Will similar forests develop on similar sites?

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Abies grandis, Taxus brevifolia, Thuja plicata, or any combination of these may dominate old-growth mesic forests of the Bitterroot Canyons, western Montana. Similar sites need not develop similar, relatively stable forests. This is shown by (i) anomalous distributional patterns of tree species, (ii) broad overlap of tree species abundance in environmental space (shown by ordination and discriminant analysis of stands in environmental space), and (iii) weak or undetectable correspondence of species × stand and site factor × stand matrices (multiple regressions of compositional dissimilarity against environmental differences; also, canonical correlation and Mantel tests). Since a one-to-one mapping from site factors to species composition in old-growth vegetation is a fundamental tenet for applications of the climax concept, caution is warranted where the concept is to be applied within a narrow range of site factors or to insular communities.


Les forêts mésiennes âgées des Bitterroot Canyons dans l’ouest du Montana peuvent être dominées par Abies grandis, Taxus brevifolia, Thuja plicata ou par l’une ou l’autre de ces espèces dans n’importe quelle combinaison. Des forêts semblables relativement stables ne se développent pas nécessairement sur des sites semblables. Les données suivantes appuient cette assertion: (i) la présence d’anomalies dans les patrons de répartition des espèces arborescentes, (ii) une large zone de chevauchement entre les espèces arborescentes dans l’espace environnemental (démontré par l’ordination et l’analyse discriminante des peuplements dans l’espace environnemental) et (iii) la correspondance faible ou indiscernable entre la matrice espèces × peuplements et la matrice facteurs stationnels × peuplements (régressions multiples de la dissimilarité de la composition sur les différences environnementales, ainsi que corrélations canoniques et tests de Mantel). Puisque l’un des aspects fondamentaux de l’application du concept du climax est qu’il doive y avoir une correspondance univoque entre la cartographie des facteurs stationnels et la cartographie de la composition spécifique dans les forêts âgées, les auteurs recommandent la prudence dans l’application de ce concept lorsque les facteurs stationnels couvrent une faible étendue ou lorsqu’on considère des communautés insulaires.

Introduction

Palmgren (1929) advocated to the International Congress of Plant Science that we strive to “estimate how wide and deep are the effects of chance.” The importance of historical accident in structuring relatively stable communities is difficult to measure. Those who address the importance of history in structuring stable communities cover a broad range of viewpoints, from determinism with lip service to historical factors the life-span of the trees, the responsible factor has long since

events. Many biotic factors are extremely variable and inaccusable and are thus historical factors. For instance, deer populations undergoing a temporary population explosion may substantially alter the composition of a cohort of stands, perhaps by a feeding preference on seedlings of a particular tree species that is colonizing a burn (Thuja is tasty). Even though the effect of the peak in deer population may last as long or longer than the life-span of the trees, the responsible factor has long since been impossible to measure.

The segregation of site factors and historical factors is somewhat arbitrary because many factors are not clearly assignable to one category or the other. For instance, consider a site that will support seedlings of a given species for 9 out of 10 years, but every 10 years or so, a drought eliminates them. The site is droughty, but this may not be directly observable except on drought years. A several-year study of vegetation and environment could easily miss this factor, making the status of occasional drought ambivalent between a site factor and an historical factor. Despite continuity between the two types of factors, the distinction between site factors and historical factors is important since it relates to ecologists’ perception of randomness in community data: both types of factors structure the data, but only one is accessible.

We sought to measure the relative influence of site factors and historical factors on species composition of old-growth forests in a narrow range of environments in the Bitterroot Canyons. A central problem in estimating the effects of historical factors is that it is difficult to know how much “unexplained” variation is intractable noise and how much could be reduced by more thorough or precise measurements. Although it is impossible to prove the null hypothesis, that the compositional variation cannot be adequately explained by site variables and has a predominantly historical origin, it can be

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Successional variation is such a strong signal that it masks many others and presents another major barrier to measuring the effects of historical factors. Successional variation can be reduced by sampling old-growth stands (without a recent major disturbance), but it is difficult to find old-growth vegetation on nearly identical, but nonadjacent, sites. However, the Bitterroot Canyons, topographic replicates in a large body of granite, provide this opportunity. The canyon bottoms support various mesic coniferous forests: one may be lined with Abies grandis, the next with Thuja plicata or Taxus brevifolia (nomenclature follows Hitchcock and Cronquist 1973). If similar sites need not develop similar communities, then we should be cautious in using climax vegetation as a standard for comparisons that rest upon the assumption that the composition at climax is solely determined by site characteristics.

