Early Successional Pathways and the Resistance and Resilience of Forest Communities

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EARLY SUCCESSIONAL PATHWAYS AND THE RESISTANCE AND RESILIENCE OF FOREST COMMUNITIES[1]

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Abstract. Vegetation changes were studied for 21 yr in two clearcut logged and slash-burned *Pseudotsuga* forests in the western Cascade Range of Oregon. Detrended correspondence analysis (DCA) was used to examine the successional relationships among six understory communities exposed to a gradient of disturbance intensity. Euclidean distances between pre- and postdisturbance samples in ordination space were used to compare community resistance to disturbance and long-term recovery, or resilience. Ordination through time for plant communities revealed a common pattern of rapid floristic change away from predisturbance composition, followed by gradual, unidirectional return. Early, but transient, convergence of successional pathways was common among mesic- and dry-site communities, reflecting the broad distribution of colonizers and the floristic similarity of predisturbance understories. Distinct sequences were observed on moist sites, reflecting more unique residual and colonizing floras. Ordinations also revealed increasing compositional change with disturbance intensity. Successional sequences were dominated by residual species on relatively undisturbed sites and by alternate suites of invading species on moderately disturbed and burned sites. Variation in the response gradient between watersheds reflected the modifying influence of local environment, stand history, and chance in succession.

Resistance and resilience varied little among plant communities but were generally lowest for the depauperate *Coptis* community and greatest for the compositionally and structurally diverse *Polystichum* and *Rhododendron–Gaultheria* types. Both measures were strongly influenced by disturbance intensity. The stability of *Pseudotsuga* understories derives from the moderate tolerance of initial understory dominants to burning and in their ability to subsequently perennate from subterranean structures. Variation in the long-term response of communities reflects complex interactions between species life history, disturbance intensity, and chance, suggesting that both deterministic and stochastic factors must be considered in evaluating community stability and response to disturbance.

Key words: clearcut logging; detrended correspondence analysis; disturbance; Euclidean distance; multiple pathways; ordination; permanent plots; resilience; resistance; stability; succession; vegetation dynamics.

Introduction

The relative stability of communities may be determined by comparing features of their responses to disturbance. Catastrophic, or large-scale, disturbances profoundly alter the composition and structure of plant communities. Subsequent patterns of change reflect the nature of disturbance (e.g., its intensity or duration), characteristics of the initial community, local environmental conditions, the influence of consumers, and the effects of chance. Consequently, multiple successional sequences are common following disturbance (Lubchenco and Menge 1978, Cattelino et al. 1979, Sousa 1979, 1984, Noble and Slatyer 1980, Turner 1983, Abrams et al. 1985, Olson 1985, Connell 1987). Communities may be considered stable if these pathways result in a return to initial composition within an appropriate time scale (Sutherland 1981). Thus, in comparing the responses of communities to disturbance, one must define successional pathways in a manner that reveals compositional change and recovery.

In this paper, I examine the successional pathways of six forest communities exposed to different intensities of soil disturbance. The data derive from a 22-yr permanent plot study of understory development following logging and burning of *Pseudotsuga* forests in the western Cascade Range of Oregon. A predisturbance classification of understory communities, and an immediate postburning evaluation of soil disturbance have facilitated study of the influence of initial composition and disturbance intensity on the long-term response of vegetation to catastrophic disturbance. In an earlier paper, Dyrness (1973) examined the influence of original community composition and disturbance intensity on compositional change for the first 5 yr of succession in one of two sites (Watershed 3) discussed here.

Interpretation of community response to disturbance may be hindered by the inherent complexity of long-term successional data. This complexity may be reduced by ordination (e.g., detrended correspondence analysis [DCA]) of the data obtained from sequential observation of permanent plots. In this manner, successional pathways may be graphically portrayed by the successive positions of samples within the resulting ordination field. The technique has been applied to data from grassland (Hopkins 1968, van der Maarel 1969, Austin 1977, Swaine and Greig-Smith 1980, Austin et al. 1981, Polley and Collins 1984, Aarssen and Turkington 1985, Belsky 1986), heathland (Hobbs and Gimingham 1984), coastal sage scrub (Westman and O'Leary 1986), and garrigue communities (Malanson and Trabaud 1987).

The relative stability of a community (sensu Sutherland 1974, 1981) is implicit in its successional trajectory, and may be characterized by its resistance (i.e., the extent to which it resists change by disturbance) and its resilience (i.e., the rate, manner, or degree to which initial community characteristics are restored following displacement). In this study, I use Euclidean distances between pre- and postdisturbance samples in ordination space to quantify the relative resistance and resilience of initial forest communities (see also Bloom 1980, Westman and O'Leary 1986, Malanson and Trabaud 1987). In this manner, ordination analysis provides a method for comparing the resistance and resilience of communities in the context of postdisturbance successional trajectories. By superimposing species abundance values on sample ordinations, species characteristics associated with community trajectories and with patterns of community stability can be identified.

STUDY AREA

Physical environment

The study areas were two watersheds of the H. J. Andrews Experimental Forest on the western slope of the central Cascade Range, 80 km east of Eugene, Oregon. Watersheds 1 and 3 (WS1 and WS3) are typical of the mature, dissected topography of the region. Elevations range from 442 to 1082 m and slopes average >50% (Rothacher et al. 1967).

Soil parent materials are derived primarily from tuffs and breccias, although basalts and andesites are also present. Soils overlay extensive colluvial deposits and are characterized by poor profile development, loamy textures, and a high porosity and water storage capacity (Dyrness 1969).

The climate of the region is maritime with mild, wet winters and warm, dry summers. Annual precipitation averages 2302 mm, yet only 6% falls between June and August (Bierlmaier and McKee, in press). Temperatures range from an average minimum of $-5.5°C$ in January and 11.9° in August, to an average maximum of 5.5° in January and 23.3° in July. Although snowfall

is common, accumulations are typically small and do not persist.

