A century of increasing pine density and associated shifts in understory plant strategies

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Abstract. We analyzed one of the longest-term ecological data sets to evaluate how forest overstory structure is related to herbaceous understory plant strategies in a ponderosa pine forest. Eighty-two permanent 1-m^2 chart quadrats that were established as early as 1912 were remeasured in 2007. We reconstructed historical forest structure using dendrochronological techniques. Ponderosa pine basal area increased from an average of 4 m^2/ha in the early 1900s to 29 m^2/ha in 2007. Understory plant foliar cover declined by 21%, species richness declined by two species per square meter, and functional diversity also declined. The relative cover of C$_4$ graminoids decreased by 18% and C$_3$ graminoids increased by 19%. Herbaceous plant species with low leaf and fine root nitrogen concentrations, low specific leaf area, high leaf dry matter content, large seed mass, low specific root length, short maximum height, and early flowering date increased in relative abundance in sites where pine basal area increased the most. Overall, we observed a long-term shift in composition toward more conservative shade- and stress-tolerant herbaceous species. Our analysis of temporal changes in plant strategies provides a general framework for evaluating compositional and functional changes in terrestrial plant communities.

Key words: functional diversity; functional traits; height; leaf economics spectrum; nitrogen; ponderosa pine; seed mass; shade tolerance; specific leaf area; specific root length; stand density.

Introduction

Plant strategies have developed over evolutionary time scales (e.g., millennia) due to selection on growth, survival, and reproduction in resource-limited environments (Grime 1979). Changes in environmental conditions and resource availability over ecological time scales (e.g., decades) could cause shifts in plant community composition because plants with traits that are best adapted to the new environment may rise to dominance (Keddy 1992). Few studies have documented shifts in functional strategies over time because complete species–trait matrices and long-term data sets are scarce. In the southwestern United States, tree densities in ponderosa pine forests have increased significantly since Euroamerican settlement in the late 1800s due to land-use changes including grazing, logging, and fire suppression, and also due to climatic events favorable to natural pine regeneration (Moore et al. 1999). In this paper, we use a set of long-term (~100 years) permanent vegetation plots to determine if changes in forest stand density were associated with shifts in herbaceous understory community structure and plant strategies.

In prior work, we found that three orthogonal strategy axes, representing Westoby's (1998) "leaf–height–seed"

model of plant strategies, captures the majority of functional variation in a ponderosa pine forest understory flora (Laughlin et al. 2010). The first strategy axis represents variation along the "leaf economics spectrum" (Wright et al. 2004) and is indicative of a species' ability to rapidly photosynthesize and respond to opportunities for rapid growth (Reich et al. 1997). The second strategy axis represents variation in seed mass, which reflects variation in dispersal capability and ability to establish in deep shade (Grime and Jeffrey 1965, Westoby et al. 1996). The third strategy axis represents variation in plant height, which reflects variation in ability to acquire light (Keddy and Shipley 1989).

This study builds on our prior work by addressing how these functional strategies may have responded to long-term changes in forest structure. The environmental conditions associated with dense ponderosa pine stands, such as shade, deep litter horizons, low soil moisture and temperature, and low available nutrients (Kaye and Hart 1998) make these environments physiologically stressful (Grime 1979). We predicted that increases in pine canopy cover over the last century would shift understory communities toward dominance by conservative graminoids and forbs, which exhibit multiple traits that confer long-term maintenance of acquired resources (Reich et al. 2003). Therefore, we predicted that increasing pine densities would be associated with (1) decreased herbaceous specific leaf area (SLA) and tissue nutrient concentrations reflecting declines along the leaf

economics spectrum, (2) increased herbaceous seed mass and declines in specific root length, (3) decreased herbaceous plant height, and (4) decreased herbaceous production and functional diversity.