Study area

The Bitterroot Canyons are a series of similar, parallel gorges on the east slope of the Bitterroot Range in western Montana (Fig. 1). Low-elevation mesic forests were sampled in the 11 major canyons from Bass Creek to Rock Creek, excluding Lost Horse Canyon, which has been logged.

Climate

Average annual precipitation in the canyon bottoms within the elevational range of this study is probably 60–90 cm (Ross and Hunter (1976) and climatic data from similar areas in western Mon-
January and July temperatures are near -5 and 15°C. Much of that coming in the winter months as snow. Mean temperature at any point--quarter method (Cottam and Curtis 1956), with a stratification by size class. This provided data on vertical structure and on species composition in relation to stand age and topographic position (McCune and Allen 1985). (ii) Species composition and environment (moisture, nutrients, and light) were sampled in 13 old-growth stands distributed among four canyons (Fig. 1). These stands were analyzed for the central question of this paper, whether similar sites necessarily develop similar vegetation. The small number of stands is a compromise between sample size and sample integrity. The narrower the range of environments included, the stronger our test. The restrictive sampling criteria required by our specific objective left few acceptable stands, and we sampled them all. Furthermore, the larger the sample size, the more consecutive nights are required for moisture stress sampling, increasing the probability of a significant change in moisture stress before all canyons were visited. Despite the small sample size our data are valuable, since the natural experiment we exploit is a rare set of circumstances that allows insights into a question that is inherently difficult to approach.

Two sets of species composition data were collected. (i) Tree species were sampled along transects through each major canyon using the point--quarter method (Cottam and Curtis 1956), with a stratification by size class. This provided data on vertical structure and on species composition in relation to stand age and topographic position (McCune and Allen 1985). (ii) Species composition and environment (moisture, nutrients, and light) were sampled in 13 old-growth stands distributed among four canyons (Fig. 1). These stands were analyzed for the central question of this paper, whether similar sites necessarily develop similar vegetation. The small number of stands is a compromise between sample size and sample integrity. The narrower the range of environments included, the stronger our test. The restrictive sampling criteria required by our specific objective left few acceptable stands, and we sampled them all. Furthermore, the larger the sample size, the more consecutive nights are required for moisture stress sampling, increasing the probability of a significant change in moisture stress before all canyons were visited. Despite the small sample size our data are valuable, since the natural experiment we exploit is a rare set of circumstances that allows insights into a question that is inherently difficult to approach.

Stands were included only if they were old-growth canyon-bottom forests dominated by Abies grandis, Thuja plicata, or Taxus brevifolia, with at least a few individuals of A. grandis in the understory for nutrient and moisture stress measurements, and in the elevation range 1260–1400 m. Old stands in the bottoms are usually small and well defined, being bounded by talus, bedrock, a creek, or younger stands.

In each stand a 375-m² circular plot was permanently marked with a 0.5-m section of 10-mm steel rod driven flush with the ground. The small plot size was used for two reasons: to fit the small size of many old-growth stands and to restrict within-plot variation so that environmental samples more closely represented the conditions affecting all the trees in the plot.

Environmental factors were measured as the plants “read” them, wherever possible. Internal moisture stress represented site moisture; foliar analysis represented site nutrients. These measures integrate many interacting environmental factors into numbers easily obtained and interpreted. Direct incident radiation was estimated from computer simulations of the sun’s trajectory over site-specific horizon maps. Temperature regimes were partly expressed in the estimates of both moisture stress and light. Other effects of temperature on composition were assumed negligible because the stands were at similar elevations and topographic positions.

