Forest disturbance accelerates thermophilization of understory plant communities

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Summary

1. Climate change is likely to shift plant communities towards species from warmer regions, a process termed "thermophilization." In forests, canopy disturbances such as fire may hasten this process by increasing temperature and moisture stress in the understory, yet little is known about the mechanisms that might drive such shifts, or the consequences of these processes for plant diversity.

2. We sampled understory vegetation across a gradient of disturbance severity from a large-scale natural experiment created by the factorial combination of forest thinning and wildfire in California. Using information on evolutionary history and functional traits, we tested the hypothesis that disturbance severity should increase community dominance by species with southern-xeric biogeographic affinities. We also analyzed how climatic productivity mediates the effect of disturbance severity, and quantified the functional trait response to disturbance, to investigate potential mechanisms behind thermophilization.

3. The proportion of north-temperate flora decreased, while the proportion of southern-xeric flora increased, with greater disturbance severity and less canopy closure. Disturbance caused a greater reduction of north-temperate flora in productive (wetter) forests, while functional trait analyses suggested that species colonizing after severe disturbance may be adapted to increased water stress. Forests with intermediate disturbance severity, where abundances of northern and southern species were most equitable, had the highest stand-scale understory diversity.

4. *Synthesis:* Canopy disturbance is likely to accelerate plant community shifts towards species from warmer regions, via its effects on understory microclimate at small scales. Understory diversity can be enhanced by intermediate disturbance regimes that promote the coexistence of species with different biogeographic affinities.

Introduction

Anthropogenic changes in global climate are expected to cause shifts in species distributions at large spatial (e.g. landscape to continent) and temporal (e.g. decade to century) scales (Lenoir et al., 2008, Bertrand et al., 2011). At the local (e.g. plot or stand) scale, plant community composition should therefore become increasingly dominated by species from lower latitudes or elevations that are better adapted to a locally warming climate, a process termed "thermophilization" (Gottfried et al., 2012). However, local environmental features such as topography can strongly alter the realized climatic niche that plants experience, potentially buffering the effects of changing regional climate and creating microclimate refugia that act to slow community thermophilization (Dobrowski, 2010, Lenoir et al., 2013, Spasojevic, Harrison et al., 2014, Rapacciuolo et al., 2014).

Forests play an important role in mediating the microclimate experienced by understory plants, by reducing understory air and soil temperatures, irradiance, and evapotranspirational demand (Norris et al., 2012, Chen et al., 1999). Therefore, increases in forest cover over large spatial and temporal scales can slow the thermophilization of understory plant communities during periods of climate warming (De Frenne et al., 2013). However, while afforestation is a slow process, forest disturbance can happen rapidly and has the potential to accelerate understory thermophilization at much smaller scales across time and space, particularly in warm, dry forests at the margin of more thermophilic plant communities. In drier forests, understory air temperatures and evapotranspirational demand are more sensitive to decreases in canopy cover than they are in more humid forests (Ashcroft and Gollan, 2013). Furthermore, drier forests are more prone to disturbances such as fire, which could provide a means for accelerated community

thermophilization by reducing competition from existing vegetation and creating recruitment opportunities (Roberts, 2004).

Previous quantification of thermophilization has relied upon assigning mean temperature scores to species based on their current geographic distributions, and calculating community temperature indices based on the scores of individual species present (Savage and Vellend, 2014, De Frenne et al., 2013). One challenge presented by this approach is that estimating climatic niches based on regional climate averages across a species' current geographic range does not account for the microclimate-mediating effects of forest cover and topography (Potter et al., 2013, Harwood et al., 2014). An alternative means of quantifying community thermophilization is to use biogeographic affinity, which describes the general climatic tolerances of taxa based on climatic conditions of the regions and time periods under which they evolved and diversified (Wiens and Donoghue, 2004). Species' biogeographic affinities have been used to predict patterns of species richness and community composition over productivity gradients (Harrison and Grace, 2007), and functional trait analyses have confirmed that biogeographic affinity classifications capture important differences in species niches, such as greater specific leaf area and leaf water content in species with more mesic biogeographic affinities (Anacker and Harrison, 2012). Therefore, biogeographic affinity may be a useful way to classify community thermophilization in response to forest disturbance, especially in fire-prone forests of topographically complex regions that contain a mixture of species with different biogeographic origins.

We examined the response of different biogeographic affinities to forest disturbance in yellow pine and mixed-conifer forests of California, USA. These montane forest types occupy a Mediterranean climate region where fire was a historically frequent disturbance, although

climatic and topographic heterogeneity led to variable fire effects and forest structure within this region (Sugihara et al., 2006). Biogeographic affinity is a particularly useful predictor of community composition in Mediterranean climates, where the relatively recent Miocene-Pliocene onset of hot, dry summers contributed to the speciation and immigration of xeric lineages, while low extinction rates – in part attributable to microclimate variation – resulted in the persistence of temperate mesic lineages that had previously diversified during the Eocene epoch (Herrera, 1992, Lancaster and Kay, 2013). In California, roughly 50% of the modern flora belongs to lineages that diversified in mesic Eocene forests and today have their centers of diversity in northern temperate regions (Lancaster and Kay, 2013, Raven and Axelrod, 1978). Much of the remaining flora diversified in southern xeric and fire-prone regions, including taxa that speciated following the onset of the Mediterranean climate in California (Lancaster and Kay, 2013, Raven and Axelrod, 1978).

If forest canopy closure influences the relative abundance between northern and southern floristic groups, then heterogeneity in canopy closure at intermediate levels of disturbance severity may lead to increased diversity by promoting coexistence of northern and southern groups at the forest stand scale. Because intermediate levels of disturbances such as fire can produce greater variation in within-stand canopy closure (Peterson and Reich, 2008), we would expect intermediate disturbance severity to lead to high beta diversity (variation in species composition among vegetation plots within a forest stand; Anderson et al., 2011). Correspondingly, when disturbance severity is greater and more homogeneous, there should be fewer microhabitat refugia (e.g. shaded areas) for species that may not tolerate post-disturbance environmental conditions (Chase, 2003), leading to increased dominance by southern floristic groups and a decline in stand-scale diversity caused by the loss of northern floristic groups.

