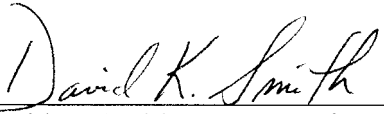
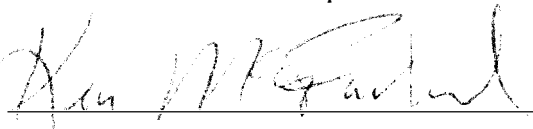
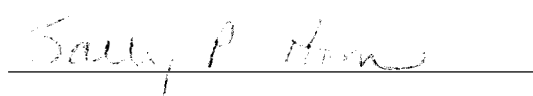


To the Graduate Council:

I am submitting herewith a thesis written by Erica Choberka entitled "A study of epixylic bryophyte ecology on Fraser fir logs in the Great Smoky Mountains National Park." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Botany.


David K. Smith, Major Professor

We have read this thesis
And recommend its acceptance:

Accepted for the Council:


Associate Vice Chancellor and
Dean of The Graduate School

A STUDY OF EPIXYLIC BRYOPHYTE ECOLOGY
ON FRASER FIR LOGS
IN THE GREAT SMOKY MOUNTAINS
NATIONAL PARK

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Erica Renee Grimm Choberka

December 1998

DEDICATION

This thesis is dedicated to my

husband, David,

and

all of my closest friends,

whose smiles and love have made this thesis possible.

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There are many people that have generously helped and encouraged me throughout the course of this research. I would particularly like to thank Dr. David K. Smith, who oversaw this research. He provided me with many valuable skills and insights. I appreciate that he shared with me his wisdom about field work. I would like to thank Dr. Sally Horn and Dr. Ken McFarland for serving on my committee and providing helpful comments, Dr. Paul Davidson for his help with liverwort identification, Bernice Stevens for providing accommodations and inspiration, Keith Langdon and Janet Rock for their issuing of a bryophyte collecting permit for the Great Smoky Mountain National Park, Jamie Estill for computer help, and Timeka Newson, Jennifer Winkler. David Sime, Mark Whited, Theresa Lange, Dr. Smith, and Dr. McFarland for helping with field work.

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Abstract

The Southern Appalachian spruce–fir forest is experiencing the chaotic conditions of ecosystem destruction resulting from the balsam woolly adelgid (*Adelges piceae* (Ratz)) infestation. In the present study, I have examined the community structure of bryophytes on fir logs in the high elevation spruce-fir forest of the Great Smoky Mountains National Park (GSMNP) to learn about the responses of bryophytes to the sudden change in forest structure.

This study has four primary objectives: 1) to provide an updated list of the epixylic bryophytes on fir logs in the spruce-fir forest of the GSMNP; 2) to compare results with previous epixylic bryophyte studies performed in the Great Smoky Mountains National Park; 3) to describe bryophyte communities on logs and describe the environmental factors that control community structure; 4) to create a quantitative method for sampling bryophyte species cover on logs.

Epixylic bryophytes on 79 Fraser fir (*Abies fraseri* (Pursh) Poir.) logs were sampled. Relative frequency values for the species were scored within the upper surface of a 60 degree arc on the log, in cm x 100 cm quadrats. Environmental variables such as general location, longitude and latitude, slope, slope aspect, elevation, dominant tree and shrub species, and canopy cover were recorded for each plot.

Three different multivariate techniques were used in this study, TWINSpan, Detrended Correspondence Analysis (DCA), and Direct Gradient Analysis (DGA). TWINSpan separated all the sites sampled into three different bryophyte communities, *Nowellia curvifolia*, *Brotherella recurvans*, and *Brotherella recurvans*/*Hypnum*

imponens. These communities were separated into nine unions that describe different combinations of species and environmental conditions. TWINSpan also separated all the species that perform similarly into six different clusters. These clusters are directly related to environmental conditions such as available light and decay stage. DCA provided a two-dimensional scatterplot of each species's overall average response within sampled sites. Finally, DGA provided insight into the environmental factors that significantly influence species distribution.

The results of this study suggest that each bryophyte species responds uniquely to environmental factors and that species replacement occurs in a unidirectional pattern. There seem to be five factors that most significantly influence the presence of a species on a log: species life strategy, species ability to colonize optimal substrate, the amount of bryophyte cover on the log, the decay class of a log, and the canopy conditions.

The epixylic bryophyte communities on Fraser fir logs in the GSMNP have drastically changed since the health of the spruce–fir forests have declined. A total of 19 species that were present on Fraser fir logs in the past are now missing completely, and many other species that were once abundant are declining. Three main union types have been lost: unions found on very wet logs, unions of corticolous species found on recently fallen fir trees, and unions of soil species found on completely decayed logs. Furthermore, there seems to have been a shift from species rich communities that used to be found on moist logs in a healthy spruce–fir forest, to less species rich communities that are currently found on dryer logs in the decimated forest.

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LIST OF ABBREVIATIONS

Anamic	<i>Anastrophyllum michauxii</i>
Baztri	<i>Bazzania trilobata</i>
Bletri	<i>Blepharostoma trichophyllum</i>
Brorec	<i>Brotherella recurvans</i>
Cepspp	<i>Cephalozia catenulata</i> and <i>Cephalozia lunulifolia</i>
cm	centimeter(s)
DBH	diameter breast height
DCA	Detrended Correspondence Analysis
Dicfus	<i>Dicranum fuscescens</i>
Dicsco	<i>Dicranum scoparium</i>
ft.	feet
GSMNP	Great Smoky Mountains National Park
ha	hectare
Hetaff	<i>Heterophyllum affine</i>
Hypimp	<i>Hypnum imponens</i>
Hyppal	<i>Hypnum pallescens</i>
Isoele	<i>Isopterygium elegans</i>
Jamaut	<i>Jamesoniella autumnalis</i>
Leprep	<i>Lepidozia reptans</i>
Lophet	<i>Lophocolea heterophylla</i>
Plarep	<i>Platygyrium repens</i>

Nowcur	<i>Nowellia curvifolia</i>
Tetpel	<i>Tetraphis pellucida</i>
Thudel	<i>Thuidium delicatulum</i>
Triexe	<i>Tritomaria exsecta</i>
TWINSpan	Two Way Indicator Species

CHAPTER 1

INTRODUCTION

The Southern Appalachian spruce-fir forest is acclaimed for its great diversity of bryophyte species. Boreal, prairie, coastal plain, and subtropical bryophytes have merged in the spruce-fir zone, and many have settled into specific microhabitats (Smith 1984). Currently the Southern Appalachian is experiencing the chaotic conditions of ecosystem destruction resulting from the balsam woolly adelgid (*Adelges piceae* (Ratz)) infestation. This exotic pest has created an epidemic of disturbance, but also a rare opportunity for baseline studies of the responses and recovery that follow such a magnitude of habitat change.

In the present study, I have examined the community structure of bryophytes on fir logs in the high elevation spruce-fir forest of the Great Smoky Mountains National Park (GSMNP) to learn about the responses of bryophytes to the sudden change in forest structure. This study has four primary objectives:

1. To provide an updated list of the epixylic bryophytes on fir logs in the spruce-fir forest of the Great Smoky Mountains National Park.
2. To compare results with previous epixylic bryophyte studies performed in the Great Smoky Mountains National Park.
3. To determine and delimit distinct communities of bryophytes on fir logs in the spruce-fir forest through multivariate techniques. This includes identifying indicator species of distinct communities and the environmental factors important in controlling community structure.

4. To create a quantitative method for sampling bryophyte species cover on logs.

Prior to this study, the majority of epixylic studies have used visual estimates.

The technique created for this study provides future researchers with a repeatable sampling method.

CHAPTER II

BACKGROUND

This chapter provides background on the spruce-fir ecosystem and of various aspects of bryophyte ecology. Section 2.1 is a general summary of information about spruce-fir forests of the Southern Appalachian Mountains. Section 2.2 describes the effects of the woolly adelgid on Fraser fir, and section 2.3 reviews basic concepts of bryophyte ecology.

2.1 The Spruce-fir forest of the Southern Appalachians

Spruce-fir forests occupy a broad region of North America, from Alaska to the eastern provinces of Canada and south along the Appalachians. These forests are the remains of a community type that, during the Pleistocene, extended in a continuous band, northeast-southwest along the Appalachian Mountains (Delcourt and Delcourt 1984). Currently, eastern spruce-fir forests are disjunct and extend southward along the Appalachian Mountains. The southernmost spruce-fir forests are on the highest peaks of the Southern Appalachians in North Carolina and Tennessee (Ramseur 1960; Pittillo, Rheinhardt, Saunders 1984; White, 1984).

Southern spruce-fir forests are biologically distinct from northern spruce-fir forests (White 1984) and represent a geographically restricted forest type (White, Pittillo, Saunders, 1984). Northern and southern spruce-fir forests are separated by a gap at the latitudes of 38 – 40 degrees. The southern spruce-fir forests experience more precipitation (greater than 200 cm per year), greater humidity, a longer growing season, and a higher minimum winter temperature (Oosting and Billings, 1951) than the northern

spruce-fir forests. Soils in the southern spruce-fir forests have a shallower organic layer (2-7 cm) than in the north (20-25 cm) (Oosting and Billings 1951), and there is faster growth, greater average tree height, and greater herb and bryophyte cover in the South. Southern spruce-fir forests also have a greater level of endemic plant species. One such example is *Abies fraseri* (Pursh) Poir. (Fraser fir). The fir species found in northern spruce-fir forests is *Abies balsamea* (L.) Mill. (Balsam fir).

The southern spruce-fir forest generally occurs at an elevation above 5500 ft.; however, the spruce-fir zone can extend downward to 5000 ft., and isolated stands can be found as low as 4000 ft. (Cooley 1954). Southern Appalachian spruce-fir forests occupy seven mountain areas with elevations greater than 5512 ft.: Mount Rogers, VA; the Balsam Mountains, NC; Grandfather Mountain, NC; Roan Mountain, TN - NC; the Black Mountains, NC; the Plott Balsam Mountains, NC; and the Great Smoky Mountains, TN - NC (Ramseur 1960).

These forests occur almost exclusively on resistant Cambrian or Pre-Cambrian bedrock (Norris 1964). The soil (Ramsey series) is podosolized to various degrees (Mc Cracken et. al 1962). The weather is relatively cold and wet. Summers are cool, and winters generally accumulate snow (Shanks, 1954). No true timber line is found in the Southern Appalachians. The peaks above 6000 ft. are flat-topped and moist due to poor drainage and high humidity (Norris, 1964).

The dominant arborescent species found in the southern spruce-fir forests are *Abies fraseri* (Pursh) Poir. (Fraser fir), *Picea rubens* Sarg. (red spruce), and *Betula lutea* Michx. F. (yellow birch) (Oosting and Billings 1951; Whittaker 1956; Pauley, Clebsch, 1990). *Acer spicatum* Lam. (mountain maple), and *Sorbus americana* Marsh. (mountain

ash) are also common in spruce-fir forests. At lower elevations, the following tree species may be present in spruce-fir forests: *Acer pensylvanicum* L. (striped maple), *Amelanchier arborea* var. *laevis* (Wieg.) Ahles (service berry), *Ilex ambigua* var. *montana* (T.&G.) Ahles, *Fagus grandifolia* Ehrh. (beech), *Quercus rubra* L. (red oak), and *Halesia carolina* L. (silver bell) (Crandall 1958; Whittaker 1956; Oosting and Billings 1951; Ramseur 1960; Busing *et al.* 1993).

The understory of the spruce-fir forests can have up to five distinct layers: 1) mosses and liverworts, 2) low herbs, 3) ferns, 4) low shrubs, 5) high shrubs (Whittaker 1956). *Oxalis montana* Raf. is a dominant species in the herb layer. *Dryopteris intermedia* (Willd.) Gray and *Dryopteris spinulosa* (Mueller) Watt are the most abundant ferns. *Viburnum alnifolium* Marsh., *Viburnum cassinoides* L., *Rhododendron* spp., *Vaccinium corymbosum* L., and *Vaccinium erythrocarpum* Michx. are dominant low shrubs, and *Sambucus pubens* Michx., *Rubus canadensis* L., and *Rubus idaeus* var. *canadensis* Richardson occur in canopy gaps as high shrubs (Smith 1997).

Southern Appalachian spruce-fir forests have an extremely rich bryophyte flora. The spruce-fir zone contains elements of subtropical, coastal plain, boreal, and prairie bryophytes in many different microhabitats (Smith 1984). The high mountain peaks form island enclaves of boreal plants (Hicks and Davison 1989). Many rare liverworts and mosses can also be found. These species often occur as endemics or disjuncts.

The high diversity of bryophytes has been attributed to the Quaternary history of the region. Vicissitudes of climate most likely widened the gap in the ranges of many species (Sharp, 1939). Although the Southern Appalachians were not glaciated during the last Wisconsinian glacial maximum, their pre-glacial and post-glacial habitats are very

different. Glacial and interglacial climatic cycles fluctuated twenty times during this period (Ruddiman and McIntyre 1976). Glaciation dammed northern rivers, creating lakes, the outwash from which assisted in the disjunction of the species currently found in the Southern Appalachians and in the Ozarks (Sharp 1941). Furthermore, fluctuating climates between interglacial and post-glacial periods allowed the migration of a variety of species. As temperatures oscillated, species of the retreating habitat migrated, senesced, or were left as endemics.

I conducted the present study in the spruce-fir forests of the GSMNP (Figure 1). The GSMNP encompasses a portion of the Southern Appalachian Mountains in Tennessee and North Carolina. Seventy-four percent of the southern Appalachian spruce-fir forests occur within the GSMNP boundary. This study was limited to spruce-fir forests of the GSMNP because of easy access to spruce-fir forest by roads and the many trails found in the park. The Appalachian trail runs through the GSMNP and conveniently connects many of the major spruce-fir zones of the Southern Appalachian Mountains.

2.2 Fraser Fir

Abies fraseri (Pursh) Poir. is a Southern Appalachian conifer that is endemic to seven localities in North Carolina, Tennessee, and Virginia (Ramsuer 1960). *Abies fraseri* increases in abundance above 6230 ft. in elevation (Busing and Clebsch, 1988), and pure fir stands were once present on exposed summits and ridges (Whittaker 1956). *Picea rubens* is dominant below 5910 ft. Fraser fir is rapidly declining in Tennessee and North Carolina due to the exotic pest, *Adelges piceae* Ratz. (balsam woolly adelgid), and it is

Spruce-Fir Forests In The GSMNP

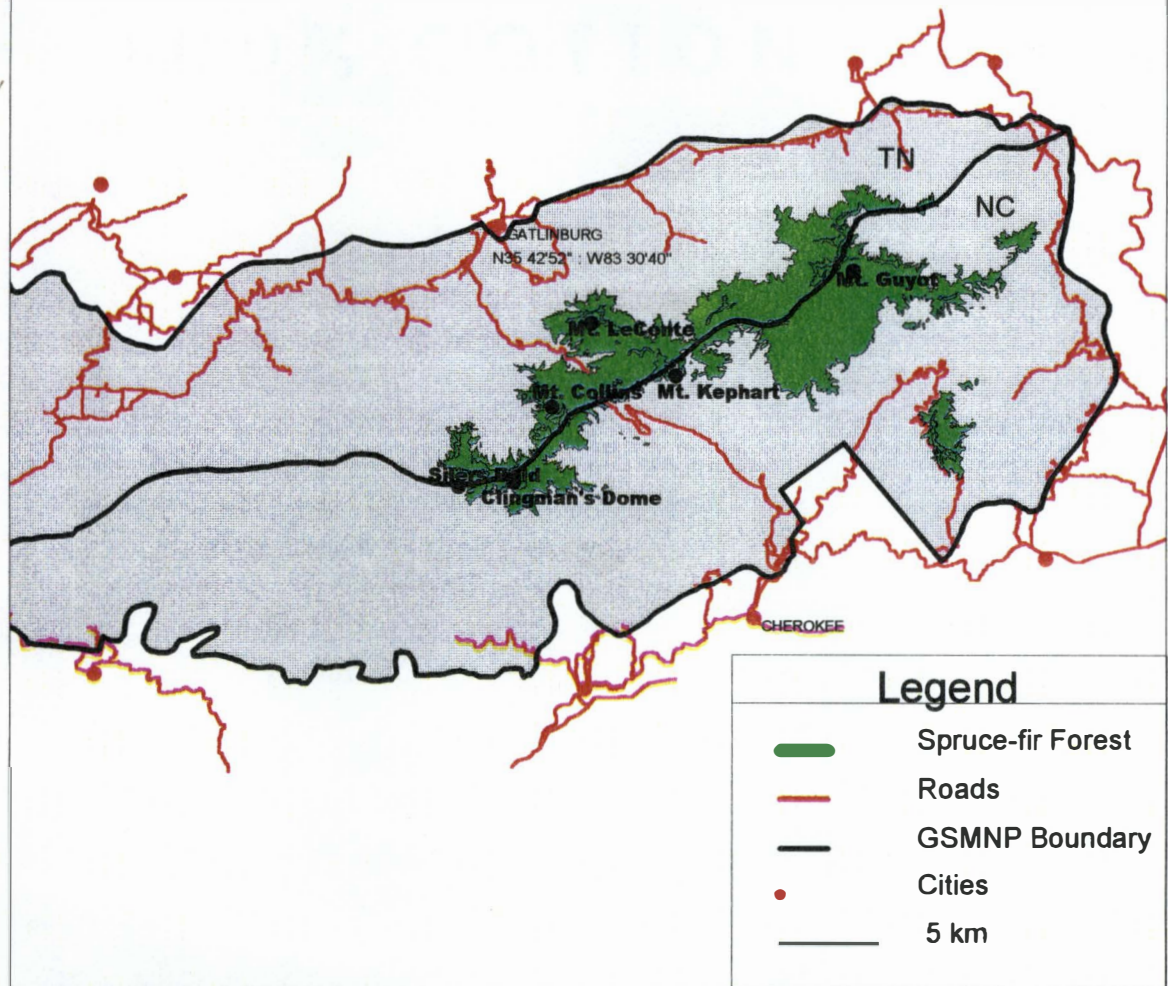


Figure 1 Map of the Southern Appalachian spruce-fir forests within the Great Smoky Mountains National Park (1996) adapted by Hermann.

now rare and imperiled. It is listed as threatened in Tennessee and is a candidate to be listed in North Carolina (Pyne and Shea 1996; Amoroso and Weakley, 1995).

The balsam woolly adelgid is a small, wingless, exotic insect that is native to the region of the Caucasus Mountain Range between the Black Sea and the Caspian Sea. Balsam woolly adelgid infestation can kill a tree in two to seven years. It was introduced in New England prior to 1908 (Kotinsky 1916) and was first reported in the Southern Appalachians on Mt. Mitchell, North Carolina, in 1957 (Speers 1958). From Mt. Mitchell, the adelgid spread throughout the Black Mountains and researchers found it on Roan Mountain in 1962 and Grandfather Mountain in 1963. Later in 1963, the balsam woolly adelgid was spotted in the GSMNP on Mt. Sterling (Ciesla *et al.* 1963). The adelgid then spread through Cataloochee Knob to the southeast slope of Mount Guyot (Ciesla *et al.* 1963, 1965; Lambert and Ciesla 1966, 1967). From Mount Guyot, the infestation spread to Mount LeConte and Clingmans Dome (Eagar 1978). It currently infests all Fraser fir stands throughout the region (Eagar 1984).

In the mid 1980's, areas dominated by Fraser fir, which were in various stages of decline, totaled 253 hectares within the GSMNP boundary (Dull *et al.* 1988). In 1997, Katherine Johnson and Glenn Taylor mapped all living Fraser fir stands greater than 1 hectare. They found only four areas greater than one hectare throughout the entire Southern Appalachian Mountains: Old Black, NC, with 1.7 ha, Mt. LeConte, TN, with 1.6 ha, Big Butt Mountain, NC, with 1.0 ha, and Mt. Kephart, TN, with 1.6 ha. The adelgid was present in all of the mapped areas.

North American adelgid populations are entirely female and parthenogenic. An adelgid lays an average of 100 eggs and up to 250 eggs, and in the Southern Appalachian

region, three to four generations are produced a year (Balch 1952; Amman and Speers 1965). During feeding, the larval instars of this wind-dispersed insect inject salivary compounds into the bole of the tree. This stimulates the tree's cambium to produce abnormally shortened, heavily lignified tracheids and a greater number of ray cells. This process causes a decrease in translocation in the sapwood and wider than normal annual rings. Tree reaction to mass infestations effectively girdles the tree by the build-up of woody tissue. The tree succumbs within two to seven years (Eagar 1984).

A healthy spruce-fir forest cycles through a continuum of live, standing dead, and fallen trees. The natural life span of fir is between 75 and 125 years. Random events and time cause individual or small groups of trees to fall (Smith 1990). These trees fall into a thick, moist bed of terricolous mosses that aid in the decay process. The moisture and light conditions on the forest floor beneath the intact canopy allow for quick decortication of logs, followed by stages of decay leading to total humification.

The sudden death of vast stretches of mature Fraser fir forest has altered the normal dynamic of tree mortality, log decomposition, and canopy replacement. Following death, trees rapidly shed their needles and stand erect for some years as skeletons. Branch pruning soon follows, leaving a spar to rot in place or be toppled by storms. Normally, fallen trees constitute a temporary substrate that cycles through various stages of decomposition. But now, the sudden decline of large tracts of Fraser fir has produced a huge overburden of debris and logs that smother the forest floor. The soil disturbance, the increased insolation, the decreased moisture, and the build up of fuel on the forest floor have created a new substrate pattern not previously present in spruce-fir forests.

Changes in the microhabitats of the fir forest are certain, but the effects of the changes are uncertain. All components of forest floor vegetation have been affected. The decrease in above-ground, live-tree, nutrient reserves may lead to nutrient losses from the overall system by leaching. Calcium is especially prone to be lost because it is concentrated in vegetation (Weaver 1972). Many herbaceous plants common under the canopy of an intact forest have been replaced by aggressive, weedy species that are more tolerant of greater sunlight and drier conditions (DeSelm and Boner 1984). These changes include a greater than 10 fold increase in the density of *Rubus canadensis* L. (thornless blackberry) (Boner 1979).

The response of bryophytes to the changes in the fir forest structure and to the sudden accumulation of log substrate is an interesting aspect of the new dynamic and future expression of the spruce-fir zone biota. Baseline studies, such as the one presented in this thesis, are critical to determine the affect that the decimation of the spruce-fir forest will have on the distribution of both rare and historically common bryophyte species.

2.3 **Bryophyte Ecology**

Bryophytes are important in natural ecosystems. There is an abundance of bryophytes in most forests, yet few ecologists consider the cryptograms anything more than an inert carpet that vascular plants may grow on. Bryophytes play an important role in nutrient interception, retention, and release. When studying bryophyte ecology, it is important to have a comprehensive understanding of the structure of and dynamics occurring in bryophyte communities.

Since 1960, a considerable amount of data on the ecology of bryophyte populations has been gathered (Esseen, 1994). Researchers have introduced terminology specific to bryophyte communities to aid their study. Slack (1982) used the term ecotope to express the merge of the “functional” and “habitat” niche concept. The functional concept of niche (Elton 1927) includes intracommunity variables such as the role of a species in a particular community. Habitat niche considers intercommunity aspects such as elevation, slope, substrate, and moisture. Thus, this term ecotope allows the discussion of bryophyte communities in a broad way that considers factors both internal and external to the community.

All natural communities are dynamic and spatially heterogeneous at any scale of resolution (Soderstrom, 1988; Soderstrom and Jonsson, 1989). A bryophyte community results from the combined interaction of each individual species' ecotope within the area. Bryophyte communities consist of a collage of individual species that are each utilizing particular portions of resources and habitat. Some communities are stable and have species with narrow niches, the breadths of which do not or only partially overlap. Other communities are not in equilibrium and include opportunistic species that have wide and overlapping niche breadths.

There are many factors important to community analysis: the successional strategy, the growth form, the niche (ecotope) breadth, and the physiological response to environmental conditions for each species present. Furthermore, the degree to which a community subdivides the habitat space and the patterns involved in species packing (Slack, 1990) are important to community analysis. It is difficult to combine all these

factors into one complete study, but the more information gathered, the better understanding we have of bryophyte distribution.

