

Change in pattern diversity during secondary succession in Estonian forests

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Abstract. Comparisons of observed variance in species diversity ($exp H'$) and in species richness with expectation assuming a random and independent distribution of species are used to assess the relative importance during succession of niche limitation (Wilson, Gitay & Agnew 1987; limitation of the abundance or occurrence of species by competitive interactions) and nucleation (Yarranton & Morrison 1974; the development of a community through chance establishment or persistence followed by vegetative expansion from those nuclei).

Wilson, Gitay & Agnew (1987) and Palmer (1987) suggest a deficit (i.e. lower than expected) in variance of richness is consistent with a 'niche limitation' process where competitive sorting makes patches more similar in species number than would be expected. In contrast, variance that is greater than expected is consistent with and could result from underlying environmental heterogeneity (i.e. 'waterhole effect'). We extend these ideas to suggest that, in addition, a deficit in variance of diversity ($exp H'$) can be interpreted as indicating niche limitation. Further, we suggest that a deficit of variance in richness need not be interpreted as resulting from niche limitation, but could result from limited dispersal and establishment followed by localized spread that causes quadrats to have less compositional overlap than might be expected if species were distributed at random. However, there is little reason to expect that such nucleation would cause a similar reduction in the variance of diversity. First, $exp H'$ is relatively insensitive to the presence or absence of rare species, and second, if local competitive processes do restrict the values of $exp H'$ through some form of niche limitation, this could well be independent of the specific species involved. Thus, a combination of lower than expected variance in richness and high variance in diversity suggests nucleation to be important, particularly if the mean pairwise similarity between samples is lower than expected.

We first examine a secondary successional sere with stands representing post-logging and mature forest. The variance of diversity is low in the establishment phase, but not in subsequent phases where the tree canopy is well developed. Significantly low variance of species richness is observed in a young forest just entering the thinning phase. Thus, nucleation may be taking place in the establishment phase of forest development, and is almost certainly important in the early thinning phase. Second, we examine communities in the process of equilibration following fertilization, logging, and paludi-

fication. All these communities have a low variance in diversity ($exp H'$) suggesting niche limitation.

Keywords: Competition; Diversity; Niche limitation; Nucleation; Variance of diversity; Variance of richness.

Nomenclature: Kuusk (1972).

Introduction

Plant species co-occurrence and co-abundance as assessed by measures of similarity or association have provided the basis for numerous studies of plant community structure (Noy-Meir & van der Maarel 1987). The study of species diversity provides a potentially powerful alternative approach to the study of plant community structure.

Most diversity studies have focussed on alpha or point diversity, especially in relation to its correlation with environmental parameters. Somewhat less attention has been paid to beta diversity which is usually defined as change in species composition along an environmental gradient. A third type of diversity, within-community diversity or pattern diversity (sensu Pielou 1966; Lewin & Westman 1973; Whittaker 1977), has been studied considerably less. Pattern diversity is conceptually similar to beta diversity in that small-scale environmental variation generally exists within vegetation and is responsible for between sample variation in vegetation composition. Thus, the beta diversity associated with the small-scale turnover of species along microenvironmental gradients is responsible for some of what we recognize as pattern diversity (Palmer 1990; Palmer & Dixon 1990). The critical conceptual difference, however, is that while beta diversity explicitly reflects compositional variation in response to underlying environmental gradients, pattern diversity is generally based on an assumption of constant background environment, and consequently is typically assumed to

reflect primarily variation resulting from species interactions within the community.

One important component of pattern diversity is small-scale variation in diversity ($N_1 = \exp H'$; see Peet 1974) and species richness ($N_0 =$ species per plot or quadrat). Palmer (1987) used the variance test to investigate whether N_0 is more or less variable than expected under the null model of no species interactions, whereas Wilson (Wilson, Gitay & Agnew 1987; Wilson & Sykes 1988; Watkins & Wilson 1992) did the same by using Monte-Carlo methods to create a null model of the independent occurrence of species. In all these studies the authors reported statistically significant departures of variance from the predictions generated using their null models, departures they viewed as ecologically interpretable.

If diversity is strongly correlated with some environmental factor that exhibits within community variation, there will be more samples with high or low concentrations of species than would otherwise be expected. Pielou (1975) has described the occurrence of high diversity on certain types of sites as the 'waterhole effect'. Both Wilson, Gitay & Agnew (1987) and Palmer (1987) interpreted higher than expected variance to be due to such environmental heterogeneity. Palmer (1987) also found some sites with the variance in N_0 lower than expected, a result he suggested might result "if the community is saturated with species, or if species-rich areas have high competitive exclusion rates." Wilson, Gitay & Agnew (1987) also looked for low variance in N_0 as an indication of niche limitation (i.e. competitive limitation of the number of species that can coexist), but found little evidence for the generality of this effect (one case in five).