We tested four specific hypotheses relating to the thermophilization of understory plant communities following disturbance, using a large replicated natural experiment across a gradient of disturbance severity. We hypothesized that: 1) species with northerly biogeographic affinities would decrease in abundance, relative to species with southerly biogeographic affinities, as forest disturbance severity increased from an undisturbed condition to high-severity fire. 2) The loss of species with northerly biogeographic affinities following disturbance would be greater at more productive sites (those with higher precipitation), where canopy cover in the absence of disturbance was greater, consistent with an important role for canopy-mediated microclimate in structuring understory communities. 3) The distribution of leaf functional traits would shift towards drought-tolerant values (lower specific leaf area and increased carbon:nitrogen ratios) with increasing disturbance severity, consistent with increased microclimatic water deficit in disturbed forest stands as a mechanism driving thermophilization. 4) Species diversity at the stand scale would be maximized by intermediate disturbance regimes that promote the coexistence of species with different biogeographic affinities (northerly and southerly). Our study took advantage of an existing statewide plot network to compare plant responses across the full continuum of disturbance severity – created by the interaction between wildfire and forest thinning treatments – which is an important unfilled need in studies of understory responses to forest disturbance (Abella and Springer, 2015). This work has implications for understanding understory vegetation shifts, and for the maintenance of species and biogeographic diversity in forests under rapid climate warming and increased fire activity (Turner et al., 2013, Dale et al., 2001).

Materials and methods

Study system

We collected floristic data from fire-adapted, yellow pine and mixed-conifer montane forests in eastern California, USA (Fig. 1), which are among the most widespread forest types in the region (Barbour et al., 2007). Forests in this region experience a Mediterranean climate of mild wet winters and hot dry summers. Prior to Euro-American settlement, the primary natural disturbance regime in these forests consisted of low- to moderate-severity fires with average return intervals ranging from 7-16 years (Van de Water and Safford, 2011). This frequent-fire regime created a heterogeneous forest structure containing large fire-resistant trees, canopy gaps, and denser clumps, with greater canopy cover at mesic sites, north-facing slopes and higher elevations (Barbour et al., 2007, Larson and Churchill, 2012, Sugihara et al., 2006). However, the majority of these forests today have been structurally homogenized by over 100 years of fire suppression (Stephens and Ruth, 2005), which has increased canopy cover, tree density, and the likelihood of high-severity wildfire (Miller et al., 2009, McIntyre et al., 2015). Increasingly, the primary management objective in these forests is to reduce potential wildfire severity by conducting fuel treatments, which remove canopy and surface fuels, often using both mechanical tree removal and prescribed fire (Agee and Skinner, 2005). Canopy reductions such as those associated with fuel treatments and fire can increase understory air temperatures by 58-124%, soil temperatures by 14-20%, photosynthetically active radiation by 7-11%, and wind speed by 24-40% while reducing relative humidity by 2-14% (Ma et al., 2010).

Field methods

We sampled the understory flora in 664 plots distributed among 12 distinct sites in yellow pine and mixed-conifer forests, between 1200 and 2300 m in elevation (Fig. 2). All 12

sites had been partially burned by wildfires within five years prior to sampling, and had been targeted by fuel treatments prior to the wildfire occurrence, such that at each site wildfire burned from untreated stands into adjacent treated stands (Safford et al., 2012, Stevens et al., 2014). The 12 sites spanned a large latitudinal gradient (from 34.3 N to 41.6 N) and a large precipitation gradient (from 40 to 180 cm annually; Table S1), spanning almost the whole range of temperature and precipitation in which this forest type occurs (Barbour et al., 2007). To standardize the effect of time-since-fire on diversity, all floristic data used were collected three years post-fire, with the exception of the Harding fire (five years post-fire) and the Cougar fire (two years post-fire). For additional site information, see Safford et al. (2012).

At each site, we established circular 12.57 m^2 (2 m radius) vegetation plots (20-113 plots per site; Table S1). Within a site, plots were divided among four disturbance classes, which were created by the four possible combinations of fuel treatments and wildfire. Class 1 stands were unburned and untreated, and represent the baseline fire-suppressed condition of the majority of yellow pine and mixed-conifer forests in California. Class 2 stands were unburned by wildfire, but had been treated with a combination of thinning and surface-fuel reduction within the previous 10 years (see Table S1 for detailed treatment information). Class 3 stands represent the interaction of fuel treatments and wildfire: they experienced the same fuel treatments as Class 2 stands but were subsequently burned by wildfire. Due to these treatments, Class 3 sites exhibited mostly low to moderate wildfire severity. Class 4 stands were untreated prior to wildfire, and generally burned at high severity, with high canopy mortality (Safford et al., 2012). As disturbance severity increases from Class 1 to Class 4, forest stands are characterized by significant decreases in live basal area, live tree density, canopy closure, litter depth and litter cover, and increases in bare soil exposure (Stevens et al., 2014).

Our sampling plots were arranged in transects that spanned the fuel-treatment boundary between Classes 1 and 2 (outside the fire perimeter), or between Classes 3 and 4 (inside the fire perimeter). Plots were spaced 20-50 m apart along transects, with an average of 11 plots per transect (range 9-15) and an average of 5 transects per site (range 2-8). When multiple transects were used within a disturbance class, the transects were placed at random locations that were relatively close together (within 1 km of one another at all but one site), so we considered all sample plots within a given disturbance class to be independent within a given site. We account for non-independence of plots in the same site relative to plots between sites, by using a hierarchical model structure described below. At each sampling plot, we visually estimated percent cover of all vascular plant species to the nearest 0.5%. This included all woody shrubs and tree seedlings in the understory layer (less than 1.4 m in height). All species were identified according to Hickman (1993); when plants were not identifiable in the field we collected pressed specimens to identify in the lab, and returned to most sites multiple times to confirm species identities. There were 329 species in our sample plot network of 664 plots (Appendix A). At each plot, we also took a point-level estimate of canopy closure using a spherical densiometer, to evaluate the understory light environment.

