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LANDSCAPE ECOLOGY OF BIRDS ON MOUNT LECONTE, GREAT SMOKY MOUNTAINS NATIONAL PARK

by

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ABSTRACT

LANDSCAPE ECOLOGY OF BIRDS
ON MOUNT LECONTE,
GREAT SMOKY MOUNTAINS NATIONAL PARK

Andreas P. Damalas
Old Dominion University, 2005
Director: Dr. Robert K. Rose

Landbirds form a significant component of wildlife resources in the Great Smoky Mountains National Park. The present study explored how forest structure and composition of deciduous-coniferous ecotones influenced diversity, richness, and relative abundance of bird species and how bird species responded to the spruce-fir community.

Using a form of the variable-circular plot method, I conducted audio-visual censuses of diurnal birds on Mount LeConte. I established 212 geo-referenced census points on six trails, which were used as gradient-oriented transects (gradsects). I measured habitat characteristics at the same census points. I used forest community types for each point on gradsects to delineate boundaries.

I applied "*The Tasseled-Cap (T-CAP)*", a graphic description of the spectral-temporal development of locations, to analyze bird-habitat relationships in order to investigate the utility of Landsat T-CAP indices in predicting forest patterns and bird species' richness and abundance. I derived elevation, slope, and aspect from differentially corrected GPS coordinates using ArcView Spatial Analyst and T-Cap indices from Landsat TM remotely sensed data for forest community types and each vegetation sampling station using Earth Resources Data Analysis System.

My results showed correlations among the abundances of many bird species and elevational, floristic, and physiogonomic features of their habitat, both for univariate and multivariate characters. Both cover type and size class (dbh) were important to the breeding avifauna; various groups of breeding birds were associated with either one or both variables. Ecotones along the gradsects among forest types were perceived by many bird species as significant discontinuities. Zones of both rapid and gradual change in bird abundance were observed. For certain bird species, patterns of bird distribution and forest types coincided. Individual species responded to patchiness, vegetation structure, and elevation, sometimes in a predictable manner. I observed clusters of species and communities along my derived zones that appeared to be different. Species expanded or contracted their distributions in localities where the homogenous ecotone was displaced upward or downward in elevation relative to the location of the ecotone on Mount LeConte. Spatial fluctuations were, in general, related to zonal transitions in forest types.

T-CAP indices were related to species' responses to changes in landscape structure and composition. Distinct patterns in vegetation that corresponded with different forest types and zones of rapid and gradual change in bird abundance were observed. *Greenness* and *wetness* values differentiated closed canopy fir stands from all other classes. *Wetness* distinguished deciduous sites from coniferous sites, with higher values associated with wetter conditions. Bird regressions with T-CAP indices as predictor variables revealed *brightness* and *greenness* were correlated in significant linear relationships. Patterns of T-CAP values, however, suggested that bird diversity measures in most cases were inversely related to *greenness* and *wetness*. This study showed that these indices could be used as pattern recognition tools to make general inferences about changes in bird diversity due to changes in forest communities, to study and predict species richness and distributional patterns, and to estimate the biodiversity status of wide areas on a broad scale.

ACKNOWLEDGMENTS

There are many people who have supported me throughout this phase of graduate school and my research. My wife, Efi, unselfishly allowed me to spend two summers in the mountains of Great Smoky Mountain National Park (GSMNP) and many hours on the computer at home and at the Laboratory for Remote Sensing and Environment (LaRSEA), Old Dominion University. During the most hectic job and research phases, Efi was always able to buffer my frustrations.

My study was performed in collaboration with a study by my advisor, Tom Allen, and colleagues entitled "Compiling field, remote, and modeling approaches to examine processes at deciduous-coniferous ecotones on Mount LeConte," in Great Smoky Mountains National Park, funded by the Geography and Regional Science Division of the National Science Foundation. The methods in the studies are complementary. These studies use a substantial co-registered spatial database produced by Twin Creeks National Resource Center, GSMNP.