CHAPTER III

LITERATURE REVIEW

There have been many attempts to describe recruitment and replacement of bryophyte communities on logs. In this chapter, I have reviewed some of them, giving attention to the design, the types of data collected, and the hypotheses about the factors that influence species presence on logs (i.e. effects of succession, decay stage, distribution patterns, and habitat fragmentation). Section 3.1 reviews general epixylic literature, and section 3.2 discusses literature about epixylic bryophyte research performed in the Great Smoky Mountains National Park.

3.1 Epixylic Bryophyte Research

One of the earliest studies addressing bryophytes on logs was performed by Jovet and Jovet, 1944, in the Savoyen Alps. The purpose of this study was to look at bryophyte succession relative to wood decay. They designated three substrate types: wood not yet decomposed, wood springy, and wood springy/ turning to humus. According to their results, four successional stages could occur for each substrate type. Pioneer stages occurred on all three substrates, but species composition on each substrate was different. From the wood springy class to the humus stage, the substrate appeared to influence the floristical composition less. This study spawned the idea that bryophytes follow a sequential species replacement pattern on logs. Thus, logs in the earliest stage of decay have an entirely different species composition than logs in middle to late stages of decay.

Raschendorfer (1949) also looked at bryophyte succession on decaying wood. She found that succession rates are much faster in humid regions than in dry regions. She also found that liverworts are more abundant in humid habitats, and mosses are more abundant in drier areas.

Schuster (1949) looked at the ecology of liverworts in New York. He concluded that succession on decaying logs was one of the few distinct examples of succession that could be treated with minimal subjectivity.

Stefureac (1969) proposed four different successional stages of a fallen log. The first stage he described was epiphytic. This is a log that still has bark. The second stage he discussed was epixylic, which is a log with no bark and whose xylem is exposed to weathering. Next were the saproliginicolous, and finally the humicolous stage. He declared that there are different combinations of species for each stage of log succession, and that succession from one stage to another was mostly unidirectional.

Muhle and Le Blanc (1975) used direct gradient analysis (Whittaker 1973) to determine the succession of cryptograms and other plant species and growth-forms on different decay stages of logs at defined elevations in the undisturbed forests of Mont Saint-Hilaire, Montreal. They took samples along an evaporational gradient from a wet/lakeshore region to a dry hilltop. They sampled nine 30.5 X 30.5 m quadrats placed 30.5 m apart. Inside each quadrat, all logs (total of 125 for study) were tagged for resampling. Only the tops of logs were sampled, and there were three microquadrat sizes. Microquadrat size one (20 x 20 cm) was used for logs with a DBH of 100-50 cm. Microquadrat size two (10 x 40 cm) was used for logs with a DBH of 50-30 cm, and microquadrat size three (5 x 80 cm) was used when a tree had a DBH of 30-15 cm.

Muhle and LeBlanc estimated degree of cover for each log using a cover class scheme (1 = 1-5%, 2=5-25%, 3= 25-50%, 4=50-75%, and 5= 75-100%). They designated the following growth forms: turfs, mats, and cushions. They defined five decay stages using bark, macroscopic and mechanical properties, chemical characteristics, twig and root condition, and material accumulated on the log surface. With slight modifications, many succeeding authors have employed this decay classification.

According to Muhle and Le Blanc, species composition changed along the gradient. Species richness and growth-form varied according to log decay stage. Species richness was greatest at the third stage of succession, and the second, fourth, and fifth stages had similar species richness. Stage one had the fewest species present. The growth forms of cryptograms in decay stages one and two were mats. Stages three and four had mats, turfs, and cushions present, while turfs and mats were found in stage five.

Slack (1982) discussed bryophytes in relation to the ecological niche theory. In this review, she suggested that bryophytes on logs are “competitive avoiders” because they are found on a temporary substrates. She hypothesized that species become extinct in one habitat because the habitat itself becomes extinct as the log decays.

Soderstrom (1987a) suggested that competition is an insufficient explanation for the distribution patterns of species growing on decaying wood. He tested the hypothesis that if dispersal of epixylic bryophytes is limited between sites, a species should be absent from some sites, but occupy the majority of available logs plus suboptimal substrates in other sites. He performed this study in ten old, isolated, spruce forests in northern Sweden. He analyzed three to five parallel transects, 10 m by 50 m, for each forest and recorded all logs, boulders, and wood litter for each site. For each log, he

recorded the following measurements: epixylic species, decay stage, diameter, highest height above ground, wood softness, percent of bark present, and wood texture.

Soderstrom measured the following levels of species frequency: regional frequency, mean local frequency, and frequency on suboptimal substrates.

Soderstrom tracked the occurrence of 19 species. He split them into two groups, core and satellite species. The core species were locally frequent and occurred on suboptimal substrates. The satellite species were divided further into two groups. One group included species that were locally infrequent and only occasionally occurred on suboptimal substrates. The second group included species that were more frequent (locally) and that often occurred on suboptimal substrate. Soderstrom concluded that this study demonstrated that effective dispersal is a major limiting factor for the distribution of bryophytes on logs.

Soderstrom (1987b) tried to evaluate the factors that regulate the distribution and abundances of species on decaying logs in the spruce forests of Sweden. (This article is a section from his doctoral thesis.) He hypothesized that species distribution on a log is determined by the interaction between epixylic bryophytes, the substrate demands among epixylic bryophytes, and the regional dynamic and dispersal abilities among bryophytes. The results of his study suggested that the substrate demands among epixylic bryophytes and the regional dynamic and dispersal abilities of bryophytes determine species distribution on a log. There was no strong evidence that interaction played a significant role in species distribution. He evaluated the interaction of species with the niche overlap theory. This theory suggests that when species occur together niche width and overlap between species should be less than when the species occur alone. Soderstrom compared

the niche overlap among bryophyte species on logs occurring alone and together. His results failed to suggest strong evidence for competition.

Soderstrom (1988) investigated how different bryophyte species respond to varying levels of decayed wood. He arbitrarily selected ten logs for each decay stage. Thirty additional logs were also selected to study the effect of a log's diameter on species distribution for each stage of decay. Soderstrom used eight different decay classes, modified from McCullough (1948), to describe the magnitude of decay. For each log, he measured the following variables: diameter, decay stage, texture of log, softness, height of log from ground, percentage of log in contact with the ground, and percent coverage of bark. He estimated the percent cover (cm^2) of all bryophytes and lichens. All the species that he found on more than five logs were used for decay variable analysis, and he used the most frequent 25 species for a more detailed analysis. Soderstrom employed a weighted average technique (Whittaker 1967) to calculate indexes of position (PI) for all measured variables.

He found 75 species in all, 40 of which occurred on at least five or more logs. The species were divided into four groups based on the PI value. The four groups are facultative epiphytes, early and late epixylics, and ground flora species. The facultative epiphyte and ground flora groups were the most clearly distinguished. The majority of the species were present over most of the decay stages. Some species were easily placed into one of the four groups, but other species were more difficult to place in a defined category.

According to Soderstrom, wood texture seemed to be the most important factor in separating and predicting colonization by species. Soderstrom suggested that logs found

high above the ground had the least number of species due to low moisture and that log diameter seemed to have a significant effect on species richness. Small logs seemed to have fewer species and were rapidly overgrown by ground flora species. Larger logs held more water and facilitated the growth of species that may be sensitive to drought.

Soderstrom (1989) studied the regional distribution patterns of bryophytes on *Picea abies* (L.) Karst. (spruce) logs in northern Sweden. In ten spruce forest stands, Soderstrom sampled all the logs found in three 20 m x 20 m plots. He recorded the decay stage, the maximum and minimum diameter, the maximum height above ground, the softness, the presence/absence of bark, the bark texture, and the cover (cm²) of each bryophyte species for each log. The presence of sexual reproduction and the production of gemmae were also recorded. Regional frequency (proportion of localities with available logs where the species was found), local frequency (mean proportion of available logs on occupied localities where the species was found), and local abundance (mean percent cover of the species on available logs in the occupied locality) were measured for each species. Soderstrom calculated the level of correlation between these measurements using Pearson's correlation equation.

Soderstrom recorded 18 species, and he distinguished four distribution patterns. He suggested that differences in patterns occur because of differences in dispersal ability and population stability. He saw four patterns: core, urban, rural, and satellite. Core species are abundant at a majority of the available localities. They usually produce spores and gemmae that are easily established. Urban species are abundant at a few localities. They are thought to have a limited dispersal ability between localities. Gemmae are produced frequently, but spores are not. Rural species occur in small populations at a

majority of the available localities. They demonstrate poor dispersal ability between localities. Satellite species are very rare and occur in small populations. They produce diaspores only occasionally and seem to have poor establishment and dispersal even within a locality. Soderstrom found no correlation between regional frequency, local frequency, or local abundance for any species.

Anderson and Hytteborn (1991) compared the substrate availability and bryophyte occurrence on decaying wood in one natural forest (Fiby urskog) with one heavily managed forest, only 1 km away, in Sweden. The natural forest was untouched since 1790, while the managed forest was thinned in 1973 and 1974. They investigated eight 10 m x 20 m sample areas, 50 m apart, for each forest and sampled a total of 458 logs or stumps. For each log, they measured the height of the log from the ground, the maximum and minimum DBH, and the decay class (adapted from Soderstrom 1987b). On five logs, they estimated the cover value of each species by using a 10 cm x 20 cm plot. Plots were placed at quarter meter intervals until the log DBH was 10 cm or less. They analyzed 101 plots.

Anderson and Hytteborn calculated the total amount of substrate for each large plot. They determined the tree species, the decay stage, and the diameter class for each log. The researchers placed each of the species they found into one of the four classifications: facultative epiphytes, epixylic, opportunistic generalists, and competitive epigenic species. They then determined the percent cover of the four classifications for each decay stage.

Anderson and Hytteborn suggested that the total amount of decaying wood in the managed forest was very different from the amount in the natural forest. The natural

forest had a greater quantity of decaying wood, a wider spectrum of decay stages, and logs with a larger DBH. Also, a greater diversity of species occurred in the natural forest, in which they found a total of 54 species. Sixteen threatened epixylic species occurred in the natural forest while only five of these species occurred in the managed forest. The authors suggested a direct relationship between epixylic species richness and increasing log diameter. According to Hytteborn and Anderson, their study demonstrated the importance of dense unmanaged forests, with their ample log substrate, stable local climate, and shelter against sunlight, wind, and drought, to the longevity of diverse bryophyte communities.

Laaka (1992) looked at 13 threatened epixylic bryophytes in a primeval forest in Finland, *Buxbaumia viridis* (DC.) Moug. And Nestl., *Cephalozia affinis* Steph., *C. catenulata* (Hub.) Spruce, *C. lacinulata* Spruce, *C. macounii* (Aust.) Aust., *Nowellia curvifolia* (Dicks.) Mitt., *Harpanthus scutatus* (Web. And Mohr) Spruce, *Scapania massalongi* (K. Mull.) K. Mull., *S. apiculata* Spruce, *Calypogeia suecica* (Arn. And Perss.) K. Mull., *Anastrophyllum michauxii* (Web.) Buch., *Lophocolea cuspidata* (Nees) Limpr. and *Jungermannia leiantha* (Grolle.) This study provides the most current records and remarks on the ecology and the status of these epixylic bryophytes. Laaka discussed the ecological demands of these bryophytes and the causes of their decline.

According to Laaka, there are many threats to the survival of these endangered epixylic species. The most serious problem is forest microclimate changes caused by deforestation. These changes include a widening of temperature extremes and drying due to increased wind. Most of the threatened epiphytes require constant humidity and shade. Another consequence of deforestation that is detrimental to these epiphytes is the overall

decrease in available substrate. Also, forest fragmentation increases the distance between available substrate. Unless a species has an effective dispersal strategy, a small population can become isolated.

Kimmerer and Young (1996) investigated the log community structure and gap utility patterns of disturbance-dependent bryophytes (A bryophyte gap is an area of disturbance in bryophyte cover caused by squirrels or some other forest activity.). They looked at the distribution of bryophyte species within a defined bryophyte gap and between different bryophyte gaps on logs. They sampled in two coniferous and two deciduous forests approximately two hectares in size. Every log with *Dicranum flagellare* or *Tetraphis pellucida* was considered in the study. The authors looked at a total of fifty-three bryophyte gaps on 26 different logs. They recorded gap dimensions, determined the decay class (modified from Soderstrom (1987)), and took a wood sample from each gap. Kimmerer and Young sampled young gametophyte cover by two perpendicular line transects. They ran a principle component ordination for each gap. The analysis included seven environmental attributes. The authors created overlays of species abundance with environmental ordinations. The level of light at each log was measured at twelve points by a LiCor quantum meter. The researchers compared propagule density of *D. flagellare* and *T. pellucida* with a student's t-test, and they used a Chi-square 2×2 contingency table to compare the amount of each species's propagules found on the top versus the side of a log. Kimmerer and Young determined the propagule germination rate of both species by gathering asexual propagules and sowing them on 18 moist coniferous logs in decay class two or on dry coniferous logs in decay class one. The authors determined the percent of germination by microscopic observation. They conducted a reciprocal

transplant experiment to determine if the microtopographic patterning of both species was the result of adult plant mortality. Shoot growth in gaps was also studied. Finally, they tested the hypothesis that the frequency of gap sizes differed between logs dominated by *T. pellucida* and *D. flagellare*.

Kimmerer and Young concluded that *D. flagellare* and *T. pellucida* exploit disturbance gaps differently. *D. flagellare* seems to inhabit small, dry gaps located on log tops, while *T. pellucida* inhabits larger, moist gaps on log sides. According to Kimmerer and Young, adult survivorship does not seem to determine species distribution; rather regeneration patterns are responsible for observed niche partitioning. Gap utilization seems to correlate with reproductive strategies, and propagule dispersal is patterned by microtopography. They determined that the relative abundance of both species depends on the availability of the correct regeneration niche and on the local disturbance. Hence, the authors proposed that the primary factor influencing community structure on logs is the interaction between the disturbance type and the niche available for regeneration.

Germano and Porto (1997) surveyed epixylic bryophytes in a seasonal, coastal, deciduous forest in Timbauba–Pernambuco, Brazil. They determined the circumference of 54 logs, the softness of their wood, their cortex texture, and their overall amount of bryophyte cover. They divided the logs into three decay classes, early, intermediate, and advanced, based on wood softness and the cortex texture. They found that the most frequent species showed no specificity relative to the decay stage of the log, but there were a few species that did show trends directly relating to decay stage. They concluded that the epixylic flora in humid tropical forests is principally composed of generalist species. Germano and Porto also found that the level of bryophyte cover was not directly

tied to species richness at a site. For instance, they found that logs that were completely colonized, often had a very low species richness.

3.2 **Epixylic Bryophyte Research in the Great Smoky Mountains National Park**

Only a few studies have included descriptions of bryophyte communities on logs in the spruce-fir forest of the Southern Appalachians. Cain and Sharp performed the first study in 1938. Prior to that, very few bryo-ecology studies had been performed in the United States (Cain and Sharp 1938). These authors looked at bryophyte unions on soil, rock, logs with no bark, tree butts, tree trunks, and tree limbs in the following types of forests: southern balsam fir, red spruce, beech gaps, buckeye/basswood, pearwood/sugar maple, and yellow poplar/sugar maple.

These authors described bryophyte communities as unions. According to Sirgo (1935) and Cain and Sharp (1938), a union is a “unistratal association concept in which each stable synusia of a phytocoenosis is considered more or less independent.” Thus, a forest association is made of many unions. A “facies of a union” was used to describe very closely related communities of subordinate rank. These terms have been used in all bryo-ecology studies of logs performed in the Great Smoky Mountains National Park.

Cain and Sharp began sampling epixylic logs by using one meter wide belt transects. On ten logs in every sample area, all the species within these transects were mapped. After a few samples, they changed this method to a 0.1 sq. m quadrat used on 19 logs. Cover was estimated for each quadrat by assigning one of six cover classes.

Within the southern fir forest association, the authors found the following unions: *Cephalozia curvifolia* (*Nowellia curvifolia*), *Sphenolobus michauxii* (*Anastrophyllum*

michauxii), *Dicranum fuscesens*, and *Hylocomium splendens*. An obvious pattern of succession was observed for these unions. The *C. curvifolia* union colonized recently fallen logs, followed by the *D. fuscesens* union, and finally the *H. splendens* union. (The *H. splendens* union has many of the same species as would be found in a soil union). The *S. michauxii* union was similar to the *C. curvifolia* union, except it was found on steep, moist north facing slopes.

Epixylic unions found in the red spruce associations were: *Cephalozia curvifolia* union, *Dicranum fuscesens* union, and the *Brotherella recurvans* union. The bryophyte communities in the spruce forests differed from those in the pure fir stands in that the *Hylocomium splendens* union was not found on logs under spruce trees even though it was abundant on the soil.

In 1939, Sharp published a paper on the taxonomy and ecology of eastern Tennessee bryophytes. In this study, he commented very briefly on the succession of the bryoflora on fir logs. His results were very similar to the results discussed in Cain and Sharp (1937).

Norris (1964) performed a study of the bryophyte unions on the major substrates of the spruce-fir zone of the Southern Appalachians. His study provides the most comprehensive data on the frequency, mean cover, and maximum cover (by visual estimate) for ten bryophyte unions found on decaying wood. He noted the successional change in bryophyte composition for different levels of substrate decay, and he assigned specific unions to different microhabitats. The following environmental data were described by Norris using only qualitative terms: intensity of light, decay of the log, and water availability. He recorded the slope degree and direction for each plot and put all of

his data on McBee keysort cards, which he arranged into unions using the Goodall (1953) method.

Norris's study is the main basis of comparison for the results of this thesis. Prior to the writing of this thesis, Norris's dissertation, written before the devastation of the fir forests, was the most current list of epixylic bryophyte communities in the spruce-fir forest of the Great Smoky Mountains National Park. The results of Norris's dissertation will be thoroughly examined in the forthcoming discussion. Although the species percent cover values can not be directly compared between the two studies, the species list and bryophyte unions found in Norris's study are directly compared to the results of this study.

CHAPTER IV

MATERIALS AND METHODS

This chapter provides an overview of the materials and methods used throughout this study. Section 4.1 describes the field site, section 4.2 discusses field methodology, section 4.3 reviews the analytical methods, and section 4.4 explains the multivariate techniques.

4.1 Field Site Description

This study was performed in the spruce-fir forest of the Great Smoky Mountains National Park, TN – NC. The area between Mt. Kephart and Double Spring Gap was most heavily investigated due to road access, the Appalachian Trail, and other trails maintained by the Great Smoky Mountains National Park. Two field excursions summited on Mt. Le Conte, and one visit each to Mt. Guyot and Old Black. (See Figure 2, for a map of the study plots.)

4.2 Field Methodology

A total of 35 field trips were incurred to accomplish sampling. Early field trips were assisted by D.K. Smith to evaluate potential sample areas, to collect specimens for identification, and to practice sample technique. Sample sites of varying levels of Fraser fir mortality were determined by advice and discussion with park personnel and D.K. Smith. Supplemental information on Fraser fir forest included a comprehensive literature

Map of Study Plots

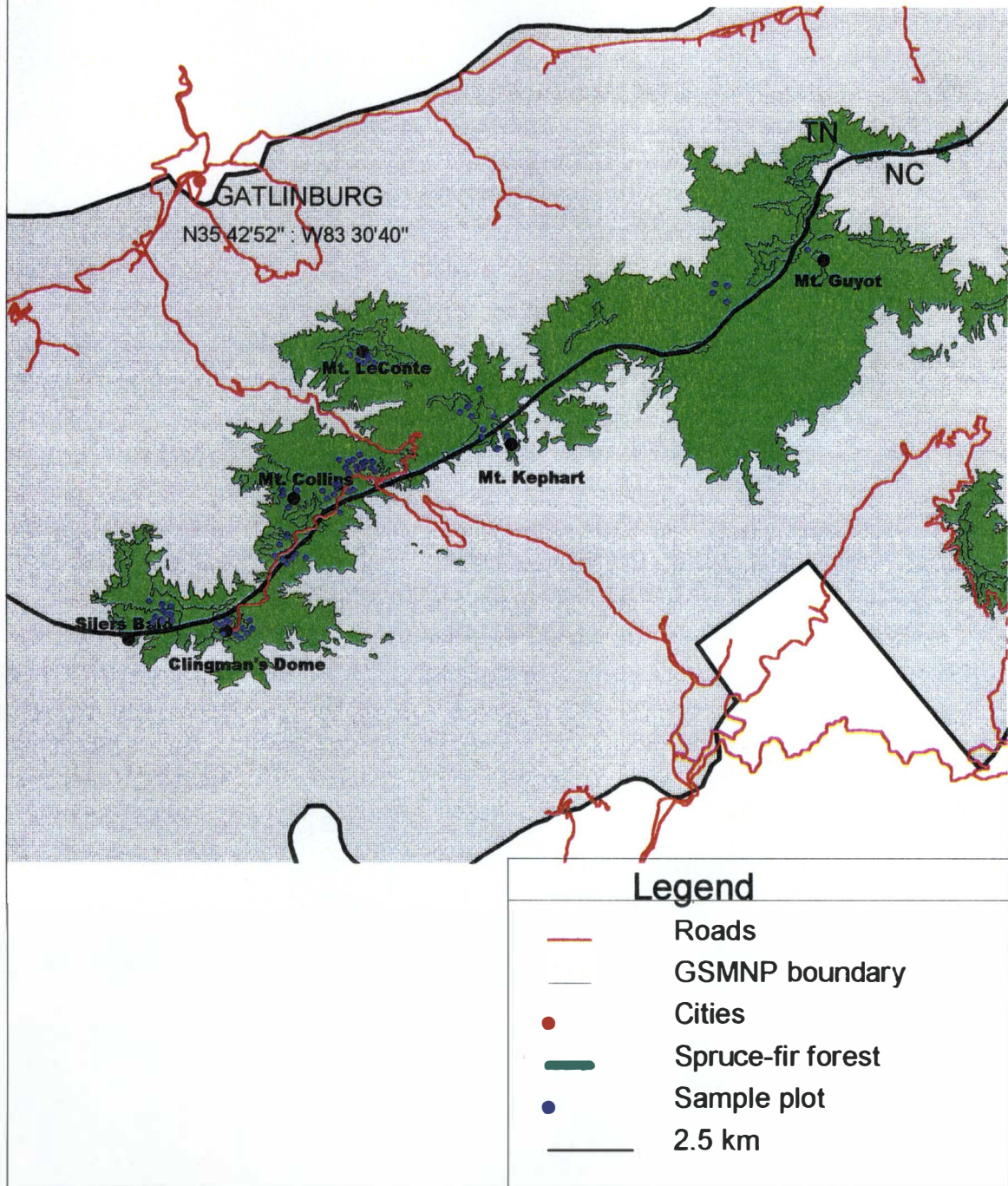


Figure 2 Map of the study plots (1996) adapted by Hermann.

search of previously sampled sites and my own field reconnaissance by hiking through spruce-fir forests.

Over the course of 30 field days, 79 fir logs ranging in DBH from nine to 26 cm were sampled. I was able to identify fir logs in all stages of decay because the only other coniferous tree of this forest type (spruce) was generally much larger and had a different decay texture than the fir logs. On a typical sampling day, I would choose a trail to hike based on the weather conditions or simply random choice. Upon reaching a fir stand that I wanted to sample, I would randomly select four to five potential logs. If a field assistant was present, he/she would assign a number for each of the potential logs. I would pick a number at each potential log, and if this number was the same as the number he/she had assigned, I would sample the log. If not, we would choose new numbers and continue until we had a match. If an assistant was not present, I used a version of the Ignorant Man Technique (Ward 1974). If a potential sample location had five logs, I would use five pennies, one yellow penny and four unpainted pennies. I then drew a penny for each log. If the yellow penny was drawn, the log was sampled.