In this paper we further develop the interpretation of variance in diversity (sensu lato) to assess community structure as pioneered by Palmer (1987) and Wilson, Gitay & Agnew (1987), and apply it to study changes in niche structure during forest succession. In contrast to Palmer's and Wilson's studies, we use the heterogeneity form of diversity (N_1) in addition to species richness (N_0) so as to incorporate evenness in our calculations. Specifically, we use N_1 because it is sensitive, not just to competitive exclusion, but to niche structure differences as evidenced in the concentration of dominance (see Whittaker 1965). If species interactions constrain niche structure, the variance of N_1 should be lower than expected. Wilson, Gitay & Agnew (1987) were aware that N_1 might prove a more sensitive indicator of competitive interactions and niche limitation than N_0 , but chose to omit it from their study, in part because they were uncertain as to the most appropriate null model for comparison. In this paper we use the bootstrap-based null model devised by Zobel & Zobel (1988a) to examine

changes in pattern diversity during forest succession.

Although Wilson, Gitay & Agnew (1987) and Palmer (1987) interpreted a deficit in variance of N_0 as an indicator of niche limitation, this is not the only possible interpretation of such a result. Another possible mechanism that could generate this result is called, in its slightly different forms, nucleation (Yarranton & Morrison 1974), positive segregation (Pielou 1966), infiltration invasion (Wilson & Lee 1989) and nascent foci (Moody & Mack 1988). Nucleation is the process where individuals of various species arrive or persist at points, or nuclei, and then spread outward (often vegetatively) creating zones of local concentration of species. The role of nucleation in driving changes in within-community pattern has been elaborated by Greig-Smith (1952, 1964), Kershaw (1958), Yarranton & Morrison (1974) and Dale & Blundon (1990), among others. Initial establishment events provide nuclei for spread with the result that the pattern becomes more pronounced during early succession. Established clumps can also provide microsites for other species to invade. During succession, as the clumps grow, coalesce and break up, the pattern declines in intensity.

The impact of the nucleation process will be evident as long as species remain clumped near where they first became established so that they have lower probabilities of occurring elsewhere in the vegetation. During this period the pool of potential species available for any particular sample location will, effectively, be smaller than if species and their propagules were randomly distributed in the vegetation. This restriction in the species pool will translate directly into lower variance in the species number because high values will be less likely. However, there is less reason to expect an influence of nucleation on the variance of N_1 . If competitive interactions of species do restrict the realized range of N_1 through niche limitation, this could well be independent of the particular species involved. Further, N_1 is relatively insensitive to the presence or absence of rare species; what matters most is the relative distribution of dominance among the more important species. Thus, if there is niche limitation, we can expect it to be first evident in a deficit in the variance of N_1 , and only in the more extreme cases evident in a deficit of variance in N_0 . If there is a significant deficit in the variance of N_0 , but not in the variance of N_1 , nucleation is likely to be responsible.

A lower than expected mean pairwise similarity of samples would provide further evidence in support of active nucleation. If there is a deficit only in the variance of N_1 , we can expect niche limitation to be the underlying mechanism. If both N_0 and N_1 have variance deficits, the processes cannot be definitively separated, though high mean pairwise similarity would be consistent with

niche limitation and competitive sorting (assuming no environmental gradient across the site), whereas low similarity would be consistent with nucleation.

Study sites

The main study area is situated in Järvelja in south-eastern Estonia. The forest under investigation belongs to the *Aegopodium - Filipendula* site-type and is on a gleyic pseudopodzolic soil (gleic podzoluvisol; see Reintam 1987). Five communities of different successional age were studied: (1) 5-yr-old clearcut, (2 - 4) forests in which the mean ages of canopy trees were 30, 70, and 150 years respectively, and (5) mature forest. Using the standard four-stage model of forest development (Bormann & Likens 1979; Oliver 1981; Peet 1981; Peet & Christensen 1987), the study sites can be classified as belonging to the establishment (1), thinning (2,3), transition (4) and steady-state (5) phases.

Secondary forest succession in Järvelja has been described in earlier papers (see Zobel & Zobel 1988a, b). In a direct gradient analysis using log-linear models (Zobel & Zobel 1988b; see Austin, Cunningham & Fleming 1984; Austin, Nicholls & Margules 1990), the frequencies of 28 of 30 abundant (constancy > 9%), field-layer species showed statistically significant differences with successional age. The frequencies of 11 species increased, 11 decreased, and 6 were unimodal along the successional gradient.