I would like to thank the chairman of my committee, Dr. Robert K. Rose, for his advice, guidance, and paramount effort and time in editing extensive prospective proposals and early versions of the dissertation manuscripts, and in providing me the opportunity and much patience to conduct this doctoral project. I am especially grateful to my other advisor, Dr. Thomas Allen, for his input, assistance and support throughout the whole research project. He and his work on Mount LeConte motivated me to pursue this project. This research project also builds upon years of interest in studying birds that was later encouraged by Dr. George Watson, my mentor and former curator of Ornithology at the Smithsonian.

Under the mentorship of the above individuals, I have succeeded in achieving my educational goals and have entered the scientific ranks of Ecology, Ornithology, and GIS.

I would like to thank Dr. Bryan Watts, Director of the Center for Conservation Biology at the College of William and Mary and a member of my dissertation committee, for his advice and editorial involvement in the dissertation manuscript. My faith in God provided the patience and persistence to tackle and finish this dissertation. I thank Brian Daniel of Leica Geosystems for providing me with the Leica GS50 GPS unit to obtain the GPS coordinates, and Doug Cribbs at Aerial Information Systems for providing me the Nature Conservancy imagery for GSMNP. Financial support for this project was provided by a grant from The Virginia Space Grant Consortium, a scholarship from "Annunciation" Greek Orthodox Church Philoptochos Society, and a grant from Sigma Xi. The National Park Service (NPS) provided spatial data, as well as housing for summer field work. I thank Keith Langdon of the NPS for logistical support. I would like to acknowledge Dr. R. Naik of the Statistics Dept at Old Dominion University and Dr. Dean Wichern, Professor, Mays Business School at Texas A & M University for their assistance in interpreting some of the multivariate analyses.

Finally, I am very grateful to Deborah Miller of the Graphics office at Old Dominion University for creating numerous figures, graphs/plots, and illustrations for my dissertation and the power point presentation for my defense.

Finally, I hope readers of this work will appreciate the complexity of studying birds in montane communities and the usefulness of a holistic perspective.

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CHAPTER I

INTRODUCTION TO THE LANDSCAPE PERSPECTIVE

Introduction

Landscape Ecology

Landscape ecology emphasizes large areas and ecological effects of spatial patterning of ecosystems. The term *landscape ecology* was first used by Troll (1939) and arose from European traditions of regional geography and vegetation science; the historical development is reviewed in Naveh (1982) and Naveh and Lieberman (1984). Landscape ecology did not really become well known to ecologists, at least in North America, until the mid-1980s (Forman and Gordon 1986; Lidicker 1988; and Turner 1989). Previously the focus of attention had been on investigating populations in patches of habitat that were as homogeneous as possible.

The definition, history, and development of landscape ecology are reviewed by Forman (1997); Forman and Gordon (1986); Gosz and Sharpe (1989); Hudson (1991); Lidicker (1999); Turner and Gardner (1991) and Urban et al. (1987); its underlying and unifying ecological mechanisms are reviewed in Wiens et al. (1993). Landscapes can be observed from many points of view, and ecological processes in landscapes can be studied at different spatial and temporal scales (Risser 1995).

Three landscape characteristics that are especially useful to consider are structure, function, and change (Forman and Gordon 1986). *Structure* refers to the spatial relationships among distinctive ecosystems, i.e. the distribution of energy and species in relation to the sizes, shapes, numbers, kinds, and configurations of components.

The model journal for this dissertation is Oecologia.

Function refers to interactions among spatial elements, i.e. the flow of energy and organisms among the component ecosystems. *Change* refers to alteration in the structure and *function* of the ecological mosaic through time. Factors creating patterns in species distribution or vegetation structure within landscapes necessarily create ecotones. In this chapter, *disturbance* refers to an ecotone-family event of sufficient intensity and severity to create a patch (minimum area ca. 0.1 ha) that differs from pre-existing and neighboring vegetation in structure and/or composition.