Vegetation

The vegetation of Watersheds 1 and 3 is typical of much of the Tsuga heterophylla zone (Franklin and Dyrness 1973). Prior to disturbance, forest canopies were dominated by a mixture of old-growth (300–500 yr old) and mature (125 yr old) Pseudotsuga menziesii (Dyrness 1973). Tsuga heterophylla varied in size and age, and dominated the subcanopy and regeneration layers. Other widely distributed tree species included Taxus brevifolia, Cornus nuttallii, and Acer macrophyllum. Castanopsis chrysophylla and Pinus lambertiana were restricted to dry, upper slopes and ridgetops, whereas Thuja plicata was locally common along moist, lower slopes. Overstory canopy cover (>8 m tall) averaged 62 and 58%, while understory tree cover (<8 m) averaged 59 and 42%, on Watersheds 1 and 3, respectively (C. T. Dyrness, personal communication). Vascular plant nomenclature and taxonomy follow Hitchcock and Cronquist (1973).

The initial understory vegetation was classified into six plant communities arrayed along a gradient of available moisture (Rothacher et al. 1967). Detailed information on understory composition, structure, and distribution has been presented elsewhere (Rothacher et al. 1967, Dyrness 1973, Halpern 1987). Plant communities were typical of sites of similar elevation and topography throughout the Experimental Forest. Although the communities were characterized by species with broad ecological amplitude, the abundance of understory dominants not only corresponded with variation in environment, but also reflected overstory canopy characteristics and local stand history. Brief descriptions of the understory communities are provided in Table 1.

METHODS

Field methods

Permanently staked sample plots of 2×2 m were established along evenly spaced, parallel transects in both watersheds during the summer of 1962, prior to logging. A total of 131 plots represented six transects on WS1 and 61 plots represented 10 transects on WS3. The position of the initial plot on each transect was determined randomly, and the remaining plots were placed at slope-corrected intervals of 30.5 m. Each plot was assigned to one of six plant communities based on the initial classification of forest understories (Table 1).

The timing and distribution of logging, burning, and artificial regeneration varied within and between watersheds (Fig. 1). The entire 96 ha of WS1 was clearcut over a period of 4 yr (fall 1962–summer 1966) and slash was broadcast burned in October 1966. In contrast, on WS3, three areas of 5, 9, and 11 ha (totaling one-quarter of the watershed) were clearcut during a

TABLE 1. Characteristics of the six forest understory communities of Watersheds 1 and 3. Information derived from Rothacher et al. (1967), Dyrness (1973), and Halpern (1987). Communities are arranged in order of increasing available moisture.

Plant community and abbreviation	Topographic position and aspect	Dominant understory growth form(s)	Dominant understory species
Corylus cornuta–Gaultheria shallon (COCO-GASH)	ridgetops; south-facing upper slopes	tall shrubs	*Corylus cornuta, Acer circinatum, Berberis nervosa*
Rhododendron macrophyllum–Gaultheria shallon (RHMA-GASH)	ridgetops; mid-slope benches	tall shrubs (herbs and low shrubs)	*Rhododendron macrophyllum, Gaultheria shallon*
Acer circinatum–Gaultheria shallon (ACCI-GASH)	mid to upper south-facing slopes	herbs and low shrubs, tall shrubs	*Gaultheria shallon, Acer circinatum*
Acer circinatum–Berberis nervosa (ACCI-BENE)	mid to lower slopes	tall shrubs	*Acer circinatum*
Coptis laciniata (COLA)	mid to lower slopes	understory trees	*Tsuga heterophylla*
Polystichum munitum (POMU)	bottom and steep, north- to east-facing slopes, seeps	herbs and low shrubs (tall shrubs)	*Polystichum munitum, Acer circinatum*

single season (winter 1962–1963), and slash was burned the following fall (September 1963). Details of aerial seeding and planting of *Pseudotsuga menziesii* are presented in Fig. 1. However, the contribution of natural and artificial regeneration to subsequent development of *P. menziesii* is unknown.

Forest understories were initally sampled during summer 1962, prior to disturbance. Within each plot, visual estimates of projected canopy cover (percent) were made for each understory vascular plant species <6 m tall (to include herbs, tall shrubs, and regenerating trees). Details of the sampling protocol have been presented in Halpern (1987).

Following the completion of logging, plots were relocated or reestablished from field notes and resampled. The watersheds were then broadcast burned. Plots were again relocated and assigned to one of four soil disturbance classes based on the following classification (Dyrness 1973).

1. *Undisturbed.* The soil surface appeared similar to that prior to disturbance, with minimal mixing of soil and litter and with no evidence of fire.

2. *Disturbed–Unburned.* Disturbance from logging was evident as litter was removed or mixed with mineral soil; however, there was little evidence of fire.

3. *Lightly burned.* Surface litter was charred by fire but was not completely removed.

4. *Heavily burned.* Surface litter was completely consumed by intense fire.

Plots were resampled the first growing season following slash burning on both sites (1967 on WS1 and 1964 on WS3) (Fig. 1). Postdisturbance remeasurements were made annually through 1973 on WS1 and through 1972 on WS3, and, for the most part, biennially thereafter.

Data reduction and analysis

Ordination analyses.—Ordination analyses were performed separately for each watershed because of differences in disturbance history and sampling schedule. Composite samples, used as input for the ordination analyses, were formed to represent the average cover of each species, for each sampling year, within each (1) plant community, (2) soil disturbance class, and (3) combination of community and disturbance class. Composites were constructed from a complete species-by-sample plots-by-dates data matrix (raw cover values) using the computer program DATAEDIT of the Cornell Ecology Program Series (Singer 1980, Gauch and Singer 1982).

Ordinations were performed using DECORANA, a FORTRAN program for detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980). The ecological literature is replete with discussion on the relative merits and limitations of diverse ordination techniques (e.g., Hill and Gauch 1980, Gauch 1982, Kenkel and Orlóci 1986, Minchin 1987, Wartenberg et al. 1987). DCA was chosen for this study because of its local availability, its computational efficiency with large data sets, and its ecologically interpretable and intuitive results. Furthermore, compared with other ordination techniques, the distances between samples along DCA axes (measured in standard deviation units) more closely represent equivalent changes in species composition (Hill 1979, Hill and Gauch 1980).

Within each ordination field, points representing the same composite sample in successive years were connected sequentially to form successional trajectories. The initial point for each trajectory represents the average species composition prior to disturbance, whereas the second and third points represent the composition during the growing seasons following logging and following slash burning, respectively. The remaining points correspond with subsequent years of sampling (see Fig. 1 for sampling schedule).

