

# U.S. NATIONAL FOREST MANAGEMENT ACT, FOREST ECOSYSTEMS DIVERSITY, AND DIVERSITY PROFILES

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**Abstract:** The National Forest Management Act of the United States (NFMA) requires that management practices maintain the diversity of forest ecosystems. An 8-year study of plant community structure and succession in managed coastal plain pine plantations and a 7-year study in an oldgrowth Douglas-fir forest following clearcut logging provide data sufficient for preliminary assessments in the spirit of NFMA.

Continuously remeasured abundances of *all plants* in second-growth pinelands and in young (< 5-year-old) plantations established by clearcutting, site preparation, and planting under two very distinct management regimes show that plant communities comprising the young plantations are more diverse than were communities comprising the antecedent second-growth forests. An analysis of similar data from pre- and post-logging periods in an old-growth Douglas-fir forest show similar results.

Recent theory is described and illustrated, including concepts of intrinsic diversity. Diversity profiles for the plantations and second-growth pine and pre- and post-logging Douglas-fir communities show that the results are index free.

## Introduction

The National Forest Management Act (NFMA) of the United States addresses the importance of information on the composition and succession of plant communities in managed forests. Such information is rare because of (i) the cost and time commitments required by oft- and long-repeated, comprehensive vegetation surveys, (ii) the traditional tendency of ecologists to concentrate on natural, or at least long undisturbed systems, and (iii) the nearly universal neglect of uncommercial species in routine inventories of managed forests. However, NFMA and related regulations require that management practices maintain the diversity of all plants (Federal Register 43(170): 39046, Federal Register 44(88):26583), based on quantitative comparisons of the diversities of managed and unmanaged forests as supporting evidence (Patil and Taillie 1982). In such assessments it is explicitly recognized one must learn what species comprise different communities and in what abundances, for it is in these ways that biological diversity is expressed (Federal Register 44(181):53975, Patil and Taillie 1982). Taken literally, the NFMA requires production functions for all plant species.

In the Southeastern Coastal Plains, comprehensive surveys of the vegetation on two experimental watersheds deliberately subjected to two quite distinct management regimes have been in progress since 1977. These watersheds were chosen to be representative of flatwoods, the dominant forest type in the slash pine ecosystem, and

the management regimes were designed to bracket those most common in the region. Hence, these surveys contain considerable information about plant composition and succession in the slash pine ecosystem: one of the most intensively managed forest ecosystems in the world.

In the western Cascades of Oregon, similar comprehensive surveys were begun in 1962 in three areas of an old-growth Douglas-fir forest. In 1963, the three areas were clearcut and a year later the slash was broadcast burned. All information on species composition for the permanent plots located in these areas in Oregon is taken from Dyrness (1973), with his kind permission. This information enables us to compare diversity trends following clearcut management in two different communities found, quite literally, at opposite ends of our country.

Much has been learned recently about the concept of species diversity and techniques for measuring it (Patil and Taillie 1982, Grassle *et al.* 1979). Compelling definitions of species diversity have been given along with unified definitions of popular indices (Patil and Taillie 1982). More than that—concepts of intrinsic diversity orderings have been given along with graphical techniques for discovering such orderings when they exist (Taillie 1979; Patil and Taillie 1979a, b; Patil and Taillie 1982).

Such analyses of the managed slash pine and Douglas-fir successional data presented here are, we believe, the most rigorous and comprehensive so far presented in the spirit of the NFMA.

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### Slash pine ecosystem

The study site is approximately 40 km north of Gainesville, in Bradford County, north central Florida. Climate is subtropical, humid, with about 135 cm of annual rainfall. Average temperature is about 20° C. Frost-free growing season is about 275 days. Topography of the study site is characteristically flat with elevations ranging only from about 43 to about 45 m.

Preharvest vegetation was typical of many flatwoods forests. Moderately well-drained soils (Arenic Paleudults) were dominated by an overstory of slash pine (*Pinus elliotii*) and longleaf pine (*Pinus palustris*) with an open understory of palmetto (*Serenia repens*) and gallberry (*Ilex glabra*). Vegetation characteristic of the poorly-drained spodosols (Ultic Haplaquods) had a thinner overstory with less longleaf pine present. The understory was dense with fetterbush (*Lyonia lucida*) and staggerbush (*Lyonia ferruginea*) occurring as common components. Cypress (*Taxodium distichum*) dominated the overstory, and fetterbush the understory on very poorly drained soil (Arenic Paleaquults).

On the 67-ha Watershed 1 (WS 1), pinelands comprised 49% of the watershed while a shallow, mixed pine and hardwood swamp occupied the interior 51% of the site.

On the 49-ha Watershed 2 (WS 2), pinelands comprised 74% of the area, and several scattered, mostly hardwood swamps occupied the remaining 26%. For a more detailed description of the study site see Conde *et al.* (1983a, 1983b).