Structural and Functional Attributes of Landscape Boundaries: Evidence for Ecological Boundary Effects

The ecological effect of different boundary surfaces or features is logical but virtually unstudied directly. Corridors, by their very nature, are characterized by ecotones and often extensive boundaries. The use of corridors by many species is well documented (e.g., Forman 1983; Merriam 1984; Harris and Gallagher 1989; Bennett 1991; Simberloff et al. 1992; Forman 1997). However, although the habitat *function* of corridors is well understood, it is little documented in most landscapes. Edge and generalist species usually predominate in corridors (Pollard et al. 1974; Verkaar 1988; Saunders and Hobbs 1991; Malanson 1993).

Habitat Edges

Formally, habitat edges, structural or compositional discontinuities in habitat features, affect the distribution or behavior of a focal individual or species in some way. This view of habitat edges generates several important corollaries:

(1) Habitat edges separate two or more different habitat types.

(2) Habitat edges often are species-specific, and possibly sex- and age-

specific.

(3) Human observers may not be able to recognize a habitat edge without careful study.

(4) It will be difficult to measure the width of habitat edges.

(5) It will be difficult to measure the length of habitat edges.

The concept of “ecotone” emerged from plant ecology and expressed the zone of tension or transition between two plant community types (Clements 1897). The term “ecotone” dates to Clements (1905), and literally means “house (place) of tension or strain”. The notion of edge effect is an insight from animal ecology and wildlife management. Its first formal presentation is generally attributed to Leopold (1933). However, as early as 1897, Clements referred to edges of plant formations as “tension zones,” and he observed that the vegetation in such places often was accentuated in size and density. It is appropriate, therefore, that, like Leopold’s edge effects, ecotones have come to be associated with emergent properties, namely increased productivity and diversity, and are sometimes detectable by the presence of edge-adapted species.

Ecologists often are concerned with boundaries around individual organisms, groups of the same kind of organism (demes), and characteristic assemblages of different kinds of organisms (community types). Landscape ecology extends this purview to focus on boundaries between adjacent but contiguous community types (Lidicker 1995). Such edges are often studied with reference to patches of habitat suitable for a particular kind or kinds of organism, or between specified community types. These discontinuities in biotic and abiotic properties across space and the responses of birds to them are the subject of my study.

Ecotones

With the beginning of the International Biological Program in the early 1970s, attention was devoted to studying entire ecosystems. Some of these investigations focused on relatively large watersheds (e.g., Hubbard Brook Experimental Forest in New Hampshire and Walker Branch and H. J. Andrews watersheds in Tennessee and Oregon, respectively). From these regional studies, it became apparent that numerous processes link different types of ecosystems across landscapes (Likens 1992). Scientists then began to study whole landscapes rather than just focusing on single vegetation or ecosystem types. Under this broader landscape approach, ecotonal (or transitional) areas became conspicuous (Risser 1990) and were considered a vegetation characteristic requiring research. The dissertation by Fortin (1992) provides perhaps the best treatise and research analyses on ecotones. After defining an ecotone quantitatively as contiguous locations of high rates of change, she investigated how edge detection methods and subgraph statistics can be employed to identify the locations of potential ecotones. These investigations were carried out using simulated and actual tree vegetation data sets from two temperate areas: the Weld forest (New York), and the forest of the Haut-Saint-Laurent (Quebec). With these data sets, she tested whether the detection of ecotones is consistent using different scales of observation (quadrat size), variable types (density, percent cover, and presence/absence data), and species assemblages (herbs, shrubs, and trees).

In static cases, edge detection algorithms and significance tests based on subgraph statistics have been found to be useful in delimiting potential ecotones. Given that significant rates of change can be identified, optimal sampling designs in the field can be established to study and monitor the functional properties of ecotones.