Measures of resistance and resilience.—Dissimilarity indices (distances in species space) are commonly used to measure temporal changes in species composition
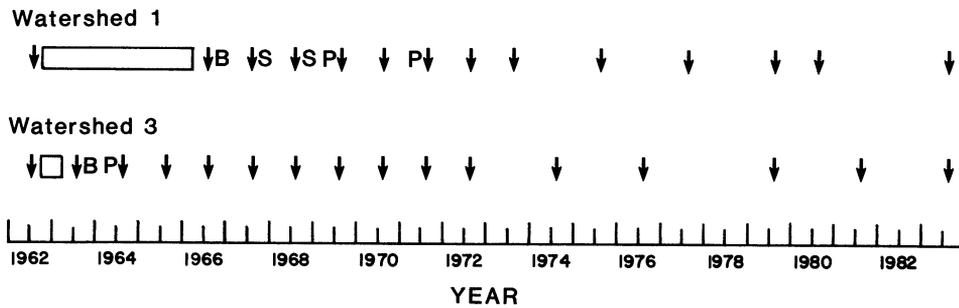
Watershed 1

Watershed 3

FIG. 1. The history of disturbance and artificial regeneration on Watersheds 1 and 3. Arrows indicate sampling years. Open horizontal bars indicate periods of logging. B = slash burning. S = aerial seeding of *Pseudotsuga menziesii* (all of Watershed 1 seeded in 1967, 10 ha in 1968). P = planting of *P. menziesii*. (Watershed 1: 1969 = entire watershed planted with 2-yr-old trees; 1971 = 40 ha planted with 2- and 3-yr-old trees. Watershed 3: each clearcut unit planted with 3-yr-old trees.)

and to express the relative displacement or recovery of communities after disturbance (e.g., Westman 1978, Sousa 1980, Smedes and Hurd 1981, Leps et al. 1982, Westman and O'Leary 1986). However, few studies have applied distances in ordination space (a species space of reduced dimensionality) to this end (but see Bloom 1980, Westman and O'Leary 1986, Malanson and Trabaud 1987). I used the Euclidean distance within a two-dimensional ordination space to measure the compositional dissimilarity between the initial and each postdisturbance composite sample. For this system, resistance to disturbance was defined as inversely proportional to the maximum Euclidean distance between pre- and postdisturbance samples. Resilience, or the degree of community recovery, was defined as inversely proportional to the Euclidean distance between predisturbance and final samples. These distance measures, rather than species-based formulations, were chosen to integrate the concepts of resistance and resilience with successional trajectories and to express individual community trends relative to the entire range of watershed pattern.

RESULTS AND DISCUSSION

Multiple pathways

Plant communities. — Ordination of community samples through time reveals parallel, as well as briefly convergent, successional trajectories (Fig. 2). However, common trends underlie all pathways. For both watersheds, predisturbance forest understory communities are aligned along Axis 2, generally corresponding with the gradient in available moisture. In response to disturbance, communities display rapid floristic change away from initial composition followed by gradual, unidirectional return. The positions of samples, 1 and 2 yr after burning, reflect widespread reductions in the abundance of understory dominants, including herbs and low shrubs (e.g., *Berberis nervosa, Gaultheria shallon,* and *Polystichum munitum*); tall shrubs (e.g., *Acer circinatum, Rhododendron macrophyllum,* and *Corylus cornuta*); and subcanopy trees (e.g., *Tsuga hetero-*

phylla). Further, they coincide with the early prominence of fugitive annuals (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*) that peaked rapidly on most sites 2 yr after burning.

Subsequent compositional changes were less dramatic. The dominant colonizing species changed gradually from annual (e.g., *S. sylvaticus* and *E. paniculatum*) to herbaceous biennial and perennial (e.g., *Cirsium* spp., *Agoseris* spp., and *E. angustifolium*) to woody perennial growth forms (e.g., *Ceanothus velutinus, C. sanguineus,* and *Rubus parviflorus*). Initially uncommon forest herbs and subshrubs showed transient (e.g., *Hieracium albiflorum, Linnaea borealis, Trientalis latifolia,* and *Whipplea modesta*) or persistent (e.g., *Rubus ursinus*) release, while initial understory dominants developed relatively slowly, with varying recovery to predisturbance levels.

Brief convergence of successional trajectories is particularly evident on WS3 (Fig. 2B). Early compositional convergence of dry- (*Rhododendron–Gaultheria* and *Acer–Gaultheria*) and mesic-site communities (*Acer–Berberis* and *Coptis*) is primarily a consequence of the broad ecological amplitude of dominant herbaceous invaders, and secondarily of the small floristic differences initally separating these forest types. Colonizing species with wide distribution included *Senecio sylvaticus, Epilobium paniculatum, E. angustifolium,* and *Ceanothus velutinus.* Subsequent divergence of successional trajectories accompanies the decline of invading herbs and the recovery of initial understory dominants. The positions of final community samples suggest return toward predisturbance composition.