Analysis

Biogeographic affinities

We classified each species as either native or non-native to California, and assigned each native species to one of two biogeographic affinities: north-temperate, which contain the "Arcto-Tertiary Geoflora", and southern-xeric, which contain the "Madro-Tertiary Geoflora" along with warm-temperate/desert elements (Raven and Axelrod, 1978). According to the paleobotanical classifications of Raven and Axelrod (1978), the Madro-Tertiary Geoflora includes taxa that

diversified with the onset of the Mediterranean climate in California during the late Tertiary and

Quaternary periods, as well as older lineages which diversified further south during drier

portions of the Tertiary, while the warm-temperate/desert taxa migrated into California from

deserts to the south and east during the Quaternary. While these southern-xeric taxa underwent

rapid speciation following the development of the Mediterranean climate, north-temperate taxa

underwent relatively little speciation during the Quaternary, and may have persisted in the region

by retreating to microclimatic refugia (Lancaster and Kay, 2013). Not counting the 17 non-native

species present in this study, we were able to assign biogeographic affinity to 302 of the

remaining 312 native species. The remaining 3.2% of species were not assigned a biogeographic

affinity by Raven and Axelrod (1978), consistent with their classification of the state's flora as a

whole. In addition to investigating the biogeographic affinity of the native flora, we also tested

the effect of disturbance class on the proportion of non-native flora at the plot-scale.

Traits

Leaf functional traits are linked to climatic productivity and covary along productivity

gradients: for example, in environments with low productivity, community-level specific-leaf

area (SLA) and leaf nitrogen (N) tend to be lower, while in more productive environments,

SLA and leaf N tend to be higher, reflecting favorable growth conditions (Westoby et al.,

2002). We obtained mean trait values of specific leaf area (SLA) and leaf carbon:nitrogen ratio

(C:N) for a subset of our species for which data were available from an existing dataset on leaf

traits of the California flora, collected elsewhere in California (Spasojevic, Damschen et al.,

2014). Trait data were available for 126 of our 329 species (Appendix A), which were randomly

distributed among biogeographic affinity classes (ANOVA, F=0.29, P=0.88) and represented

63% of total vegetation cover in the dataset. For each of 643 plots, we calculated abundance-

weighted mean SLA and C:N values by multiplying the species-specific mean trait value for each species present, by the relative abundance of each species in the plot, determined by percent cover.

We compiled information on plant life form following the Raunkiaer (1934) classification system. Plants were classified as phanerophytes (woody above-ground secondary growth), chamaephytes (perenneating buds from woody base close to ground), hemicryptophytes (herbaceous plants with buds at ground level), geophytes (buds in below-ground storage organs) and therophytes (annual plants). Classifications were made for 325 of 329 species using information from Kew Botanical Gardens (http://apps.kew.org/wcsp), the US Forest Service Fire Effects Information System (feis-crs.org) and the University of California Jepson Herbarium (http://ucjeps.berkeley.edu). We additionally analyzed the distribution of dispersal syndromes (ant, wind, vertebrate, and passive) among different disturbance classes. We had dispersal information for 150 of our 329 species (data from Anacker and Harrison, 2012).

Species diversity

We measured species richness as a count of species present in a plot, and calculated alpha diversity within plots using the Shannon-Weiner index to account for differences in evenness of cover among plots (Magurran, 1988). We quantified plot-scale beta diversity, e.g. variation in species presence/absence among plots within a single stand, using Raup-Crick (RC) dissimilarity scores scaled from 0 (more similar) to 1 (less similar) (Raup and Crick, 1979). RC scores adjust for the positive relationship between alpha diversity and beta diversity by generating a null distribution of pairwise dissimilarities based on random draws from the regional species pool (Chase et al., 2011). We calculated RC dissimilarity scores based on a regional species pool defined separately for each of our 12 sites. Mean pairwise dissimilarity scores are not

independent of each other when calculated for each plot's dissimilarity to all other plots in a site

(Anderson et al., 2011). We accounted for this by estimating the distance-to-centroid (hereafter

RC distance scores) for each plot, where the centroid is calculated in multivariate space for each

disturbance class based on the RC dissimilarity scores (Anderson et al., 2011), using the

betadisper function in the R package Vegan (Oksanen et al., 2011). We calculated gamma

diversity within each of the four disturbance classes by multiplying the independently-derived

estimates of alpha and beta diversity (Jost, 2007), to compare stand-scale estimates of diversity

among disturbance classes.

Statistical models

In order to test our primary set of hypotheses that biogeographic affinity, leaf functional

traits and diversity metrics should vary among the four disturbance classes in this study

(hypotheses 1, 3 and 4), we adopted a generalized multilevel regression-based modeling

approach (Bolker et al., 2009). We fit mixed models to the data that included fixed effects for the

effect of disturbance class (the treatment variable), and random effects for site. The general

structure of these models is as follows:

$$y_i \sim N(\mu_i, \sigma^2); \; \mu_i = \beta_{D[i]} + \theta_{s[i]}$$
Eq. 1

where y_i is the *i*th observation of the response variable, μ_i is the model fitted value for that

observation, and σ^2 is the plot-level variance. The regression equation contains $\beta_{D[i]}$, which

represents the coefficients of the categorical variable for disturbance class, *D*. Because there is

no overall intercept, β_D represents the estimated mean level of y in each disturbance class. The

random effects $\theta_{s[i]}$ are random intercepts for each of the 12 sites *s* sampled in this study, with

$\theta_{s[i]} \sim N(0, \sigma_{site}^2)$. Including these site random effects allows the model to account for potential

non-independence of the observations taken at the same site relative to observations taken at

different sites (Gelman and Hill, 2007). These models were fit using the lme4 package in R

(Bates et al., 2013).

To test our hypothesis that the effect of disturbance on biogeographic affinity would vary

among sites based on climatic productivity (hypothesis 2), we modified Eq. 1 as follows:

$$y_i \sim N(\mu_i, \sigma^2); \; \mu_i = \beta_{D[i]S[i]}$$

Eq. 2

In this model, $\beta_{D[i]S[i]}$ is a set of coefficients for D, as was $\beta_{D[i]}$ in Eq. 1, but these coefficients

now vary across sites s. We were then able to model these coefficients $\beta_{D[i]S[i]}$ against site-level

precipitation values, using simple linear regression to relate precipitation to variation among sites

in the effect of disturbance.