Definition of an Ecotone

Quantitatively, a boundary on either side of an ecotone can be viewed as the location in space at which the rate of change of a given variable (or assemblage of variables) is the highest. Given that ecotones are mainly recognized by changes in characteristics, such as having either a greater or lower number of species than either adjoining communities, I shall define an ecotone operationally to be the set of locations where the majority of variables (species or environmental factors) show the highest rate of change (van der Maarel 1976, 1990). When quantitative data are available, such as density or abundance, high rate of change will refer to magnitude of the gradient between adjacent sampled points; when only qualitative data are available, such as the presence/absence of species, high rate of change will refer to the amount of turnover in species composition between adjacent sampled points. Furthermore, the locations in such a set should be spatially contiguous and linked to create either long and narrow or short and wide boundaries.

This definition of ecotone mostly concerns the identification of the structural aspects of ecotones, such as their location, shape, and width. However, it also emphasizes that an ecotone is detected by the co-occurrence of changes in more than one variable and is independent of scale. Furthermore, by defining an ecotone as a set of locations of high rate of change, I do not specify the direction of change so that the ecotone can either have more or less diversity than the adjacent communities. This is a desirable property because not all ecotones show the same types of changes (van der Maarel 1976, 1990).

I shall investigate whether this definition is sufficient to adequately perform the first step in the study of ecotones, namely the spatial delimitation of their location and associated bird species. Only after having adequately detecting ecotones in the static situation can their dynamics be analyzed (Hobbs 1990). The dynamics of ecotones through time refers to their functional aspects, such as stability and resiliency.

Origin and Types of Ecotones

Depending on the type and intensity of causal factors, ecotones can either be sharp or smooth (Whittaker 1977; Ferson 1988). According to Yahner (1988), there are two types of ecotones: inherent ones due to natural processes (ecotones), and induced ones produced and maintained physically by man (edges).

Recent studies have analyzed vegetation responses under environmental changes due to pollution (Botkin et al. 1984; Westman 1987) or climatic conditions (Brubaker 1986; Holland 1988a). Furthermore, Brubaker (1986) has pointed out that there is evidence for treeline movements due to climate change. Thus, it is possible to use the change in local vegetation and ecotones to analyze the impacts of pollution (e.g., acid rain) and climate change (e.g., greenhouse effect). However, such boundary movements should be studied on inherent ecotones rather than on induced ones because only the former indicate direct physiological responses to environmental changes (van der Maarel 1990). Therefore, it is important to be able to differentiate between natural and induced ecotones (Forman and Gordon 1986; Yahner 1988).

Importance of Ecotones

Ecotones are of concern in several fields of fundamental and applied research in ecology. For instance, in conservation biology and wildlife management, ecotones and edges are important because they usually show special properties, such as an increase in abundance, diversity, or primary productivity (Leopold 1933; Elton 1966). However, as noted by Yahner (1988), edge effects cannot only be positive but negative as well, since they can increase predation, parasitism (Brittingham and Temple 1983), and competition among species.

Ecotones frequently contain relatively high levels of biodiversity, especially those ecotones that cover significant areas and are stable for prolonged time periods (Delcourt and Delcourt 1992; Hansen et al. 1992). Transitions between two ecosystems contain compositional and structural characteristics of the adjacent habitats as well as distinctive microhabitats found only in the ecotonal area. Ecotones that are stable over long periods facilitate dispersal into and establishment of species in the ecotone (Gosz 1992). Near a species' periphery of distribution, habitats are likely to be fragmented, with merging communities, further leading to higher biological diversity. Whitcomb et al. (1981) provide an example supporting these patterns in bird communities of deciduous forests of the eastern United States, where biodiversity is high and life-history characteristics, such as population density and feeding and nesting preference, correlate with the type, size, and distribution of habitats within the ecotone (Hansen and Urban 1992).

Despite the general belief that biodiversity increases within ecotones, empirical data are available for relatively few studies (e.g., Delcourt and Delcourt 1992; Hansen et al. 1992). As additional data are collected, it is likely that it will become possible to better understand the relationship between biodiversity and ecotones. For now, it is clear that patterns of biodiversity in and adjacent to ecotones are influenced by several factors, including size and distribution of habitats within and near the ecotone, steepness of environmental gradients impinging on the ecotone, and specific life-history and demographic characteristics of organisms that allow them to invade and persist in the ecotone (Hansen et al. 1992).