In comparison, successional trajectories for moist-site communities (i.e., *Polystichum*) remain relatively distinct, reflecting the sequential expansion of species with greater site fidelity. Annual (e.g., *Montia sibirica*) and perennial invaders (e.g., *Anaphalis margaritacea* and *Rubus parviflorus*) were followed by initially subordinate (e.g., *Galium triflorum, Oxalis oregana,* and *Vancouveria hexandra*) and dominant forest herbs (e.g., *Polystichum munitum*). Trajectories for the *Polysti-*
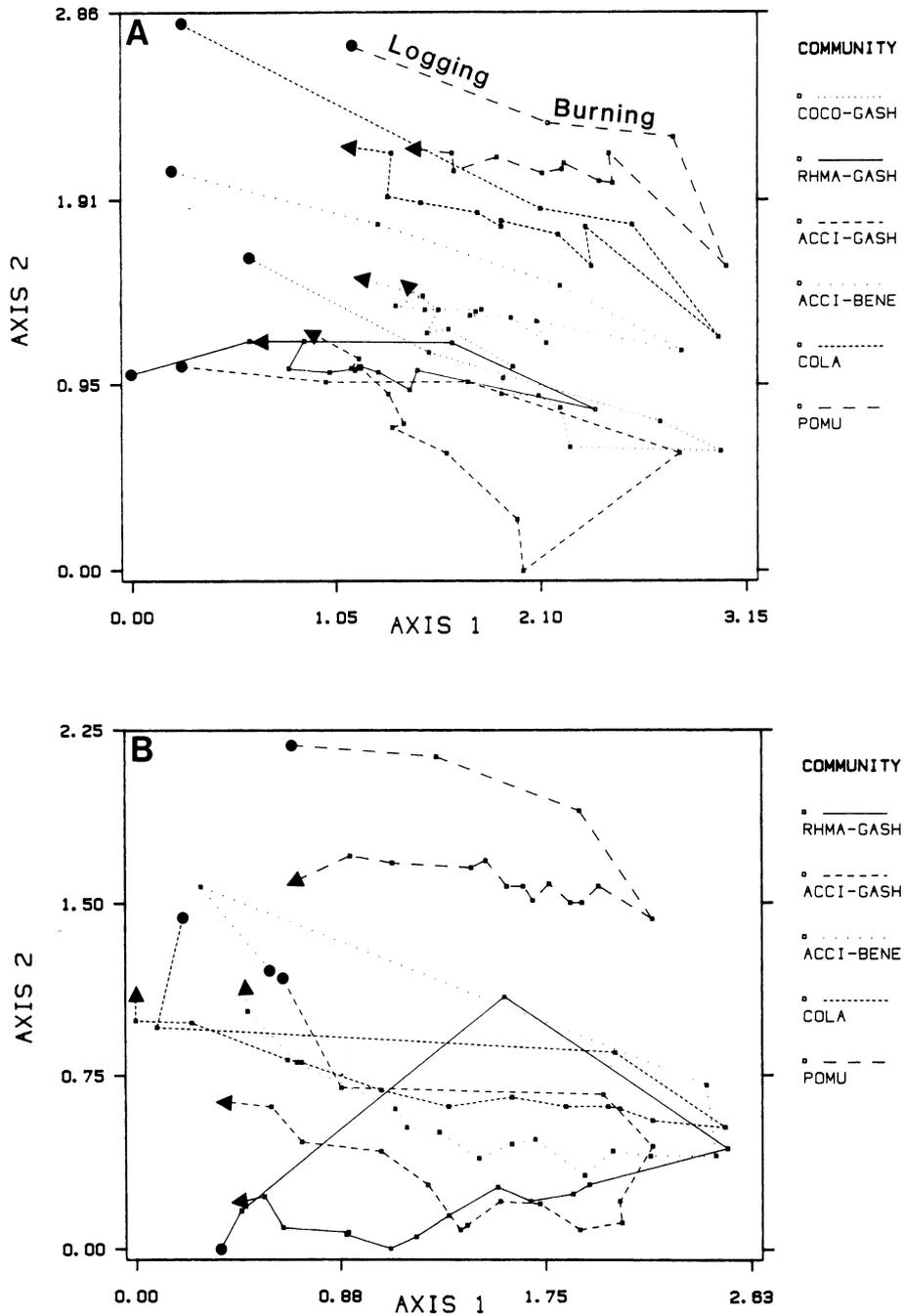
FIG. 2. Detrended correspondence analysis (DCA) ordination through time of composite samples representing the initial understory communities of Watersheds 1 (A) and 3 (B). Lines connect the same composite sample in subsequent years. Solid circles represent the predisturbance communities; arrowheads coincide with the final sample and indicate the direction of change through time. Axes display standard deviation units. See Fig. 1 for sampling dates. Community abbreviations are defined in Table 1.

chum community are further distinguished from other community pathways by the limited development of *Ceanothus velutinus,* the principal colonizing shrub of mesic and dry sites.

Thus, pronounced changes in composition typified

the response of all communities to disturbance. Annual and perennial colonizers rapidly, but temporarily, dominated initial understory species. Early convergence of community composition depends both on the ecological amplitude of invading species and on the
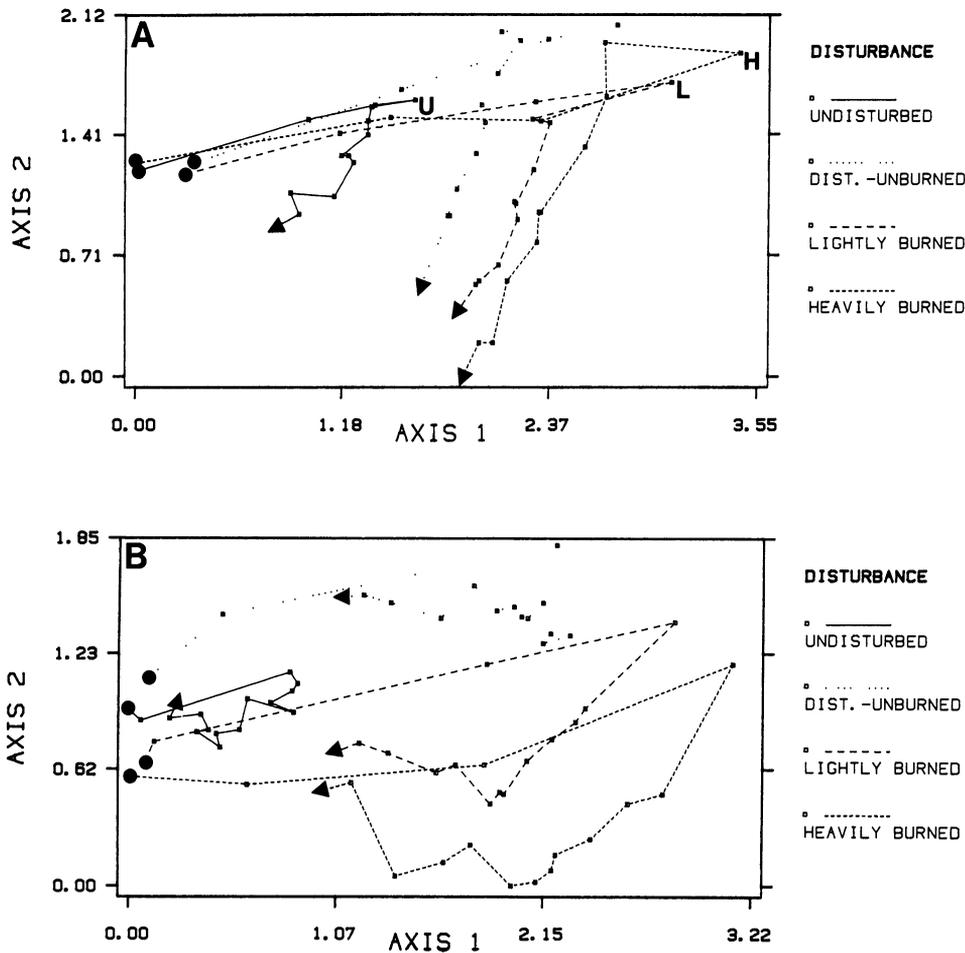
FIG. 3. DCA ordination through time of composite samples representing the soil disturbance classes of Watersheds 1 (A) and 3 (B). The disturbance classes represented by U (undisturbed), L (lightly burned), and H (heavily burned) are more fully described in Results and Discussion: Multiple Pathways: Intensity of Soil Disturbance. See Fig. 2 caption for details of data presentation.