### Douglas-fir ecosystem

This study site is located in the H.J. Andrews Experimental Forest in the western Cascade Mountains of Oregon. Annual precipitation averages about 230 cm, with summers very dry. In contrast to the flat topography of the slash pine ecosystem, slopes here are generally steep, averaging close to 60%.

Treatment was applied to three distinct clearcuts totaling 25 ha located within a 117-ha watershed. Prior to clearcut logging, overstory vegetation consisted primarily of (300 to 500 years) old-growth Douglas-fir (*Pseudotsuga menziesii*) and various age classes of western hemlock (*Tsuga heterophylla*), with lesser amounts of western redcedar (*Thuja plicata*), sugar pine (*Pinus lambertiana*), big-leaf maple (*Acer macrophyllum*), and dogwood (*Cornus nuttallii*). For a more detailed description of the climate, geology, soil, and undisturbed vegetation of the area, see Rothacher *et al.* (1967).

### Methods: Slash pine ecosystem

#### Treatments

Pinelands of WS 1 were clearcut harvested in November and December 1978. All merchantable pine trees were felled, delimbed, sectioned, and stacked by hand for transport from the woods by a small tractor. Logging debris and residual vegetation were chopped with a roller

drum chopper in April and again in August 1979. Planting beds were formed in September and October by a single pass of a bedding harrow, and machine planted in November 1979 with a nominal 1,850 1-0 slash pine seedlings per hectare.

The interior swamps were not disturbed on either watershed.

Pinelands of WS 2 were clearcut harvested also in November and December 1978. All merchantable pine trees were sheared at the stump and stacked by a heavy, articulated, rubber-tired feller buncher. Stacks of trees with crowns intact were dragged by large skidders to central loading areas where tops were severed and tree-length boles were loaded on trailers. Resin-soaked stumps were collected and removed from the site. Even prior to site preparation, residual vegetation was considerably reduced by these machines. Harvested portions of the watershed were burned in May 1979. Woody material surviving the fire was pushed into parallel windrows (of about 2.5 m<sup>2</sup> cross-sectional area and approximately 47 m apart) with a large tractor. Inadvertently substantial litter and soil was also displaced (Morris *et al.*, 1983). Areas between windrows were disced in August with an agricultural offset harrow-creating a relatively clean mineral soil surface. Machine bedding and planting by November 1979 with 1,850 slash pine seedlings per hectare was conducted as on the companion watershed.

Management regimes for southern pine plantations vary by site and ownership. Regeneration regimes commonly practiced on a large-scale are all intermediate in destructiveness between the regimes imposed on WS 1 and WS 2; hence those regimes may be called minimum and maximum treatments, respectively.

#### Surveys

In 1977, a 100-m grid was surveyed and permanently marked on each watershed. Twenty-seven of the resulting grid points on WS 1 and 18 on WS 2 were randomly selected for permanent transects. Three 10-m transects were surveyed beginning 10 m from these monumented grid points. All plant species intercepting a vertical projection of these transects were identified and extent of crown cover was measured. In the summers of 1980, 1982, and 1984 those 26 transects on WS 1 and 24 transects on WS 2 that fell wholly within the areas harvested, site prepared, and planted were thrice resurveyed using exactly the same techniques. Only crown cover data from these 26 + 24 transects are reported in this paper.

### Douglas-fir ecosystem

#### Treatments

The same treatment was applied to all three clearcuts studied in Oregon. After permanent plots were located and data taken from them in 1962, the area was clearcut logged. One year later, after data had been once again taken from the plots, the remaining slash was broadcast burned. However, due to the topography of the area and

unequal distribution of the slash, some plots were more severely burned than others (Dyrness 1973). This is an inevitable occurrence in an area with steep slopes, and so data from all plots in the three clearcuts were combined.

### Surveys

Prior to logging in the summer of 1962, 61 permanent plots were placed at 30.5-m intervals along randomly-located transects in the three cutting units. The plots were square, 2 m on a side, with one-quarter of each plot subdivided into nine subplots. Crown cover of shrubs and trees up to 6 m in height occurring within each plot was estimated and recorded by species. For herbaceous and low shrub species (< 0.6-m tall), percent crown cover on each 0.33 m<sup>2</sup> subplot was estimated and recorded by species. Plots were inventoried in late July or August of 1962, 1963, 1964, 1966, and 1968 (Dyrness 1973).

### Analytical Procedures

Two graphical methods were used to determine a partial intrinsic diversity ordering of the plant communities a year before and 1, 3, and 5 years after treatment. For the young slash pine plantations, the analytical method employed was simply that of graphing *relative diversity profiles* (Patil and Taillie 1979 a, b, 1982; Taillie 1979), where «relative» derives from the fact that plantation diversity profiles were always contrasted with diversity profiles for the antecedent second-growth forests. For the data on the old-growth Douglas-fir forests, profiles of the  $\Delta\beta$  parametric family of indices (Patil and Taillie 1979b) for the years 1962, 1963, 1964, 1966, and 1968 were drawn.

