

**Natural Recovery of Logged and Burned
Plant Communities in the Lake Winnipeg
East Forest Section, Manitoba-
TECHNICAL APPENDICES.**

by

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Table of Contents

<u>Section</u>	<u>Description</u>	<u>Page</u>
Appendix C	Methodology for evaluating treatment effects in an observational study.	1
C.1	Steps involved.	1
C.2	Selection of a criterion to assess sustainability.	1
C.3	Indicators of community resilience.	3
C.4	Time series or chronosequence approach to temporal change?	9
C.5	Sampling design.	11
C.5.1	The principles of randomization and replication applied to observational studies.	11
C.5.2	Experimental or statistical control for substantial causal factors other than treatment- the role for a model of vegetation dynamics.	12
C.6	Important decisions related to data analysis.	12
C.6.1	Initial data analysis and the selection of a transformation.	12
C.6.2	Treatment of outliers.	13
C.6.3	Treatment of violations of assumptions of techniques employed.	14
C.6.4	Defining ecological distance in a manner compatible with study objectives.	16
C.6.5	Univariate or multivariate approach, or both, to testing for treatment effects?	19
C.6.6	Criteria for identifying species which characterize treatment differences or a site type.	23
C.7	Evaluating ecological relevance in the event of statistical significance.	26
Appendix D	The effects of sample size on the estimation of species richness and certain other species composition parameters.	28
D.1	Statement of the problem.	28
D.2	Formulation of a method to determine what the sample represents in terms of the species present in the community.	34
D.3	Pragmatic application of the method to the problem of evaluating environmental impacts.	39
Appendix E	Validation of the site type classification.	44
	Literature Cited	49

Appendix C

Methodology for evaluating treatment effects in an observational study.

C.1. Steps involved.

Numerous steps and decisions are involved in a comparison of treatment effects in the context of an observational study. At a general level, they include:

- I. Selection of criteria and indicators to evaluate treatment effects;
- II. Time series or chronosequence approach to temporal change;
- III. Sampling design:
 - a) Randomization and replication;
 - b) Experimental or statistical control for substantial causal factors other than treatment;
- IV. Variables to measure in the field;
- V. Empirical form of variables selected;
- VI. Defining ecological distance in a manner compatible with study objectives so that appropriate decisions can be taken during the steps involved in data analysis;
- VII. Data analysis:
 - a) Treatment of outliers;
 - b) Data transformation or standardization;
 - c) Treatment of violation of assumptions of techniques employed;
 - d) Univariate or multivariate approach or both? Which methods to use;
 - e) If a multivariate approach is taken, additional concerns are:
 - (1) Resemblance measure;
 - (2) Which species to retain;
 - (3) Method for reducing dimensionality;
 - (4) Method for conducting hypothesis tests.
- VIII. Does statistical significance imply ecological relevance?

Each of these decisions, by themselves or in conjunction with others, influence whether or not a treatment effect can and will be detected. Clearly, these constitute the key decisions of any study conducting hypothesis tests and deserve special attention. Unfortunately, although there are many works which thoroughly address some of these decisions (for instance, Cochran 1977, 1983; Eberhardt and Thomas 1991; Green 1979; Greig-Smith 1983; Harris 1985; Hurlbert 1984; Mueller-Dombois and Ellenberg 1974; Orloci 1978; Pielou 1984), there is no established protocol for community level observational studies which provides a guide for their design and analysis (Eberhardt and Thomas 1991). Because each step has the potential to determine which, or if any, effects will be detected, a study should be explicit about the steps and decisions taken in arriving at the final results.

C.2. Selection of a criterion to assess sustainability.

The introduction to this report discussed the reasons why human activities in the boreal forest must be sustainable. In response to that need, community resilience, that is, the ability of a disturbed community to return to its pre-disturbance state (Halpern 1988; Westman 1978; Westman and O'Leary 1986), was selected as the community level criterion for sustainability. For a particular type of disturbance, ecological sustainability is implied if a disturbed community can repeatedly return to a species composition typical for the site conditions and climate. On the assumptions that the mean fire return interval in the study area is 100 years and that boreal vegetation has been

present on an uninterrupted basis for approximately 4,000 years, most of the forest found in the study area has undergone about 40 fire rotations. Presumably this is a sufficient number of rotations to establish the sustainability of fire.

Only limited statements can be made about the sustainability of logging given the short period of time during which it has occurred. Less than one-quarter of the study area has been logged for pulp fiber once; none of it is on second rotation¹. Even if no effects are visible yet, there could still be single rotation impacts on ecological processes which do not manifest themselves as treatment differences in species composition until 100 years later or after the second rotation. One factor which may defer the manifestation of impacts on ecological processes is "ecological capital" built up in the system. For example, soil organic matter is an important source of cation exchange capacity in the coarse to medium textured soils common in the study area. Removal of tree boles from the site will eliminate one potential source of soil organic matter. This is not expected to have an immediate impact given the length of time it takes for a bole killed by fire to become soil organic matter. In burned forests, either there must be a surplus of organic matter at the time of fire which is depleted until the tree enters the soil, tree boles do not make a substantial contribution to soil organic matter or the rate of some other process is temporarily altered to meet the shortfall.

This example indicates why regeneration to the pre-disturbance species composition after logging is not sufficient to establish that ecological processes have not been disrupted and the activity is sustainable. It would require a number of rotations to provide strong support for that inference. Society cannot wait that long to assess impacts. During the interim, it can do at least two things. First, it can examine single rotation effects on community resilience. If the impacts on ecological processes are dramatic then presumably they will be manifested in species composition during the first rotation. Second, processes known to be ecologically important can be subjected to direct study. Nutrient cycling, soil temperature cycling, decomposition rates, the atmospheric CO₂ cycle, productivity and the maintenance of soil organic matter are a few examples.

It should be noted that is not expected that a disturbed community will regenerate exactly back to its pre-disturbance species composition. There are many factors which influence vegetation dynamics and thus there are many possible temporal pathways of species composition. It is assumed that regeneration to a species composition typical of a mature post-fire community for the site type is adequate to maintain the integrity of ecological processes. The many factors which influence vegetation dynamics makes a range of species composition possible for a site type. If this range is classified into vegetation types (cf. the vegetation types of the Forest Ecosystem Classification for Northwestern Ontario (Sims et al.)) then a frequency distribution of mature post-fire vegetation types can be attached to each site type. A management goal might be to maintain this frequency distribution across the landscape. When the objective is to compare the effects of logging with fire, one approach to variability is to specify a typical composition based on the "average" composition of the frequency distribution. Multivariate methods can be used to perform this calculation (these are described below). Immature successional stages can be characterized in the same way.

Evaluation of community resilience based on typical composition is a coarse filter approach. Some vegetation types are rare because some of the species within them require very specialized conditions within a site type. The community types these vegetation types represent² will not be properly evaluated unless they are identified beforehand and separate studies conducted for them.

It is expected *a priori* that logging will cause the early post-logging pathway of community species composition to differ from that of fire due to treatment differences in immediate effects. However, the null hypothesis is that the community is resilient to logging's impacts and, therefore,

¹ Some of the area is being selectively logged for the second time. Other human activities have also raised the proportion of the area subjected to direct human disturbance.

² A community is defined as the plants found within specified spatial and temporal boundaries. In the context of this paragraph, the boundary of the community is defined by the area where vegetation type and site type are homogenous.

species composition in cutovers will approximate that of the typical mature state after an appropriate length of time. A standard for appropriate time is guided by:

- 1) the mean fire return interval for the site type;
- 2) the mean length of time required for the species composition of post-fire communities to return to a typical mature state.

The mean fire return interval for the site type is the average number of years between fires. It will be determined not only by the site type but also the pre-fire community type, the surrounding spatial pattern of community types, landforms and water bodies. If species composition has not returned to its typical state by the time fire recurs then recovery to a typical mature state may be prevented (Payette 1992). Mean fire return intervals may be as short as 30 - 50 years for outcrops and shallow soils and as long as 150 years for lowland areas. Due to the high variance of mean fire return intervals, many boreal species have developed strategies that enable them to regenerate from within a burn even after a fire return interval much shorter than the mean (Heinselman 1981). Jack pine and black spruce can produce cones as early as 10 years of age (Sims et al. 1990).

An upper time boundary for the direct assessment of community resilience is set by the mean fire return interval. The lower boundary is set by time it takes for the species composition of post-fire communities to become relatively stable. Development of the tree canopy eliminates many of the species which invaded immediately after the fire. It also facilitates the establishment of species which require conditions associated with it. Once the tree canopy has developed, physiognomy has stabilized. For the next 50 years, changes in species composition primarily involve small changes in relative abundances rather than floristics.

Van Cleve and Viereck (1981) describe typical successional pathways for upland black spruce in the central part of Alaska. The area differs climatically from the study area; it is in the permafrost zone. Their results are not directly comparable to ours since climatic differences may lead to differences in typical species composition or slow the rate of vegetation change. Bearing these caveats in mind, they note that changes in species composition are subtle once the "tree canopy is well established". This stage occurs in central Alaska from 50 - 100 years after fire. Warmer climate and soil temperatures in the study area may shorten the length of time taken to reach the relatively stable stage of species composition. During the stage following the mature one, mortality of the fast-growing tree species eventually leads to their replacement by the slower growing ones provided that this process is not interrupted by fire. Typically, this means that jack pine or aspen is replaced by black spruce or balsam fir (Cayford and McRae 1983; Heinselman 1973).

Ahlgren (1974) describes the post-fire vegetation dynamics of jack pine/ black spruce stands in northern Minnesota. It is the description most comparable to this study in terms of climate and overstorey composition although some of the abundant understorey species were not abundant or encountered in the study area. His review indicates that the pre-fire species composition is substantially restored by about 50 years after fire. Based on Ahlgren (1974) and Van Cleve and Viereck (1981), we conclude that the typical mature state for either pure or mixed upland jack pine and black spruce occurs during the period of 50 - 100 years after fire. Van Cleve and Viereck (1981) indicate that the age range of mature black spruce lowland communities is similar to that of upland black spruce.

C.3 Indicators of community resilience.

It has already been stated that species composition is one indicator of community resilience. Others include productivity, vertical stratification of vegetation or rates of nutrient accumulation. An explanation of how species composition relates to concerns about sustainable forestry and biodiversity conservation is now provided.

Mooney and Chapin (1994) have stated that . . . "Two of the principal concerns of the ecological community during the past decade have been the loss of biodiversity and the consequences of global change". They identify three prevailing views amongst ecologists on what impact the loss of biodiversity will have on ecosystem function. They are:

1. Each species is like a rivet on an airplane so that the loss of each species increases the probability of sudden, catastrophic change. In graphic terms, the airplane falls out of the sky.
2. Some ecosystem processes (e.g. the cycling of carbon and nutrients) can be carried out effectively by a relatively small number of species; species redundancy exists so that the loss of some species will not affect ecosystem function.
3. Species diversity serves as insurance against change in ecosystem function if a species is lost. Even if a species currently does not perform an important role in ecosystem function it may in a future system which has been modified by global change or large scale human intervention (e.g. logging or fire suppression).

They go on to point out that, despite its potential importance, scientists currently know very little about the role of biodiversity in ecosystem function³ (see also Risser 1995; Walker 1995).

Biodiversity is a concept which arises in most discussions on the sustainability of human activities. Therefore, it is important to explain what the term means, which components of it are most meaningful in an evaluation of environmental impacts or community resilience and how the selected components are measured.

What does the term biodiversity mean? This is a question which has been the focus of an extensive and sometimes confusing literature. The confusions relate not only to theoretical problems involved in the definition and measurement of biodiversity but also the broad range of concepts conservation biology has incorporated into usage of the term. The Canada Country Study of Biodiversity (Mosquin and Whiting 1992) identifies four components to the biodiversity concept:

1. Genetic diversity- variability within individuals in a population or species.
2. Taxonomic diversity- the number and abundance of species, genera, families, etc. that an area has within it.
3. Ecosystem/ community diversity- the number and extent of different types of ecosystems/ communities within an area.
4. Functional diversity- ecosystems perform a variety of necessary functions and provide services such as production of oxygen or soil creation.

Some omit ecological function as a component of biodiversity. Its inclusion ensures that the biodiversity concept spans the entire range of spatial, temporal and hierarchical scales of ecological processes. A study which encompasses a large contiguous geographical area will incorporate all levels of biodiversity.

All the components of biodiversity are relevant to an evaluation of sustainability. However, practical limitations usually preclude the measurement of more than one component of biodiversity. The selection of a component can be guided by the scale of the human activity. For example, although logging can have impacts on landscape level ecological processes each cutover occurs on a much smaller scale. It is the aggregation of individual cutovers which may create a cumulative effect on such things as climate or the global carbon cycle. Logging operations are targeted on particular community types which suggests that a community scale of analysis is appropriate. Recalling the four components of biodiversity, the community scale precludes a direct evaluation of ecosystem or community diversity. This leaves genetic and taxonomic diversity. In the context of the limited information on logging's impacts, taxonomic diversity is a component of biodiversity which

³ Besides its role in ecosystem function, biodiversity is also important for economic, social and philosophical reasons similar to those discussed in Section 1 of the main report.

can be evaluated across a wide a range of site conditions to provide an overview of impacts. In the process, priority areas for further research can be identified.

Ambiguity and confusion still arise even when the biodiversity concept is confined to the species level of taxonomic diversity. To avoid some of the confusion associated with the term diversity, it should be recognized that species diversity is an abstraction which serves a useful purpose in discussions at a very general level. However, it can not be observed any more than the statistician's "average" person. It presents no problems in a discussion which involves two communities which are the same in all respects except that the first one has more species (that is, has a higher species richness) than the other. The species diversity concept is intended to embody the intuitive notion that the first community is more diverse than the other. Likewise, if two communities have the same species richness but the individuals in one community mainly belong to one species and in the other they are evenly distributed between all the species then the community with the even distribution of individuals amongst species is considered to be more diverse.

As can be seen from these two examples, the term species diversity combines the concepts of species richness and the distribution of abundance among species. This usage is adequate for general discussions, especially when applied to ecosystems which are very different. For example, it is difficult to argue against the statement that tropical forests are more diverse than boreal forests. Species richness and evenness is much higher in tropical forests. However, the concept breaks down once comparisons stray from these trivial ones and an attempt is made to measure species diversity. The problems arise because species diversity combines richness and evenness into a composite measure. An example of one of the problems which arises is that values for some species diversity indices can go up while species richness goes down. This happens when greater evenness overcompensates for lower richness. This may be a reasonable result if we want to weight evenness more highly than richness. Each of the species diversity indices weights these two components differently so that it is possible for diversity to go up when measured by one index but go down for another. When a species diversity index is used then it is important that it weights richness and evenness in a manner consistent with the study's objectives. It is also important that whenever results are reported the name of the index is included (e.g. "Shannon's diversity was higher") so the reader immediately appreciates the type of taxonomic diversity being referred to.

The ambiguity related to determining exactly what each diversity index is measuring or what the appropriate application is for each one has prompted assessments such as: ". . . they are answers waiting for a question" (Poole 1974) or "The recent literature on species diversity contains many semantic, conceptual, and technical problems. It is suggested that, as a result of these problems, species diversity has become a meaningless concept, that the term be abandoned, and that ecologists take a more critical approach to species-number relations . . ." (Hurlbert 1971).

Although it has been over 20 years since both these statements were published, little progress has been made towards the adoption of empirical methods suitable for broad classes of study objectives related to species diversity. Some further problems will be raised in the ensuing discussion which draws on an extensive literature. The more influential sources include Heltshe and Bitz (1979), Hughes (1986), Hurlbert (1971), James and Rathbun (1981), Kempton (1979), Kempton and Taylor (1974, 1976), Kempton and Wedderburn (1978), Magurran (1988), May (1975), Peet (1974, 1975), Pielou (1966a, 1966b, 1975, 1977), Taylor et al. (1976), Wolda (1981) and Zahl (1977).

One of the first problems which must be tackled is bringing the species diversity concept down to an operational level. Several possible groups of empirical measures of diversity at the community scale are possible. The first group includes those which focus on species richness alone⁴ and thereby avoid the weighting problem.

⁴ Some authors use the terms species richness and species diversity interchangeably. We follow the recommendation of other authors (Begon et al. 1990) and treat species richness as a concept separate from species diversity.

Measurement of species richness introduces a second problem- one which is common to the measurement of a number of community parameters. Boundaries must be constructed so that one knows when to stop counting species. One method used to set boundaries is to count the number of species within a fixed area, for instance, the number of species per hectare (Hurlbert 1971; Magurran 1988). This will be referred to as species density. Another approach expresses the number of species relative to the number of individuals present. For example, 30 species in an area containing 1,000 individuals, that is, 30 species per 1,000 individuals. This concept will be referred to as species richness⁵ (Hurlbert 1971; Magurran 1988). Both approaches suffer from the flaw that the number of species recorded will also be dependent on the comparability of the areas sampled vis-a-vis substantial causal factors of vegetation (Section 3.1). Consequently, a refinement applied to both of these definitions is to measure species density or richness using ecologically comparable parameters so that comparisons will be meaningful. Two examples are the number of species per square meter found on dystric brunisols less than 20 cm in depth in the Manitoba Model Forest or the number of species per hectare found in a white spruce/ balsam fir mixedwood vegetation type in the Manitoba Model Forest⁶. Both of these examples are attempts to refine the definition of species richness or density to an ecologically meaningful level, that is, to the community.

Clearly, community level species richness or density will be highly dependent on how community boundaries are defined. The community concept is another theoretical abstraction which is constructed for analytical purposes and, as such, cannot be collected in the real world. This does not mean that the community concept cannot be rendered operational. To do so, requires the definition of boundaries which can be identified in the field. We define a community as a group of interacting plants within defined spatial and temporal boundaries. Spatial boundaries can be delimited operationally based on the abundance of particular indicator species or on site conditions and other substantial causal factors which generally lead to characteristic vegetation. When the objective is to compare the effects of two treatments on vegetation, the former approach would lead to confounding. To apply the latter approach, site type categories can be constructed based on soil and topographic variables which are known to substantially affect vegetation (Section 3.1). For example, a community might be defined as the vascular plants, bryophytes and lichens growing on a particular site type which had been disturbed by fire 20 years ago. In theory, communities defined in this way are operational units because the site types can be mapped in the field. The "in theory" part of the last statement is added since the production of a site type map for an area would be very expensive and time consuming. Fortunately, it is not necessary to map site types in order to sample the communities as defined, provided that the appropriate data are collected at each plot and edge effects are minimized.

Communities can be classified into types which represent ranges of species composition associated with particular site types. An example of this approach is the "forest ecosystem type" of the NWO FEC (Sims et al. 1989) which is defined by combinations of NWO FEC vegetation types and soil types. The community type concept was applied in the discussion of community resilience where it was stated that resilience meant that a post-disturbance community had regenerated to a species composition typical of the site type. Here the potential confusion between the general use and the theoretical or operational uses of the term community can be made apparent. When we talk about a plant community we often think only of an assemblage of plants. Although this is the entity of interest, it is not possible to collect data on a community without setting some type of boundary for

⁵ A further complication is introduced by plants. Conceptualizing animals as discrete, similar sized individuals generally presents few difficulties. However, the same is far from true for plants. Plant individuals of the same species and age can vary as much as a thousandfold in size. Often, with clonal or rhizomatous species it is not apparent where one individual ends and another begins. Therefore, using individuals as the units for species richness has limited meaning. If species richness is to be reported then it should be with reference to some other measure of individual abundance such as total square meters of cover.