similarity of initial floras. Although convergence was common, it was transient, as gradual decline of invaders and recovery of initial understory dominants returned communities toward their distinct predisturbance compositions. Where initial and invading floras displayed greater community fidelity, successional pathways remained more distinct.

Intensity of soil disturbance.—The intensity of soil disturbance profoundly influenced the magnitude and direction of vegetation change. Ordinations reveal increasing compositional change with disturbance intensity (Fig. 3). On WS1, for example, composition on undisturbed sites changed relatively little after slash burning (U, Fig. 3A) as initial dominants persisted. On lightly and heavily burned sites, however, major changes in composition occurred; sample positions after 2 yr (L and H, Fig. 3A) coincide with the maximum abundance of annual colonizers (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*). Their local prominence two

growing seasons after burning reflects the combined effects of (1) copious seed production, (2) interaction of a winter annual life cycle with fall burning (Halpern, *in press*), and (3) an affinity for the high soil fertility associated with recent burns (West and Chilcote 1968).

Long-term compositional changes among disturbance classes differed between watersheds, as reflected in their different paths of recovery. On WS1, composite samples uniformly progress downward along the second ordination axis (Fig. 3A). Compositional change in this direction coincides with a gradual physiognomic transition from herb- to tall shrub-dominated understories. Trajectory lengths increase with disturbance intensity, reflecting differences in the distribution of dominant tall shrub species. Undisturbed sites were reoccupied by resprouting understory dominants (e.g., *Acer circinatum* and *Rhododendron macrophyllum*). In contrast, disturbed and burned sites were dominated by invaders; *Rubus parviflorus* characterized dis-
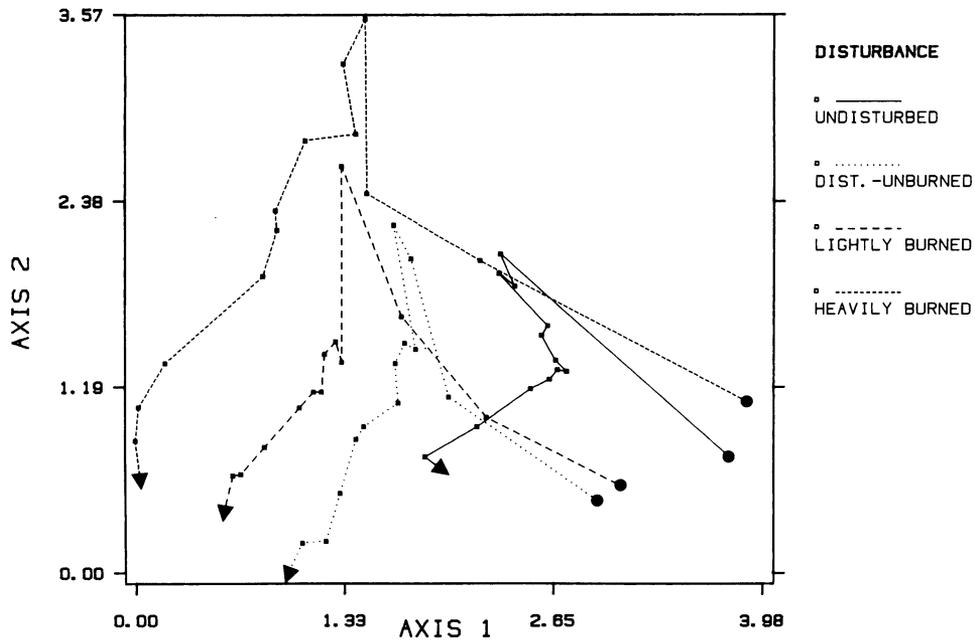
FIG. 4.   DCA ordination through time of composite samples experiencing four intensities of disturbance within the *Polystichum munitum* community of Watershed 1. See Fig. 2 caption for details of data presentation.

turbed–unburned sites, and *Ceanothus velutinus* and *C. sanguineus,* burned sites.

On WS3, however, successional trajectories are directed toward predisturbance points (Fig. 3B), indicating relatively greater compositional recovery than on WS1. Here, the second ordination axis segregates alternate successional sequences initiated by different intensities of disturbance. Although invading tall shrubs on WS3 generally showed the same affinities for disturbed and burned soils as on WS1, widespread recovery of residual shrubs occurred on all sites. Successional trajectories further suggest that the magnitude of long-term compositional recovery on disturbed and burned soils was not related to disturbance intensity; distances were similar between each initial and final composite sample (Fig. 3B), unlike WS1 (Fig. 3A).

Differences in recovery between watersheds are partly explained by three observations (Halpern 1987):

1) Invading tall shrubs were more abundant and persistent on WS1 than on WS3. These differences were probably historical and stochastic in nature. First, the paucity of *Ceanothus sanguineus* on WS3 was most likely due to a limited availability of buried seed. Second, a dramatic decline of *C. velutinus* in response to severe winter frost was limited to WS3, probably reflecting local differences in climate or the reduced vigor of older individuals.