For both equations, where the response variable was modeled as a count or proportion,

we assumed a Poisson or binomial distribution, respectively, instead of a normal distribution. For

all models, we evaluated the effect of disturbance class by comparing the penalized log-

likelihood value from the model in Eq. 1, with a null model that excluded the effect of

disturbance class, using ΔAIC as our comparison metric (Burnham and Anderson, 2002). We

tested whether pairwise differences in means between the four disturbance classes were

significantly non-zero using Wald-Z scores (Bolker et al., 2009).

Results

Forest disturbance had a strong effect on the proportion of understory flora within a plot

from different biogeographic affinities (Tables 1 and S3). The proportion of the total native flora

with a north-temperate biogeographic affinity decreased with increasing disturbance severity

(Fig. 2a), while the proportion of native flora with a southern-xeric biogeographic affinity

increased with disturbance severity (Table 1). All pairwise comparisons were significantly

different except for the proportion of north-temperate flora between Class 1 (undisturbed) and

Class 2 (fuel treatment only; Table 1). Correspondingly, there was a significant positive effect of canopy closure on the proportion of north temperate flora (Fig. 2b, effect size=0.5%, Wald $Z =$ 10.66, $P<0.001$) and a significant negative effect of canopy closure on the proportion of southern xeric flora (effect size=-0.5%, Wald $Z = -10.97$, $P<0.001$).

Precipitation interacted with disturbance class to affect the proportion of north-temperate origin species (Fig. 3). The main effect of precipitation on north-temperate species abundance was positive and highly significant ($F=54.2$, $df=1$, $P<0.001$), and the interaction between precipitation and disturbance class was marginally significant ($F=2.72$, $df=3$, $P=0.057$). For a given precipitation level, disturbance reduced the predicted proportion of north temperate flora, however, the degree to which disturbance reduced the proportion of north-temperate flora was greater at sites with higher precipitation (Fig. 3).

When we analyzed the abundance-weighted mean plot-level leaf trait values, we found a significant effect of disturbance class for leaf C:N but not for log-SLA (Table 1, Fig. S1). Plots in unburned Classes 1 and 2 had significantly higher average C:N values than those in burned Classes 3 and 4, and the intermediate-severity Class 3 had significantly higher average C:N values than high-severity Class 4 (Table 1). Although the plot-level SLA values did not significantly differ among any of the four disturbance classes (Tables 1 and S2), there was a strong negative correlation between abundance-weighted mean log-SLA and C:N at the plot level (Pearson's r=-0.56, 95% CI=(-0.61, -0.50), $R^2=0.31$), suggesting that overall, plots dominated by species with lower C:N also had higher mean SLA values (Fig. S2). We investigated differences in this relationship among disturbance classes by extracting the residuals from a linear multilevel model that regressed logSLA on leaf C:N with random site effects, and then checking for associations between residuals of this model and disturbance class, as well as

canopy closure and the proportion of north-temperate species in the plot. We found that the residuals from the plot-level SLA-C:N model were significantly less than zero in the high-severity disturbance class (Wald Z=2.37, *P*=0.019). Furthermore, we found a significant positive effect on the plot-level residuals of both canopy closure (Wald Z=2.97, *P*=0.003), and proportion of north-temperate flora (Wald Z=2.2, *P*=0.028). Collectively, these results indicate that plots in highly disturbed stands have lower than expected SLA values for a given C:N value, and plots in more heavily forested stands have higher than expected SLA values for a given C:N value.

Disturbance class also explained differences in plant life forms and dispersal traits (Table S2). Phanerophytes (woody plants) were more abundant relative to other life forms in undisturbed (Class 1) and high-severity (Class 4) stands (Table S4). In Class 1 stands this trend was driven by a mixture of tree and shrub species in the understory, while in Class 4 stands phanerophyte diversity was primarily among shrub species. Among herbaceous species, chamaephytes and hemicryptophytes decreased, and therophytes (annuals) increased as a proportion of the total flora at higher levels of disturbance severity (Table S4). Further, the proportion of wind-dispersed species increased with disturbance severity, while the proportion of vertebrate-dispersed species decreased (Table S4).

We found strong effects of disturbance class on species richness, alpha diversity and beta diversity: multilevel models for these variables containing a parameter for disturbance class always had more support, based on ΔAIC values, than null models containing only random effects for site (Table S2). At the plot scale, increased disturbance was associated with greater species richness and alpha diversity, although Class 3 and Class 4 stands were not significantly different from each other at this scale (Fig. 4a, Tables 1 and S3). Increased disturbance was also

associated with a significantly higher proportion of non-native species at the plot scale, although the proportion of non-native flora was low overall, peaking at 8% in Class 4 stands (Table S3).

Disturbance class had a strong effect on among-plot beta diversity, with mean RC distance-to-centroid scores highest in the intermediate disturbance classes and lowest in the high disturbance class (Fig. 4b). Gamma diversity, the product of alpha and beta diversity, was therefore highest in the intermediate disturbance classes (Fig. 4c). Pairwise comparisons between the four disturbance classes from the multilevel model indicated significantly lower between-plot beta diversity in Class 4 compared to all other classes (Table 1). None of the other three disturbance classes differed significantly from one another in beta diversity (Table 1). We tested whether canopy closure was also less variable in Class 4 stands by calculating the standard deviation of canopy closure measurements for each disturbance class within each site, and conducting an analysis of variance on the standard deviations. Disturbance class had a significant effect on the variability of canopy closure (F =5.058, df=3, P=0.004), and Tukey's HSD test indicated that Class 4 canopy closure had significantly lower standard deviations than each of the other disturbance classes (all $P < 0.05$).

Discussion

Disturbance severity strongly influenced understory plant community composition and diversity at small spatial and temporal scales. We draw three principal conclusions from this work: First, the decrease in abundance of northern species and increase in abundance of southern species with disturbance severity demonstrate that community thermophilization is strongly influenced by disturbance characteristics at small spatial scales. Second, the mechanisms driving community thermophilization appear to be related to understory microclimate, which is strongly

affected by tree canopy cover. Microclimatic water deficit is generally higher in forest stands with lower canopy cover, as demonstrated by interactions between climatic productivity and disturbance severity, and by the response of leaf functional traits to disturbance severity. Therefore, the effects of disturbance may be more pronounced in more productive forests. Third, low- to moderate-severity wildfire, which in this study is associated with forests that had previously been treated to reduce fuels, supports the highest levels of plant diversity at the stand scale, relative to more or less severe disturbances. This intermediate-disturbance peak in diversity coincides with a more equitable coexistence of species from northern and southern biogeographic affinities at the plot-scale, relative to high-severity disturbance, which produces stands dominated by southern-xeric species, and the absence of disturbance, which is associated with dominance of north-temperate species (Fig. 2).

