.6 \pm 2.6	3.6 \pm 2.7
<i>Verbena urticifolia</i>	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0	2.4 \pm 1.4
Grass				
Grass spp.	479.8 \pm 131.3	437.3 \pm 45.9	282.6 \pm 39.0	670.3 \pm 130.7
<i>Microstegium vimineum</i>	77.7 \pm 72.5	13.9 \pm 10.7	7.2 \pm 6.2	18.8 \pm 18.8

Table A1. Continued.

Species	Ambient	Precip	Warm	Warm + Precip
Trees				
<i>Acer rubrum</i>	3.4 ± 3.4	0.0 ± 0.0	16.5 ± 14.0	4.3 ± 4.3
<i>Acer saccharum</i>	37.1 ± 30.1	1.0 ± 1.0	20.0 ± 16.6	19.4 ± 10.7
<i>Betula lenta</i>	0.0 ± 0.0	3.4 ± 2.1	1.5 ± 0.9	0.0 ± 0.0
<i>Carya ovata</i>	1.1 ± 1.1	0.6 ± 0.6	18.0 ± 7.3	0.0 ± 0.0
<i>Carya tomentosa</i>	1.6 ± 1.6	6.2 ± 6.2	0.0 ± 0.0	13.8 ± 9.2
<i>Fraxinus</i> spp.	56.2 ± 33.4	33.0 ± 13.0	52.6 ± 40.9	33.2 ± 21.6
<i>Liriodendron tulipifera</i>	27.1 ± 23.9	43.7 ± 18.0	34.7 ± 20.3	3.5 ± 2.0
<i>Pinus</i> spp.	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
<i>Populus grandidentata</i>	0.0 ± 0.0	7.5 ± 3.7	23.7 ± 23.7	43.1 ± 43.0
<i>Populus tremuloides</i>	0.0 ± 0.0	14.3 ± 9.2	0.3 ± 0.3	0.0 ± 0.0
<i>Prunus serotina</i>	74.7 ± 48.5	0.0 ± 0.0	17.9 ± 17.9	120.2 ± 44.0
<i>Quercus alba</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	12.8 ± 11.4
<i>Quercus rubra</i>	0.0 ± 0.0	0.0 ± 0.0	15.2 ± 15.2	9.0 ± 9.0
<i>Quercus velutina</i>	6.5 ± 6.5	0.0 ± 0.0	15.9 ± 15.9	20.2 ± 12.1
<i>Sassafras albidum</i>	0.0 ± 0.0	1.5 ± 1.5	6.3 ± 6.3	0.0 ± 0.0
<i>Ulmus rubra</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	32.2 ± 32.2
Shrubs				
<i>Amelanchier</i> spp.	0.0 ± 0.0	0.0 ± 0.0	5.4 ± 5.4	0.0 ± 0.0
<i>Ceanothus americana</i>	26.7 ± 26.7	6.1 ± 2.7	0.8 ± 0.8	9.7 ± 5.9
<i>Cornus racemosa</i>	4.7 ± 3.0	4.0 ± 4.0	46.7 ± 32.7	29.2 ± 17.6
<i>Ilex verticillata</i>	0.0 ± 0.0	3.7 ± 3.7	0.0 ± 0.0	0.0 ± 0.0
<i>Lindera benzoin</i>	6.4 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>Lonicera</i> spp.	0.3 ± 0.3	0.7 ± 0.7	9.9 ± 9.9	7.1 ± 7.1
<i>Rosa multiflora</i>	0.4 ± 0.4	22.8 ± 22.1	0.0 ± 0.0	13.6 ± 7.9
<i>Rubus</i> spp.	361.4 ± 185.0	573.1 ± 130.4	565.5 ± 142.2	510.1 ± 156.0
<i>Viburnum</i> spp.	0.0 ± 0.0	0.0 ± 0.0	2.8 ± 2.8	0.0 ± 0.0
Small trees				
<i>Cornus florida</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	7.3 ± 7.3
<i>Crataegus</i> spp.	18.1 ± 6.1	6.6 ± 5.6	6.4 ± 4.9	85.7 ± 42.4
<i>Hamamelis virginiana</i>	14.5 ± 14.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>Rhus glabra</i>	0.0 ± 0.0	12.2 ± 12.2	0.0 ± 0.0	0.0 ± 0.0
<i>Sambucus canadensis</i>	11.2 ± 11.2	0.0 ± 0.0	4.3 ± 4.3	0.0 ± 0.0
<i>Viburnum prunifolium</i>	0.0 ± 0.0	4.5 ± 4.5	0.0 ± 0.0	30.7 ± 30.7
Vines				
<i>Amphicarpa bracteata</i>	0.6 ± 0.6	0.0 ± 0.0	4.6 ± 4.6	0.0 ± 0.0
<i>Celastrus orbiculatus</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.7 ± 1.7
<i>Clematis virginiana</i>	0.0 ± 0.0	11.0 ± 11.0	3.0 ± 3.0	0.0 ± 0.0
<i>Dioscorea</i> spp.	0.0 ± 0.0	0.0 ± 0.0	2.4 ± 2.4	0.0 ± 0.0
<i>Parthenocissus quiquefolia</i>	0.0 ± 0.0	0.0 ± 0.0	3.4 ± 3.4	4.4 ± 3.6
<i>Vitis</i> spp.	37.5 ± 20.6	3.7 ± 1.9	170.1 ± 63.0	114.7 ± 46.9