2) The abundance of invaders on WS1 varied directly with intensity of disturbance, reflecting the distributional patterns of annual (e.g., *Senecio sylvaticus* and *E. paniculatum*) and woody perennial species (e.g., *C.*

sanguineus and *C. velutinus*). The abundance of invaders on WS3, in contrast, was similar among disturbed and burned soil classes.

3) The fact that complete recovery of initial understory dominants was limited to undisturbed sites on WS1, but was widespread among disturbed and burned sites on WS3 may reflect: (1) reduced competition from invading shrubs on WS3 and (2) a more favorable physical environment within the smaller clearcut units of WS3.

Interactions of initial composition and disturbance intensity. — Multiple successional paths may reflect the combined influence of initial composition and disturbance intensity. The effects of this interaction were examined with separate ordinations of each plant community and soil disturbance class for each watershed. The successional relationships revealed by these analyses are illustrated with the following examples from WS1. Generally similar interactions between initial composition and disturbance intensity were observed on WS3.

1. *Polystichum munitum community.* — Successional patterns varied in the *Polystichum* community (Fig. 4). Alternate trajectories can be attributed to the differential response of dominant invading and residual species to variation in the timing and intensity of disturbance. For example, on undisturbed sites, dominance rapidly shifted from invading to residual growth forms. Early prominence of the perennial invader *Epilobium angustifolium* reflected its vigorous rhizomatous spread prior to burning, as most undisturbed plots
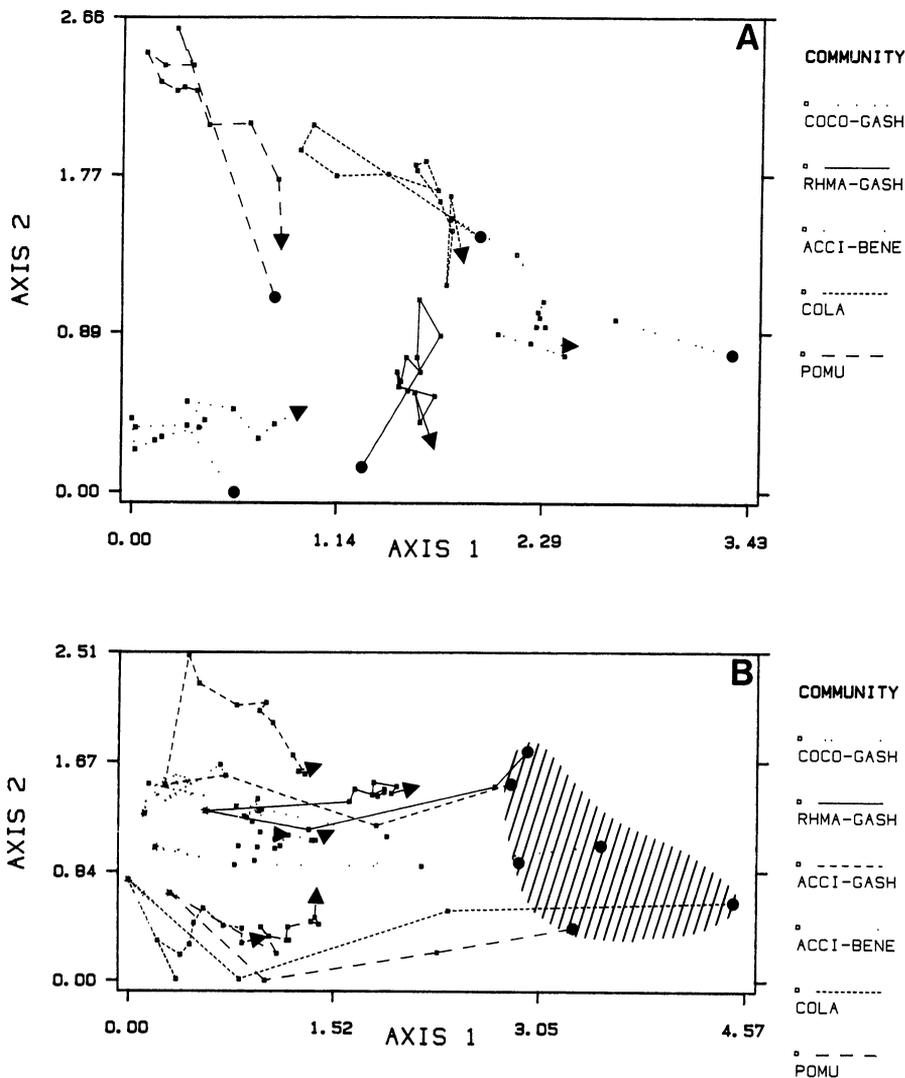
FIG. 5. DCA ordination through time of composite samples representing the initial understory communities on (A) undisturbed sites and (B) lightly burned sites on Watershed 1. Shaded areas illustrate temporary convergence from predisturbance (hatched) to postburning (stippled) composition. Community abbreviations are defined in Table 1. See Fig. 2 caption for details of data presentation.

had been logged during the first of 4 yr of staggered harvesting in WS1 (Halpern 1987). This expansion was followed by dramatic, but temporary, release of the residual trailing subshrub *Whipplea modesta* and subsequent recovery of the initial dominant *Polystichum munitum*. In contrast, heavily burned sites were persistently dominated by invaders: initially by annuals (e.g., *Senecio sylvaticus, E. paniculatum,* and *Montia sibirica*), secondarily by biennials and small-statured perennials (e.g., *Agoseris* spp., *Anaphalis margaritacea,* and *Rubus leucodermis*), and subsequently by tall, woody perennials (e.g., *Ceanothus velutinus, C. sanguineus,* and *Rubus parviflorus*). Although subordinate forest herbs were also released, understory dominants were greatly reduced (e.g., *Polystichum munitum*) or eliminated (e.g., *Tsuga heterophylla*).

2. *Undisturbed vs. lightly burned sites.*—Undisturbed community samples on WS1 maintained their initial floristic character through time (Fig. 5A). Successional trajectories are variously directed, occupying relatively small, discrete areas within the ordination field. There is little evidence for a distinct temporal or environmental gradient, in contrast with the response of communities to the average disturbance regime (Fig. 2A). Although the principal ordination axes are complex, plant communities remain well segregated by floristic differences.

