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Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory–understory interactions

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Abstract. Stem exclusion and understory reinitiation are commonly described, but poorly understood, stages of forest development. It is assumed that overstory trees exert strong controls on understory herbs and shrubs during the transition from open- to closed-canopy forests, but long-term observations of this process are rare. We use long-term data from 188 plots to explore patterns and correlates of variation in understory richness and abundance 15–45 years after clear-cut logging and burning of two experimental watersheds in western Oregon, USA. We test whether variation in the temporal dynamics of plots can be explained by topoedaphic factors that influence resource availability (insolation and soil moisture), variation in the pace and intensity of overstory development, or characteristics of the vegetation prior to canopy closure. Changes in forest structure were substantial over the study period; canopy cover increased fourfold, stem density by 75%, and bole biomass by two orders of magnitude, although trends were highly variable among individual plots. In contrast, understory richness, foliar cover, and biomass declined only 30–40%, driven by loss of early-seral colonists, not residual forest species. Canopy closure occurred earlier on north aspects but declines in understory biomass, reflecting loss of colonizing shrubs (without concomitant increases in forest shrubs), were limited to south aspects. In contrast, variation in effective soil moisture had little influence on the pace of decline. Temporal trends were highly asynchronous among plots: nearly 50% of plots experienced some form of decline, but >35% showed no discernible trend. Declines were more likely in plots with greater tree influence before or at peak overstory development, but also in plots with greater understory development prior to canopy closure. Quantile regression models indicated weak relationships between understory biomass and overstory structure at most points in time. Our long-term data support a model of understory dynamics in which characteristics of the pre-closure vegetation are as important as overstory structure in determining the timing and nature of decline. Long-term studies are critical for elucidating patterns and processes that cannot be inferred from short-term experiments or space-for-time substitutions.

Key words: competition; forest development; forest structure; forest succession; long-term studies; Pacific Northwest; permanent sample plot; species richness; understory biomass.

INTRODUCTION

Stem exclusion and understory reinitiation are commonly described, but poorly understood, stages in the structural development of forests (Bormann and Likens 1979, Peet and Christensen 1987, Oliver and Larson 1996, Franklin et al. 2002). Stem exclusion is described as a period of intense tree competition, density-dependent mortality, and marked reductions in light at the forest floor. Overstory development during this stage is assumed to exert strong controls on the understory, substantially reducing plant abundance and diversity. Understory reinitiation is described as a period of reduced tree density and competition, ascension of the lower crown, and increased understory light: conditions that allow for reinvigoration of the understory either through vegetative reproduction of surviving plants (Lezberg et al. 1999) or recolonization by seed dispersal. Despite general acceptance of this model, direct, long-term observations of these processes are lacking. Instead, trends have been inferred indirectly through the use of chronosequences (e.g., Alaback 1982, Schoonmaker and McKee 1988, Moola and Vasseur 2004, Jules et al. 2008). However, these space-for-time substitutions offer limited ability to infer process from pattern, typically have coarse temporal resolution, and are susceptible to bias associated with sample selection (Pickett 1988, Johnson and Miyanishi 2008, Walker et al. 2010). Here, we present the first empirically based critique of these models using direct observations from a 30-year study of overstory–understory interactions in secondary forests transitioning from open- to closed-canopy conditions. We focus on the patterns and correlates of temporal variation in the understory.

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Several factors are likely to contribute to variation in understory decline during canopy closure: the pace or intensity of closure, variation in resource supply, the extent to which trees preempt these resources, and the ability of understory species to tolerate the conditions. Numerous factors may influence the pace of overstory development, including post-disturbance seed limitations, resource or other environmental constraints, and competition with early-seral vegetation (Seidel 1979, Graham et al. 1982, Haeussler and Coates 1986, Donato et al. 2012). Topography and soils jointly determine the supply of light, soil moisture, and nutrients to the understory, but trees can preempt these resources. It is generally assumed that light is the limiting resource for understory plants (Oliver 1981, Peet and Christensen 1988, Klinka et al. 1996). However, where soil moisture is seasonally limiting, belowground competition with tree roots can be intense (Coomes and Grubb 2000, Hubbert et al. 2001). Soil trenching experiments demonstrate that root competition from trees, which can be acute in dense coniferous forests (Vogt et al. 1983), greatly limits productivity in the herb layer (Tuomey and Keinholz 1931, Riegel et al. 1992, Lindh et al. 2003).

Topoedaphic factors that influence resource availability or mediate environmental stress can accentuate or temper the effects of canopy closure. For example, in topographic settings with reduced insolation (steep north aspects), effects of canopy closure may be accentuated, resulting in more rapid and complete loss of the understory. On the other hand, if competition for soil moisture is the principal constraint during closure, effects may be tempered in sites with greater resource supply (moist toe slopes; Montgomery et al. 2010). Indirect effects of stress or resource variation, mediated through patterns of stand development, are also likely. For example, in stressful or low-productivity sites (south aspects or dry upper slopes), rates of forest development may be slower, delaying canopy closure. Under these conditions, shading by trees can have positive (facilitative) effects on understory development (Callaway et al. 1991, Haugo and Halpern 2010) resulting in increases, rather than declines, in species richness and abundance. Conversely, in more productive sites (moist toe-slopes), the pace of forest development may be greater (Larson et al. 2008), leading to more rapid closure of the canopy, greater light reduction, and more dramatic declines in the understory.

Species' life histories and tolerances of changing resource conditions also shape the nature of understory development. Pre-closure communities dominated by early-seral species with high light requirements (Grime 1977, Bazzaz 1979) should show more rapid declines in cover and diversity than those comprising more shade-tolerant, residual forest species. Plant size is also relevant; short-statured herbs may decline more rapidly than taller woody species that have greater access to understory light. Alternatively, if plant stature and shade tolerance are inversely related (Givnish 1982, Thomas and Bazzaz 1999), shrubs may be more susceptible to shading by trees (Tilman 1984, Goldberg and Miller 1990). Timing and intensity of decline may thus depend on the representation of species with differing functional or growth-form traits prior to closure, which may be determined much earlier in succession (e.g., as a function of pre-disturbance composition or disturbance severity [Halpern 1988, Halpern and Franklin 1990, Schimmel and Granstrom 1996]).

Here we use direct, long-term observations to elucidate the influence of resource variation, overstory development, and characteristics of the pre-closure vegetation on the dynamics of forest understories during stem exclusion. We use data from 188 paired overstory–understory plots in two clearcut watersheds in the H. J. Andrews Experimental Forest Long-term Ecological Research (HJA-LTER) Site (Oregon, USA). Established in 1962, prior to disturbance, these plots form the basis of the longest and most intensive study of secondary succession in forests of western North America (Dyrness 1973, Halpern 1988, 1989, Halpern and Franklin 1990, Halpern and Spies 1995, Lutz and Halpern 2006, Dovčiak and Halpern 2010). Steep north- and south-facing hillslopes create natural contrasts in resource availability (insolation and soil moisture) and environmental stress that have contributed to heterogeneity in forest development (Lutz and Halpern 2006): ideal conditions for exploring patterns and correlates of variation in understory dynamics during canopy closure. We address the following questions: (1) How do understory richness and abundance (cover and biomass) change during the transition from open- to closed-canopy forest? Do understory richness and abundance converge among plots during this transition? (2) How do species with differing growth forms and life-history strategies contribute to these trends? (3) Do topoedaphic factors that influence resource availability accentuate or temper the effects of canopy closure? (4) To what extent is understory abundance constrained by overstory structure and do these relationships change over time? (5) How variable are individual plots in their temporal dynamics? Can this variation be explained by resource environments, patterns of overstory development, or vegetation characteristics prior to canopy closure?

Study Area

Physical environment, vegetation, and disturbance history

Watersheds 1 and 3 (WS1 and WS3) occur at low to moderate elevations (442–1082 m) in the HJA-LTER, 80 km east of Eugene, Oregon (WS1, 44.2047° N, 122.2489° W; WS3, 44.2138° N, 122.2321° W). Both are ~100-ha basins characteristic of the western Cascade Range. The primary stream channels flow southeast to northwest, creating steep north- and south-facing hillslopes (Fig. 1). Soils are shallow to moderately deep, originating from andesites, tuffs, breccias, and basalt flows (Rothacher et al. 1967). They are moderately productive (site class II–IV; King 1966), varying with depth and topographic position (A. Mckee, *personal communication*). Textures are mostly loamy and porosity and water-storage capacity are generally high (Dyrness 1969).