Application of Ellenberg's indicator values (1979, 1982) demonstrated that earlier species were more shade intolerant, more hydrophilous, and slightly more nitrophilous (Zobel 1989). Soil conditions were consistent across all stages (Zobel 1990), except that five years post-logging the nutrient content, as indicated by nitrate nitrogen and pH, was higher in the upper layer of the humus horizon.

Three supplemental study areas illustrate changes in vegetation induced by field manipulations, either natural or planned. These sites were selected to represent community changes with strong competitive interactions between field-layer species.

The first supplemental site, Pikasilla, was a middle-aged, dry *Pinus sylvestris* forest of the *Vaccinium vitis-idaea* site-type in central Estonia. The site was fertilized ($N_{15}:P_{10}:K_{10}$) in spring 1987 and sampled in summer 1988. The untreated control is typical poor heath vegetation dominated by *Vaccinium vitis-idaea* and *Pleurozium schreberi*. After fertilization *Calamagrostis epigeios* and *Convallaria majalis* increased enormously, while the previous dominants decreased. Five new species invaded.

At the second supplemental site, Einby, two types of

vegetation change were observed in old-growth *Pinus sylvestris* forest of the *Vaccinium vitis-idaea* site-type. The first was in forest that had been cleared two years before with the result that shade-intolerant species such as *Calluna vulgaris*, *Lerchenfeldia flexuosa* and *Empetrum nigrum* had increased significantly relative to the control. The second type of change was progressive paludification where invading sphagna (*Sphagnum fallax*, *S. nemorum*, *S. warnsdorfii*), present in 80% of the quadrats, facilitate the invasion of mire and mesophytic species. Again, the dry forest was viewed as the control.

Tipu, the third supplemental site, also demonstrated progressive paludification, in this case for *Pinus sylvestris* - *Picea abies* forest with abundant bryophytes. The site was on the edge of a large bog where the ca. 30 cm of peat and the virtually complete cover by bryophytes (mainly *Sphagnum angustifolium* and *S. centrale*) indicated the first stage of paludification. Strong competitive effects of *Sphagnum* species on mesophytic species (*V. vitis-idaea*, *Dryopteris carthusiana*, and forest mosses), plus facilitative effects (sensu Connell & Slatyer 1977) on bog species (*Eriophorum vaginatum*, *Menyanthes trifoliata*), can be assumed. There was no control.

Field methods

The composition of each community was sampled using 32-40 randomly located, square, 1-m² quadrats. Soil samples were taken from all horizons in all quadrats, and cover percentages of bryophytes, lichens, herbs and dwarf shrubs were estimated for each quadrat. Further details of field methods are presented in Zobel (1989).

Early work by Greig-Smith and associates (see Kershaw & Looney 1985; Austin & Nichols 1988) suggested that the role of plant-plant interactions is typically important at small scales, but that the physical environment dominates at large scales. Consequently, niche limitation might be expected to be readily observed at small scales where plants are expected to interact directly, but to be relatively difficult to detect at larger scales because many small neighborhoods of interaction are averaged together. Wilson, Gitay & Agnew (1987), in a study employing quadrats from 0.0004 - 1.0 m², found relatively little evidence for quadrat size influence. However, Palmer (1987), using quadrats from 0.01 - 10 m², found that in all six of his case studies the smaller quadrats showed lower variance in N_1 relative to expectation than the larger quadrats. Although data were also collected for 100-m² plots, the present study was based exclusively on the 1-m² quadrats because these were considered the more likely to allow detection of differences in niche limitation.

Statistical methods

The statistical procedure is based on measuring the shift between two empirical distributions realized after recombining two-way tabular data of the importances of I ($i = 1, 2, \dots, I$) species in J ($j = 1, 2, \dots, J$) quadrats (samples) in two different ways.

First, m (we used $m = 1000$) bootstrap replicates (samples) are drawn from the set of J original quadrats. This is done by choosing randomly new sets of J quadrats from the original set with replacement, thus compiling m new tables. In any of the tables each quadrat can be represented several times or not at all. Subsequently, the value of the community characteristic is evaluated for each table. After counting the values that fall into previously fixed subintervals of the range of the characteristic, one obtains the empirical bootstrap frequency distribution which approximates the hypothetical distribution that would be observed after repeating sampling m times.