For each sample log, I recorded the following site conditions: general location, longitude and latitude (using a Magellan NAV 5000 GPS), slope, slope aspect, elevation, dominant tree and shrub species, and canopy cover. Canopy cover values were determined by taking a densiometer reading from the center of a log and by assigning a qualitative canopy cover class (Appendix A-1) to each site. For each log, I recorded the DBH, position of the log (Appendix A-2), decay class (Appendix A-3 (Modified from Soderstrom, 1988)), presence/absence of bark, and bryophyte cover class (Appendix A-

4). Determining the position of the log included recording whether the log was in contact with the ground or above the ground, and if it was parallel or perpendicular to the slope.

The design of the sampling method used in this study is my own. The concept for this sampling technique was a product of ideas from Muhle and LeBlanc (1975), Huntzinger (1985), and D.K. Smith (personal discussion). It has been determined in past literature that the tops and sides of logs differ in species composition. To simplify my study, I decided to sample only the tops of logs. Thus, quadrats of different sizes were necessary to accommodate logs with different width (dbh). My design sampled the area forming a 30 degree arc to both sides of the center perpendicular axis of the log (Appendix B). The plot width marks the edge of the 30 degree arc for both sides of the log center. I used a standard 1m for plot length. At each of the four corners of a plot, I placed a large pin. The perimeter of the plot was outlined in yarn, and a total inventory of all bryophyte species was recorded.

Ten percent of the total plot area was sampled. Sampling ten percent of each plot was tested and determined to be an adequate sample size based on a logistics curve of multiple samplings of different percentages of the plots (3-75%). The cover values for each species based on a different percentage of the plot sampled were compared using the Chi square Goodness of fit test. There was no significant difference in cover value for any species between sample sizes ranging from 75 to ten percent of the 60 degree arc using an alpha of 0.01.

Presence and cover values of each species were measured by the use of belt transects. Each belt was 1m long and had 100 holes spaced 0.3 cm apart with the diameter of 0.625 cm punched into the belt. This size of hole was selected because only

one or possibly two species could occupy the area. The area of each hole was 0.30679 cm². Transects of 100 holes were laid out. The first belt transect was placed down the very center of the log. The second transect was placed along the inside edge of the plot to the right of the center. If subsequent transects were needed, they were equally spaced from the center transect and alternated from right to left transects. In partial transects (less than 100 holes) the number of holes to be sampled were equally placed along the 1 m transect length. For example, if 30 holes were to be sampled in the last transect, every third hole would be recorded until 30 was reached.

In many epixylic studies by various authors, cover value for each species was based on visual estimates. The utility and precision of data sampled in such a manner depends on the expertise of the researcher. The sampling method used in this study allowed for greater precision in estimating species cover, and it favors repeatability by future researchers. Furthermore, extremely small and very rare liverworts were rarely overlooked or missed when this technique was applied.

A field assistant or a cassette tape recorded the hole number and species present in the hole. Recordings on tape were transferred to data sheets upon returning from the field. Although most identifications were made in the field, a small number of unknown species were taken back to the laboratory for critical examination.

A field notebook was kept, and notes of each sample site were recorded. The notes recorded data such as weather conditions, field assistants, and bryo-ecology observations.

A voucher specimen of each species encountered in this study has been deposited in the bryophyte herbarium at the University of Tennessee [TENN]. Nomenclature

adopted for the mosses follows Crum and Anderson (1981), and nomenclature adopted for liverworts follows Schuster (1966-1980).

4.3 Analytical Methods

Percent cover and frequency values were calculated for each species in each plot. These values were recorded in separate matrices. Percent cover was determined by taking the total sum of the species presence (if a species was only present in one-half of the hole, it received a value of one-half) and dividing by the total number of holes sampled. Frequency values were calculated by taking the total number of hits (holes the species was present in) and dividing by the total number of holes sampled. A species received a frequency and percent cover value from one to 100. These values were rounded up if the first decimal place was five or above. All values between >0.0 and 1 were rounded up to one.

Relative percent cover, relative percent frequency, and presence/absence matrices were also calculated from the data set. Relative percent cover is the proportion of a species's coverage compared to all other species in the community. It was calculated by taking the percent cover of a species and dividing it by the sum of the percent covers of all species in the community. Likewise, the relative frequency of a species is the proportion of a species' frequency compared to all other species in the community. It is calculated in the same manner as relative percent cover.

A species's percent cover, frequency, relative percent cover, relative frequency, and presence absence data differ slightly in value for each plot. Although all these matrices were used in preliminary analyses, the relative frequency matrix was used to

determine the results reported in this thesis. The relative frequency matrix was used because this value adjusts for the difference in species size, and best represents community structure.

The uniformity of the data were inspected and checked for outliers. The data appeared to meet all requirements and assumptions necessary to apply statistical analysis.

4.4 Multivariate Techniques

Each sample site from this study is described by a certain number of species and environmental factors. The data gathered for each log is complex, bulky, and in some cases only indirectly interpretable. For these reasons, I used multivariate statistics to explore how the abiotic environmental variables influence the biotic composition on logs. Multivariate statistics allowed the data to be treated as one, even though all the measurements were not of the same type (ie. it allowed the combined use of qualitative and quantitative data for analysis). It also helped reduce noise within the data set and show relationships among samples, species, samples/species together, habitat preferences, and environmental data (Gauch, 1982).

Three types of multivariate analyses were performed on the data set: direct gradient analysis, ordination (indirect gradient analysis), and classification (cluster analysis). Each of these multivariate tests revealed different aspects within the data. Without using all three techniques, the results of this study would be limited.

4.4.1 Direct Gradient Analysis

Direct gradient analysis reflects the trends of species distribution along environmental gradients. It plots the direct distribution of a species along a specifically

measured environmental gradient by a stepwise linear position. Each gradient is observed individually for each species. By using this type of analysis, one can explore how a species responds to what seems an obvious environmental influence. The software used to perform direct gradient analysis was SPSS student version 6.1.3.

4.4.2 Ordination (Indirect Gradient Analysis)

Ordination is a technique that tries to represent species and sample relationships in a low dimensional space. According to Gauch (1982), there are four aspects of ordination: it is effective for showing relationship, reduces noise, helps identify outliers and disjunct data, and summarizes data redundancy. It uses species composition as important indicator of environment rather than any set of environmental variables. It produces a two dimensional graph where similar samples and/or species are grouped near one another. Points that lie close together correspond to sites with similar species composition, and points that are far apart correspond with sites that have a very dissimilar species composition. This technique leaves environmental interpretation of the data to a separate step, and it helps determine if important environmental variables were previously overlooked. For example, an important environmental variable is most likely overlooked if there is no relation between mutual positions of the samples in the ordination and the measured environmental variables. An excellent summarization of this process is seen in Appendix C (diagram from Jongman *et al.* 1995).

Detrended Correspondence Analysis (DCA) was the ordination technique used in this study. DCA is an eigenvector ordination technique based on reciprocal averaging. It is a heuristic modification of Correspondence Analysis (CA) that tries to correct the major faults of CA by detrending. Detrending ensures that at any point along the first

axis, the mean value of a sample score is near zero on the subsequent axis. This process of detrending is built into a two-way weighted average algorithm. Each subsequent axis is derived by detrending with respect to each pre-existing axis. This technique provides an eigenvalue for each division of the data set. The closer the eigenvalue is to one, the further separated the groups are from one another, and the fewer species the two samples have in common.

DCA was performed with the PC-ORD Software Package which uses a modified version of DECORANA from the Cornell Ecology Program series (McCune and Mefford, 1995). It was applied to a sample-by-species relative frequency data set. All rare species occurring in less than 5% of the plots were ignored in the analysis. All program default settings were used for data analysis.

This version of DCA has many additional features that facilitate interpretation. One such option is called a joint-plot. It allows for the overlapping of species and samples onto the same 2-D diagram. This allows one to predict the rank order of species within a plot. One may also overlap environmental gradients onto a species, or a sample 2-D diagram. This allows one to see how a species responds to various environmental variables. Furthermore, one can rotate the axes to bring into clearer view the environmental gradient that is of interest to the researcher. To perform the joint plot using environmental axes, a sample-by-environmental variables matrix must also be generated.

To interpret DCA diagrams, a few pointers should be given. Species that are found on the edge of the diagram are often rare species that prefer extreme environmental conditions, and species that are found in the very center of the plot can have a unimodal

distribution with their optima at the center, a bimodal distribution, or a distribution that is unrelated to the ordination axis.

4.4.3 Classification (Cluster Analysis)

Classification is a technique that considers all species a single cluster initially and then partitions them into smaller clusters. It is used to give information on the concurrence of a species, establish community types, and detect relationships between communities and their environment (Jongman *et al.* 1995). TWINSpan was used for the classification analysis and was applied to the relative frequency data gathered for this study. The TWINSpan analysis was performed with PC-ORD software package, which uses the modified version of TWINSpan from Cornell Ecology Program Series (McCune and Mefford, 1995). All program default settings were used for this process, and rare species (occurring in less than 5% of all plots) were excluded from the data matrix.

TWINSpan is one of the most widely used programs in community ecology (Jongman *et al.* 1995). It classifies and constructs a two-way table from a sites-by-species matrix. Each species within the data matrix is assigned a pseudo-species value. The pseudo-species concept is based on the idea that each group of sites can be characterized by a group of differential species. A pseudo-species is a qualitative equivalent of species abundance (Hill *et al.* 1975). Thus, a more abundant species is assigned a higher pseudo-species value. This is a way of substituting a quantitative variable by several qualitative variables, or a process called cojoint coding (Heiser 1981). Cojoint coding provides an advantage in the situation that a species abundance is skewed. In this situation, cojoint coding produces a pseudo-species response curve that differs in the pseudo-species optimum.

TWINSPAN ordines samples using correspondence analysis. This takes place in a series of ordinations. For each dichotomy produced, TWINSPAN performs each of the following ordinations. The first ordering division occurs at the center of the starting group. All the species preference scores are added together. The group is then divided into two clusters assigned positive and negative positions. After this division, an iterative character weighting is performed to improve the arrangement of the samples within their clusters. An absolute preference score of one is assigned to each pseudo-species that is at least three times more frequent in one cluster than the other cluster. Rare pseudo-species are down-weighted in this step. In the second ordering division, an average of the preference scores for each site is determined. This step does not down-weight rare species, and less strongly polarizes the non-preferential species. Finally, a refined ordination is performed on the scores in both orderings, and the refined ordination is then divided near the center. For data sets where sites are close to the point where the refined ordination process was divided, a third ordering is performed.

TWINSPAN creates an extremely valuable species-by-plots table. This is done by first arranging the dichotomies described above, and then classifying species based on site classification. One can then take this table and compare the environmental conditions of all the sites placed into a particular group. Combining environmental and species data results in hypothetical community types. These community types include a description of indicator species (species that are found with high relative frequency values within this group relative to all other groups) and environmental conditions. An example of the species-by-plots table for this data is found in Appendix D, and an example of the environmental variables-by-plots table is found in Appendix E.

CHAPTER V

RESULTS/ DISCUSSION

This chapter summarizes and discusses the results of this study. Section 5.1 provides a comprehensive species list of all the epixylic bryophytes that I found on Fraser Fir logs in the Great Smoky Mountain National Park. Section 5.2 is a summary of the results from TWINSpan, and section 5.3 discusses these results. Section 5.4 describes the results from DCA and section 5.5 discusses them. Finally, the results from Direct Gradient Analysis are reported in section 5.6 and section 5.7 discusses them.

5.1 Species list

In this study, I found a total of 30 species. Fifteen of these species were mosses, and 15 were liverworts. Five of the moss species and five of the liverwort species are considered rare because they were found in less than five percent of all the plots sampled. Appendix F provides a comprehensive species list.

5.2 Twinspan Results

I used TWINSpan to create two dendrograms from the species relative frequency-by-plots data matrix (Appendix D). The first dendrogram (Figure 3) separates all the sites sampled into nine different groups. Each one of these groups represents a Union. (See Appendix G, p. 116 for the plot/union listing.) The second dendrogram (Figure 4) groups species that perform similarly into six different clusters.

Bryophyte Unions

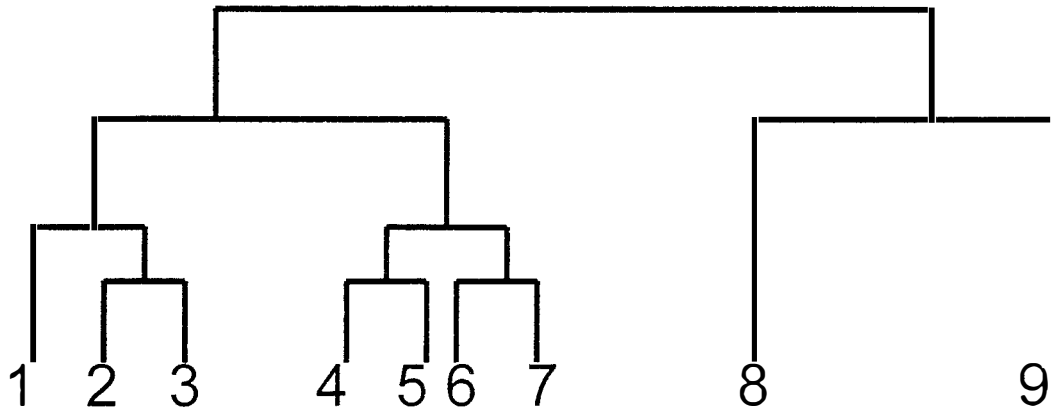


Figure 3 TWINSpan Bryophyte Unions

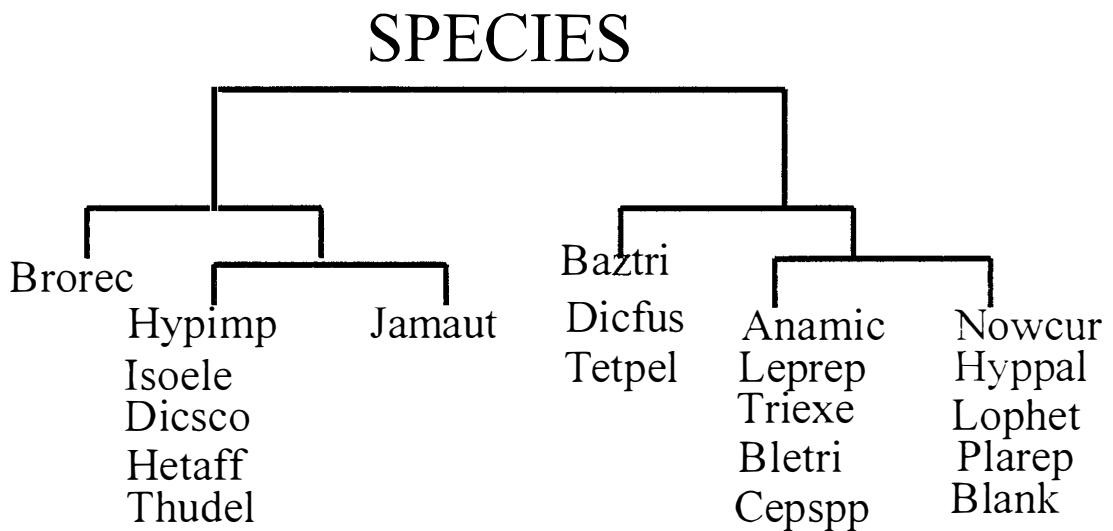


Figure 4 TWINSpan Species Groups

5.3 TWINSpan Discussion

In order to make sense of the bryophyte unions and species clusters delineated by TWINSpan, it is necessary to look at the environmental and species data for each plot and compare it with the TWINSpan results. This section provides an interpretation and discussion of the TWINSpan results based on the species relative frequency-by-plots matrix (Appendix D) and the environmental variables-by-plots matrix (Appendix E).

5.3.1 TWINSpan Bryophyte Unions

The first division of the “Bryophyte Unions” dendrogram divides sample sites based on the level of bryophyte cover. Sites on the left of the dendrogram include plots that have a low bryophyte cover, and plots on the right of the dendrogram have a greater amount of bryophyte cover (Figure 5).

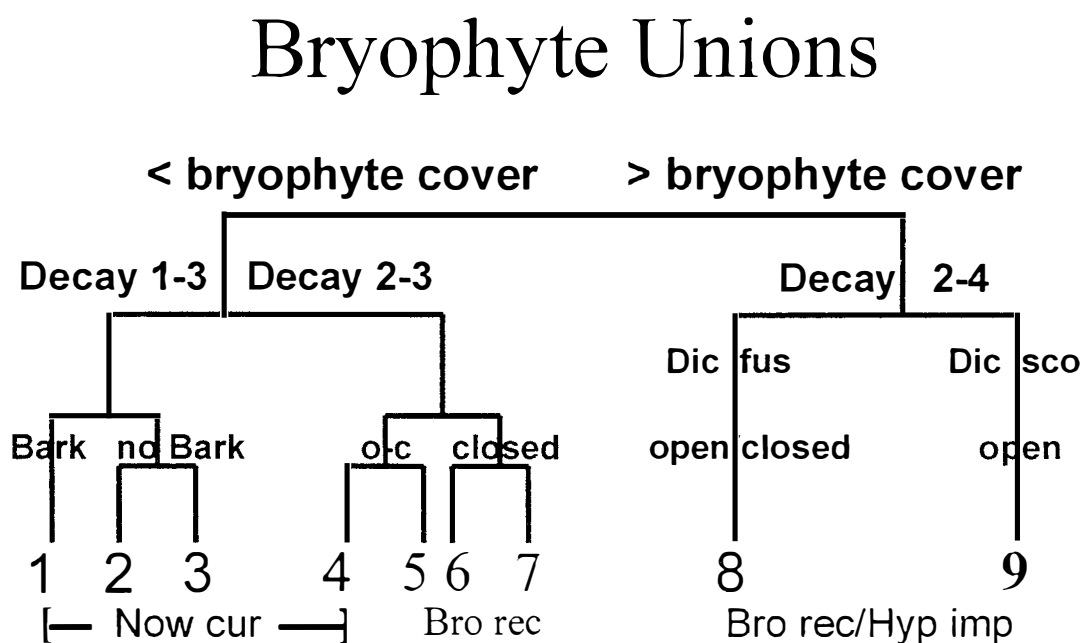


Figure 5 TWINSpan Bryophyte Unions Interpretation

The left-hand side of the dendrogram is broken into two different bryophyte communities: *Nowellia curvifolia* and *Brotherella recurvans*. These two communities are divided into seven unions (Figure 5). The species present in each union varies slightly. (See Table 1 for indicator species/union listing.) Groups 1,2,3, and 4 are variations of the *Nowellia curvifolia* community. Group 1 represents a union found on a corticulous log that has just fallen (decay stage 1-2). This union can be found at all levels of light. The indicator species of this union are *Nowellia curvifolia*, *Hypnum pallescens*, and *Platygyrium repens*. Group 2 is a union that I found on logs that are in middle to late stages of decay (decay stage 2-4) and in closed to moderately shaded forests. *Nowellia curvifolia*, *Cephalozia* spp., and *Isopterygium elegans* are species that define this group. Group 3 consists of a *Nowellia curvifolia* community that I found on epixylic logs in early stages of decay (decay stage 1-2) and in varying levels of light. *Nowellia curvifolia* is the only indicator species of this union. The last *Nowellia curvifolia* union, Group 4, was found on logs in moderate to late stages of decay (decay stage 2-3) in very open forest. Indicator species of this group are *Nowellia curvifolia*, *Dicranum fuscescens*, *Anastrophyllum michauxii*, and *Tritomaria exsecta*.

Groups 5,6, and 7 describe the *Brotherella recurvans* community. Group 5 represents a union found on logs in moderate levels of decay (decay stage 2-3) and in all types of light conditions. This union has the following indicator species: *Brotherella recurvans* and *Dicranum fuscescens*. Small amounts of *Nowellia curvifolia* can also often be found in this union. Groups 6 and 7 are unions that I found on logs in moderate levels of decay (decay stage 2-3) and in forests that are moderately shaded to closed. *Brotherella recurvans* and *Dicranum fuscescens* are the dominant species within these

Table 1 Indicator species present in each TWINSPAN union.

Community	Union #	Species Present
<i>Nowellia curvifolia</i>	1	<i>Nowellia curvifolia</i> <i>Hypnum pallescens</i> <i>Platygyrium repens</i>
<i>Nowellia curvifolia</i>	2	<i>Nowellia curvifolia</i> <i>Cephalozia</i> spp. <i>Isopterygium elegans</i>
<i>Nowellia curvifolia</i>	3	<i>Nowellia curvifolia</i>
<i>Nowellia curvifolia</i>	4	<i>Nowellia curvifolia</i> <i>Dicranum fuscescens</i> <i>Anastrophyllum michauxii</i> <i>Tritomaria exsecta</i>
<i>Brotherella recurvans</i>	5	<i>Brotherella recurvans</i> <i>Dicranum fuscesens</i> <i>Nowellia curvifolia</i>
<i>Brotherella recurvans</i>	6	<i>Brotherella recurvans</i> <i>Dicranum fuscesens</i> <i>Bazzania trilobata</i>
<i>Brotherella recurvans</i>	7	<i>Brotherella recurvans</i> <i>Dicranum fuscesens</i> <i>Tetraphis pellucida</i> <i>Blepharostoma trichophyllum</i> <i>Cephalozia</i> spp. <i>Lepidozia reptans</i> <i>Nowellia curvifolia</i>
<i>Brotherella recurvans</i> / <i>Hypnum imponens</i>	8	<i>Brotherella recurvans</i> <i>Hypnum imponens</i> <i>Dicranum fuscesens</i>
<i>Brotherella recurvans</i> / <i>Hypnum imponens</i>	9	<i>Brotherella recurvans</i> <i>Hypnum imponens</i> <i>Dicranum scoparium</i> <i>Thuidium delicatulum</i>

unions. Group 6 differs from 7 in that Group 6 has an additional indicator species, *Bazzania trilobata*. Group 7 has a greater relative frequency of *Tetraphis pellucida* and also small liverworts such as *Blepharostoma trichophyllum*, *Cephalozia* spp., *Lepidozia reptans*, and *Nowellia curvifolia*.

The right hand side of the dendrogram (Figure 5) is broken into two unions: 8 and 9. Groups 8 and 9 represent variations within the *Brotherella recurvans*/*Hypnum imponens* community. Both of these unions are found on logs in mid to late stages of decay (decay 2-4). Union 8 can be found in very open to very closed forests. In addition to *Hypnum imponens* and *Brotherella recurvans*, *Dicranum fuscescens* is an indicator species. Group 9 is found in very open conditions. *Thuidium delicatulum* and *Dicranum scoparium* are additional indicator species for group 9.

5.3.2 TWINSPAN species groups

TWINSpan used the species-by-plots data matrix to group species that respond in a similar way. This process resulted in six different groups of species (Figure 4). Figure 6 provides an interpretation of the environmental variables that greatly influence species composition within the TWINSpan groups.