The climate is maritime with mild, wet winters and warm, dry summers. For 1971–2000, mean minimum temperatures at 430 m were −1.3°C (January) and mean maxima were 28.6°C (July). Annual precipitation averages ∼2200 mm (falling mostly as rain), but only 6% occurs between June and August leading to frequent summer drought (Bierlmaier and McKee 1989; data *available online*).[4] Vegetation is characteristic of the *Tsuga heterophylla* zone (Franklin and Dyrness 1988). Prior to harvest, forests were dominated by mature (125–300 years old) and old-growth (300–500 years old) *Pseudotsuga menziesii* and *Tsuga heterophylla* with a diversity of shade-tolerant conifers and hardwoods in the subcanopy (Lutz and Halpern 2006). Understory composition reflected strong topoedaphic controls on soil moisture availability, the principal resource gradient structuring understory composition in these forests (Dyrness et al. 1974, Zobel et al. 1976, Hemstrom et al. 1987). Six communities were defined along this gradient, from dry ridgetops with shallow soils to moist toe-slopes with deeper soils: *Corylus cornuta*/*Gaultheria shallon*, *Rhododendron macrophyllum*/*Gaultheria shallon*, *Acer circinatum*/*Gaultheria shallon*, *Acer circinatum*/*Berberis nervosa*, *Coptis laciniata*, and *Polystichum munitum* (Rothacher et al. 1967; see also Dyrness 1973, Halpern 1988, 1989).

WS1 was clearcut over the period 1962–1966; a skyline cable was used to transport logs to a landing at the base of the watershed. Slash was broadcast burned in fall 1966. WS3 was partially clearcut in 1962–1963 creating three 5–11 ha harvest units; high-lead cables were used to transport logs to roadside landings. Slash was broadcast burned in fall 1963. Attempts at reforestation included aerial seeding or planting of *Pseudotsuga menziesii*, but seed germination and survival were low. Thus, most regeneration has occurred through natural seed dispersal from adjacent forests or stump sprouting of hardwoods (Lutz and Halpern 2006).

METHODS

Field sampling

Prior to disturbance (1962), permanent understory plots (2 × 2 m, slope corrected) were established at 30.5-m intervals along multiple transects in both watersheds (132 plots on six transects in WS1, 62 plots on 10 transects in WS3). Plots were assessed for slope and aspect and assigned to one of the six plant communities (Rothacher et al. 1967, Dyrness 1973). In 1979 and 1980 (14–16 years after burning), circular overstory plots (250 m^2; 8.92 m radius) were established over each understory plot (one corner of the latter served as plot center). Understory and overstory plots were sampled at 2–6 year intervals, but not in the same year (typically one year apart; Table 1). Six of the initial plots were dropped from the analysis because one or more samples were missed, yielding a total of 188 plots (129 in WS1; 59 in WS3).

FIG. 1. Aerial view of Watershed 1 (WS1), H. J. Andrews Experimental Forest-LTER, Oregon, USA, taken in 1988, 22 years after disturbance. The steep terrain is characteristic of the western Cascade Range. The primary stream channel flows east-southeast (110°) to west-northwest (290°), creating a strong contrast in aspect between the principal hillslopes. Photo credit: USDA Forest Service.

At each understory sampling date we estimated canopy cover (%) of all vascular plant species (herbs, tall shrubs, and trees). Several taxa that were difficult to distinguish were combined at the genus level (Appendix A). For tall shrubs (and most ferns) rooted in each plot, we also measured the basal diameter of each stem (or frond length), from which we estimated aboveground biomass (henceforth, biomass; see *Methods: Plot and species classification and data reduction*). At each overstory sampling date, all conifers ≥1.4 m tall were tagged (if not previously tagged), measured for diameter, and recorded as live or dead. Conifers with breast height diameter (dbh) >2 cm were measured at dbh;

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[4] http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS001

TABLE 1. Dates of sampling of understory and overstory plots on Watersheds 1 and 3 (WS1 and WS3) and their relationships to time since disturbance.

Understory				Overstory				
Date	WS1 (yr)	WS3 (yr)	Ave. (yr)†	Date	WS1 (yr)	WS3 (yr)	Ave. (yr)†	Time since disturbance (yr)‡
1979	13	16	14.5					
1980–1981§	14	18	16.0	1979–1980¶	14	16	15	15.5
1983	17	20	18.5	1984	18	21	19.5	19.0
1987	21	24	22.5	1988	22	25	23.5	23.0
1990	24	27	25.5	1991	25	28	26.5	26.0
1994	28	31	29.5	1995	29	32	30.5	30.0
1997	31	34	32.5					
2002	36	39	37.5	2001	35	38	36.5	37.0
2008	42	45	43.5	2007	41	44	42.5	43.0

† Time since disturbance averaged between watersheds.
‡ Time since disturbance averaged for understory and overstory plots.
§ Understory was sampled in 1980 in WS1 and in 1981 in WS3.
¶ Overstory was sampled in 1980 in WS1 and in 1979 in WS3.

smaller trees were measured at the base (dba). Hardwoods, typically stump sprouts, were either tagged and measured at dbh (stems $\geq$5 cm dbh) or tallied by diameter class (<3 and 3–4.9 cm). For details, see Lutz and Halpern (2006).

Plot and species classifications and data reduction

Data from the two watersheds were combined for analysis because physical environments and vegetation were similar and our emphasis is on overstory–understory interactions. The dates of logging and burning differed between watersheds; thus we express time as "time since disturbance" (years after broadcast burning). Measurements made in the same year in different watersheds thus represent an average time since disturbance (Table 1). Understory plots (including tree cover) were sampled nine times and overstory plots (tree diameters), seven times. For analyses of overstory–understory relationships we used the seven closest temporal pairings of the data (difference of $\leq$1 yr; Table 1).

To explore the influence of resource supply on understory trends (question 3), plots were assigned to contrasting resource environments (insolation and effective soil moisture) as follows. Plots on opposing hillslopes (Fig. 1) were assigned to contrasting light environments: north (N) aspects (northwest to northeast; n = 83) and south (S) aspects (southwest to southeast; n = 57). Plots with east or west aspects (n = 48) were not considered for this comparison. Using predisturbance plant community type as an indicator of soil moisture availability (Rothacher et al. 1967, Dyrness 1973, Zobel et al. 1976) we assigned plots to one of three distinct site types: xeric (*Corylus cornuta*/*Gaultheria shallon* and *Rhododendron macrophyllum*/*Gaultheria shallon* types; n = 44); mesic (*Acer circinatum*/*Gaultheria shallon*, *Acer circinatum*/*Berberis nervosa*, and *Coptis laciniata* types; n = 97); and moist (*Polystichum munitum* type; n = 47).

Each taxon was assigned to a growth form (herbaceous or tall shrub) and life-history strategy (seral group: colonist or residual forest species) based on previous classifications (Dyrness 1973, Halpern and Franklin 1990, Halpern and Spies 1995, Dovčiak and Halpern 2010; Appendix A). Forest species were those present prior to disturbance; colonists established thereafter. Several taxa could not be assigned to a seral group and were omitted from analyses of seral-group responses; however, these contributed minimally to understory richness or abundance. Plant nomenclature follows Hitchcock and Cronquist (1973).

Biomass was estimated using species-specific allometric equations developed in or adjacent to HJA-LTER (Gholz et al. 1979, Means et al. 1994, Halpern et al. 1996) (Appendix D). For most herbaceous species, biomass was predicted from cover (or for ferns, from stem basal diameter or frond length). For tall shrubs, biomass was predicted from basal diameter. Where equations did not exist, we substituted equations of species of similar growth form (Appendix D). For trees, estimates of bole biomass (live and dead) were based on equations of Means et al. (1994) with modifications as described by Lutz and Halpern (2006).

Analyses

Trends in overstory structure.—For each overstory plot × sampling time (time since disturbance), we computed three measures of overstory structure that served as proxies for resource preemption: total (summed) cover of tree species (maximum >100%), tree density (stems/ha), and bole biomass (Mg/ha). We computed means for the full set of plots (n = 188) and for plots representing contrasting resource environments (N vs. S aspects and xeric, mesic, or moist sites).