⁶ Note that for each of these species density examples the value is for the specified plot area and not a scalar which can be used to calculate density for different plot areas because species density and richness are a function of plot size.

the sampling. If the boundaries are based on ecologically relevant criteria then the assemblage of plants represents an entity from which generalizations can potentially be drawn. Otherwise, the data simply represents the collection of plants found within the area sampled and will probably include more than one community type. Any reference to a community implicitly, if not explicitly, must have a limitation attached to it which identifies its boundaries.

Species richness measures are one group of measures which arise from the species diversity concept. The other group of measures are the composite ones already mentioned which collapse species richness and relative abundance information (evenness) into one or two numbers so that comparisons of communities can be made. Where species diversity measures differ from each other is in their relative emphasis on richness and evenness⁷. The approach is no different from using a mean, median or mode to summarize the central tendency. Each of these three measures has the same general purpose but emphasizes different aspects of the data and is, therefore, suited to different objectives or data structures. In some situations, all three must be used in order to accurately represent a variable's behavior. Usually, a second statistic, the standard deviation is also reported. Often, additional statistics such as skewness must supplement measures of central tendency and dispersion if the data pattern are to be accurately conveyed. Species diversity measures which are a single number include the Simpson Index, Shannon-Wiener Index and the parameter α of the log-series distribution⁸. Species diversity measures which use two numbers fit a statistical or mathematical model to the community's species abundance distribution. These models can be fully specified with two parameters. For example, a lognormal distribution can be characterized by the number of species in the modal class and the standard deviation of the distribution. Log-series α can also fall into this category if an additional parameter such as the total number of species is included.

Despite what may have been construed from the earlier quotations, species diversity measures are not useless. Rather, a study must first establish what community attributes are theoretically and practically important and then determine which, if any, of the diversity measures adequately represents them. In terms of the important attributes, it has already been noted that biodiversity conservation has become a widespread concern. The discussion thus far has attempted to scope that concern down to something precise and practical. One way to further this process is to identify what plant ecologists consider to be theoretically important.

Keddy (1989; 1990) has stated that the overall objective of plant ecology is to develop the ability to predict, given an initial species assemblage and species pool, the identity and abundance of the species which will be present following a specified disturbance. This sounds like a simple objective until one considers its implications. The identity and abundance of the species present at a given time is just another way of referring to a community's species composition. If one has the ability to reliably predict temporal changes in species composition then there must be an understanding of the underlying processes. A vegetation theoretical framework such as the one identified in Section 3.1 is a first step in the development of a predictive model.

Species composition is the appropriate vegetation descriptor for a model of vegetation dynamics, however, the level of detail involved makes the task of comprehending and analyzing species composition information a challenge. It is natural that efforts have been made to construct simple measures such as species diversity measures for comparison purposes. While species diversity measures have exploratory utility, several problems limit their usefulness in the evaluation of treatment effects. Firstly, in view of the limited information that exists on the impacts of logging, the overriding consideration is that measures be as sensitive as practically possible to treatment differences in species composition. Species diversity measures ignore information on species

⁷ Some indices are also influenced by differences in total abundance.

⁸ Log-series α is an example of a species diversity measure which attempts to characterize the shape or other aspect of the community's species abundance distribution by collapsing relative abundances into a single number without regard for the identity of species.

identities and this can lead to difficulties. One occurs where two communities have exactly the same species richness and evenness but the dominant species in one community could be an exotic species which will eventually displace the natural dominant (e.g. purple loosestrife). Alternatively, a scarce species which performs an important ecological function or has high economic or medicinal value may be replaced by another. If either of these situations is present then a desirable characteristic of a measure is the ability to detect them since they may precipitate drastic changes in species composition over time.

A second problem with diversity measures is that the mathematical properties of some of them lead to ambiguous interpretations. As already noted, species diversity can go up while species richness goes down. Various solutions to these ambiguities have been proposed. However, it is not the mathematical properties which are the fundamental problem. The ambiguities arise because an attempt is being made to summarize the complexity of species composition in a single number (or two in the case of the parameters of a mathematical or statistical distribution such as the lognormal distribution). To build upon an earlier analogy, although the mean is a useful summary of the central tendency of a parameter, when two groups are being compared a number of additional statistics such as standard deviation, median, skewness and coefficient of variation are also considered. Use of only one summary statistic easily leads to erroneous conclusions about the nature of similarities or differences between groups. Species composition information is too complex to be meaningfully collapsed into one or two numbers except at a very general level.

Thirdly, most species diversity measures are highly sensitive to sample size (see Appendix D for a detailed discussion of the sample size problem and a suggested method for dealing with it) or require the assumption that a specific species abundance distribution (a histogram of species abundances or a bar chart of abundances in rank order) is present. If a particular species abundance distribution is assumed then circularity is introduced because diversity measures essentially summarize some aspect of the shape of the species abundance distribution.

In the final analysis, one must ask: if species composition is what is really of interest then why not measure it? The major problem with this approach is that it necessitates the comprehension of a large amount of information. For instance, if the species list obtained from two communities contains 50 species it is difficult to construct a mental image of the communities and compare them by scanning species names and associated abundances. Similarity coefficients and multivariate dimensionality reduction techniques have been developed specifically to address this difficulty. Their advantage in principle is that they incorporate all the information found in a species abundance distribution and retain species identity information. In the process, however, a theoretical problem is introduced. Namely, some measure of ecological resemblance is required and the choice of this measure requires a decision as to how community characteristics such as total abundance or richness are to be weighted. The advantages that similarity coefficients and multivariate dimensionality reduction techniques have over diversity measures include: species identities are retained and the choice of how to weight characteristics is explicit and based on ecological theory (Green 1979). An added benefit of multivariate methods is the information can be presented in as many dimensions as warranted by the data structure.

Table C.1 summarizes the types of measures associated with each indicator and provides examples of them. Species composition has been identified as the main indicator of community resilience due to its central position in plant ecology. A conservative approach to its measurement, that is, one which retains species identities is recommended. Although many multivariate techniques implicitly incorporate differences in species richness into their calculations it is recommended that species richness be included as an ancillary indicator of resilience⁹. Species richness is an important parameter in conservation biology where it is assumed that the maintenance of a natural level of native species richness maximizes a community's ability to adapt to global change or large

⁹ See Appendix C for a discussion of the problems involved in estimating species richness and a suggested method for dealing with them.

scale human intervention (Maser 1994; Walker 1995). It is analogous to the manner in which a large range of genotypic variability within a population renders it less susceptible to extirpation when extreme stresses prevent most members of the population from reproducing.

Table C.1. Measures Associated with the Two Indicators Used to Compare Treatment Effects at the Community Level.

INDICATOR	TYPE OF MEASURE	EXAMPLES OF MEASURES
Species Richness	Observed* Richness Observed Density	42 species/ 100 m ² of plant cover 3.3 species/ m ²
Species Composition		
a) Species identities <u>not</u> used (species diversity measures)	Species Diversity Indices Parameters of Mathematical or Statistical Models	Shannon-Wiener; Log-Series α Log-Series α ; Modal number of species and variance of lognormal distribution
b) Species identities used	Similarity Coefficients; Multivariate Dimensionality Reduction Methods	Czekanowski coefficient. PC Scores from Principal Components Analysis

* Observed richness or density is a sample statistic which is a function of sample size. It is not an estimate of the total richness of a community.

C.4. Time series or chronosequence approach to temporal change?

An evaluation of community resilience ideally uses data from plots sampled in a community prior to disturbance and a series of progressively older post-disturbance states for the same plots. Such data are extremely difficult to obtain in the boreal forest where time spans of at least 50 years (and possibly up to 100) are required to test for resilience. Consequently, studies which examine questions related to boreal vegetation dynamics frequently use the chronosequence approach. This approach assumes that patterns observed in space substantially represent patterns in time (Pickett 1989)¹⁰. That is, post-disturbance communities of different ages are linked together in order of ascending age to form a temporal pathway of species composition for the community type¹¹. This assumes that the communities in the chronosequence were influenced by similar causal factors such as pre-disturbance species composition and disturbance characteristics.

When using the chronosequence approach, historical information on disturbance characteristics and pre-disturbance species composition is often not available. When this is the case, some decisions or further assumptions must be made if resilience is to be evaluated.

¹⁰ There are many ecological factors which can be confounded when space is substituted for time. Many of these would also be confounded in a field experiment which burned and cut sites and then monitored them for 80 years because some causal factors cannot be replicated. Examples are global change or changes in logging methods. In addition to this difficulty, practical concerns dictate that the evaluation of impacts cannot wait for the results of long-term monitoring projects. The temporal patterns identified by the chronosequence approach should not be considered as being definitive but as suggestive of certain patterns which can be tested by future studies.

¹¹ This is sometimes referred to as a successional pathway. We generally avoid the use of this term because it is sometimes taken to mean that a series of species replacements occurs and, in the boreal forest, this is usually the case only for a subset of species. In its place we use the term "vegetation dynamics" which refers to the "temporal pathway of species composition".

Information on disturbance characteristics is difficult to obtain. It is rarely available for fire (Viereck 1983) although fire intensity can be partially assessed since there is often evidence which indicates whether the overstorey was killed. Fires in the main boreal zone generally are of similar intensity. "Most fires are crown fires, or severe surface fires, killing and regenerating whole stands" (Heinselman 1981). Fire severity is more difficult to assess than intensity. It can have a substantial effect on which species regenerate in a post-fire community. A decision must be made as to whether the absence of fire severity data introduces a bias into a comparison of two different types of disturbance such as fire and logging. It is expected that the main effect will be to introduce greater variability into the data and thereby reduce the precision and statistical power of hypothesis tests. This is not a fatal flaw when the comparison involves two treatments which are so different in their immediate ecological effects. On the other hand, if the objective was to elucidate the mechanisms of post-fire or post-logging vegetation dynamics then more specific information on disturbance characteristics would be required.

When information on the pre-disturbance species composition of the community is not available the community is assumed to be from a community type that typically occurs on the site type. This assumption is consistent with the earlier conclusion that resilience does not require that a given community regenerate back to its pre-disturbance species composition (Section C.2). Community resilience simply requires that a community regenerate back to a mature one typical for the site type¹². Thus, data from mature communities is used to represent both the pre-disturbance and the typical mature state of the vegetation.

A direct evaluation of resilience is accomplished by comparing mature communities sampled from each treatment. In the case of fire and logging, logging methods have undergone several substantial changes in terms of their ecological effects. Consequently, it may not be possible to obtain suitable data for mature post-logging communities. If this is the case then it is suggested that resilience be evaluated in several steps. The first step confirms the expectation that post-fire communities in the study area are regenerating to a typical mature state and that immature post-fire communities represent natural states. This is done by examining the post-fire temporal pathway of species composition of a chronosequence of immature communities to see if they are recovering towards the typical mature state. Obviously, the strength of this type inference will be an increasing function of the number of age classes in the chronosequence and the closer the oldest community in it is to a mature age. If the post-fire chronosequence is typical, then a post-logging chronosequence using the same age classes can be examined to determine if it also leads to the mature state and if its rate of return to the mature state is the same as that of fire. In the final step, the species composition of specific age classes can be examined across treatments to elucidate where the differences lie and suggest explanations for any differences.

¹² See the proviso in Section C.2 regarding the coarse filter approach.

C.5. Sampling design.

C.5.1. The principles of randomization and replication applied to observational studies.

The importance of randomization and replication are well known and essential to drawing inferences from hypothesis tests (Green 1979). Replication is the basis for comparing treatments (or communities, age classes) by providing estimates of variation within treatments which can be compared with variation between treatments. More replicates are always better than less since they improve the precision of estimates and minimize the possibility that chance events will lead to spurious conclusions (Hurlbert 1984). However, the number of replicates which can be obtained is limited by the constraints of total sampling effort available or the size of the sampling frame. The other basis for drawing inferences is randomization. Randomization minimizes biases arising from two sources: unknown but systematic differences within treatments and the subjective biases of the investigator.

Several complications arise when these two statistical principles are applied to observational studies, that is, studies which do not randomly apply treatments. Firstly, there may be systematic differences in the treatment units¹³ which would result in vegetation differences even in the absence of a treatment. For example, even though burns and cutovers can be randomly selected from a sampling frame, burns may contain a higher percentage of rock outcrop than cutovers or they may be located in a portion of the study area having a drier climate. The higher proportion of rock outcrop may predispose the area to a higher frequency of disturbance leading to systematically different vegetation when compared to logged areas. This type of problem is common in observational studies and an attempt must be made to control for it during the construction of the sampling frame.

Other unknown factors may not create systematic biases but can affect results in other ways. For instance, in a study of post-fire vegetation, there is no way of knowing whether the intensity or severity (Bonan and Shugart 1989; Viereck 1983) of replicate fires is the same. The impact of this is that the variance of burn parameters may be higher than would have occurred in a controlled situation, thereby reducing the statistical power of hypothesis tests. In other words, the probability that a significant difference of a specified level will not be detected, even if it exists (Type II error level), is increased by the higher variability in treatment attributes. Unfortunately, the increased variance generally cannot be offset by increasing replication as the size of the sampling frame is limited. It is unusual for an observational study¹⁴ to have as many as four replicates (Hurlbert 1984). Higher variability is accepted as a tradeoff for the higher degree of generality possible in an observational study relative to an experiment.

Complete randomization is not always desirable when replication is low since it may easily result in a lack of interspersion of replicates (Hurlbert 1984). In other words, randomization might result in each treatment's replicates being clustered in different parts of the study area. Inferences drawn then relate to differences in location and not in treatment. For this reason, blocking and systematic sampling are often applied. Randomization can be applied at the various stages of sampling such as the Blocks, sub-blocks within Blocks and subsamples. The consequence for inferences is the same as that for the Block level. The best way to ensure that the desired inferences can be drawn is to locate sampling units so that they are interspersed and their locations

¹³ Although this is an observational study, the terminology developed for experiments will be used. This is in accordance with other authors (Cochran 1983) who point out that the principles of design are the same for both types of studies with the major difference being the inability to randomly apply a treatment in the former type. A treatment unit is an area which has been either burned or logged once since 1900 but not otherwise disturbed. From this point onward, the term Block will be used to refer to treatment units.

¹⁴ Mensurational study in Hurlbert's terminology.

are independent. In an observational study, this is often accomplished with a combination of randomization, blocking and systematic sampling.

A clarification of what randomization means in plant ecology is in order. While it is possible to construct a sampling frame of burns or cutovers, it is not feasible to randomly sample the communities within any one of them. Even if the communities or site types within a burn or cutover could be mapped, the best that could be achieved is a random siting of sample plots within the community or site type. When species composition is the indicator measured, estimation of the mean abundances of species is required. The sampling frame from which a random sample of species would be drawn is a map of the spatial distribution of species in addition to a map of communities. Production of such a map would obviate the need for sampling. A more detailed discussion of this problem and a suggested method of dealing for with it is provided in Appendix D.

C.5.2. Experimental or statistical control for substantial causal factors other than treatment- the role for a model of vegetation dynamics.

A comparison of treatment effects should involve communities that have been defined so that the only difference between them in terms of causal factors is the type of treatment they have been exposed to. There are a multitude of causal factors involved in vegetation dynamics, some of which have a very small influence. Factors whose effects are not small relative to treatment are termed substantial causal factors. Experimental or statistical control¹⁵ of substantial causal factors prevents confounding their effects with that of treatment. Although causal factors which have small influences are of interest and may be substantial under certain conditions, constraints on total sampling effort available preclude their inclusion.

Site type is one obvious example of a substantial causal factor. To identify the other substantial causal factors for design purposes, a theoretical model of vegetation dynamics is required¹⁶. Due to the importance of such a model in identifying causal factors and variables to measure in the field, it is reviewed in the Section 3 of the main report (Ehnes and Shay 1995).

C.6. Important decisions related to data analysis.

C.6.1. Initial data analysis and the selection of a transformation.

The purposes of initial data analysis (Chatfield 1992; Krzanowski and Marriott 1994) are to:

- 1) Test for gross violations of the typical assumptions of statistical models, that is, normality, independence of errors and homogeneity of variance;
- 2) Suggest whether a data transformation prior to further analysis is desirable;
- 3) Provide an additional opportunity to identify data entry or setup errors;
- 4) Identify and evaluate outliers and remove those which can be theoretically justified;
- 5) Identify the nature of the data structure so as to suggest empirical methods for use during exploratory data analysis;

Most types of quantitative methods are affected by the introduction or exacerbation of non-linearities in data structure, non-normality, correlation of errors and heterogeneous variances. As a reflection of scarce species and sampling phenomena, vegetation data typically contains a high proportion of zeros and this contributes to non-normality and non-linearity. This difficulty must be dealt with. Some authors advocate the retention of as many species as possible on the grounds that

¹⁵ Experimental control is achieved by selecting treatment units which are homogenous with respect to the factor; statistical control by incorporating replication for different levels of the factor.

¹⁶ The spatial pattern of vegetation is merely a snapshot of a temporal process. Therefore, if we can predict temporal processes we will also describe spatial patterns.

it may not be known *a priori* which are the 'important' species (Orloci 1978). Typically, certain species are excluded using a method such as:

- 1) Retaining species whose abundance can be predicted by other species (Orloci's (1978) variable ranking method). This method assumes that the interesting species are the ones which are good predictors of other species. Unfortunately, poor predictors of other species may be highly correlated with specific treatments;
- 2) Eliminating species which have small loadings in a principal components analysis (Krzanowski and Marriott 1994). This is somewhat circular since the results of PCA are distorted by a large number of zeros and dependent on the species included. The latter shortcoming can be partially evaluated by comparing the results with and without the 'uninformative' species;
- 3) Eliminate double zeros, that is, pairwise species absences, in data analysis (Legendre and Legendre 1983). This approach is mainly applicable to the calculation of resemblance measures;
- 4) A common approach in plant ecology is to exclude species occurring in only a few plots. Scarce species are thought to be more likely the result of unusual circumstances.

All species contain some interesting information. The question is whether the information conveyed by some species is relevant to the objectives of a particular study. When a study attempts to ensure that, to the extent possible, plots are statistically independent and that factors expected to have a substantial influence on species composition are controlled for by the sampling design, it is likely that species which occur in only a few plots within a site type category are more likely there as a result of accidental factors¹⁷. If there are several species which occur in a few plots in only one Block then this may indicate that the Block is an outlier in terms of some unmeasurable factor such as ecological history. On this basis, species which occur in less than four plots within a site type category can be deleted prior to initial data analysis. An exception to this rule are species which occurred in three plots within a single Block. Methods to deal with violations of assumptions identified by initial data analysis are discussed in Section C.6.3.

C.6.2. Treatment of outliers.