Data for WS 1 consisted of *ranked abundance vectors* (Patil and Taillie 1982):

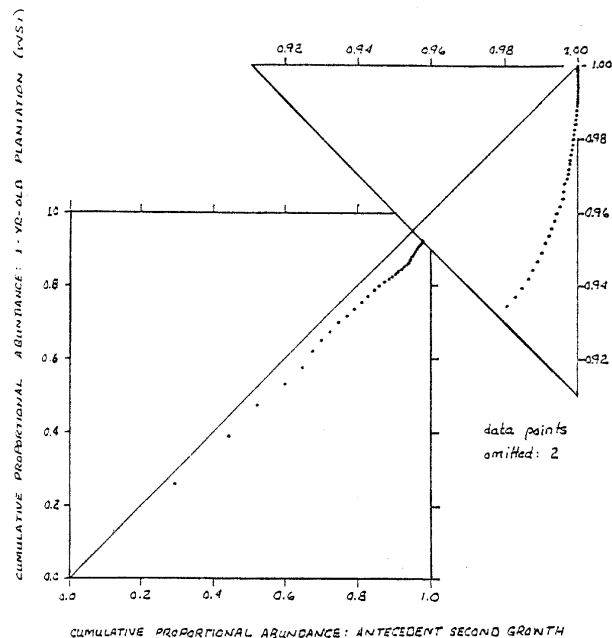


Fig. 1. Relative diversity profile (based on measured crown cover of all plants) for 1-yr-old plantation on minimum treatment watershed 1 in pine flatwoods of north Florida.

$$i\mathbf{m} = (i\mathbf{m}_1 \geq i\mathbf{m}_2 \geq i\mathbf{m}_3 \geq \dots \geq i\mathbf{m}_{S_i}) ,$$

where  $i = -1, 1, 3, \text{ or } 5$  to denote time of survey as pretreatment or plantation age 1, 3, or 5 years, respectively,

$i\mathbf{m}_j$  = measured proportional abundance (as indicated by crown cover) of the  $j$ th most abundant species at time  $i$ , and lowercase  $m$  is a reminder that data are from WS 1, the minimum treatment watershed.

Exactly analogous data from WS 2, the Maximum treatment watershed, are denoted

$$i\mathbf{M} = (i\mathbf{M}_1 \geq i\mathbf{M}_2 \geq i\mathbf{M}_3 \geq \dots \geq i\mathbf{M}_{S_i}) .$$

In order to discover whether any intrinsic diversity orderings existed between plant communities comprising the second-growth forests and the two plantations at any age ( $i = 1, 3, 5$ ), we plotted six relative diversity profiles:

$$\begin{array}{llll} 1\mathbf{m} & \text{versus} & -1\mathbf{m} & (\text{Fig. 1}), \\ 3\mathbf{m} & \text{versus} & -1\mathbf{m} & (\text{Fig. 2}), \\ \dots & \dots & \dots & \dots \\ 5\mathbf{M} & \text{versus} & -1\mathbf{M} & (\text{Fig. 6}), \end{array}$$

where  $1\mathbf{m}$  versus  $-1\mathbf{m}$ , for example, consists of the successive data points (Figure 1, beginning lower left)

$$(x_1, y_1) = (-1\mathbf{m}_1, 1\mathbf{m}_1),$$

$$(x_2, y_2) = (-1\mathbf{m}_1 + -1\mathbf{m}_2, 1\mathbf{m}_1 + 1\mathbf{m}_2),$$

$$(x_3, y_3) = (-1\mathbf{m}_1 + -1\mathbf{m}_2 + -1\mathbf{m}_3, 1\mathbf{m}_1 + 1\mathbf{m}_2 + 1\mathbf{m}_3),$$

...

Notice that if the  $J$ th point in this construction plots below the line  $y = x$ , i.e., if

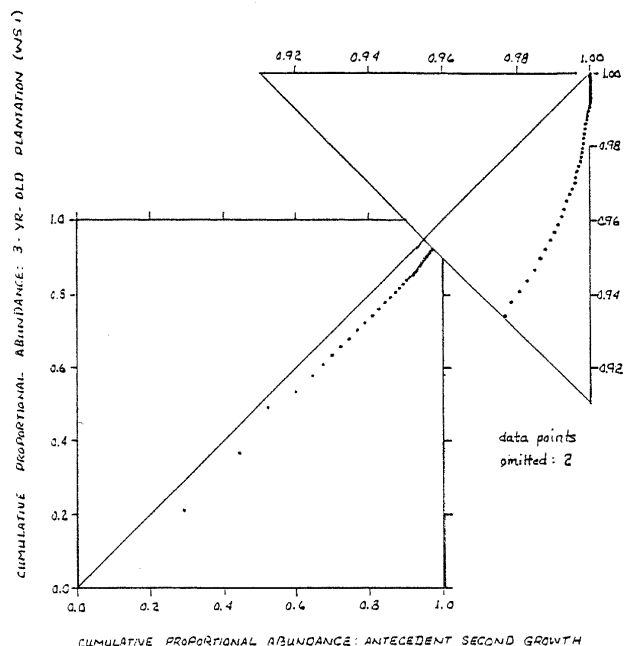


Fig. 2. Relative diversity profile for 3-yr-old plantation on watershed 1.