Second, an analogous distribution is computed for the null model conditions. As species distributions are considered independent, tables are compiled after bootstrapping all species separately. For each I species, a bootstrap sample is drawn from the corresponding set of abundance (e.g. cover, presence/absence) values. For example, to get the first row in such a table, we choose randomly with replacement J values from the set $a_{11}, a_{12}, \dots, a_{1j}$, where a_{ij} is the abundance estimate of the i -th species in the j -th quadrat. The I independent bootstrap samples are compiled and the value of the community characteristic is computed. This procedure is repeated m times and the corresponding m values of the community characteristic form the second null distribution ('independent random distribution', of Zobel & Zobel 1988a) which is compared with the first bootstrap distribution. The comparison is made as in the Kolmogorov-Smirnov two-sample test, by measuring the relative shift between the two empirical distributions. The resulting statistic \mathbf{W} (with range -1 to 1) is derived from the Kolmogorov-Smirnov statistic (with range 0 to 1) by assigning it a sign depending on the direction of the shift. A zero value of \mathbf{W} indicates full coincidence of the two distributions and thus validity of the null model.

We employed variance of N_1 as a measurable community characteristic that responds to variation in niche structure. Deviation of observed variance from expected was computed as described above resulting in the statistic \mathbf{W}_{VD} ($-1 \leq \mathbf{W}_{\text{VD}} \leq 1$). The statistic was designed to have positive values indicate low variance and negative values high variance. The analogous statistics based on variance of species richness (N_0) and mean pairwise similarity (percentage similarity) are denoted as \mathbf{W}_{VR} and \mathbf{W}_{S} respectively (positive values of \mathbf{W}_{S} indicating

greater similarity than expected).

The Kolmogorov-Smirnov test for significance is not appropriate for use in the above described procedure because this test assumes independent random sampling of an infinite population (Pratt & Gibbons 1981). In the case of bootstrap distributions, this basic assumption is violated and statistical inference could be biased. Also, we cannot say with certainty that in case the null hypothesis is valid the two distributions compared using this procedure will necessarily be identical for each particular random set of quadrats (although this would be true if we used actual resampling instead of bootstrap-sampling to evaluate the deviation from the null model conditions).

To overcome the problem of bias in the statistical inference, we empirically estimated the significance levels (p values) for the calculated \mathbf{W}_{VD} and \mathbf{W}_{VR} , again using bootstrap methods. For all five successional stages, 200 bootstrap replicates were drawn from the original set of quadrats (choosing with replacement an identical number of quadrats) and for each of them \mathbf{W}_{VD} and \mathbf{W}_{VR} were determined. The aim of the procedure was to test the null hypothesis that \mathbf{W} is not different from zero. Here, unequal proportions of negative/positive \mathbf{W} -values in the bootstrap distribution is evidence against the null hypothesis, and the empirical probability that \mathbf{W}

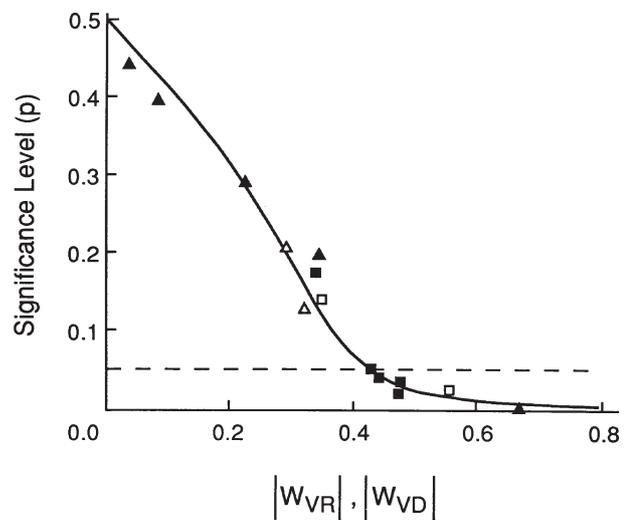


Fig. 1 Empirically estimated significance levels (p) for the absolute values of \mathbf{W}_{VD} (square symbols) and \mathbf{W}_{VR} (triangular symbols). The p 's were determined for the original data tables describing the five successional stages in Järvelja (filled symbols), and for two additional subsets of quadrats chosen randomly from the original 5-yr and 30-yr old forest data (empty symbols). The curve describing the p vs \mathbf{W} relationship is hand-drawn. The $p = 0.05$ significance level is indicated by the broken line.

takes values with sign opposite to the original (mean) value can be treated as an estimate of the significance level for the statistic. Such an estimate of p is not dependent on m (number of bootstraps in calculating \mathbf{W}), as long as m is sufficiently large.