Two principal trends account for these patterns. First, invading species, most noticeably the fugitive annuals, played a minor role on undisturbed sites. Second, initial community dominants persisted through disturbance and generally recovered to initial abundance.

TABLE 2. Relative resistance and resilience measures on Watershed 1, derived from Euclidean distances (ED) between pre- and postdisturbance samples in a two-dimensional DCA ordination space. Distances are in standard deviation units.

	Number of plots	Maximum ED (SD units)	Relative resistance (rank)	ED at final sampling (SD units)	Relative resilience (rank)
A) Soil disturbance classes					
Undisturbed	11	1.63	1	0.87	1
Disturbed–Unburned	40	2.56	2	1.47	2
Lightly burned	70	3.00	3	1.74	3
Heavily burned	10	3.51	4	2.24	4
B) Plant communities					
Corylus–Gaultheria	12	2.60	4	0.82	4
Rhododendron–Gaultheria	20	2.39	2	0.68	2
Acer–Gaultheria	7	2.59	3	0.71	3
Acer–Berberis	34	2.76	5	1.14	6
Coptis	23	3.16	6	1.06	5
Polystichum	32	2.20	1	0.61	1
C) Undisturbed sites					
Corylus–Gaultheria	1	1.72	5	0.92	5
Rhododendron–Gaultheria	3	0.96	2	0.41	3
Acer–Berberis	2	0.70	1	0.56	4
Coptis	3	1.11	3	0.13	1
Polystichum	2	1.57	4	0.33	2
D) Lightly burned sites					
Corylus–Gaultheria	8	2.79	3	1.80	3
Rhododendron–Gaultheria	12	2.42	1	0.93	1
Acer–Gaultheria	4	2.56	2	1.50	2
Acer–Berberis	20	3.30	5	2.03	5
Coptis	8	4.47	6	3.52	6
Polystichum	17	2.99	4	1.90	4

In contrast, where soils were lightly burned on WS1, community composition changed profoundly in response to fire. Burning resulted in persistently reduced cover of many forest residuals, and it initiated seres dominated by invading species. Within the ordination, predisturbance samples (hatched area, Fig. 5B) are aligned along Axis 2, roughly coinciding with a gradient of available moisture. After disturbance, however, community trajectories briefly converge (stippled area, Fig. 5B) due to rapid and pervasive establishment of the invading annuals *Senecio sylvaticus* and *Epilobium paniculatum* in response to burning. Trajectories subsequently diverge as communities displayed rather distinct patterns of development. For example, an otherwise uncommon suite of annual (e.g., *Conyza canadensis*) and perennial species (*Vicia americana* and *Arctostaphylos columbiana*) invaded the *Acer–Gaultheria* community, whereas other uncommon perennials (e.g., *Equisetum arvense, Epilobium watsonii,* and *Ribes* spp.) colonized the *Coptis* community. The recovery of original community composition on WS1 was slower on lightly burned (Fig. 5B) than on undisturbed sites (Fig. 5A), as indicated by the distances separating predisturbance and final samples.

Successional patterns on disturbed–unburned sites (not shown) were intermediate to those on undisturbed and lightly burned sites. In addition, successional trends on heavily burned sites (not shown) indicate stronger

convergence of community composition following burning and poorer long-term recovery than on lightly burned sites.

Measures of resistance and resilience

The degree to which community composition changes and recovers after disturbance may depend on characteristics of the resident assemblage and of the perturbation itself. To illustrate how disturbance intensity and initial composition influence community resistance and resilience, I present four examples from WS1. For brevity, I do not examine the corresponding patterns for WS3, although similar relationships may be derived directly from the WS3 ordinations.

Intensity of disturbance. — Both resistance and resilience varied inversely with the intensity of disturbance (Table 2A). Resistance to disturbance declines with the loss of aboveground structures. Within *Pseudotsuga* understories, loss of canopy cover appears directly related to burning severity. Although species such as *Polystichum munitum* commonly survive intense fire, aboveground structures may be absent for several years following burning (Haeussler and Coates 1986). Resistance also decreases with early establishment of invading species. In these systems, the importance of wind-dispersed annuals is enhanced by disturbance, since the availability of germination sites on mineral soil increases with fire severity. Further, the high fer-

tility of recently burned soils promotes establishment of fugitive species such as *Senecio sylvaticus* (West and Chilcote 1968). Thus, the decline in resistance with disturbance intensity encompasses not only loss of the initial assemblage, but also invasion of nonresident species.

The resilience, or long-term recovery, of *Pseudotsuga* forest understories is typically dependent on the vegetative spread of surviving individuals because reproduction from seed is poor (Sabhasri 1961, Anderson 1967, Russel 1974, USDA 1974, Haeussler and Coates 1986, Halpern 1987). Although species such as *Acer circinatum* and *Gaultheria shallon* may sprout basally even after heavy burning, recovery is typically slower than on unburned sites. Community resilience also declines with the persistence of invading species. In this study, both the magnitude and the duration of dominance of the principal invading shrubs, *Ceanothus sanguineus* and *C. velutinus,* increased with soil disturbance on WS1. Originating from buried seed, the abundance of *Ceanothus* spp. typically increases with fire severity in response to elevated soil temperatures (Biswell 1961, Gratkowski 1962, Dyrness 1973, Orme and Leege 1976, Conard et al. 1985). At final sampling on WS1, total *Ceanothus* cover ranged from 11% on undisturbed sites to 57% on heavily burned sites (Halpern 1987). Thus, the decline in resilience with disturbance intensity reflected the reduced recovery of initial understory dominants, as well as the greater persistence of invading tall shrub species. However, it is evident in the greater return of disturbance class trajectories on WS3 (Fig. 3B), that historical and stochastic factors (e.g., heterogeneity in the seed bank of *Ceanothus* and in the effect of local frost [Halpern 1987]) may greatly modify the influence of disturbance intensity on resilience.