TWINSpan first separated species that are influenced by the amount of light from species that are influenced by the level of decay of the log. The groups on the left are species that respond most significantly to the availability of light. *Brotherella recurvans* is in its own group (group 1). It is the species that is most abundant in closed canopies. Its relative frequency increases when the level of light on the canopy floor decreases. Group two includes species whose relative frequencies increase

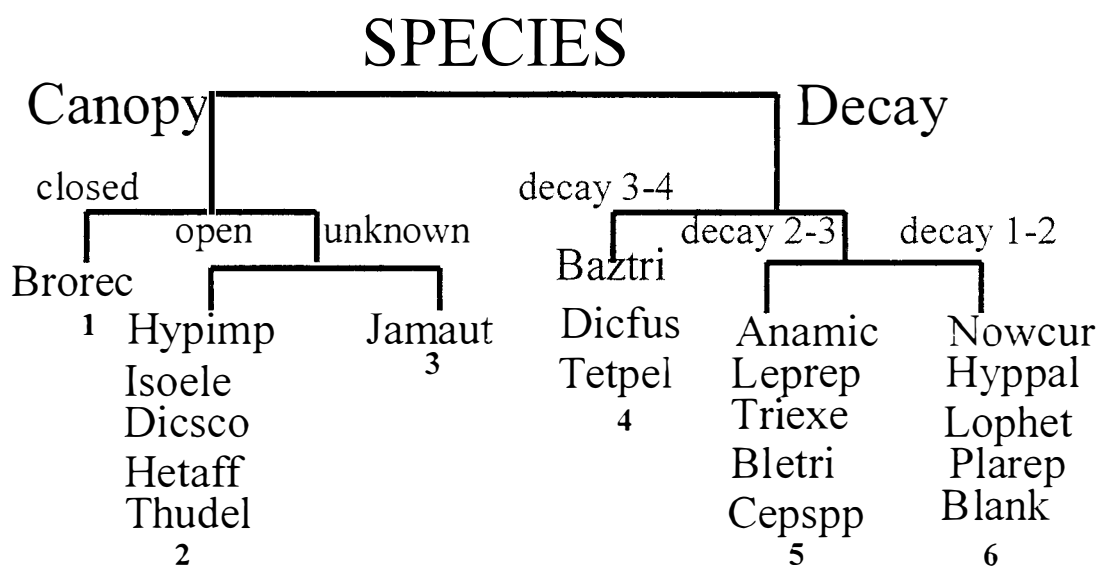


Figure 6 TWINSpan Species Groups Interpretation

when the light on the forest floor increases. This group includes the following species:

Hypnum imponens, *Isopterygium elegans*, *Dicranum scoparium*, *Heterophyllum affine*,

and *Thuidium delicatulum*. The last group on this side (group 3) has only one species in

it, *Jamesoniella autumnalis*. This species does not appear to respond directly to light. The

methods used in this study may not be able to determine in what community type it is

most abundant.

The species on the right of the dendrogram are those that respond most to the level of decay of the log. I found *Bazzania trilobata*, *Dicranum fuscescens*, and *Tetraphis pellucida* (group 4) on logs in the late stages of decay. I found *Anastrophyllum michauxii*, *Lepidozia reptans*, *Tritomaria exsecta*, *Blepharostoma trichophyllum*, and *Cephalozia* spp. (group 5) on logs that were in moderate levels of decay. Finally, *Nowellia curvifolia*, *Hypnum pallescens*, *Lophocolea heterophylla*, *Platygyrium repens*, and blank holes (group 6) were found on logs that were in early stages of decay.

5.4 DCA Results

I performed Detrended Correspondence Analysis ordination on the species-by-plots data matrix. The result of this ordination was a two-dimensional scatterplot of each species's overall average response within sampled sites (Figure 7).

Axis one has an eigenvector value of 0.6491 and axis two has a value of 0.4180.

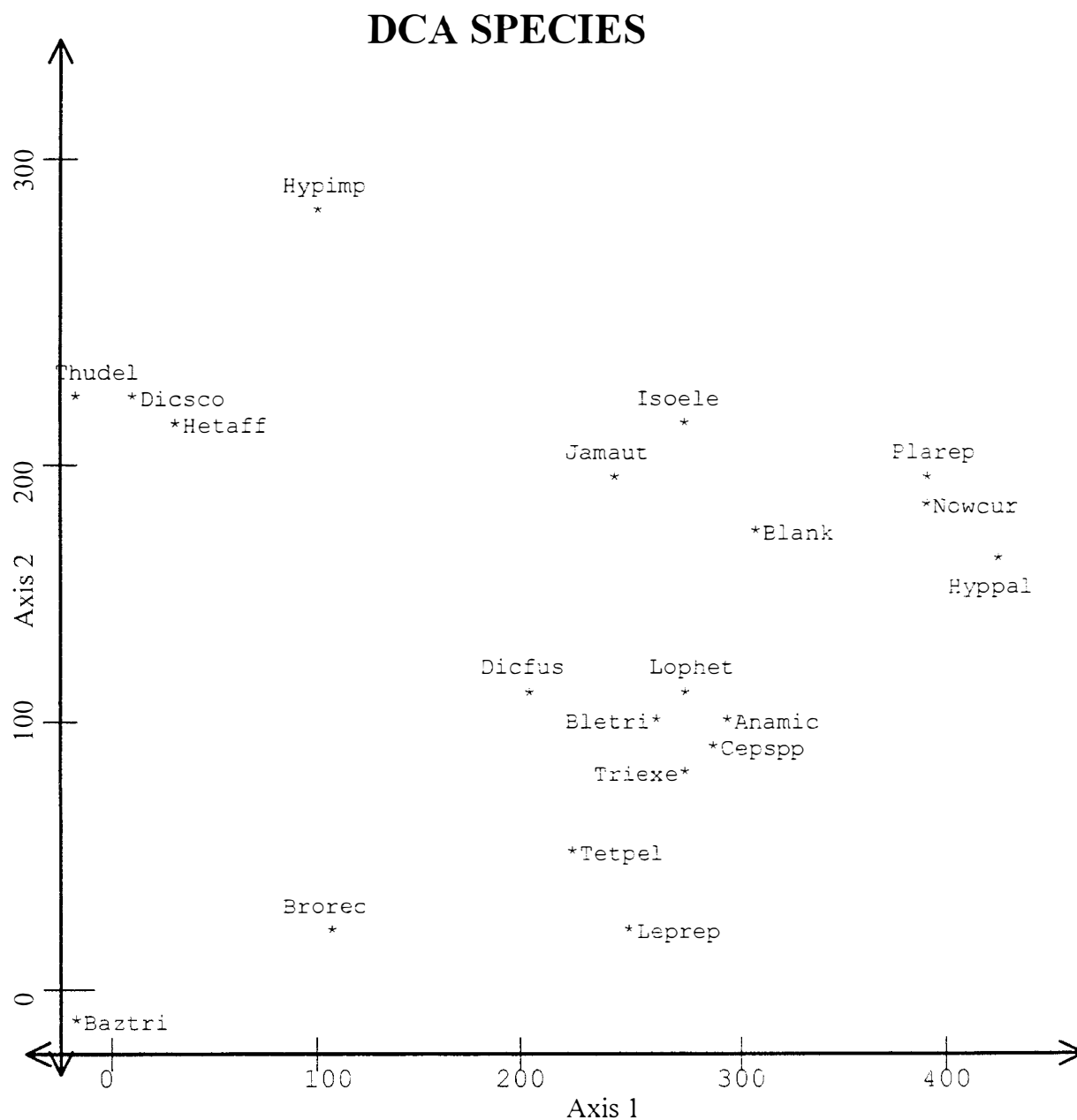


Figure 7 DCA ordination of species

5.5 DCA Discussion

In order to interpret the results of DCA, I used the environmental-by-plots data matrix (Appendix F) to determine if axes one and two are influenced by measured environmental gradients.

Axis one of the DCA scattergram, the predominant underlying environmental gradient, appears to be related to the level of substrate decay (figure 8). Species found toward the far right end of the scattergram are species that are often found in early stages of decay. Likewise, species found on the far left of the scattergram are species that are found during late stages of decay. I found *Nowellia curvifolia* and *Hypnum pallescens* as well as empty spaces on logs in the early stages of decay (decay stage 1-2).

Blepharostoma trichophyllum, *Cephalozia* spp., and *Anastrophyllum michauxii* are species that I found on moderate levels of log decay (decay stage 2-3). Lastly, *Heterophyllum affine* occurred on logs in the late stages of decay (decay stage 3-4).

Axis two appears to be related to the environmental gradient of light availability. Species that are found in the top half of the dendrogram can tolerate far greater levels of light than the species found in the lower half of the scattergram. The distribution of one species, *Hypnum imponens*, is particularly influenced by light. This species is a very tolerant, generalist species that takes advantage of all situations, but which increases in abundance with a high level of light.

Many other species respond to both light and decay gradients. I found *Dicranum fuscescens*, *Tetraxis pellucida*, *Lepidozia reptans*, *Lophocolea heterophylla*. and *Tritomaria exsecta* on logs that are in decay stages of 2 or 3 in forests that are moderately shaded to closed. *Dicranum scoparium* and *Thuidium delicatulum* grew on logs in mid to

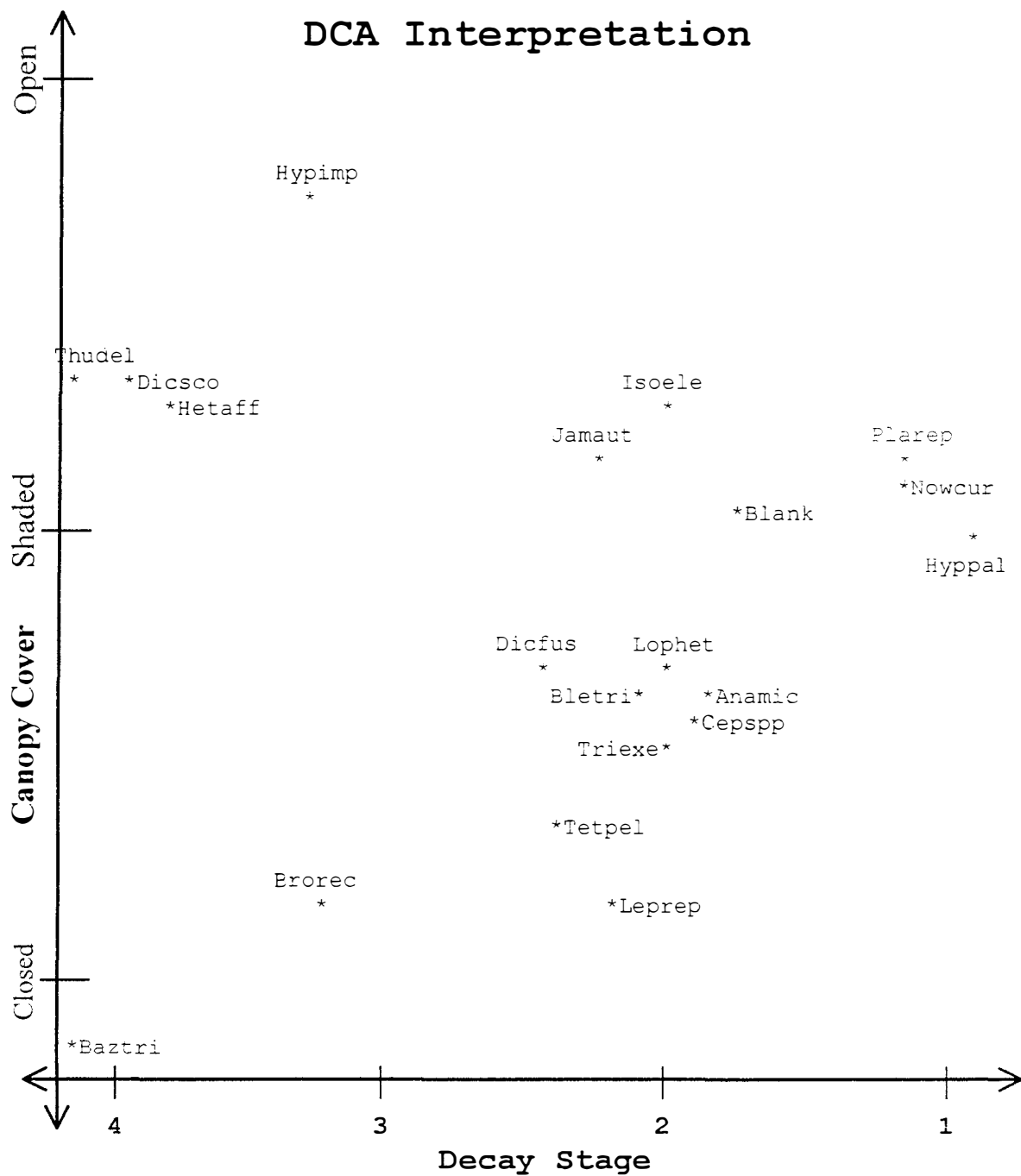


Figure 8 Interpretation of DCA ordination

late stages of decay in forests that were very open to moderately shaded. *Brotherella recurvans* preferred logs in moderate to late stages of decay (decay stages 3-4) and under closed canopy conditions. *Bazzania trilobata* flourished in late stages of decay (decay stage 4) and in closed forests.

Another feature of DCA is its ability to display the relative frequency of each species on a two dimensional diagram. A scattergram produced from this feature has the same axes interpretation as the one just discussed, but it displays only one species at a time. This function is very valuable because it shows the entire distribution of a species rather than just its average relative frequency. This allows us to probe deeper into each species's overall strategy and to determine which species take advantage of a wide array of niche openings and which species occupy very narrow niches and are intolerant of suboptimal conditions.

When I examined the entire distribution for each species individually, I found three species that have a much wider range in two-dimensional space than it appears on the DCA scatterplot. These species are *Platygyrium repens*, *Jamesoniella autumnalis*, and *Isopterygium elegans*. *Platygyrium repens* occurred in greatest relative frequency in early stages of decay (decay stage 1-2) and tolerated all levels of light. *Jamesoniella autumnalis* was present in almost all levels of decay (decay stage 1-3) and under all light conditions. Lastly, I found *Isopterygium elegans* in moderate levels of decay (decay stage 1-3) and in forests that are slightly open to moderately shaded.

5.6 Direct Gradient Analysis Results

Throughout this study, I measured many different environmental variables for

each log. Direct Gradient Analysis was performed on all non-rare species for the following environmental gradients: decay stage, canopy cover, log position, log orientation, site location, log diameter, and amount of bryophyte cover. Only the environmental factors that significantly influenced species distribution (decay, canopy class, bryophyte cover, and log position) are summarized in this section. For each variable, I created three separate graphs: dominant species, small liverworts, non-dominant mosses. Grouping the species this way allows the response of each species to be displayed on a scale relative to its size and relative frequency. Figures 9-11 summarize how each species responds to the decay stage of a log. Figures 12-14 show the relationship between canopy cover and species relative frequency, and figures 15-17 summarize each species relative frequency relative to bryophyte cover. Lastly, figures 18-20 show how species respond to log position.