An outlier is a plot whose species composition differs dramatically from the other plots within its grouping. If retained within the dataset, it will exert a substantial influence on the results regardless of the multivariate technique employed. Numerous methods are available for the detection of outliers (Dillon and Goldstein 1984; Green 1979; Hair et al. 1987; Krzanowski and Marriott 1994). Two simple approaches are suggested- one univariate and the other multivariate. The univariate approach consists of calculating the mean of normalized species values¹⁸ for each plot by site type and treatment. Any plot which has a mean of normalized species values greater than 2.0 is considered to be an outlier (Hair et al. 1987). This means that, on average, the species abundances in that plot are at least two standard deviations greater than average for that treatment and site type category. From the multivariate perspective, outliers can be detected using non-hierarchical cluster analysis, centered principal components analysis (PCA) and correspondence analysis (CA) applied to the raw and square root transformed data. Plots which are "distant" from the "swarm" of plots in an ordination scattergram are considered to be outliers. The lowest weight should be placed on the results from CA since the double standardization implicit in it has the effect of zeroing in on what is different about each plot. Outliers are more common in the results of CA.

¹⁷ A critical caveat to this relates to the effect sample representativeness has on which species appear to be infrequent or scarce (Appendix D).

¹⁸ That is, from each data value is subtracted the mean of the species it belongs to and then that result is divided by the standard deviation of that species.

Once outliers are identified they must be examined to determine if their removal can be justified. Causton (1988) recommends that an outlier not be removed unless there is a sound theoretical reason for doing so. For example, a causal factor unrelated to the objectives of the study may affect only one plot and produce an unusual assemblage of species in that plot. Such a plot will affect relative plot distances in multivariate analysis and have two different effects on the variability of the data. It will reduce the statistical power of univariate comparisons and multivariate tests if the abundance of the one species overwhelms the others in the plot. For multivariate tests, the degree to which the plot is unusual must be weighed against the reduction in statistical power which would result from its removal. For example, a plot containing 25 species may be identified as an outlier if a species which typically has moderate abundance has a high abundance in that plot. CA is particularly sensitive to this type of situation which may simply be a sampling artefact for that species. Dropping this plot would remove the information provided by 24 species for the sake of 1 species. This may be justified if the unusual abundance of the 1 species is linked to unusual levels of some substantial causal factor.

C.6.3. Treatment of violations of assumptions of techniques employed.

Vegetation data are rarely consistent with the assumptions typically employed in statistics even after transformation. In many cases, several steps using different techniques are required to prepare the data for hypothesis tests (e.g. PCA to reduce dimensionality for MANOVA). Violations are compounded as each of these steps may involve violations of assumptions even if the final step does not.

Violations have three main effects. They may introduce bias into the results, reduce the power of statistical tests or cause the true level of α to deviate from the specified one (Green 1979 p. 45). The latter two effects have a direct impact on hypothesis tests and result from violations of the assumptions of normality or homoscedasticity. Harris (1985) states that it is virtually certain that these assumptions are not met for any real dataset. Therefore, the possibility that true levels of α deviate from those specified is pervasive throughout ecology. Fortunately, Harris and others (Green 1979; Zar 1974) point out that t-tests and ANOVA are quite robust to violations of the assumptions of normality and homoscedasticity provided that the number of replicates in each group is approximately equal and not less than ten. This is especially true when tests are two-tailed. Harris (1985) points out that the results dealing with robustness have not been extended to the multivariate situation although there is no obvious reason why they should not apply there also.

An observational study is often able to conform to most of the constraints outlined above. An approximately equal number of replicates and subsamples can often be obtained for hypothesis tests. All tests can be two-tailed and logarithmic or square root transformations can often be used to reduce deviations from normality and homoscedasticity. Replication is the main problem. It is unusual to have as many as four replicates (Hurlbert 1984).

The possibility that the true level of α will deviate from the nominal level should not be considered to invalidate hypothesis tests (Harris 1985) or be a justification for not conducting tests. Being realistic, large scale human disturbance will neither wait for the development of methods to treat violations nor methods known to be robust to violations and still maintain high statistical power. The risk that a test is being conducted at a level of $\alpha = 10\%$ or 1% rather than 5% is less of a concern than to not evaluate treatment effects at all. Consequently, we must proceed with the best methods available and use other, less appropriate, methods to validate the results obtained. Validation is discussed further in Section C.6.5 where the issues of experimentwise error rates in multiple comparisons and statistical power are reviewed.

The second main potential effect of violations of assumptions is the introduction of bias into the data. This is a concern primarily where a multivariate technique is used as an intermediate step to the application of another technique. For example, an ordination technique is used to reduce the number of variables input to MANOVA. Ordination techniques do not alter the data. By creating a linear combination of the original variables they can present the data in a manner in which the strongest patterns in the data are readily observable. The procedure is analogous to rotating a large cube so you are looking at it from an angle rather than straight on from one face. Viewing it from an angle allows you to see more of the cube at one time.

A pitfall of the mathematics of ordination techniques is that they will distort interplot relative distances when the data structure is not linear. Vegetation data are highly non-linear when collected over a large portion of an ecological gradient. When these data are manipulated with eigenanalysis ordination techniques, the distance of plots relative to each other is altered and results in the well-known arch or horseshoe effect. In the event that the alterations in relative distances are not systematic as far as treatment is concerned, variances may be inflated thereby reducing the statistical power of hypothesis tests. If they are systematic then a spurious treatment effect may be detected or a true one not at all.

Alternatives to linear models include rank order techniques and non-linear models. Both of these possess much lower statistical power for the same sample size. Sample size in this study, as in most ecological studies, is small. Green (1979) points out that the greater robustness provided by rank order techniques is often offset by a consequent loss of power and information. Therefore, these methods are generally not the preferred options.

Various methods exist to reduce or deal with non-linearities. One option is to ignore them. Overall, classification and ordination techniques have been found to be fairly reliable at recognizing natural species groups. That is, the distinct patterns in the data are accurately reproduced. Where they are deficient with heterogeneous data is in their portrayal of the relative distance between groups and between plots within a group. When plots are to be used as observations for hypothesis tests, then the preservation of relative interplot distances becomes paramount and further steps are required. One is to apply multivariate techniques to relatively homogenous vegetation. For instance, data which has been stratified by site type and age class. Each plot will then have a relatively high proportion of species in common with other plots. Another method used to minimize non-linearity is to reduce the number of zeroes in the data. As already mentioned, dropping infrequent species is a common method of dealing with this and other mathematical problems. Other methods include the use of resemblance measures which are less sensitive to non-linearities (e.g. correlation coefficient is quite sensitive, Legendre and Legendre 1983) and logarithmic or square root transformations of the data.

There is no foolproof linearity test which can be applied to multivariate datasets. Scattergrams of one species against another can be plotted for all pairwise combinations of species. The data can also be analyzed using different resemblance measures and techniques. Non-metric multidimensional scaling (NMDS) is useful in this regard since it assumes a monotonic rather than a linear structure. Despite its apparent superiority over other techniques based on this assumption, it generally should not be applied as the dimensionality reduction technique precedent to hypothesis tests since it merely preserves rank order and not relative distances between plots. It should be noted that obtaining results from NMDS similar to those of other ordination techniques does not establish the absence of non-linearities. On the other hand, if NMDS generates substantially different results then this may indicate that non-linearities are distorting the results.

Cluster analysis is another useful technique for corroborating the results of the dimensionality reduction technique. It is not a linear technique although the resemblance measure it uses may be affected by non-linearities. Therefore, it is suggested that the techniques serve the classification objective without distorting the subsequent data analysis.

To sum up, violations of assumptions are inevitable in any study using field data. This should not stop scientists from attempting to address many immediate scientific and practical problems. Many methods are sufficiently robust to be used in a complementary fashion to corroborate each other. The strength of inference is not as great as under ideal conditions but still strong enough for the purposes of impact evaluation. The recommended strategy is to apply ANOVA and other multivariate techniques (the "primary techniques") where appropriate after steps have been taken to minimize violations of assumptions. Alternative techniques can be used to corroborate these results. If the corroborative techniques suggest quite different patterns from the primary techniques then the original results should be reexamined and a subjective judgment made as to whether the results should be allowed to stand.

C.6.4. Defining ecological distance in a manner compatible with study objectives.

The multivariate techniques used in this study require a resemblance matrix for analysis. In some cases, the decision regarding which resemblance measure¹⁹ will be used is explicit and in others implicit (e.g. correspondence analysis). Two causes for concern arise. Firstly, it is shown below that even raw data may not accurately reflect ecological distance. Secondly, the relative distance between plots is altered when a resemblance measure is applied. Both these factors can introduce a bias into the results and must be considered. Otherwise, a spurious treatment effect may be detected or a true one not at all. The discussion below begins with a presentation of the fundamental problem and then provides an overview of the components of ecological distance which should be considered when the objective is to evaluate treatment effects. The discussion concludes with the selection of the transformation and resemblance measure used in this study.

Our everyday notion of distance is Euclidean in nature. Euclidean distance is an accurate representation of the physical relationships of objects in space. That is, when the coordinates of objects represent their physical locations in three dimensional space. However, Euclidean distance is not an accurate analog for ecological distance. For example, a scattergram of plots in species space shows that two plots that have no species in common can have a shorter straight line (Euclidean) distance than two plots with all species in common (Van Tongeren 1987). Table C.2 provides an example of ten plots containing two species. Figure C.1 is a scattergram of the data in Table C.2. Each point in the scattergram is labeled with its plot name from Table C.2. Plots A and B have no species in common. Plots J and D have both species in common at similar levels of abundance. However, the straight line (Euclidean distance) between plots A and B is less than that between J and D (see G and H also). Ecologically, two plots with no species in common cannot be more similar (i.e. closer together) than two plots with all species in common at similar abundances. In this example, Euclidean distance does not reflect ecological distance.

As will be elaborated upon below, Euclidean representations of ecological distance are also distorted in other ways even when plots have species in common (Legendre and Legendre 1983). Therefore, Euclidean and ecological space are not equivalent. If this is true then it calls into question the entire practice of graphing raw ecological data unless the data are transformed in such a way that Euclidean space reflects the "ecological distance" one wishes to portray. Ecological distance is a representation of plots such that the straight line relative distances between pairwise comparisons of them reflects an ecological perception of their relative dissimilarity. Such an ecological perception will incorporate how, among other things, species are to be weighted based on components such as their abundance, relative frequency or absence. Ecological distance is not an

¹⁹ Resemblance measure is a general term for any measure of similarity, dissimilarity or distance (Sneath and Sokal 1973). A distance measure satisfies the triangle inequality whereas a dissimilarity measure does not. Certain techniques, such as principal coordinates analysis require a distance matrix for subsequent manipulation and analysis. For this reason and because graphical representation of raw data or resemblance is implicitly distance based, most of the discussion which follows refers to distance.

absolute concept but must be defined in relation to a study's objectives. Once this distance has been defined, a data transformation, standardization, resemblance measure or combination of the three may be able to present the data in such a way that our Euclidean perception of it reflects the ecological information we are attempting to extract. In other words, the space separating two plots on paper should reflect the ecological distance between them.

Table C.2. Abundance (percent cover) of two species in ten plots.

	Plot Name									
	A	B	C	D	E	F	G	H	I	J
Species 1	10	0	40	30	30	0	40	70	20	50
Species 2	0	10	30	50	0	30	70	40	50	40

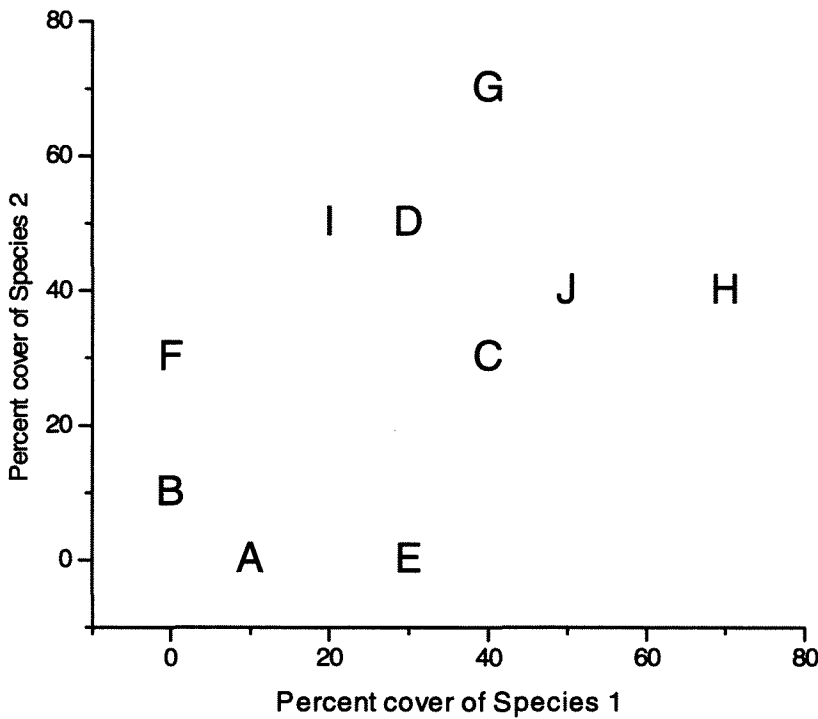


Figure C.1. Scattergram of plots from Table C.2 in species space.

Incongruity between Euclidean and ecological distance has consequences for many multivariate methods since they generally operate either explicitly or implicitly on a Euclidean space. The major concern when testing for treatment effects is that the relative ecological distance between plots may be represented by the mathematics of the method in a way that distorts the relative placement of plots. In other words, a bias is introduced. Referring back to the last example, assume that the plots of burns and cutovers have no species in common. It is then possible that a distance measure will find little difference between them even though they are completely different. To find that burns and cutovers have no species in common is highly unlikely (it would also obviate the need for statistics), however, it illustrates a problem which exists to lesser degrees as a result of joint absences and other factors. All have the effect of misrepresenting the relative dissimilarity of plots in ecological terms. Therefore, the objective is to have the relative spaces between plots in a

scattergram to be reflective of our perception of how ecologically dissimilar they are (i.e. their ecological distance). To accomplish that, the components of ecological distance must be identified and then evaluated relative to a study's objectives.

What are the components which need to be considered when assessing the ecological distance of two plots? Clearly, maximum distance between two plots is attained when the plots have no species in common²⁰. If the plots have species in common then distance is greater when the abundances of those species are greatly different than when abundances are similar. Beyond these two intuitively obvious situations, ecological distance becomes more complex. An example illustrates a few subtleties. In some cases, two plots may not only contain the same species but also have them represented by the same relative abundances. The only difference between the two plots is that absolute abundances are higher in one. Should two plots in which the species have the same relative abundances be considered to have zero ecological distance? This is a complex question since the total abundance of a plot is determined by factors in addition to treatment effects. Many of those factors cannot be measured in an observational study (e.g. moose browsing) so it will be impossible to separate them from treatment effects. In any event, if plot abundances are consistently lower in one treatment then that needs to be detected and represented.

The translation from a conception of ecological distance to a resemblance matrix is complicated by two things. In the first place, there are two different and, sometimes, complementary ways of making the translation: transformations/ standardizations and distance measures. Many distance measures implicitly incorporate a transformation or standardization or both so that the effects of the two are confounded. Secondly, distance measures can be sensitive, all other things being equal, to a number of the components of ecological distance. The individual effects of the components may work in opposite directions relative to the desired representation of ecological distance.

Some of the components of ecological distance which must be considered when choosing a resemblance measure are (Greig-Smith 1983; Van Der Maarel 1979):

- 1) Species abundance- most quantitative methods weight species in proportion to their abundance. That is, a 1% increase in the abundance of an abundant species can negate a 500% decrease in the abundance of a scarce species. Abundant species have a tolerance for a wide range of ecological conditions so they may be less affected by treatments they are not adapted to than a scarce species. Nevertheless, lower abundance in one treatment may be an indicator of treatment effects. A compromise must be reached between giving the scarce and abundant species equal weight (as in conversion to presence data or PCA on a correlation matrix) and allowing the abundant species to overwhelm the scarce.
- 2) Equal abundances- if there are four plots which are identical in their species composition except that two plots have one additional species present in the same amount, some resemblance measures would yield identical distances for pairwise comparisons of these plots whether or not the additional species was included. Most ecologists would consider that ecological distance is less between two plots which contain the additional species than two other plots which do not.
- 3) Differences in absolute but not relative abundances- certain distance measures will find no difference between two plots which have species in the same proportions but different

²⁰ Plots with no species in common can create problems for ordination techniques whose objective is indirect gradient analysis. The problems are manifested as the "arch" or "horseshoe" effect. Essentially, it occurs when three or more plots have no or a small proportion of species (which are scarce) in common with each other reflecting the fact that they represent three or more community types on the gradient. A distance measure which has a maximum will find the three plots to be equidistant even though two of them represent opposite extremes on the gradient. If information on the gradient and the relationships of vegetation to the gradient is available then the plots can be ordered along an axis. Alternatively, if the plots have some species in common with one plot but not the other (intermediate species) then their interplot distances can be linked in a chain-like fashion.

absolute abundances. When dealing with plots which have been grouped on causal variables in an appropriately designed study, consistently higher abundances in one treatment may indicate a treatment effect. Therefore, relative distance measures are not adequate for hypothesis testing.

The relevance of these and other components of ecological distance to this study's objectives was considered in conjunction with the findings of others (Campbell 1978; Causton 1988; Faith et al. 1987; Greig-Smith 1983; Hadju 1981; Legendre and Legendre 1983; Orloci 1978; Van Der Maarel 1979). It was decided that the resemblance measures which provide the most appropriate representation of ecological distance in Euclidean space were percentage difference or relative Manhattan and that these measures should be applied to square root or logarithmically transformed data. The choice of transformation is influenced by the other functions which a transformation performs (Section C.6.1).

C.6.5. Univariate or multivariate approach, or both, to testing for treatment effects?

Multivariate tests have no applicability when only one parameter is of interest. For instance, species richness comparisons. However, once the focus shifts to comparisons of species composition, a decision must be made as to whether hypothesis testing takes a univariate, multivariate or combined approach. Univariate tests involve comparisons on a species by species basis. They are more powerful than multivariate tests until the problem of experimentwise error rates is considered (Harris 1985). An example will illustrate how the problem arises. When one species is tested for a treatment difference in means at a level of $\alpha = 5\%$ the chances are 1 in 20 that a significant difference will be detected simply as a result of chance. If 50 species are found within a site type category and 50 such comparisons are made then one expects to find significant differences for 2.5 species (50/20) simply due to chance. To correct for this, the nominal level of α must be divided by the number of species involved to obtain the level of α to be used in each comparison (Bonferroni adjustment) so that the experimentwise level of α is equal to the nominal level. In this example, a level of $\alpha = 0.1\%$ would have to be used in each comparison to maintain a nominal level of $\alpha = 5\%$. This would make it extremely difficult to detect a difference even if one exists unless a large number of replicates are available. This is not the case in this study or for plant ecology in general. One option would be to select only a few species for comparison but that would require prior knowledge on which species are most affected by logging. Another option is to accept a higher level of α in order to maintain a particular Type II error level. It is sometimes argued that, due to the risks involved, environmental impact assessment should be more concerned with not rejecting the null hypothesis of no treatment effect than falsely rejecting it. The only way to simultaneously lower one type of error rate and maintain or lower the other type is to increase replication. This is usually not possible.