Composition
The species, basal area, height, and age of every living or dead tree >1.5 m tall in each plot were recorded. Tree seedlings (<1.5 m tall) were identified and aged, and their heights were measured. When scarce, all seedlings in the plot were tallied, while plots with numerous seedlings were sampled with 30 quadrats (1 x 1 m) arrayed along five parallel lines through the plot.

Moisture
Site moisture, as measured by predawn xylem potentials in Abies grandis, was sampled four times in each plot, twice during both summers of 1980 and 1981. The same trees were sampled throughout, to exclude variation between sampling times arising from consistent differences between trees on the same site. Three Abies grandis individuals with foliage in arm’s reach were selected per plot, although in three plots, only two trees qualified. The average tree used for moisture stress sampling was 1.4 dm² in basal area, 7.0 m tall, and 98 years old.

During each moisture stress sampling session, all plots in a canyon were sampled on the same night, the four canyons on consecutive nights. A different canyon order was used for each four-night session. Each session began after long periods of dry weather to sample maximum moisture stress with minimal changes in stress during a session. Three of four sessions were completed without rain during the session, these three constituting the moisture stress sample.

Sampling began at 0300 Mountain Standard Time and were completed before dawn. In each plot six branchlets 1.5–3.0 m above the ground were clipped and their moisture stress was measured (Waring and Cleary 1967). On the same day, the current year’s growth was clipped for nutrient analysis and dried.

Within-plot variation in moisture stress arising from differences in branch vigor was removed by regressing moisture stress on dry weight per shoot tip (after square-root transformation of weight per shoot tip, \( r^2 = 0.20, 0.12, 0.17 \) for sessions 1, 3, and 4, respectively; \( p < 0.01 \)). Residuals were used to adjust moisture stress values to the condition
of average vigor. Adjusted stress values were averaged across the three acceptable sampling sessions, and this composite variable was used in the analysis.

**Nutrients**

Site nutrient availabilities were compared using foliar analysis of nitrogen and phosphorus, apparently the two nutrients most often deficient in forests (Pritchett 1979). The 1980 samples were analyzed for total N, samples from 1981 for total P. Nutrient analyses were based on the current year’s growth of branchlets used for moisture stress determinations.

Since nutrient concentrations may vary temporally and spatially within the same tree (van den Driessche 1974), precautions were taken to ensure comparability between sites. Lower crown samples were used in all cases and seasonal differences were avoided by taking all samples for a given nutrient within a few days of each other.

Individual samples were kept separate for N, while the two or three samples per tree were combined for P. The dried (24 h, 70°C), ground (40-mesh screen in Wiley mill) samples of 1980 were wet ashed using Caro’s acid digest (Miller and Miller 1948). Digests were colorimetrically analyzed for total N with a Technicon Auto Analyzer II (Anonymous 1974). Results were expressed as percents of dry weight.

Samples from 1981 were treated to prevent volatilization of P (Jackson 1958, p. 335), then dry ashed and analyzed with the vanadomolybdate method (Bertramson 1942). Colorimetric determinations from a Spectronic 100 spectrophotometer were expressed as percents of dry weight.

**Light**

Since the plots are surrounded by steep topography, different horizon configurations may result in differences in incident radiation. We estimated direct incident radiation for each plot by constructing horizon maps and superimposing the sun’s daily trajectories by computer simulation.

Horizon maps were constructed from field and map measurements with a resolution of 5° of azimuth. The sun’s trajectory in 1-h increments was superimposed on the horizon maps, using formulae from Satterlund and Means (1978) and Satterlund (1977). Each hour of sunshine was weighted by the proportion reaching the earth, based on a transmission coefficient of 0.78, a reasonable value based on data in Satterlund and Means (1978, p. 368).

**Data analysis**

Our central analytical question was “How well do the site variables account for compositional differences?” Thus, we sought a measure of the strength of the relationship between two sets of variables, drawn from the same set of stands. Two matrices are involved: (i) species abundances in each stand and (ii) the level of each environmental variable in each stand.