METHODS

Chart quadrats

The ponderosa pine forest ecosystem covers approximately 3.5 million ha of land across uplands in the southwestern United States. Our study was conducted on a ~12 000 ha landscape on the Coconino National Forest in northern Arizona between the elevations of 2000–2500 m on relatively flat sites. Ponderosa pine is the dominant tree species and forms extensive pure stands, but sometimes occurs with Gambel oak (*Quercus gambelii* Nutt.). Quadrats were located within a range of soil types developed in basalt, limestone, and sandstone parent materials. Grazing by native ungulates and domestic livestock still occurs across the study area, though grazing intensity has declined considerably over time (Bakker and Moore 2007). The mean annual precipitation of Flagstaff, Arizona is 56 cm and the mean annual temperature is 7.7°C.

In 1905, Frederic Clements suggested that plant communities be studied using fine-grained 1-m^2 maps called "chart quadrats" that show the location and basal area of individual plants (Clements 1905). At least 98 chart quadrats were established in northern Arizona between 1912 and 1938. Raw data were preserved in the Fort Valley Experimental Forest Archives (U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona, USA). We found the exact location of 82 chart quadrats because their corners were permanently marked with angle iron or galvanized steel pipe and a metal tag (Appendix A).

Historically, professional botanists compiled a complete species list and mapped the basal cover (i.e., area of ground occupied by a plant) of every plant on each quadrat. Graminoids with measurable basal area were mapped as polygons, and other species were mapped as points. Shrubs were recorded, but were too sparse to include in this analysis. We replicated the historical measurements and digitized historical and recent chart quadrat maps in a geographical information system (ArcView GIS version 3.3; ESRI, Redlands, California, USA) to facilitate the calculation of basal cover of each species on each plot (Appendix A). We lumped some taxa to higher taxonomic levels due to observer errors, uncertain identification of some species in vegetative state, and ambiguity of common names used in historical sampling (Appendix B).

Functional traits

We measured a core set of functional traits on all plant species detected on these plots. We measured specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration ([N]), fine root [N], seed mass, specific root length (SRL), canopy

TABLE 1. Results of the principal components analysis of the 78 species × 8 functional traits matrix.

Factor	PC1	PC2	PC3
Eigenvalues	2.4	2.0	1.3
Percentage	30	25	16
Cumulative percentage	30	55	71
Eigenvectors			
Specific leaf area	**0.49**	−0.06	−0.00
Leaf dry matter content	**−0.51**	0.06	0.18
Leaf [N]	**0.48**	0.32	0.14
Fine root [N]	**0.42**	0.27	0.24
Seed mass	−0.04	**0.56**	0.12
Specific root length	0.20	**−0.55**	0.10
Height	−0.19	0.14	**0.75**
Flowering date	0.10	**−0.43**	**0.55**

Notes: All traits were log$_{10}$-transformed prior to data reduction. Eigenvectors > |0.40| are shown in boldface text. Percentages are the percentages of total variance (i.e., the sum of the diagonal elements in the correlation matrix) accounted for by each principal component. The principal component scores obtained with these eigenvectors were used to calculate community-weighted strategy axis scores.

height, and mean Julian flowering date. Trait measurement methodology is described in Laughlin et al. (2010).

We calculated two functional diversity indices. First, FD$_{pg}$ (Petchy and Gaston 2002) is the sum of the branch lengths of a functional trait dendrogram and does not take into account the relative abundances of the species. Second, FD$_{rao}$ (Botta-Dukát 2005), also known as "Rao's quadratic entropy," uses a distance matrix (calculated from a species–trait matrix) and weights the index by the relative abundance of the species in the community. We used code written for R (version 2.11.1; R Development Core Team 2010) by Owen Petchy and Evan Weiher to calculate indices.