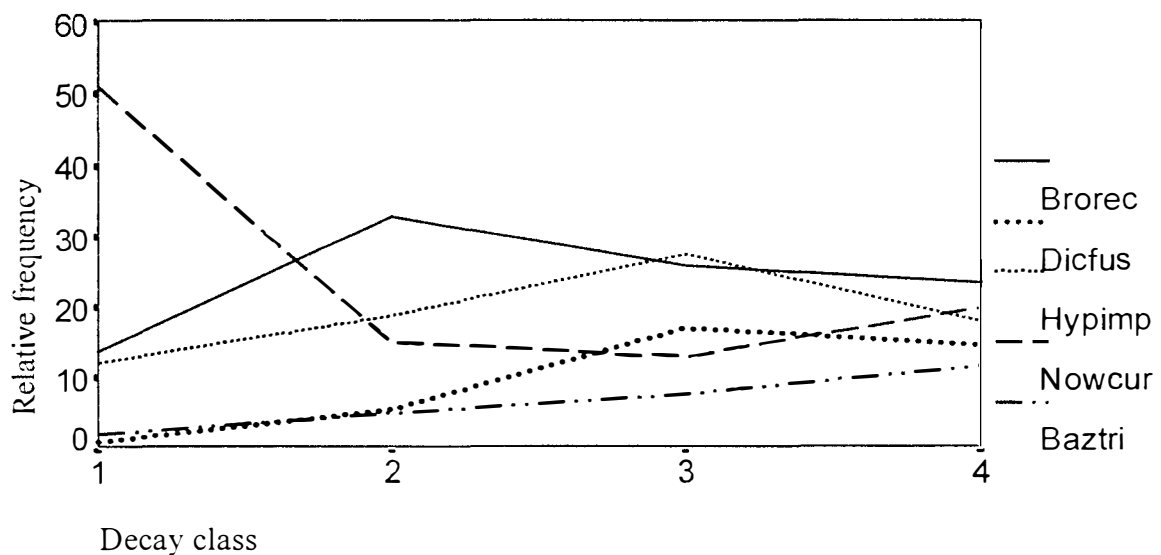


Figure 9 Dominant Species Relative Frequency vs. Decay Class

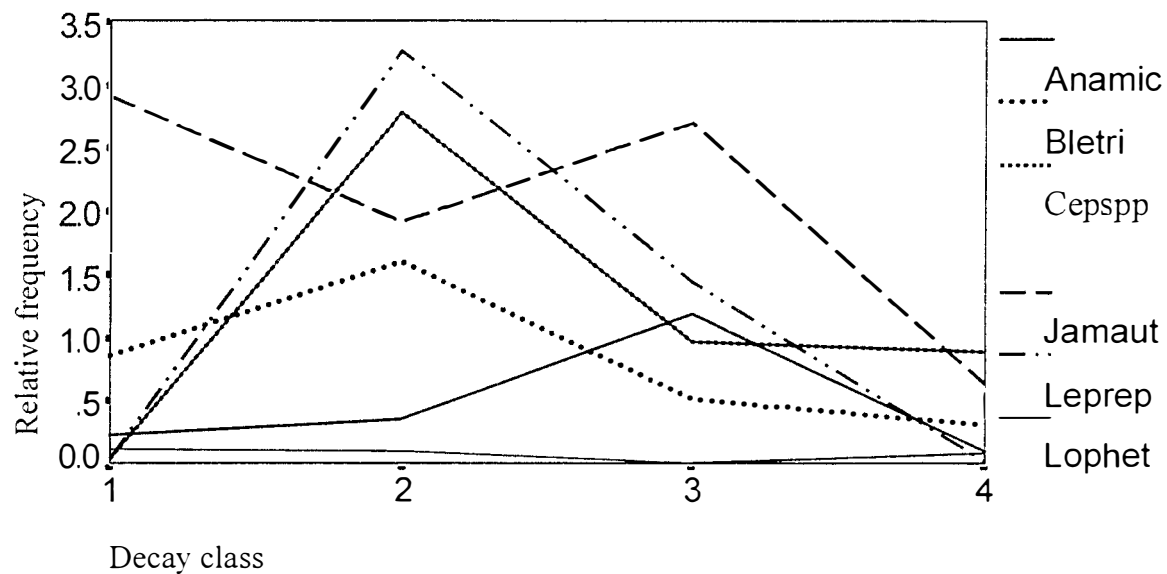


Figure 10 Small Liverworts Relative Frequency vs. Decay Class

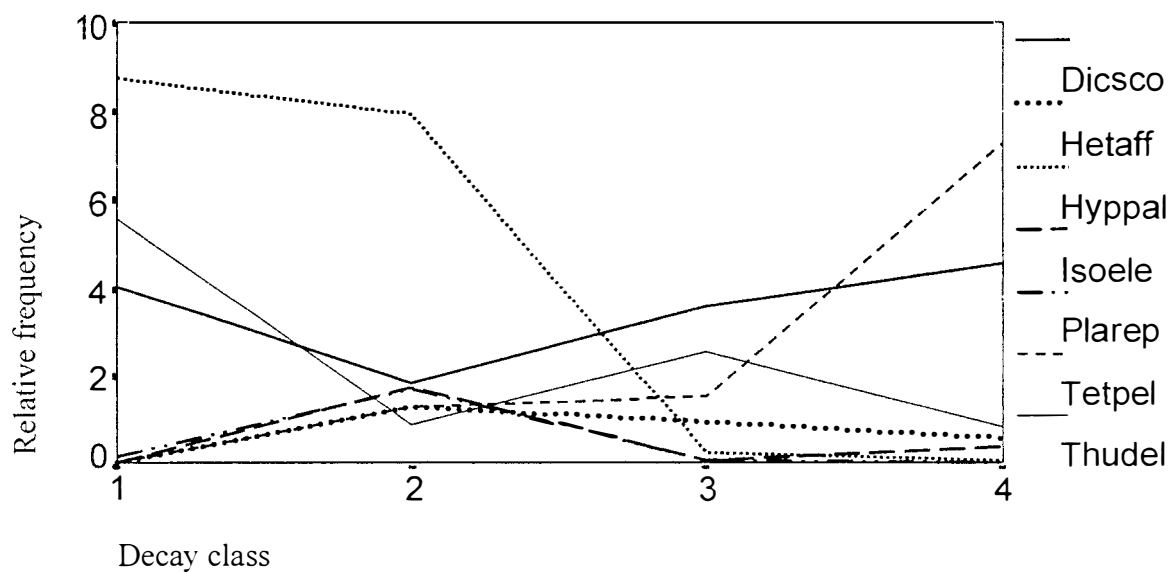


Figure 11 Non-dominant Moss Species Relative Frequency vs. Decay Class

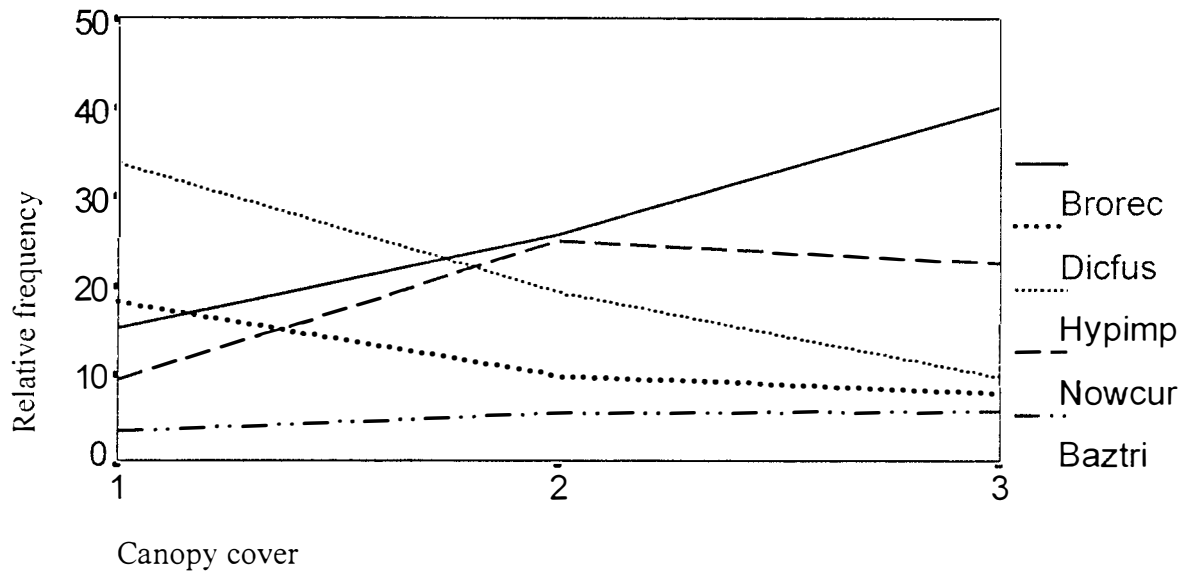


Figure 12 Dominant Species Relative Frequency vs. Canopy

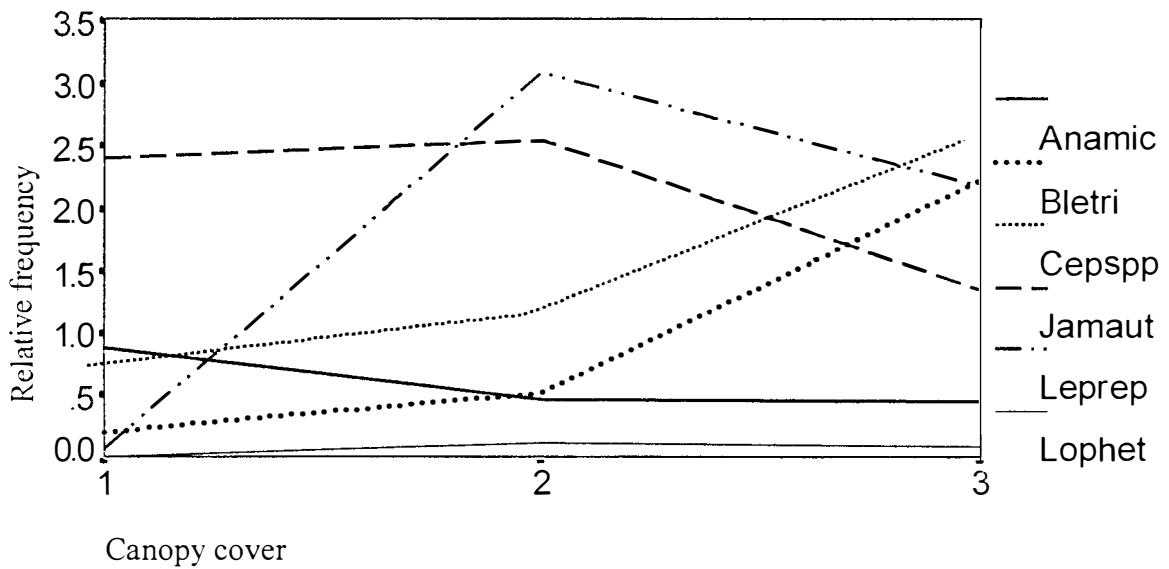


Figure 13 Small Liverworts Relative Frequency vs. Canopy

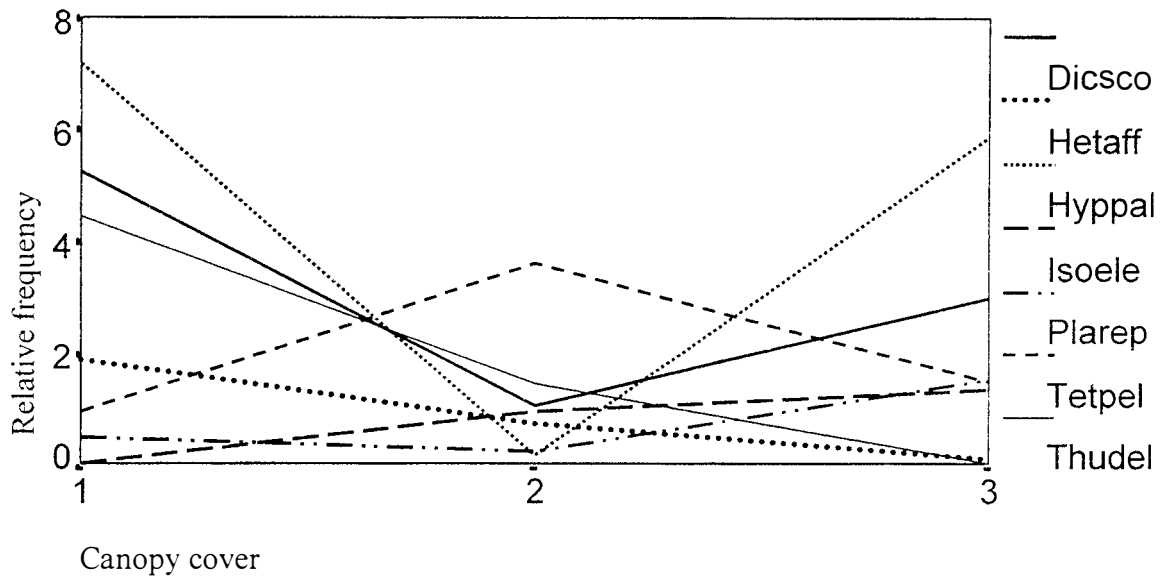


Figure 14 Non-dominant Moss Species Relative Frequency vs. Canopy

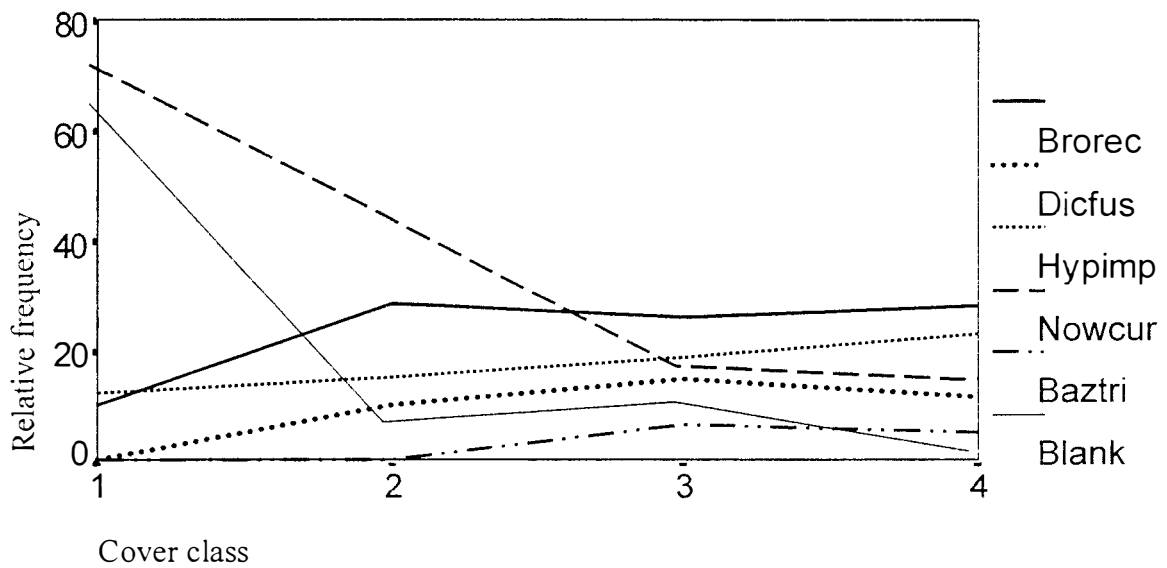


Figure 15 Dominant Species Relative Frequency vs. Bryophyte Cover Class

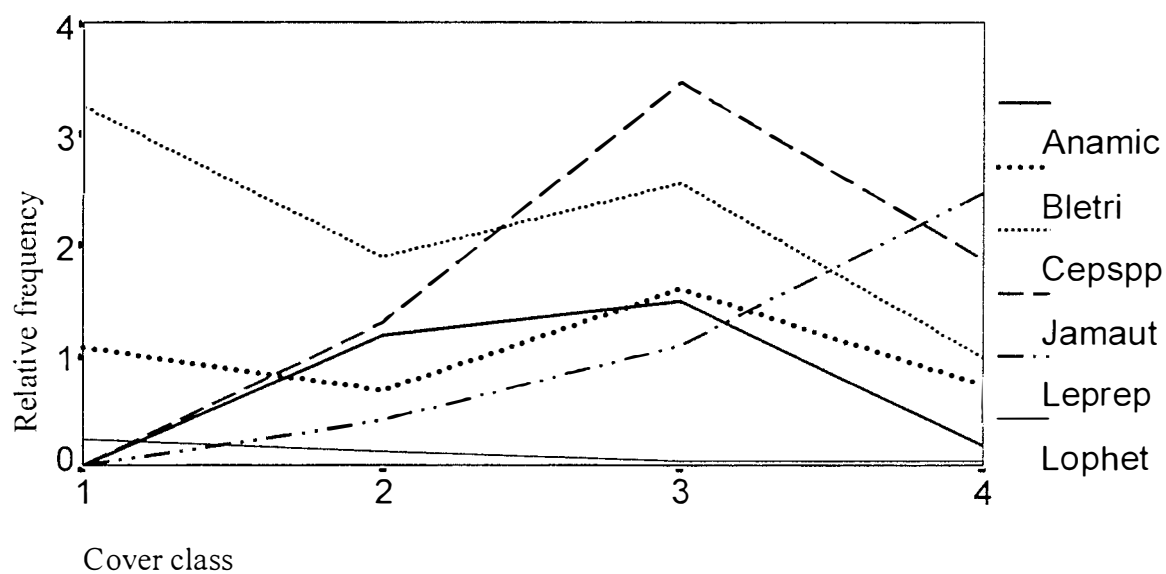


Figure 16 Small Liverworts Relative Frequency vs. Bryophyte Cover Class

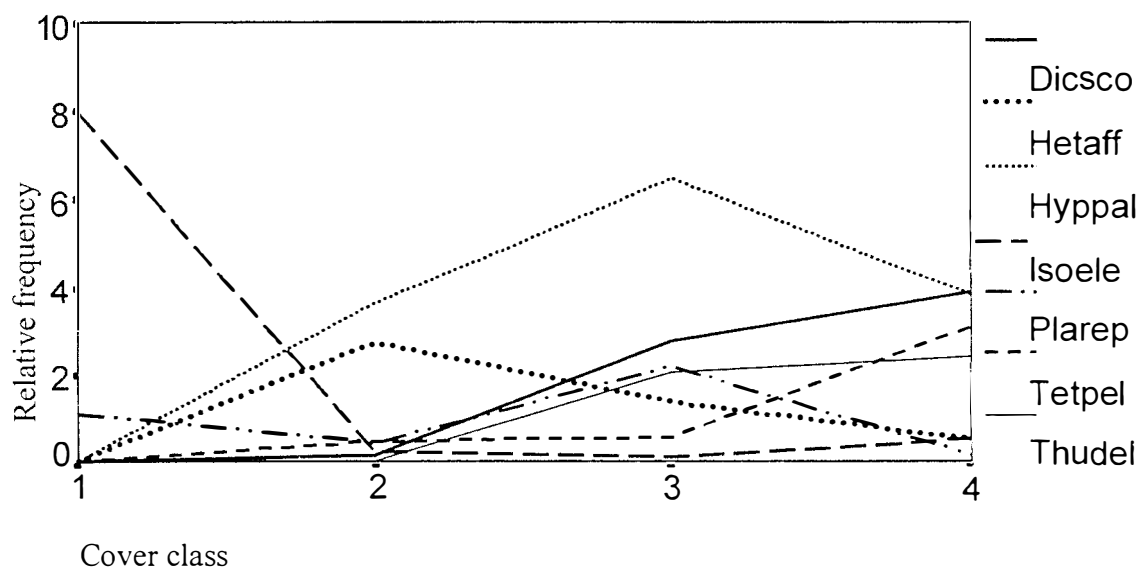


Figure 17 Non-dominant Moss Species Relative Frequency vs. Bryophyte Cover Class

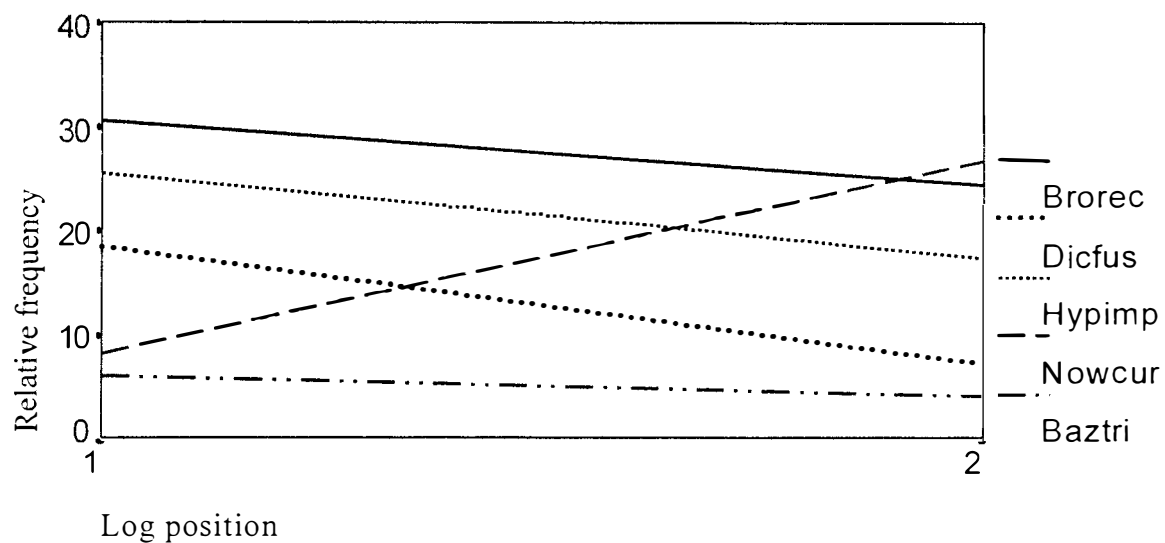


Figure 18 Dominant Species Relative Frequency vs. Log Position

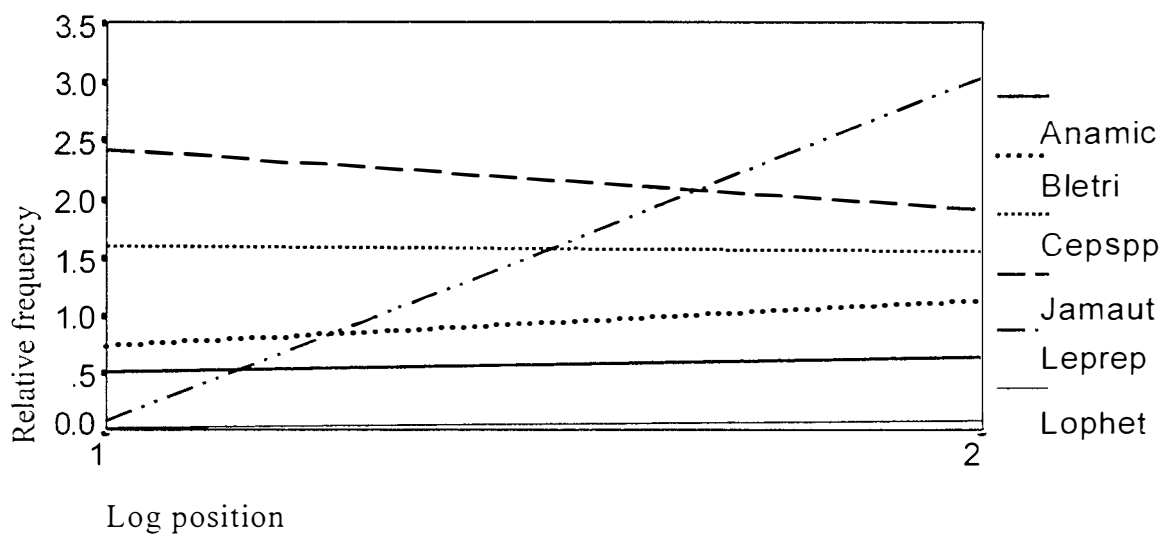


Figure 19 Small Liverworts Relative Frequency vs. Log Position

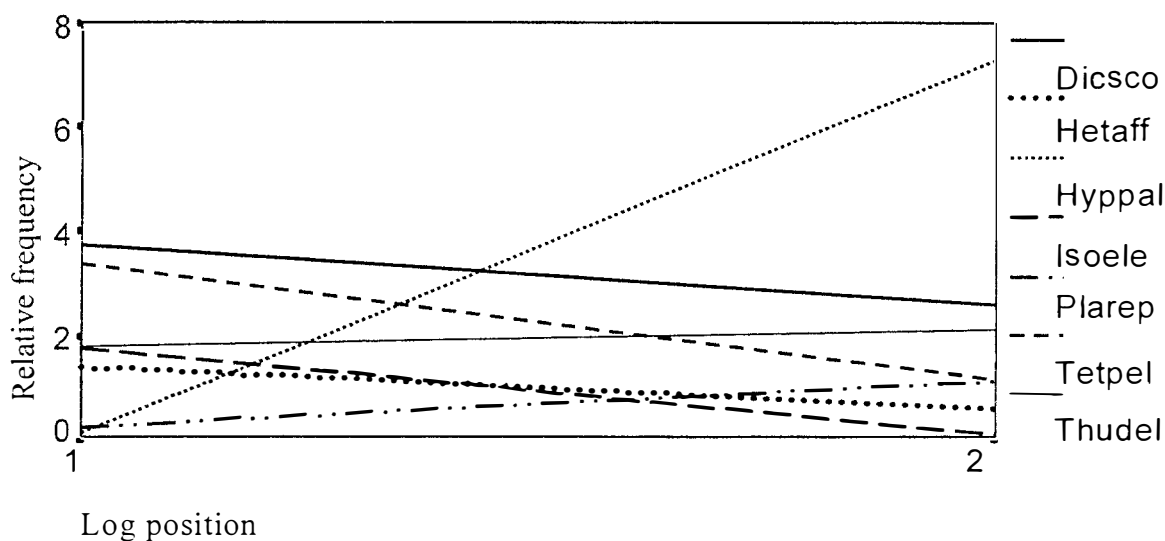


Figure 20 Non-dominant Moss Species Relative Frequency vs. log Position

5.7 Direct Gradient Analysis Discussion

In order to interpret the results of Direct Gradient analysis, it is necessary to look at each species individual response to one environmental variable at a time. In this section, each species response to the following environmental variables: log decay stage, canopy cover, bryophyte cover, and log position are discussed.

5.7.1 Species Relative Frequency vs. Decay

Figures 9-11 summarize how each species responded to the environmental variable of decay class. Decay class seems to greatly influence some species. These species demonstrate large peaks and troughs in their relative frequency vs. decay stage. Other species seem to be affected, but their response is less dramatic. *Nowellia curvifolia* (Figure 9), *Dicranum fuscescens* (Figure 9), *Bazzania trilobata* (Figure 9), *Anastrophyllum michauxii* (Figure 10), *Blepharostoma trichophyllum* (Figure 10),

Cephalozia spp. (Figure 10), *Jamesoniella autumnalis* (Figure 10), *Lepidozia reptans* (Figure 10), *Dicranum scoparium* (Figure 11), *Hypnum pallescens* (Figure 11), and *Tetraxis pellucida* (Figure 11) are the species that seem most influenced by decay.

Hypnum pallescens and *Nowellia curvifolia* had a much greater relative frequency on logs in early stages of decay. The abundance of *Anastrophyllum michauxii*, *Blepharostoma trichophyllum*, *Cephalozia* spp., *Jamesoniella autumnalis* and *Lepidozia reptans* peaked on logs in the middle stages of decay. Lastly, *Dicranum fuscescens*, *Bazzania trilobata*, *Dicranum scoparium*, and *Tetraxis pellucida* flourished on logs in late stages of decay.

5.7.2 Species Relative Frequency vs. Canopy Class

The frequency of many species seems to be directly related to light conditions: *Brotherella recurvans* (Figure 12), *Dicranum fuscescens* (Figure 12), *Hypnum imponens* (Figure 12), *Blepharostoma trichophyllum* (Figure 13), *Cephalozia* spp. (Figure 13), *Jamesoniella autumnalis* (Figure 13), *Lepidozia reptans* (Figure 13), *Heterophyllum affine* (Figure 14), *Isopterygium elegans* (Figure 14), *Platygyrium repens* (Figure 14), and *Thuidium delicatulum* (Figure 14). Of these species, *Dicranum fuscescens*, *Hypnum imponens*, *Heterophyllum affine*, *Jamesoniella autumnalis*, and *Thuidium delicatulum* increased in relative frequency when there was an increase in light availability; *Lepidozia reptans* and *Platygyrium repens* preferred habitat under canopies that moderately shaded the forest floor; and the relative frequency of *Brotherella recurvans*, *Blepharostoma trichophyllum*, *Cephalozia* spp., and *Isopterygium elegans* peaked under dense canopies.

5.7.3 Species Relative Frequency vs. Amount of Bryophyte Cover

Figures 15-17 summarize how species respond to total bryophyte cover on logs.

Three species are found on logs with very low levels of bryophyte cover: *Nowellia curvifolia* (Figure 15), *Lophocolea heterophylla* (Figure 16), and *Isopterygium elegans* (Figure 17). Many small liverworts, such as *Anastrophyllum michauxii* (Figure 16); *Blepharostoma trichophyllum* (Figure 16), *Cephalozia* spp. (Figure 16), *Jamesoniella autumnalis* (Figure 16), and one moss, *Hypnum pallescens* (Figure 17) occurred most often on logs that have 50 to 75 percent of bryophyte cover. *Lepidozia reptans* (Figure 16), *Dicranum scoparium* (Figure 17), *Tetraxis pellucida* (Figure 17), and *Thuidium delicatulum* (Figure 17) had their greatest relative frequency on logs that have 75 to 100 percent bryophyte cover.

5.7.4 Species Relative Frequency vs. Log Position

Figures 18-20 summarize how species respond to log position. The log's position seems to only slightly influence most species. In general, these species slightly favor logs that are in contact with the soil. Three species showed strong preference to log position. All three of these species, *Nowellia curvifolia* (Figure 18), *Hypnum pallescens* (Figure 20), and *Lepidozia reptans* (Figure 19), prefer logs that are not in contact with the ground.

CHAPTER VI

CONCLUSION

This section is divided into three parts. In section 6.1, I discuss the community structure of the epixylic bryophytes sampled in this study. In section 6.2, I compare my results to Norris's, and in the final section, 6.3, I compare my results to results reported in current epixylic literature.

6.1 Community Structure of Bryophytes on Fraser Fir Logs in the Great Smoky Mountain National Park

Communities are naturally occurring groups of organisms that interact in a defined environment by fixing, utilizing, and transferring energy in some way. Most bryophyte communities form a vegetation continuum rather than rigid groups or associations that are separated without intermediates. Within a community, a species never responds as an isolated individual, but as a part of the community. The way species interact within a community involves the individual life strategy and reaction to environmental conditions of each species as well as the broad variables of time and space.

One of the main purposes of this study was to describe the community structure of epixylic bryophytes on fir logs. I applied three different multivariate techniques to the raw data, and these techniques allowed me to interpret how each species responded to measured environmental variables and in relation to the other species found within the community. This provided insight to the life strategies of the species found on fir logs,

the environmental factors that influence them, and the effect of interaction within the community on each. Thus, these results allowed me to draw conclusions about the overall strategy (profile) of each species and to determine if epixylic bryophyte species form well defined “natural communities” in response to environmental gradients, or if they tend to intergrade in a continuous fashion with each species responding in a unique way to changing conditions.

6.1.1 **Species Strategies**

Each species appears to respond as an individual. Species dispersal of spores, strategy of reproduction, response to competition, and width of dispersion along environmental gradients are unique. Thus, each species has an individual niche or “space”. The overall community structure found on a log is the result of the niche stacking of all the species present on the log at that given time.

More than one main condition can dictate the occurrence of a species on a given log. Although it is difficult to separate all the factors of a species’s niche and rank them in order of importance, this study seeks to create a species strategy profile for each species for the niche preferred by each species. Since this study is descriptive and exploratory, I base each species strategy profile on my field observations, TWINSpan, DCA, and DGA results, and extrapolation of trends from the results of the multivariate programs.

Five conditions/strategies seem to have the greatest influence on species occurrence on epixylic logs in the spruce-fir forest: 1) life strategy, 2) ability to colonize optimal substrate, 3) the amount of bryophyte cover on the log, 4) decay class, and 5) canopy conditions. The clearest way to divide the bryophytes is according to overall life

strategies, because bryophytes are usually generalists or specialists. A generalist species has a very wide niche and can be found almost anywhere. A species with a specialist life strategy has a much more narrow niche and is less tolerant of suboptimal conditions.

In this study, only two species displayed a generalist life strategy, *Hypnum imponens* and *Brotherella recurvans*. *Hypnum imponens* and *Brotherella recurvans* were dominant species on rotten fir logs in nearly any type of niche condition. Interestingly, the data first suggested that *Hypnum imponens* and *Brotherella recurvans* had a specialist life strategy. However, this impression was drawn from the observation that both of these species had a definite peak in their performance resulting from their ability to exploit a space in which no other specialist species could flourish. *Hypnum imponens* was extremely tolerant of extreme exposure to light, and it took full advantage of a niche opening on a log in the middle to late stages of decay under a very open canopy. *Brotherella recurvans* was the inverse of *Hypnum imponens*. Its relative frequency increased as the level of light decreased.

Aside from the species with a generalist life strategy, the decay level of the log seems to have the greatest influence on species composition. The decay level of a log can directly or indirectly influence species composition. The majority of the species that are directly influenced by decay stage seem to flourish on their preferred decay level requirement regardless of other conditions. The relative frequencies of *Hypnum pallescens*, *Frullania asagrayana*, *Platygyrium repens*, *Dicranum fuscescens*, and *Bazzania trilobata* are directly tied to decay stage. Of these species, *Hypnum pallescens* and *Frullania asagrayana* are predominately epiphytic on living trees, and logs are a suboptimal substrate for them. Thus, the communities I found were remnants of

communities that had populated live trees. I rarely found these species on logs with a decay stage greater than one. Another of the species, *Platygyrium repens* also prefers early stages of decay. It seems to be able to colonize logs with very tight and smooth bark. *Dicranum fuscescens*, in contrast, is successful during moderate to late stages of decay (decay stage 3-4) in a wide range of light intensity, and *Bazzania trilobata* tends to propagate during late stages of decay. It can tolerate all light conditions, but it seems to be most abundant in closed canopy forests.