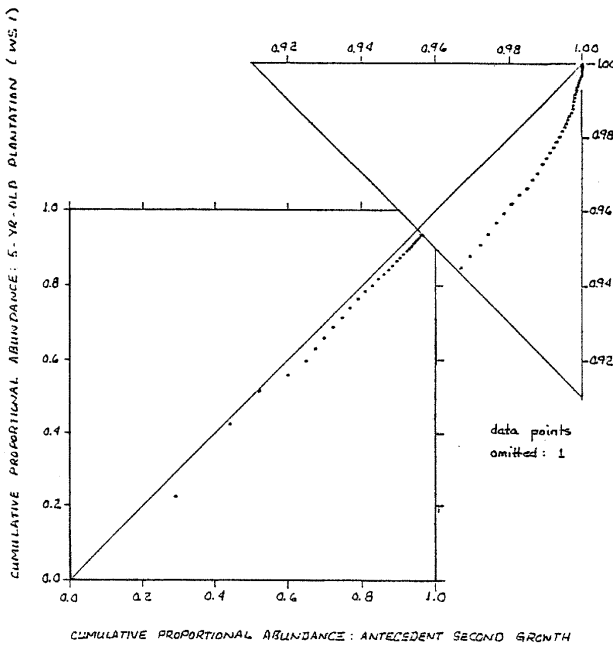


Fig. 3. Relative diversity profile for 5-yr-old plantation on watershed 1.

$$y_j = \sum_{j=1}^J 1m_j < \sum_{j=1}^J -1m_j = x_j$$

that means the  $J$  most abundant plants in the 1-year-old plantation were proportionally less abundant in that community than were the  $J$  most abundant plants in the antecedent second-growth forest.

Figures 2-6 were similarly constructed, and have the same property.

Data for the Douglas-fir forests consisted of (unranked) abundance vectors (Patil and Taillie 1979)

$$\pi = (\pi_1, \pi_2, \dots, \pi_s)$$

where  $\pi_j$  = proportional abundance of species  $j$ ,

$$\sum_{j=1}^s \pi_j = 1, \text{ and}$$

$s$  = total number of species present.

In this case, proportional abundance was measured in two different ways: First, as the proportion of the total crown cover on the sample plots belonging to species  $j$ ; and second, as the proportion of total species-plots belonging to species  $j$  (a species-plot is the occurrence of a given species on a given plot; a plot possessed with twelve different species has twelve species-plots). In the second case,  $\pi_j$  may be interpreted as the proportion of species plots belonging to species  $j$ . Surely, this is a measure of relative abundance. We term this measure species-plot frequency. Measures of abundance, other than frequency or cover, such as total or foliage biomass belonging to species  $j$ , are

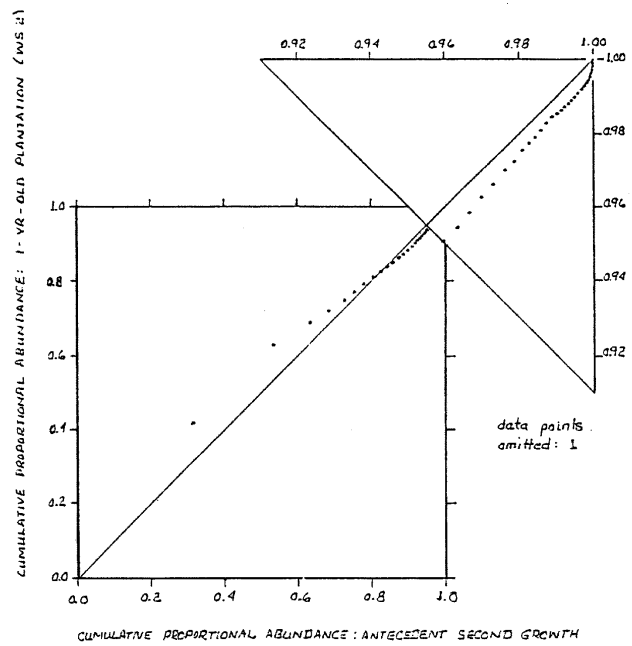


Fig. 4. Relative diversity profile for 1-yr-old plantation on maximum treatment watershed 2 in pine flatwoods of north Florida.

appropriate when such data are available (Conde *et al.* 1983a, b).