In order to clarify the possible effect of data table size (the original dataset includes tables with 32-40 quadrats), p was also estimated for \mathbf{W}_{VD} and \mathbf{W}_{VR} in two randomly selected sub-sets of 20 quadrats in the case of the first two successional stages. Results of these computations indicate that in this study p values can be assigned to \mathbf{W}_{VD} and \mathbf{W}_{VR} according to a single rule (Fig. 1). Also, there is no apparent reason for correcting the p vs \mathbf{W} relationship for data table size, as long as data tables with 20-40 quadrats are analyzed. The graph implies that the $p = 0.05$ critical value of \mathbf{W} , 0.425, is applicable for all the datasets studied. As such empirical estimation of significance levels is extremely computer-intensive, p values were assigned to \mathbf{W}_{S} 's for all plots and to all \mathbf{W} 's for additional datasets by extrapolation from the relationship in Fig. 1.

For comparison of observed variance in N_1 with that expected from a null model, we used the bootstrap technique described above (also see Zobel & Zobel 1988a) for several reasons. (1) In contrast to Palmer's (1987) method, this method allows a test against the null hypothesis of independent species distributions for any community characteristic that is evaluated as a single numerical measure (e.g. mean pairwise similarity among samples, mean pairwise correlation between species, variance in species richness, variance in *exp H'*). (2) No assumptions are made concerning species distributions; the bootstrap procedure uses the observed empirical distributions that form the initial data table. Finally, (3) the observed and expected error distributions (approximated by bootstrap distributions) of a community characteristic are examined instead of simply the observed and expected point estimations. In this way, along with the variances of the error distributions, we also determine their shape and possible systematic biases in estimating the mean, such as might result from non-randomly placed quadrats.

Results

Experiments with artificial data

We first present some simple examples to illustrate the differences in behavior of the variance of N_1 (\mathbf{W}_{VD}) and mean pairwise similarity (\mathbf{W}_{S}) generated by extreme data structures. Mean pairwise similarity of samples can be of value for identifying variation within communities unrelated to diversity. The example data

demonstrate situations where differences in species replacement rates along compositional gradients can be detected in species abundance and diversity values, but where N_0 shows no effect.

These artificial data were generated by randomly sampling three different artificial coenoclines, each containing two species. The coenoclines were designed to represent situations where there is (1) rapid replacement of one species by another resulting in two different communities with a narrow zone of overlap (Fig. 2a), (2) a zone of dominance by each species separated by a broad zone of coexistence (Fig. 2b), and (3) simple linear replacement of one species by the other along the underlying environmental gradient (Fig. 2c).

Each of these three coenoclines was sampled 1000 times by means of 10 randomly placed plots. For each set of plots, the values of \mathbf{W}_{VD} and \mathbf{W}_{S} were computed. The corresponding frequency distributions of \mathbf{W}_{VD} and \mathbf{W}_{S} are shown in Fig. 2. \mathbf{W}_{VD} can be seen to measure the strength of interactions that the three situations were designed to characterize, whereas \mathbf{W}_{S} hardly detects any difference. Alternatively, \mathbf{W}_{S} would be the better indicator if the intent were to detect compositional differences where N_1 was relatively constant. Note that the value of \mathbf{W}_{VR} (based on variance of richness) is necessarily zero for all three coenoclines.

Successional trends in \mathbf{W}_{VD} and \mathbf{W}_{VR}

The values of \mathbf{W}_{VD} for the five stands in the successional sere are presented in Fig. 3. In the 5-year-old clear-cut a strong variance deficit is observed. For all other stages, especially those with a well-defined tree layer, there is a variance excess (i.e. the variance of N_1 is markedly greater than predicted by the null model). In all but one case (middle-aged forest) the deviation from the null model is significant ($p < 0.05$). The differences between the later forest stages are small.

To gain further information about changes in niche structure with succession, we determined \mathbf{W}_{VR} for the five successional stages (Fig. 3). The rather small positive value of \mathbf{W}_{VR} in the initial stage suggests the deficit in variance of N_1 (that is, the strongly positive \mathbf{W}_{VD} value) was caused by some mechanism other than nucleation. In contrast, the extremely high value of \mathbf{W}_{VR} ($p < 0.005$) in the early thinning phase with \mathbf{W}_{VD} much less than zero indicates nucleation. The evidence for nucleation drops off in the late thinning phase (i.e. \mathbf{W}_{VR} is not significantly different from 0) and cannot be detected in the last two stages.