Biogeographic affinity of the understory community responded very strongly to the different disturbance classes created by the interaction of fuel treatments and wildfire. Mesic north-temperate species decreased in abundance as disturbance severity increased (Fig. 2). This suggests that canopy shading in xeric environments selects for species from regions or lineages less tolerant of moisture-stress (Valiente-Banuet et al., 2006, De Frenne et al., 2013). The relative increase in annuals with disturbance severity, which are generally drought-adapted and speciose within southern-xeric lineages (Raven and Axelrod 1978) provides additional support for the role of understory moisture stress. Importantly, the introduction of low- to moderate-severity fire (Class 3) and high-severity fire (Class 4) each further depress the proportion of mesic lineages below levels found in stands that were only subject to fuel reduction treatments, suggesting that these north-temperate derived lineages are generally not fire adapted.

Without refugia from high-severity or high-frequency fire conditions, mesic lineages may be at enhanced risk of local extinction. Over longer time scales, this may influence the composition of the regional flora. For instance, in regions such as South Africa and Australia, which had very high fire frequency during the onset of the Mediterranean climate in the late Tertiary, mesic lineages may have had higher extinction rates than xeric lineages (Cowling et al., 1996). However, evidence from California indicates that Cenozoic extinction rates have been low across all biogeographic lineages, while the concurrent increase of fire and diversification within lineages of the California Floristic Province suggests that the long-term, large-scale coexistence of these two groups may have been attributable to spatial variation in fire and microclimatic refugia (Lancaster and Kay, 2013). Slope aspect is an important source of microclimatic refugia for species less well adapted to high temperatures and moisture stress, both in xeric regions (Copeland and Harrison, 2015, Harrison et al., 2010) and more mesic regions (Warren, 2008, Lipscomb and Nilsen, 1990, Cantlon, 1953), where community composition on equatorial-facing slopes may reflect future community composition under a warming climate. Our study reveals that at a small scale, changes in forest canopy cover may be an equally important source of microclimatic refugia or accelerated community shifts. Because the coexistence of northern mesic and southern xeric lineages in our study was most equitable under low- and moderate-severity fire conditions, where total diversity was also highest (Figs. 2 and 4), the simultaneous conservation of these biogeographically distinct floras may be maximized under intermediate disturbance conditions.

Microclimatic water deficit, an important measure of drought stress that is strongly affected by both temperature and precipitation, is likely an important mechanism driving community composition in these dry forests. Our finding that north-temperate species were more

abundant at sites with greater precipitation even when highly disturbed (Fig. 3) is consistent with work that has shown an affinity of these northern species to more mesic areas within the region (Harrison and Grace 2007). However, these species are more responsive to increases in canopy cover with precipitation than to increases in precipitation alone (Fig. 3, Class 1 vs Class 4), reinforcing that local disturbance processes are at least as important as regional climatic change to predict understory thermophilization (Rapacciuolo et al., 2014). In general, disturbances such as fire appear to exert a stronger influence on communities at higher levels of productivity (Safford and Mallek, 2011).

We expected increased water stress in disturbed stands to cause a shift in leaf functional traits towards reduced SLA and increased C:N, traits associated with sclerophylly and drought tolerance (Chaves et al., 2003, Reich, 2014). However, we found no change in community SLA, and a decrease in community C:N with disturbance (Table 1). The decrease in foliar C:N may be explained by higher leaf nitrogen content associated with increased maximum photosynthetic rates selected for by high-light conditions (Cornelissen et al., 2003), suggesting that understory plants in disturbed stands may be able to sustain high photosynthetic rates despite water limitation. However, despite the strong negative correlation between community-weighted mean SLA and C:N (Fig. S2), we did not observe SLA increasing with disturbance (Fig. S1). We attribute this result to two factors: first, some shade-tolerant understory plants in dense forests have high SLA values (Cornelissen et al., 2003), and second, water stressed environments can lead to lower than expected SLA for given irradiance levels. In highly disturbed plots (Class 4), climatic water deficit is likely constraining SLA: canopy reductions may select for species with greater water use efficiency, which have reduced SLA to alleviate transpirational water loss but also have higher nitrogen levels to support high maximum photosynthetic rates (Wright et al.,

2001). Previous work has shown that SLA is lower for a given leaf N content at low-rainfall sites than at high-rainfall sites (Wright et al., 2001), indicating that water stress may constrain SLA values when higher max-photosynthetic rates would otherwise support higher productivity and leaf turnover. Our results extend this idea from large-scale climate gradients to local microclimates, where disturbance can constrain optimal SLA values in open forest patches. Further, this selection for high leaf N and relatively low SLA may be driving the positive response by species from southern-xeric lineages in disturbed forest, and is a potentially important mechanism behind thermophilization.

In ecosystems of intermediate productivity, theory predicts that plant diversity should generally increase after individual wildfire events (Bond and van Wilgen, 1996, Safford and Mallek, 2011). We find this to be true at the plot scale (Fig. 4), where increased diversity after fire can be attributed to removal of competitive dominants, creation of bare soil surfaces suitable for germination, removal of surface litter, increased canopy light penetration, or heat-stimulation of fire-dependent seed banks (Pickett and White, 1985, Bond and van Wilgen, 1996). However, theory also predicts that at intermediate productivity levels, diversity may decline at high disturbance frequency or severity (Safford and Mallek, 2011). We find support for this prediction more strongly at the stand scale, where high-severity disturbance stands had the lowest beta diversity and the lowest variation in canopy closure. Because variation in canopy closure provides a diversity of regeneration niches for different understory species (Roberts, 2004), increasing canopy homogeneity within high-severity disturbance patches could explain decreases in understory beta diversity.