Trends and variation in understory richness, cover, and biomass.—For each understory plot × sampling time we computed species richness (species/plot), total cover (maximum >100%), and biomass (Mg/ha) for the full community and each growth form × seral group. Means and variation (SD and CV) were computed for the full set of plots (questions 1 and 2). Means (and SEs) were also computed for plots representing each resource environment. We then assessed whether rates of change over time (regression slopes) differed among resource environments (question 3). To do so, we used generalized linear models to test the environment × time interaction; significant interactions were followed by pairwise comparisons of slopes. We also tested whether individual or pooled slopes (as appropriate) differed from zero. Although temporal trends for a small number of variable × environment combinations were hump shaped, use of linear models to approximate change over the study period did not alter our interpretations. We did not test whether intercepts differed among resource environments because these represented differences that predated effects of closure. Regression analyses were conducted within the glm module of SPSS version 14 (SPSS 2005).

Overstory–understory relationships.—To test relationships between overstory structure and understory abundance (question 4), we used constraint-line analysis or quantile regression, which is based on the upper quantile of a distribution (Guo et al. 1998, Scharf et al. 1998, Cade et al. 1999). This method of modeling "maximum" (rather than mean) response is useful for isolating the effect of a hypothesized constraint (e.g., tree cover or density) on a response variable (e.g., understory biomass) when there are additional unmeasured factors that can contribute to the response. We used linear quantile regression (Cade and Noon 2003) to explore relationships between maximum understory biomass and each measure of overstory structure (tree cover, density, and bole biomass). Given strong contrasts in structural development on N and S aspects, we tested relationships separately for each aspect. We also tested whether relationships changed over time, using separate models for each temporal pairing of overstory–understory data (Table 1). Emergence of a significant relationship or a change in slope over time could reflect a shift in the distribution of a constraining variable (e.g., toward greater values of tree cover, density, or bole biomass) or a cumulative effect over time. To assess the sensitivity of these relationships to selection of the upper quantile (τ), we compared three quantiles, $\tau = 0.80$, 0.90, and 0.95. Analyses were performed in R version 2.14.1 (R Development Core Team 2011) using the quantreg package version 4.44 (*available online*).[5]

Variation in and predictors of temporal trends.—Temporal trends in understory abundance varied substantially among plots, ranging from decline and reinitiation (or not), to no change, to a continuous increase with time. To characterize the diversity and frequency of these temporal patterns (question 5), we fit trends in understory abundance (cover and biomass) in each plot to one of six model types (Fig. 2). Four of these models captured differences in the onset or rate of decline (or reinitiation); these were termed "reinitiating," "crashing," "declining," or "peaking" (the latter, typically declining only at the last measurement) (Fig. 2). The two remaining models represented instances of no decline and were termed "stabilizing" or "increasing." A model was accepted as significant at $\alpha = 0.05$. If multiple models were accepted for a plot, we identified the "best-fit" model as that with greatest adjusted R^2.

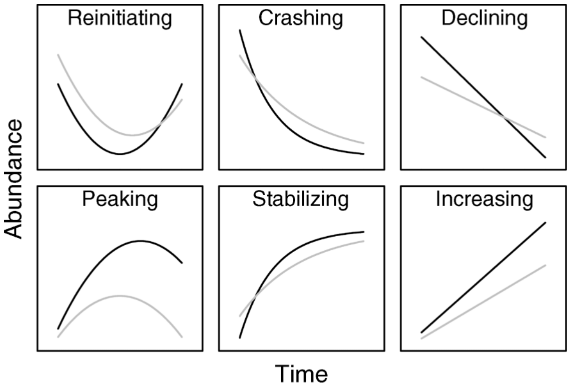

FIG. 2. Schematic representation of the six model types to which temporal trends in plot abundance (cover or biomass) were fit. Black and gray lines illustrate variation in the magnitude or rate of change in abundance within a model type. Models represent plots that differed in the pace or timing of decline (upper row) or that showed a delay in, or no effect of, canopy closure (bottom row).

We then used multinomial logistic regression (MLR; Hosmer and Lemeshow 1989, Trexler and Travis 1993) to test whether plots with similar temporal trends (based on best-fit models) shared similar characteristics, i.e., resource environments, patterns of structural development, or vegetation characteristics prior to canopy closure (question 5). MLR is useful for identifying variables (categorical or continuous predictors), that differentiate among multiple outcomes, in this case, model types. Separate regressions were run for understory cover and biomass. We tested multiple predictors of six general types: (1) resource environments (N vs. S aspects; xeric, mesic, or moist sites); (2) pre-closure tree influence (tree cover, density, or bole biomass at 14–16 yr); (3) rate of overstory development (timing of minimum or maximum tree cover, density, or bole biomass); (4) intensity of overstory development (minimum or maximum tree cover, density, or bole biomass); (5) post-closure disturbance (bole biomass lost to mechanical disturbance, a proxy for increased resource availability (Lutz and Halpern 2006); and (6) seral group abundance prior to canopy closure (cover or biomass of colonizing and residual forest species). Due to the small sample sizes of several model types, some plots were reclassified to the next best-fitting model and regressions were run on fewer model types. Specifically, for cover, plots modeled as "stabilizing" ($n = 3$) were reclassified, resulting in five model types. For biomass, plots classified as "declining" ($n = 12$), "stabilizing" ($n = 1$), and "increasing" ($n = 11$) were reclassified, resulting in three model types: "reini-

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[5] http://cran.r-project.org/web/packages/quantreg/index.html

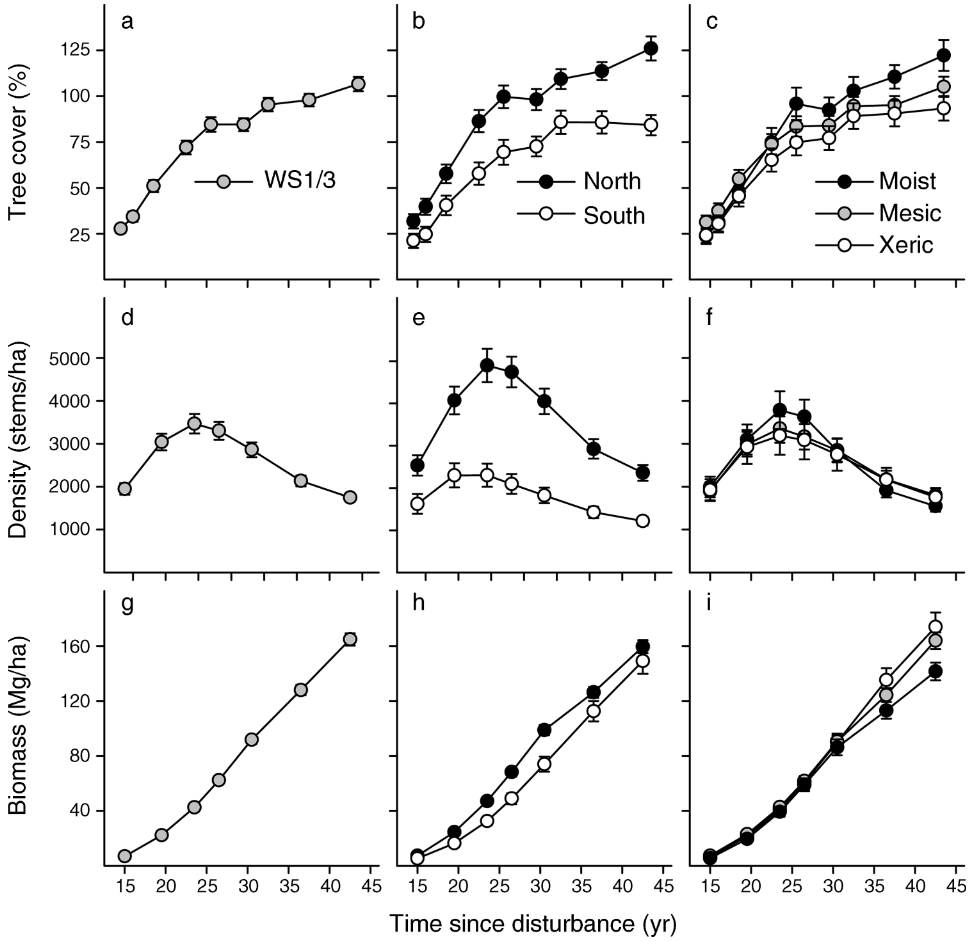

FIG. 3. Trends in (a–c) total (summed) tree cover, (d–f) stem density, and (g–i) bole biomass for the full set of plots ($n = 188$ plots) and for plots from contrasting aspects (north vs. south; $n = 83$ and 57 plots, respectively) and topoedaphic contexts (moist-, mesic-, and xeric-site communities; $n = 44$, 97, and 47 plots, respectively). Values are means ± SE.

tiating," "crashing," and "peaking." For each regression, the set of plots showing no temporal trend was chosen as the reference category (required in MLR), allowing each of the final model types to be compared with a common "null" model. The significance of predictors was determined stepwise, using the likelihood ratio as a removal test with $\alpha = 0.05$. Analyses were conducted in SPSS version 14 (SPSS 2005).