The amount of bryophyte cover on of a log is usually related to the decay stage of a log. Logs in early stages of decay usually have a low level of bryophyte cover, but there can be exceptions. In this study, I was fortunate to have examples of logs of every decay stage with varying amounts of bryophyte cover. This indirectly provided insight into the ability of species to compete during different stages of the decay process. In general, a species whose relative frequency depended on low bryophyte cover tended to have a generalist life strategy in all respects other than the amount of bryophyte cover it can occur in. For example, *Tritomaria exsecta* and *Anastrophyllum michauxii* are very small liverworts that peaked in performance during decay stage 2-3. These species were present during decay stage 4, but their relative frequencies were much lower. I found them on logs of all bryophyte cover classes, but only rarely on logs with a cover class above three. The reason that their performance peaks at decay stage 2-3 maybe that they are being pushed out by larger growth forms that are able to compete better for the space during decay stage 4. However, if the spores of a larger growth form are not in proximity, then the species that are already present will sustain during decay stage 4.

Nowellia curvifolia is another liverwort species whose performance during varying levels of bryophyte cover suggests that it is influenced by competition. This species is the dominant species that first colonizes a log. This does not mean that the log must be in decay stage 1 for this species to flourish, but rather that the log must have a very low bryophyte cover. Its relative frequency greatly decreases as the amount of bryophyte cover on a log increases. This suggests that *Nowellia curvifolia* is good at establishment but is a poor competitor.

Lophocolea heterophylla and *Isopterygium elegans* are a liverwort and moss whose presence appears to be limited by amount of bryophyte cover on a log. *Lophocolea heterophylla* occurred on logs that were in early to moderate stages of decay and that had 0-50 percent bryophyte cover. *Isopterygium elegans* occurred on logs in moderate to late stages of decay with less than 50 percent bryophyte cover.

In contrast to the species with a very wide niche and a limiting response to bryophyte cover, many species in this study had very narrow niche parameters. *Blepharostoma trichophyllum*, *Cephalozia* spp., *Lepidozia reptans*, and *Tetraphis pellucida* tolerated only a very narrow range in the decay stage and light intensity gradients. I found all of these species predominately in middle to late stages of decay (decay stage 2-4) and in moderately shaded to closed canopy.

Some species were generalist species with respect to decay stage, but they exploited niche openings created by extremes in the amount of available light. Species of this sort usually peaked in performance at extreme ends of the light gradient because there was less competition from other species. Most species preferred moderate light requirements, and were not sustained at high or low threshold levels. *Heterophyllum*

affine, *Dicranum scoparium*, and *Thuidium delicatulum* were greatly influenced by the availability of light, because these species thrived in light conditions that many of the other bryophytes could not tolerate. I was able to find these species on a log in any decay stage as long as the canopy was very open.

This study provided no insight on the species strategy of *Jamesoniella autumnalis*. I found it in small amounts in all decay stages, types of canopy cover, and succession levels. This suggests that its dispersal method may play an important role in its establishment on a log.

The remaining species in the study, *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus squarrosus*, *Polytrichum pallidisetum*, *Calypogeia suecica*, *Geocalyx graveolens*, *Riccardia palmata*, and *Scapania nemorosa*, are infrequent. I am reserved to speculate on a species strategy when the species occurred in less than 5 percent of the sampled plots. According to literature. *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus squarrosus*, *Polytrichum pallidisetum*, and *Calypogeia suecica* are species that occur on soil, so their rareness may be related to suboptimal substrate conditions.

6.1.2 Log Succession

Succession is the replacement of species and communities by another. A repeated theme in the bryological literature is that epixylic communities demonstrate unidirectional succession (Jovet and Jovet, 1944; Stefureac, 1969; Soderstrom, 1988; Schuster, 1949). This is the idea that a log is an ever changing substrate, and that the species present on the log correspond to the current conditions of a log.

The results of this study suggest that there is an observable pattern of bryophyte succession on logs, and that this succession is usually directly or indirectly related to the decay stage of the log. TWINSpan divided the species into three small units or communities: the *Nowellia curvifolia* community, the *Brotherella recurvans* community, and the *Brotherella recurvans* / *Hypnum imponens* community. These communities were then divided into nine different unions. Each one of the unions has a slightly different species composition and different environmental requirements. By combining community information with the strategy profile of each species, I have created a model for Fraser fir log succession in the Great Smoky Mountain National Park.

Figure 21 is a flow chart that hypothesizes when a particular union of bryophytes will occur on a log. When I suggest more than one union for a log, any of the unions listed can be occurring separately or in combination with one another. While this flow chart is a good model for predicting bryophyte community composition at various stages in a log's decay process, it is still a generalization of the dominant trends that I have observed. Furthermore, it is important to note that there are important factors missing from the flow chart that influence community composition. Some of these factors were investigated in this study, and other suggestions are hypotheses that this study did not address, but should be tested in the future.

The height of the log from the forest floor and the location of the log are examples of factors this study suggested as possible influences on community composition, but figure 21 does not take into consideration. The results of Direct Gradient Analysis suggest that a log's distance from the ground is very important to species composition on the log. A log that is in contact with the forest floor can have any species from this study

SUCCESSION OF LOGS

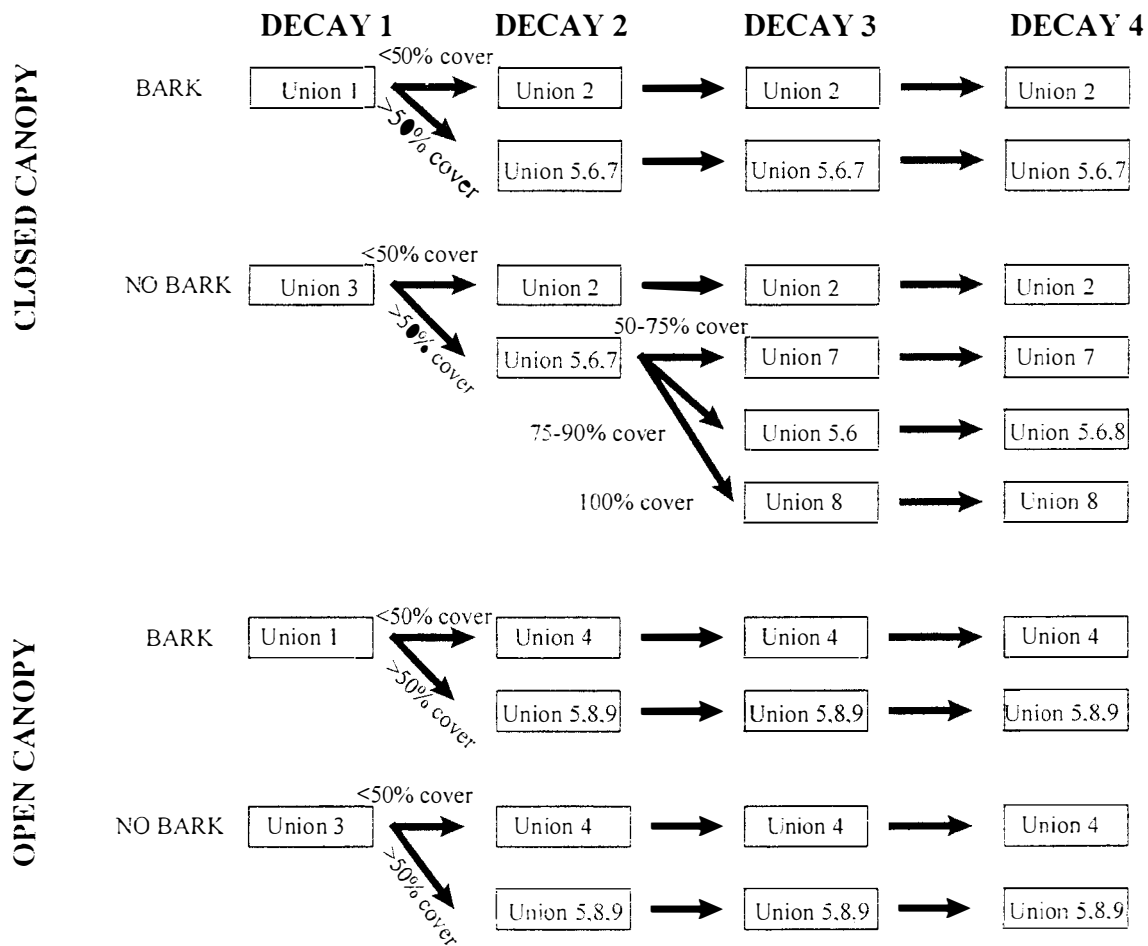


Figure 21

Hypothetical succession patterns of logs in the spruce-fir forests

Union 1: *Nowellia curvifolia*, *Hypnum pallescens*, *Platygyrium repens*; Union 2: *Nowellia curvifolia*, *Cephalozia* sp., *Isopterygium elegans*; Union 3: *Nowellia curvifolia*; Union 4: *Nowellia curvifolia*, *Dicranum fuscescens*, *Anastrophyllum michauxii*, *Tritomaria exsecta*; Union 5: *Brotherella recurvans*, *Dicranum fuscescens*; Union 6: *Brotherella recurvans*, *Dicranum fuscescens*, *Bazzania trilobata*; Union 7: *Brotherella recurvans*, *Dicranum fuscescens*, *Blepharostoma trichophyllum*, *Cephalozia* sp., *Lepidozia reptans*, *Tetraphis pellucida*; Union 8: *Hypnum imponens*, *Brotherella recurvans*, *Dicranum fuscescens*; Union 9: *Hypnum imponens*, *Brotherella recurvans*, *Dicranum fuscescens*, *Thuidium delicatulum*, *Dicranum scoparium*

on it, and it follows the flow chart very well. On the other hand, logs that have no contact with the ground seem to have a high relative frequency of *Platygyrium repens*, *Hypnum pallescens*, *Lepidozia reptans*, and *Nowellia curvifolia*. Because I usually found these species during early stages of decay, their relative frequency on elevated logs can be indirectly tied to the fact that most of the logs that have no contact with the forest floor are in early stages of decay. Once a log comes in contact with the forest floor its rate of decay usually increases.

Direct Gradient Analysis also suggests that the location of a log is important to species composition. This is particularly true for rare species, such as *Geocalyx graveolens*. I found this species in three samples out of five on Mt. LeConte, but in no other samples throughout the study. This suggests that *Geocalyx graveolens* might have only local occurrences such as on Mt. LeConte. This isolation could be historical or a result of decline due to a requirement for a very closed canopy. If the latter, the patterns of Fraser fir mortality and the opening of the canopy will detrimentally influence the species distribution. Likewise, I found *Ptilidium crista-castrensis*, *Hylocomium splendens*, and *Rhytidiadelphous squarrosus* only in samples of pure fir forests.

There are many factors that may influence community composition that this study did not answer. These include the physiological and anatomical structure of the species, the time of year, the elevation of the forest, and the canopy composition. Each species has a different physiological and anatomical structure. For example, some species prefer more moisture than other species. Thus, the amount of moisture the log is acquiring and the weather conditions may influence the abundance of a species at a particular time. Similarly, each species may have different growth rates and reproduction ability during

the different seasons. Some species may go relatively dormant in winter months, while other species may remain semi-active. Finally, the canopy composition and elevation of a log may be important to the community composition. At lower elevations, spruce, fir, and yellow birch dominate the forests. In contrast, the high elevations are composed only of Fraser fir. Thus, in the winter, the light conditions in the partially deciduous, lower elevation forests, are significantly different than the light in pure evergreen forests. Furthermore, the high elevation forests are pure fir forests, and most of these forests are completely devastated from the woolly adelgid, a disturbance that may have numerous, rapid effects on species distribution.

6.2 Comparison of Current Epixylic Communities With Historical Records

In his dissertation, Norris (1964) looked at bryophyte growth form, at bryophyte ecology, and at the species present on various substrates, including soil, trees, decaying wood, and rocks, within the spruce-fir forests of the Great Smoky Mountains National Park. Based on his sampling, he placed all the species present into bryophyte unions. In this section, I compare the results of Norris's dissertation to the overall community trends that I found.

Norris found that the primary factor influencing the type of bryophyte community on decaying wood is the degree of decay. He found that as the log decayed the communities changed. He highlighted three important events in the decay of a log: decortication, softening of the outer woody cylinder, and complete humification of the log. His results suggest that the tree species does not influence species distribution after the decortication process, but he found that the position of the log on a slope and whether

the log was in contact with the soil were important factors in determining species composition.

Beyond highlighting the important events of decay of a log, Norris grouped species that occurred together on logs into ten unions. Seven of these unions occurred on the tops of logs: *Frullania asagrayana*, *Nowellia curvifolia*, *Brotherella recurvans*, *Hylocomium splendens*, *Sphenolobus* sp., *Polytrichum ohioense*, and *Sphagnum* sp. Within each of these unions, he always listed the most abundant species first and less important species last, and I have repeated his convention.

The *Frullania asagrayana* union occurred on logs prior to decortication. The composition of this union was influenced by the tree species. Once the log shed its bark, some species of this union would reestablish for a short period, while others disappeared from the community. Norris includes the following species in the *Frullania asagrayana* union: *Frullania asagrayana*, *Paraleucobryum longifolium*, *Brotherella recurvans*, *Herberta hutchinsiae*, *Sphenolobus exsectus*, *Hypnum reptile*, *Bazzania trilobata*, *Dicranum fuscescens*, *Ulota crispa*, *Zygodon viridissimus*, *Plagiochila tridenticulata*, *Microlejeunea ulicina*, and *Anomylia cuneifolia*.

Norris found the *Nowellia curvifolia* union on decorticated logs in the early stages of decay. *Nowellia curvifolia* was the only dominant species of this community, but the following species were present in small amounts (relative cover <10%): *Brotherella recurvans*, *Dicranum fuscescens*, *Riccardia palmata*, *Bazzania trilobata*, *Cephalozia* sp., *Hypnum imponens*, *Sphenolobus exsectus*, *Sphenolobus michauxii*, *Lepidozia reptans*, *Jamesoniella autumnalis*, *Dicranodontium denudatum*, *Thuidium delicatulum*, and *Dicranum scoparium*.

In Norris's study, the *Sphenolobus* union occurred on logs in decay stage one or two. This union took the place of the *Nowellia curvifolia* union on logs with excessive amounts of moisture. It included the following species: *Sphenolobus michauxii*, *Brotherella recurvans*, *Lepidozia reptans*, *Dicranodontium denudatum*, *Sphenolobus exsectus*, *Bazzania trilobata*, *Dicranum fuscescens*, *Jamesoniella autumnalis*, *Hypnum imponens*, *Heterophyllum affine*, *Cephalozia* sp., *Riccardia palmata*, *Dicranum scoparium*, *Hylocomium splendens*, *Mnium punctatum*, *Geocalyx graveolens*, *Blepharostoma trichophyllum*, *Lophozia incisa*, and *Ptilium crista-castrensis*.

Norris found the *Brotherella recurvans* union on 79 percent of all logs in decay stage three. He included the following species in this union: *Brotherella recurvans*, *Dicranum fuscescens*, *Lepidozia reptans*, *Hylocomium splendens*, *Hypnum imponens*, *Bazzania trilobata*, *Dicranum scoparium*, *Thuidium delicatulum*, *Hylocomium brevirostre*, *Heterophyllum affine*, *Jamesoniella autumnalis*, *Blepharostoma trichophyllum*, *Ptilium crista-castrensis*, *Sphenolobus michauxii*, *Polytrichum ohioense*, *Sphenolobus exsectus*, *Plagiothecium laetum*, *Cephalozia* sp., *Dicranodontium denudatum*, *Calliergonella schreberi*, *Sphagnum* sp., *Geocalyx graveolens*, and *Mnium punctatum*. Among Norris's various examples of this union, he discovered that different species dominated. In general, *Brotherella recurvans* and *Dicranum fuscescens* were most abundant. *Dicranum scoparium* and *Dicranodontium denudatum* flourished on very moist logs, while *Hypnum imponens* and *Thuidium delicatulum* dominated logs in high light conditions.

Norris also designated a *Hylocomium splendens* union that developed on logs in the very late stages of decay. This union included the following species: *Hylocomium*

splendens, *Brotherella recurvans*, *Hylocomium brevirostre*, *Rhytidiadelphus triquetrus*, *Dicranum fuscescens*, *Polytrichum ohioense*, *Ptilium crista-castrensis*, *Thuidium delicatulum*, *Bazzania trilobata*, *Calliergonella schreberi*, *Hylocomium umbratum*, *Dicranum scoparium*, and *Lepidozia reptans*.

On logs that were so advanced in their decay that their surface was a layer of mineral rich soil, Norris noted the *Polytrichum ohioense* union. (Current taxonomy accords *Polytrichum pallidisetum* as the upper elevation replacement for *Polytrichum ohioense*.) The species found in his study was most likely *Polytrichum pallidisetum*.) It included *Polytrichum ohioense*, *Bazzania trilobata*, *Hylocomium splendens*, *Ptilium crista-castrensis*, *Brotherella recurvans*, *Lepidozia reptans*, *Dicranum fuscescens*, *Hylocomium brevirostre*, *Calliergonella schreberi*, *Dicranum scoparium*, *Hypnum fertile*, *Pohlia nutans*, and *Dicranella heteromalla*.

Norris suggested that a *Sphagnum* union flourished on any substrate that accumulated water, including logs. He found the following species in this union: *Sphagnum quinquefarium*, *Bazzania trilobata*, *Polytrichum ohioense*, *Scapania nemorosa*, *Lepidozia reptans*, *Mnium punctatum* var. *elatum*, *Brotherella recurvans*, *Sphagnum girgensohnii*, *Atrichum crispum*, *Cephalozia* sp., *Dicranum scoparium*, *Sphenolobus michauxii*, *Thuidium delicatulum*, *Ptilium crista-castrensis*, *Hylocomium splendens*, and *Blepharostoma trichophyllum*.

In section 5.3.1, I discussed in detail the unions I found in my study. Some of the unions Norris described are present in my study and some are not. I found the *Frullania asagrayana*, *Nowellia curvifolia*, and *Brotherella recurvans* unions, but not the *Sphenolobus*, *Sphagnum*, *Hylocomium splendens*, and *Polytrichum ohioense* unions.

Portions of the *Frullania asagrayana* union can be found in my study.

Furthermore, Norris found the *Frullania asagrayana* union on live trees. If the species he found on live trees were taken out of his union, and he used it to specifically describe a union on logs, it would be similar to union 1 from my study. Species included in Norris's union that usually grow on live trees include *Paraleucobryum longifolium*, *Herberta hutchinsiae*, *Ulota crispa*, *Zygodon viridissimus*, *Plagiochila tridenticulata*, *Microlejeunea ulicina*, and *Anomylia cuneifolia*.

Norris's *Nowellia curvifolia* union is similar to unions 2 and 3 from my TWINSpan results, with the exclusion of *Dicranodontium denudatum* and *Sphenolobus exsectus*. I never found either of them.

Norris's *Brotherella recurvans* union is also present in my study. My results break his *Brotherella recurvans* union into five separate unions, unions 5,6,7,8, and 9. Each one of these unions differ slightly in species composition and the decay stage in which it occurs. In his union, he listed the following species that are not present in the similar unions of my study: *Hylocomium splendens*, *Hylocomium brevirostre*, *Ptilium crista-castrensis*, *Polytrichum ohioense*, *Sphenolobus exsectus*, *Plagiothecium laetum*, *Dicranodontium denudatum*, *Sphagnum* sp., and *Mnium punctatum*.

Norris found the *Hylocomium splendens* union during late stages of decay. This union was not found in my study; and possibly has been eliminated from the fir forest. During my study, I did find a few of these species (*Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Ptilium crista-castrensis*, and *Calliergonella schreberi*), but they were extremely rare, and never in the same plot.

Many of the species that Norris groups with this union (*Hylocomium splendens*, *Hylocomium brevirostre*, *Rhytidiadelphus triquetrus*, *Ptilium crista-castrensis*, *Calliergonella schreberi*, *Hylocomium umbratum*) grow on humus in a very moist, boreal forest floor. Although I did not sample the forest floor, I saw very few sites where these species were present in the abundance that is suggested in literature. This suggests that the forest floor and logs are much drier as a result of the canopy being opened by Fraser fir mortality. Even the canopies that I considered closed were second generation fir forests, regrown after a woolly adelgid infestation. Likewise, I did not find the *Sphenolobus* and *Sphagnum* unions that Norris described. No logs in my study were as wet as Norris described when he observed these community types. This further suggests that the spruce-fir forest is much drier as a result of forest fragmentation and of the death of fir trees.

I found the *Polytrichum ohioense* (*Polytrichum pallidisetum*) union only once in my study. Norris found this union on logs that had accumulated large amounts of soil, and its species composition was similar to the *Hylocomium splendens* union. Therefore, I conclude that it was not often present in my study because the soil species that would colonize a log under these conditions were not present.

The following is a list of species that have apparently waned or disappeared from the epixylic substrates found in the spruce-fir forests of the GSMNP: *Paraleucobryum longifolium*, *Herberta hutchinsiae*, *Sphenolobus exsectus*, *Ulotia crispa*, *Zygodon viridissimus*, *Plagiochila tridenticulata*, *Microlejeunea ulicina*, *Anomylia cuneifolia*, *Dicranodontium denudatum*, *Mnium punctatum*, *Lophozia incisa*, *Hylocomium brevirostre*, *Plagiothecium laetum*, *Sphagnum* sp., *Hylocomium umbratum*, *Sphagnum*

quinquefarium, *Mnium punctatum* var. *elatum*, *Sphagnum girgensohnii*, and *Atrichum crispum*. The apparent disappearance of many of these species is alarming. Prior to the destruction of the spruce-fir forest, species such as *Sphenolobus exsectus*, *Dicranodontium denudatum*, *Mnium punctatum*, *Lophozia incisa*, *Hylocomium brevirostre*, *Sphagnum* sp., *Hylocomium umbratum*, and *Mnium punctatum* var. *elatum* were common on logs.

By comparing Norris's unions and mine, we can examine how the spruce-fir bryophyte ecosystem has changed as a result of Fraser fir death. There are three main union types that appear to have been lost since Norris's study: unions found on extremely wet logs, unions of corticolous species found on recently fallen live fir trees, and unions of soil species found on completely humified logs. It appears that the forest floor is drier than in the past. Species that require the very moist, shaded conditions that existed before the forest declined are no longer present or have been astonishingly reduced in abundance. Corticolous species that used to be present on logs in very early stages of decay are now absent. This is because live trees no longer fall to the ground with their bark still intact. Instead, death resulting from the adelgid infestation causes fir trees to lose their bark and stand erect as skeletons for some years before falling to the ground. Lastly, soil species that used to be abundant in thick carpets have dramatically declined to sparse, scattered mats, and are no longer able to engulf logs in the late stages of decay. Thus, there is no longer a fluid succession of species from live trees to logs to soil in the pure fir forest.

Beyond these direct conclusions, I also see a change in species abundance between the two studies. Norris never mentions *Hypnum imponens* as a dominant species.

In my study however, *Hypnum imponens* is abundant enough that it can be the dominant species, and defines a union. Interestingly, *Hypnum imponens* is a species that can tolerate great levels of light. While there is epixylic substrate in closed canopies, there seems to be an increase of substrate in open canopies.

New unions of species, such as unions 8 and 9 from my study, are beginning to take advantage of substrate present in the increased light. Thus, union types are beginning to shift from species that are found in wet and dark conditions to species that can tolerate more light and drier conditions. Hence, we are seeing sensitive liverworts decline, while weedy mosses that can tolerate these conditions flourish.

6.3 The Results of This Study Compared to Current Literature

Some authors have attempted to describe how and why bryophyte communities on logs change. Since epixylic bryological research is such a small field, it is easy to summarize most of the main hypotheses on the distribution patterns for epixylic bryophytes and compare them to my own study.