Detection of Ecotones

Ecotones are relatively heterogenous compared to the adjacent homogenous units they separate. Without the identification and characterization of these adjacent homogeneous units, ecotones cannot be adequately defined, making the concept of ecotone irrelevant or of little value. An important step in the definition of ecotones, therefore, is the determination of the adjacent homogeneous units described as communities or patches. Community is commonly defined in the literature both as "any group of organisms belonging to a number of different species that co-occur in the same habitat or area and interact through trophic and spatial relationships" and "...typically characterized by reference to one or more dominant species" (Lincoln et al. 1982). By contrast, a patch refers to "a surface area differing from its surroundings in nature or appearance" (Wiens 1976) or "implies a relatively discrete spatial pattern, but (without) any constraint on patch size, internal homogeneity, or discreteness" (Pickett and White 1985). I define ecotone as a transition line, strip, or area of vegetation between two communities, which has characteristics of both types of adjacent vegetation as well as characteristics of its own. Ecotone will be applied to the relatively discontinuous bounding zones. Therefore, the ecotone concept, itself vague quantitatively, refers to the separation between entities (communities or patches), which themselves are difficult to delimit quantitatively.

Furthermore, there is no reason for a boundary to completely surround and delimit a patch. Indeed, some ecotones may surround a patch, such as in mountains where the alpine vegetation of the peak is separated from the vegetation below by an ecotonal belt. However, other ecotones simply denote a local discontinuity in rate of change of density, structure, or composition between adjacent systems, corresponding only to the location where the processes and forces are changing (O'Neill et al. 1986).

Other important factors in the detection of ecotones, in addition to spatial scale, are different life-history stages of plants (seeds, saplings, and trees) and different types of vegetational physiognomy (herbs, shrubs, and trees). Indeed, even though the major factor that creates an ecotone can be identified, it is difficult to determine all the factors that create and maintain its location and properties through time. For example, using multiple regressions, Ranney et al. (1981) showed that the highest amount of variance of edge-width is not always explained by the same variable. The width of edges can vary depending on their orientation to the sun, wind direction, age of the patch, and man-made disturbances, among others (Forman and Gordon 1986). Edge width can also vary depending on whether it is measured with respect to vegetation structure or animal territories. Gates and Mosher (1981) found an edge whose width, when measured by vegetation structure, was less than 13 m, but was about 64 m when nest sites of birds were considered.

Therefore, studies of ecotones should be conducted at different scales of observation and with different vegetational physiognomies. By doing so, analysis of the spatial hierarchical organization of vegetation can be improved and the functional and quantitative descriptions of ecotones can be established (Allen 1987; Urban et al. 1987). Such studies should be made on areas (length x width) rather than gransects (length only). Gransect studies provide no information about the variation in width and shape of the ecotone. Because ecotones are variable and can be homogeneous in space and time, their study and especially their monitoring require intensive and frequent sampling (Jeffers et al. 1989).

Several researchers (e.g., Sharp and Keddy 1986) have suggested the use of changes in vegetation as indicators of change in environmental conditions. Indeed, given the availability of aerial photographs and remotely sensed images of vegetation types, researchers can use automated techniques to detect ecotones and their movement. Wiens et al. (1985) studied the factors that influence the location of vegetation boundaries and concluded that edaphic factors are the most important. However, as Johnston and Naiman (1987) showed, changes in edaphic variables are not always reflected by changes in the vegetation composition or abundance. Hence, it is not always the case that vegetation patterns respond to environmental change. Therefore, depending on the purpose of the study, it may be necessary to analyze more than just canopy structure when using aerial photographs or remotely sensed images.