RESULTS

Trends in forest structure

Total tree cover increased continuously (Fig. 3a), with 80% of plots reaching ≥100% cover within the 30 years of study. Closure occurred earlier on N aspects (>100% cover at ~25 yr) than on S aspects (peak cover of 86% at ~32 yr; Fig. 3b). Cover was consistently greater in moist- than in mesic- or xeric-site communities (Fig. 3c). Tree density peaked much earlier (~22 yr; Fig. 3d) than did cover, with 75% of plots reaching maximum density within ~25 years. Maximum density on N aspects was more than twice that on S aspects (~4900 vs. 2300 trees/ha), but subsequent declines were steeper (Fig. 3e). Peak densities tended to be greater in moist- than in mesic- or xeric-site communities, but these differences were small (Fig. 3f). Bole biomass increased continuously (Fig. 3g). Biomass was greater on N than on S aspects for most of the study period (Fig. 3h), but was similar among moist-, mesic-, and xeric-site communities until the final measurement (Fig. 3i).

Trends and variation in understory richness, cover, and biomass

Variation among resource environments.—Species richness declined significantly over the study period (Fig. 4a). Declines reflected continuous loss of colonizing species, offset in part, by small gains in forest species (Fig. 4a–c). Declines were steeper on N than on S aspects (Fig. 5a). Colonizing species declined on both aspects, but forest species declined only on N aspects (Fig. 5b–e). Declines in total richness were comparable among xeric-, mesic-, and moist-site communities (Fig.

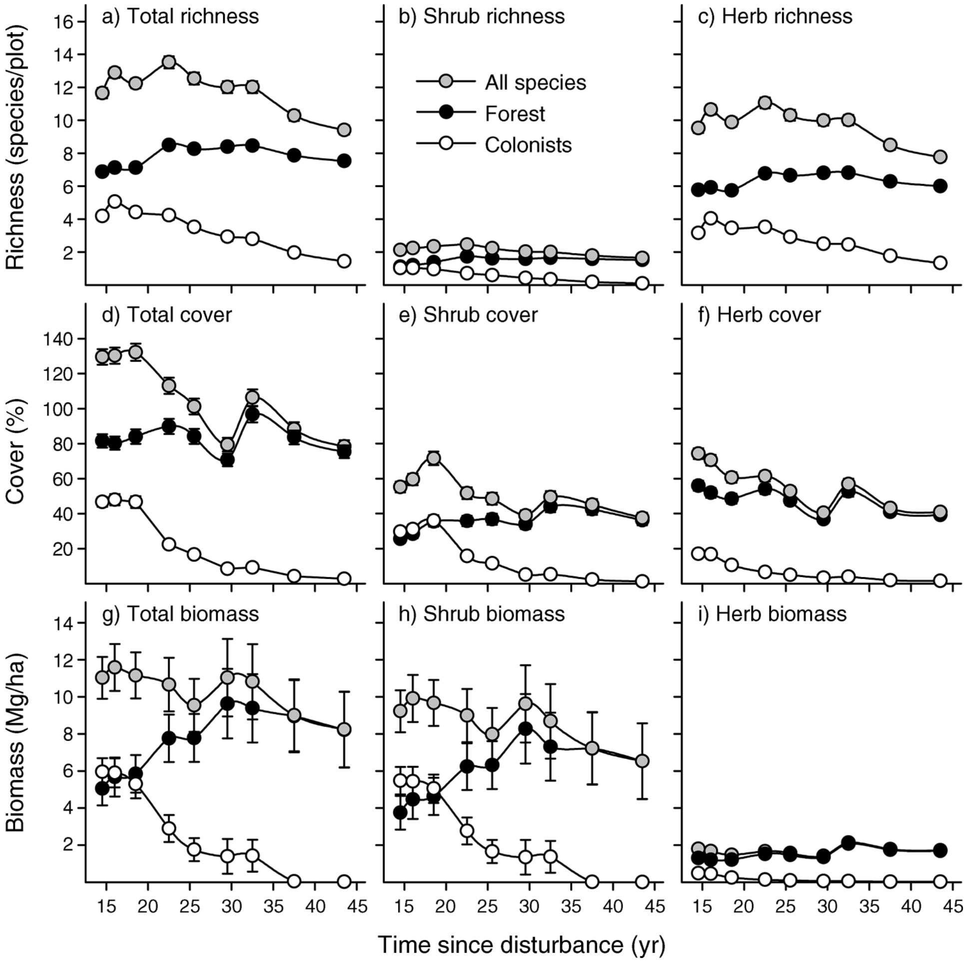

FIG. 4. Trends in (a–c) understory richness (species/plot), (d–f) total (summed) cover, and (g–i) biomass for the full set of plots ($n = 188$ plots), including the contributions of colonizing and residual forest species. Understory totals (left column) are partitioned by growth form (middle and right columns). Values are means ± SE.

5f), but for colonizing herbs they were steepest in moist sites (Fig. 5i).

Total understory cover declined earlier and at a steeper rate than did richness. Nevertheless, mean cover did not fall below ~80% (Fig. 4d). Declines reflected loss of the dominant colonizing shrubs (*Ceanothus sanguineus*, *C. velutinus*, *Rubus parviflorus*), and herbs (*Epilobium angustifolium*). In contrast, cover of forest shrubs (mainly *Acer circinatum*) increased (Fig. 4e). Declines were comparable on N and S aspects for all plant groups except forest shrubs, which showed no change on N aspects but continuous increase on S aspects (Fig. 6c). Declines (or increases in forest shrubs; Fig. 6h) were also comparable among moist-, mesic-, and xeric-site communities.

Understory biomass, dominated by shrubs, declined less steeply than did cover (Fig. 4g). Similar to trends in cover, colonizing shrubs (primarily *Ceanothus* spp.) declined and forest shrubs (primarily *Acer circinatum*) increased (Fig. 4h). Declines in total biomass were significant on S aspects, where colonists dominated the pre-closure vegetations (Fig. 7a–c). However, there was no net change on N aspects: declines in colonists were balanced by increases in forest shrubs (Fig. 7a–c). Total biomass declined more steeply in xeric- than in mesic- or moist-site communities (Fig. 7f). Declines in colonizing shrubs were comparable among site types (Fig. 7g), but rates of increase among forest shrubs differed (greatest for mesic-site communities; Fig. 7h).

Plot-scale variation.—Individual plots exhibited a broad range of variation (one to two orders of magnitude) in total understory richness, cover, and biomass (Fig. 8a–c). Variation in richness and cover changed little or declined slowly, but variation in biomass increased markedly over time (Fig. 8d, e).

Overstory–understory relationships

Quantile regression models indicated weak relationships between maximum understory biomass and overstory structure (Fig. 9). Although understory biomass tended to decline with tree cover, density, and bole biomass, few models produced significant relation-