We assessed changes in the functional strategies of the community using two approaches. First, we used a traditional approach that examines changes in the relative abundance of plant functional types (C$_4$ graminoids, C$_3$ graminoids, C$_3$ forbs, and C$_3$ legumes). Second, we examined temporal shifts along the three plant strategy axes. As recommended by Webb et al. (2010), we used principal components analysis (PCA) to reduce the dimensionality of the 78 species × 8 functional trait matrix; three axes represented 71% of the variation in the correlation matrix. The resulting eigenvectors (Table 1) were used to calculate species scores on each of the three orthogonal strategy axes. We scaled these species-level strategies up to the community level for each plot in each time period by calculating a matrix of community-weighted mean strategy axis scores (**C**) as follows: $\mathbf{C} = \mathbf{RS}$, where **R** is an $n \times p$ matrix of species' relative abundances (see Appendix B), n is the number of plots (82 plots × 2 time periods = 164), p is the number of species (78), **S** is a $p \times t$ matrix of principal component axis scores, and t is the number of principal components (3). Changes in herbaceous understory plant strategies were quantified by subtracting the historical community-weighted mean strategy

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TABLE 2. Vegetation attributes (mean ± 95% confidence interval) in historical (1912–1938) and recent (2007) time periods.

Vegetation attribute	Historical	Recent	Mean change per century	Wilcoxon signed-rank test	
				T	P
Overstory structure					
Ponderosa pine basal area (m²/ha)	3.7 ± 1.0	29.3 ± 3.4	29 ± 4	1495	<0.001
Ponderosa pine stem density (trees/ha)	268 ± 162	908 ± 192	720 ± 280	1214	<0.001
Herbaceous understory structure					
Foliar aerial cover (%)	25.4 ± 3.0	7.7 ± 1.7	−21.1 ± 4.0	−1602	<0.001
Basal cover (%)	12.9 ± 2.1	3.9 ± 1.2	−10.7 ± 2.5	−1489	<0.001
Species richness (no. species/m²)	7.7 ± 0.6	5.4 ± 0.8	−2.6 ± 1.1	−775	<0.001
Species evenness ($e^{\text{Shannon } H}$/richness)	0.57 ± 0.03	0.59 ± 0.06	0.03 ± 0.07	231	0.2894
Unweighted functional diversity (FD$_{pg}$)	0.47 ± 0.04	0.34 ± 0.04	−0.15 ± 0.7	−729	<0.001
Weighted functional diversity (FD$_{rao}$)	0.46 ± 0.04	0.38 ± 0.04	−0.09 ± 0.07	−494	0.019

Notes: The mean difference between time periods is expressed on a per-century scale to account for different plot establishment dates. Pine basal area and density were measured on 20 × 20 m plots, and herbaceous cover and diversity were measured on 1-m² plots ($n = 82$).

axis score from the recent community-weighted mean strategy axis score for each of the three axes. Our analysis assumes that trait values have not changed appreciably within species over the last century. This is reasonable because many phenotypic traits are conserved within species over much longer time scales, permitting the identification of plant material preserved for tens of thousands of years (e.g., Cole 2010).

Forest structure

We measured overstory trees on 20 × 20 m plots centered on each chart quadrat. For each tree (live and dead) we recorded species, condition, and diameter at breast height (dbh; 1.37 m) and calculated basal area (m²/ha) and live tree density (trees/ha). Because data on the overstory were not recorded in historical measurements, we reconstructed historical tree densities and basal areas for each 20 × 20 m plot at the dates of plot establishment. We cored all live trees ($N = 3000$ increment cores total) at 40 cm height for dendrochronological analyses and used a forest reconstruction model to calculate historical basal areas and densities (R code from Bakker et al. 2008). In addition, historical and recent timber harvest histories were compiled for each plot to determine death dates of stumps. The model also uses a decay submodel to account for current snags that may have been living at the time of plot establishment. These methods have been validated and demonstrated to be reliable within ±10% (Moore et al. 2004). The relationship between (log$_{10}$-transformed) pine basal area and stem density among the 82 stands is significantly positive in both the historical time period ($R^2 = 0.26$, $P < 0.0001$) and the recent time period ($R^2 = 0.80$, $P < 0.0001$); thus, increases in stem density were also associated with increases in basal area on these plots.

