SPECIES PAIRWISE ASSOCIATIONS OVER NINE YEARS OF SECONDARY

SUCCESSION: ASSESSING ALTERNATIVE EXPLANATIONS

AND SUCCESSIONAL MECHANISMS

by

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ABSTRACT

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The importance and mechanisms of species interactions are undetermined in most successional systems. I used correlations and null modeling to detect pairwise species associations between 33 plant species in the first nine years of secondary succession after logging and burning in a western Oregon Cascade forest. I tested for correlations between each species and soil nutrients, nonvegetative ground cover, and surrounding vegetation. More positive than negative associations were found at all sampling times. The proportion of positive associations decreased and negative associations increased through time. Up to 42% of associations at a sampling time were explicable by shared positive correlations with surrounding vegetation. One dominant shrub species, *Berberis nervosa*, may be primarily responsible for the decline of four early seral species. The associations indicated diffuse facilitation is of primary importance in the stressful early successional environment, and microsite availability and interspecific competition become more important later.

ACKNOWLEDGMENTS

Jim Haefner spent much patience, perseverance, and good humor motivating and training me in my thesis work, classes, lab meetings, and teaching roles. My other committee members, Jim MacMahon and Richard Inouye, asked the right questions at the right times.

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My mother Dorothy Rozzell and sisters Sheri and Shara contributed years of moral support and perspective. Happily, the fellow graduate students, friends, and companions of many species who contributed similarly are too numerous to mention here.

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INTRODUCTION

Early work on succession in North America emphasized plant interaction as a driving mechanism of succession and debated the extent and nature of the interactions (e.g. Clements 1916, Gleason 1926, Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1977). More recent and extensive successional studies shifted emphasis to the combination of influences such as plant interactions, plant life histories, disturbance type, biological legacies, and abiotic factors. Knowledge of the relative importance of these variables is crucial to understanding succession, but difficult to obtain. Isolating the variables as they act in concert upon a site is difficult; their importance varies through time and space, and they interact. One important example of interaction between successional factors is the relationship between environmental stress and plant interaction. In more stressful environments, facilitation assumes greater importance (Bertness and Callaway 1994, Callaway 1994, Pugnaire and Haase 1996, Kikvidze and Nakhutsrishvili 1998, Pugnaire and Luque 2001, Callaway et al. 2002). Odum (1969) postulated a gradient of decreasing abiotic stress in succession with increased time since disturbance. As time since disturbance increases, the dominant form of plant interaction influencing a site may shift from facilitation to competition.

Analysis of changing patterns in species associations can indicate the relative importance and types of species interaction through successional time (Aarssen and Turkington 1985, O'Connor and Aarssen 1987, Morris and Wood 1989, Myster and Pickett 1992, del Moral and Wood 1993, Gitay and Wilson 1995, Soro et al. 1999). Species associations are similarly useful to assess the importance of interaction in plant

communities not specifically identified as successional (Grieg-Smith 1952, Rogers 1983, O'Connor and Aarssen 1987, Myster and Pickett 1992, Silvertown and Wilson 1994, Gitay and Wilson 1995, Nuñez et al. 1999, Floren and Linsenmair 2000, Gavilán et al. 2002, Michalet et al. 2002).

The analysis and interpretation of spatial associations are subject to well-known ambiguities (Connor and Simberloff 1979, Schluter 1984). Detection of associations depends on the timing and location of sampling, and may be merely coincidental (Gleason 1926, Whittaker 1957, Hastings 1987, Austin and Smith 1989). Even when an association is observed consistently over time or space, the underlying mechanism for the association is not revealed by study of the spatial pattern alone (Connor and Simberloff 1979, 1984, Schluter 1984). Positive spatial associations may result from factors such as the ubiquity of species due to dispersal success, shared responses to environmental conditions, or facilitative interaction between species.   Negative spatial associations may result from rarity or dispersal limitations of species, differing responses to environmental conditions, or competitive interaction. Ecologists are often forced to intuit among these potential explanations due to lack of evidence. In a few instances, correlation has been used to examine pairwise associations and variables that might explain the associations. Maguire and Forman (1983) looked for associations between species and correlations with possible explanatory variables (soil pH, soil moisture, light intensity, total herb and tree seedling cover) in hemlock-hardwood forests. Thomson et al. (1996) tested the correlation between adult and seedling lilies as well as the relationships of both with soil moisture, soil rockiness, and pocket gopher activity. Albrecht and Gotelli (2001) tested correlations between ant species and between the species and air temperature. With

sufficiently detailed data on abiotic and biotic factors and previous studies of species

ecology, it becomes possible to evaluate effectively the alternative explanations for

associations (Rejmánek and Lepš 1996).

This paper analyzes pairwise plant species associations through nine years of

early secondary succession after clearcutting and slashburning in an Oregon forest. I

analyzed data from fifteen post-disturbance sampling times, allowing assessment of

recurring associations. I analyzed species correlations with nonvegetative ground cover,

soil nutrients, and surrounding vegetation to find alternative explanations for spatial

associations. I also performed association tests with a null model specifically constrained

to incorporate site heterogeneity and relative abundance of the species, and to test for

spatial patterning not attributable to these two causes (Gotelli and Graves 1996).

I address three fundamental questions. How do the importance and types of

species interactions, as reflected in associations, change over time? How important are

environmental factors such as nonvegetative ground cover, total surrounding vegetation,

and soil nutrients in explaining species distributions and associations? Does the pattern

of associations, combined with previously documented ecology of the species, indicate

that decline of early seral species is attributable to species interaction?

METHODS

Site and data description

The 4-hectare site is located on the west side of the Cascade Range in Oregon, at 730 m elevation on a gentle, east-facing slope. The surrounding landscape is a mosaic of mature and old-growth forest, young plantations, and recent clearcuts of varying age (Halpern et al. 1997). The climate is maritime with mild, wet winters and warm, dry summers (Bierlmaier and McKee 1989). The pre-disturbance community consisted of mature forest dominated by *Pseudotsuga menziesii*, with *Tsuga heterophylla* and *Thuja plicata* common in the lower canopy. The understory was dominated by the shrubs *Gaultheria shallon*, *Rhododendron macrophyllum*, and *Berberis nervosa*.

Prior to logging at the site, twenty-five blocks (ca. 11 x 11 m) were established, each containing nine 1-m2 plots, separated from other plots by approximately 2 m. Pre-disturbance sampling data were collected for all plots in 1990. The site was clear-cut and slash-burned in 1991. Investigators recorded cover percentages for all species in each plot. As of 2003, cover sampling is ongoing once annually in the summer; the dataset used for this study extends to 1999. For the first five years after disturbance, sampling was conducted two or three times per growing season.

Soil samples were collected within 0.5 m of 135 plots at the predisturbance sampling time, and once annually for the following three years. Samples were analyzed for total and extractable nitrogen and total carbon (for further details of soil study see Antos et al. 2003).

Eight experimental treatments and one control plot were monitored in each block. Experimental treatments included removal of one or two species, or removal of all plants

within the plot excepting one or two species. Removals were conducted seasonally or

annually for the duration of the study. Experimental removals of one or two species had

little observable effect. Species were chosen for removal based on their dominance in

previous studies (Halpern 1989), but did not necessarily reach equivalent dominance on

this site. Often, the removal species were not present to be weeded from the removal

plots, or occurred only rarely across the entire site. For instance, Yerkes (1958) reported

that *Epilobium angustifolium* and *Senecio sylvaticus* represented nearly 70 percent of

herbaceous cover for the first two years after disturbance, and on plots in this study they

represented less than 25 percent of herbaceous cover during that time. Because the one-

species or two-species removal treatments showed minimal effects, they were included

with the control plots in the analysis. When testing for associations involving a removal

species, removal plots were excluded from the analysis.   The number of plots analyzed

also differed with sampling time because some removal treatments were abandoned in

later years when removal species had largely disappeared from the site (Table 1).

One hundred twenty vascular species were observed on the site. To make the

species-level analysis manageable, I tested for associations between all possible pairs of

thirty-three focal species that were common on the site through some or all of the study

(Table 2). The 33 focal species accounted for over 93% of the occurrences recorded at

the site and represented 94% of the biomass present on the site in 1999. Halpern (1989)

assigned species to groups according to life history, morphology, and seral status.

Species common in the forest before disturbance are described as "residuals" and species

generally appearing only after severe disturbance are "colonizers." Species displaying

peak abundance in the first five years following disturbance are described in this paper

Table 1. Number of plots used for analysis of removal species and all other species at each sampling time. Sampling time is expressed in years relative to disturbance, with the predisturbance sampling represented at the time of "-1." There were 25 control plots, 75 community removal plots, and 125 plots with one or two species removed. Community removal plots were not used in any analyses after treatments began.

Sampling Time (years)	Species	Number of Plots
-1	All	225
0.8 – 5.2	All (except removal species)	150
	Rubus ursinus, Berberis nervosa, Gaultheria shallon	125
	Senecio sylvaticus, Epilobium angustifolium	100
6	All (except removal species)	125
	S. sylvaticus, R. ursinus, B. nervosa, G. shallon	100
	E. angustifolium	75
7	All (except removal species), *S. sylvaticus*	100
	E. angustifolium, R. ursinus, B. nervosa, G. shallon	75
8, 9	All (except removal species), *S. sylvaticus, E. angustifolium*	75
	R. ursinus, B. nervosa, G. shallon	50

as "early-seral" species and those displaying peak abundance later are described as "mid-seral," even though most species were present to some extent throughout the sampling period.

Analytical methods

I used two analyses to address the questions - a correlation of cover abundances and a null modeling procedure.

Correlation of species abundance measures

I tested the correlation of species cover percentages between all possible species pairs at each sampling time. Species were included when they were observed on at least five plots. Because sampling distributions varied by species and were not normally distributed, I used Spearman rank correlation to test for associations between pairs of

Table 2. Focal species and classifications. Group classifications are from Halpern (1989), with modification. Life histories are perennial (P) or annual (A). Seral groups are residual (R) or colonizers (C). The "colonizer" seral species were termed "invasives" in Halpern (1989).