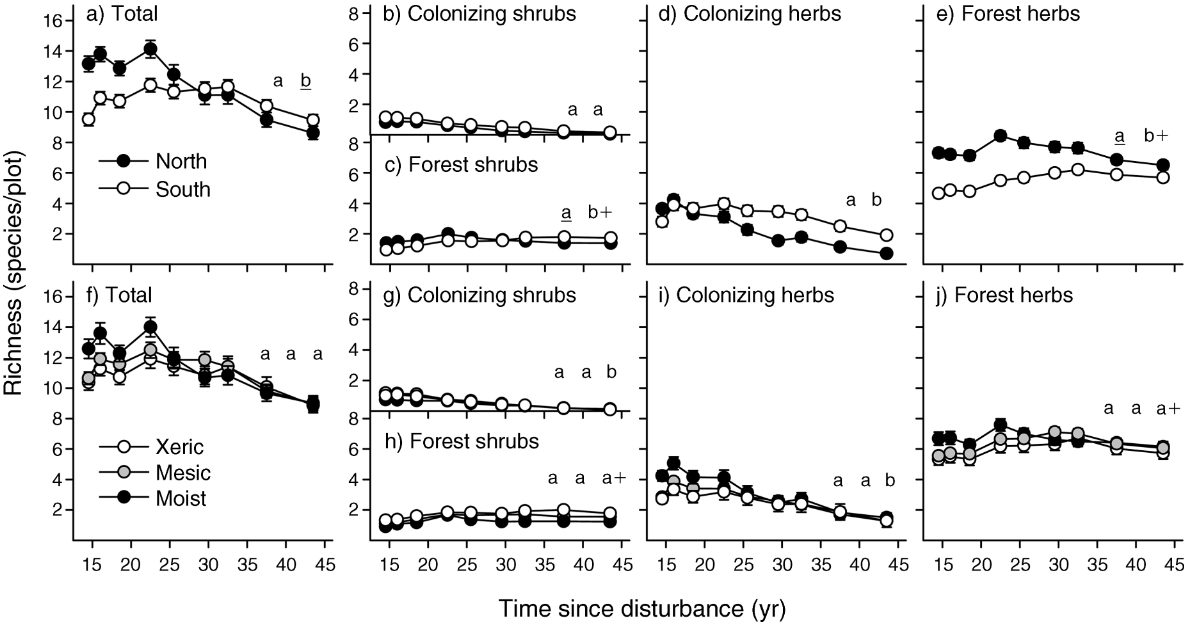

FIG. 5. Trends in understory richness for plots from (a–e) contrasting aspects and (f–j) topoedaphic contexts (moist-, mesic-, and xeric-site communities). Understory totals (left column) are partitioned by growth form and seral group (remaining columns). Scaling of the *y*-axis is the same in all panels. Different lowercase letters above symbols represent significant ($P \leq 0.05$) differences in regression slopes among resource environments (north vs. south, respectively; or xeric, mesic, and moist, respectively). A plus ("+") sign is used to indicate a positive slope, and an underscore indicates a slope that does not differ from zero. Values are means ± SE.

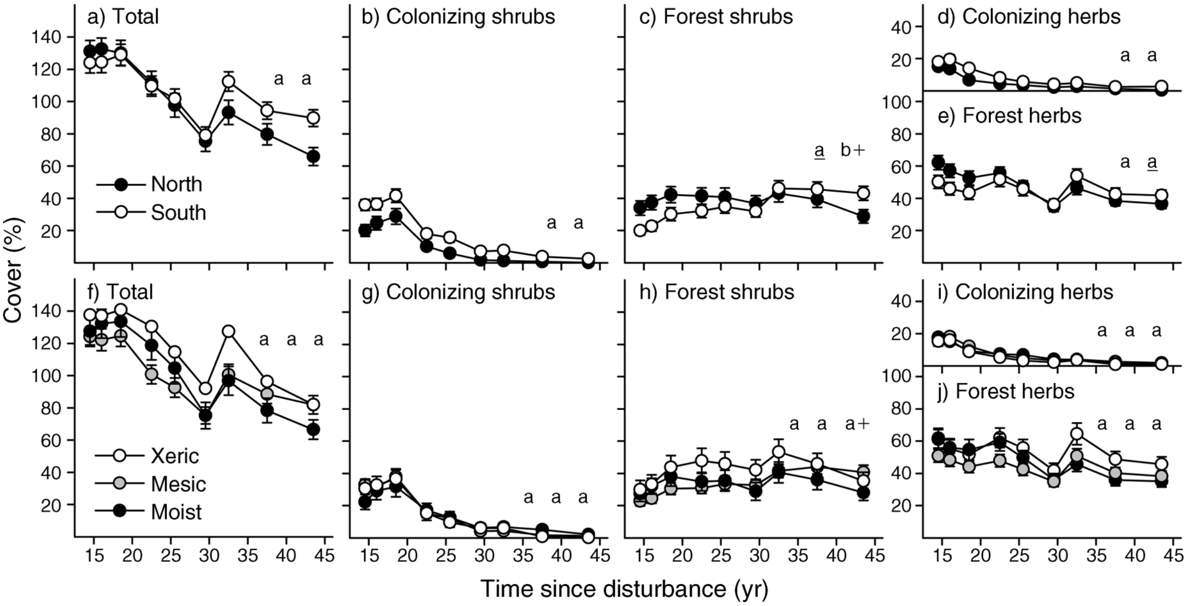

FIG. 6. Trends in understory cover for plots representing (a–e) contrasting aspects and (f–j) topoedaphic contexts (moist-, mesic-, and xeric-site communities). Understory totals (left column) are partitioned by growth form and seral group (remaining columns). Scaling of the *y*-axis is the same in all panels. Different lowercase letters above symbols represent significant ($P \leq 0.05$) differences in regression slopes among resource environments (north vs. south, respectively; or xeric, mesic, and moist, respectively). A plus ("+") sign is used to indicate a positive slope, and an underscore indicates a slope that does not differ from zero. Values are means ± SE.

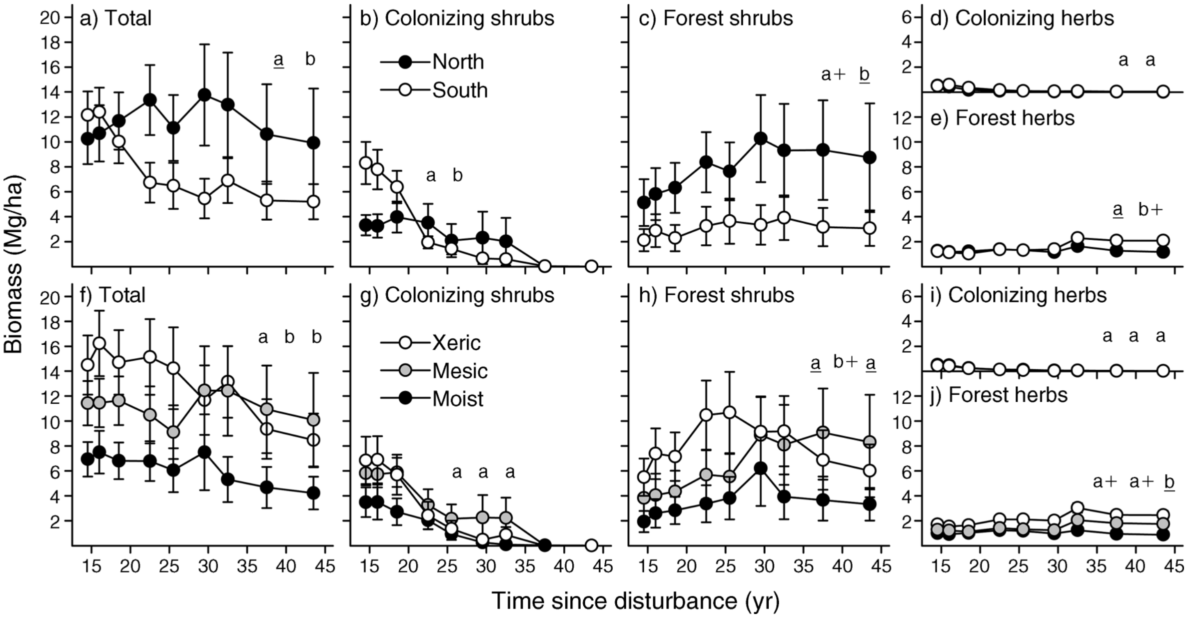

FIG. 7. Trends in understory biomass for plots representing (a–e) contrasting aspects and (f–j) topoedaphic contexts (moist-, mesic-, and xeric-site communities). Understory totals (left column) are partitioned by growth form and seral group (remaining columns). Scaling of the *y*-axis is the same in all panels. Different lowercase letters above symbols represent significant ($P \leq 0.05$) differences in regression slopes among resource environments (north vs. south, respectively; or xeric, mesic, and moist, respectively). A plus ("+") sign is used to indicate a positive slope, and an underscore indicates a slope that does not differ from zero. Values are means ± SE.

ships for any of the upper quantiles tested: five of 42 models (overstory–understory combinations × times) at $\tau = 0.80$, three at $\tau = 0.90$, and four $\tau = 0.95$. Most of these occurred early in stand development ($\leq$19 yr), prior to peak density or canopy cover.