APPENDIX B

Table B1. Additional results from analysis of community composition: p-values from PERMANOVA community composition analysis. PERMANOVA was run with a Bray-Curtis distance measure and 1000 permutations.

Fixed effect	Short forbs	Tall forbs	Trees	Shrubs/Small trees/Vines	All species
Block	0.67	0.55	0.05	0.28	0.27
Warm	0.11	0.89	0.07	0.33	0.11
Precip	0.61	0.37	0.88	0.38	0.37
Warm × Precip	0.63	0.75	0.03	0.25	0.15

APPENDIX C

Table C1. Additional GAMM results: p-values from GAMM analysis of functional group cover over time.

Fixed effect	Short forbs	Tall forbs	Grass	Trees	Shrubs/Small Trees/Vines	Total cover
Warming	0.163	0.144	0.081	0.811	0.092	0.262
Precipitation	0.025	0.164	0.519	0.361	0.706	< 0.001
Year	0.092	0.833	0.001	0.010	0.001	0.661
Warm × Precip	0.288	0.870	0.004	0.242	0.453	0.002
Warm × Year	0.481	0.253	0.689	0.632	0.491	0.757
Precip × Year	0.150	0.973	0.931	0.747	0.287	0.335
Warm × Precip × Year	0.454	0.651	0.589	0.628	0.229	0.798
Model R ²	0.289	0.459	0.364	0.475	0.534	0.800

APPENDIX D

Table D1. Predictor importance scores for short forb random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	133	44	93	16	71
	Soil density	12	22	41	19	23
	Soil pH	12	23	23	47	26
	Soil clay	16	19	13	21	17
	Soil sand	15	45	32	18	27
	Soil silt	13	21	19	48	26
Time	GDD5_year	35	43	20	12	27
	Julian day	26	14	15	11	16
	Year	14	32	16	73	34
Plant cover	Short forbs					
	Tall forbs	40	24	35	12	28
	Grass	30	8	13	11	15
	Trees	22	34	28	83	42
	Shrubs/Small trees/Vines	39	46	17	18	30
Temperature	GDD5_sum	15	15	15	−2	11
	Tsoil_Avg	30	18	16	15	20
	Tsoil_Max	17	14	15	18	16
	Tsoil_Min	29	22	19	29	25
	Tsurface_Avg	14	12	9	11	11
	Tsurface_Max	3	10	−2	16	7
	Tsurface_Min	33	12	32	22	25
Moisture	Precipitation	1	5	2	−6	1
	SoilH2O_Avg	7	24	6	7	11
	SoilH2O_Max	16	24	25	4	17
	SoilH2O_Min	4	21	19	12	14

Table D2. Predictor importance scores for tall forb random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	23	84	40	36	46
	Soil density	21	4	39	33	24
	Soil pH	22	28	40	28	29
	Soil clay	10	27	11	30	19
	Soil sand	15	3	12	27	14
	Soil silt	11	4	13	35	16
Time	GDD5_year	22	20	29	27	24
	Julian day	23	12	30	29	24
	Year	3	0	15	15	8
Plant cover	Short forbs	28	14	21	24	22
	Tall forbs					
Temperature	Grass	17	6	4	20	12
	Trees	26	50	41	30	37
	Shrubs/Small trees/Vine	47	36	24	28	34
	GDD5_sum	9	1	12	11	8
	Tsoil_Avg	18	22	40	25	26
	Tsoil_Max	13	46	26	22	26
	Tsoil_Min	17	46	42	29	34
	Tsurface_Avg	17	13	13	23	16
	Tsurface_Max	9	9	6	17	10
	Tsurface_Min	18	37	30	39	31
Moisture	Precipitation	2	-5	5	8	2
	SoilH2O_Avg	24	23	15	28	22
	SoilH2O_Max	23	19	8	22	18
	SoilH2O_Min	27	19	6	31	21