Given the abundance vector, we then calculated

$$\Delta_\beta(i) = (1 - \sum_{j=1}^s \pi_j \beta_j) / \beta \quad -1 \leq \beta \leq +1,$$

where  $\Delta_\beta(i)$  is the diversity index parameterized by  $\beta$  using the data for year  $i$  (Patil and Taillie 1979b). Graphs of  $\Delta_\beta(i)$  versus  $\beta$  were then simultaneously graphed for  $i = -1, 0, +1, +3$ , and  $+5$  (using data for the years 1962, 1963, 1964, 1966, and 1968, respectively). Since two measures of abundance were used, two graphs were produced. The plant community of year  $i$  is said to be intrinsically more diverse than plant community of year  $i'$  if

$$\Delta_\beta(i) \geq \Delta_\beta(i'), \text{ for all } \beta \text{ (Patil and Taillie 1979b).}$$

This will occur if the graph of  $\Delta_\beta(i)$  versus  $\beta$  lies entirely above the graph of  $\Delta_\beta(i')$  versus  $\beta$ . Should the graphs of the two communities intersect, we say that the communities are not intrinsically comparable with respect to diversity.

## Results and discussion

### Watershed 1

Figure 1 displays the plot of  $1m$  versus  $-1m$ . Let us now be more specific about the data that are displayed there.

The pretreatment survey in the second-growth pinelands on the minimum treatment WS 1 revealed 69 plant species

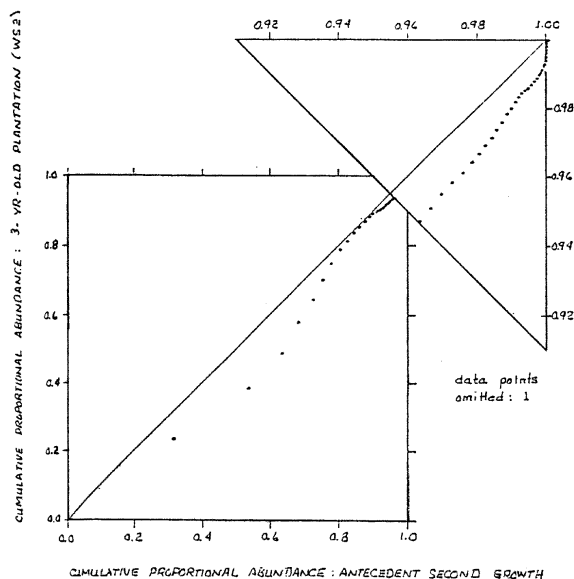


Fig. 5. Relative diversity profile for 3-yr-old plantation on watershed 2.

intercepted the permanent transects. The three most abundant species were:

*Pinus elliotii* with 57.15% crown cover,  
*Ilex glabra* with 29.58% crown cover, and  
*Serenoa repens* with 15.88% crown cover.

Two of the least abundant species were:

*Osmunda cinnamomea* with 0.04% crown cover and  
*Lycopodium* spp. with 0.04% crown cover.

Total crown cover of all species was 197.22% (Conde *et al.* 1983a).

Consequently, the ranked proportional abundance vector (with 69 elements) for the second-growth forest on WS 1 was

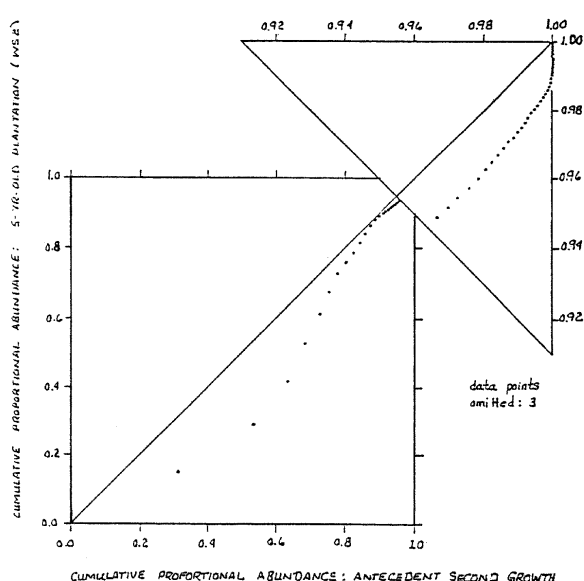


Fig. 6. Relative diversity profile for 5-yr-old plantation on watershed 2.

$$\begin{aligned} \underline{1m} &= \left( \frac{57.15}{197.22}, \frac{29.58}{197.22}, \frac{15.88}{197.22}, \dots, \frac{0.04}{197.22}, \frac{0.04}{197.22} \right) \\ &= (.2898, .1500, .0805, \dots, .0002, .0002). \end{aligned}$$

Analogous data (Conde *et al.*, 1983a) for the 1-year-old plantation on WS 1, as revealed in the 1980 resurvey of the same transects, was

$$1m = (.2618, .1276, .0859, \dots, .0007, .0007)$$

where  $1m$  has 85 elements since 85 species intercepted the transects in the 1980 survey. The three most abundant species were *Panicum* spp., *Ilex glabra*, and *Andropogon capillipes*, respectively. *Rhexia virginica* and *Polygala setacea* were among the least abundant.