Mean similarity (\mathbf{W}_{S}) is consistently higher than predicted from the null model, though only in the case of the clear-cut area was the deviation from the null model significant ($p < 0.005$). This is probably because our null

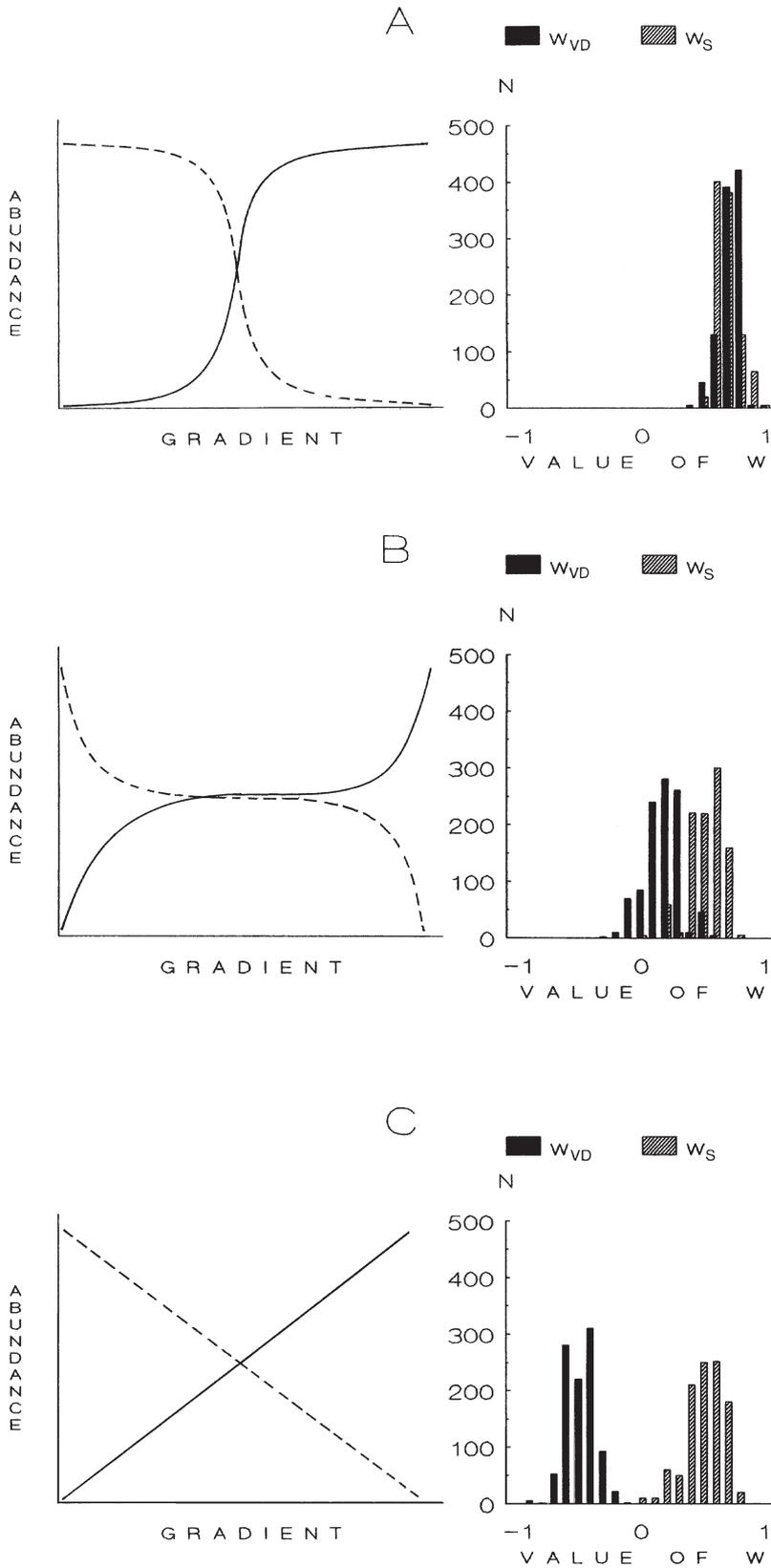


Fig. 2. Three simulated coenoclines with two species (solid and broken line). Frequency distributions of the two statistics determined by randomly sampling the coenoclines are shown on the right. W_{VD} (solid bars) measures the deviation of the variance in diversity from that predicted with the null model, positive values indicating a variance deficit. W_S (striped bars) shows the deviation in mean pairwise similarity from that expected from the null model.