Perhaps the more important justification for not adopting a univariate approach as the primary one in the comparisons of species composition is that, by definition, the interest is in collective species changes. Univariate tests are not sensitive to simultaneous small differences. To illustrate, imagine that a fisherman tells you that fish caught in Lake A are bigger than Lake B. You take a random sample of fish from each lake and obtain measurements on length, girth and taper. ANOVA performed on each variable indicates no statistically significant difference. You are puzzled because when you look at the samples from the two lakes it seems obvious to you that the fish from one lake are consistently slightly larger than the other. In effect, when we look at the fish our brain evaluates all three size variables simultaneously. When MANOVA is applied to the fish data it detects a highly significant difference between the size of the fish in the two lakes. This occurs because it also takes into consideration all three size variables simultaneously.

Another example of the advantage of the multivariate approach, involves the relation of vegetation to soil depth and moisture regime. There may be no relationship between vegetation and either of these variables individually because there is too much variability within each of the soil variables. However, there may be differences between the vegetation on deep dry versus deep wet soils that can be detected by a multivariate approach.

The main disadvantage of multivariate methods is that their power is lower than univariate methods. This disadvantage may be illusory if a large number of species are involved. Once Bonferroni adjustments are applied, the power of univariate tests may be similar to multivariate. Even when the number of variables is small, the lower power of multivariate methods is offset, to a situation specific degree, by their sensitivity to simultaneous changes amongst variables.

MANOVA is the multivariate method recommended for species composition comparisons. Other available multivariate techniques which could be used include Hotelling's T^2 and canonical variates analysis²¹. The advantage of MANOVA over Hotelling's T^2 is that it allows us to model Block as a random effect and then test for differences between Blocks. Canonical variates analysis suffers from the same drawback as Hotelling's T^2 . In addition, it currently lacks an unbiased estimate of R^2 and cannot test the statistical significance of the canonical variate coefficients (Harris 1985). Nevertheless, it can be used to assist in the interpretation of MANOVA results. Interpretation is required as a result of the need to reduce the number of variables (i.e. dimensionality) prior to application of MANOVA.

Dimensionality reduction is a requirement which is a consequence of having more species than replicates. The maximum number of variables which can be handled by MANOVA is limited by the number of replicates available. In our case this will be either three or four. Drastic reductions in the number of variables are required given that the average number of species in an age class/ site type combination is 55. Dropping species is, therefore, not a viable option.

Conceptually and mathematically, each species is a dimension in ecological space when plots are compared with each other based on their species composition. Consequently, the number of variables can be reduced by principal components analysis (or some other eigenanalysis ordination technique) and retention of only the first p components (Gauch 1982b; Green 1979; Harris 1985). It is assumed that the first p components represent the structure resulting from ecological factors and treatment effects. The last q components represent noise and are dropped. Noise is defined as species responses which reflect random effects and have nothing to do with substantial environmental factors or treatment effects. PCA, and eigenanalysis ordination techniques in general, produce a linear transformation of the original data such that coordinated species responses are recognized and represented by the first p axes in decreasing order of importance in terms of relative variation. Uncoordinated responses present themselves as noise on the last q axes (Pielou 1984)²². Gauch (1982b) cites other authors who found that noise usually constitutes 10 - 50% of the variation in a typical vegetation dataset. He then present results from a simulation study. The simulations were conducted by constructing a series of single coenocline datasets which were noiseless, contained complete noise or had a mixture of the two. PCA and CA were applied to the resulting datasets. Generally, it was found that the first component corresponded to structure, the next few to spurious polynomial effects and the remaining components to noise. Structure was found to correspond to high eigenvalues, spurious polynomial effects to intermediate eigenvalues and noise to low eigenvalues.

It is unknown how far these results can be extended from a single environmental gradient to the number typically expected in vegetation data. Gauch makes some general statements which

²¹ All three of these techniques and ANOVA are special cases of the more general canonical correlation model.

²² This does not mean that noise does not represent interesting information. To the contrary, if only one scarce species responds to the treatment then it will appear as noise (Green 1979; Krzanowski and Marriott 1994). A requirement that an approach be sensitive to a treatment effect which involved only one scarce species is too stringent. If these situations are to be recognized then a fine filter approach must be developed for them.

presume that the investigator has information on the number and length of the gradients. Gauch (1982a, 1982b) also argues that only a few environmental factors exert a substantial influence in any one location. Most species abundances will be related to these variables in a systematic, albeit potentially complex, manner. If that is true then the number of axes which represent structure or structure mixed with polynomial effects is limited unless there are strong non-linearities in the data. The likelihood that this will occur is much reduced when the data are stratified on substantial causal factors.

Noise is always present in ecological data. In any area, there are usually species whose distribution is localized due to specialized microhabitat requirements or random events. It is also the case that the probability of collecting a scarce species, even if it is widespread, is small unless the plot and sample size are large. A sample will contain such species in one to a few plots. An entire principal component with a low eigenvalue may be dedicated to such species. If there are a number of infrequent species in the dataset then a large number of components will be required to capture all the variation in the data.

Even if the data structure is approximately linear, the first few axes may capture as little as 20% of the total variation. This can occur if there are a large number of species and a number of them have patterns of abundance independent from the rest. It does not mean that the ordination is ineffective. In this case, it means that there is a significant amount of noise which is also being captured. The amount of variation captured on the first few axes will be a function of the amount of noise, degree of non-linearity, resemblance measure and a number of other factors.

The upshot is that there are valid arguments for suggesting that only the first few axes need be retained without biasing the results of an hypothesis test. Unfortunately, there is no objective way of determining how many of the first few axes are capturing the salient structure in the data (Chatfield and Collins 1980). The generally accepted procedure is to review the results to determine whether they have an ecological interpretation. Other methods include the retention of components with eigenvalues greater than the average or the plotting of eigenvalues (or percentage of variation) in rank order (scree test; Dillon and Goldstein 1984). In the latter approach, if there is structure in the data then a curve approximating a negative exponential distribution is produced. The point where the curve begins to level off suggests the transition from structure (which includes spurious polynomial effects) to noise.

Thus far, a particular ordination technique has not been identified as being suited to dimensionality reduction in the context of this study's objectives. Statements are found in the literature regarding the differences in PCA, CA and principal coordinates analysis (PCO). PCO is generally described as preserving interplot distances in a lower dimensional space, PCA as representing the real pattern of the data in two or three dimensions (Pielou 1984) and CA as highlighting the block structure of a dataset (Ter Braak 1987). Despite the fact that these are valid descriptions of the techniques, it should be emphasized that all eigenanalysis ordination techniques can follow the same general algorithm and thus be conceptualized as special cases of PCO. All of these techniques eigenanalyze a resemblance matrix. Their results differ because they emphasize different aspects of the data by perform eigenanalysis on a different resemblance matrix. The resemblance matrix is the product of four explicit or implicit decisions:

- 1) Transform the raw data?
- 2) Center the data?
- 3) Standardize the data?
- 4) Which dissimilarity measure?

One of the ways to get the same results from PCO as would be obtained from PCA using covariances is to answer yes to the first two questions, no to the second and choosing Euclidean

distance as the dissimilarity measure²³. CA is equivalent to PCO performed on a matrix of chi-squared distances.

The four required ordination decisions emphasize that there are many decisions involved in data analysis. Sixteen different matrices could be produced for eigenanalysis if only one transformation, standardization and resemblance measure are considered. Imagine the number of combinations when several of the transformation or resemblance measure options become candidates. Selection of an appropriate ordination technique is important and implies simultaneous decisions regarding a number of other issues. Section C.6.4 identified percentage difference of relative Manhattan as the resemblance measures most appropriate to a comparison of treatment effects. PCO is the only ordination technique which can use these measures.

A disadvantage of PCO is that its results do not have a direct interpretation in terms of the species. PCO simply ensures that the relative ecological distances between the plots in the reduced space resemble their original distances in species space as closely as possible. The results produced by PCO can be corroborated by cluster analysis, PCA, CA and NMDS and frequency and abundance data. It is expected *a priori* that the overall pattern exhibited by all the techniques will be the same unless there are substantial polynomial effects distorting the results. Cluster analysis has the dual advantages of making no assumptions about the structure of the data and it represents the results in a two-dimensional space. Non-linearities in the data affect it only to the extent that they affect the resemblance measure used. PCA and CA emphasize different aspects of the data than PCO using percentage dissimilarity. NMDS makes the less restrictive assumption of monotonicity rather than linearity. If the pattern suggested by any of these techniques differs greatly from that of PCO, in depth examination of the data is required to reevaluate the efficacy of percentage dissimilarity.

An added benefit of the corroboration techniques is that they provide an effective means of conducting exploratory data analysis and interpreting the final results. Frequency and abundance data are also available for use at all stages of analysis. Obvious trends will be apparent from scanning these data. Multivariate output can then be examined to ensure that these techniques faithfully represent any obvious patterns.

One of the shortcomings of using MANOVA as the primary test for differences in species composition is that does not provide direct or indirect indications of which species or combinations of species are affected by the treatment. This is not simply because the input to MANOVA is the first few principal coordinates derived from PCO and these principal coordinates have no interpretation vis-a-vis the original species. Consider the most straightforward situation in which species data are used. MANOVA implicitly constructs discriminant functions of the input variables. When the treatment effect is significant it may be the case that but none of the species are found to demonstrate significant differences on their own. Treatment effects must then be interpreted in terms of linear combinations of species in the same way that a principal component is a linear combination of species. This complicates the interpretation of the results.

Assume now that too many species are involved for species data to be used in MANOVA. Instead, the first few components from PCA rather than PCO are used. MANOVA constructs a linear combination of the components which are themselves linear combinations of the species. The result is something which is difficult to interpret and requires resort to sources of information external to MANOVA.

PCA distorts the representation of ecological distance germane to this study's questions. PCO is the recommended alternative but it suffers from the drawback that its components cannot be interpreted in terms of the species. Although this is true, the overall pattern it presents should be similar to cluster analysis, PCA, CA and NMDS. Exploratory data analysis prior to hypothesis tests

²³ The scale of the axes will differ by a proportionality factor but this is unimportant since the overall objective is to preserve relative and not absolute ecological distances.

should be used to confirm this. The results of these techniques are interpretable in terms of the species and can also be used to help interpret the results of MANOVA. In short, regardless of the form of species data input into MANOVA, other techniques are required to assist in the interpretation of its results and identify differences in species composition. The other techniques can also be used to identify differences in species composition when it appears that insufficient statistical power exists for MANOVA to detect differences.

Some of the other methods which can supplement ordinations to interpret the results of MANOVA include ANOVA²⁴, canonical variates analysis, cluster analysis, frequency and means. ANOVA can be used to identify which species exhibit significant differences between treatments. When used as a corroborative technique, Bonferroni adjustments will not be made since statistical power will already be low given only three or four replicates and the maintenance of power is considered more important than the maintenance of a particular experimentwise error rate.

To summarize, the suggested approach to multivariate hypothesis testing involves the use of PCO to reduce the number of variables to three or four. The new variables serve as the input to MANOVA which then tests for treatment differences in species composition. The results of other ordination techniques and ANOVA are used to corroborate the results of PCO and assist in the interpretation of MANOVA results.

C.6.6. Criteria for identifying species which characterize treatment differences or a site type.

An approach was developed to characterize, firstly, post-fire communities and, secondly, treatment differences in species composition in a more understandable way than possible in an ordination diagram or a series of tables. It was based on different notions of what was required for each of these two objectives but the result was substantially the same method. Characterization of post-fire communities across the site types is intended to provide a description of the natural state. The goal is to identify the species one would expect to be conspicuous in communities on the site type. With regard to treatment comparisons, the goal is to characterize substantial treatment differences in species composition. For both types of comparison, the interest is in identifying species which have an "affinity"²⁵ either for a site type or a treatment. A species with a site type affinity is one which is conspicuous on the site type whereas a species with a treatment affinity is more conspicuous in one of the treatments on a particular site type. When site type affinities are assigned, a given species may have an affinity with more than one site type. On the other hand, a given species can only have an affinity with one treatment.

Concepts applied in traditional approaches to the classification of vegetation (Whittaker 1978) provide a natural starting point from which to outline a method for identifying species with an affinity. They are useful because they developed criteria to group plots based on species composition measures. The Braun-Blanquet approach has been used extensively in Europe to group plots into community types based on species presence, relative and percent cover, constancy²⁶, density and vitality (Westhoff and Van Der Maarel 1978).

²⁴ In particular, mixed model ANOVA where Block is the random effect.

²⁵ Webster's New World dictionary (Guralnik 1973) defines affinity as: 1. relationship by marriage, 2. close relationship, 3. a likeness implying a common origin, 4. a spontaneous attraction to, or liking for, a person or thing. Affinity is used in the second sense herein. That is, if one is standing on a certain site type within a treatment, what species would they expect to find and how abundant are those species? Other ecological terms which have similar connotation are in use (e.g. characteristic species). However, they all have specific definitions which are not equivalent and would, therefore, introduce confusion. Affinity has been used to describe the similarity of communities but this usage is uncommon.

²⁶ Constancy should be distinguished from two related statistics. Presence-degree is the percentage of relevés (sample plots from different stands) in which a taxon occurs; constancy is the special form of presence-degree which occurs when the size of the sample plot is the same for all stands being compared. Frequency is the percentage of plots within a single stand or quadrats within a plot in which a taxon

A drawback of the traditional approaches is that they are univariate in nature. Multivariate statistical techniques incorporate, to various degrees, the vegetation characteristics that are applied in the Braun-Blanquet approach along with the added benefit of sensitivity to simultaneous changes amongst species. Canonical variates analysis (Gittins 1985) is the technique most suited to identification of the species which distinguish one site type from the others. Canonical variates analysis is a special case of canonical correlation analysis (as are PCA and MANOVA) in which species relationships are used to find the linear combination of species which maximizes the between group F ratio based on a known group membership variable. The grouping variable used is either treatment (for a particular site type and age class) or site type (for post-fire communities from a particular age class). The former grouping variable is used to assess treatment effects and the latter to characterize the vegetation found on each site type in the "natural" state. The exclusive application of multivariate techniques is precluded by two concerns. Canonical variates analysis is effective for exploratory analysis of data but cannot be used for hypothesis tests since it treats the plots as replicates and would result in pseudoreplication (Hurlbert 1984). An analysis based on plots is necessary due to the large number of observations required to detect multivariate relationships between the species.

A second problem with canonical variates analysis is that high canonical structure correlations derived from a canonical variates analysis can be misleading as they are based on plots and not Blocks. A species may be given a high structure correlation based on a high frequency and mean cover in only one Block. Mixed model ANOVA, treating Block as a random effect, is used to help detect this. ANOVA is inadequate on its own since it suffers from low statistical power and is insensitive to interspecific associations. Even when these two techniques are coupled, frequency and mean cover data are required to deal with the drawbacks which still remain. Canonical variates analysis and ANOVA identify exclusive and characteristic species effectively. They are less effective at identifying companion (ubiquitous) species. Treatment differences are not characterized by companion species but these species are important in the characterization of post-fire communities across the site types. Frequency and mean cover data can be used to identify companion species and situations where low statistical power may be precluding the detection of treatment or site type differences.

When these four methods are coupled together they identify species which have either a site type or treatment affinity based on their frequency and fidelity at the plot and Block levels. Because frequency and fidelity are a function of plot size, affinity should be assessed at two strength levels for the site type characterizations. Species moderately to very abundant on a site type will be found in most plots. Since we expect to find these species in or adjacent to each plot, they are called characteristic species. There will be another group of species which are less frequent because they have a lower relative abundance or higher mean patch size. They still occur in most communities but the plot size is too small to collect them. These are called associated species.

Empirical criteria for assigning affinities can now be developed. The criteria used to establish affinity incorporate the concepts of coordinated species responses, constancy, fidelity and distribution of cover at the plot and Block level. They are developed from knowledge of the strengths and weaknesses of the statistical techniques and traditional approaches to vegetation classification.

For a particular site type, a species was short-listed for the treatment affinity designation if it:

- 1) Had a high canonical structure correlation (≥ 0.3 in absolute value) with a treatment;
- 2) Had a significant treatment difference at $\alpha = 5\%$ when analyzed with mixed model ANOVA using Block as a random effect. Bonferroni adjustments were not applied;

occurs (Westhoff and Van Der Maarel 1978). In this study, sample plots representing a particular site type are generally located in different communities. Constancy is the term which is applied.

- 3) Occurred in both treatments but with a much higher frequency or mean cover in one treatment (e.g. 60% frequency on outcrops in burns and 5% in cutovers). These species may be missed by the first two criteria if variability is high.
- 4) Was present in only one treatment and had an overall frequency of at least 50% and a Block frequency of at least 75% for that treatment. Canonical variates analysis and ANOVA will identify species which meet this criterion. The problem is that they will also identify species with much lower frequencies than set out. When this occurs, it is possible that the species' absence in one treatment is an artefact of sampling and should not be considered to be an indicator of a treatment effect.

All four criteria had to be considered simultaneously since they were intended to complement the drawbacks of each other. Species identified by one criterion might be disqualified by another.

Site type affinities are derived in a similar way and at two levels: conspicuous and associated species. A species was short-listed for the conspicuous site type affinity designation if it:

- 1) Had a high canonical structure correlation (≥ 0.3 in absolute value) with a site type;
- 2) Had a significant site type difference at $\alpha = 5\%$ when analyzed with mixed model ANOVA using Block as a random effect. For species which were found to have a significant difference, this was followed by a Bonferroni adjusted comparison of means across site types to identify the site types in which the species had a significantly different mean cover;
- 3) Was present in only one site type or treatment and had an overall frequency of at least 50% and a Block frequency of at least 75% for that site type;
- 4) Had an overall and Block frequency greater than or equal to 75%. This criterion identified companion species.

Once again, all four criteria were considered simultaneously.

Associated species met criteria 1) and 2) but had a lower frequency than in 3). They had much higher frequency or mean cover in one site type compared with all others (e.g. 60% frequency on outcrops and 0% - 5% on all others).

C.7. Evaluating ecological relevance in the event of statistical significance.

Assuming significant treatment differences are detected, what do they imply²⁷? Treatment differences in species composition are direct observations which may be indirect indications about impacts on ecological processes and functions. Interpretation of differences in species composition is complex and can be reduced to evaluations of particular species or groups of species. The question which then arises is: how large does a statistically significant difference have to be before it is considered to be ecologically significant? To illustrate, let's assume that it is found that the mean cover of Species X is 15% in burns and 10% in cutovers. Here, a 5% absolute and 33% relative reduction in abundance is associated with logging. Is this reduction ecologically significant? What are the factors which must be incorporated into such an evaluation?

Hurlbert (1971) has grappled with this question and suggests that importance in terms of ecological function may be defined as:

$$I = \sum_{i=1}^S |P_{i,t=1} - P_{i,t=0}|$$

where S = the number of species in the forest ecosystem, P = productivity, $P_{i,t=0}$ represents productivity of all species prior to removal of species i, $P_{i,t=1}$ is productivity of all species after removal of species i allowing enough time for other species to adjust.

Measuring ecological importance in this way is complicated by the possibility that a species may not be completely removed or that a number of species are affected and their effects on the forest ecosystem are confounded. In addition, very substantial practical problems are involved in such a measurement.