The understory thermophilization documented here reflects community composition in the 2-5 year post-fire range (up to 12 years post-disturbance in the fuel-treatment only Class 2

stands). Longer-term community changes may be driven in large part by post-disturbance successional trajectories and subsequent disturbance regimes (Webster and Halpern, 2010). Species diversity and vegetation cover, particularly by shrubs, can continue to increase for up to 10-20 years post-fire in western conifer forests (Shive et al., 2013, Webster and Halpern, 2010). Certain species lost from the community after high-severity disturbances (e.g. north-temperate, shade-tolerant and/or fire-intolerant species) may be able to subsequently re-colonize, but the relative importance of their environmental tolerances vs dispersal abilities to this process is uncertain. We observed an increase in wind-dispersed species relative to vertebrate-dispersed species with increasing disturbance severity, but post-fire stands are well known to be favored by many vertebrate species, including browsers attracted by increased vegetation cover and post-fire habitat specialists (Swanson et al., 2011), suggesting that dispersal limitation may not be driving the shift in community composition. Perhaps more important is the forest canopy recovery rate following high-severity fire, which is likely to depend on interactions between high-severity patch size, shrub cover, and re-burn probability. At our study sites, abundance of tree seedlings in high-severity patches was very low, suggesting low forest resilience to high-severity fire (Stevens et al., 2014). Furthermore, with increasing fire severity in many Californian forests (Miller et al., 2009) and the high likelihood that high-severity patches will re-burn at high-severity and further delay tree regeneration (van Wagtendonk et al., 2012), the associated community thermophilization may be long lasting.

Our findings have significant implications for the conservation of species diversity in forests that evolved under frequent wildfire regimes. We show that active management, including fuel reduction treatments, can achieve desirable effects on understory plant diversity in such forests where fire has been suppressed, but also that fuel treatments are not complete fire

surrogates from a plant diversity perspective. Treatments alone increased plot-level diversity, and facilitated the establishment of species from southern lineages, but additional gains in diversity were achieved by subsequent burning of treated forest by wildfire (Fig. 4). Plant diversity is often greater in moderate-severity burns than in low-severity burns (Webster and Halpern, 2010). In this study, by including stands that burned at the full range of severity levels (Safford et al. 2012), we show that beta-diversity is reduced in high severity stands relative to low-moderate severity stands, indicating a homogenization of environmental filters. In a future of increasing temperature and disturbance frequency, management of disturbance itself will become an increasingly important part of conservation planning in ecosystems worldwide (Pressey et al., 2003). In forests with a history of frequent fires, restoration of historic disturbance processes appears to be an important tool for the conservation of floristic diversity.

Data Accessibility

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.q2n8p

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SUPPORTING INFORMATION
Additional supporting information may be found in the online version of this article:

Appendix S1: List of species in this study

Table S1: General information from the sampled fuel treatments

Table S2: AIC values from model comparisons

Table S3: Additional model estimates for biogeographic affinity and diversity

Table S4: Additional model estimates for plant life form and dispersal syndromes

Figure S1: Disturbance effects on community-weighted trait values

Figure S2: Correlation between abundance-weighed mean trait values at the plot scale

Table 1: Model estimates for each disturbance class.

Plot-level response variable	Disturbance class	Class mean value[1]	Effect size[2]	pairwise |Wald Z test statistic| (P) Class 1	Class 2	Class 3
Proportion north-temperate affinity	Class 1	0.63 (0.55,0.71)				
	Class 2	0.59 (0.51,0.67)	-0.15 (-0.35,0.04)	1.27 (0.115)		
	Class 3	0.47 (0.39,0.55)	-0.66 (-0.83,-0.49)	7.60 (0.001)	5.97 (0.001)	
	Class 4	0.38 (0.31,0.46)	-1.02 (-1.21,-0.85)	11.31 (0.001)	9.86 (0.001)	4.88 (0.001)
Proportion southern-xeric affinity	Class 1	0.29 (0.23,0.35)				
	Class 2	0.33 (0.27,0.40)	0.20 (0.01,0.40)	2.01 (0.045)		
	Class 3	0.48 (0.40,0.55)	0.80 (-0.63,0.98)	8.97 (0.001)	6.95 (0.001)	
	Class 4	0.57 (0.50,0.64)	1.19 (1.02,1.38)	12.86 (0.001)	11.07 (0.001)	5.27 (0.001)
Log (specific leaf area)	Class 1	4.74 (4.57,4.90)				
	Class 2	4.68 (4.52,4.86)	-0.05 (-0.16,0.06)	0.85 (0.40)		
	Class 3	4.76 (4.60,4.92)	0.02 (-0.08,0.13)	0.44 (0.66)	1.37 (0.17)	
	Class 4	4.73 (4.57,4.90)	-0.003 (-0.11,0.10)	0.06 (0.95)	0.85 (0.40)	0.56 (0.58)
Carbon-Nitrogen ratio	Class 1	32.84 (30.2, 35.5)				
	Class 2	32.83 (30.2, 35.5)	-0.01 (-1.81,1.78)	0.16 (0.99)		
	Class 3	30.65 (28.1, 33.2)	-2.19 (-3.83,-0.56)	2.63 (0.009)	2.58 (0.01)	
	Class 4	28.46 (25.9, 31.0)	-4.39 (-6.06,-2.71)	4.39 (0.001)	5.09 (0.001)	2.91 (0.004)
Alpha diversity (Shannon-Weiner)	Class 1	1.21 (1.01,1.40)				
	Class 2	1.42 (1.22,1.61)	0.21 (0.08,0.34)	3.14 (0.002)		
	Class 3	1.57 (1.38,1.75)	0.36 (0.24,0.48)	5.94 (0.001)	2.4 (0.016)	
	Class 4	1.51 (1.32,1.70)	0.3 (0.18,0.42)	4.78 (0.001)	1.4 (0.167)	1.1 (0.27)
Beta Diversity (Raup-Crick)	Class 1	0.24 (0.22,0.28)				
	Class 2	0.27 (0.24,0.30)	0.03 (-0.01,0.06)	1.43 (0.15)		
	Class 3	0.27 (0.24,0.30)	0.02 (-0.01, 0.05)	1.36 (0.17)	0.22 (0.83)	

Class 4	0.19 (0.15,0.22)	-0.06 (-0.09,-0.03)	3.53 (0.001)	4.98 (0.001)	5.45 (0.001)

1- Estimates of mean values from disturbance class + site random effect model (with 95% confidence intervals). For proportion data, estimates have been back-transformed from the logit-scale.
2- Estimates of effect size of a given disturbance class, relative to class 1 (with 95% confidence intervals). For proportion data, estimates are on the logit-scale

Figure Legends

Figure 1: Study sites in California, located within Yellow Pine Mixed Conifer (YPMC) forest types (in white).