Species	Family	Life history	Seral group	Growth form
Pseudotsuga menziesii	Pinaceae	P	R	Tree
Thuja plicata	Cupressaceae	P	R	Tree
Tsuga heterophylla	Pinaceae	P	R	Tree
Rubus ursinus	Rosaceae	P	R	Subshrub
Whipplea modesta	Hydrangeaceae	P	R	Subshrub
Arctostaphylos columbiana	Ericaceae	P	C	Shrub
Berberis nervosa	Berberidaceae	P	R	Shrub
Ceanothus sanguineus	Rhamnaceae	P	C	Shrub
Gaultheria shallon	Ericaceae	P	R	Shrub
Rhododendron macrophyllum	Ericaceae	P	R	Shrub
Rubus parviflorus	Rosaceae	P	R	Shrub
Agoseris grandiflora	Asteraceae	P	C	Herb
Anaphalis margaritacea	Asteraceae	P	C	Herb
Cirsium vulgare	Asteraceae	A	C	Herb
Conyza canadensis	Asteraceae	A	C	Herb
Collomia heterophylla	Polemoniaceae	A	C	Herb
Crepis capillaris	Asteraceae	A	C	Herb
Epilobium angustifolium	Onagraceae	P	C	Herb
Epilobium paniculatum	Onagraceae	A	C	Herb
Epilobium watsonii	Onagraceae	P	C	Herb
Fragaria vesca	Rosaceae	P	C	Herb
Gnaphalium microcephalum	Asteraceae	P	C	Herb
Hieracium albiflorum	Asteraceae	P	R	Herb
Lactuca serriola	Asteraceae	A	C	Herb
Lotus crassifolius	Fabaceae	P	C	Herb
Lupinus latifolius	Fabaceae	P	R	Herb
Madia gracilis	Asteraceae	A	C	Herb
Pteridium aquilinum	Dennstaedtiaceae	P	R	Herb
Senecio sylvaticus	Asteraceae	A	C	Herb
Trientalis latifolia	Primulaceae	P	R	Herb
Viola sempervirens	Violaceae	P	R	Herb
Deschampsia elongata	Poaceae	P	C	Grass
Elymus glaucus	Poaceae	P	C	Grass

species (SAS Institute 1998). In the Spearman rank correlation, species abundances are transformed to ranks, and the Pearson product moment correlation is then performed on the paired columns of ranks for all possible pairs of species. Spearman rank correlation or Pearson correlation have been used to investigate temporal trends in associations of plant species in deciduous forests (Rogers 1983), abandoned sand quarries (O'Connor and Aarssen 1987), oldfields (Ogle and Reiners 2002), and in tall tussock grasslands (Gitay and Wilson 1995).

This analysis required many non-independent tests to include all possible pairs of species at each time. It was inevitable that a number of the tests appeared statistically "significant" due to Type I error. My interest lay in describing the changing sets of associations between species, rather than testing a hypothesis about each association. This reduced the need to apply adjustments to the significance level (Myster and Pickett 1992, Stewart-Oaten 1995). I use $\alpha = 0.025$ at each tail of the probability curve, and discuss all associations meeting this cutoff value as "significant." The question of Type I error is addressed throughout the presentation of results and interpretation. If an association appears significant due to Type I error, the probability of it appearing so repeatedly over time is much reduced. Focusing on associations that recur through time, as described below, should avoid over-interpretation of associations that appear significant due to chance alone.

Null model analysis

Patterns of interspecific association are heavily influenced by ecological factors other than interspecific interaction (Simberloff and Connor 1979). Ecological factors of major influence include plot heterogeneity, species dispersal abilities and relative

abundance of species in the surrounding forest and on the site itself (Jackson et al. 1989).

Creating simulated communities incorporating these factors allows comparison of

associations in the simulated communities with associations in the observed community

(Gotelli and Graves 1996). When associations in the observed community appear

significantly different from associations in the simulated communities, it should be from

patterns of co-occurrence not attributable to the relative abundance or dispersal

effectiveness of the species, or heterogeneity among plots. I used a null modeling

process to create simulated communities according to constraints reflecting relative

species frequencies and plot heterogeneity. Constraints on species frequencies correct

for mathematical bias toward finding associations in high-frequency species, and can

reflect species dispersal limitations. Similar null modeling procedures have been used to

examine associations in plant and animal communities (e.g. Rice and Belland 1982,

Wilson 1988, Silvertown and Wilson 1994, Wołek 1997, Bartha and Kertész 1998,

Gotelli 2000, Virágh et al. 2000, Peres-Neto et al. 2001, Gotelli and McCabe 2002). The

null modeling procedure and consistency with previous null model use are detailed in

Appendix A.

Assessing patterns to answer the questions

    Changes in associations

To monitor the sitewide degree of association over time, I quantified associations

according to the number detected at each sampling time as a percentage of the number of

associations possible at the sampling time. For instance, only 15 of the 33 focus species

were present in the predisturbance sampling forest; at this sampling time there were only

105 possible pairwise species combinations. When all 33 species were present later,

there were 528 possible pairwise combinations. Sixteen significant associations are reported as 15% (16/105) in the first year, and 3% (16/528) in later years. To allow comparison with other studies investigating changes in interaction using association analysis over time, I first report all associations, and then in a separate section assign alternative explanations for associations.

Many associations were observed at only one sampling time. These transient associations may appear due to Type I error, or they may reflect species interaction or other distributional influences that only operate during a limited time in the life history of the plant (Callaway and Walker 1997). To focus on the associations that were detectable on the site over longer periods of time, I report a subset of recurring associations. I classified associations as "recurring" if they were statistically significant ($\alpha < 0.05$) in at least 25% of the sampling times, and "transient" if they were significant at fewer sampling times. It was possible for a species to be common on the site for as short a period as two years and still be included in recurring associations (four of the 16 sampling times), since sampling was done at least twice per year for the first five years after disturbance.

Alternative explanations for species associations

In addition to the pairwise species analysis, I also tested correlations between the plot cover of each species and several other variables. I correlated the abundances of each species with the percent coverage of coarse woody debris, litter, and bare ground within the plots, and with three soil nutrients (extractable and total nitrogen and total carbon) sampled directly outside the plots. I tested the relationship between each species

and the surrounding plant community by correlating the cover of each species and the
summed cover of all other vegetation in each plot.

     To assess the relative importance of species interaction and other factors in
structuring associations, I adopted a conservative approach favoring explanations
involving abiotic factors over explanations involving species interactions (Strong et al.
1979). Whenever both species involved in a significant association were also correlated
with another variable, the association was classified as explicable by the variable. For
instance, if *Berberis nervosa* and *Trientalis latifolia* were positively associated two years
after disturbance, and both showed a positive correlation with litter cover at that time, I
characterized the association as explicable by the shared positive correlation with litter.
If *B. nervosa* and *Crepis capillaris* were negatively associated at the same time, and *C.*
capillaris showed a negative correlation with litter cover, then the association was
explicable by their opposite correlations with litter.

     I also focused on the subset of recurring associations and alternative explanations.
If both species in a recurring association shared correlations at four or more sampling
times with a nonvegetative ground cover variable or total surrounding vegetation, then
the association was classified as explicable by that variable. Fig. 1 illustrates a
theoretical set of recurring associations and the subsets of associations explicable by
variables other than species interaction. The larger ellipse on the left represents
associations found with correlation, and the ellipse on the right represents associations
detected by null modeling analysis. The null modeling procedure (see Appendix A) was
designed to find associations not attributable to site heterogeneity, or species' relative
abundances. Recurring associations found with both correlation analysis and with null

modeling, without alternative explanations from shared environmental correlations, are most likely to involve species interaction (hatched area, Fig. 1).

Mechanisms of successional change

Interactions involving one early-seral and one mid-seral species are of particular interest, since I am interested in finding mechanisms for species replacements in succession. I compare the trends in recurring associations of the dominant species with the ecology of these species observed in prior studies.
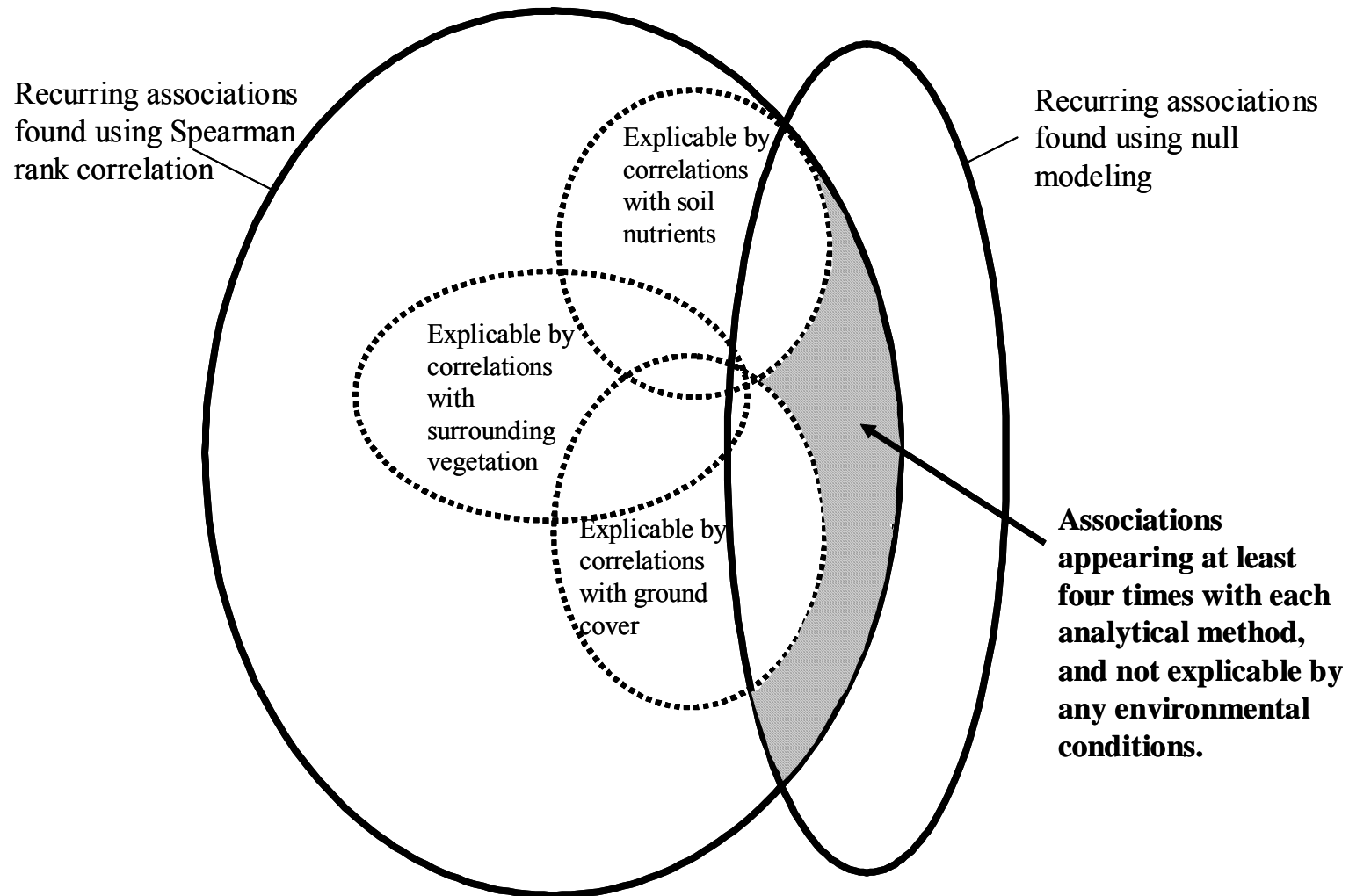
Fig. 1. Recurring associations found using two tests, and possible alternative explanations for the associations. Recurring associations found using both correlation and null modeling, and not explicable by measured environmental variables, are represented by the crosshatched area. These associations are more likely to reflect pairwise species interaction.