Canonical correlation directly relates two sets of variables but is not wholly satisfactory, as discussed below. Lacking a single powerful and general method, we therefore chose to diversify the analysis using (i) multiple regressions of abundance of individual species against environmental variables, (ii) ordination of stands in environmental space with overlays of dominant species, (iii) multiple discriminant analysis of dominance types in environmental space, (iv) canonical correlation between the species \( x \) stand and environment \( x \) stand matrices, and (v) Mantel tests and multiple regression of dissimilarity in the tree layer against differences in environmental variables. Following remarks on our strategy for variable selection, we give the rationale for using each method.

A small sample size necessitates restricting the number of independent variables allowed to enter a multivariate analysis, since a large set of noisy variables will “explain” virtually any dependent variable. Thus, we chose (i) not to transform site variables, since within the small ranges of the site variables linear approximations should suffice; (ii) to exclude variables which are nearly equal among sites (elevation); and (iii) to select the strongest variables from groups of related, partially redundant variables. For example, “stand age” can be expressed in several ways: age of the oldest tree, modal age, or the

![FIG. 2. Relative dominance of major shade-tolerant tree species in each plot by age-class, basal area (BA) relativized among just three species, *Thuja plicata*, *Taxus brevifolia*, and *Abies grandis*.](image-url)
Ordinations in environmental space

Plots were ordinated on pairs of environmental axes. The dominants best represented across a spectrum of age and size classes were then superimposed on the ordinations to evaluate subjectively whether or not species as dominants occupied different parts of environmental space. Although examining pairs of axes for segregation of species is a clumsy method for reducing dimensionality, it is not burdened by the assumptions of classical multivariate analysis such as multivariate normality.

Discriminant analysis

Stands were classified by dominants and the resulting groups subjected to multiple discriminant analysis (DA) (Klecka 1975). DA was used to seek the best linear combination of environmental variables for separating dominance types. We used stepwise selection (Wilks’ lambda criterion) of site variables, maximizing the F-ratio for the test of differences among dominance centroids in environmental space (Klecka 1975). Stepwise rather than direct DA was chosen to reduce the high number of independent variables relative to the sample size. DA evaluates the relationship between vegetation and environment in a single analysis, but only at the price of substantially reducing the compositional data to a qualitative statement of the dominant.

Canonical correlation

Canonical correlation measures how much of the variability in two sets of variables can be accounted for by the relationships between them (Jeffers 1978). This method maximizes the correspondence between the cluster of stands in environmental space and the cluster of stands in species space. This is done essentially by performing two simultaneous variance maximizing procedures (cf. principal-components analysis), one on each variable set, rotating each point cluster to maximize the correlation between stand projections onto each successive pair of axes extracted. This is a direct method for measuring the redundancy of two matrices (performed with MANOVA procedure in SPSS (see Nie 1983, p. 518)), but it cannot identify certain types of correlation structures in the data (Warwick 1975, p. 518) and performs poorly when relationships between variables are even modestly nonlinear (Beals 1984).

Comparison of dissimilarity matrices

Dissimilarity in tree composition (relative dominance) was regressed against differences in environmental variables. Dissimilarity was measured with the quantitative version of Sørensen’s index (Bray and Curtis 1957; Mueller-Dombois and Ellenberg 1974, p. 226). This measure of sociological distance can be more closely linear with respect to environmental difference than Euclidean measures (Beals 1984). Strata were regressed both separately and combined. In each case, the three best site factors were used to construct the regression equation. Differences in site factors were expressed as the absolute value of the arithmetic difference between stands. One additional site factor was added to the pool of available independent variables, the daily differences in direct incident radiation summed through the year, thus accounting for differences in the timing of direct radiation between sites.

The intuitive appeal of this analysis is that if two stands are quite dissimilar in tree composition, and the difference is environmentally determined, then environmental differences should likewise be relatively great. On the other hand a low $R^2$ value would suggest that tree dissimilarity is largely unrelated to the observed site differences.

Since there is partial dependence in dissimilarity matrices, some degrees of freedom are lost, and one should not stress parametric interpretations of the outcome. Instead, the results should be taken as loosely indicative of the strength of the relationship between the matrices.