Table D3. Predictor importance scores for grass random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	48	19	18	42	32
	Soil density	21	10	13	11	14
	Soil pH	21	11	7	13	13
	Soil clay	49	9	16	63	34
	Soil sand	27	11	11	15	16
	Soil silt	24	11	18	13	16
Time	GDD5_year	20	26	45	18	27
	Julian day	23	25	28	21	24
	Year	35	35	92	69	58
Plant Cover	Short forbs	48	25	26	30	32
	Tall forbs	32	27	31	13	26
Temperature	Grass					
	Trees	26	23	14	17	20
	Shrubs/Small trees/Vines	27	24	32	47	33
	GDD5_sum	8	18	12	8	11
	Tsoil_Avg	31	20	16	13	20
	Tsoil_Max	21	19	16	13	17
	Tsoil_Min	28	22	15	12	19
	Tsurface_Avg	15	21	13	12	15
	Tsurface_Max	8	16	8	7	10
	Tsurface_Min	17	24	14	3	15
Moisture	Precipitation	3	20	9	11	11
	SoilH2O_Avg	21	21	8	25	19
	SoilH2O_Max	18	19	11	25	18
	SoilH2O_Min	17	25	22	46	27

Table D4. Predictor importance scores for tree random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	36	35	56	17	36
	Soil density	16	14	14	7	13
	Soil pH	16	11	25	14	16
	Soil clay	34	18	5	5	16
	Soil sand	19	13	5	14	13
	Soil silt	16	15	5	5	10
Time	GDD5_year	26	33	37	59	39
	Julian day	17	27	18	19	20
	Year	14	5	48	43	28
Plant Cover	Short forbs	18	14	49	71	38
	Tall forbs	33	47	37	14	33
	Grass	29	14	7	17	17
	Trees					
Temperature	Shrubs/Small trees/Vines	30	44	67	64	52
	GDD5_sum	15	19	8	11	13
	Tsoil_Avg	10	24	31	15	20
	Tsoil_Max	9	15	16	10	12
	Tsoil_Min	14	40	27	16	24
	Tsurface_Avg	8	14	11	13	12
	Tsurface_Max	2	7	10	4	6
	Tsurface_Min	21	25	25	45	29
	Precipitation	2	9	1	7	5
Moisture	SoilH20_Avg	13	20	4	15	13
	SoilH20_Max	17	13	8	17	14
	SoilH20_Min	9	18	0	11	9

Table D5. Predictor importance scores for shrub/small tree/vine random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	37	78	38	24	44
	Soil density	36	4	6	25	17
	Soil pH	35	23	59	20	34
	Soil clay	5	6	4	12	7
	Soil sand	19	46	27	32	31
	Soil silt	6	7	32	24	17
Time	GDD5_year	32	84	65	40	55
	Julian day	25	20	23	17	21
	Year	9	32	17	49	27
Plant Cover	Short forbs	17	46	16	25	26
	Tall forbs	81	35	14	22	38
	Grass	12	5	2	18	9
	Trees	38	151	98	110	99
Temperature	Shrubs/Small Trees/Vines					
	GDD5_sum	17	10	18	15	15
	Tsoil_Avg	19	19	22	12	18
	Tsoil_Max	19	15	24	12	18
	Tsoil_Min	31	20	22	14	22
	Tsurface_Avg	12	16	26	15	17
	Tsurface_Max	5	12	17	11	11
	Tsurface_Min	25	8	41	20	23
	Precipitation	4	13	3	16	9
Moisture	SoilH20_Avg	21	25	6	12	16
	SoilH20_Max	15	22	20	14	18
	SoilH20_Min	13	16	15	14	14

Table D6. Predictor importance scores for total cover random forest models.

Class	Variable	Treatment				Mean
		Ambient	Precip	Warm	Warm + Precip	
Plot	Block	12	6	15	16	12
	Soil Density	6	5	7	6	6
	Soil pH	6	2	5	5	4
	Soil clay	10	1	4	11	6
	Soil sand	5	2	7	6	5
	Soil silt	10	6	6	8	8
Time	GDD5_year	49	67	37	20	43
	Julian Day	21	16	23	33	23
	Year	9	10	8	22	12
Plant cover	Short forbs	132	80	90	88	98
	Tall forbs	38	56	49	38	45
	Grass	39	70	32	39	45
	Trees	37	116	41	86	70
	Shrubs/Small trees/Vines	48	32	47	53	45
Temperature	GDD5_sum	11	16	5	10	10
	Tsoil_Avg	18	12	15	13	15
	Tsoil_Max	7	14	12	13	12
	Tsoil_Min	18	24	21	28	23
	Tsurface_Avg	13	10	25	15	16
	Tsurface_Max	3	17	8	8	9
	Tsurface_Min	83	20	65	50	54
Moisture	Precipitation	12	11	14	7	11
	SoilH20_Avg	19	10	5	17	13
	SoilH20_Max	17	9	26	9	15
	SoilH20_Min	13	7	13	17	12