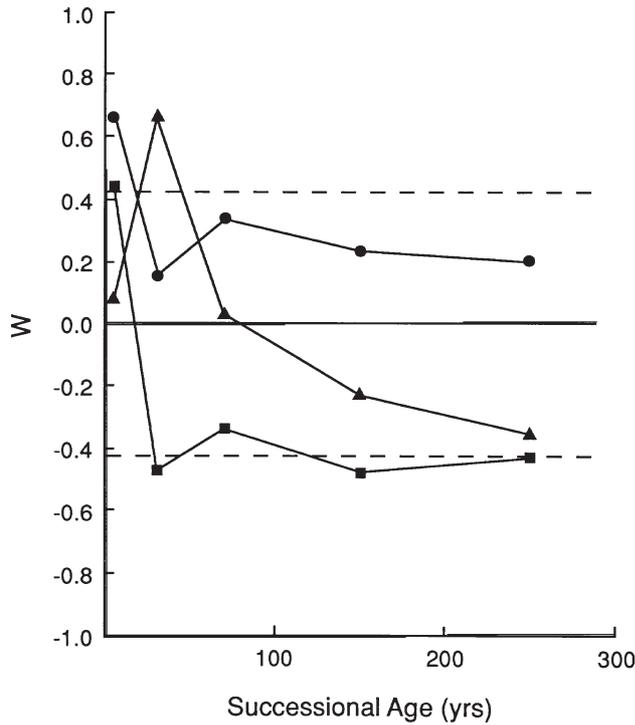


Fig. 3. Change during secondary forest succession in W as based on variance of diversity (W_{VD} = ■), variance of richness (W_{VR} = ▲), and mean pairwise similarity (W_S = ●). Positive values of W indicate a deficit in variance of diversity, a deficit in variance of richness, or greater than expected mean similarity, respectively. The broken lines indicate the $p = 0.05$ critical value for W .

model places no constraints on the total abundance that can be encountered in a stand. A somewhat different null model, where the stand totals were bootstrapped and the bootstrapped species values were adjusted accordingly, might have produced W_S values closer to 0. Note, however, that mean similarity is very high in the 5-yr stand, but exhibits a pronounced dip in the 30-yr stand. The maximum for W_S in the 5-yr stand is consistent with our niche limitation interpretation because it suggests the individual samples are more similar than by chance alone, which could result from competitive sorting constraining the possible niche structure. Further, the minimum in W_S in the 30-yr stand is consistent with the nucleation hypothesis because nucleation is characterized by numerous patches which differ from each other in species but not necessarily species richness or relative abundances.

A possible explanation for the high variance in N_1 in mature stands is heterogeneity of the abiotic environment, the explanation invoked by Palmer (1987) and Wilson, Gitay & Agnew (1987). In addition, heteroge-

Table 1. Numbers of field-layer species, mean species richness per quadrat (N_0), and mean species diversity (N_1) for 32 - 40 1-m² quadrats in each of five stands representing a secondary successional sequence.

Successional stage	Number of species	Richness per 1 m ²	Diversity ($exp H'$)
5-yr-old clear-cut	64	13.6	4.9
Young forest	44	10.2	5.3
Intermediate-aged forest	43	10.3	5.3
Submature forest	38	10.0	5.5
Mature forest	41	9.9	5.7

neity in the light environment could result from irregularities in the canopy. Nevertheless, when the early successional stand and stands representing subsequent stages are compared in the field, it appears that there are insufficient between-stand differences in environmental heterogeneity to account for the difference in N_1 variance observed. The variance in soil conditions does not appear to change during succession except in mature forests where wind-throw pits and mounds occur.

The total number of field-layer species, richness per 1 m² and species diversity (N_1) for each successional stage in Järvelja are shown in Table 1. The total numbers and the mean values of richness for forest stages fall within the narrow ranges 38 - 44 and 9.9 - 10.3 respectively. Slightly higher richness was observed in the establishment phase community as some shade intolerant pioneer species, as well as more hydrophilous species which did not occur in the closed forest, were found in the clear-cut area. This can be explained partially by the increase in soil moisture after logging due to reduced transpiration, and perhaps also by lower competitive preemption of resources as reported by Christensen & Peet (1984). Species diversity is lower in the early successional community due to strong dominance by such species as *Calamagrostis canescens*, *C. epigeios*, *Rubus idaeus* and *Filipendula vulgaris*.

To further test the effectiveness of W_{VD} for revealing the strength of competitive interactions we applied the method to data from the three supplemental study areas (Table 2). All of these sites had experienced recent changes in environmental conditions (e.g. fertilization, increased soil moisture, increased light) and had also experienced consequent changes in community composition. Because new species had invaded and population densities of some species had increased considerably, competitive interactions can be assumed to have changed. In each of these cases a deficit in variance of N_1 (i.e. positive values of W_{VD}) was observed, in one case significant at $p < 0.01$. In all control situations where

Table 2. Values of W_{VD} for supplemental study areas, indicating a deficit (positive values) or excess (negative values) of variance in species diversity (N_1) relative to values predicted using a null model with independent, randomly distributed species.