Figure 2: Proportion of plot-level species pool that is of north-temperate evolutionary origin, (a) grouped by disturbance class and (b) plotted against canopy closure. Bars in (a) represent +/- 1 standard error around the mean for each disturbance class. The line in (b) indicates predicted values from the fixed-effects regression component of the multilevel binomial model of proportional north temperate flora conditional on canopy cover. N = 664 plots (137, 130, 216 and 181 plots for Classes 1-4 respectively). Disturbance classes are arranged from Class 1 to Class 4 (from control to wildfire-only plots) in order of increasing disturbance severity.

Figure 3: Proportion of total flora with north-temperate biogeographic affinity at each of the twelve sites in the study (points), and predicted proportions based on a regression against precipitation (lines). Precipitation values are averaged annual values from 1981-2000. Disturbance classes are arranged in legend from control to wildfire-only plots in order of increasing disturbance severity.

Figure 4: Alpha (a), beta (b) and gamma (c) diversity indices within each of the four disturbance classes. Alpha diversity was estimated using the Shannon-Weiner index, beta diversity was estimated using Raup-Crick distance-to-centroid scores, and gamma diversity was calculated as the product of alpha and beta indices. Bars in (a) and (b) represent +/- 1 standard error around the

mean for each disturbance class. N = 664 plots. Disturbance classes are arranged from Class 1 to