An important concept that is very common throughout epixylic literature is that although the community compositions found on logs in varying areas are different, bryophyte communities assume a mostly unidirectional succession (Jovet and Jovet, 1944; Stefureac, 1969; Soderstrom, 1988; Schuster, 1949). All of these authors discuss succession based on the fact that decay causes several changes to the composition of a log. They put species into different successional groups that correspond to the decay stages of the log. For instance, Soderstrom (1988) tried to divide the epixylic species in his study into four groups: facultative epiphytes, early epixylics, late epixylics, and

ground species. He found however, that many of the species from his study were present over a larger part of the decay period and that only species in the facultative epiphyte and the ground species stages could be placed in a definite group. To explain this, he suggested that many of the species overlap decay stage because an entire log does not decay at the same rate. He points out that the hardness of a log is different on different parts of the log and argues that species distribute themselves relative to the hardness of the log at a particular area. He concludes that wood texture is the most important variable for distribution.

I agree that succession on epixylic logs tends to be unidirectional, and I agree that the decay stage of a log most greatly influences species distribution. Nonetheless, I think it is important to stress the indirect ways that decay influences distribution, rather than just describing species that occur during a decay class. This is important because some species do not respond to the actual texture or decay level of the log, but rather to certain other circumstances that usually occur on a log at a particular level of decay. For example, *Nowellia curvifolia* can be found during all levels of decay, but it is most abundant on logs in early stages of decay. This is because during early stages of decay there is generally a low level of bryophyte cover on a log. Thus, if one were basing bryophyte distribution preferences on logs only on decay stage, one might overlook the fact that *Nowellia curvifolia* is only indirectly responding to the decay stage and is directly responding to the level of competition. The assumption that all species respond directly to decay stage can lead to a biased analysis and simplistic results. Rather than describing species roles throughout succession by breaking the process into groups that correspond with decay stages, I suggest creating flow charts such as Figure 21 to describe

possible modes of succession relative to an array of circumstances that may affect any log, or portions of logs.

Germano and Porto (1997) introduced a new idea to epixylic literature. They looked at overall colonization cover on a log in addition to the decay stage of a log. They found that the most frequent species on a log had no specificity with regard to decay stage, but that some less frequent species did have such direct relations to decay. They also discovered that species richness is not directly related to the intensity of colonization; sometimes logs with a small number of species are completely covered.

Based on my results, I think that the extent to which a log is colonized is a very important influence on species distribution. I had similar results with respect to species richness. Logs that had lower levels of bryophyte cover seemed to be more species rich. This may be due to the fact that small liverworts cannot compete on heavily colonized logs.

Soderstrom (1989) suggested that dispersal is a major limiting factor for distribution among epixylic bryophytes. By observing the strategy, distribution, and frequency of occurrence of each species, he broke the species into four groups: core species, urban species, rural species, and satellite species. According to Soderstrom, core species are abundant at the majority of all available localities, and they usually produce spores and gemmae that are easily established. Urban species are abundant at a few localities, and they are thought to have a limited dispersal ability between sites. Rural species occur in small populations at the majority of available localities, and they tend to demonstrate poor dispersal ability between localities. Lastly, satellite species are very

rare and occur in very small populations. These species seem to demonstrate poor dispersal and poor establishment even within a locality.

Even without performing a formal analysis of the factor, the data from my study does seem to suggest that species can be grouped according to dispersal strategies. For instance, species that are incapable of competing on heavily colonized logs seem to colonize logs in the early stages of decay and logs that are not in contact with the forest floor. It would be very interesting to formally examine the epixylic bryophytes from my study to see if examples could be found of all four groups that Soderstrom describes. Furthermore, I think that including the dispersal strategy of a species would enhance both my flow chart and species union concept.

Soderstrom based his hypothesis that dispersal is a limiting factor for species distribution on the premise that competition is very slight and plays an insignificant role in distribution (Soderstrom 1987b). Slack (1982, 1990) also agreed with this. Soderstrom and Slack suggested that because logs are temporary substrates, bryophytes never fully saturate them, and thus competitive exclusion for space is minimized. While I have never looked singly at dispersal patterns of epixylic logs, or specifically at competition, I think it is incorrect to say that competition does not occur on logs since it seemed to influence many species in my study. Rather, I suggest that competition and species dispersal strategies are both very important to species distribution. An example of competition and dispersal ability influencing a distribution pattern of a species can be found by looking at *Nowellia curvifolia*'s strategy profile. This species can occur during any stage of decay and on logs that are not in contact with the ground. Furthermore, it has a high relative frequency of occurrence when the bryophyte cover of a log is very low. Therefore, this

species seems to be good at colonizing substrates that are difficult to get to. Thus, this species is very good at distribution, but once other species have colonized the log, it cannot compete.

The exploratory nature of my study provided new insight into the current concepts of species distribution on logs. It allowed multivariate techniques to group the species based only on species data, and it used environmental conditions as a secondary description of why the species were present.

CHAPTER VII

SUMMARY

The purpose of this study was to describe the community structure of bryophytes on Fraser fir logs in the Great Smoky Mountains and to determine if there has been a change in community composition since the forests have become infested with the balsam woolly adelgid. The analysis used three multivariate techniques to determine community structure: TWINSpan, DCA, and DGA.

The results of this study suggest that each species responds uniquely to environmental factors and other species, and that each species follows a characteristic life strategy. Another important conclusion is that while a log seems to change community composition in a unidirectional pattern, there are at least five main factors that seem to influence the presence of a species on a log: species life strategy, species ability to colonize optimal substrate, the amount of bryophyte cover on the log, the decay class of a log, and the canopy conditions.

The results of my study delineated nine different unions. Some of these unions have similar community composition to those found in Norris's study (1964), but many of his union types and 19 of the species found in his study were not present in mine. Seven of the species that were very abundant in his study were rarely encountered in my study. Many of the species missing or currently rare used to be very common on logs prior to the forest decline.

There are three main union types that appear to have been lost since Norris's study: unions found on extremely wet logs, unions of corticolous species found on

recently fallen live fir trees, and unions of soil species found on completely humified logs. Furthermore, there seems to be a shift from the species rich communities found on dark and moist logs to the less species rich communities found on drier logs exposed to a greater light intensity. While the moisture level on the forest floor was not measured in my study, these results suggest that the spruce-fir forests in the GSMNP are drier than they were before the woolly adelgid infested the forest and caused fir mortality.

In conclusion, this study contributes many ideas to existing literature on epixylic bryophytes, it provides many suggestions that could enrich our understanding of epixylic community structure, and it suggests many hypotheses that need to be tested in a quantitative sense. This study also provides insight into the changes in epixylic bryophyte communities that are occurring in response to Fraser fir decline. Many of these changes are more drastic and have occurred sooner than previously predicted (Smith, personal discourse).

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APPENDICES

APPENDIX A

Qualitative Environmental Tables

Table 1 Canopy

<u>Canopy Type</u>	
1. (O) Open	– Canopy heavily decimated; Sun constantly directed upon the site. Less than 50% of the canopy intact.
2. (MS) Moderately shaded	– Canopy somewhat intact; Log exposed to some sun and part shade. Aprox. 50 - 75% of the canopy still intact
3. (C) Closed	– Complete canopy; Log very shaded. Greater than 75% of the canopy intact

Table 2 Position

<u>Log Position</u>	
L	Log perpendicular to the slope
ll	Log parallel to the slope
C	Log in contact with the soil
NC	Log elevated from the soil

Table 3 Decay

<u>Decay History</u>	
<u>Decay Stage</u>	<u>Characteristics</u>
1	Wood hard and very smooth; probe 1-2 cm
2	Wood hard , but the log surface is beginning to roughen; probe 2-3 cm
3	Wood starting to soften, and log texture is very rough; probe 3-4 cm
4	Wood very soft. log is losing cylindrical shape, and is very rough: probe > 4 cm

Table 4 Cover Class

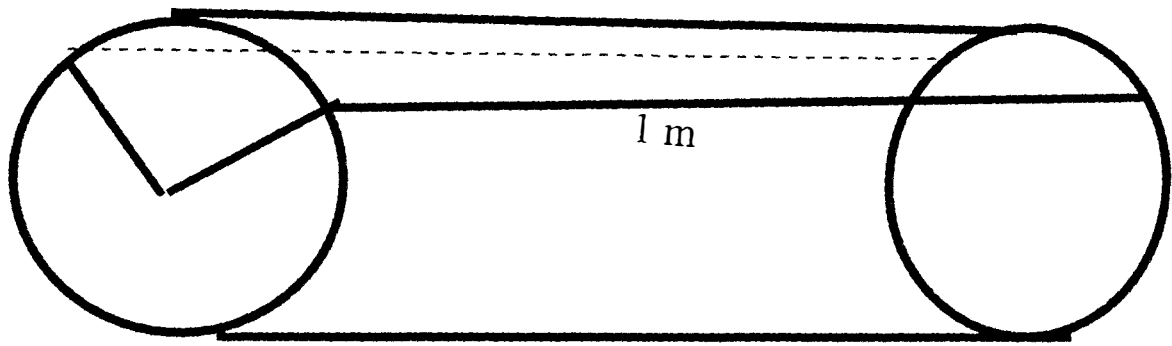
<u>Cover Class</u>	
<u>Class</u>	<u>Cover</u>
1	< 25% of the plot
2	25 – 50% of the plot
3	50 – 75% of the plot
4	75 – 100% of the plot

APPENDIX B

Plot Diagram

SAMPLE PLOT

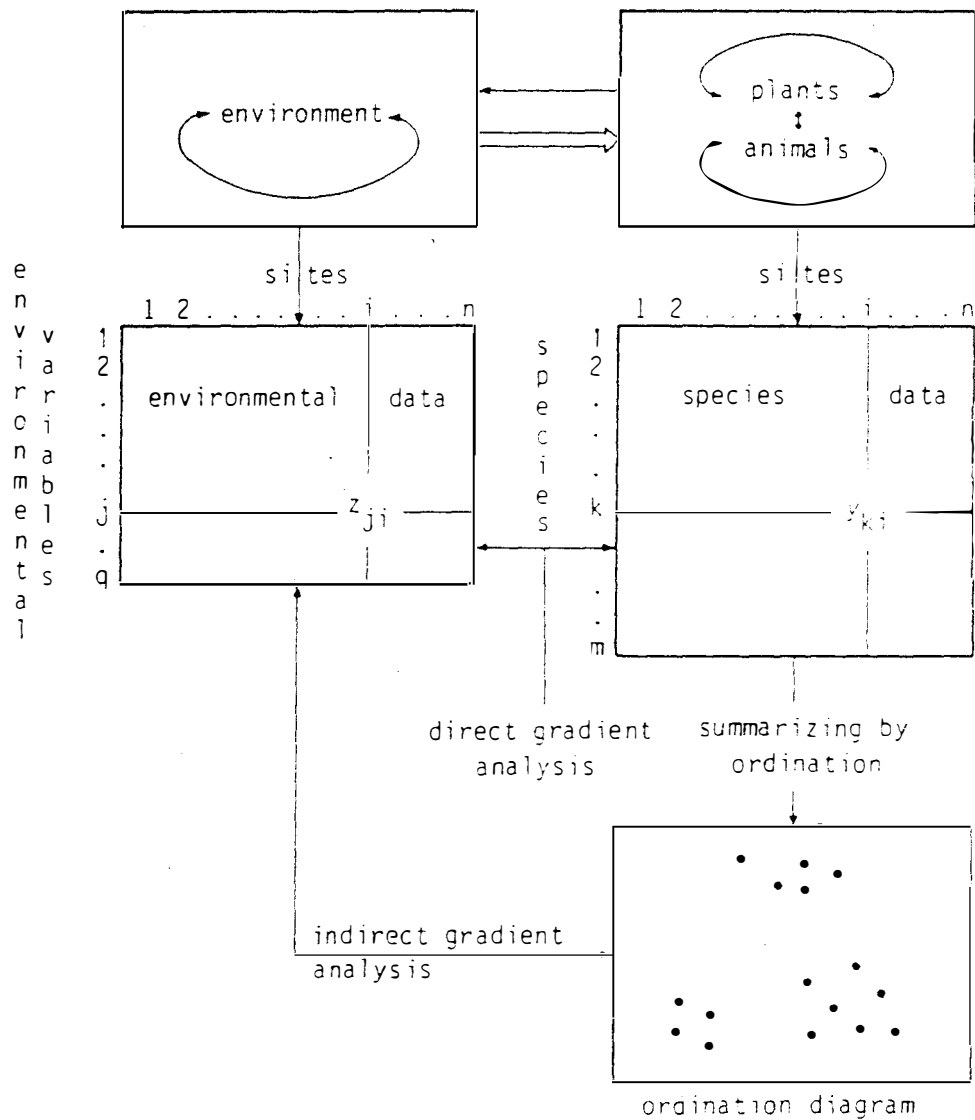
60 degree arc



APPENDIX C

Summary of Ordination

ROLE OF ORDINATION IN COMMUNITY ECOLOGY



*Summary of Ordination from Jongman et. al 1995.

APPENDIX D

Species Relative Frequency-by-Plots Matrix

	Anamic	Baztri	Blepht	Calysu	Ceph	Fruasa	Geogra
p1	0	0	0	0	0	0	0
p2	0	0	0.019685	0	0	0	0
p3	0	0	0	0	0	0	0
p4	0.002079	0.014553	0	0	0.010395	2.08E-05	0
p5	0.009091	0	0.015152	0	0.015152	4.59E-05	0
p6	0.006	0.522	0	0	0.008	0.000016	0
p7	0	0.017341	0.028902	0	0.052023	0.000301	0
p8	0	0	0	0	0	0	0
p9	0	0	0	0	0	0	0
p10	0	0	0	0	0	0	0
p11	0	0	0	0	0.011019	3E-05	0
p12	0	0.1860465	0	0	0	0	0
p13	0	0.6396867	0	0	0	0	0
p14	0	0	0	0	0.041783	0.000109	0
p15	0	0.0203562	0	0	0	0	0
p16	0	0.0008264	0	0	0.005785	4.76E-06	0
p17	0	0.010274	0	0	0	0	0
p18	0	0	0	0	0	0	0
p19	0	0	0	0	0	0	0
p20	0	0	0	0	0	0	0
p21	0	0	0.007732	0	0.007732	1.86E-05	0
p22	0	0.0248227	0	0	0.010638	2.9E-05	0
p23	0	0	0	0	0	0	0
p24	0	0	0	0	0	0	0
p25	0	0	0	0	0	0	0
p26	0	0	0	0	0	0	0
p27	0	0.9140625	0	0	0	0	0
p28	0	0	0.043478	0	0.130435	0.000526	0
p29	0	0	0	0	0.005263	2.77E-05	0
p30	0	0	0.041096	0	0.003425	1.15E-05	0
p31	0	0	0	0	0	0	0
p32	0.042553	0	0	0	0	0	0
p33	0	0	0	0	0	0	0
p34	0	0	0	0	0	0	0
p35	0	0	0	0	0	0	0
p36	0	0	0	0	0	0	0
p37	0	0	0	0	0	0	0
p38	0	0	0	0	0	0	0
p39	0	0	0	0	0	0	0
p40	0	0.0540541	0	0.004914	0.009828	2.25E-05	0
p41	0.011538	0	0	0	0.057692	0.000222	0
p42	0	0.7677903	0.003745	0	0.108614	0.000388	0
p43	0	0	0	0	0.012397	3.56E-05	0
p44	0	0	0.225664	0	0.265487	0.000763	0
p45	0	0.032967	0	0	0.164835	0.000868	0
p46	0	0	0	0	0.167742	0.000964	0
p47	0	0	0	0	0	0	0
p48	0	0	0	0	0	0	0
p49	0	0	0	0	0	0	0

	Jameau	Lepire	Lophhe	Lophoz	Nowcur	Ricpal	Scanem
p1	0	0	0	0	0	0	0
p2	0	0	0	0	0.417323	0	0
p3	0	0	0	0	0.096591	0	0
p4	0.29106	0	0	0	0	0	0
p5	0.075758	0	0	0	0.009091	0	0
p6	0.01	0	0	0	0	0	0
p7	0.00578	0.011561	0.011561	0	0.057803	0	0
p8	0	0	0	0	0	0	0
p9	0	0	0	0	0	0	0
p10	0	0	0.008523	0	0.965909	0	0
p11	0	0	0	0	0	0	0
p12	0.015504	0	0	0	0	0	0
p13	0	0	0	0	0.002611	0	0
p14	0.05571	0	0	0	0.022284	0	0
p15	0	0	0	0	0	0	0
p16	0.002479	0.002479	0.009091	0	0.856198	0	0
p17	0.010274	0	0	0	0	0	0
p18	0	0	0	0	0	0	0
p19	0.003279	0	0	0	0.996721	0	0
p20	0.013812	0	0	0	0.690608	0	0
p21	0.113402	0	0.010309	0	0.046392	0	0
p22	0.01773	0	0	0	0.404255	0	0
p23	0	0	0	0	0	0	0
p24	0	0	0	0	0.303249	0	0
p25	0	0	0	0	0.4	0	0
p26	0.063927	0	0	0	0.059361	0	0
p27	0	0	0	0	0	0	0
p28	0	0	0	0	0.492754	0.043478	0
p29	0.010526	0	0	0	0.226316	0	0
p30	0.017123	0.003425	0	0	0.123288	0	0
p31	0	0	0	0	0.007813	0	0
p32	0	0	0	0	0.29078	0	0
p33	0	0	0	0	0.009009	0	0
p34	0	0	0	0	0	0	0
p35	0	0	0	0	0.75	0	0
p36	0	0	0	0	0	0	0
p37	0.018307	0	0	0	0	0	0
p38	0	0	0	0	0	0	0
p39	0.02551	0	0	0	0	0	0
p40	0.02457	0.420147	0.007371	0	0	0	0
p41	0	0	0	0	0.926923	0	0
p42	0	0.011236	0	0	0.007491	0	0
p43	0	0.016529	0	0	0.946281	0	0
p44	0.004425	0.150442	0	0	0.336283	0	0
p45	0	0.208791	0	0	0.32967	0	0
p46	0	0	0	0	0.832258	0	0
p47	0	0	0	0	0	0	0
p48	0	0	0	0	0.598765	0	0
p49	0	0	0	0	0	0	0

	Brorec	Dicfus	Dicsco	Hetnem	Hylspl	Hypimp	Hyppal
p1	0	0.192308	0	0	0	0.70979	0
p2	0	0.043307	0	0	0	0.653543	0
p3	0.221591	0.0625	0	0	0	0	0
p4	0.484407	0.043659	0	0.064449	0.006237	0.280665	0
p5	0.012121	0.048485	0	0.009091	0	0.948485	0
p6	0.762	0.174	0	0	0	0	0
p7	0.971098	0.00578	0	0	0	0	0
p8	0.246212	0.246212	0	0	0	0.589015	0
p9	0.936118	0.238329	0	0.022113	0	0	0
p10	0	0	0	0	0	0	0
p11	0	0	0.294766	0	0	0.870523	0
p12	0.325581	0	0.426357	0.015504	0	0.131783	0
p13	0	0.201044	0	0.130548	0	0.255875	0
p14	0.066852	0.412256	0	0.169916	0	0.462396	0
p15	0.770992	0.381679	0	0	0	0.020356	0
p16	0	0.057851	0	0	0	0.028926	0
p17	0.386986	0	0.078767	0.044521	0	0.462329	0
p18	0.896266	0	0.033195	0.024896	0	0.024896	0
p19	0	0	0	0	0	0	0
p20	0	0.016575	0	0	0	0.287293	0
p21	0.703608	0	0.048969	0.025773	0	0.025773	0
p22	0	0	0.141844	0.007092	0	0.450355	0
p23	0.018229	0	0	0	0.440104	0	0
p24	0.068592	0.01444	0	0	0	0	0.371841
p25	0	0	0.010811	0	0	0.335135	0.254054
p26	0.054795	0.054795	0	0	0	0	0.844749
p27	0.097656	0	0	0	0	0	0
p28	0	0	0	0	0	0	0
p29	0.852632	0.031579	0	0	0	0.005263	0
p30	0.380137	0	0.366438	0	0	0.171233	0
p31	0	0	0.003906	0.011719	0	0.976563	0
p32	0.080378	0.742317	0	0	0	0.01182	0
p33	0.481982	0.504505	0	0	0	0.04955	0.004505
p34	0	0.044355	0	0.008065	0	0	0.983871
p35	0	0	0	0	0	0.5	0
p36	0.236842	0.1	0	0	0	0.7	0
p37	0.853547	0.043478	0	0	0	0.084668	0
p38	0.378571	0.053571	0	0	0	0.567857	0
p39	0.418367	0.112245	0	0	0	0.086735	0
p40	0.083538	0.063882	0	0.004914	0	0.036855	0
p41	0	0.003846	0	0	0	0	0
p42	0.044944	0.071161	0	0	0	0	0
p43	0	0	0.008264	0	0	0.008264	0
p44	0.013274	0	0	0	0	0	0
p45	0.214286	0.208791	0	0	0	0	0
p46	0	0	0	0	0	0	0
p47	0	0.109661	0	0.044386	0	0.866841	0
p48	0.407407	0	0	0	0	0	0
p49	0.149798	0.117409	0	0	0	0.62753	0

	Isoele	Platre	Plesch	Polypa	Pticri	Rhytri	Tetpel
p1	0	0	0	0	0	0	0
p2	0	0	0	0	0	0	0.043307
p3	0	0	0	0	0	0	0.011364
p4	0	0	0	0	0	0	0
p5	0.012121	0.015152	0	0	0	0	0.00303
p6	0	0	0	0	0	0	0.002
p7	0.017341	0.028902	0	0	0	0	0.017341
p8	0	0	0	0	0	0	0.022727
p9	0	0	0	0.004914	0	0	0
p10	0	0.014205	0	0	0	0	0
p11	0	0	0	0	0	0	0
p12	0	0	0	0	0	0	0.046512
p13	0	0	0	0	0	0	0
p14	0	0	0	0	0	0	0
p15	0	0	0	0	0	0	0
p16	0.004132	0	0	0	0	0	0
p17	0.037671	0	0	0	0	0	0.006849
p18	0	0	0	0	0	0	0
p19	0	0	0	0	0	0	0
p20	0	0	0	0	0	0	0
p21	0.012887	0	0	0	0	0	0.007732
p22	0	0.095745	0	0	0	0	0
p23	0	0	0	0	0	0	0
p24	0	0.306859	0	0	0	0	0
p25	0	0	0	0	0	0	0
p26	0	0	0	0	0	0	0
p27	0	0	0	0	0	0	0
p28	0.318841	0	0	0	0	0	0
p29	0	0	0	0	0	0	0
p30	0	0	0	0	0	0	0
p31	0	0	0	0	0	0	0
p32	0	0	0	0	0	0	0.002364
p33	0	0	0	0	0	0	0
p34	0	0	0	0	0	0	0
p35	0	0	0	0	0	0	0
p36	0	0	0	0	0	0	0.005263
p37	0	0	0	0	0	0	0.002288
p38	0	0	0	0	0	0	0
p39	0	0	0	0.02551	0	0.137755	0.010204
p40	0	0	0	0	0	0	0.090909
p41	0	0	0	0	0	0	0
p42	0	0	0	0	0	0	0.011236
p43	0	0	0	0	0	0	0
p44	0	0	0	0	0	0	0.017699
p45	0	0	0	0	0	0	0
p46	0	0	0	0	0	0	0
p47	0	0.023499	0	0	0	0	0
p48	0	0.030864	0	0	0	0	0
p49	0	0	0	0	0.044534	0	0.004049