As is the case with most other steps in the evaluation of community resilience, ideal techniques are not available. Consequently, pragmatic criteria must be suggested based on theoretical propositions. Some of those are:

1. Has previous research suggested that the species performs an important ecological function?
2. Is its reduction in abundance compensated for by other species which perform a similar ecological function?
3. If there is no particular ecological function associated with the species, is its reduction in abundance offset by increases in other species? In other words, is the abundance of all species combined less in post-logging communities than in post-fire communities?
4. If there are new species found in cutovers, are they exotics? Is it suspected that they will eventually have detrimental impacts on species composition or richness (e.g. purple loosestrife)?
5. Are there groups of species which have changed in a systematic manner indicating some broader impact than would be interpreted from a single species?

Points 1) to 3) relate to the view that redundancy exists in a forest ecosystem and implies that some species are dispensable as far as function is concerned. In the short term, it is easy to imagine that the species composition of a community will change following disturbance. The indirect evidence that the disturbance has not adversely impacted ecological processes and functions is that species composition eventually returns to a typical mature state after a series of repetitions of the disturbance. If redundancy exists then this means that not all species must return or even most species with the exact same abundance. Even if redundancy is not present, natural variability and the multiple potential successional pathways possible for any given set of abiotic conditions ensures that exact regeneration will rarely occur.

²⁷ No two Blocks are exactly alike and neither are any two groups of Blocks. A difference can always be detected provided that enough replicates are obtained. The difficulty that observational studies have securing replicates means that the detection of minute differences is not an issue simply due to its impracticality. When differences are detected in this context, they are likely to be large in relative terms.

When evaluating differences in species composition, emphasis should be placed on community dominants, species or groups of species which play an important role in vegetation dynamics, species which perform important ecological functions²⁸ and species which are important for other reasons (e.g. they are rare). In boreal plant communities, the two groups of species which play a key role in dynamics are the trees and mosses and reindeer lichens. The dominant canopy species can have very substantial effects on species composition through its effects on shading, microclimate, snow accumulation, soil pH and smothering by leaf litter. Mosses and reindeer lichens can have a substantial influence on seedling survival, soil moisture and soil temperature. Substantial treatment differences in the composition or abundance of these species will be important.

Two other points must be considered when a significant result is obtained and species differences are being evaluated.

1. Do the differences observed reflect true differences or sampling variability?
2. Is the species economically or socially important? There are many examples of scarce species which have no apparent substantial ecological function but are very important medicinally or in ceremonies.

One component of sampling variability is taken into account when the level of α is specified. It is not this variability that is of concern but that associated with sample size problems in the representation of species abundances in general and scarce or clumped species in particular (see Appendix D). This is a very real problem and explains why only the Common species are used in species richness comparisons herein.

Once we go beyond the pulpwood use of trees, the evaluation of ecological significance becomes more difficult. Evaluating economic, medicinal, spiritual and social importance is complicated by the fact that there are many alternative uses of plants and no simple way of evaluating them. This issue is beyond the scope of this report.

Last, but not least, what does it mean if a significant difference is **not** found? It certainly is not a proof that there are no differences. Replication is low due to limitations on the size of sampling frames. Inevitably, this will lead to situations in which statistical power is too low to detect a treatment difference. In general, differences will only be detected if they are relatively large or within treatment variation is low relative to between treatment variation. The latter condition is a decreasing function of sample size. Insignificant results should be accompanied by a statement of power. That is, an estimate of the probability that the test would detect a specified difference between treatments at the given significance level. For example, the test has an 80% chance of detecting an absolute difference of 10% in percent cover of Species X at $\alpha = 5\%$. Calculating power for univariate tests is relatively straightforward, however, it becomes quite complex for multivariate hypothesis tests. The corroborative methods can be used for this purpose (Section C.6.5).

²⁸ We know very little about the ecological functions that species perform so we must perform our evaluations with the best information available and realize that our efforts will contribute more to the generation of new hypotheses than providing understanding.

Appendix D

THE EFFECTS OF SAMPLE SIZE ON THE ESTIMATION OF SPECIES RICHNESS AND CERTAIN OTHER SPECIES COMPOSITION PARAMETERS.

D.1. Statement of the problem.

Plant ecologists are well aware that the number of species observed in a community increases with area sampled. Plotting species collected against cumulative area sampled provides what is known as a species area or collector curve (Pielou 1975)²⁹. Figure D.1 illustrates the collector curves for two hypothetical communities. As is typical for real communities, both collector curves initially rise rapidly and then level off at different rates. This is the case whether nested quadrats or the cumulative area of randomly located plots are used although the curve resulting from the latter sampling approach will generally rise more rapidly because individuals and species usually do not have random spatial distributions.

There are three points to note about these curves. Firstly, the number of species collected in a sample (a collection of plots of a given size and shape) is a biased estimator of total species richness³⁰ despite it being an unbiased estimator of the mean number of species collected in a plot of a fixed area. In other words, the mean species richness of an infinite number of samples of A m² (Figure D.1) in Community 1 is expected to equal X species. The only way to reach total species richness is by increasing sample size to area B. Intuitively, the difference between estimating the mean number of species per plot and total species richness is that, in the former case, the mean value of some attribute of the individuals (i.e. the species affiliation of the individual) encountered in the plot is being estimated. Data for this attribute is collected in each plot by grouping individuals into species and then counting the number of species. Species identities are not required when the mean for all plots is being calculated. For total species richness, the objective is to estimate the number of groups in the entire community and not just the average number in a plot. Species identities must be retained as plots are added to the data so that one can keep track of which species have already been recorded. Estimation of total species richness also differs in another fundamental manner. It requires an estimate of how many new species will be found in the plots which have not been sampled. Sample sizes in observational studies in plant ecology typically constitute less than 1% of the area of a community. Consequently, the probability that many species have not been collected is high unless species richness is low and evenness is high.

To illustrate how the sampling problem arises, imagine what would be happening under field conditions. Assume that equal sized plots of 1 m² are randomly located in a community in which the individuals and species are approximately randomly distributed (Figure D.2). Each of the three plots contains 5 species. Each plot also has 1 species unique to it. As each new plot is sampled, mean species density remains constant across all plots while observed richness increases from 5 to 6 to 7. If 30 plots were sampled it is expected that each plot would still contain about 5 species but observed richness would continue to rise slowly. If enough plots were sampled, all species inhabiting the community would eventually be collected.

²⁹ To avoid potential confusions, these two terms will be applied to two different situations. A species area curve will refer to the number of species observed in communities or islands of different areas or the cumulative area of samples of the same size in replicate communities from the same community type. It summarizes cross-sectional data. In contrast, a collector curve represents the number of species observed as the cumulative area sampled within a single community increases. It represents a sampling phenomena. A species area curve has no theoretical upper limit whereas a collector curve does provided that the boundaries of the community have been precisely defined.

³⁰ Appendix C discussed the definitions of species richness and species density. The unit for species richness is abundance (e.g. 14 species per 1000 individuals) and that of species density is area. This creates a semantic problem. Often when species richness is being discussed, the results actually relate to species density. This probably occurs because the term species richness is being used in the more general sense of the number of species in a community. However, the effect of sample size (i.e. number of individuals or area sampled) on species richness means that results need to be precise in stating which measure is being used. In this theoretical discussion, we will make the assumption that the number of individuals/ total plant cover is proportional to area so that the two terms can be used interchangeably (May 1975).

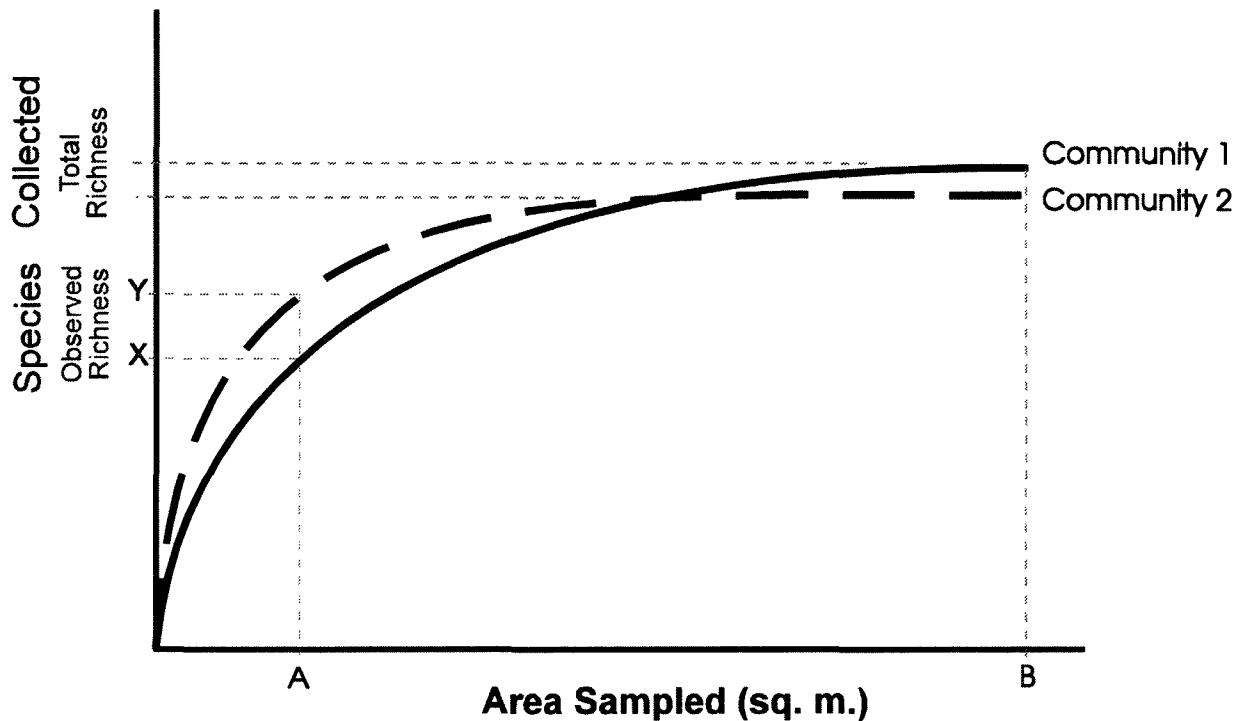


Figure D.1. Collector curves for two hypothetical communities.

The second point to note about the collector curves is that a comparison of the total species richness of two or more communities is not possible without having information on a large portion of the collector curve for each community. This is the case because community collector curves may cross. When this happens, the community with the higher observed species richness may actually have the lower total species richness. Comparisons of species richness based on sample information will lead to erroneous conclusions regarding total species richness unless the sample size is large (the interpretation of "large" is discussed below).

The third point to be made about the collector curves (Figure D.1) is that their shape is determined by how the individuals³¹ are distributed among the various species within the community. A mathematical relationship exists between this diagram and the theoretical shape of the collector curve (May 1975) (the actual shape of the collector curve will deviate from the theoretical if individuals and species are patchy in their distribution). One way of representing the distribution of abundance among species is in a bar chart with the relative abundance of each species in rank order. This is called an abundance-rank diagram.

Figure D.3 presents the abundance-rank diagram for two hypothetical communities, both containing 61 species. Community 1, represented by the dark bars, has what is referred to as a log-series distribution of abundance. That means that the community consists of several very abundant species and a large number of scarce ones. In contrast, Community 2 has several very abundant species, a large number of moderately abundant species and a few scarce ones. This type of species abundance distribution is termed lognormal. When the bars are labeled with species

³¹ Or whatever measure of abundance is being used. For example, percent cover or biomass. Numbers of individuals are generally used since, being discrete objects of similar size, they simplify the presentation of concepts and the development of theoretical constructs. This conception of an individual is unsuited to plants since individuals of the same species can vary a thousand-fold in size. Clonal species present a different problem. With them it is often not clear where one individual ends and another begins. Consequently, percent cover or biomass are often used in the empirical application of the concepts. This appendix will use the number of individuals as the measure of abundance for the presentation of concepts and the development of a method to deal with the sample size problem. Once the method is applied empirically, percent cover is substituted.

names, an abundance-rank diagram provides complete species composition information for the community.

Species composition and one of its components, species richness, can be used as indicators of community resilience or treatment effects. All of the comparison measures associated with these indicators are strongly affected by sample size regardless of the shape of the community's underlying species abundance distribution. This arises in two ways. Firstly, as already noted, the expected value of the estimator changes with the sample size used. Secondly, since the sample size effect is a non-linear one based on some unknown species abundance distribution, predicting how the estimator changes with sample size requires additional information not available in a small sample (Baltanas 1992; Palmer 1990, 1991). In the case of species richness, the degree of dependence on sample size varies between estimators. Studies have shown that a "large" sample is generally at least 80% of the species and sometimes also 80% of the community's abundance (Baltanas 1992). Samples of this size are impractical. Even if sample size could be dramatically increased, available methods do not indicate when 80% of the community's species or individuals have been collected. The other option frequently employed is to assume a particular species abundance distribution such as the lognormal. However, if the objective is to determine whether differences in species composition exist then this is circular. The shape of the species abundance distribution (i.e. a summary of species composition) is assumed so that parameters can be estimated for comparison purposes.

These factors lead to the possibility of collector curve crossover and should dissuade us from making comparisons of total species richness based on the sample sizes typical of plant ecology.

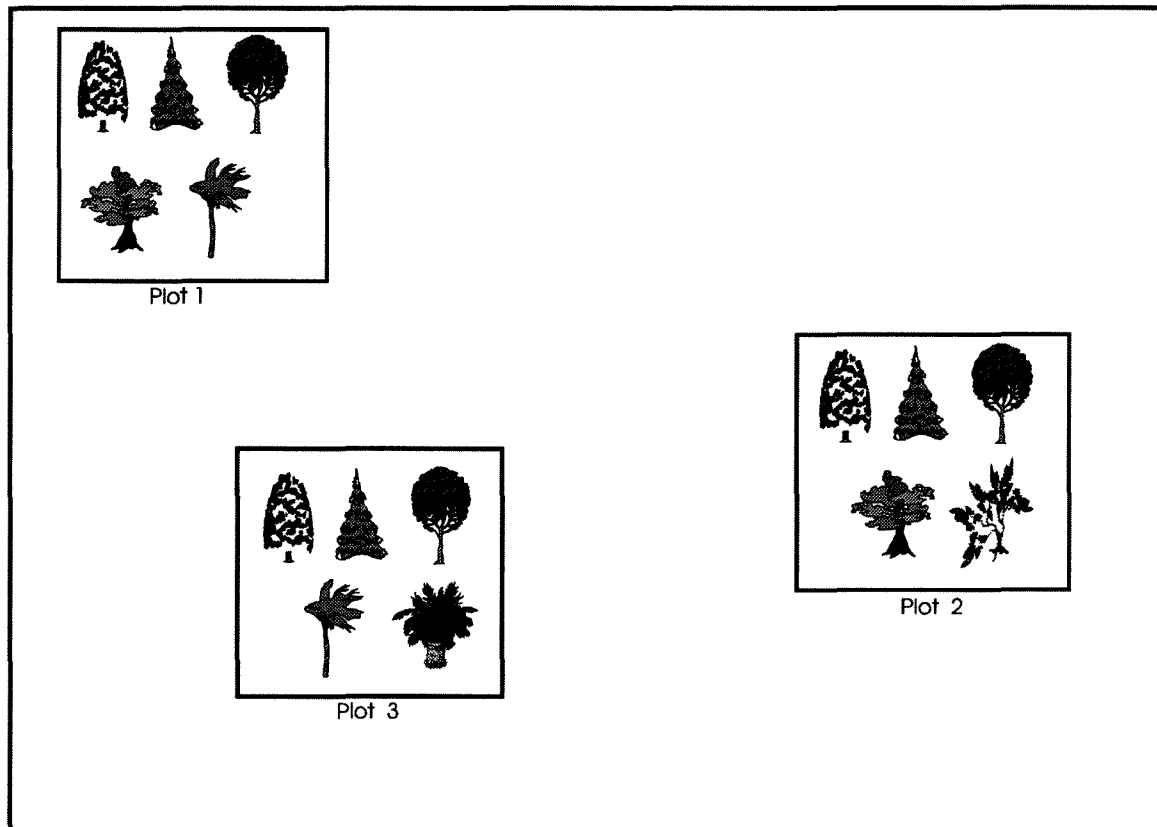


Figure D.2. Species collected in plots randomly located in a community.

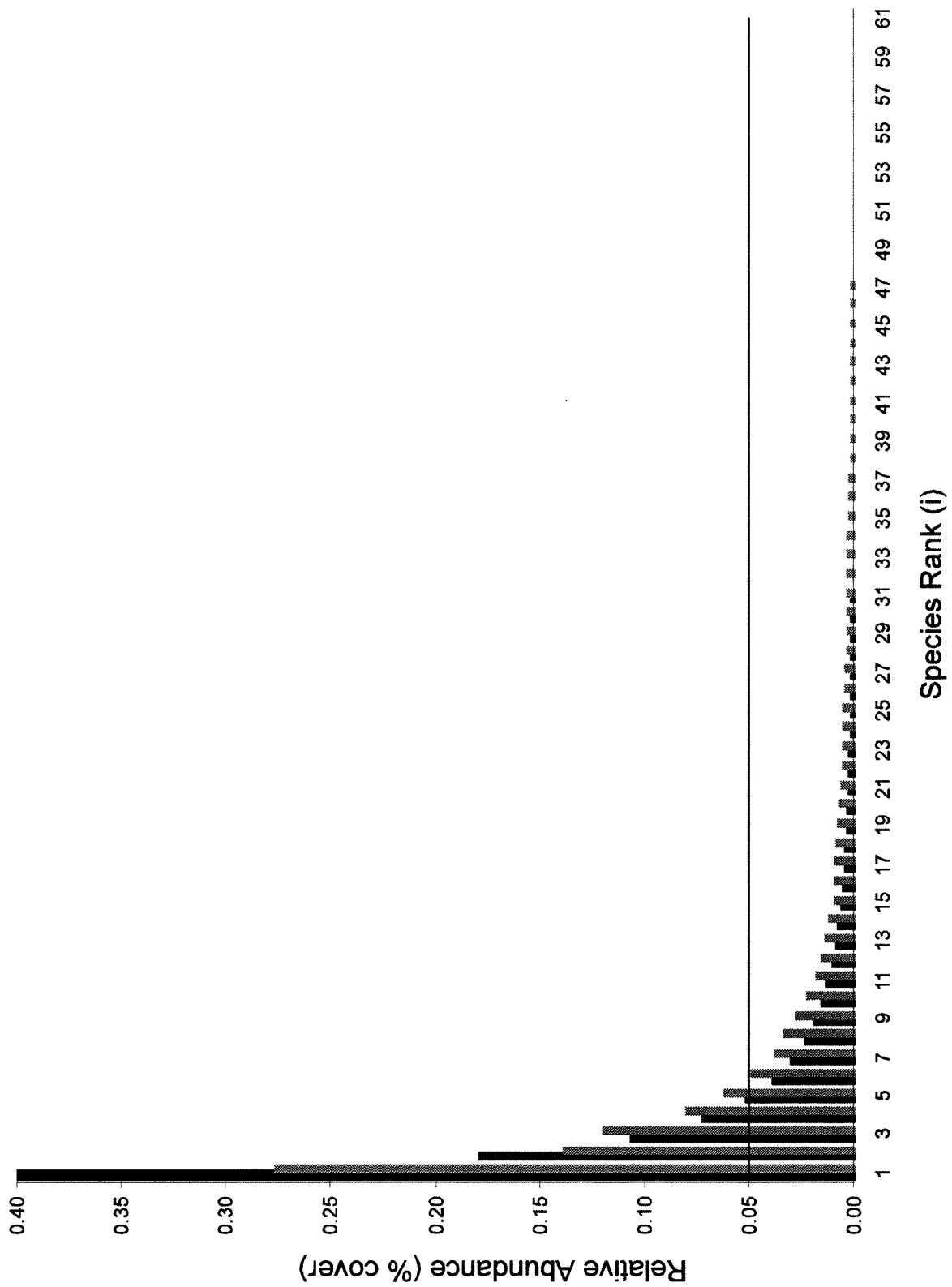


Figure D.3. Abundance-Rank Diagrams for two communities. Community 1 represented by light bars; Community 2 by dark bars. Values for some species too small to be visible.