Class 4 (from control to wildfire-only plots) in order of increasing disturbance severity.
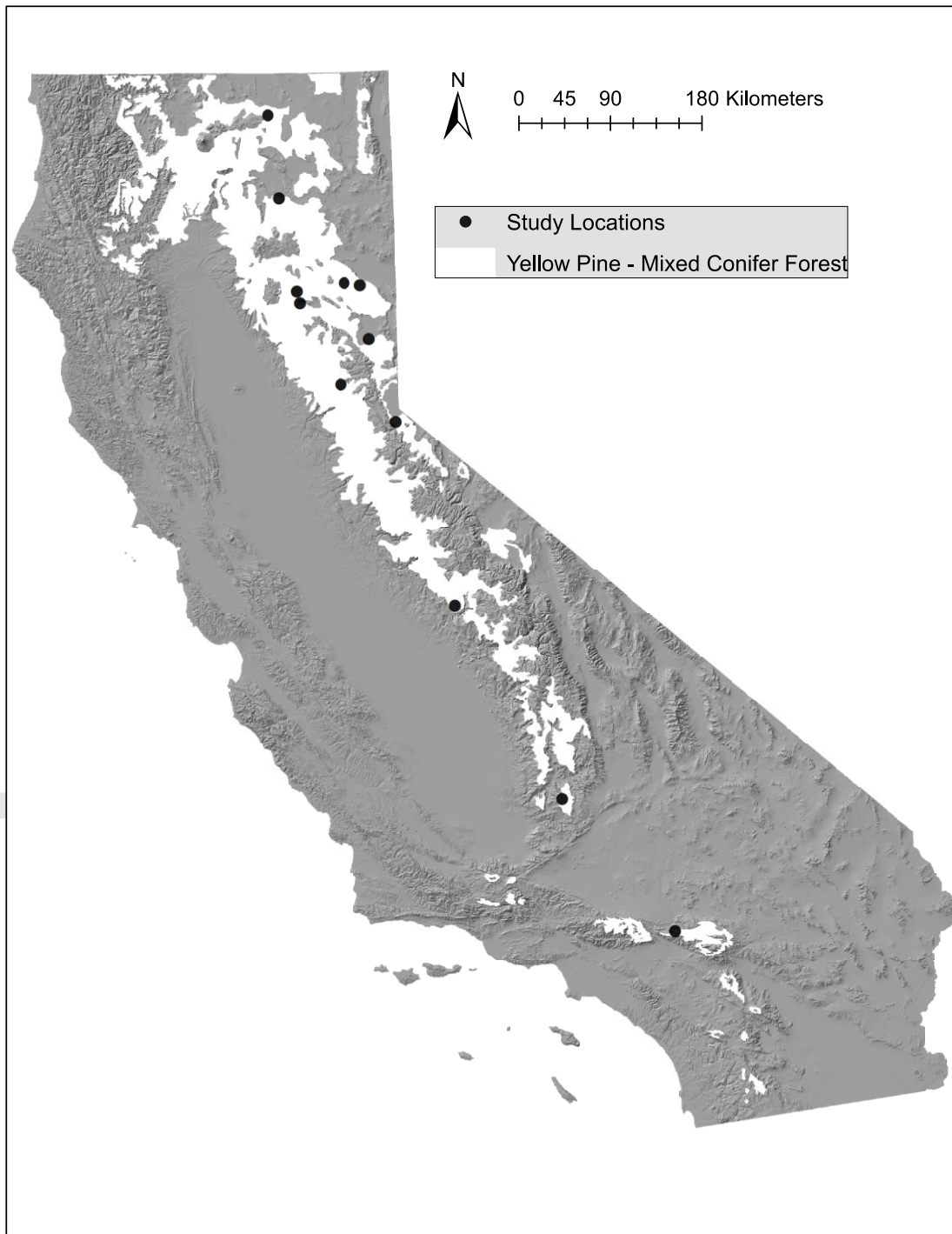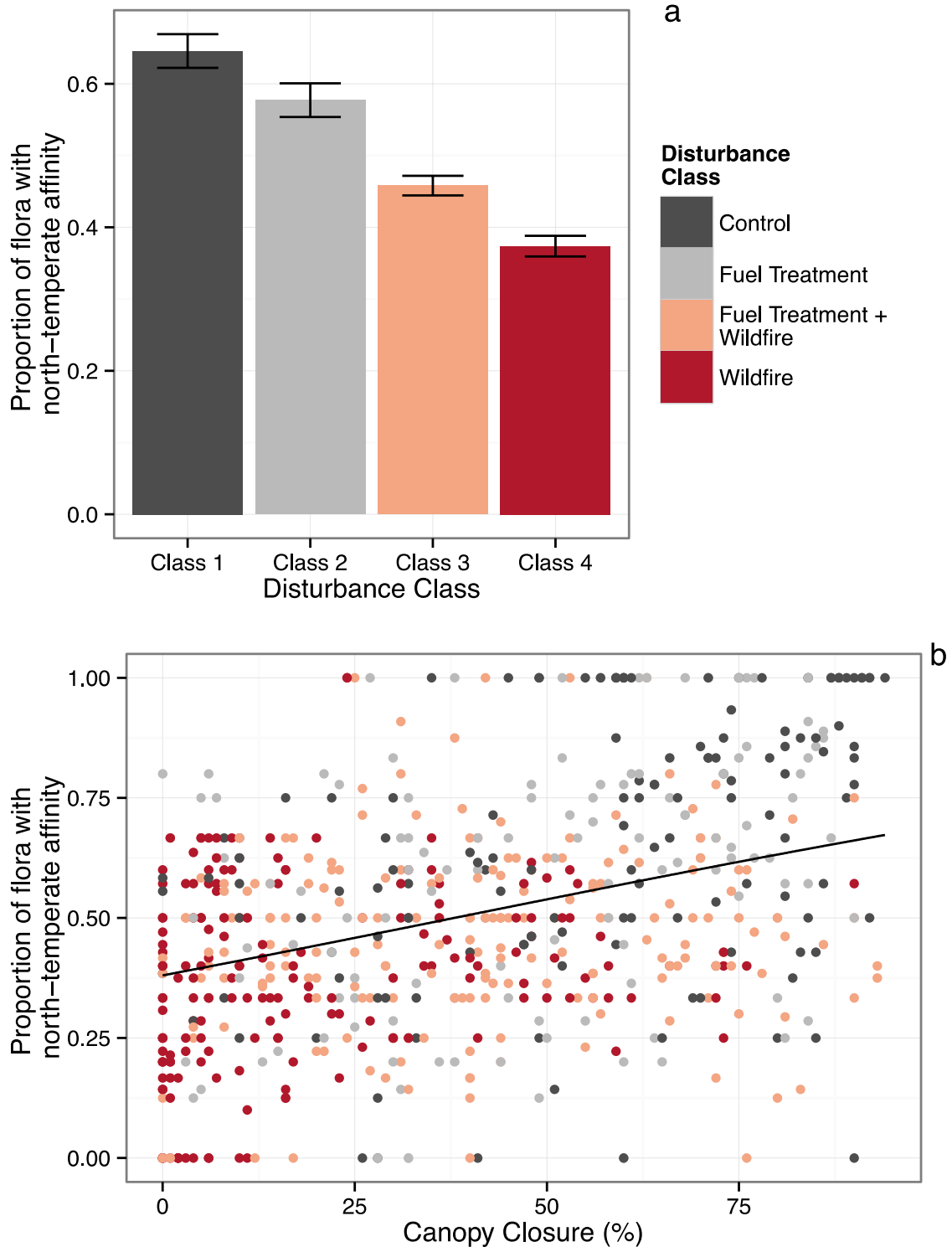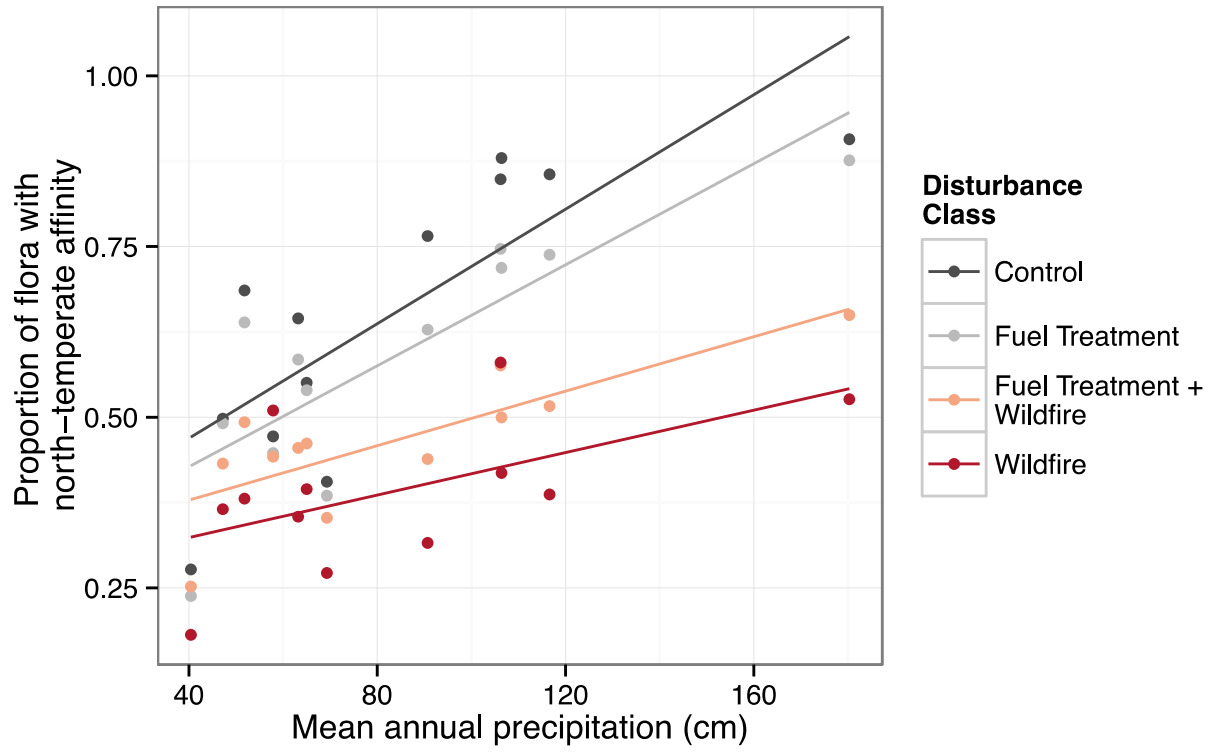
Figure 1

Figure 2

Figure 3

Figure 4