The Mantel test is an alternative to regressing distance matrices that circumvents the problem of partial dependence in these matrices (Douglas and Endler 1982; Mantel 1967). We used the Mantel test to compare site difference matrices with compositional dissimilarity matrices. Unfortunately, this method allows comparison of only two matrices at a time. Although the site variables could be combined into a single composite site difference matrix, we did not do this, since site variables vary greatly in their importance to vegetation, and the inclusion of weak factors with strong on an equal basis can only weaken the site difference matrix. Thus, we used the Mantel test to compare individual matrices while we used multiple regression to relate compositional dissimilarity to several site difference matrices simultaneously.

Results

Distributional patterns of trees

The anomalous distribution of tree species among the canyons (Fig. 3) suggests the insularity of the canyon-bottom communities and the possibilities for alternative climax communities on similar sites, if we assume that the canyons are similar. The only tree species shown are, within Montana, largely restricted to low, moist sites. Several of these species (Abies grandis, Taxus, Thuja) are near the eastern edge of an outlying
lobe of their Pacific Coastal distributions.

The canyons are similar in form and bedrock, yet the vegetation is strikingly variable. If each canyon offers a similar range (even if in different proportions) of landforms and microclimates, then the distributional pattern (Fig. 3) cannot be due to site differences, and the conclusion that different relatively stable plant communities may develop on similar sites is inescapable. However, it is possible that the environmental similarity of the canyons is superficial and that vegetational differences may be attributable to site differences; hence, a quantitative analysis of the relationship between vegetation and site is given below.

**Environmental differences among plots**

Before discussing correlations between vegetation and environment, the range of variation in environmental variables should be considered (Table 1). Moisture stress and elevation were so restricted in variation from site to site that statistical selection of these variables for explanatory power should be suspect on biological grounds. Other site factors (light, nitrogen, phosphorus) varied through a range that could conceivably affect the relative abundance of dominants. Variation in each potentially important environmental factor is considered below.

Average moisture stress was 3–4 bars (1 bar = 100 kPa) in all cases (Table 1), a low and narrow range. The higher stress in two plots may relate more to poor health of the sample trees than to site differences. The insignificance of differences in moisture stress within the range of sites sampled here is further suggested by the weak correlation of radial growth increments of the seven major species with precipitation (67 years of record, average $r^2 = 0.07$, maximum $r^2 = 0.14$ (method in McCune 1983)). It is likely, therefore, that water supplies in the canyon bottoms are fairly reliable, although moisture stress samples in drought years are needed to state this with confidence.

The yearly totals for potential direct incident radiation in the canyons are 85–95% of the radiation on flat topography (Table 1). This may be a higher percentage than one would expect, based on the large proportion of the sun’s trajectory that is blocked by the canyon walls. However, since the canyon bottoms are shaded primarily at low angles of the sun, much of the lost radiation does not contribute greatly to the yearly totals.

Foliar nitrogen was nearly identical among the canyons, although some differences were found between plots (Table 1). Foliar phosphorus varied considerably from plot to plot, though much of the variation was between canyons. There may be a north–south gradient in available phosphorus, despite the uniformity of the bedrock.

**Relationships between site and vegetation**

All of the analytical methods failed to account for most of the compositional variation with the measured site factors.

**Multiple regressions for individual species**

Relative dominance for two of the four species tested was somewhat predictable with measured environmental factors (Table 2). Residual compositional variation after removal of stand age (>89% of the variance remained for each species, see $R^2$ for stand age in Table 2) was partially explained in two species (*Thuja* and *Taxus*) by environmental factors, while regression coefficients were nonsignificant ($p > 0.10$) in both *Abies grandis* and *Picea*. Relative dominance of *Thuja* was greater on better lit sites, while dominance of *Taxus* was greater on sites with higher nitrogen.