Species richness estimation is not the only area for concern. Sampling effects can also introduce problems where the objective is to describe or compare communities based on species composition. This is because there is no established way of knowing what the sample represents in terms of the species present in the communities. Some of the potential biases associated with small samples include:

- 1) Equal sized samples taken from two communities with the same total species richness but different species abundance distributions will collect more species in one community than the other. Any data transformation, resemblance measure or quantitative method which incorporates species richness will distort the differences between the communities and may identify differences that do not exist. For example, calculation of the correlation coefficient will use zero abundance values for some plots when the true value is some positive number. This measure treats double zeros as indications of high similarity.
- 2) If the sample size is too small to include a species, its sample abundance will be an unreliable estimate of its community abundance. A test for a difference in mean abundance of the species in two communities using ANOVA (where the replicate is modeled as a random effect) might determine that a significant difference exists when it does not.
- 3) It is a common practice when applying multivariate methods to analyze species composition data to drop species which occur in only one plot on the basis that scarce species have limited ecological significance in a community. However, when doing this, you may actually be deleting a moderately abundant species. The only reason it appears to be scarce is that the plot size was too small.
- 4) A species may appear in a sample from one community but not another even though its abundance is the same in both communities. A comparison of the communities based on composition will be affected by the spurious absence of this species.

The effect of sample size on the reliability of abundance estimates (point 2 above) can be illustrated by comparing the way sampling is typically conducted in plant ecology with the approach advocated by statisticians. To obtain an estimate of a population parameter using the statistician's approach one would construct a sampling frame for the population of interest, randomly select X individuals from the sampling frame, measure the parameter for each individual and then calculate the parameter's mean and variance. The resulting estimate of the mean is unbiased. That is, the mean of an infinite number of such sample means is expected to equal the population mean. Increasing the number of individuals sampled from X to $1.5X$ has the effect of increasing the precision of the single sample obtained.

Figure D.4 shows how this approach would be applied to a plant community. Species A and B are present in this community and are shown by different shading. For each species, each individual is numbered beginning at 1 and its spatial coordinates (x,y) are shown in brackets. Assume a sample size of three individuals for each species. Individuals can be selected from a random number table. The plant ecologist then uses the geographic coordinates to locate the individuals in the field so that the surface area of the vertical projection of their foliage can be measured. Once relativized to the total area of the community and multiplied by 100, an unbiased estimate of percent cover for the species is obtained. Estimated mean cover for Species A and B in Figure D.4 based on three randomly selected individuals are $1.4\% \pm 3.2\%$ and $2.5\% \pm 4.0\%$, respectively.

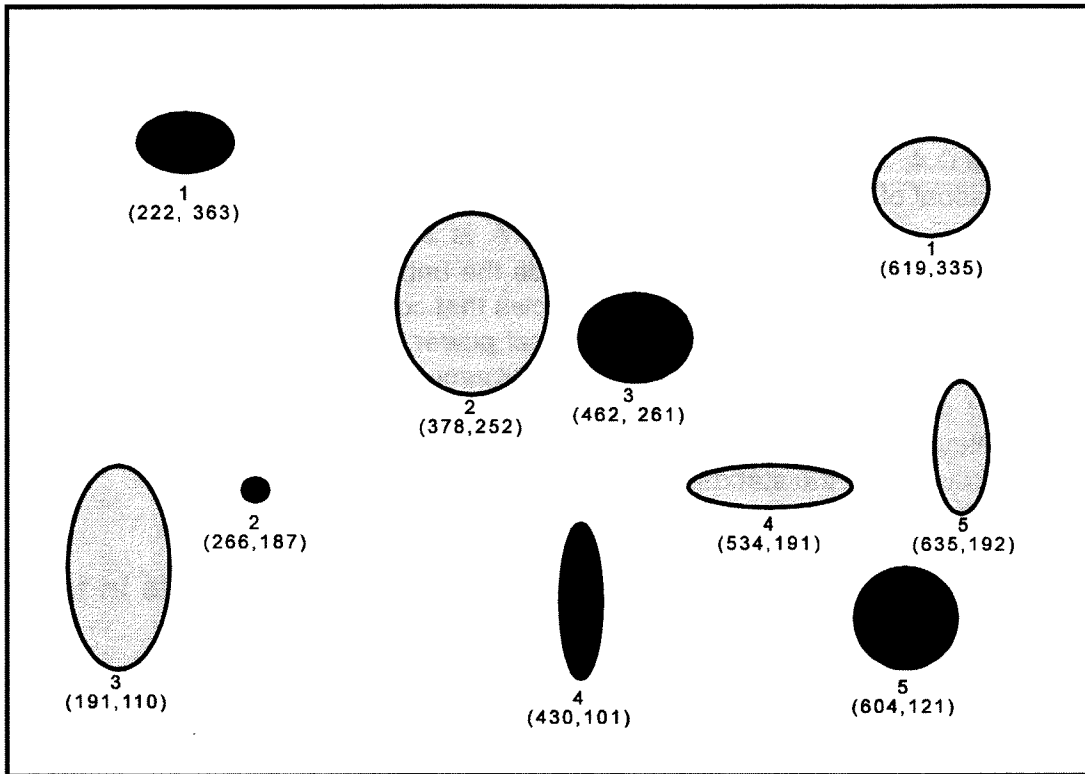


Figure D.4. Map of Species A and B in a community showing area covered and coordinates of center of individual. Species A is stippled; Species B is solid. Spatial coordinates in parentheses.

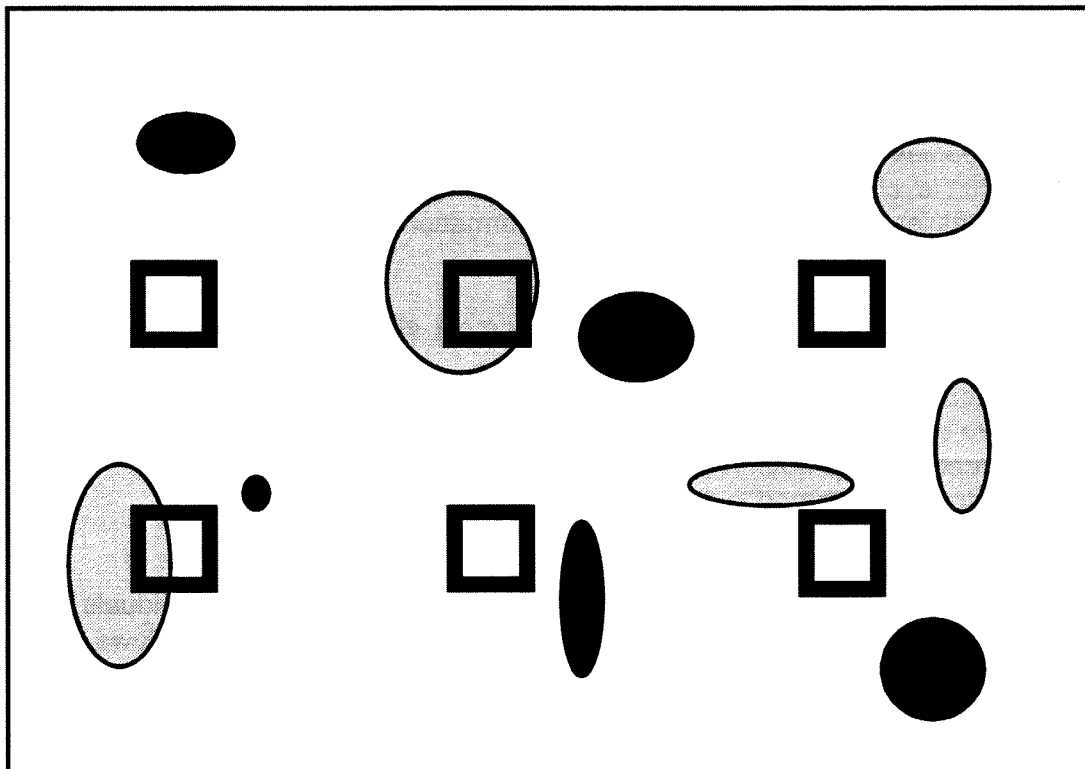


Figure D.5. Six plots systematically located in the community of Figure D.4.

Plant ecologists rarely sample communities in this way because species sampling frames (i.e. maps showing the spatial distribution of individual plants by species) are not available. Instead, plots are systematically or randomly placed within the community and the percent cover or density of each species encountered within the plots is measured. Figure D.5 shows 6 plots systematically located in the community of Figure D.4. In this example, Species A does not fall within any of the plots and only a portion of one individual of Species B covers all of one plot. Mean cover estimates are $0\% \pm 0\%$ and $22.5\% \pm 104\%$. The results imply that Species A is absent in the community. The confidence interval for Species B is broad enough to include the unbiased estimate for this species calculated from the species sampling frame but is so imprecise that comparisons between species or for the same species across communities will lack statistical power. Ecologists often obtain more than three but usually less than 10 subsamples within a community. Increasing the number of subsamples from 3 to 10 will increase the probability that Species A will be collected and the precision of estimates. Nevertheless, an increased probability cannot compare with the certainty and increased precision provided by the standard approach.

D.2. Formulation of a method to determine what the sample represents in terms of the species present in the community.

It appears that measures used to compare species composition or species richness across treatments or communities are subject to potentially serious sampling problems. These problems result from the combination of small sample size, spatial aggregation of individuals and species and the ecologist's inability to randomly sample individuals and species within a community. At best, a sample can only be expected to collect all the abundant species in a community. The sample will also include some moderately abundant and scarce species. It would be useful to know what the sample actually represents in terms of the community's species composition and whether a particular species' sample abundance is a reliable estimate of its community abundance. This appendix will propose a method which is intended to answer the following questions:

- 1) Which species is the sample expected to collect?
- 2) How do we set the sample size so that it is large enough to collect all the moderately to very abundant species in the community?
- 3) Alternatively, what level of relative abundance is the sample size capable of detecting?
- 4) Is the sample sufficiently representative that its information can be used to estimate total species richness?

In order to present the proposed method with the utmost clarity, a number of simplifying assumptions are made.

- 1) Abundance is measured as the number of individuals.
- 2) All individuals are similar in their size/ aerial extent;
- 3) Individuals are randomly distributed in space;
- 4) Species are randomly distributed in space;
- 5) The plot size is larger than the patch size of most individuals;
- 6) Plots are randomly located in the community;
- 7) There is a proportional relationship between plot size and the number of individuals found in a plot. This is a reasonable assumption given assumptions 2) to 5) and allows for the use of individuals and area interchangeably in the presentation.

These are simplifying assumptions only and the consequences of their relaxation must be dealt with at some point. It should be noted that most quantitative methods presently applied to vegetation data make assumptions equivalent to 2) - 6) either explicitly or implicitly.

From basic statistics, it can be stated that the probability of collecting an individual of species i in a sample size of 1 is equal to its proportional representation in the community (Eq. 1).

$$\text{Eq. 1) } p_i = \frac{N_i}{N}$$

where p_i = probability of collecting species i ; N_i represents the abundance of species i in the community and N the abundance of all species in the community; N is large.

In other words, the probability of collecting species i in a sample size of 1 is equal to its relative abundance.

The probability of collecting at least one individual of species i in a sample size larger than 1 (without replacement) can be obtained from the hypergeometric distribution (Eq. 2).

$$\text{Eq. 2) } \Pi_k = 1 - \frac{\binom{N - N_i}{k}}{\binom{N}{k}}$$

where k = sample size, Π_k = probability of collecting species i in a sample size of k and the combinatorial term represents the probability of not collecting species i .

The with replacement equivalent is given by the multinomial distribution. Its value for Π_k approximates Eq. 2 when $N > 1,000$, $k < .05N$ and $N_i > 0.04N$ is³²:

$$\text{Eq. 3) } \Pi_k = 1 - \left(1 - \frac{N_i}{N}\right)^k \text{ or } \Pi_k = 1 - (1 - p_i)^k$$

where p_i is from Eq. 1.

Eq. 3 is introduced as it facilitates the use of relative rather than absolute abundances. This will become very useful when it comes time to draw inferences from samples. Eq. 3 indicates that the probability of collecting a species in this ideal community is dependent only on two things- its relative abundance and the sample size. Taking the logarithm of both sides of Eq. 3 and solving for k yields the sample size required to collect at least one individual of species i at a given probability level with replacement (Eq. 4).

$$\text{Eq. 4) } k_i = \frac{\ln(1 - \Pi)}{\ln(1 - \frac{N_i}{N})}$$

The behavior of Eq. 4 can be illustrated with sample size curves for various probability levels and relative abundances (Figure D.6). Increasing the probability of collecting a species (Π) results in small increases in sample size (k) until the probability approaches 1.0. Once a level of approximately 0.95 is reached, k increases drastically. Eq. 4 is the multinomial equivalent of the without replacement version (Eq. 2). The sample size curves rise more rapidly for the multinomial version. A mathematical solution for Π from Eq. 2 was not derived but values can be derived by a series of substitutions. Inserting a probability level of 0.9999 into Eq. 4 yields the result that species whose relative abundances 25% and 5% will be collected in sample sizes of 32 and 180 individuals,

³² The multinomial equation is the "with replacement" version of the hypergeometric equation and that is why it approximates it for large N . A mathematician needs to derive exact values for this proposition. The value 0.04 was derived iteratively in a spreadsheet application.

respectively, for any community containing more than 1,000 individuals³³. The same values from Eq. 2 were 31 and 158 individuals. In a community of 10,000 individuals, these sample sizes represent 0.3% and 1.6% of the entire community, at most. The ability to determine the absolute sample size required to collect a species of a given relative abundance is a useful tool.

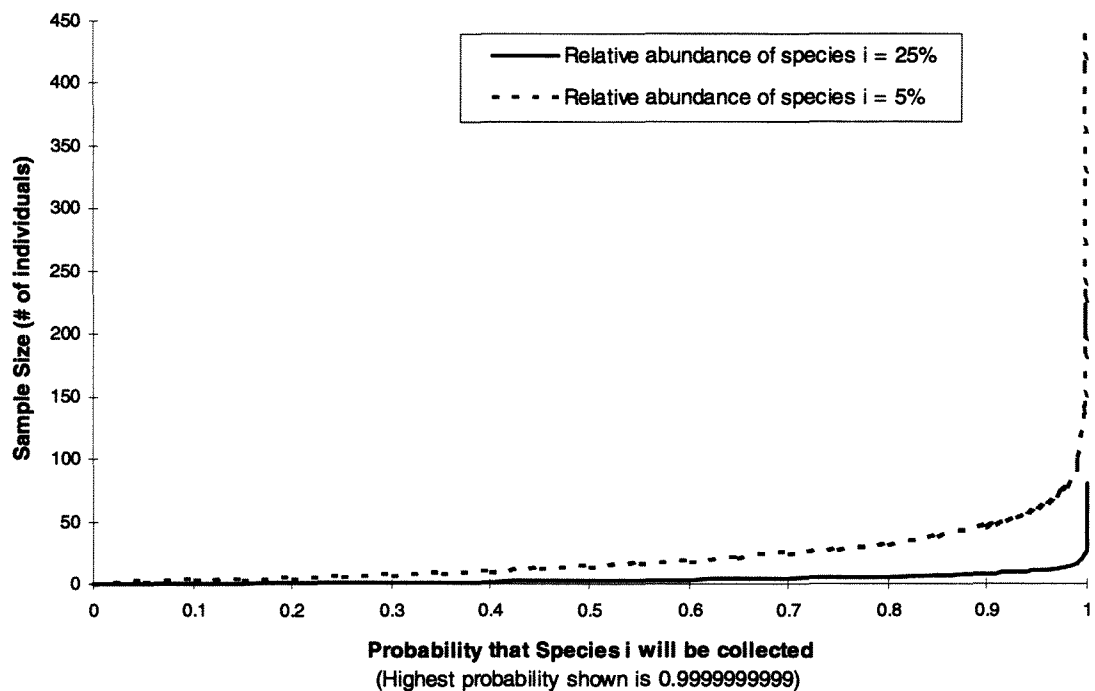


Figure D.6. Sample Size Curves.

We return now to the abundance-rank diagram shown previously. The results derived thus far can be used to determine which species are expected to be collected in samples of different sizes for communities of 1,000 individuals or more (Figure D.7). Horizontal lines in Figure D.7 represent different sample sizes. The discussion will focus on the dotted line which represents a relative abundance of 5%. Based on Eq. 4, any species whose relative abundance is equal to or greater than the line's ordinate value has a probability of 99.99% of being collected in the sample. For these species, it will be stated hereinafter that the sample size is expected to "reveal" the species. Preston (1948) described the effect sample size has on revealing species abundance distributions with his use of the "veil line". As sample size is increased, the relative abundance revealed by it decreases.

A sample will also collect a number of species whose relative abundance falls below the sample size line. By summing over all species using Eq. 2 and Eq. 3 (see Eq. 5 and Eq. 6), the total number of species expected in a sample of size k can be calculated (Hurlbert 1971). The total will include all those above the sample line plus some unidentified subset of those below it.

$$\text{Eq. 5) } S_k = \sum_i \left(1 - \frac{\binom{N - N_i}{k}}{\binom{N}{k}} \right)$$

³³ The sample size required to collect a species of a given relative abundance and probability approaches an asymptotic value at about 1,000 individuals.

$$\text{Eq. 6) } S_k = \sum_i \left[1 - \left(1 - \frac{N_i}{N} \right)^k \right]$$

This elucidates one of the distortions that sampling can introduce. Both communities in Figure D.7 contain 61 species, but, their abundance distributions differ. For any given sample size, more species are collected in the community with the more even distribution of abundance- in this example it is the one with the light bars. The number of species expected to be collected at each sample size is shown next to the horizontal line. SCN equals the number of species collected in the lognormally distributed community i.e. the light bars; SCS is the number collected in a community with a log-series distribution. Both communities have the same total number of species but a sample is expected to collect more species in Community 2 (light bars in figure) leading to the erroneous conclusion that Community 2 has a higher species richness. This reiterates why a relationship between the number of species in the sample and total species richness cannot be inferred without knowledge of the community's species abundance distribution.

A second distortion is also clarified by the figure. Two successive samples of 158 individuals taken from Community 1 (solid bars in Figure D.7) are each expected to collect 17 species. The first time Community 1 is sampled, the 5 common plus 12 of the 56 remaining scarce species are expected to be collected. A second sample from the same community is expected to collect the same 5 common species again plus 12 of the rare. It is quite possible that the 12 scarce species in the second sample will be a different 12 than were collected in the first. Consequently, the two samples taken from the same community would apparently indicate that the community's composition had changed between samples. Likewise, a constant sample size applied to two communities with identical species composition will yield different species lists leading to the erroneous conclusion that the communities differ in their species composition. Common sense would cause a plant ecologist to question the result obtained from the two samples taken from the same community if the second sample was obtained immediately after the first. What about the situation involving two different communities?