Statistical analyses

Because these data are repeated measurements on permanent plots, we used the Wilcoxon signed-rank test to evaluate whether changes in community attributes

differed significantly from zero ($\alpha = 0.05$ for all tests). In order to determine whether changes in vegetation attributes were associated with changes in forest structure, we regressed the changes in vegetation attributes on changes in pine basal area. In Appendix C we report ANCOVA results where time is the main effect and pine basal area is the continuous covariate. We evaluated changes in the relative foliar cover of each of four functional type categories with a likelihood ratio contingency test (χ^2).

RESULTS

Pine basal area and stem density increased significantly between the early 1900s and recent measurements (Table 2). Understory plant foliar and basal cover declined by 21% and 10%, respectively, since the early 1900s (Table 2). Changes in herbaceous foliar cover and basal cover were negatively correlated with changes in pine basal area (Fig. 1a, d). A total of 78 understory species were detected in the quadrats; 53 in historical samples and 66 in the recent samples. Despite this increase in total detected species, plot-level species richness declined (Table 2) by approximately two species per square meter. Changes in species richness were negatively and linearly correlated with changes in pine basal area (Fig. 1b), but evenness changes were uncorrelated with changes in pine basal area (Fig. 1e). Both indices of functional diversity decreased over time (Table 2), and were negatively correlated with increases in pine basal area (Fig. 1c, f).

The relative abundances of C$_4$ and C$_3$ graminoids were nearly equal in the historical time period. However, C$_4$ relative abundance declined by 18%, C$_3$ relative abundance increased by 19%, and legume relative abundance declined by 2% (Fig. 2). Shifts in the first strategy axis were weakly negatively correlated with changes in pine basal area (Fig. 1g), indicating a shift in dominance toward species with lower leaf [N], fine root [N], and SLA, and higher LDMC. Shifts in the second strategy axis were positively correlated with changes in
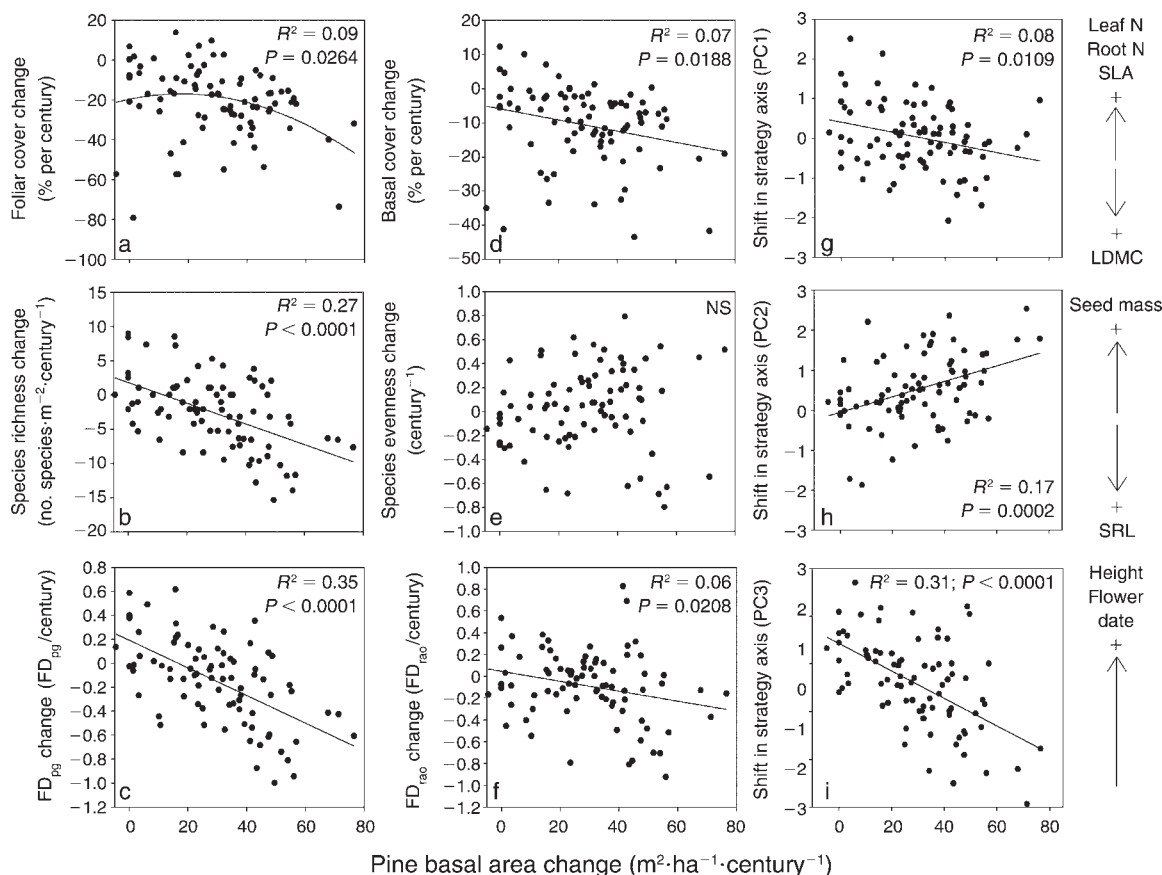
FIG. 1. Relationships between long-term changes in pine basal area and changes in understory (a) plant foliar cover, (b) species richness, (c) unweighted functional diversity (FD_{pg}), (d) basal cover, (e) species evenness (defined as exp[Shannon H]/richness), (f) weighted functional diversity (FD_{rao}), (g) community-weighted leaf economics spectrum (PCA axis 1), (h) community-weighted seed mass spectrum (PCA axis 2), and (i) community-weighted height spectrum (PCA axis 3). Community-weighted strategy axes in panels (g)–(i) are spectra of multiple correlated functional traits represented as principal components (Table 1). Key to abbreviations: [N], nitrogen concentration; SLA, specific leaf area; LDMC, leaf dry matter content; SRL, specific root length.