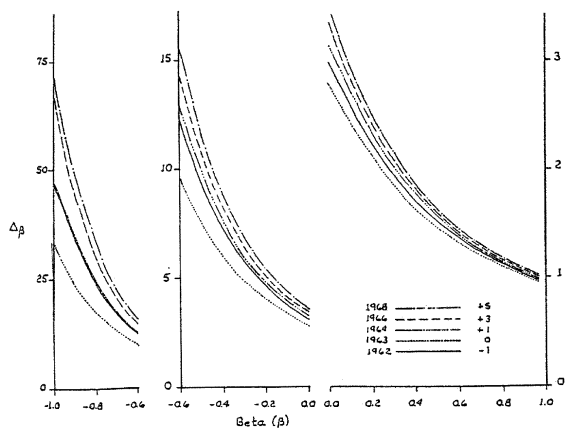


Fig. 7.  $\Delta\beta$  diversity profiles (based on measured frequency) for 1962 (-1), 1963 (0), 1964 (+1), 1966 (+3), and 1968 (+5) for Douglas-fir in Oregon Cascades. (Parenthetical numbers are years from harvest).

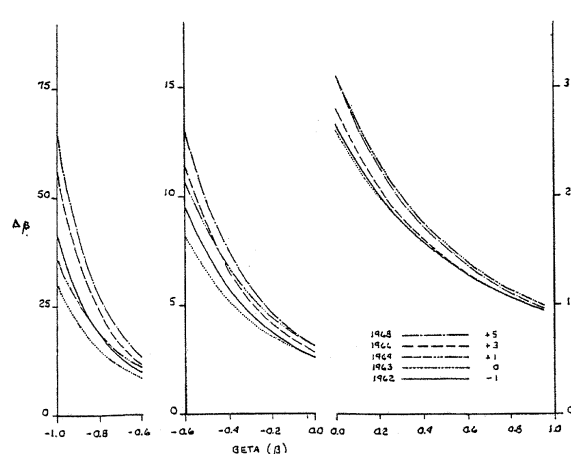


Fig. 8.  $\Delta\beta$  diversity profiles (based on measured crown cover) for 1962 (-1), 1963 (0), 1964 (+1), 1966 (+3), and 1968 (+5) for Douglas-fir.

The first (lower left) data point in Figure 1 is the Cartesian representation of the first element of  $\mathbf{1m}$  and  $\mathbf{1m}$ , i.e.,

$$(x_1, y_1) = (\mathbf{1m}_1, \mathbf{1m}_1) = (.2898, .2618).$$

It plots below the line  $y = x$ , reflecting the fact that the most abundant species (*Panicum* spp.) in the 1-year-old plantation was proportionally less abundant than was the most abundant species (*Pinus elliottii*) in the second growth.

The second data point in Figure 1 is the Cartesian representation of the sum of the first two elements of  $\mathbf{1m}$  and  $\mathbf{1m}$ , i.e.,

$$\begin{aligned} (x_2, y_2) &= (\mathbf{1m}_1 + \mathbf{1m}_2, \mathbf{1m}_1 + \mathbf{1m}_2) \\ &= (.2898 + .1500, .2618 + .1276) \\ &= (.4398, .3894). \end{aligned}$$

It also plots below the line  $y = x$ , reflecting the fact that the two most abundant species (*Panicum* spp. + *Ilex glabra*) in the 1-year-old plantation were proportionally less abundant than were the two most abundant species (*Pinus elliottii* + *Ilex glabra*) in the second growth.

Indeed, visual inspection of Figure 1 reveals that every data point plots below the line  $y = x$ , i.e., the  $J$  most abundant species in the 1-year-old plantation were proportionally less abundant than were the  $J$  most abundant species in the second growth, for every  $J = 1, 2, 3, \dots$ . This is a necessary and sufficient condition for the plantation to be *intrinsically more diverse* than the second growth (Taillie 1979, Patil and Taillie 1979a, b; Patil and Taillie 1982). An obvious and intuitive description is: the most abundant species in the plantation were less dominant than the most abundant species in the second growth, however «most» is defined. Conversely, species other than those most abundant were more abundant in the plantation, however «most» is defined.

Figure 2 gives exactly analogous information for the 3-year-old plantation on WS 1. All data points plot below the line  $y = x$ , showing that the plantation at age 3 years was also intrinsically more diverse than the second growth.

Figure 3 gives exactly analogous results for the 5-year-old plantation — with the same conclusion.

A sequential examination of Figures 1, 2, and 3 shows the influence on diversity of early succession on WS 1. While the plantation at all surveyed ages (1, 3, and 5 years) was intrinsically more diverse than the second growth, there is an obvious trend in the aging plantation toward the diversity profile of the second growth, as evidenced by a strong tendency of nearly all data points to converge with time to the line  $y = x$ .

#### Watershed 2

Figures 4, 5, and 6 display analogous information for the maximum treatment WS 2 at plantation age 1, 3, and 5 years, respectively.

Figure 4 shows that the initial (1st year) response to the more disruptive treatment imposed on WS 2 is quite different from the response on WS 1: there was no intrinsic

diversity ordering between the 1-year-old plantation on WS 2 and the antecedent second growth. This is reflected in Figure 4 in the crossing of the line  $y = x$  by the relative diversity profile. Thus, various diversity indices may differ in their ordering of the two plant communities. Indeed, Shannon's (and Simpson's) diversity index decreased with treatment while species count increased (Conde *et al.* 1983b).