RESULTS

General successional trends

Before disturbance, mean summed plot cover of understory species (all plants under 1.4 m in height) was 130% (Fig. 2). Logging and burning removed most of the aboveground vegetation, but many species maintained living underground parts or quickly recolonized. Eight months after the burn, mean plot cover was only 4%, but 47 species were observed. Mean vegetation cover, litter cover and bare ground changed rapidly in the first two to three years after disturbance, and changed very little after year four. These trends are consistent with earlier observations at nearby sites (Yerkes 1958, Halpern 1989). The first and second years after disturbance appeared to be the times of highest abiotic stress, with little vegetative or litter cover on the plots to ameliorate harsh summer environmental conditions. On similar clearcut sites in the Oregon Coast Range, Robinson (1964) recorded air temperatures up to 130º F under first-year clearcut vegetation.

Several colonizing herbs appeared after disturbance, achieved conspicuous peaks in abundance and declined or disappeared from the plots within the nine-year postdisturbance sampling period. The frequency, mean plot cover, and associations of these species are represented in Fig. 3. *Senecio sylvaticus* peaked in the second year, and then largely disappeared by the fifth year, while *Conyza canadensis* and *Lactuca serriola* were present in over three quarters of the plots in the fourth year and disappeared by the ninth year. Other species peaking and then declining conspicuously in cover or frequency were *Cirsium vulgare*, *Crepis capillaris*, *Epilobium paniculatum, Gnaphalium microcephalum,* and *Madia gracilis*. Species increasing markedly in
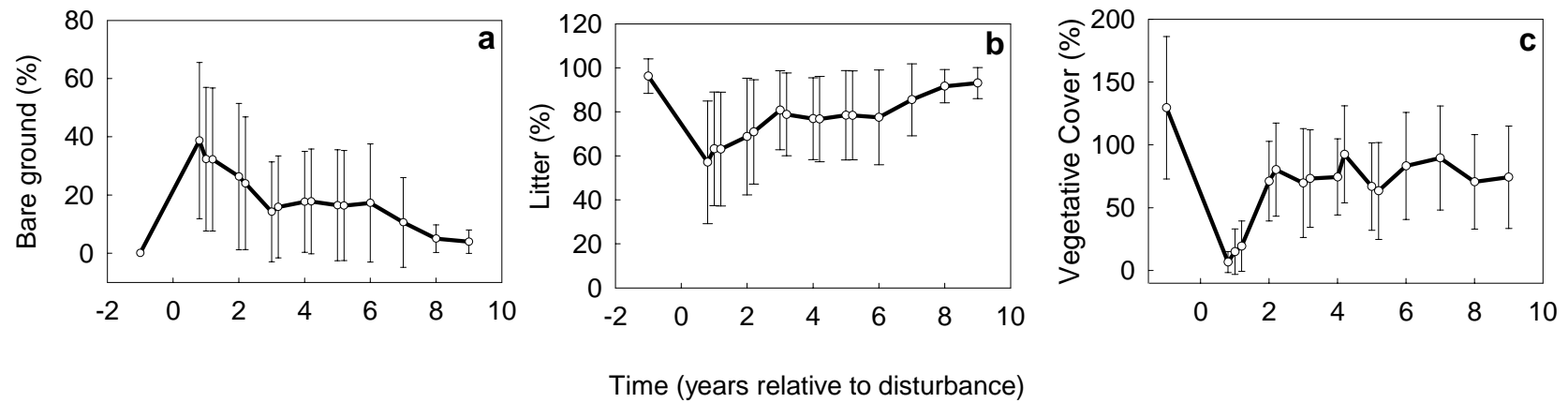
Fig. 2. General successional trends. Mean and standard deviation of a) bare ground, b) plant litter, and c) vegetation as percent cover within 1-m² plots.

Sampling time (years relative to disturbance)
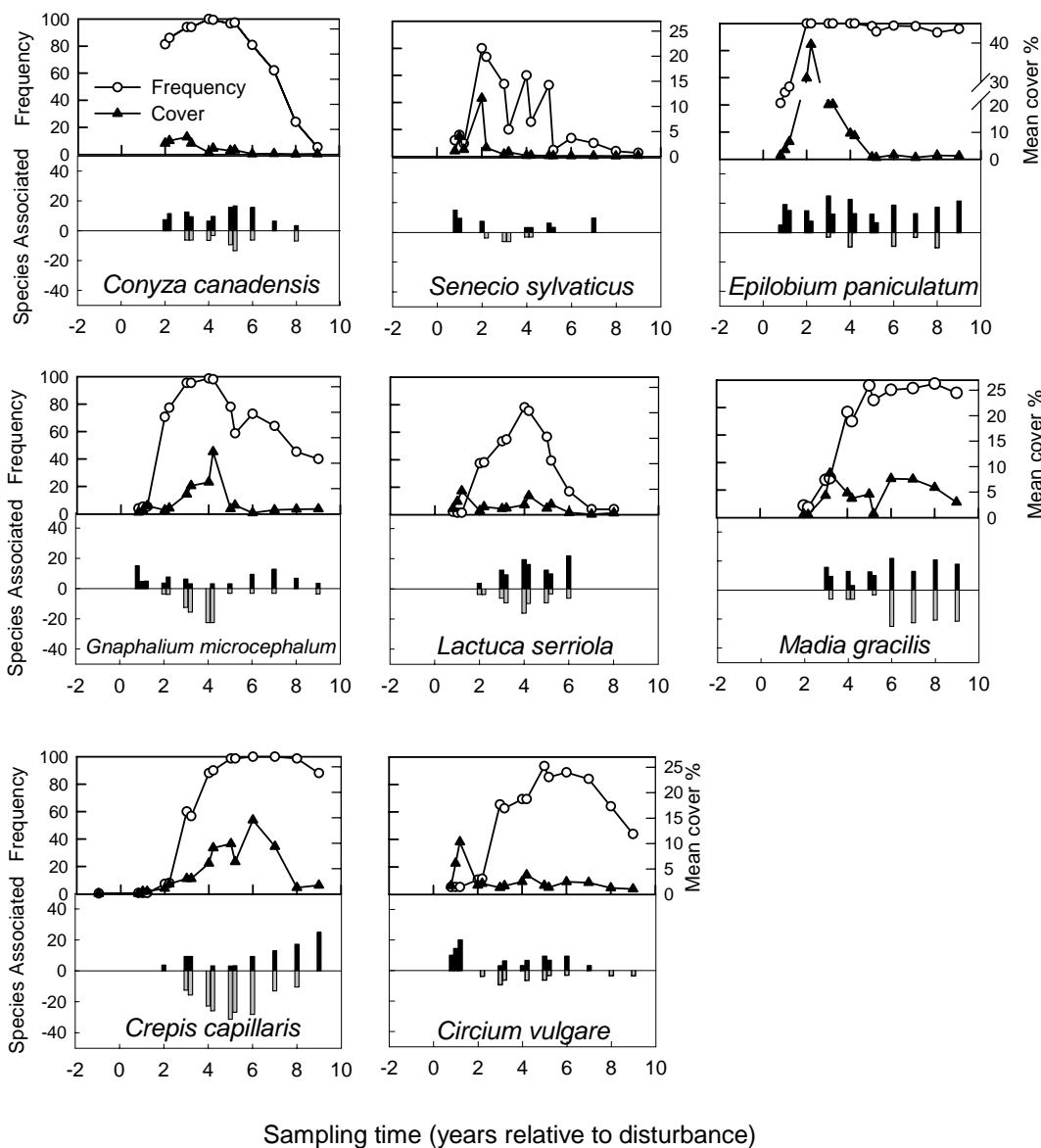
Fig. 3. Frequency, cover, and associations of invasive species attaining peak abundance and declining early in succession. Frequency is represented on the upper left y axis as the percentage of plots sampled at a given sampling time that contained the species. Cover is on the upper right y axis and is the mean cover percentage per m² plot in which the species was present. Associations are presented in the lower graph as the percentage of species present at the sampling time that were significantly associated with the graphed species. The percentage of positively associated species appears above the x axis and the percentage of negatively associated species extends below the x axis.

abundance as the early-seral species declined are likely candidates for species interaction as a driving mechanism for successional change. Candidate species included the shrubs *Berberis nervosa, Gaultheria shallon, Rubus ursinus, Rhododendron macrophyllum, Whipplea modesto,* and the perennial herbs *Lotus crassifolius, Lupinus latifolia,* and *Fragaria vesca* (Fig. 4). Associations of each species (lower panels in Fig. 3-4) are analyzed below to see which are most likely to be interacting.

Changes in associations

A relatively large percentage of tests yielded significant associations in the predisturbance forest (Fig. 5). After disturbance, cover correlations produced significant associations ranging from 9-21% of possible associations at a given time. Null modeling resulted in 4-11% of possible associations showing significance.

There were more positive associations than negative ones at all sampling times with both tests, with one exception in the fourth year after disturbance. Positive associations spiked conspicuously in the first year, and then dropped sharply (Fig. 5b). Positive associations increased again until year 6, and then leveled off and decreased. For the first two years after disturbance, there were almost no negative associations (Fig. 5c). Type I error was expected to create significant negative associations in 2.5% of the possible associations. Negative associations reached a maximum of 7.6% of possible associations in the cover correlations, and showed little change after the fourth year.