Site	'Treatment'	Values of W_{VD}	
		Treated	Control
Dry <i>Pinus</i> forest in Pikasilla	Fertilization by N_{15} : P_{10} : K_{10} in 1987, sampled in 1988	+ 0.108 ($p \approx 0.40$)	- 0.089 ($p \approx 0.45$)
Dry <i>Pinus</i> forest in Einby	Logging in 1982, sampled in 1987	+ 0.138 ($p \approx 0.35$)	- 0.884 ($p < 0.005$)
Dry and moist <i>Pinus</i> forests in Einby	Progressive paludification of forests near the edge of a transitional mire	+ 0.298 ($p \approx 0.20$)	- 0.884 ($p < 0.005$)
Moist, mixed forest in Tipu	Strong paludification of forest near the margin of a bog	+ 0.688 ($p < 0.01$)	-

environmental conditions were not changing, an excess of variance (negative values of W_{VD}) was recorded, in two cases significant at $p < 0.005$. These results are consistent with niche limitation taking place in the equilibrating stands, plus they suggest strong interactions in these transient communities.

Discussion

The results from the supplemental study areas indicate that a deficit in variance of N_1 is often associated with transient conditions. These special cases mainly represent situations where one or several species increase quickly and temporarily preempt a large portion of the available resources. Similarly, the results from Järvelja suggest N_1 variance deficits to characterize the establishment phase community, but that all the older phases, which have had time to reequilibrate, are characterized by a high excess of variance.

The clear-cut area is overgrown by taller dominants (*Calamagrostis canescens*, *C. epigeios*, *Rubus idaeus*, *Filipendula ulmaria*), but with most of the forest species persisting despite considerable decreases in abundance. The simultaneous weak deficit in variance of N_0 and strong deficit in variance of N_1 precludes clear discrimination between nucleation and niche limitation as the primary mechanisms responsible for pattern diversity in this phase of community development. However, the

near zero value of W_{VR} suggests niche limitation to be more likely, as does the high value of similarity (W_S).

A clearer situation is observed in the young, 30-yr-old forest where N_0 exhibits a strong variance deficit, but the variance of N_1 shows an excess. These results are consistent with nucleation as a structuring mechanism. The nucleation process begins with the formation of a closed tree canopy which takes place 15–20 yr after logging. Rapid changes occur in the field layer as most of the light-demanding species disappear, though the vegetation of the 30-yr-old forest is already quite similar to that of older stands. Rapid re-establishment of the forest community after canopy closure, starting from the sparse patches (nuclei) of forest species which have survived, can be the reason why nucleation becomes pronounced only during the transition from the establishment to the thinning phase. Closed forest species, which do not regenerate much under a dense canopy of light-demanding herbs and grasses, become able to expand quickly, both underground (*Mercurialis*, *Aegopodium*) and above-ground (*Galeobdolon*) following tree canopy closure. After most of the early successional species have disappeared, clumps of these dominants rapidly increase and preempt available free space. At this stage, relatively large but low diversity patches have formed which differ in dominants, while there are few quadrats with high numbers of species. This interpretation is supported by the associated decline in mean similarity.

The process of nucleation whereby the forest field layer is re-established is no longer evident in the intermediate-aged (70-yr) forest; W_{VR} has already dropped to nearly 0. In the two last stages, as forest development continues, variance of N_0 and N_1 increases, probably in response to 'niche differentiation' (Wilson, Gitay & Agnew 1987). That is, different numbers of niches are available in different microsites. This change could be due to the increased correlation between microsite conditions and diversity which occurs during forest development and which leads to greater beta diversity (Christensen & Peet 1984; Peet & Christensen 1988, Palmer 1990).

Physical site conditions did not change during the succession except in the last mature stage (for soil conditions see Zobel 1990), so the differentiation of niches cannot be the result of increasing environmental heterogeneity. The increased sorting of species can only be of biological origin, perhaps through intensified competition or perhaps caused by the influence of tree-layer species on light conditions or strength of root competition.

Conclusions

Evidence from measures of variance of N_0 , N_1 , and mean pairwise similarity show patterns of vegetation response to disturbance consistent with results from earlier studies of spatial pattern (e.g. Greig-Smith 1952; Pielou 1966), and dominance diversity relations (e.g. Whittaker 1965; McNaughton & Wolf 1970). Specifically, recovery from a moderate disturbance is generally accompanied by rapid growth of a few potential dominants with the result that a deficit in variance of N_1 can be observed. When the disturbance is more severe and results in destruction of the original stand of vegetation, recovery is slower and often contains one or more early stages where nucleation is a dominant structuring process. The techniques we have developed should allow researchers to examine other successional sequences to test the generality of these results.

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