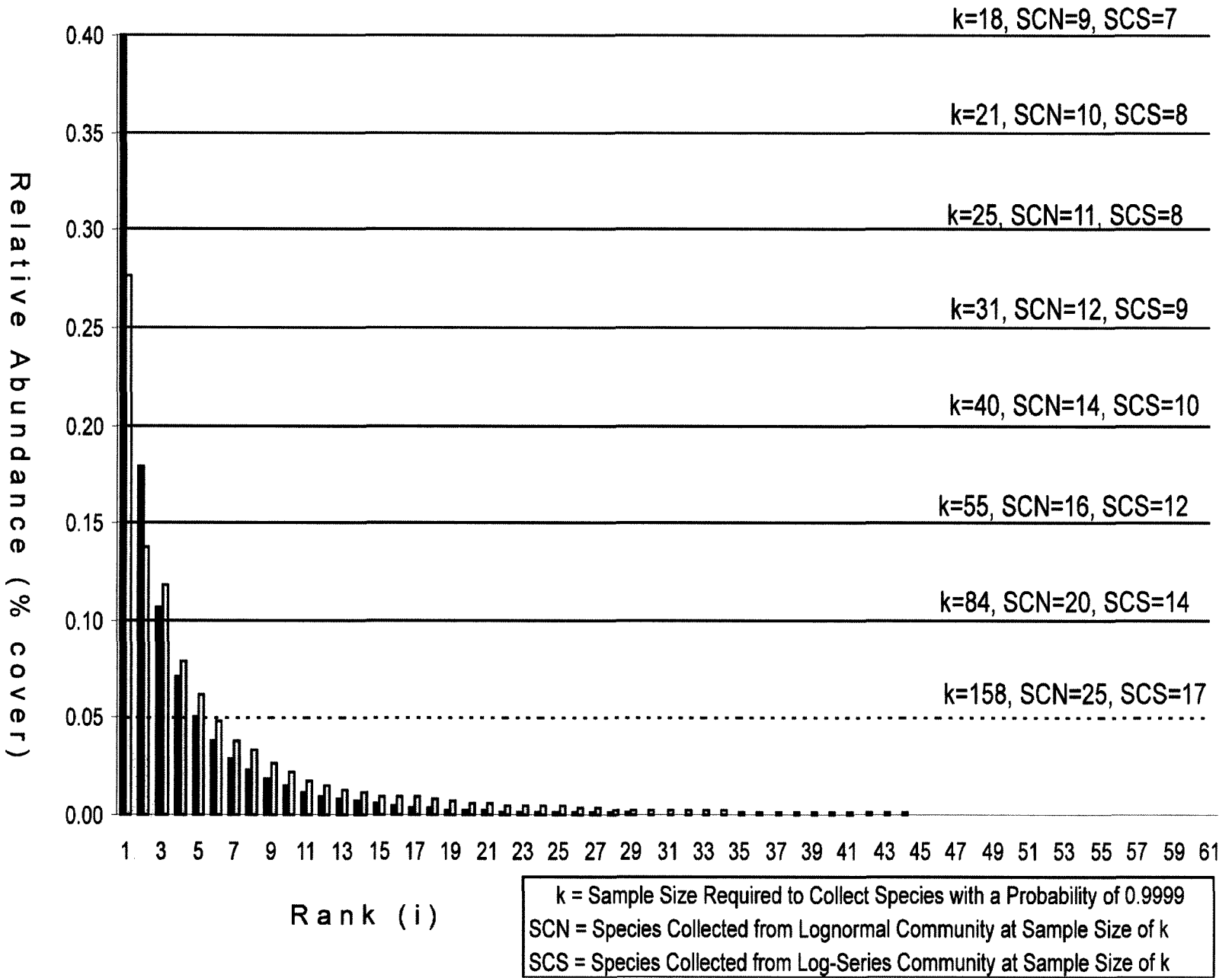
Now assume that the sampling unit referred to in Figure D.7 relates to subsamples (i.e. plots of a fixed size within a community) rather than sample size (i.e. the total number of individuals or area sampled). Every species whose relative abundance reaches the plot size represented by a particular horizontal line is expected to occur in every plot. Define m to equal the mean number of individuals per plot and r as the minimum level of relative abundance that the study wishes to reveal. For the moment, set $r = 5\%$. Plot size (m) can then be varied until it equals k_r . In other words, if

$$\text{Eq. 7) } m \geq k_r$$

where m = plot size and k_r = the minimum subsample size required to collect a species with a relative abundance of r .

then each plot is expected to contain each species whose relative abundance is equal to or greater than r with a probability of 99.99%. **Therefore, and this is the key to the method, it follows that there is a relationship between relative abundance, plot size and frequency.** The relationship has been derived statistically by demonstrating that, for appropriate combinations of plot size and relative abundance, the expected frequency of a species is 100%. **This relationship is mathematical and can be inverted to form the proposition that if a species appears in all the plots then the plot size is representative for this species and its sample relative abundance is a reliable estimate of its community relative abundance.** In short, the plot size has revealed the relative abundance of the species through frequency.

Figure D.7. Sample Sizes and Abundance-Rank Diagrams of a Log-Series and Lognormal Community. The relative abundance of species at the right is too small to be visible.



The method presented is founded on a relationship between plot size, frequency and relative abundance. It should be emphasized that the objective is not to estimate abundance or compare communities using frequency data. Rather, frequency data are being used to identify those species whose relative abundance has been revealed by the sample. These species can then be used in further analysis.

To summarize, descriptions or comparisons of communities based on sample data may lead to erroneous conclusions. An objective method has been proposed to determine: 1) whether the plot size is adequate to collect all the common species, 2) which of the species collected are the common ones and 3) which can be excluded from analysis based on rarity. These results are based on a number of conditions and simplifying assumptions. They are:

- 1) The community, as defined by its conceptual boundaries, is homogenous;
- 2) There are not large differences in the size of an "individual" plant;
- 3) There is no spatial aggregation among individuals or species;
- 4) Sub-associations of species within the community do not exist;
- 5) Plots are randomly located;
- 6) The size of the plot is much larger than most individuals or sub-associations within the community.

These assumptions are clearly not realistic. The consequences of relaxing them is still be worked through. Nevertheless, the method has practical application and may take us one step further than can be taken with existing methods. In the first place, all existing methods which estimate community parameters based on the random (or equivalent) location of sampling units employ, either explicitly or implicitly, the same or similar assumptions. The presentation above has attempted to establish that, in addition to the calculated statistical risk that a 1 in 20 random event has occurred, some unquantifiable but highly probable bias results from the small sample sizes typical of observational studies and not being able to construct sampling frames based on individuals and species. The method is intended to address this bias at the theoretical level. That is the same level at which the other sampling techniques commonly employed are constructed. Applied during study design, the method may facilitate the reduction or elimination of this bias. It does so by establishing which species, in terms of relative abundance, the sample is expected to collect.

D.3. Pragmatic application of the method to the problem of evaluating environmental impacts.

Prior to applying the method to field data, some additional complicating factors need to be dealt with. Large differences in species composition can result from small differences in ecological history- events as simple as a beaver cutting down trees, a bear digging up an ant's nest, fires of different intensities or fires followed by different amounts of precipitation for the balance of the growing season. An observational study has no ability to control for some of these differences either experimentally or statistically. A reduction in precision must be accepted as a tradeoff for generality. A consequence of high within Block variability is that a requirement of 100% frequency in order to consider that a species' relative abundance has been revealed would be too restrictive. It is recommended that a frequency equal to the number of plots minus one divided by the total number of plots sampled in the community be used as the threshold.

A second complicating factor which arises when applying the method to field data relates to measuring the central tendency of a species' relative abundance across plots within a community. Some species have very patchy distributions. Consequently, one plot may have a very high abundance value for a species. When a large number of plots are available, this very high abundance value will be averaged with many small ones to provide a reliable estimate of the species abundance. However, as the example of Figure D.4 illustrates, when the number of plots is small,

this is not the case. In this situation, the median is a better measure of central tendency than the mean. Therefore, it is used when the method is applied to field data.

What does the method predict for sample data? Most importantly, the selected plot size and shape will collect all species whose distribution is not localized and whose relative abundance is above a certain value determined by the plot size. The relative abundance which the plot size reveals can be determined by comparing absolute frequency and relative abundance data for each species in the community. A scattergram of presence versus relative abundance can facilitate this (Figure D.8).

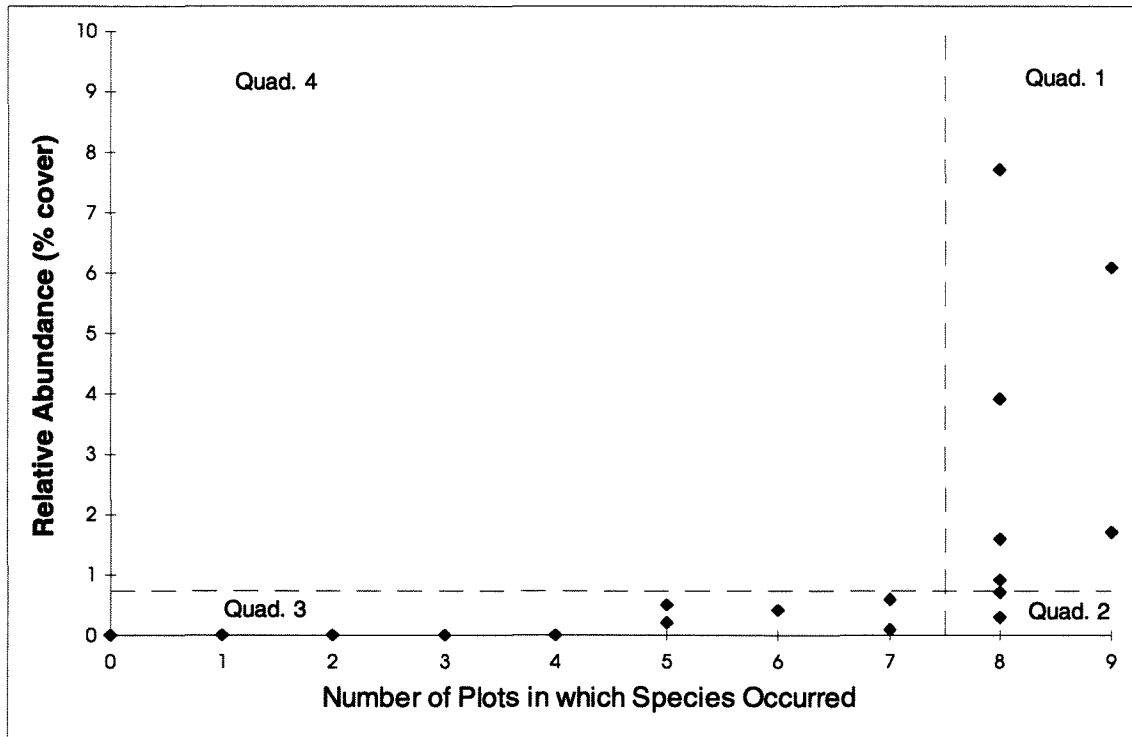


Figure D.8. Relative abundance (% cover) vs. number of plots in which species occurred.

Let x equal the number of plots sampled. A vertical line set between $(x-2)$ and $(x-1)$ splits the scattergram into two halves (Figure D.8). Species to the right of this line have their abundance revealed by the plot size and are referred to as Revealed species. A horizontal line can be placed on the scattergram at a level so that none of the species to the left of the vertical line are located above the horizontal. Species appearing above this line are the Common ones for this plot size. A distinction is made between Revealed and Common species. Once the minimum relative abundance for a Common species is determined, all species having at least that relative abundance are expected to be collected unless their distribution is localized³⁴. Scarcer species are also collected in all plots but only if their patch size is below a maximum level determined by the plot size. The average size of an individual is species specific. Some species occur as small solitary individuals (e.g. *Maianthemum canadense*) and others in large, scattered patches (e.g. *Arctostaphylos uva-ursi*). To illustrate, assume there are two widespread species with a relative abundance of 1%. One species makes up its total abundance in the community in patches of 1 m² while the other is in patches of 0.001 m². The latter species is more likely to occur in all plots of a small sample than the former and be one of the Revealed species. Revealed species include those

³⁴ Species density also influences what level of relative abundance will be common.

species which do not have a localized spatial distribution and, if they are scarce, their patch size is relatively small.

The scattergram in Figure D.8 is divided into four quadrants by the two dotted lines. Quadrant 1 contains the Common species for which the plot size will provide a reliable estimate of relative abundance. Quadrant 2 contains scarce species whose abundance is revealed due to their approximately random distribution and small mean patch size (e.g. *Maianthemum canadense* or *Oryzopsis pungens*). In Quadrant 3 are found the scarce species which occur in the community but whose relative abundance is not revealed by the plot size. Finally, Quadrant 4 contains the Common species, that is, the species that the plot size is expected to collect but whose sample abundance is not expected to be a reliable abundance estimate of their community abundance³⁵. This quadrant will include species which are localized or patchy in their distribution or for which the plot size is too small. The horizontal line should be located so that only species that obviously meet the criteria of Quadrant 4 are contained within it.

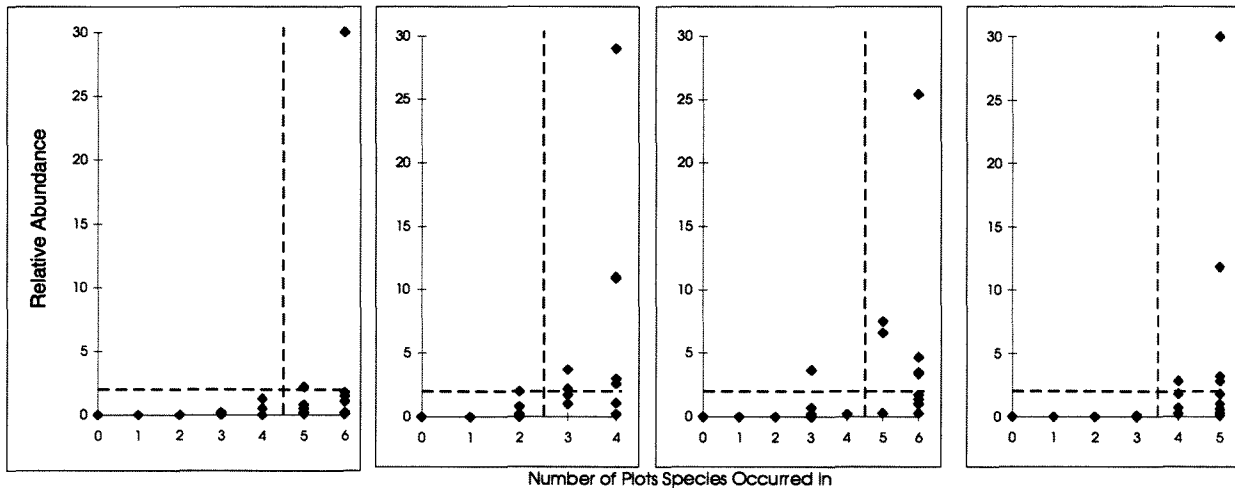
What is the anticipated effect of altering various sample size parameters. Increasing the number of plots sampled will not shift existing species to different quadrants but will add more species to Quadrant 3 since total area sampled will have increased (i.e. the sample size effect on species richness). Enlarging the plot size will shift some species from Quadrants 3 and 4 to Quadrants 1 and 2 and, concomitantly, lower the horizontal line. It will also add new species to Quadrant 3 due to the increase in total area sampled.

In this *ex post* application of the method, we are letting the data determine what the boundary for Common should be. Ideally, the process should begin with a decision on the minimum relative abundance to be detected. This would be followed by a pilot study to determine the plot size and shape required to collect all such species.

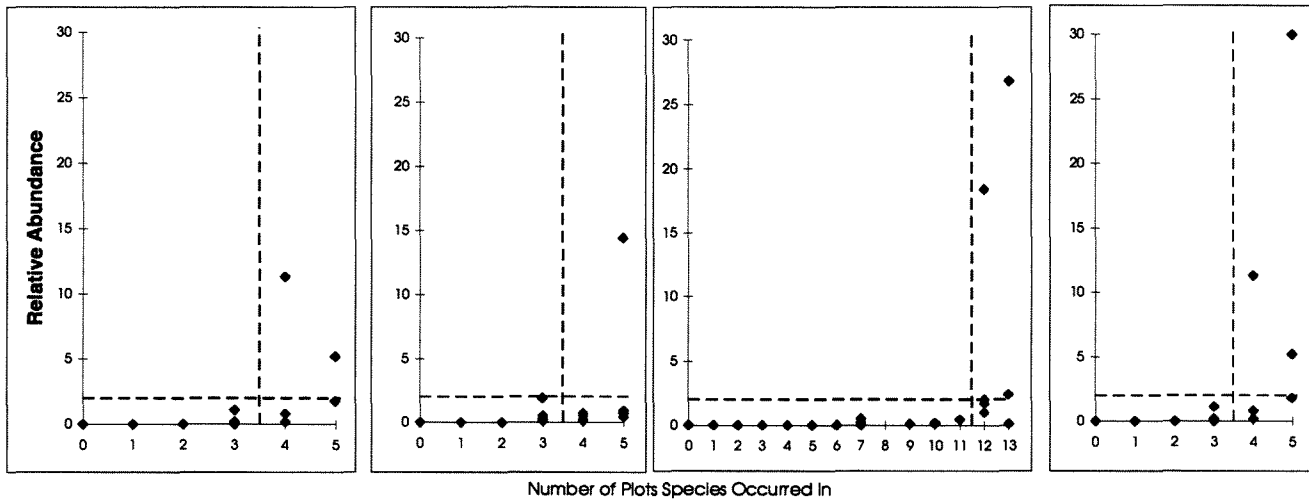
The results which follow are based on study data for 37 year old post-fire and post-logging communities found on shallow soils. For each species in each Block, median relative abundance and frequency were calculated. Figure D.9 provides the relative abundance vs. absolute frequency scattergrams for the burns of the 37 year old age class. The horizontal line has been set at 2%- a level which results in only one occurrence of a species in Quadrant 4. Notice the reverse L-shaped configuration of points in each scattergram. Despite the fact that these data were not collected with any aspect of this method in mind, it displays the characteristics predicted by it. This provides some support for the robustness of the method when applied to natural conditions.

Further support for the method is provided by application of it to the other site type categories in this age class. Table D.1 summarizes the number of occurrences of species whose relative abundance was in a particular category and the number of those species in each of those categories which appeared in Quadrant 4. There was only one situation out of 63 where a species with a relative abundance greater than 10% did not appear in Quadrant 1. It was a tall shrub. In the 5-10% class, 5 of 24 fell into Quadrant 4. Three of these five were tall shrub or tree species. It is easy to imagine that the plot size may be too small for these species. Four of 34 occurrences in the 3-5% class landed in Quadrant 4. One was a tall shrub. Subjective assessment of the remaining three species indicates that they are typically patchily distributed.

³⁵ This quadrant may contain numerous species if the boundaries of the community are poorly defined ecologically.



Replicate burns on shallow soils.