Variation in and predictors of temporal trends

For most plots, temporal trends in understory abundance conformed to one or more of the six model types (Fig. 2, Table 2). Trends in cover could be modeled for 117 plots (62%) and trends in biomass for 123 plots (65%). Trends could not be modeled in 35–38% of plots. The most frequent model types were reinitiating, crashing, and declining (71–87 plots; 38–46%). The most frequent best-fit model for cover was reinitiating (51 plots, 27%) and, for biomass, it was crashing (45 plots, 24%). Trends less often conformed to peaking, stabilizing, or increasing forms (1–21 plots; <1–11%).

Multinomial logistic regression models were highly significant ($P < 0.001$), successfully differentiating among model types (Tables 3 and 4). For trends in cover, significant predictors included topoedaphic context (soil moisture availability, $P = 0.02$), pre-closure tree cover ($P < 0.001$) and density ($P = 0.006$), and pre-closure understory development (cover of colonizing and forest species, $P < 0.001$ and $P = 0.001$; Table 3). Relative to the reference group (no temporal trend), plots that declined in cover (reinitiating, crashing, declining, or peaking) had significantly greater tree influence (cover or density) prior to closure and, for all but the peaking group, significantly greater understory development (cover of colonizing or forest species; see parameter mean values in Table 3). Plots in the peaking group were much more likely to be xeric site communities and less often mesic site communities. Plots in which cover did not decline (increasing) had limited understory development prior to closure.

For trends in biomass (reduced to three model types; Table 4), significant predictors included timing and intensity of overstory development (timing of maximum tree density and cover, $P < 0.001$ and $P = 0.02$) and pre-closure understory development (biomass of colonizing and forest species, $P < 0.001$ and $P = 0.003$). All model types attained maximum tree density earlier than the reference group (see parameter mean values in Table 4). Plots characterized by earlier or more rapid declines (reinitiating and crashing) had greater biomass of colonizing species prior to canopy closure. Plots in which declines occurred later (peaking), had significantly greater biomass of forest species. Surprisingly, plots that experienced significant (30–50%) loss of overstory biomass to gap-forming disturbance (Lutz and Halpern 2006) did not share similar responses.

DISCUSSION

Conventional models of early forest development describe the stem-exclusion phase as one of intense tree competition, low light at the forest floor, and dramatic declines in the abundance and diversity of understory plants (Bormann and Likens 1979, Peet and Christensen

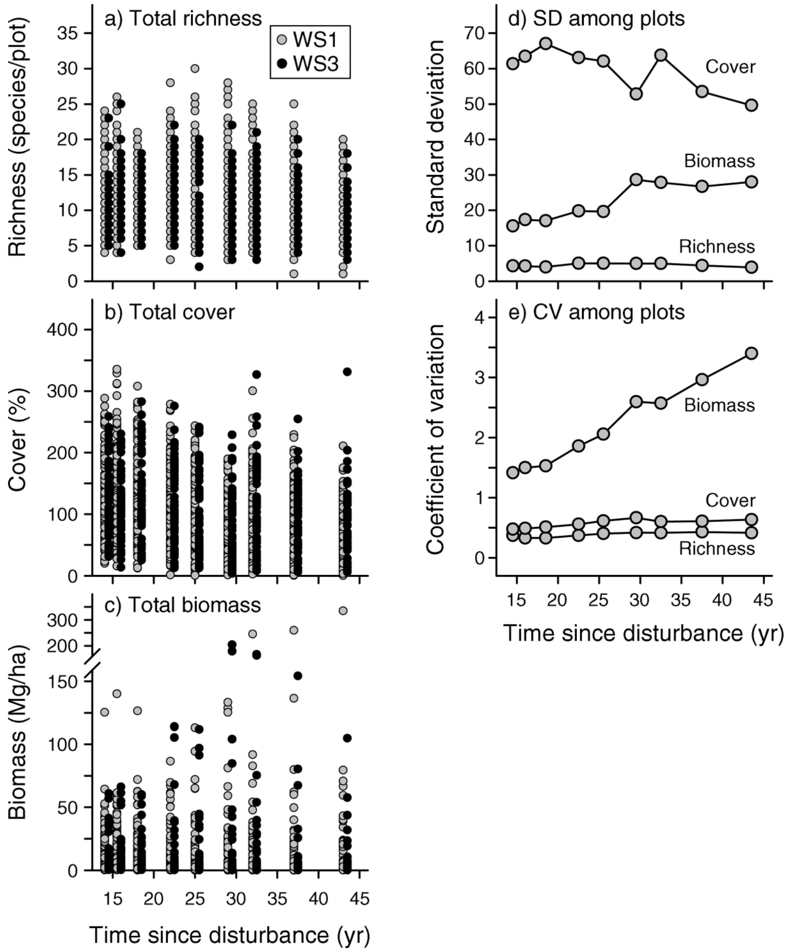

FIG. 8. Plot-level variation in understory (a) richness, (b) cover, and (c) biomass, and associated trends in the (d) SD and (e) CV of each measure. Plots from WS1 ($n = 129$ plots) and WS3 ($n = 59$ plots) are coded separately and displaced to reduce overlap; SD and CV are based on the full set of plots ($n = 188$ plots).

1987, Oliver and Larson 1996). Our permanent-plot observations, even when aggregated at larger spatial scales (comparable to those implicit in conventional models), illustrate much less dramatic declines in the abundance and diversity of the understory. Recent criticisms and elaborations of these models emphasize their simplicity and limited relevance to the broader range of pathways initiated by natural disturbances. In particular, they fail to acknowledge the potential for delayed or incomplete closure of the canopy (Franklin et al. 2002, Donato et al. 2012). Our long-term studies provide a rich and detailed picture of this variation and, more importantly, that it can arise from a common (single) disturbance (see also Halpern 1988).

General trends in overstory and understory characteristics

Forest structure changed significantly over the three decades of study (15–45 yr after disturbance). Canopy cover increased fourfold (25% to >100%), tree density nearly doubled to ~3500 stems/ha then declined comparably, and biomass accumulated linearly (from 7 to 160 Mg/ha; also see Lutz and Halpern 2006). However, changes in the understory were moderate by comparison. Richness, cover, and biomass declined by 30–40% (~10% per decade), reflecting loss of colonizing species that had peaked earlier in succession (Dyrness 1973, Halpern 1989, Halpern and Franklin 1990). In contrast, residual forest species changed little (herbs) or increased significantly (shrubs). Moreover, the small decline in forest herbs was attributable to a small number of "release" herbs (e.g., *Rubus ursinus*; Appendix B [McKenzie et al. 2000, Lindh and Muir 2004]): species of low initial abundance that expanded rapidly after overstory removal (Halpern 1989). Similar declines were not observed for the vast majority of forest species, including old-growth dominants (*Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*; Appendices B and C; see Plate 1). In fact, understory richness and cover following closure were comparable to levels observed prior to disturbance (Dyrness 1973, Halpern and Franklin 1990). Rather than causing wholesale suppression of the understory, stem-exclusion thus