**Ordinations of stands in environmental space**

Dominance types were poorly separated on even the best (Fig. 4) of 10 projections of stands onto pairs of environmental axes (all combinations of the following: stand age, moisture, nitrogen, phosphorus, and light (Fig. 4)). Again, *Thuja* domi-
nated more exposed sites, contrary to expectations, as discussed under results from multiple discriminant analysis. Sites dominated by *Taxus* tended to have more available nitrogen.

**Discriminant analysis**

DA was, at best, moderately successful in separating dominance types, using site factors (Table 3; Fig. 5). DA selected the most powerful site variables from the following: stand age, moisture, nitrogen, phosphorus, and light. Unequal variances and nonnormal distributions prevent a strict parametric interpretation of the F-ratio. However, the F-ratio suggests a loose separation of dominants in environmental space. Group separation is also expressed by the proportion of stands that are correctly classified, according to the discriminant functions. Since 4 of the 13 stands should have had a different dominant, based on their positions in environmental space, group separation was unclear.

The first two DA axes were related to light and nitrogen as shown by the standardized discriminant function coefficients (Table 3). Thus, there is a resemblance between the DA ordination (Fig. 5) and the ordination of stands in axes of light and nitrogen (Fig. 4). According to these figures, *Taxus* tends to dominate on high-nitrogen sites, *Thuja* on some high-light sites, and *Abies grandis* on a wider variety of sites. Interpretation of these results is problematic since relative placement of species on the light gradient is contrary to results from studies of longer gradient segments. *Thuja* is generally more successful on wetter sites on north slopes or in stream bottoms than *Abies grandis* (Antos and Habeck 1981; Pfister et al. 1977) in contrast to our finding greater dominance by *Thuja* on better lit sites. One possible reconciliation is that well-lit sites in the canyons may be warmer and less frost prone, these factors being more important to *Thuja* than moisture differences if the canyon-bottom sites are subirrigated. On the other hand, it is possible that the differences in light are insignificant and the correlation structure is spurious, DA merely having selected the best of a noisy set of variables. This is suggested by the weaker segregation of *Thuja* with the more finely divided dominance classification used on the direct ordination

**Regression of tree dissimilarity on environment**

Tree dissimilarity matrices were virtually unrelated to site dissimilarity matrices, with both the multiple regression approach (Table 4) and Mantel tests (*p* > 0.2 in all cases). This was true for size classes considered either separately or combined. Regressions using stepwise selection of three environmental difference variables had overall *R*² values of 0.10–0.14 (Table 4). Large differences in vegetation among plots were not always accompanied by large site differences, and conversely, similar vegetation need not occur on similar sites. In fact, sites that were more similar in moisture stress were less similar in vegetation (*p* < 0.05)!

**Convergence**

Convergence of the vegetation on various sites in a limited area towards a common composition does not often occur (Gleason 1926; Whittaker 1953; Olson 1958; Matthews 1979; Christensen and Peet 1981). However, fewer authors (Gleason 1926, Oliver 1981) have criticized the concept that within a local region, similar sites will support similar climax communities.

If our plots are converging towards a common composition, then similarity between plots should be higher in smaller size classes. This was not found (Fig. 6), except for the seedling
are graphed separately from comparisons between plots in different canyons. Vertical bars are 95% confidence intervals for the means. Comparisons between plots in the same canyon are also shown by (i) divergent compositional vectors representing vertical trends in ordinations of the transect data (Fig. 2 in McCune and Allen 1985) and (ii) age structures (Fig. 2) and size structures in the plots. The wide differences in the younger and smaller classes suggest that the plots will maintain considerable differences in composition, despite the similarity of the size structures in the plots. The wide differences in the younger and smaller classes suggest that the plots will maintain considerable differences in composition, despite the similarity of the sites. However, plots in the same canyon are more similar and more likely to converge than plots from different canyons (Fig. 6).

**Discussion**

About 10% of the compositional variation was attributable to measured site factors, based on multiple regression of compositional dissimilarity on differences in site variables (Table 4). The remaining 90% is attributable to historical factors, unmeasured site variables, suboptimal mathematical models, and imprecise measurements (descending order of importance in our estimation).