Replicate cutovers on shallow soils.

Figure D.9. Relative abundance vs. absolute frequency scattergrams for the burns and cutovers on shallow soils in the 37 year old age class.

Table D.1. Number of occurrences of relative abundance by relative abundance class.

	Relative Abundance Class					Total
	<2%	2-3%	3-5%	5-10%	>10%	
Occurrences of relative abundances $\geq 2.0\%$ (Quadrants 1 and 4)	0	33	34	24	63	154
Occurrences falling into Quadrant 4	0	8	4	5	1	18
Occurrences of relative abundances $< 2.0\%$ which are revealed (Quadrant 2)	76					76

1599 occurrences fell into Quadrant 3.

To make reliable species richness comparisons, it is suggested that one only include those species which are expected to be collected regardless of their patch size, that is, the Common species (species in Quadrants 1 and 4 in Figure D.8). Typical approaches to reporting richness include the observed number of species in the sample or a jackknife estimate of total species richness. In these approaches the number of species reported will generally include all the moderately to very abundant species, all the widespread, small patch size, scarce species and some unknown proportion of the remaining scarce species. The latter group causes problems for the estimation of total species richness because there is no way of knowing what proportion of them have been collected. As previously noted, two communities with the same total species richness will usually have different observed richness (since the species abundance distributions of the communities are rarely the same) leading to the erroneous conclusion that one has a higher total richness than the other. When Common species are used for species richness comparisons, all species whose relative abundance is greater than or equal to the horizontal line in Figure D.8 are expected to appear in the sample unless its distribution is localized or very patchy (all replicates must be taken into consideration when the level of the line is being established so that a consistent minimum relative abundance can be applied³⁶). Consequently, species richness comparisons are based on the species which the plot size is expected to collect *a priori*. While not being that which is ideally desired, pragmatically, it is the next best thing that can be achieved by a study whose main interest is in species composition. The sampling design of a study interested primarily in species richness would be quite different and not provide data appropriate for the analysis of species composition.

Revealed species (species contained in Quadrants 1 and 2) can be used for species composition comparisons. Occurrence to the right of the vertical line (Figure D.8) suggests that a species' sample relative abundance is a reliable estimate of its community relative abundance. To evaluate the effects of including species which are not Revealed in species composition comparisons, ordination and cluster analysis were applied to this study's 37 year old post-fire data. Results based on dropping species which occurred in less than 4 plots or retaining only Revealed species were compared. The results differed little and this was attributed to two factors³⁷. First, the species composition of the plots in any given comparison were similar since they were stratified by age class and site type. Second, the multivariate methods used to summarize species composition information (except correspondence analysis) are relatively insensitive to infrequent, scarce species³⁸. On this count, the inclusion of species which are not Revealed may not be great. The main effect of their inclusion is to increase the number of species and proportion of zeros in the dataset. This adds to computational effort and exacerbates non-linearities in the data structure. Due to the problems associated with a large number of zeros, generally the first step in multivariate analysis is to drop species which occur in only a few plots on the basis that they have limited ecological significance. This will have the effect of eliminating some of the species which are not Revealed.

The next step in the method's development is a sensitivity analysis which explores the effects of plot size, sample size, individual patch size and spatial aggregation at various scales on this method using data from real and simulated communities. Even in its present state, application of the method to species richness estimation is expected to substantially improve the reliability of species richness comparisons.

³⁶ Since the minimum relative abundance of a Common species is set by the plot size, it may be the case that such a species has a relative abundance as low as 1%.

³⁷ Because the analysis did not include a variety of resemblance measures or techniques, general conclusions cannot be drawn regarding the effects of including species which are not Revealed in multivariate analyses.

³⁸ As a consequence of the resemblance matrix it operates on, correspondence analysis effectively focusses on how each plot differs from the others. That has the effect of placing high weight on species which have an unusually high abundance in one plot (especially if it is a species poor plot).

Appendix E

Validation of the site type classification.

One of the first questions addressed in data analysis following the second field season was whether the site type categories being used produced an ecologically meaningful grouping of the plots were statistically efficient (i.e. maximized the precision of estimates), and operationally useful.

The efficiency of the site type classification was of concern because it was derived based on univariate criteria using the most frequent and abundant species and a pilot study which lacked replication. Site type categories were constructed as part of a simultaneous decision which also determined the plot, subsample and sample size and were corroborated by the NWO FEC (Sims et al. 1989).

Cluster analysis was used to validate the classification since it has several attractive features. It automatically forms groups or clusters of plots and outputs its results in two dimensions so there is no need to make a judgment as to how many "axes" to retain (as in ordination methods). Cluster analysis makes no explicit assumptions about data structure. It is also put forward as a non-linear technique but this can be misleading since the method operates on a resemblance measure which itself may be sensitive to aspects of data structure such as non-linearity.

Cluster analysis has weaknesses such as sensitivity to outliers, the cluster algorithm and, where applicable, the number of clusters the algorithm is directed to retain in the final solution. Punj and Stewart (1983) provide an assessment of a number of different clustering algorithms. K-means clustering is the algorithm least sensitive to outliers, resemblance measure chosen and sampling errors (Hair et al. 1987). Its drawbacks are that it requires a starting cluster configuration and a specification of the number of clusters to be produced. If the starting clustering is chosen randomly or on some other criterion such as the plots having maximum distance then it may produce a final solution which is nonsensical in ecological terms. The use of a hierarchical method such as Ward's as a first step is designed to minimize this shortcoming. Punj and Stewart's (1983) suggest a three step approach to cluster analysis to avoid pitfalls:

1. Obtain an initial clustering using Ward's method or average linkage;
2. From the results, determine the desired number of clusters in the final solution;
3. Using the clusters obtained from Ward's method as a starting configuration, perform a K-means cluster analysis.

This was the approach we adopted. Percentage difference was selected as the resemblance measure preceded by a logarithmic transformation³⁹ of cover values on the basis that this combination most accurately reflects the concept of ecological distance implicit in the objectives of this study (Austin and Greig-Smith 1968; Campbell 1978; Clymo 1980; Faith et al. 1987; Greig-Smith 1983; Hadju 1981; Jensen 1970; Lamont and Grant 1979; Noy-Meir 1973; Noy-Meir et al. 1975; Van Der Maarel 1979, Appendix C). Outliers were removed prior to cluster analysis⁴⁰. Ward's method was the algorithm used in the first step of cluster analysis.

Only burns were included in cluster analysis since this is considered to be the 'natural' state with which logging is compared. Amalgamation of burns and cutovers could lead to a confounding of treatment with site type effects in the cluster solution. Data from the outcrop, shallow mineral, moderately deep mineral, deep dry mineral, deep wet mineral and organic site type categories were included in the analysis (see Section 7.1 of main report for description of categories). Clustering was performed on the vegetation and not the site data (soils and topographic variables). Given the

³⁹ Note that data analysis after the final field season determined that a square root transformation performed better than a logarithmic (see Section 7 of the main report).

⁴⁰ An outlier is defined as a plot in which the mean of normalized species values is greater than 2. In the two field season dataset, this occurred for five plots in post-fire communities and no plots in post-logging communities.

manner in which the Blocks were selected, site type variables are expected to be the main causal variables influencing the vegetation within a burn. Thus, the vegetation should generally reflect underlying differences in site type characteristics. The objective of the site type classification is to minimize within group variability so that the statistical power of treatment comparisons can be maximized. A site type classification derived from a cluster solution using the methods proposed, by definition minimizes within group variation and maximizes between group variation and will be the most efficient for use in hypothesis testing⁴¹ provided that the cluster solution has an ecological interpretation both in terms of the vegetation and site type variables.

Results from a 6 group K-means clustering of site variables are included for comparison purposes. The procedure followed was the same as for the vegetation data. All site variables were standardized by their range. The variables included were percent canopy closure, aspect, percent slope, plot shape, slope length, upslope length, depth of organic material, depth of solum, depth to bedrock, depth to distinct mottling, depth to prominent mottling, depth to gleying, depth to water table, drainage regime, moisture regime and percent stoniness.

Determination of the number of groups to be carried forward to K-means clustering was based on changes in inter-group distances. An increasing number of groups maintained relatively large inter-group distances up to five groups. Changes in intergroup distance then became small until a nine group cluster solution was reached⁴². A nine group classification was not feasible given the total sampling effort available. Four, five and six level clusterings were examined further.

Any clustering which has ecological meaning should recognize the vegetation types which the research of others has shown to be distinct. In this study, these were the vegetation of organic soils (wet, very to moderately nutrient poor) and outcrops (dry, nutrient poor). Examination of the four, five and six level groupings produced by Ward's method clustering revealed an ecological interpretation for each level of clustering. In all three, the organic and outcrop site types were the most distant from each other. The major difference in the clusterings was the manner in which the vegetation on intermediate site conditions was grouped. Because the resolution of the four group solution was too low, only the five and six group solutions were carried forward to the next step. One note of interest was that each Block was represented in each group of each clustering (except where no plots were available for a Block in the site type category). This suggested that differences in site type variables had more influence on the vegetation than differences in location within the study area.

K-means clustering, using the groups produced by Ward's method as starting configurations, was the next step in analysis. K-means clustering reclassified 5 out of the 97 plots from the five group solution and 4 from the six group solution. All reclassifications related to plots from intermediate moisture regimes. Ward's method and K-means clustering created similar groupings for this dataset.

Cluster solutions obtained from K-means clustering were reviewed for their ecological interpretation using Baldwin and Sims (1989), Bell (1991), Klinka et al. (1989), Sims et al. (1989) and Vitt et al. (1988). The five and six level of groupings both had a defensible ecological interpretation in terms of the vegetation. That is, the groups contained species which commonly occur together and, where applicable, give similar indications about site conditions. Based on the indications of species, both clusterings appeared to group vegetation most strongly on moisture regime. Mineral soil depth appeared to be next in importance. The six group solution provided better resolution of the vegetation on soils with intermediate moisture regimes.

Our site data was used to examine the ecological interpretation of the clusterings further. ANOVA was performed on site variables with plots grouped based on the five and six cluster

⁴¹ An incidental benefit is that, by focusing on the vegetation, methodological problems which would arise in an analysis of site variables are also avoided. Those problems relate to variables selection and standardization to remove scale differences.

⁴² As a word of caution, Sneath and Sokal (1973) indicate that cluster analysis is better at representing between plot distances within groups than between group distances.

solutions. Means for those site variables which had a significantly different mean ($\alpha=5\%$) for at least one group within a cluster solution are given in Table E.1. It should be noted that the test does not indicate which group's mean was different or whether the mean was different in more than one group (a Scheffe's contrast, for example, would be required for that). This is the approach to the interpretation of cluster results advocated by Hair et al. (1987). In the tables that follow, the group numbers used for each cluster solution are intended to correspond to similar vegetation types across the two clusterings.

Table E.1. Mean values for site variables which had a statistically different mean in at least one group within a cluster solution.

	Five Group					Six Group					
	0	1	2	4	5	0	1	2	3	4	5
Percent canopy closure						24	26	34	33	14	36
Plot Aspect (degrees North, 0 = no aspect)	166	155	78	144	0	166	156	75	97	144	0
Plot Slope (%)	10	7	4	3	0	10	8	3	6	3	0
Site Slope Length (m)	15	20	21	42	0	15	21	29	8	42	0
Site Upslope Length (m)	4	6	7	15	0	4	6	9	4	15	0
Depth of Organic Layer (cm)	1	6	6	6	24	1	6	6	7	6	24
Depth of Solum (cm)	4	26	59	55	27	4	23	60	57	55	27
Depth to Bedrock (cm)	4	29	81	85	81	4	26	87	66	85	81
Depth to Distinct Mottling (cm)	n/a	87	69	67	97	n/a	89	69	70	67	97
Depth to Water Table (cm)	n/a	94	77	78	18	n/a	96	83	67	78	18
Drainage Regime *	0.4 (rapid)	0.9	3.5	3.3	5.6 (poor)	0.4 (rapid)	0.9	4.3	1.6	3.3	5.6 (poor)
Moisture Regime *	0.0 (dry)	0.6	2.9	2.6	6.3 (wet)	0.0 (dry)	0.6	4.0	0.9	2.6	6.3 (wet)
Stoniness in Soil Profile (%)	3	25	13	25	1	3	26	6	25	25	1
Existing Site Type Category **	0.2	1.7	2.9	3.0	5.0	0.2	1.6	3.2	2.4	3.0	5.0
	Outcrop				Organic	Outcrop					Organic

* Drainage regime runs from 0 for very rapid to 7 for very poor. Moisture regime runs from 0 for dry to 9 for very wet. Moisture regime is a composite variable derived from drainage regime, depth to bedrock and soil texture. It is intended to reflect moisture availability throughout the growing season. ** Existing site type categories range from 0 for outcrops (dry) to 5 for organic (wet).

As expected, the variables depth to water table, drainage regime, moisture regime and existing site type category all reflected the trends in the moisture gradient detected in the vegetation clusterings. Each clustering also exhibited patterns in depth of solum and depth to bedrock consistent with the ecological interpretation of the clusterings. Patterns are the strongest for the first, second and last groups in the five and six level solution whereas there are no strong trends for the middle groups. The site variables analysis also indicated that the creation of group 3 in the six cluster solution separated out drier sites from group 2 of the five cluster solution. This was consistent with the vegetation interpretation given to group 3.

An ecological interpretation for the five and six group cluster solutions was possible. Selection of the number of groups to be used in the site type classification proceeded to an analysis of cluster solution minimized within group variance. This was accomplished by summing each species' variance within a group for each level of clustering and choosing the cluster solution with the lowest overall variance. Admittedly, this was a crude means of comparison. Canonical variates analysis of the vegetation using the clusterings as group membership variables was one alternative

method of evaluating the efficiency of cluster solutions. However, a canonical variates analysis of the vegetation could be circular since the clustering was based on the vegetation. Therefore, variance summation was used as a mathematically independent method to evaluate the cluster solutions and its results were corroborated by canonical variates analysis. A canonical variates analysis would be appropriate for the site type variables and was undertaken.

A six group clustering provided the lowest overall variance in vegetation (Table E.2). Increasing the number of groups from five to six resulted in a small decrease in Group 1 variance, a large decrease in Group 2 (interpreted as closed fresh coniferous stands) variance along with a concomitant variance in newly created Group 3 (interpreted as closed dry coniferous stands) which is lower than the mean group variance of the five group clustering. Vegetation in groups 2 and 3 are commonly logged.

Table E.2. Variance of species means summed for each group for 5 and 6 group K-means clusterings, existing site type categories and 6 group K-means clustering of site variables.

Classification	Group						Mean
	0 Outcrop	1	2	3	4	5 Organic	
Five Group K-Means Clustering	2.96	3.30	3.31		4.67	3.84	3.62
Six Group K-Means Clustering	2.96	3.25	2.39	3.56	4.67	3.84	3.44
Site Type Classification	2.76	3.88	4.32	4.17	5.09	3.84	4.01
Site Variables Clustering	4.75	4.93	5.12	4.98	5.89	4.05	4.95

Table E.3. Variance of site variable means summed for each group for 5 and 6 group K-means clusterings, existing site type categories and 6 group K-means clustering of site variables.

(Variables included were percent canopy closure, aspect, percent slope, plot shape, slope length, upslope length, depth of organic material, depth of solum, depth to bedrock, depth to distinct mottling, depth to prominent mottling, depth to gleying, depth to water table, drainage regime, moisture regime and percent stoniness. Each site variable standardized to its maximum across all groups).

Classification	Group						Mean
	0 Outcrop	1	2	3	4	5 Organic	
Five Group K-Means Clustering	2.85	6.20	9.59		7.74	4.85	6.25
Six Group K-Means Clustering	2.85	6.11	9.13	7.74	7.82	4.85	5.42
Site Type Classification	2.55	3.69	7.23	6.78	5.83	4.85	5.16
Site Variables Clustering	3.54	7.25	5.71	6.08	5.37	2.47	5.07

The site type classification is only superior in variance minimization of vegetation data for the outcrop grouping. It performed as well for the organic group but for the other mineral soil groups it performed more poorly than any of the vegetation clusterings (Table E.2). Also included in Table E.2 are vegetation variance values resulting from a clustering based on site variables. It was indicated above that this is the alternative approach to creating site type categories. As anticipated, the groups created by the site variable clustering performed more poorly at minimization of vegetation variance than any of the other approaches.

The variance of site type variables was also examined (Table E.3). Based on variance alone, it would appear that the six group solution performs better than the five. In contrast with the vegetation results (Table E.2), the site type classification and the site variables clustering did a better job of minimizing within group variance than the K-means vegetation clusterings. Although the site

variables clustering had the lowest overall variance, it did more poorly than the 6 group K-means classification for 2 of 6 groups. Examination of the data indicated why the site variable clustering was inferior to the others at minimizing vegetation variance despite its better performance on the site variables. The site variable clustering moved a number of plots from the organic group, a vegetation type that we know is distinctive, into other very different vegetation types. This may be a reflection of the methodological problems involved with site type variables and could be altered by changing the variables included in the analysis or the standardization applied. The variables sampled were included based on prior ecological knowledge and theory. Changes in variable selection would require a review of that theory and knowledge- something not justified at this stage especially when the existing site type categories already did a better job of minimizing the variance of site variables than either of the K-means classifications (Table E.3). The site variables classification was disqualified from further consideration based on its poor performance in the vegetation variance, site variable total variance for groups 0 and 1 and its misclassification of some organic plots.

A series of canonical variates analyses performed on the site variables using the same four classifications produced a trend of variance similar to that of the variance summation method (Table E.4). A considerable improvement in Wilk's Lambda was obtained by increasing the number of groups from five to six. The existing site type categories were substantially superior to both of the K-means vegetation classifications based on R^2 , Chi-Square and Wilk's lambda. The vegetation approach to clustering appeared to separate two vegetation types which both occurred on a more broadly defined intermediate site category- one mixedwood or deciduous and the other coniferous. In other words, two major vegetation types were encountered in that cluster group. What caused one to be present and not the other was just as likely to be a function of historical factors, dispersal, stochastic events, etc. as of the most recent fire. Therefore, while cluster analysis of vegetation data accomplished its variance minimization objective for the vegetation data, it did so in a manner which went beyond grouping plots based on site conditions to further resolution based on other unmeasurable causal factors. When variance minimization of the vegetation and soils was considered in conjunction with ecological interpretation and operational usefulness, the existing site type categories performed best.

The ecological resolution of the vegetation found on deep mineral soils (Groups 3 and 4) is still poor. Earlier results indicated that at least three more site type categories would be required to improve resolution for these two groups. This was not feasible given the implications for sampling effort. Moreover, it would be the infrequent categories which would gain higher resolution.

A review of the existing site type categories using cluster analysis indicated that they minimized within-group variance for site related variables. Cluster analysis could create a classification which would result in lower vegetation variance for some groups. However, this seemed to be accomplished by recognizing different vegetation types across a broad range of site conditions. Treatment effects were thereby confounded with other ecological factors. Consequently, the site type classification was not revised.

Table E.4. Summary statistics from canonical variates analysis of site variables using various classifications as the group variables.

Classification	R^2	Chi-Square	Wilk's Lambda
Five Group K-Means Clustering	0.91	319	0.239
Six Group K-Means Clustering	0.91	348	0.017
Site Type Classification	0.93	500	0.003

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