	Thudel	Hylbre	Tritex				
p1	0.129371	0	0				
p2	0	0	0				
p3	0.085227	0	0				
p4	0.091476	0	0				
p5	0.012121	0	0				
p6	0	0	0				
p7	0	0	0				
p8	0	0	0				
p9	0	0	0				
p10	0	0	0				
p11	0.008264	0	0				
p12	0.007752	0	0				
p13	0	0	0				
p14	0	0	0				
p15	0.005089	0	0				
p16	0	0	0				
p17	0.010274	0	0				
p18	0.020747	0	0				
p19	0	0	0				
p20	0	0	0				
p21	0.03866	0	0				
p22	0	0	0				
p23	0.5	0	0				
p24	0	0	0				
p25	0	0	0				
p26	0	0	0				
p27	0	0	0				
p28	0	0	0				
p29	0	0	0				
p30	0	0	0				
p31	0.003906	0	0				
p32	0	0	0				
p33	0	0	0				
p34	0.004032	0	0				
p35	0	0	0				
p36	0.015789	0	0				
p37	0	0	0				
p38	0	0	0				
p39	0.163265	0	0				
p40	0	0	0				
p41	0	0	0				
p42	0	0	0				
p43	0	0	0				
p44	0	0	0				
p45	0	0	0				
p46	0	0	0				
p47	0	0	0				
p48	0	0	0				
p49	0.072874	0	0				

	Anamic	Baztri	Blephtr	Calysu	Ceph	Fruasa	Geogra
p50	0	0	0	0	0.06875	0.000397	0
p51	0	0	0	0	0	0	0
p52	0	0	0	0	0	0	0
p53	0.083333	0	0.016667	0	0.038889	0.000185	0
p54	0.112971	0	0	0	0.100418	0.000289	0
p55	0.01	0	0	0	0	0	0
p56	0	0	0	0	0	0	0
p57	0	0	0	0	0	0	0
p58	0	0	0.038922	0	0.038922	0.000112	0
p59	0	0	0.025	0	0	0	0
p60	0.005618	0.005618	0.05618	0	0.179775	0.000856	0
p61	0	0	0.02027	0	0.202703	0.001172	0
p62	0	0	0	0	0	0	0
p63	0	0.0748899	0.057269	0	0	0	0.017621
p64	0	0.0264317	0.017621	0	0	0	0
p65	0	0	0.0025	0	0.005	1.25E-05	0
p66	0.020595	0	0	0	0	0	0
p67	0	0	0	0	0	0	0
p68	0	0.0404624	0.011561	0	0	0	0
p69	0.050691	0	0.013825	0	0.036866	0.000162	0
p70	0	0	0	0	0	0	0
p71	0	0	0	0	0	0	0
p72	0	0	0	0	0	0	0
p73	0	0	0.011561	0	0	0	0
p74	0	0	0.045455	0	0.011364	6.42E-05	0
p75	0	0.0505415	0.021661	0	0	0	0
p76	0.105882	0.0647059	0	0.011765	0.4	0.002222	0.041176
p77	0	0	0.014085	0	0.035211	0.000207	0
p78	0.006667	0	0	0	0.006667	2.22E-05	0
p79	0	0.3184358	0	0	0.002793	7.61E-06	0

	Jameau	Lepire	Lophhe	Lophoz	Nowcur	Ricpal	Scanem
p50	0.0125	0.025	0	0	0.575	0	0
p51	0	0	0	0	0	0	0
p52	0.083551	0	0	0	0	0	0
p53	0.011111	0.016667	0	0	0.838889	0	0
p54	0	0	0	0.008368	0	0	0
p55	0	0	0	0	0.18509	0	0
p56	0	0	0	0	0	0	0
p57	0	0	0	0	0	0	0
p58	0.017964	0.011976	0	0	0	0	0
p59	0.0125	0	0	0	0.68125	0	0
p60	0.08427	0.02809	0	0	0.241573	0	0
p61	0	0.033784	0	0	0.013514	0	0
p62	0	0	0	0	0	0	0
p63	0.008811	0.096916	0	0	0	0	0
p64	0.013216	0.171806	0	0	0	0	0
p65	0.1175	0.015	0.005	0	0	0	0
p66	0.098398	0	0	0	0.361556	0.004577	0
p67	0.010526	0	0	0	0	0	0
p68	0.115607	0	0	0	0	0	0
p69	0.050691	0.082949	0	0	0.493088	0	0
p70	0.022026	0	0	0	0	0	0
p71	0.080952	0.004762	0	0	0	0	0.004762
p72	0	0	0	0	0	0	0
p73	0.017341	0	0	0	0	0	0
p74	0.051136	0	0	0	0	0	0
p75	0	0.068592	0	0	0.01083	0	0
p76	0	0.011765	0	0	0.164706	0	0
p77	0.042254	0	0	0	0	0	0
p78	0	0	0	0.006667	0	0	0
p79	0	0	0	0	0	0	0

	Brorec	Dicfus	Dicsco	Hetnem	Hylspl	Hypimp	Hyppal
p50	0.025	0	0	0	0	0.3875	0
p51	0.014368	0	0.12931	0	0	0.841954	0
p52	0.469974	0	0	0	0	0.336815	0
p53	0.05	0.05	0	0	0	0	0
p54	0	0.786611	0	0	0	0	0
p55	0.089974	0.652956	0	0	0	0	0
p56	0	0.936975	0	0	0	0.021008	0
p57	0	0	0	0	0	0	0
p58	0.748503	0.086826	0	0	0	0	0
p59	0.2875	0	0	0	0	0	0
p60	0.483146	0.129213	0	0	0	0	0
p61	0.425676	0.587838	0	0	0	0	0
p62	0.964856	0.015974	0	0	0	0.019169	0
p63	0.898678	0.202643	0	0	0	0	0
p64	0.823789	0.039648	0	0	0	0.008811	0
p65	0.2825	0.145	0	0	0	0.55	0
p66	0	0.009153	0	0	0	0.011442	0.787185
p67	0	0	0.057895	0.026316	0	0.868421	0
p68	0.554913	0.202312	0	0	0	0.121387	0
p69	0.156682	0.105991	0	0	0	0.02765	0.041475
p70	0.568282	0.035242	0	0.088106	0	0.220264	0
p71	0.085714	0	0.228571	0	0	0.666667	0
p72	0.3	0	0.133333	0	0	0.457143	0
p73	0.317919	0	0.260116	0	0	0.33526	0
p74	0.198864	0	0	0	0	0.539773	0
p75	0.617329	0.458484	0	0	0.025271	0.036101	0
p76	0.458824	0.029412	0	0	0	0	0
p77	0.183099	0.112676	0	0	0	0	0
p78	0.166667	0.046667	0	0	0.013333	0	0
p79	0.27933	0.360335	0.145251	0	0	0	0

	Isoele	Platre	Plesch	Polypa	Pticri	Rhytri	Tetpel
p50	0	0	0	0	0	0	0
p51	0	0	0	0	0	0	0
p52	0	0	0	0	0	0	0
p53	0	0	0	0	0	0	0.016667
p54	0	0	0	0	0	0	0
p55	0	0	0	0	0	0	0.113111
p56	0	0	0	0	0	0	0
p57	0	0	0	1	0	0	0
p58	0	0.04491	0	0	0	0	0.098802
p59	0	0	0	0	0	0	0
p60	0	0	0	0	0	0	0.067416
p61	0	0	0	0	0	0	0.094595
p62	0	0	0	0	0	0	0
p63	0	0	0	0	0	0	0
p64	0	0	0	0	0	0	0.07489
p65	0	0	0	0	0	0	0.0225
p66	0	0.002288	0	0	0	0	0
p67	0	0	0	0	0	0	0
p68	0	0	0	0	0	0	0
p69	0	0	0	0	0	0	0.073733
p70	0	0	0	0	0	0	0.022026
p71	0	0	0	0	0	0	0
p72	0	0	0	0	0	0	0
p73	0	0	0	0	0	0	0
p74	0.193182	0	0	0	0	0	0.005682
p75	0	0	0	0	0	0	0.01444
p76	0	0	0	0	0	0	0
p77	0	0	0	0	0	0	0.704225
p78	0	0	0	0.823333	0	0	0.006667
p79	0	0	0.002793	0	0	0	0

	Thudel	Hylbre	Tritex				
p50	0	0	0				
p51	0.048851	0	0				
p52	0.057441	0.007833	0				
p53	0	0	0.055556				
p54	0	0	0.07113				
p55	0	0	0.264781				
p56	0	0	0				
p57	0	0	0				
p58	0	0	0				
p59	0	0	0				
p60	0	0	0				
p61	0	0	0				
p62	0	0	0				
p63	0	0	0				
p64	0	0	0				
p65	0	0	0				
p66	0.002288	0	0				
p67	0.026316	0	0				
p68	0	0	0				
p69	0.004608	0	0				
p70	0.026432	0	0				
p71	0	0	0				
p72	0.090476	0	0				
p73	0.086705	0	0				
p74	0	0	0				
p75	0	0	0.050542				
p76	0	0	0.052941				
p77	0	0	0				
p78	0	0	0				
p79	0.00838	0	0				

APPENDIX E

Environmental Variables-by- Plots Matrix

plot	Latitude	Longitude	Location	aspect	Canopy
1	N/A	N/A	Spruce/fir destruction trail	0	open
2	N/A	N/A	Spruce/fir destruction trail	10	open
3	35 34'00"	83 29'03"	Clingman Dome Road	130	open
4	35 35'24"	83 28' 16"	Mt Collin	290	open
5	35 35	83 27'	Fork Ridge Trail	21	shaded
6	35 35'57"	83 27'24"	Clingman Dome Road	76	shaded
7	35 36'07"	83 27'21"	Clingman Dome Road	73	closed
8	35 33'56"	83 32'19"	Near Double Gap Springs	198	open
9	35 33'56"	83 32'19"	Near Double Gap Springs	160	closed
10	35 35'43"	83 27'36"	Spruce/fir destruction trail	318	shaded
11	35 35'43"	83 27'36"	Spruce/fir destruction trail	318	open
12	35 35'25"	83 28'23"	Clingman Dome Road	224	open
13	35 35'25"	83 28'22"	Clingman Dome Road	220	open
14	35 35'27"	83 25'21"	Clingman Dome Road	168	open
15	35 35' 27"	83 25'21"	Clingman Dome Road	198	open
16	35 36'29"	83 26'51"	Indian Gap area	236	closed
17	35 36'27"	83 27'01"	Indian Gap area	248	shaded
18	35 35'47"	83 27'41"	Spruce/fir destruction trail	4	shaded
19	35 35'47"	83 27'41"	Spruce/fir destruction trail	284	shaded
20	35 35'47"	83 27'42"	Spruce/fir destruction trail	284	shaded
21	35 35'46"	83 27'41"	Spruce/fir destruction trail	328	shaded
22	35 36'31"	83 26'53"	Indian Gap area	160	open
23	35 36'31"	83 26'53"	Indian Gap area	160	open
24	35 37'04"	83 27'04"	Indian Gap area	180	closed
25	35 37'04"	83 27'04"	Indian Gap area	184	closed
26	35 37'04"	83 27'04"	Indian Gap area	184	closed
27	35 35'34"	83 28'24"	Mt Collin	306	closed
28	35 35'34"	83 28'24"	Mt Collin	306	closed
29	35 35'34"	83 28'24"	Mt Collin	306	closed
30	35 33'54"	83 32'32"	Double Spring Gap	82	closed
31	35 33'58"	83 32'30"	Double Spring Gap	130	open
32	35 33'52"	83 32'22"	Double Spring Gap	80	shaded
33	35 34'00"	83 32'27"	Double Spring Gap	90	open
34	35 34'02"	83 32'26"	Double Spring Gap	90	open
35	35 33'59"	83 32'27"	Double Spring Gap	116	closed
36	35 33'54"	83 32'23"	Double Spring Gap	136	open
37	35 33'52"	83 32'03"	Double Spring Gap	248	closed
38	35 33'52"	83 32'03"	Double Spring Gap	248	closed
39	35 33'52"	83 32'03"	Double Spring Gap	248	shaded
40	35 33'52"	83 32'03"	Double Spring Gap	248	shaded
41	35 33'45"	83 30'02"	Clingman Dome	8	shaded
42	35 33'45"	83 30'02"	Clingman Dome	8	shaded
43	35 33'45"	83 30'02"	Clingman Dome	8	closed
44	35 33'45"	83 30'02"	Clingman Dome	8	closed
45	35 33'45"	83 30'02"	Clingman Dome	8	shaded
46	35 33'45"	83 32'02"	Clingman Dome	8	shaded
47	35 35'52"	83 27'35"	Spruce/fir destruction trail	344	open

plot	Densimeter value	Slope %	Slope Class	Log Position	Position to Ground
1	60	8	1	horizontal	contact w/ soil
2	52	7	1	horizontal	contact w/ soil
3	55	20	3	horizontal	no contact w/ soil
4	30	15	2	horizontal	contact w/ soil
5	12	8	1	horizontal	contact w/ soil
6	14	25	3	horizontal	no contact w/ soil
7	6	30	4	slanted	no contact w/ soil
8	26	35	4	slanted	no contact w/ soil
9	13	8	1	horizontal	contact w/ soil
10	17	13	2	horizontal	no contact w/ soil
11	27	13	2	horizontal	contact w/ soil
12	50	9.5	1	horizontal	contact w/ soil
13	27	11	2	horizontal	no contact w/ soil
14	39	12	2	horizontal	contact w/ soil
15	17	8	1	horizontal	contact w/ soil
16	7	9	1	horizontal	contact w/ soil
17	13	11	2	horizontal	contact w/ soil
18	11	14	2	horizontal	contact w/ soil
19	14	12	2	horizontal	contact w/ soil
20	18	12	2	horizontal	contact w/ soil
21	16	5	1	horizontal	no contact w/ soil
22	31	42	5	slanted	no contact w/ soil
23	31	42	5	slanted	no contact w/ soil
24	13	10	2	horizontal	no contact w/ soil
25	9	5	1	horizontal	no contact w/ soil
26	14	5	1	horizontal	no contact w/ soil
27	8	7	1	horizontal	contact w/ soil
28	8	7	1	horizontal	contact w/ soil
29	14	7	1	horizontal	contact w/ soil
30	10	9	1	horizontal	contact w/ soil
31	21	32	4	horizontal	contact w/ soil
32	12	14	2	horizontal	contact w/ soil
33	15	12	2	horizontal	contact w/ soil
34	0	16	2	slanted	no contact w/ soil
35	10	11	2	horizontal	no contact w/ soil
36	10	16	2	horizontal	contact w/ soil
37	10	3	1	horizontal	contact w/ soil
38	10	3	1	horizontal	no contact w/ soil
39	16	3	1	horizontal	contact w/ soil
40	15	3	1	horizontal	no contact w/ soil
41	16	35	4	slanted	no contact w/ soil
42	20	35	4	slanted	contact w/ soil
43	11	30	4	slanted	no contact w/ soil
44	8	35	4	slanted	no contact w/ soil
45	10	30	4	slanted	no contact w/ soil
46	7	35	4	slanted	no contact w/ soil
47	71	11	2	horizontal	no contact w/ soil

plot	Orientation to slope	Decay class	Cover Class
1	perpendicular	3	3
2	perpendicular	4	4
3	perpendicular	3	3
4	parallel	3	3
5	parallel	3	3
6	perpendicular	3	3
7	parallel	2	2
8	parallel	3	3
9	perpendicular	2	2
10	perpendicular	1	1
11	parallel	2	3
12	perpendicular	4	4
13	perpendicular	3	3
14	parallel	2	2
15	perpendicular	3	3
16	perpendicular	4	4
17	parallel	4	4
18	parallel	3	3
19	Slope	1	2
20	Slope	1	2
21	perpendicular	2	3
22	perpendicular	2	3
23	perpendicular	1	4
24	parallel	2	3
25	parallel	2	2
26	perpendicular	2	3
27	perpendicular	4	4
28	perpendicular	2	1
29	parallel	2	4
30	parallel	1	4
31	parallel	3	4
32	parallel	3	3
33	perpendicular	4	4
34	perpendicular	2	4
35	parallel	1	1
36	perpendicular	3	4
37	perpendicular	2	4
38	perpendicular	3	4
39	perpendicular	2	4
40	perpendicular	2	4
41	parallel	4	4
42	parallel	2	4
43	parallel	2	3
44	perpendicular	2	3
45	perpendicular	3	4
46	perpendicular	3	4
47	parallel	2	4

plot	Latitude	Longitude	Location	aspect	Canopy
48	35 35'40"	83 27'27"	Spruce/fir destruction trail	340	shaded
49	35 35'40"	83 27'27"	Spruce/fir destruction trail	340	shaded
50	35 35'40"	83 27'27"	Spruce/fir destruction trail	340	shaded
51	35 36'27"	83 27'01"	Indian Gap area	248	shaded
52	35 36'18"	83 26'54"	Indian Gap area	248	open
53	35 33'44"	83 30'02"	Clingman Dome	348	open
54	35 33'46"	83 30'01"	Clingman Dome	8	open
55	35 33'46"	83 30'01"	Clingman Dome	8	open
56	35 33'46"	83 30'01"	Clingman Dome	348	open
57	35 33'46"	83 30'01"	Clingman Dome	348	open
58	35 42'5"	83 15'46"	Tricorner Knob shelter	18	closed
59	35 42'5"	83 15'46"	Tricorner Knob shelter	18	closed
60	35 42'5"	83 15'46"	Tricorner Knob shelter	18	closed
61	35 42'5"	83 15'46"	Tricorner Knob shelter	18	closed
62	35 42'5"	83 15'46"	Tricorner Knob shelter	18	closed
63	35 35'40"	83 28'21"	Mt Collin	316	closed
64	35 37'45"	83 23'28"	Mt Kephart	296	closed
65	35 37'45"	83 23'28"	Mt. Kephart	296	shaded
66	35 37'45"	83 23'28"	Mt. Kephart	296	open
67	35 37'45"	83 23'28"	Mt. Kephart	296	open
68	35 37'45"	83 23'28"	Mt. Kephart	296	shaded
69	35 37'43"	83 23'23"	Mt. Kephart	88	shaded
70	35 37'43"	83 23'23"	Mt. Kephart	88	shaded
71	35 37'43"	83 23'23"	Mt. Kephart	88	closed
72	35 37'43"	83 23'23"	Mt. Kephart	88	open
73	35 37'43"	83 23'23"	Mt. Kephart	88	open
74	35 37'43"	83 23'23"	Mt. Kephart	88	shaded
75	35 39'00"	83 26'30"	Mt. LeConte	238	shaded
76	35 39'00"	83 26'30"	Mt. LeConte	238	closed
77	35 39'00"	83 26'30"	Mt. LeConte	238	shaded
78	35 39'00"	83 26'30"	Mt. LeConte	238	shaded
79	35 39'00"	83 26'30"	Mt. LeConte	238	closed

plot	Densiometer value	Slope %	Slope Class	Log Position	Position to Ground
48	12	10	2	horizontal	no contact w/ soil
49	17	10	2	horizontal	contact w/ soil
50	15	10	2	horizontal	no contact w/ soil
51	11	11	2	horizontal	no contact w/ soil
52	12	9	1	horizontal	no contact w/ soil
53	36	23	3	slanted	no contact w/ soil
54	0	29	4	slanted	contact w/ soil
55	47	29	4	slanted	contact w/ soil
56	42	23	3	slanted	contact w/ soil
57	24	23	3	slanted	contact w/ soil
58	4	37	4	slanted	contact w/ soil
59	5	37	4	slanted	no contact w/ soil
60	2	37	4	slanted	no contact w/ soil
61	6	37	4	slanted	no contact w/ soil
62	1	37	4	slanted	no contact w/ soil
63	6	7	1	horizontal	no contact w/ soil
64	6	3	1	horizontal	no contact w/ soil
65	13	3	1	horizontal	no contact w/ soil
66	26	3	1	horizontal	no contact w/ soil
67	27	3	1	horizontal	no contact w/ soil
68	21	3	1	horizontal	contact w/ soil
69	14	13	2	slanted	no contact w/ soil
70	7	13	2	slanted	contact w/ soil
71	7	13	2	slanted	no contact w/ soil
72	17	13	2	slanted	no contact w/ soil
73	7	13	2	slanted	no contact w/ soil
74	14	13	2	slanted	contact w/ soil
75	15	1	2	horizontal	contact w/ soil
76	14	1	2	slanted	contact w/ soil
77	18	1	3	slanted	contact w/ soil
78	26	1	3	slanted	contact w/ soil
79	14	1	3	slanted	contact w/ soil

plot	Orientation to slope	Decay class	Cover Class
48	perpendicular	2	1
49	perpendicular	4	4
50	parallel	2	4
51	perpendicular	3	4
52	perpendicular	3	4
53	parallel	3	2
54	parallel	3	3
55	parallel	3	4
56	perpendicular	4	4
57	perpendicular	3	4
58	parallel	2	4
59	perpendicular	1	4
60	perpendicular	3	3
61	perpendicular	3	4
62	perp	4	4
63	parallel	2	4
64	parallel	2	4
65	parallel	2	4
66	Slope	1	4
67	perpendicular	2	4
68	parallel	1	4
69	perpendicular	3	4
70	perpendicular	2	4
71	perpendicular	3	4
72	perpendicular	3	4
73	perpendicular	3	4
74	perpendicular	2	4
75	perpendicular	2	4
76	perpendicular	2	3
77	perpendicular	4	4
78	perpendicular	2	4
79	perpendicular	3	4

APPENDIX F

Species List

Mosses	Liverworts
<i>Brotherella recurvans</i> (Mx.) Fl.	<i>Anastrophyllum michauxii</i> (Web.) Buch
<i>Dicranum fuscescens</i> Turn.	<i>Bazzania trilobata</i> (L.) S. Gray
<i>Dicranum scoparium</i> Hedw.	<i>Blepharostoma trichophyllum</i> (L.) Dum.
<i>Heterophyllum affine</i> (Hook. ex Kunth) Fl.	<i>Calypogeia suecica</i> * (Arn. & Perss.) K. Muell.
<i>Hylocomium splendens</i> * (Hedw.) BSG	<i>Cephalozia catenulata</i> (Huben.) Lindb.
<i>Hypnum imponens</i> Hedw.	<i>Cephalozia lunulifolia</i> (Dum.) Dum.
<i>Hypnum pallescens</i> (Hedw.) P.-Beauv.	<i>Frullania asagrayana</i> * Mont.
<i>Isopterygium elegans</i> (Brid.) Lindb.	<i>Geocalyx graveolens</i> * (Schrader.) Nees
<i>Platygyrium repens</i> (Brid.) BSG	<i>Jamesoniella autumnalis</i> (DeCand.) Steph.
<i>Pleurozium schreberi</i> * (Brid.) Mitt.	<i>Lepidozia reptans</i> (L.) Dum.
<i>Polytrichum pallidisetum</i> * Funck	<i>Lophocolea heterophylla</i> (Schrader.) Dum.
<i>Ptilium crista-castrensis</i> * (Hedw.) DeNot	<i>Nowellia curvifolia</i> (Dicks.) Mitt.
<i>Rhytidiadelphus triquetrus</i> * (Hedw.) Warnst.	<i>Riccardia palmata</i> * (Hedw.) Carruth.
<i>Tetraphis pellucida</i> Hedw.	<i>Scapania nemorosa</i> * (L.) Dum.
<i>Thuidium delicatulum</i> (Hedw.) BSG	<i>Tritomaria exsecta</i> (Schmid.) Schiffn.

* indicates found in < 5% of all plots

APPENDIX G

Plot Number / TWINSPAN Union

Group	Plot Number
Union 1	p24 p34 p66
Union 2	p16 p28 p41
Union 3	p22 p35 p43 p02 p20 p25 p50 p10 p19 p46 p48
Union 4	p53 p54 p55 p76
Union 5	p26 p29 p32 p78 p03 p09 p33 p56
Union 6	p27 p06 p42 p63 p75
Union 7	p40 p45 p60 p64 p69 p58 p61 p77 p07 p44 p59
Union 8	p47 p04 p65 p68 p70 p13 p14 p15 p79 p05 p01 p49 p36 p37 p38 p39 p62
Union 9	p23 p30 p71 p18 p21 p17 p31 p52 p74 p12 p51 p72 p7 p11 p67

VITA

Erica Renee Grimm Choberka was born on July 18, 1974 in Peoria, IL. She attended St. Bernard's Grade school from 1980 to 1988 and graduated from Peoria Woodruff High School in 1992. In 1992, she entered Southern Illinois University at Carbondale and received her Bachelor of Arts in Plant Biology in May 1996. In that same year, she entered The Graduate School of The University of Tennessee, Knoxville to study bryophyte ecology. She received her Masters of Science degree in December, 1998.