Recurring associations

About one half of the species pairs were never significantly associated. Nearly half of the pairs showing significance were only associated at one of the sixteen sampling
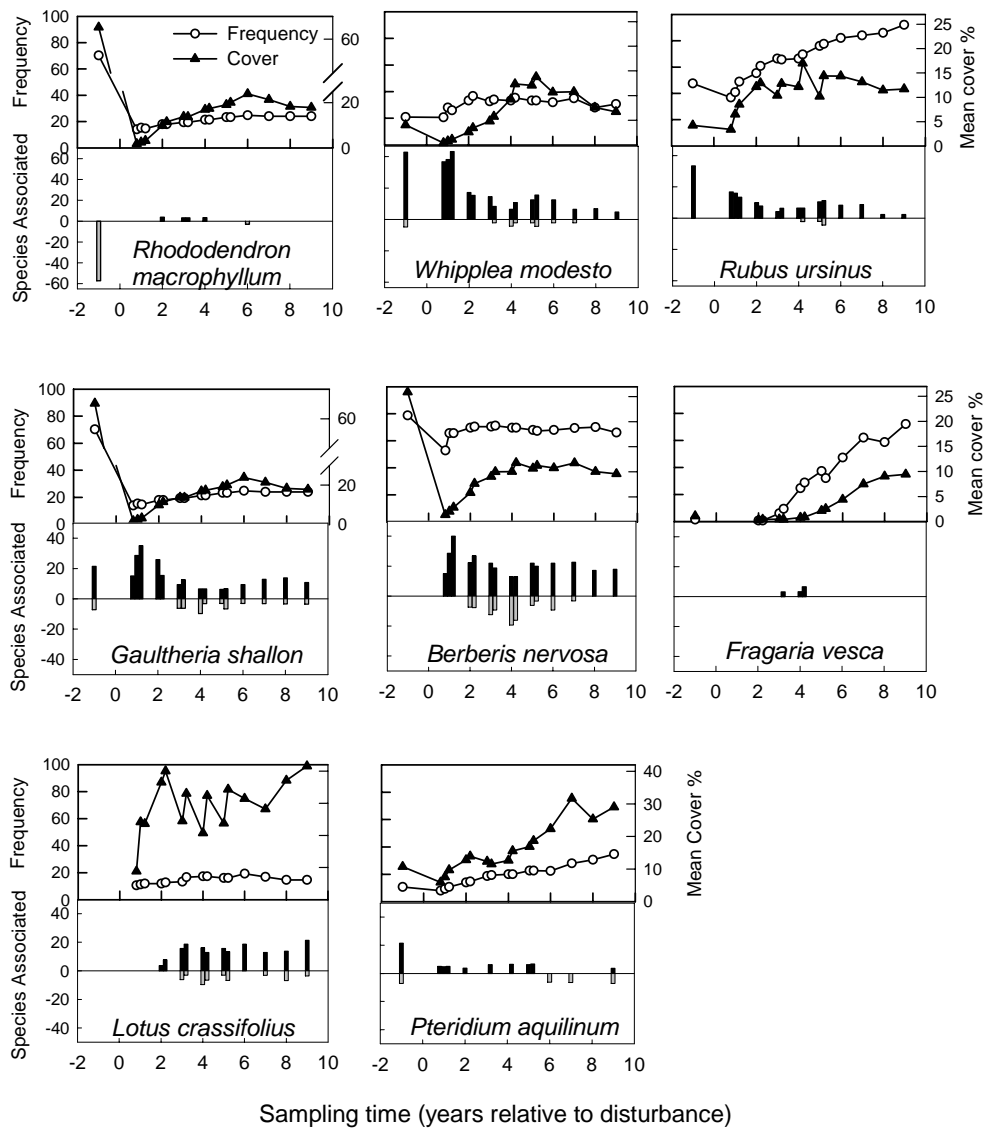
Fig. 4. Frequency, cover, and associations of species with marked increases in abundance during the sampling period. Note differences in Y axes. See Fig. 3 for details.
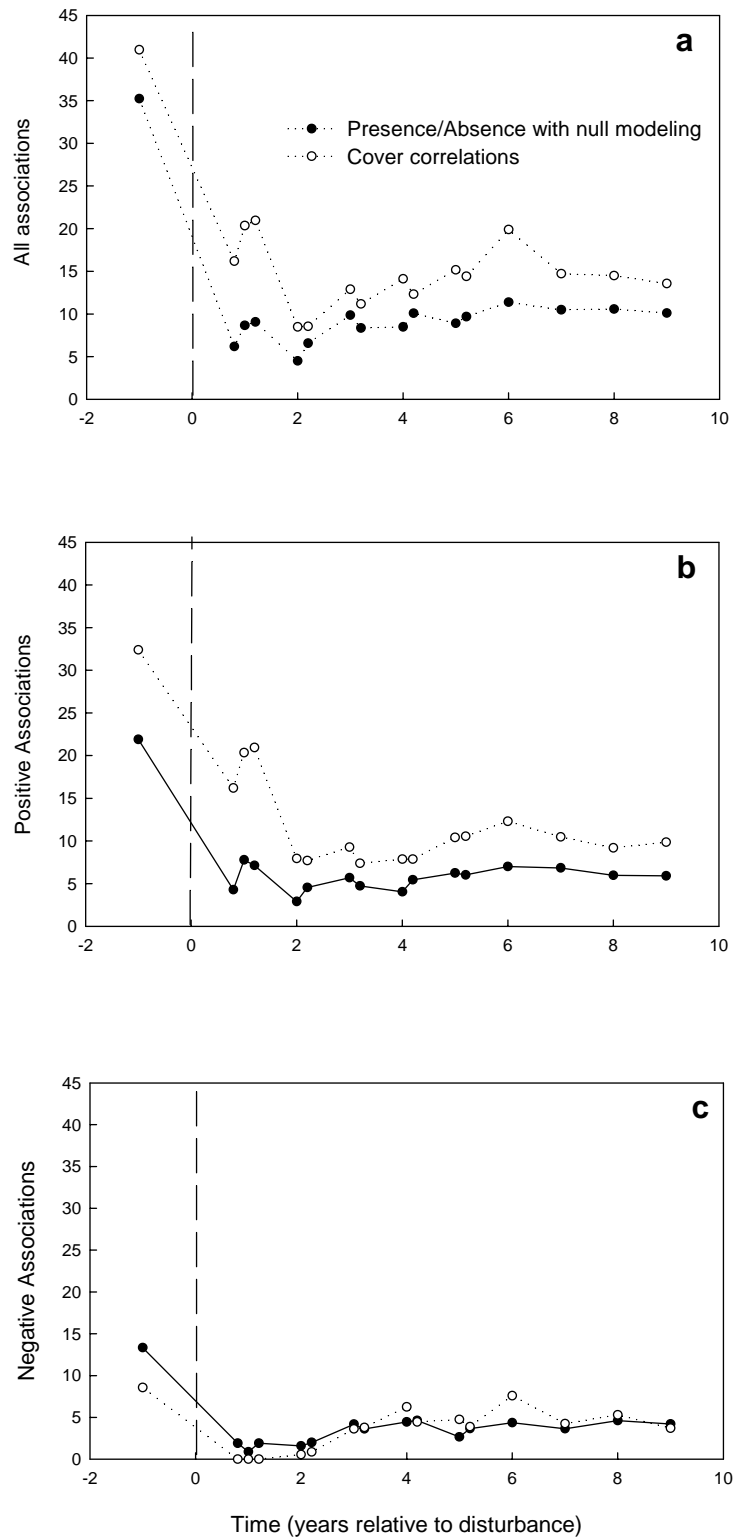
Fig. 5. Significant associations (as percentage of associations possible). Vertical dashed lines emphasize time of disturbance.

times (Fig. 6). Associations appearing significant in four or more sampling times were considered "recurring associations," and were used to assess successional mechanisms. A primary concern was avoiding overrepresentation of perennial plants in recurring associations, and also determining whether temporal autocorrelation was an important sampling influence within growing seasons. However, perennial plants were not more abundantly represented in recurring associations than in all associations, and associations recurred at a one-year interval more often than they recurred within a year. Matrices summarizing recurrences of each pairwise association are in Appendix B.

Alternative explanations for associations

I report overall patterns of species correlations with environmental variables and alternative explanations for associations. I also examine the subset of recurring associations explicable by recurring correlations with plot environmental variables.

Correlations with environmental conditions

Soil samples were collected during predisturbance sampling and once annually for the three years following disturbance. Since there was little change between the second and third year of sampling (Antos et al. 2003), I tested the soil variable measures from the third year with fourth and fifth year species abundances. No species showed significant correlation with soil nutrients before disturbance. At each of the three postdisturbance sampling times, up to 15% of the species present were correlated with one of the three soil nutrients (Table 3). However, the species correlated with soils were generally not involved in significant associations, so few pairwise associations were explicable by soil correlations (Table 4). Due to limited sampling times, the recurrence of soil correlations
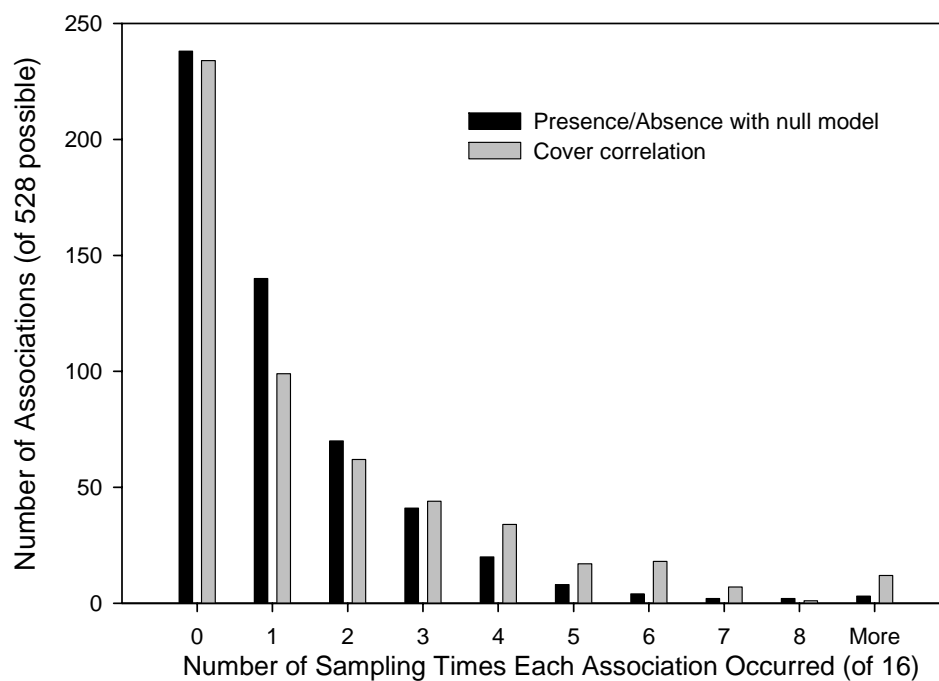
Fig. 6. Recurrence of significant associations. There were 528 possible pairwise combinations of focal species. The figure summarizes the number of times that each of the pairwise associations was found significant, using two different statistical testing procedures. It was possible for an association to be found significant a maximum of sixteen times over the sampling period.

Table 3. Percentage of species present at each time that are significantly correlated with plot environmental conditions. Expected percentage from Type I error is 5%. Total row represents the percentage of all species distributions across all sampling times significantly correlated with the variable. (na, not available due to lack of sampling).

Sampling Time (Years relative to disturbance)	Percent of species correlated with:						
	Surrounding vegetation	Bare ground	Litter	CWD	Total Carbon	Total Nitrogen	Extractable Nitrogen
-1	33	27	13	27	0	0	0
0.8	38	5	5	0	10	5	5
1	36	5	14	9	na	na	na
1.2	33	5	14	5	na	na	na
2	14	0	0	7	4	14	11
2.2	15	7	11	11	na	na	na
3	27	18	15	9	0	15	12
3.2	21	15	12	12	0	12	15
4	22	13	9	19	0	16	16
4.2	22	22	16	9	6	6	16
5	30	30	12	12	3	6	15
5.2	29	19	16	16	3	13	13
6	21	33	18	9	na	na	na
7	9	22	16	9	na	na	na
8	7	23	17	3	na	na	na
9	7	21	14	7	na	na	na
Total	22	17	13	11	na	na	na

Table 4. Percentage of positive and negative associations at each sampling time explicable by a shared correlation with an environmental variable. Time is reported as years relative to disturbance. The "Total" row represents the percentage of associations summed across all sampling times that were explicable by a variable. No negative associations were explicable by shared correlations with soil (na, not available due to lack of sampling; --, no associations explicable because no associated pairs of species both showed correlations with the variable).