pine basal area (Fig. 1h), indicating a shift in dominance toward species with larger seed mass and lower SRL. Changes in the third strategy axis were negatively correlated with increases in pine basal area (Fig. 1i), indicating a shift in dominance toward shorter species that flower earlier in the growing season.

DISCUSSION

A century of increasing ponderosa pine density was associated with shifts in herbaceous plant strategies and reduced functional diversity. Shade- and stress-tolerant herbaceous plants that use a more conservative strategy for acquiring and maintaining resources have increased in relative abundance over time likely because light, water, and nutrients have become more limiting beneath the dense overstory.

Increases in pine density were associated with slight shifts along the first strategy axis toward communities dominated by plants with low SLA, low leaf and root [N], and high LDMC. Species with low leaf and fine root tissue [N] are generally slower-growing, stress-tolerant

species that conserve their acquired nutrients and dry mass (Reich et al. 1997). Species with low fine root [N] are adapted to persist in low nutrient soils (Grime 1979) such as those found beneath dense stands of pine (Kaye and Hart 1998). Decomposition rates have likely declined with increasing pine basal area due to both the increase of recalcitrant pine needles on the forest floor and the shift toward herbaceous understory species with slower decomposition rates (Laughlin et al. 2010). This understory shift may also be partly responsible for slower N mineralization and nitrification rates beneath dense pine canopies (Kaye and Hart 1998).