Since all sites had similar parent materials and topographic positions, measured site differences were small, and compositional differences were large (Table 1), we believe that additional unmeasured site variables are unlikely to explain much of the large residual variation in species composition. Historical factors are probably responsible for much of this variation, not unexpectedly, considering the insularity of the canyon-bottom communities, the similarity of sample sites, and the diversity of species capable of growing on a given site.

Following examples of how historical events may influence species composition, we discuss implications for applications of the climax concept.

**Compositional shifts with stand establishment**

Stand establishment provides the greatest opportunity for compositional changes among shade-tolerant species, since resources are temporarily freed from mature trees. The shade-tolerant tree species that often colonize a burn are long-lived, say 300 years (McCune and Allen 1985). Since on the average 99% of the stands in the canyons burned before an age of 300 years in the presettlement forests (McCune 1983), it follows that most of the dominant trees in the canyon bottoms arrived in the first wave of establishment, and successions between tolerant tree species during fire-free intervals were unlikely. Most of the opportunity for compositional flux among shade-tolerant species occurred, therefore, with disturbance, when the vagaries of seed production, weather, insects, and disease during a few years may be amplified to a compositional effect lasting hundreds of years.

Some examples follow. If two or more tree species can survive on a site, then the relative timing of good seed crops and weather conditions following disturbance may strongly affect the future species composition. Differential seedling mortality in a young stand from a single summer frost may be preserved as a local species composition that is more frost hardy than adjacent stands originating in normal years. The preference of deer for *Thuja* seedlings may affect some stands more than others, depending on the coincidence of stand regeneration and peak deer populations. Deer may have affected the regional abundance of *Thuja* seedlings in the nearby Clearwater drainage in Idaho (Habeck 1978).

The importance of local abundance in affecting stand establishment is particularly great in insular communities such as the Bitterroot Canyons. Small populations will have difficulties acquiring the space for which the species is best adapted. For example, *Thuja* is apparently restricted to a narrower range of sites and is less abundant than *Abies grandis* in the canyons. However, the abundance of *Abies* may restrict *Thuja* more than environmental tolerances would dictate, simply because *Abies* exerts a stronger immigration pressure on sites suitable for *Thuja* than *Thuja* itself. In other words, “possession is eleven points in the law” (Cibber 1697).

**Competition and forest dynamics**

We too found “alternate, stable, invasion-resistant communities” (Diamond 1975). However, there seems to be no reason to believe that these canyon-bottom communities are
"integrated by diffuse competition" or that the species obey "assembly rules," since we found no "forbidden combinations" (Diamond 1975) of the major shade-tolerant tree species.

This is not to say that competition does not occur in these forests. On the contrary, trenching experiments demonstrate root competition in similar moist forests (B. McCune, unpublished data). However, the rate constants for substantive effects of competition, e.g., exclusion of one species by another, are much too slow (relative to disturbance frequencies in the context of individual longevity) to play an overriding role in structuring these forest communities.

Applications

The utility of the climax concept depends on the degree of stand-to-stand similarity on similar sites (Whittaker 1953, p. 58). Climax communities are used as standards for comparison: standards for comparing sites on both local and regional scales, standards of relative stability for community dynamics, and standards for evaluating the effects of disturbance and pollution by humans. These uses of the climax concept (Whittaker 1974) require a stable and faithful expression of site factors by undisturbed vegetation.

Since pronounced differences in climax vegetation can be unrelated to site differences, the climax concept should be applied with caution. We would not, however, expect the degree of independence between site and vegetation that is found in the Bitterroot Canyons to be the rule (the influence of historical factors is dependent on the range of variation included in the sample (Grigal and Arneman 1970; McCune and Antos 1981; Wiens and Rotenberry 1981), the insularity of the communities, and the intensity of competition for scarce resources (Christensen and Peet 1981)). Since we studied insular sites with low environmental variability, site and vegetation were largely independent. While these conditions are extreme, they are not uncommon. A similar independence of site and species composition is to be expected in widely scattered woodlots in agricultural regions, isolated islands in bodies of water, alpine tundra on mountain peaks, and in any other set of samples taken from a narrow range of insular communities.

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