Time	Coarse Woody Debris +	Coarse Woody Debris −	Ground Litter +	Ground Litter −	Bare Ground +	Bare Ground −	Total Surrounding Vegetation +	Total Surrounding Vegetation −	Total carbon +	Total nitrogen +	Extractable nitrogen +	Extractable nitrogen −
-1	7	2	--	2	7	5	9	--	--	--	--	--
0.8	--	--	--	--	--	--	41	--	3	--	--	--
1	2	--	--	--	--	--	43	--	na	na	na	na
1.2	--	--	5	--	--	--	34	--	na	na	na	na
2	3	--	--	--	--	--	3	--	--	3	3	3
2.2	3	--	--	--	--	--	3	--	na	na	na	na
3	3	--	9	--	9	1	16	3	--	6	4	4
3.2	2	--	2	--	2	2	5	8	--	3	5	--
4	1	3	1	--	3	--	3	9	--	6	4	1
4.2	--	2	3	--	7	2	7	7	--	--	3	3
5	3	--	1	--	8	--	13	4	--	--	4	--
5.2	--	--	3	--	4	--	19	3	--	1	3	--
6	1	--	3	1	14	11	3	1	na	na	na	na
7	--	--	4	--	11	5	--	--	na	na	na	na
8	--	--	5	5	11	6	--	2	na	na	na	na
9	--	--	4	2	16	2	2	--	na	na	na	na
Total	1	<1	3	1	7	3	11	3	<1	1	2	1

could not be assessed in the same manner as the other environmental variables.

More species abundances were correlated with coarse woody debris (CWD) or plant litter than with any single soil variable, but these two variables did not provide alternative explanations for many pairwise associations (Tables 3 and 4). CWD provides protection for seeds during slash burning, and retains moisture and provides shade, enhancing seedling establishment and plant growth (Hofman 1924, Gray and Spies 1997). CWD may have been relatively unimportant on this site because mean plot cover by CWD averaged less than ten percent at all sampling times, compared to plot averages of 60-98% for litter and up to 40% for bare ground. Litter cover is the least interpretable of the nonvegetative ground cover variables, because litter is the product of the species as well as a variable affecting their distributions. Generally, early-seral weedy annuals were negatively correlated with litter and mid-seral species were positively correlated. This is consistent with an effect in either direction, since later seral species tend to have more robust plant parts that resist decay. The species most likely to demonstrate an association with self-generated litter was *R. macrophyllum* (Whiles et al. 1993), which was positively correlated with litter at eight sampling times. *G. microcephalum*, *C. canadensis*, and *Collomia heterophylla* all demonstrated later negative associations with litter and with each other. All three species were present on more than half the plots at these times, though in very low cover percentages (less than one percent in each plot where present). Up to one third of the species abundances at a sampling time were correlated (either positively or negatively) with bare ground, and bare ground correlations provided an alternative explanation for ten percent of all associations (Totals row in Table 4). Eight

species had recurring correlations with bare ground (Table 5). Four were successional colonizers with bare ground correlations beginning in the third year after disturbance or later, when bare ground for germination was becoming scarce, and a likely limiting factor.

The bare ground and litter readings had a correlation coefficient of -0.94. It was expected that the sets of species correlated with them would be similar or identical, with opposite sign. There were several unexpected differences (Tables 3 and 4). Measures of litter on the site may not have been correlated too closely with species abundances because cover area is not the best representation of litter abundance. Depth of litter, rather than areal coverage, better represents the ability of the litter to retain soil moisture and enhance or impede seedling growth (Hofman 1924, Isaac 1938).

Species abundances were most often correlated with surrounding vegetation cover (Table 3). After disturbance, nearly all correlations between individual species and the surrounding vegetation were positive. The few negative correlations were consistently found for *C. heterophylla*, *C. capillaris*, *G. microcephalum*, *M. gracilis*, and *S. sylvaticus*, all colonizing herbs. The positive correlations with surrounding vegetation decreased conspicuously over time, while the negative correlations increased more slowly. Surrounding vegetation cover provided an alternative explanation for up to 43% of the associations at a sampling time. All the negative associations explicable by significant correlations with surrounding vegetation involved one species positively correlated with surrounding vegetation and another that was negatively correlated.

Ninety-five of the 528 species pairs were significantly associated at least four times using Spearman rank correlation (Fig. 7). When two species in a recurring

Recurring associations
found using Spearman
rank correlation. N = 95

CWD
N=2

Bare
ground
N=6

Litter
N=1

Recurring associations
found using null
modeling. N= 39

Surrounding
vegetation
N = 16

**Associations appearing
at least four times with
each analytical
method, and not
explicable by any
environmental
conditions.
N = 23**
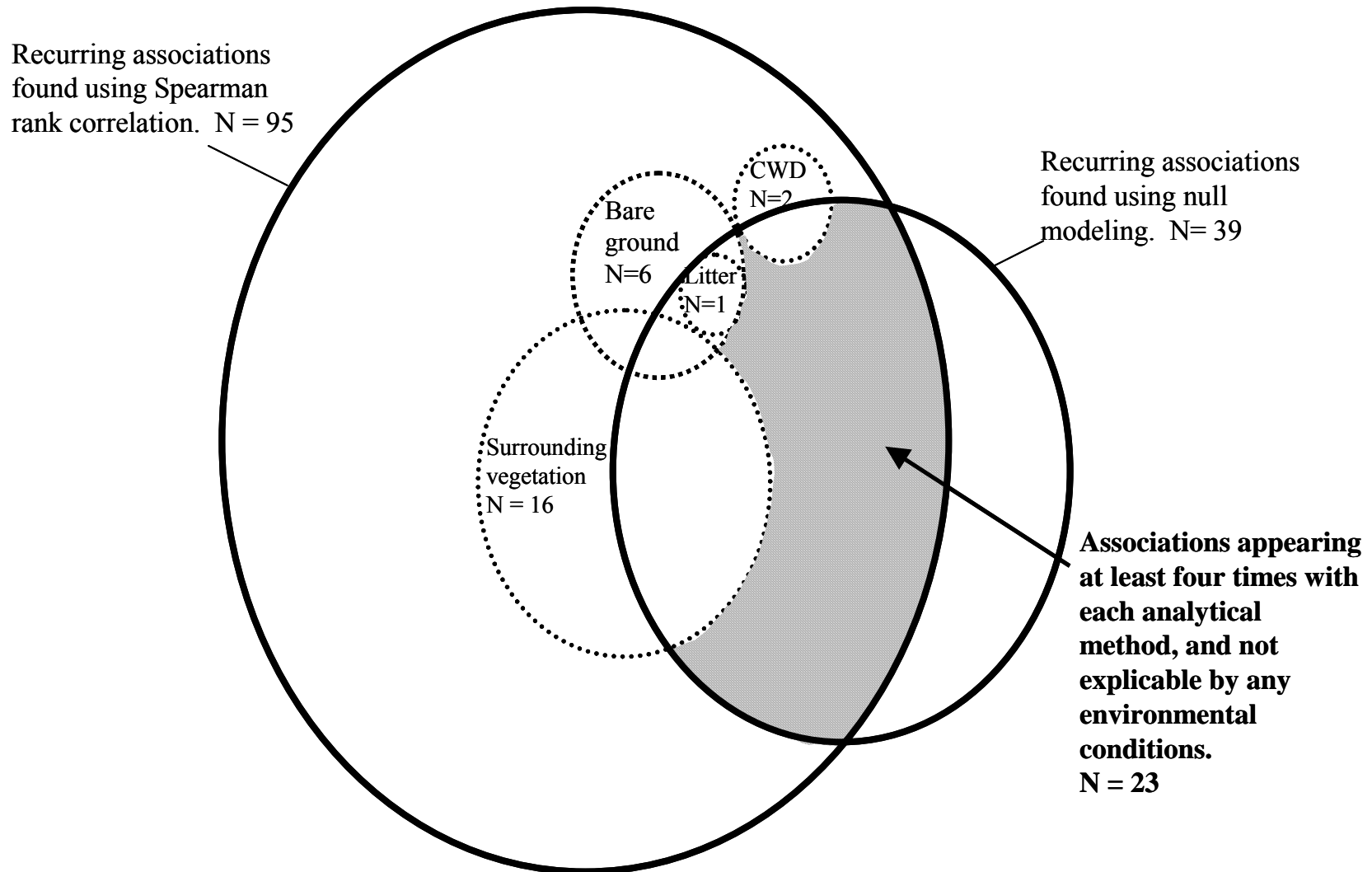
Fig. 7. Proportional representation of the sets of associations identified in Fig. 1. Cross-hatched area represents associations most likely to reflect pairwise interaction. "N" = number of pairwise associations.

Table 5. Species correlated with environmental variables at four or more sampling times.

Species	Type of correlation	Number of sampling times	Seral group
Bare Ground			
Epilobium watsonii	−	6	Colonizer
Berberis nervosa	−	5	Residual
Rhododendron macrophyllum	−	5	Residual
Trientalis latifolia	−	7	Residual
Collomia heterophylla	+	5	Colonizer
Epilobium paniculatum	+	7	Colonizer
Gnaphalium microcephalum	+	4	Colonizer
Madia gracilis	+	5	Colonizer
Litter			
Epilobium watsonii	+	4	Colonizer
Berberis nervosa	+	8	Residual
Rhododendron macrophyllum	+	8	Residual
Rubus ursinus	+	4	Residual
Trientalis latifolia	+	9	Residual
Coarse woody debris			
Berberis nervosa	−	6	Residual
Fragaria vesca	+	4	Colonizer
Gnaphalium microcephalum	+	4	Colonizer
Thuja plicata	+	4	Residual
Surrounding vegetation			
Crepis capillaris	−	6	Colonizer
Gnaphalium microcephalum	−	5	Colonizer
Madia gracilis	−	4	Colonizer
Ceanothus sanguineus	+	6	Colonizer
Epilobium watsonii	+	10	Colonizer
Lotus crassifolius	+	6	Colonizer
Rubus parviflorus	+	6	Colonizer
Rubus ursinus	+	4	Residual
Thuja plicata	+	4	Residual
Trientalis latifolia	+	7	Residual
Viola sempervirens	+	6	Residual
Whipplea modesto	+	11	Residual
Extractable nitrogen			
Lotus crassifolius	+ −	4	Colonizer
Lactuca serriola	−	5	Colonizer
Total nitrogen			
Lotus crassifolius	+	7	Colonizer
Whipplea modesto	+	7	Residual

association were also correlated with the same plot environmental variable at least four times, the association was classified as explicable by that variable (Tables 5 and 6). The most important alternative explanation for recurring associations was shared correlations with surrounding vegetation. Shared correlations with bare ground, litter, and CWD explained a few recurring associations (Table 6). Twenty-three associations recurred in the results of both tests and were not explicable by any shared correlations with environmental variables (Table 7). Fig. 7 illustrates the sets of associations identified in Fig. 1, scaled proportionally to the findings of the study. Of these 23 associations, five were negative, 15 were positive, and three switched signs over time. All the negative associations were between residuals and colonizers. Four of the fifteen positive associations involved nitrogen-fixing species (*Ceanothus sanguineus* or *L. crassifolius*).