We observed long-term shifts along the second plant strategy axis toward communities dominated by plants with larger seed mass and lower SRL, perhaps due to the reported advantage of large seeded species when germinating in deep litter and shade (Grime and Jeffrey 1965). Nutrients are less available in soils beneath dense forest stands because nutrients are tied up in the canopy biomass and because recalcitrant pine needles release N into the soil slowly (Kaye and Hart 1998). Therefore,
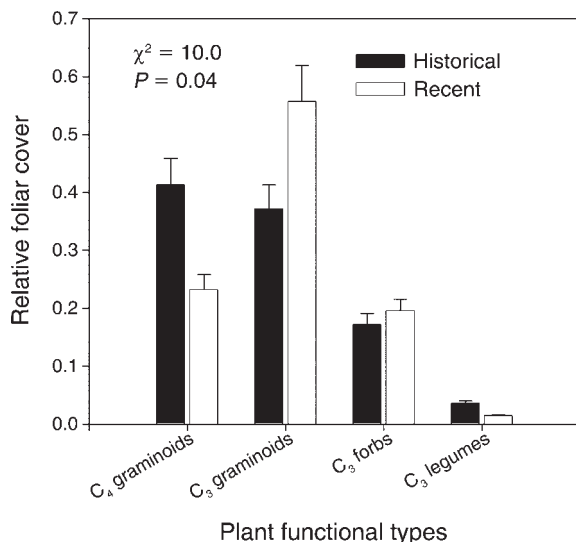
FIG. 2. Changes in relative foliar cover (means + SE) of four plant functional types from the historical (1912–1938) to recent (2007) time periods ($n = 82$). The change in relative abundances between time periods was significant and was driven primarily by declines of C_4 graminoids, increases of C_3 graminoids, and declines of legumes.

dense forest conditions might favor herbaceous species with low SRL that slowly acquire and conserve mineral nutrients.

We also observed shifts along the third strategy axis toward dominance by shorter plants that flower earlier. Tall species are better able to acquire light (Keddy and Shipley 1989), but beneath dense canopies it is more important to be shade-tolerant than to be able to acquire light. In this flora, shorter species also tend to flower earlier in the growing season (Laughlin et al. 2010). We speculate that earlier flowering times may be indicative of a temporal segregation of belowground competition because fine root production in ponderosa pine is highest late in the growing season (Gaylord et al. 2007). In addition, the change in mean flowering time reflects the increases in cool-season C_3 graminoids and decreases in warm-season C_4 graminoids. The decline in C_4 graminoid abundance with increases in pine basal area suggests that species with high photosynthetic water-use-efficiency are adapted to persist in the warmer, high light, and likely drier environment of open forest stands (Naumburg and DeWald 1999). The increase in the relative abundance of C_3 species might also be the result of higher concentrations of carbon dioxide in the atmosphere (Poorter 1993).

These permanent quadrats permitted us to examine vegetation dynamics over a ~100-year time period. Our findings illustrate how the usefulness of historical plots extends beyond their original objectives. Nevertheless, this long-term data set is not without its limitations. The permanent quadrats were not established within an experimental design framework that allows rigorous hypothesis testing. Our analyses of this long-term

"natural experiment" were therefore necessarily correlative. However, significant relationships between long-term changes in pine basal area and changes in herbaceous understory attributes provide stronger support for causal relationships than spatial association within one time period. Nonetheless, forest structure is but one environmental gradient that influences the assembly of understory plant communities in this ecosystem. Other factors that could have contributed to the observed changes in functional trait distributions include past land-uses (e.g., livestock grazing), soil properties, climate change, and fire. We view fire and grazing as indirect factors in this study since both factors influenced the long-term increase in pine density (Bakker and Moore 2007). However, the direct effects of fire and grazing on understory trait distributions are also likely important in this system. Though we could not analyze grazing effects with this data set directly, we speculate that release from heavy grazing would favor perennial graminoids, thereby decreasing community-weighted mean SLA and increasing height and seed mass (Laughlin et al. 2010).

Our analysis of temporal changes in plant strategies provides a general framework for evaluating compositional and functional changes in terrestrial plant communities. Detecting species turnover over time does not equate to shifts in function unless the traits of the community have also changed. Reducing multiple correlated traits to orthogonal strategy axes (Reich et al. 2003, Webb et al. 2010) increases the generality of the analysis and facilitates comparisons with other ecosystems where similar functional gradients among species have been observed.

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APPENDIX A

Map of study area and repeat photographs (*Ecological Archives* E092-047-A1).

APPENDIX B

Quality control and related issues when analyzing long-term historical data sets (*Ecological Archives* E092-047-A2).

APPENDIX C

ANCOVA results (*Ecological Archives* E092-047-A3).

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