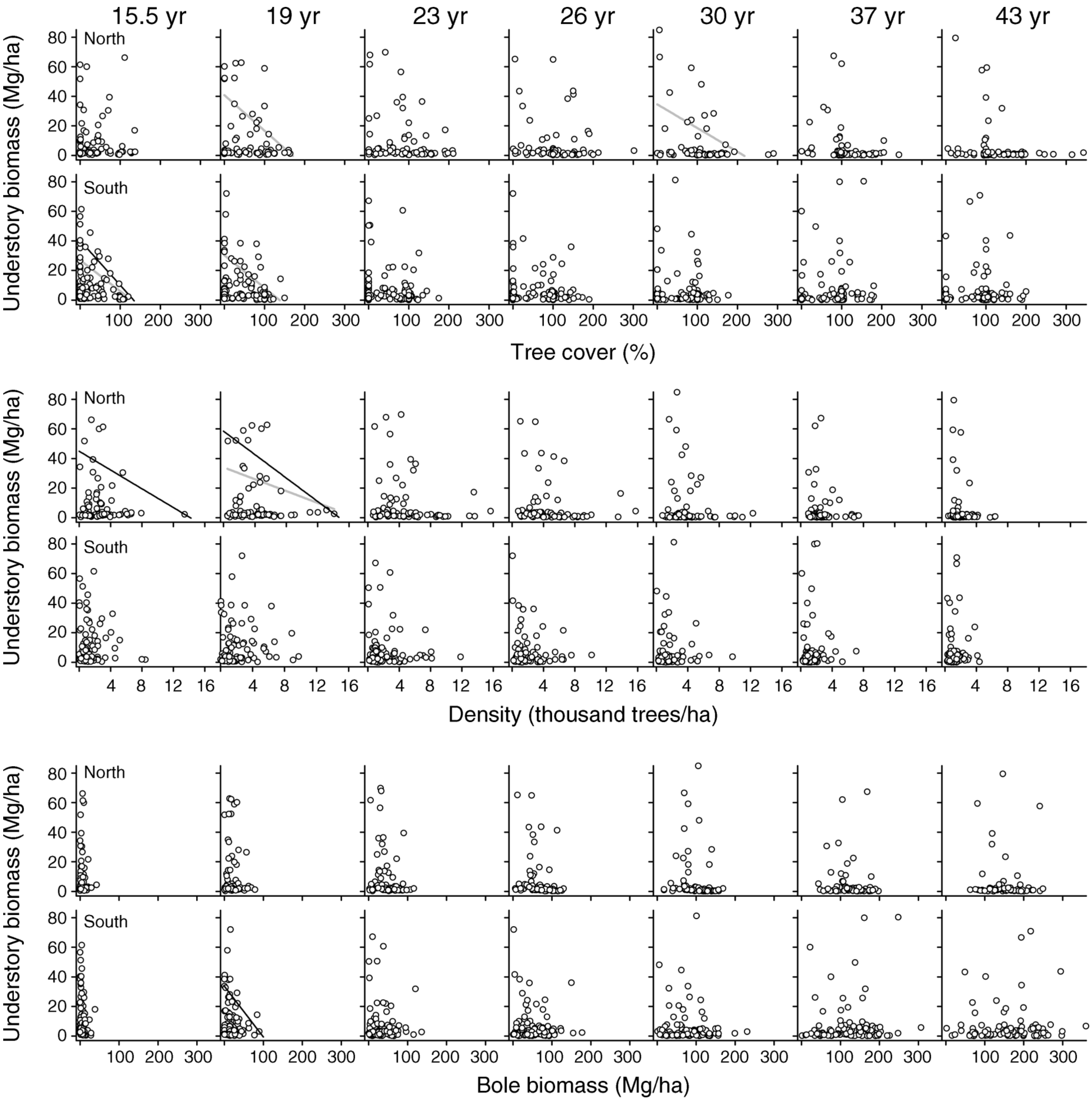

FIG. 9. Relationships between measures of overstory structure (bole biomass, tree density, and total cover) and understory biomass for each of the seven temporal pairings of overstory and understory plots. Quantile regression lines are shown for significant relationships ($P \leq 0.05$) for $\tau = 0.90$ (black lines) and $\tau = 0.80$ (gray lines); the four significant relationships for $\tau = 0.95$ are not shown. For clarity, plots in which understory biomass exceeded 85 Mg/ha are not shown but were included in analyses ($n =$ 1–6 per temporal sample).

appears to act as a filter, selectively removing the shade-intolerant colonists from a highly enriched post-disturbance community.

Similar trends in understory richness and cover have been described from a chronosequence of *Pseudotsuga*-dominated stands in western Oregon, albeit for a limited sample of post-closure sites and a much narrower range of environments (i.e., *Rhododendron*/*Gaultheria* community [Schoonmaker and McKee 1988]). However, trends in biomass have not been described for this system and make apparent how interpretations of understory decline can differ with the metric of abundance: herbs and shrubs contributed comparably to declines in cover, but shrubs dominated the decline in biomass. Although the gradual accumulation of stem wood has a tempering effect on biomass increase in shrubs, when stems die, it results in an abrupt and substantial loss. Our results reinforce the idea that in physiognomically diverse vegetation, species' contributions to community properties are highly dependent on the measure of abundance (Guo and Rundel 1997, Chiarucci et al. 1999).

TABLE 2. Numbers of sample plots for which temporal trends in total understory cover and biomass conformed to one or more of six model types.

Name	Model type	Cover Fit	Cover Best fit†	Biomass Fit	Biomass Best fit†
Reinitiating	$y = y_0 + at + bt^2$; $b > 0$	71	51	75	33
Crashing	$y = ae^{-bt}$; $b > 0$	87	17	82	45
Declining	$y = y_0 + at$; $a < 0$	86	24	73	12
Peaking	$y = y_0 + at + bt^2$; $b < 0$	27	15	28	21
Stabilizing	$y = a(1 - e^{-bt})$; $b > 0$	11	3	20	1
Increasing	$y = y_0 + at$; $a > 0$	11	7	17	11
No trend			71		65

Notes: Temporal trends were modeled for 188 plots (nine sampling dates per plot). A model was accepted as significant at an alpha of 0.05. The response variable, y, is cover or biomass; y_0 is the intercept; a and b are coefficients; and t is time since disturbance. See Fig. 2 for the shape of curves associated with each model type.

† Model with the highest adjusted R^2 among accepted models.

Variation across resource and environmental stress gradients

We hypothesized that topoedaphic factors that influence resource availability or that mediate environmental stress, could temper or exacerbate rates of understory decline, either directly through effects on resource supply (Fahey et al. 1998) or indirectly by influencing the pace of overstory development (Larson et al. 2008). Indeed, aspect had a dramatic effect on the pace and intensity of overstory development, with canopy closure occurring >10 yr earlier on N than on S aspects. Substantially greater densities of *Pseudotsuga* and shade-tolerant *Tsuga* (Lutz and Halpern 2006) are indicative of a less stressful regenerative environment on N aspects (Isaac 1943, Silen 1960, Larson and Franklin 2005). Although aspect-related declines in understory richness and cover were consistent with a model of resource preemption (i.e., greater canopy shading or greater root competition with trees [Coomes and Grubb 2000, Lindh et al. 2003]), the differences between aspects were much less dramatic than those of the overstory. In stark contrast, understory biomass declined on S, but not N aspects. This counterintuitive result can be explained by the spatial distribution and successional dynamics of the principal colonists: seed banking shrubs in the genus *Ceanothus*. *Ceanothus* spp. showed greater development on S aspects, where warmer sites, greater burn severity, and more open, post-disturbance conditions are likely to have enhanced germination and growth (Mueggler 1965, Hickey and Leege 1970, Orme and Leege 1976, Noste 1985, Halpern 1989). However, *Ceanothus* is sensitive to even moderate levels of shading and has a relatively short lifespan in this system (Mueggler 1965, Zavitkovski and Newton 1968, Conard et al. 1985). Greater accumulation of biomass on S aspects thus resulted in greater loss of biomass when stems died. Because biomass and foliar cover are poorly correlated in mature stems (C. B. Halpern, personal observation), mortality did not have the same effect on relative loss of cover. In sum, aspect-related declines in understory biomass are better explained by variation in the initial abundance of colonists than by resource supply.

TABLE 3. Multinomial logistic regression coefficients and parameter mean values for predictors that differentiate among plots of five model types representing differing trends in total understory cover.

Predictors	Reinitiating	Crashing	Declining	Peaking	Increasing	No trend
Regression coefficients						
Intercept	**−4.335**	**−5.570**	**−4.192**	**−4.878**	**0.632**	
Moisture						
Moist-site community	0.942	0.927	1.137	**2.156**	−1.078	
Xeric-site communities	−0.301	1.019	0.032	**2.244**	−0.143	
Pre-closure tree cover	**0.019**	**0.033**	−0.004	−0.015	−0.004	
Pre-closure tree density	**0.000**	0.000	**0.000**	**0.000**	0.000	
Pre-closure colonizing species cover	**0.032**	0.036	**0.018**	0.015	−0.039	
Pre-closure forest species cover	**0.009**	**0.002**	**0.016**	0.009	−0.021	
Parameter mean values						
Moisture						
Moist-site community (% of plots)	29.4	17.6	37.5	**33.3**	10.0	31.0
Mesic-site communities (% of plots)	56.9	47.1	41.7	**13.3**	70.0	46.5
Xeric-site communities (% of plots)	13.7	35.3	20.8	**53.3**	20.0	22.5
Pre-closure tree cover (%)	**46.7**	**55.8**	23.2	17.7	34.6	27.8
Pre-closure tree density (trees/ha)	**2709**	1898	**2072**	**2353**	1323	1620
Pre-closure colonizing species cover (%)	**59.8**	63.4	**46.6**	44.5	19.4	42.6
Pre-closure forest species cover (%)	**85.9**	**67.5**	**114.8**	98.6	44.1	77.4

Notes: From the original classification (Table 2), the three plots modeled as "stabilizing" were reclassified to the next best-fitting model, "increasing." The reference category for the regression was the set of plots whose temporal trends did not fit any of the model types ("no trend"). Only predictors with significant contributions are shown (significant parameters [$P \leq 0.05$] are in boldface type). For a list of the full set of predictors considered, see *Analyses: Variation in and predictors of temporal trends*. See Fig. 2 for the shape of curves associated with each model type.