Mechanisms of succession

The patterns of decline of early seral species (Fig. 3) may be attributed to life history constraints, changing plot environmental conditions, interaction with another species, or interaction with total surrounding vegetation. Predation or disease may also play a role, but such observations were not within the scope of this study. The decline of these species in the first few years of succession is well-documented on nearby sites (Yerkes 1958, Brown 1963, Robinson 1968, West and Chilcote 1968, Gashwiler 1970, Dyrness 1973, Kraemer 1977, Halpern 1989); anomalous predation or disease events were unlikely to have played a role. I look at a limited set of associations, most likely to be interacting (Fig. 7), to attribute the declines of these species to one or more of the factors above.

Table 6. Recurring associations explicable by species' recurring correlations with environmental variables.

Pairwise Association		Type	Seral Groups
Bare Ground			
† *Berberis nervosa*	*Trientalis latifolia*	+	Residual/Residual
Collomia heterophylla	*Epilobium paniculatum*	+	Colonizing/Colonizing
Epilobium paniculatum	*Gnaphalium microcephalum*	+	Colonizing/Colonizing
Epilobium paniculatum	*Madia gracilis*	+	Colonizing/Colonizing
† *Epilobium watsonii*	*Trientalis latifolia*	+	Residual/Colonizing
Gnaphalium microcephalum	*Madia gracilis*	+	Colonizing/Colonizing
Litter			
† *Berberis nervosa*	*Trientalis latifolia*	+	Residual/Residual
Coarse woody debris			
Berberis nervosa	*Gnaphalium microcephalum*	−	Colonizing/Residual
Berberis nervosa	*Thuja plicata*	+	Residual/Residual
Surrounding vegetation			
Crepis capillaris	*Thuja plicata*	−	Colonizing/Residual
Crepis capillaris	*Trientalis latifolia*	−	Colonizing/Residual
Gnaphalium microcephalum	*Lotus crassifolius*	−	Colonizing/Colonizing
Ceanothus sanguineus	*Whipplea modesta*	+	Colonizing/Residual
Epilobium watsonii	*Lotus crassifolius*	+	Colonizing/Colonizing
† *Epilobium watsonii*	*Trientalis latifolia*	+	Colonizing/Residual
Epilobium watsonii	*Viola sempervirens*	+	Colonizing/Residual
Rubus parviflorus	*Viola sempervirens*	+	Colonizing/Residual
Rubus parviflorus	*Whipplea modesta*	+	Colonizing/Residual
Rubus ursinus	*Viola sempervirens*	+	Residual/Residual
Rubus ursinus	*Whipplea modesta*	+	Residual/Residual
Thuja plicata	*Trientalis latifolia*	+	Residual/Residual
Thuja plicata	*Viola sempervirens*	+	Residual/Residual
Trientalis latifolia	*Viola sempervirens*	+	Residual/Residual
Trientalis latifolia	*Whipplea modesta*	+	Residual/Residual
Viola sempervirens	*Whipplea modesta*	+	Residual/Residual

† Association explicable by more than one environmental variable

Table 7. Pairwise species associations that recur in results from correlation testing and from null modeling, and are not explicable by shared correlations with any other factors (see hatched area in Fig. 1). Classifications by seral group from Halpern (1989).

Pairwise Association		Type	Seral groups
Berberis nervosa	*Crepis capillaris*	−	Colonizing/Residual
Berberis nervosa	*Gnaphalium microcephalum*	−	Colonizing/Residual
Berberis nervosa	*Lactuca serriola*	−	Colonizing/Residual
Hieracium albiflorum	*Lactuca serriola*	−	Colonizing/Residual
Hieracium albiflorum	*Lotus crassifolius*	−	Colonizing/Residual
Crepis capillaris	*Madia gracilis*	−,+	Colonizing/Colonizing
Anaphalis margaritacea	*Ceanothus sanguineus*	+	Colonizing/Colonizing
Anaphalis margaritacea	*Rubus parviflorus*	+	Colonizing/Colonizing
Arctostaphylos columbiana	*Whipplea modesto*	+	Colonizing/Residual
Berberis nervosa	*Gaultheria shallon*	+	Residual/Residual
Berberis nervosa	*Pseudotsuga menziesii*	+	Residual/Residual
Ceanothus sanguineus	*Pseudotsuga menziesii*	+	Colonizing/Residual
Deschampsia elongata	*Lotus crassifolius*	+	Colonizing/Colonizing
Epilobium angustifolium	*Gaultheria shallon*	+	Colonizing/Residual
Gaultheria shallon	*Trientalis latifolia*	+	Residual/Residual
Hieracium albiflorum	*Pseudotsuga menziesii*	+	Residual/Residual
Hieracium albiflorum	*Viola sempervirens*	+	Residual/Residual
Lotus crassifolius	*Madia gracilis*	+	Colonizing/Colonizing
Pseudotsuga menziesii	*Thuja plicata*	+	Residual/Residual
Pteridium aquilinum	*Rubus ursinus*	+	Colonizing/Residual
Thuja plicata	*Tsuga heterophylla*	+	Residual/Residual
Berberis nervosa	*Madia gracilis*	+,−	Colonizing/Residual
Collomia heterophylla	*Whipplea modesto*	+,−	Colonizing/Residual

In the subset of species pairs most likely to be interacting, four species with conspicuous declines (*G. microcephalum*, *L. serriola*, *C. capillaris,* and *M. gracilis*) were negatively associated with *B. nervosa*. Antos and Halpern (1997) performed root excavations at the study site to compare root/shoot biomass ratios among species, and *B. nervosa* had the highest root/shoot ratio of all species excavated by a factor of ten. *B. nervosa* often dominates the understory in mid to late succession (Halpern 1989).

Isaac (1940) observed that *S. sylvaticus* dominated early clearcut sites in such abundance and disappeared so rapidly that total vegetative cover often declined conspicuously. West and Chilcote (1968) attributed the disappearance of *S. sylvaticus* to reduced nitrogen availability and competition from surrounding species. Halpern et al. (1997) showed experimentally that *S. sylvaticus* declines in the absence of surrounding vegetation. In this study, *S. sylvaticus* showed few associations with other species (Fig. 3), and was negatively associated with surrounding vegetation only in the third year after disturbance. *S. sylvaticus* appears to decline from post-clearcut sites in the third or fourth year after disturbance due to life history or nutrient constraints, and the lack of interspecific associations in this study is consistent with earlier findings.

E. paniculatum was positively correlated with bare ground at seven sampling times. It has a pattern unique among the declining species, appearing consistently on nearly all plots after the first year but at very low cover values from years five to nine. Individual plants of *E. paniculatum* were much smaller after the second year (Antos and Halpern 1997). As the bare ground available on plots decreases over time, *E. paniculatum* appears able to germinate, grow, and reproduce from year to year, but only to produce a limited number of very small plants. Two other species declining early in

succession (*C. vulgare*, and *C. canadensis*) did not show recurring negative correlations with other species, environmental variables, or surrounding vegetation.

Eight mid-seral species showed conspicuous increases in abundance on the site during the sampling period (Fig. 4). These species represented a range of life histories and reproductive strategies. With the exception of *B. nervosa*, as mentioned above, the recurring associations of these species, and most of the temporary associations, were positive (Fig. 4 and Table 7).

DISCUSSION

Changes in associations

Although the predisturbance forest had a high proportion of significant associations, the postdisturbance community displayed no clear, continuous trend toward increasing association over the first nine years of secondary succession. Other studies show conflicting results in the changes in associations over time, and interpretations of the associational patterns vary. Soro et al. (1999) found more associations in older bogs, and Aarssen and Turkington (1985) found that associations were more stable in older pastures. O'Connor and Aarssen (1987) saw decreasing association with increasing community age in sand quarries, as did Myster and Pickett (1992) in old fields. Gitay and Wilson (1995) invoked a three-phase model with negative associations important in the first and third decades of postfire grassland succession, and unimportant in the second decade. While ecologists conducting association studies generally postulate that a site (or sampling time) with more associations demonstrates greater species interaction, findings of few or no associations have also been interpreted as evidence for ubiquitous, diffuse competitive interaction not detectable at the species level (Rogers 1983, O'Connor and Aarssen 1987). The trends in associations at this site, however, do not support conclusions of diffuse competition. Many species are positively associated with other individual species and with surrounding vegetation, indicating diffuse *facilitation* (Carlsson and Callaghan 1991, Nuñez et al. 1999, Bruno et al. 2003). The term is used broadly to signify favorable habitat modification within a plot, including purely structural effects such as trapping seeds (Walker and del Moral 2003).

Positive associations outnumbered negative associations at nearly all sampling times. The high percentage of positive associations, particularly in the first year of succession, can be interpreted as evidence for facilitation or as a product of site heterogeneity. If plants were clustered together at a few highly favorable sites, many species would appear positively associated. The null modeling procedure minimized findings of significant associations due to favorable conditions on certain plots, since the null matrices were constructed to reflect site heterogeneity as reflected in the species richness on each plot. In the three sampling times in the first year after disturbance, Spearman rank correlations were significant and positive in 16-21% of possible associations. The null modeling procedure showed positive significance in 4-8% of possible associations. I expected about 2.5% of possible associations to be significantly positive due to Type I error. The difference between the two metrics indicated that many of the correlation associations are due to favorable site clumping, but facilitation was also affecting the spatial association of species. Most likely, the two factors interact so that plots especially suitable for early establishment have high cover that increases shade and moisture, producing positive feedback among species in the earliest years.

The pattern of associations at this site is consistent with other research showing the importance of facilitation in environments of high abiotic stress (Callaway and Walker 1997, Callaway et al. 2002). As cover increased on this site, mitigating the harsh summer conditions, the importance of positive associations decreased. The trend in the first nine years of succession was toward decreasing importance of facilitation, but the associations did not reflect a commensurate increase in competition. The low percentage of significant positive and negative associations in the fifth through ninth year of

succession reflected a period of relative neutrality; competition may become more important in later years.

Alternative explanations for associations

This study is a first attempt to explicitly quantify the relative importance of alternative explanations of pairwise associations (but see Maguire and Forman 1983, Thomson et al. 1996, Albrecht and Gotelli 2001). The relative importance of the factors changed with time and abiotic stress on the site.

Shared correlations with surrounding vegetation appeared as alternative explanations for many more associations than any single soil or nonvegetative ground cover variable, and were most important in earliest succession. The number of associations explicable by shared correlations with surrounding vegetation nearly equaled the sum of associations explicable by all other measured variables. However, the influence of surrounding vegetation in structuring associations decreased over time. The influence of surrounding vegetation also changed in nature – in early succession many positive associations were explicable by the positive correlation of both species with surrounding vegetation, and in later succession more negative associations were explicable by the dissimilar correlations of two species with surrounding vegetation.

Few pairs of species shared soil correlations. CWD was also relatively unimportant as an explanatory variable for species distributions and for associations, though this may be attributed to the low coverage of CWD on the site. The pattern of associations explicable by bare ground and litter was more complex than expected. Bare ground was important in explaining positive associations of the early seral species, especially as bare patches became scarce later in succession. Litter cover, though

strongly negatively correlated with bare ground, appeared as an explanation for very few associations. While litter is important to many species for seed germination and moisture retention, it can also inhibit growth and raise air and soil temperatures (Robinson 1964, Chapin et al. 1994). It may not be possible to effectively characterize litter with one measure – a combination of depth, area, and texture or composition may be necessary to reflect the effects of litter.