Plant communities. — Measures of resistance and resilience varied little among plant communities (Table 2B). However, the greatest contrast (between *Coptis* [low] and *Polystichum* or *Rhododendron–Gaultheria* communities [high]) reflected differences in initial composition and structure. Specifically, the *Coptis* community is typified by dense subcanopies of the tree *Tsuga heterophylla,* with combined herb and shrub cover averaging only 14%. Invading species and initially subordinate residuals dominated postdisturbance communities. The limited abundance of understory dominants resulted in poor long-term recovery. In contrast, initial understories of the *Polystichum* and *Rhododendron–Gaultheria* communities are richer and more structurally complex, with combined herb and shrub cover averaging 86 and 102%, respectively. Although invaders briefly dominated the postdisturbance flora in both communities, residuals were also abundant. Surviving herbs and shrubs served as centers for vegetative expansion, promoting relatively rapid community recovery.

The measures of resistance and resilience presented above portray the response of communities to the average level of disturbance. Among individual soil disturbance classes, however, community responses varied dramatically. This heterogeneity reflects changes in the response of major residual and invading species along the disturbance gradient. On undisturbed sites, for example, resistance of the *Coptis* community was intermediate and its resilience was high (Table 2C). Surviving *Tsuga heterophylla* quickly reestablished a dense understory tree canopy, largely preempting annual and perennial invaders. In contrast, resistance and resilience were relatively low for lightly burned sites in the *Coptis* community (Table 2D). Seral communities were dominated by invading species, displaying enhanced establishment on burned soils, and by initially uncommon forest residuals that were released from competition. Without a well-developed residual flora, long-term recovery on burned *Coptis* sites may require canopy closure to eliminate perennial invaders. However, reestablishment of the *Tsuga heterophylla* subcanopy will be slower than on undisturbed sites, as reproduction must be from seed.

CONCLUSIONS

Early successional patterns in this study support the growing number of models that incorporate both deterministic factors and chance to explain alternate pathways of succession (e.g., Lyon and Stickney 1976, Cattelino et al. 1979, MacMahon 1980, Noble and Slatyer 1980, Morgan and Neuenschwander 1985, Olson 1985, Steinhorst 1985). The deterministic basis of these models lies in the life history characteristics of the available species (e.g., modes of species persistence or reproduction) and in the competitive relationships of species following disturbance. In *Pseudotsuga* forests, predictable features of early succession are also founded in the life history traits of major understory species, particularly in their ability to resprout and expand vegetatively following fire. As a result, communities exhibited an inherent tendency to return toward original composition. Moreover, successional trajectories in ordination space largely remained ordered along an initial moisture gradient, suggesting that the influences of initial species composition and local environment may persist through catastrophic disturbance.

The stochastic component of successional models commonly includes variation in the timing, intensity, or frequency of disturbance, in the availability of species, or in the local environment (e.g., Cattelino et al. 1979, MacMahon 1980, Noble and Slatyer 1980, Morgan and Neuenschwander 1985, Olson 1985, Steinhorst 1985). In this study, multiple paths of succession were largely the result of variation in the intensity of logging and burning disturbance. Alternate successional pathways reflected the disturbance gradient not only in differences in the immediate response of initial vegetation and buried seed, but also in subsequent effects asso-

ciated with a heterogeneous postdisturbance environment (e.g., with respect to nutrient pools or germination sites). In addition, watershed-level differences in the long-term response to this gradient illustrate the potential modifying influence of historical, stochastic, and environmental factors on successional pathways that are largely governed by disturbance intensity (Halpern 1987, *in press*).

The persistence of community composition in *Pseudotsuga* understories is a property other authors have referred to as stability (Holling 1973, May 1973, Orians 1975), adjustment stability (Sutherland 1981, Connell and Sousa 1983), resilience (Westman 1978, 1985, Pimm 1984, Keeley 1986, Westman and O'Leary 1986), or elasticity (Cairns and Dickson 1977). Theoretical studies have focused on the relationship between the structural and functional properties of ecosystems and their stability (e.g., Margalef 1969, Odum 1969, Holling 1973, May 1973, Orians 1975, Harrison 1979, Pimm 1984). However, results of empirical studies (e.g., Smedes and Hurd 1981, Sutherland 1981, Leps et al. 1982, Dethier 1984, Turner 1985, Westman and O'Leary 1986, Malanson and Trabaud 1987) suggest that community stability largely depends on properties of the component species rather than on emergent properties of the system itself. That is, community stability may simply reflect the ability of resident species to resist change, or, if altered by disturbance, their ability to readjust or recover. Rapid compositional recovery following fire has been described for many terrestial ecosystems in which the regeneration of species derives from either surviving individuals or from a persistent seed bank (e.g., Hanes 1971, Naveh 1975, Black and Bliss 1978, Viereck and Dyrness 1979, Trabaud and Lepart 1980, Gill 1981, Mallik and Gimingham 1983, Christensen 1985, Keeley 1986, Westman and O'Leary 1986, Malanson and Trabaud 1987). The widespread stability of *Pseudotsuga* understory communities is founded in the ability of dominant herb and shrub species to resprout from subterranean structures following even intense fire. The degree to which the life history traits of resident species may confer stability on a community was evident in comparing the average resistance and resilience of the depauperate *Coptis* community (dominated by regenerating *Tsuga heterophylla*) with that of the well-developed *Polystichum* and *Rhododendron–Gaultheria* types.

However, the relationship between community stability and species' life histories is complex. For example, the recovery patterns of the *Coptis* community on undisturbed vs. lightly burned sites suggests that the nonlinear responses of key species (e.g., *Tsuga heterophylla*) may shift the relative stability of communities along a disturbance gradient. Large-scale stochastic or historical phenomena that promote the recovery of initial species or the limited establishment or elimination of long-lived colonizers, may also affect community stability. On WS3, for example, the paucity

of *Ceanothus sanguineus* and the dramatic decline of *C. velutinus,* suggest that seed bank distributions and local climatic fluctuations may enhance community resilience. Further, small-scale stochastic factors or random species variation may influence community responses at a local level. Loss of understory dominants on undisturbed soils or persistent release of initially subordinate species may modify the relationship between species' life histories and community persistence (Halpern 1987). Thus, stability at the plot, rather than at the community, level is particularly sensitive to random events and to small-scale variation manifested in the local extinction or atypical expansion of species (see also Sutherland 1981, Connell and Sousa 1983).

In recent years, an appreciation has emerged for the interaction of deterministic and stochastic factors in producing alternate successional pathways. Extending the analysis of pathways by examining the resistance and resilience of communities has shown that species' life histories, stand history, and chance also influence community stability.

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