By age 3 years (Figure 5), however, and persisting at least through age 5 years (Figure 6), the plantation on WS 2 was also intrinsically more diverse than the antecedent second-growth forest, as evidenced by relative diversity profiles always less than the line  $y = x$ .

Sequential examination of Figures 4, 5 and 6 shows that the effects of early succession on plant diversity are quite different on WS 2 as compared to WS 1. On WS 2, there is no convergence of the diversity profiles of the plantation with time toward the profile of the second growth. Indeed, the more prevalent trend through age 5 years is divergence from the profile of the second growth, as evidenced by the tendency of most data points to diverge with time from the line  $y = x$ . This clearly heightens interest in future diversity trends as this plantation ages.

Various authors (Conde *et al.*, 1983 a, b; Swindel *et al.*, 1983, 1984) have reported that common indices of diversity (Shannon's, Simpson's, species count) tended to increase with treatment on these watersheds through plantation age 3 years. The results reported here show that the increases in diversity persist through plantation age 5 years, and that the results are indec free.

#### Douglas-fir

Results of the analysis of the Douglas-fir ecosystem are in Figures 7 and 8. Figure 7 shows the  $\Delta_\beta$  diversity profiles for the years 1962, 1963, 1964, 1966, and 1968 (−1, 0, +1, +3, and +5 years after treatment, respectively) computed using the species-plot frequency measure of abundance. *None of the graphs intersect*, implying that, at least with this measure of abundance, a complete intrinsic diversity ordering of the plant communities is possible. In particular:

$$\Delta_\beta (+5) \geq \Delta_\beta (+3) \geq \Delta_\beta (+1) \geq \Delta_\beta (-1) \geq \Delta_\beta (0).$$

Intrinsic diversity decreased immediately after treatment (year 0), but then increased above the levels of the antecedent forest (year −1) in following years. After treatment, intrinsic diversity is seen to increase monotonically with time. At the present time it is unknown how long this trend will continue, but it certainly encourages analysis of the community in subsequent years.

Figure 8 is completely analogous to Figure 7 except that here the proportion of total crown cover attributable to species  $j$  was used as the measure of abundance for that species. The results from this graph are not as orderly as the results from the previous graph, as now there are many intersections. However, from Figure 8 we may make the following intrinsic diversity comparisons:

$$\begin{aligned}
\Delta_{\beta} (+1) &\geq \Delta_{\beta}(0) \\
\Delta_{\beta} (+5) &\geq \Delta_{\beta} (+3) \\
\Delta_{\beta} (+5) &\geq \Delta_{\beta} (0) \\
\Delta_{\beta} (+5) &\geq \Delta_{\beta} (-1)
\end{aligned}$$

We conclude that the community 1 year after treatment is intrinsically more diverse than the community immediately after treatment, and that the community appearing 5 years after treatment is intrinsically more diverse than the communities before treatment, immediately after treatment, and 3 years after treatment. The most significant statement is that 5 years after treatment the community is intrinsically more diverse than the preceding old-growth Douglas-fir community. Comparisons for other years will lead to the conclusion that the communities are not intrinsically comparable with respect to diversity. These results are consistent with the results obtained using species-plot frequency as a measure of abundance, although the conclusions are not as strong. That is, whenever we can say community *i* is intrinsically more diverse than community *i'* using crown cover as the measure of abundance, we can make the same statement using species-plot frequency as the measure of abundance.

#### Analytical Methods

The choice of which measure of abundance is most appropriate for a particular diversity analysis is an issue which is unresolved. Perhaps it is best left to the intuition or rationale of the investigator. Undoubtedly, consistency of results from analyses using various measures of abundance will provide the best solution.

It is possible to show that the issues involved in using different measures of abundance are similar to those involved in using *estimates* of abundance. In this paper, we disregard the effect of using estimates of abundance in place of the actual abundances. We use the abundances in the sample to estimate the actual community abundances, then use these estimates to obtain our graphs, ignoring sampling error. Consider the community abundance vector

$$\underline{\pi} = (\pi_1, \pi_2, \dots, \pi_s)$$

as previously defined, and consider the abundance vector for the sample plots:

$$\begin{aligned}
\pi' &= (\pi'_1, \pi'_2, \dots, \pi'_s) \\
&= (p_1 \pi_1, p_2 \pi_2, \dots, p_s \pi_s)
\end{aligned}$$

where the  $p_j$  are unknown, non-negative constants, and

$$\sum \pi'_j = \sum p_j \pi_j = 1.$$

Note that the  $p_j$  are not a common function of the  $\pi_j$  or  $\pi'_j$ . We see that  $\underline{\pi}'$  is a transformation of  $\underline{\pi}$ . Now consider the community abundance vector using one measure of abundance:

$$\underline{\pi} = (\pi_1, \pi_2, \dots, \pi_s)$$

as previously defined, and consider an abundance vector of

the *same* community using a different measure of abundance:

$$\begin{aligned}
\lambda &= (\lambda_1, \lambda_2, \dots, \lambda_s) \\
&= (v_1 \pi_1, v_2 \pi_2, \dots, v_s \pi_s)
\end{aligned}$$

where the  $v_j$  are unknown, non-negative constants and

$$\sum \lambda_j = \sum v_j \pi_j = 1.$$

Note that the  $v_j$  are not a common function of the  $\pi_j$  or  $\lambda_j$ . Once again we see that the one abundance vector is a transformation of the other, and that the transformation is similar to the previous one. While rigorous statistical analysis of the diversity profiles may remove the problems arising from estimation, it will not solve the question of which measure of abundance to use. Therefore, rigorous statistical analysis of diversity profiles should not be sufficient to reach conclusions on intrinsic orderings of communities unless various measures of abundance are used.

We have presented two methods for comparing the intrinsic diversity of two (or more) communities. Each has its advantages. The relative diversity profiles are easy to compute and graph, and are readily interpreted in light of the working definition of «intrinsically more diverse» (Taillie 1979, Patil and Taillie 1979b).

The  $\Delta_{\beta}$  diversity profiles are much more difficult to compute and graph, but do have several advantages. The first is that many of the common diversity indices are special cases of the  $\Delta_{\beta}$  family: the Simpson index  $1 - \sum \pi_j^2$  for  $\beta = 1$ ; the Shannon index  $-\sum \pi_j \ln \pi_j$  for  $\beta = 0$ ; and species richness  $s-1$ , for  $\beta = -1$ . Also, the distributional properties of  $\Delta_{\beta}$  are known and may be used in conjunction with alternate estimation techniques (*e.g.*, jackknifing) to perform statistical tests. These tests determine if intersections of diversity profiles are real and not an artifact of the sampling scheme (Patil and Taillie 1979b). Perhaps the most important feature is that  $\Delta_{\beta}$  is sensitive to rare species when beta is small (close to  $-1$ ) and sensitive to abundant species when beta is large (close to  $+1$ ). This has the practical consequence that when  $\Delta_{\beta}$  is used as a test statistic, it can detect changes in both rare and abundant species (Patil and Taillie 1979b).

An example of this varied sensitivity may be seen by looking at the  $\Delta_{\beta}$  profile for the 1966 crown cover data. We see that for small beta the index is relatively large, and that for large beta it drops off considerably. This may be explained by the successional stage the community is in at that time. This is a period when residual species are just beginning to be established and are rare, while the invading species are peaking in dominance, and hence, are very abundant (Dyrness 1973). Since many rare species are present, we see a high value for  $\Delta_{\beta}$  for small beta. Alternatively, since a few invading species have become very abundant, we see that  $\Delta_{\beta}$  drops relatively rapidly as beta gets large. In the community at this time, rare species are diverse while abundant ones are not, and  $\Delta_{\beta}$  is large for small beta and small for large beta.

We have presented analyses of intrinsic diversity trends following clearcut treatment for two completely different

forest ecosystems. In one system we analyzed data for maximum and minimum treatment while in the other we used two different measures of relative abundance. In *all* cases the intrinsic diversity of the post-treatment forest community was greater than that of the antecedent community within 5 years of treatment. Also of interest is the magnitude of the differences between the two forest communities—one exists on the flat terrain of subtropical Florida dominated by rapidly-growing pines while the other exists in the rugged mountainous terrain of Oregon dominated by the slower-growing Douglas-fir. Yet the results are excitingly similar. However, we should refrain from extrapolating these results to all commercial forest ecosystems and other management regimes; we have examined two forest systems exposed to various types of clearcut management.

We remind the reader that this is a preliminary assessment of diversity trends and extends only 5 years post treatment. There is little doubt that as the pine plantations mature their intrinsic diversity will decrease and may very well become less diverse than the antecedent community. What will happen in the Douglas-fir ecosystem is more obscure. However, to abide by regulations set forth in NFMA, we must be able to answer the question of how to compare the post-treatment community, considered over its entire rotation length, with that of the preceding community. Somehow the information on intrinsic diversity of the post-treatment community will have to be integrated over all years it exists and then comparison made. At the present time this methodology does not exist. Development of such methodology presents a significant challenge to theoreticians working in the field of diversity, and is demanded by NFMA.

### Conclusions

Early second-growth Douglas-fir communities become more diverse than the antecedent old-growth communities within 5 years of clear-cutting. Plant communities comprising young ( $\leq 5$  years) plantations in the flatwoods of the slash pine ecosystem are more diverse than the plant communities in the second growth that preceded them. Harvesting, site preparation, and planting regimes affect such diversity, and successional trends in the young plantations may be altered by different regimes. Nevertheless, the stated conclusion is quite general—in particular, it is independent of the index chosen to quantify diversity.

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