The null modeling test produced fewer significant associations at all sampling times than cover correlations. Some associations found with cover correlations and not found with null modeling are attributable to the factors built into the null model: site heterogeneity, species frequencies, or dispersal abilities. However, other associations found only with cover correlations reflect subtle effects of species on others' abundances, since the null model association coefficient was based on presence/absence.

Mechanisms of succession

Four early seral species may decline due to negative interactions with *Berberis nervosa*, a dominant understory species in mid-successional and mature forests. One disappearing species (*Senecio sylvaticus*) showed very few associations, in accordance with earlier field studies and experiments documenting its decline due to life history or nutrient constraints (Isaac 1940, Halpern et al. 1997). No explanations for the decline of three other early-seral species were obvious from association analysis.

Excepting *B. nervosa*, mid-seral species were mostly involved in positive associations, both temporary and recurring. Most mid-seral species either survived the fire and resprouted, or re-appeared early in the sere. Their increasing dominance appeared to be a slow process of regrowth, facilitated by neighbors. These results are not

anomalous; Mueggler (1965) found mostly positive associations between shrubs of the cedar-hemlock zone in Idaho on 2- to 60-year-old burn sites. Kraemer (1977) made predictions about associations of many species based on qualitative observations in nearby forests, and predicted mostly positive associations among mid-seral shrubs. Nitrogen fixers may play an important facilitative role on the site, as they were strongly represented in the set of associated pairs most likely to be interacting.

Association analysis over the first nine years of secondary succession at this site reveals the changing relative importance of diffuse facilitation, species-specific competition, and microsite limitation. Diffuse facilitation is highly important in earliest succession, especially the first year. As the system moves along gradients of increasing successional time and decreasing abiotic stress, positive interactions still dominate the site, but one dominant shrub species inhibits the continuing growth and establishment of several abundant early-seral herbs. The continuing presence of these herbs is also increasingly dependent on limited bare spaces for germination and establishment. Experimental studies are needed to verify mechanisms with certainty, but the repeating patterns of association and previous ecological studies from this site allow inference of influential mechanisms.

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APPENDICES

Appendix A. Null modeling method and consistency with previous use

Tests for interspecific association may be heavily influenced by patterns attributable to ecological factors other than interspecific interaction. Very rare species may appear to have many negative associations because they seldom co-occur with other species. Interpretation of the negative associations as evidence for competitive exclusion misses the ecological reality that few propagules for the species arrived on the site. An example at this site is *H. albiflorum*, which is sparsely scattered in the predisturbance forest (Halpern 1989). Positive associations may appear due to clumping of plants in a few plots that are particularly favorable due to high nutrients or moisture. Interpretation of these results as evidence for facilitation fails to recognize heterogeneity among plots in the field. When associations in the observed community appear significantly different from associations in the simulated communities, it should be from patterns of co-occurrence that are not attributable to the dispersal effectiveness of the species or heterogeneity among plots. The null modeling procedure consists of the following steps, slightly modified from Gotelli and Entsminger (2003):

1. Choose an index that reflects the degree of association between each pair of species. Calculate the index from the observed data for each pair of species.

2. Create a simulated community, using Monte Carlo simulations with appropriate constraints (detailed below).

3. Calculate the index for each species pair in the simulated community.

4. Repeat steps 2 and 3 100,000 times for each field sampling time. Create a distribution of index values for each species pair from the simulated communities.

5. Within the cumulative frequency distribution of simulated indices, locate the observed index value. Classify the association as significant if the observed value is in the $\alpha < .025$ tail at either end of the distribution.

6. Repeat the procedure for each of the sixteen sampling times.

We used the Baroni-Urbani index to measure association between species, based on presence/absence data (Baroni-Urbani and Buser 1976). The index formula is

$$\frac{\sqrt{(A*D)} + A}{\sqrt{(A*D)} + A + B + C}$$

where the contingency table takes the form shown in Table A1. This index decreases the importance of plots where both species are absent and is a reasonable approach in the early years of this study when many plots were sparsely populated.

The simulated matrices were generated beginning with a blank matrix and filling in the cells with presences or absences, subject to certain constraints. Rows of the matrix represent plots sampled and the columns contain species (Table A2). Each species was constrained to occur in the number of plots in which it was actually observed at that sampling time. Constraining species frequencies in this way reflects the reality that some species have much wider ecological amplitude than others or can disperse more effectively. The probability of placing a species into a particular plot was proportional to

Table A1. Contingency table used for calculation of Baroni-Urbani and Buser coefficient. The letters A, B, C, and D represent the number of plots containing the combination of species indicated.

	Species 1	
Species 2	Present	Absent
Present	A	B
Absent	C	D

Table A2. Generating simulated matrices from observed data matrices. In generating a simulated matrix, species frequencies are held constant, while plots are filled in a manner proportional, but not absolutely constrained, to their observed richness. Note that in the simulated matrix, co-occurrences of the pairs of species are different than those seen in the matrix of observed data.

a. Observed matrix

Plot Number	AGGR	ANMA	BENE	CRCA	COHE	Plot richness
1	1	1	1	1		4
2			1			1
3	1		1			2
4			1	1	1	3
5	1	1				2
6	1		1			2
7			1			1
8	1			1	1	3
9			1			1
Species frequency	5	2	7	3	2	

b. One possible simulated matrix

Plot Number	AGGR	ANMA	BENE	CRCA	COHE	Plot richness
1	1		1	1	1	4
2	1		1			2
3			1	1		2
4	1	1				2
5			1			1
6			1		1	2
7	1		1			2
8	1			1		2
9		1	1			2
Species frequency	5	2	7	3	2	

the number of species observed in that plot. Constraining the richness within plots

incorporated the differing suitability of plots for colonization and establishment, due to

factors such as distance from colonizing sources and microsite variability (Connor and

Simberloff 1979). The constraint was achieved by breaking a [0,1] number line down

into segments, each representing one plot on the site. The length of each segment was

proportional to the number of species observed on the plot. A random number was

generated between zero and one, and placed onto the number line. The species

occurrence was assigned to the plot corresponding to the segment on the number line.

Plots with greater observed richnesses occupy a greater length on the number line,

increasing the probability that a given random number will fall into their assigned

segments (e.g. Gotelli and Entsminger 2003).

The controversy over the particular form of null models is reviewed in Harvey et

al. (1983), Colwell and Winkler (1984), and Gotelli and Graves (1996). Simberloff and

Connor (1979) wrote "ideally one would wish independent assessments of the dispersal

and persistence abilities for all N_t species. However, comprehensive data for an entire

species pool on either ability are rare." Their solution was to use weighted or fixed totals

to fill in the 'randomly' generated community matrices, as we have done.

The inclusion of too many ecological constraints in the null model may

incorporate effects of species interaction, invalidating the model as a reasonable null

hypothesis for species interactions (Wright and Biehl 1982, Colwell and Winkler 1984).

We chose not to use an incidence function (constraining species occurrence by

surrounding richness) and we assigned plot richnesses in a manner proportional, but not

strictly equal, to observed richness (Gilpin and Diamond 1982). Gotelli (2000) compared

null modeling constraints on simulated and real-world datasets, and found that this

algorithm of conserved species frequencies and probabilistic plot richnesses (referred to

as "SIM4") was not prone to either elevated Type I or Type II error rates.

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Appendix B. Matrices of associated species pairs

Table B1. Number of times that each species pair was significantly positively associated, tested with cover correlations as described in the "Analytical Methods" section.

```
Agoseris grandiflora
.   Anaphalis margaritacea
2   .   Cirsium vulgare
1   .   2   Conyza canadensis
1   .   .   2   Collomia heterophylla
3   .   .   4   1   Crepis capillaris
.   .   .   1   3   3   Deschampsia elongata
.   .   1   .   .   2   .   Elymus glaucus
.   .   3   1   .   .   .   .   Epilobium angustifolium
3   .   .   8   4   4   4   .   .   Epilobium paniculatum
.   3   .   .   .   .   2   .   .   6   Epilobium watsonii
.   .   .   .   .   .   .   .   .   2   .   Fragaria vesca
.   .   .   2   2   3   2   .   .   4   1   .   Gnaphalium microcephalum
3   .   5   5   .   3   2   .   .   5   .   .   .   Lactuca serriola
1   .   1   2   1   3   1   4   .   4   7   .   .   6   Lotus crassifolius
1   .   1   1   3   2   7   .   .   4   .   .   4   4   9   Madia gracilis
.   .   .   2   2   1   1   .   .   1   .   .   .   .   .   .   Senecio sylvaticus
.   2   .   .   1   .   .   .   .   3   .   2   1   .   .   .   .   Arctostaphylos columbiana
.   4   .   .   .   .   .   .   .   2   3   .   .   .   .   .   1   2   Ceanothus sanguineus
.   2   .   .   2   .   .   1   7   .   1   .   3   .   .   .   .   2   .   Hieracium albiflorum
2   .   3   2   2   .   .   .   .   1   1   .   1   .   .   .   .   1   .   2   Lupinus latifolius
.   1   .   .   .   .   .   .   1   .   .   .   .   .   .   .   .   2   1   .   4   Pteridium aquilinum
1   .   1   .   .   .   .   .   6   1   4   .   .   .   3   1   1   1   5   3   .   Trientalis latifolia
.   2   .   .   1   .   .   .   1   6   .   .   .   .   .   2   .   5   3   .   6   Viola sempervirens
.   2   .   .   .   .   .   .   3   .   1   .   .   .   2   1   3   6   9   .   .   14   5   Berberis nervosa
.   .   .   .   2   .   .   4   1   .   .   .   .   .   .   1   .   .   1   5   1   6   4   14   Gaultheria shallon
.   .   .   .   3   .   .   .   1   .   .   .   .   .   .   .   .   .   .   .   .   .   .   .   .   Rhododendron macrophyllum
.   6   3   .   .   .   .   1   2   .   1   .   .   .   .   .   .   2   3   2   .   .   3   9   9   3   .   Rubus parviflorus
.   .   .   .   .   .   3   1   .   2   .   .   1   .   2   .   .   .   .   5   1   14   .   11   .   6   Rubus ursinus
.   .   2   2   2   .   .   2   4   4   1   .   .   .   1   .   2   6   6   3   1   .   6   16   6   5   .   16   12   Whipplea modesta
.   2   .   .   .   .   .   .   1   4   .   .   .   .   .   .   5   9   1   .   3   7   5   1   .   1   1   4   Pseudotsuga menziesii
.   2   .   .   .   .   1   5   .   3   .   .   .   2   1   .   1   4   .   1   5   7   7   .   .   1   .   2   6   Thuja plicata
.   2   .   .   .   .   .   2   .   .   .   .   .   .   .   .   .   1   .   .   .   .   1   .   .   .   .   1   2   5   Tsuga heterophylla
```