Table 4. Multinomial logistic regression coefficients and parameter mean values for predictors that differentiate among plots of three model types representing differing trends in total understory biomass.

Predictors	Reinitiating	Crashing	Peaking	No trend
Regression coefficients				
Timing of maximum tree density	**−0.088**	**−0.041**	**−0.058**	
Maximum tree cover	**0.009**	0.004	0.001	
Pre-closure colonizing species biomass	**0.081**	**0.082**	0.020	
Pre-closure forest species biomass	0.044	−0.009	**0.066**	
Parameter mean values				
Timing of maximum tree density (yr)	**24.8**	**26.7**	**25.5**	29.2
Maximum tree cover (%)	**142.8**	124.9	117.5	113.0
Pre-closure colonizing species biomass (Mg/ha)	**7.9**	**9.3**	3.6	3.2
Pre-closure forest species biomass (Mg/ha)	5.5	2.9	**13.6**	3.2

Notes: The intercept term was not significant in any model (significant parameters [$P \leq 0.05$] are in boldface type). From the original classification (Table 2), the 24 plots modeled as "declining," "stabilizing," or "increasing" were reclassified to the next best-fitting model: six to "reinitiating," eight to "crashing," six to "peaking," and four to "no trend." See Table 3 for other details. See Fig. 2 for the shape of curves associated with each model type.

In contrast to the response to aspect, differences in the pace or intensity of overstory development were small among sites with differing effective soil moisture. Trends in stem density were remarkably similar among xeric-, mesic-, and moist-site communities, and although moist sites developed greater canopy cover (reflecting greater establishment of sub-canopy *Tsuga*), they accumulated less bole biomass. Similarly, there was scant evidence that moisture supply had a moderating influence on understory decline. Declines in richness of colonizing herbs were steepest in moist-site communities, and declines in total biomass were steepest in dry-site communities, locations where colonists were either most diverse or most abundant, respectively. Even among residual forest shrubs that did not suffer declines during closure, biomass trends did not correlate with proxies for resource supply. Biomass accumulated on N but not S aspects (despite greater insolation and reduced canopy shading) and in mesic, but not moist or xeric site communities. These differences in growth likely reflect inherent compositional variation in the shrub layer: prevalence of more shade-tolerant *Acer* (Russel 1974, O'Dea et al. 1995) on N-facing and mesic sites and less tolerant *Rhododendron* and *Corylu*s on S-facing and xeric sites.

Understory variation in time and space

We expected resource preemption during canopy closure to reduce not only the average richness and abundance of the understory, but also the variability among plots, leading to convergence in community properties (Christensen and Peet 1984). Implicit in the models of Clements (1916), convergence during succession has been the subject of considerable theoretical and empirical study (Margalef 1968, Facelli and D'Angela 1990, Leps 1991, Frelich and Reich 1995, Walker et al. 2010). Although it is typically viewed from the perspective of species composition, the underlying mechanism, interspecific interactions that sort among species, should result in convergence of other community properties as well (Wilson et al. 1987, Zobel et al. 1993). Here we saw limited evidence of convergence in the richness, cover, or biomass of plots, either in the range of values or in simple measures of variability (CV and SD). Lack of convergence in the understory could reflect corresponding heterogeneity in the overstory. Indeed, variation in forest structure either remained high (tree density) or increased over time (bole biomass; Lutz and Halpern 2006). However, this explanation would also imply a strong negative relationship between overstory and understory characteristics, which was not apparent in the broad scatter of plots used in quantile regressions (Fig. 9). Moreover, among the few significant models of maximum understory response, most occurred well before peak tree density or canopy cover. Both of these outcomes, the lack of convergence and the quantile regression results, run counter to a model in which understory decline is driven by overstory influences. However, they are consistent with the dynamics of colonizing shrubs which dominated the decline process.

Early stand development in this system may be more accurately described as a spatiotemporal mosaic of vegetation states and transitions, with asynchrony among individual forest patches (or plots) dampening any directional trends at larger scales. Although cover and biomass were most often modeled as reinitiating or crashing, delays (peaking) or no evidence of decline were also common, even after four decades, a sharp contrast to the simple dynamics of decline described by conventional models. The results of multinomial logistic regression provide insights into this variation. Declines were more likely to occur where there was greater tree influence (cover or density) before or at peak overstory development, and where there was greater initial cover or biomass in the understory (thus greater potential for decline). Not surprisingly, plots with greater biomass of colonizing species followed "faster" trajectories (reini-

PLATE 1. Dense, post-closure stand in Watershed 1 (WS1) with a well-developed understory of *Polystichum munitum*. Photo credit: C. B. Halpern.

tiating or crashing), plots with greater biomass of forest species "slower" trajectories (peaking), and plots with limited understory development either an increase or no discernible trend. Interestingly, however, plots that lost significant overstory biomass to gap-forming disturbance (Lutz and Halpern 2006) did not respond positively (increasing or reinitiating), suggesting that damage or burial of the understory by treefall may balance the benefits of sudden increases in light or belowground resources. Although gap formation early in succession may contribute to the structural complexity of older forests (Lutz and Halpern 2006, Lutz et al. 2012), it does not appear critical to reinitiation of the understory.

The ability to link variation in post-closure dynamics to characteristics of the pre-closure vegetation highlights the value of long-term studies for elucidating patterns and processes that are difficult (or impossible) to infer with a chronosequence approach. Indeed, variation in the characteristics of the pre-closure vegetation (e.g., dominance by colonizing species or relative shade-tolerance of forest shrubs) may be as important as the pace or intensity of overstory development. We do not address the causes of this variation: disturbance severity and pre-disturbance composition (described in Halpern 1988, Halpern and Franklin 1990, Halpern and Spies 1995). Rather, we emphasize that this pre-closure variation exists and has important consequences for the post-closure dynamics of these forests, either by accentuating or dampening the pace of decline.

Conclusions

Although there is heuristic value to conventional, stage-based models of stand development, their relevance to forests initiated by natural disturbance has been questioned (Franklin et al. 2002, Donato et al. 2012). It has been argued that these simple models fail to account for the complexity of structures and diversity of regeneration pathways initiated by natural stand-replacing disturbances. For example, they ignore the potential for protracted, low-density recruitment that can result in slow or incomplete closure of the canopy (Tappeiner et al. 1997, Franklin et al. 2002, Donato et al. 2009, 2012, Turner et al. 2009). Although the disturbances in these experimental watersheds were not "natural," the variability of subsequent regeneration patterns clearly supports this view (Lutz and Halpern 2006). They also suggest a more complex model of understory development, one in which the dynamics of the understory and overstory are loosely coupled in space and time, and in which the characteristics of the understory vegetation are as important as those of the overstory in the timing and nature of decline. Natural disturbances that create greater diversity of live and dead structures (or biological legacies), would likely enhance this spatial and temporal variability. Just as structural diversity can arise early in the development of forests in ways that advance future complexity (Swanson et al. 2011, Donato et al. 2012, Lutz et al. 2012), so too can diversity in the understory. Clearly, in this system, the notion of stem-exclusion as a temporal bottleneck in the development of the understory does not hold. Our long-term studies of structural and compositional change provide novel insights into successional processes that cannot be gained from short-term experiments or space-for-time substitutions.

ACKNOWLEDGMENTS

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SUPPLEMENTAL MATERIAL

Appendix A

Frequency of occurrence (number of plots) of understory taxa in WS1 and WS3, H. J. Andrews Experimental Forest, Oregon, over the study period (1979–2008) (*Ecological Archives* M083-008-A1).

Appendix B

Mean cover of understory taxa in WS1 and WS3, H. J. Andrews Experimental Forest, Oregon, over the study period (1979–2008) (*Ecological Archives* M083-008-A2).

Appendix C

Mean biomass of understory taxa in WS1 and WS3, H. J. Andrews Experimental Forest, Oregon, over the study period (1979–2008) (*Ecological Archives* M083-008-A3).

Appendix D

Equations used to estimate aboveground biomass of understory taxa in WS1 and WS3, H. J. Andrews Experimental Forest, Oregon (*Ecological Archives* M083-008-A4).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/1q88j