Colonizing herbs

Colonizing shrubs

Residual herbs

Residual shrubs

Trees

Table B2. Number of times that each species pair was significantly negatively associated, tested with cover correlations as described in the "Analytical Methods" section.

```
    Agoseris grandiflora
 3  Anaphalis margaritacea
 .  2  Cirsium vulgare
 .  .  .  Conyza canadensis
 .  .  .  .  Collomia heterophylla
 .  2  .  .  .  Crepis capillaris
 .  .  .  .  .  .  Deschampsia elongata
 .  .  .  .  .  1  .  Elymus glaucus
 2  .  .  1  1  8  2  .  Epilobium angustifolium
 .  .  .  .  .  .  .  .  1  Epilobium paniculatum
 1  .  .  .  .  1  .  .  .  .  Epilobium watsonii
 .  .  .  .  .  .  .  .  .  .  .  Fragaria vesca
 .  .  .  .  .  1  .  .  1  .  3  .  Gnaphalium microcephalum
 .  1  .  .  .  .  .  .  .  .  .  .  .  Lactuca serriola
 .  .  .  .  .  3  .  .  .  .  .  4  .  Lotus crassifolius
 .  1  .  1  .  3  .  .  3  .  .  .  .  .  .  Madia gracilis
 .  .  1  .  .  .  .  .  1  1  .  .  .  .  2  Senecio sylvaticus
 .  .  .  .  .  .  .  .  .  .  .  .  .  .  2  .  Arctostaphylos columbiana
 1  .  .  .  1  1  .  .  .  .  .  .  .  .  2  .  Ceanothus sanguineus
 1  .  4  2  2  3  .  .  .  1  .  .  6  4  3  .  .  .  Hieracium albiflorum
 .  .  .  .  .  .  .  .  .  .  .  .  3  1  .  .  .  .  Lupinus latifolius
 .  .  .  .  .  2  .  .  .  .  1  .  .  2  .  .  .  1  .  Pteridium aquilinum
 1  .  .  1  1  6  2  .  .  1  .  .  .  .  3  .  .  .  .  .  Trientalis latifolia
 1  .  .  1  3  .  .  .  .  .  .  2  5  .  3  .  .  .  .  .  Viola sempervirens
 .  .  3  4  1  6  .  .  .  1  .  .  5  6  .  2  .  .  .  1  .  .  Berberis nervosa
 .  .  .  3  .  5  1  .  .  1  .  .  .  1  1  3  .  .  .  1  .  .  .  .  Gaultheria shallon
 .  .  .  1  .  .  .  .  .  .  .  .  .  .  .  .  .  1  .  1  1  1  .  .  Rhododendron macrophyllum
 .  .  .  .  .  .  .  .  .  .  4  .  .  .  .  .  .  .  .  .  .  .  .  Rubus parviflorus
 1  .  .  .  3  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  Rubus ursinus
 3  .  .  1  2  .  .  .  .  .  .  3  .  .  .  .  .  .  .  .  .  1  .  .  Whipplea modesta
 4  .  2  3  2  4  2  .  .  2  .  .  5  1  .  4  .  .  .  1  .  .  .  1  .  .  Pseudotsuga menziesii
 4  .  2  1  2  7  .  .  .  3  .  .  1  .  1  .  .  .  .  1  .  .  .  Thuja plicata
 .  .  .  .  1  1  .  .  .  .  .  .  .  .  .  .  .  .  .  1  .  .  .  Tsuga heterophylla
```

Colonizing herbs

Colonizing shrubs

Residual herbs

Residual shrubs

Trees

Table B3. Number of times that each species pair was significantly positively associated, tested with null modeling as described in the "Analytical Methods" section.

```
Agoseris grandiflora
 .   Anaphalis margaritacea
 1   .   Cirsium vulgare
 1   .   1   Conyza canadensis
 .   .   .   1   Collomia heterophylla
 1   .   .   1   .   Crepis capillaris
 1   .   .   .   4   .   Deschampsia elongata
 .   .   1   .   .   .   .   Elymus glaucus
 .   .   .   .   .   .   .   .   Epilobium angustifolium
 1   .   .   .   2   1   .   .   .   Epilobium paniculatum
 .   2   .   .   .   .   1   .   .   1   Epilobium watsonii
 .   .   .   .   .   .   .   .   .   .   .   Fragaria vesca
 2   1   .   1   1   1   1   .   .   .   1   .   Gnaphalium microcephalum
 2   .   2   3   1   2   2   1   .   .   .   .   .   Lactuca serriola
 .   .   .   .   1   .  10   3   .   .   3   .   .   3   Lotus crassifolius
 1   .   .   1   2   2   3   .   1   3   1   .   2   .   5   Madia gracilis
 .   .   .   1   .   .   .   .   .   .   .   .   1   .   .   .   Senecio sylvaticus
 .   1   .   .   .   .   .   2   .   1   1   2   1   .   .   1   .   Arctostaphylos columbiana
 .   4   .   1   .   .   .   .   .   4   .   1   .   .   .   .   1   Ceanothus sanguineus
 .   1   .   .   2   .   .   1   3   .   .   1   1   .   .   .   .   .   .   Hieracium albiflorum
 2   .   2   .   1   .   .   .   .   .   .   .   1   .   .   .   .   2   1   1   Lupinus latifolius
 .   1   .   1   .   .   .   .   1   .   .   .   .   .   .   .   .   2   .   .   2   Pteridium aquilinum
 .   .   1   .   .   .   .   .   1   .   .   .   .   .   1   .   .   2   1   .   .   .   Trientalis latifolia
 .   2   .   .   1   .   .   .   .   3   .   .   .   .   .   .   .   2   1   4   .   .   3   Viola sempervirens
 .   .   .   .   .   .   .   .   .   4   .   .   .   6   4   .   .   3   3   .   .   5   1   Berberis nervosa
 2   .   1   .   .   .   .   3   .   1   .   .   .   .   1   .   .   .   1   .   3   .   8   Gaultheria shallon
 .   .   .   1   .   .   .   .   1   .   .   .   .   .   .   .   1   1   .   2   .   .   2   Rhododendron macrophyllum
 .   7   1   .   .   .   .   1   .   .   1   .   .   .   .   .   2   3   1   .   .   3   4   .   .   .   Rubus parviflorus
 .   .   .   1   .   .   .   2   .   .   .   .   .   .   1   2   .   1   1   5   1   5   .   2   .   2   Rubus ursinus
 .   1   .   .   .   .   2   1   .   .   .   .   1   .   4   4   2   1   .   6  10   .   .   1  11   3   Whipplea modesta
 .   3   .   .   .   .   .   3   .   .   1   .   .   .   5   8   .   .   3   .   4   .   .   1   2   3   Pseudotsuga menziesii
 .   2   .   .   .   .   1   3   .   2   .   .   1   2   1   .   .   .   3   .   1   5   5   2   .   .   1   .   2   4   Thuja plicata
 .   1   .   .   .   .   .   .   .   .   .   .   .   .   1   .   .   .   .   .   .   .   .   .   .   .   .   1   1   5   Tsuga heterophylla
```

Group brackets (right side):
- Colonizing herbs: *Agoseris grandiflora* through *Senecio sylvaticus*
- Colonizing shrubs: *Arctostaphylos columbiana*, *Ceanothus sanguineus*
- Residual herbs: *Hieracium albiflorum* through *Viola sempervirens*
- Residual shrubs: *Berberis nervosa* through *Whipplea modesta*
- Trees: *Pseudotsuga menziesii* through *Tsuga heterophylla*

Table B4. Number of times that each species pair was significantly negatively associated, tested with null modeling as described in the "Analytical Methods" section.

```
                                                                          ⎫
Agoseris grandiflora                                                      │
 4  Anaphalis margaritacea                                               │
 .  1  Cirsium vulgare                                                   │
 .  .  .  Conyza canadensis                                             │
 .  4  .  .  Collomia heterophylla                                      │
 .  .  .  .  .  Crepis capillaris                                        │
 .  .  .  .  .  .  Deschampsia elongata                                 ⎬ Invasive herbs
 .  .  .  .  .  1  .  Elymus glaucus                                     │
 3  .  1  1  .  .  1  1  Epilobium angustifolium                        │
 .  .  .  .  .  .  .  .  2  Epilobium paniculatum                       │
 1  .  2  .  1  .  .  1  .  1  Epilobium watsonii                       │
 1  .  .  .  .  .  .  .  .  .  .  Fragaria vesca                        │
 .  .  .  .  .  .  .  .  .  .  .  .  Gnaphalium microcephalum           │
 .  2  .  .  .  .  .  1  .  .  .  .  .  Lactuca serriola                │
 .  1  .  .  1  2  .  .  .  1  .  .  2  .  Lotus crassifolius           │
 .  .  .  .  4  .  1  .  .  .  .  .  .  .  .  Madia gracilis            │
 .  .  .  1  .  1  .  .  .  1  .  .  .  .  2  Senecio sylvaticus        ⎭
 2  .  .  .  .  .  .  .  .  .  1  .  .  .  .  .  Arctostaphylos columbiana  ⎱ Invasive
 3  .  .  .  3  .  .  1  .  .  .  .  .  .  .  .  2  .  Ceanothus sanguineus ⎰ shrubs
 .  2  .  1  .  1  .  .  .  .  .  7  5  .  1  .  .  Hieracium albiflorum   ⎫
 .  .  .  .  .  .  1  .  1  .  .  .  4  1  .  .  .  2  Lupinus latifolius  │
 .  .  .  .  2  1  .  .  .  .  .  1  .  .  1  .  .  .  3  .  Pteridium aquilinum ⎬ Residual herbs
 .  .  .  1  2  2  2  .  .  .  .  .  .  .  .  .  1  2  .  .  .  .  Trientalis latifolia │
 1  .  .  1  3  .  .  .  .  .  .  .  3  3  .  .  .  .  .  .  .  .  Viola sempervirens  ⎭
 .  .  3  2  .  4  .  .  .  1  .  1  4  6  .  .  .  .  .  .  1  1  .  1  Berberis nervosa     ⎫
 .  .  .  3  .  2  3  .  1  .  .  2  .  .  3  .  1  .  1  1  .  .  1  1  .  Gaultheria shallon  │
 .  .  .  2  .  .  .  1  .  .  .  .  .  .  .  .  .  .  1  .  1  1  .  1  1  .  Rhododendron macrophyllum ⎬ Residual shrubs
 1  .  1  .  .  1  .  .  .  .  .  .  .  .  .  .  .  .  .  .  1  .  .  .  .  .  1  Rubus parviflorus │
 .  2  .  .  .  2  1  1  .  .  .  .  .  .  .  .  .  .  1  .  .  .  .  .  .  .  1  .  Rubus ursinus  │
 3  .  .  .  4  .  1  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  .  1  .  .  Whipplea modesta ⎭
 3  .  1  1  2  .  3  .  .  1  .  .  3  3  1  2  1  .  .  .  1  1  .  .  .  1  .  .  .  .  Pseudotsuga menziesii ⎱ Trees
 3  .  2  .  3  2  2  .  .  .  .  .  .  .  .  .  1  .  1  .  .  .  .  3  .  .  .  .  1  .  .  Thuja plicata   ⎰
 .  .  .  .  1  .  .  .  .  .  .  .  .  .  .  .  1  .  .  .  .  .  .  .  .  .  1  .  .  .  1  .  Tsuga heterophylla
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