Background

The Great Smoky Mountains National Park (GSMNP) straddles the crest of the southern Appalachian Highlands along the Tennessee-North Carolina boundary and includes the southern-most limit of spruce-fir forest and the largest continuous expanse of old-growth spruce-fir forest in eastern North America. An International Biosphere Reserve with the most extensive old-growth forest stands in the Southern Appalachians, it also contains one of the highest diversities of breeding birds in temperate North America. Vegetation changes in response to complex gradients of temperature and moisture are themselves related to elevation, topography, and soils. Stands above elevations 1500 to 1800 m are dominated by red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*), with yellow birch (*Betula lenta*) also present as a minor canopy tree. Fraser fir, endemic to the Southern Appalachians, is found in nearly pure stands above 1800 m. Some ridges and rocky slopes within the spruce-fir zone are dominated by heath balds composed of evergreen broadleafed shrubs (e.g., *Rhododendron catawbiense* and *Vaccinium* spp.). The Southern Appalachian spruce-fir forest is one of the 21 most endangered ecosystems of the United States (Leslie et al. 1996).

Some types of vegetation in the GSMNP are in nearly virgin condition, except for the loss of American chestnut (Kendeigh and Fawver 1981) since the 1920s. Coniferous forests of different types and past history occur at both low and high elevations. Secondary as well as primary forest types are represented since only about 40 percent of the total area of the GSMNP is occupied by virgin forest (Braun 1967; Kendeigh and Fawver 1981).

Almost regardless of slope, exposure and steepness, chestnut forest prevailed at moderate elevations. Formerly the dominant species, all of the large chestnut trees have died since the 1920s. The virgin chestnut-dominated forest is but a ghost forest. Secondary succession, the assumption of dominance by one or several of the usual understory species, will in time result in the development of mature communities. Which of these may ultimately become the climax tree species for such sites is moot. On some of the lower ridges, a pine-heath community occupies the dry southerly slopes, giving way abruptly to xeric oak species. Locally, at moderate elevations, and not always on southerly slopes, the pine-heath community interrupts the prevailing deciduous forest.

Contact may be abrupt and sometimes appears to be related to substratum rather than slope. At the lowest elevations and in some of the outlying valleys where a red soil is present, oak forest has developed.

Restricted to high elevation sites with cool, moist conditions, red spruce and Fraser fir dominate approximately 17,900 ha in the GSMNP, 68% of which is old-growth forest (Pyle 1984). The old-growth forest has no history of logging; however, in recent decades Fraser fir has experienced high mortality from balsam woolly adelgid (*Adelges piceae*), a non-native insect pest (Speers 1958; Amman and Speers 1965; Eagar 1984). Fir mortality has been enough to adversely affect community composition and ecosystem dynamics (Witter and Ragenovich 1986; Busing et al. 1988; Nicholas et al. 1992). Although southern Appalachian red spruce does not exhibit the widespread decline observed in the northern Appalachians (Siccama et al. 1982; Vogelmann et al. 1985, Peart et al. 1992), the potential for negative responses to air pollution or climate change is a major concern (Johnson and Fernandez, 1992). These changes may lead to long-term alterations in the structure and dynamics of the spruce-fir forests (Busing and Clebsch 1988).

Until the introduction of the balsam woolly adelgid, dynamic processes in spruce-fir forests were dominated by the filling of small canopy gaps created by the death of one to a few overstory trees (White et al. 1993). Because gaps were small, replacement was primarily by advanced regeneration of fir or spruce, both of which are shade-tolerant species. The wave of fir mortality caused by the invasion of the adelgid, however, has significantly altered the microclimatic conditions in the forest understory. With increased fir mortality, deciduous trees and shrubs (*Betula sp., Sorbus americana, Prunus* *pensylvanica, Rubus canadensis, Sambucus pubens*) have increased in percentage cover in many stands formerly dominated by spruce and fir (e.g., Pauley and Clebsch 1990). Should this trend continue, the loss of southern spruce-fir forest ecosystems is also a possibility (White et al. 1993).

In the GSMNP, empirical evidence exists for vegetation zonation (Whittaker 1956, 1967). Ecotones were first investigated by Whittaker (1956), but Schofield (1960) contributed the only study of ecotone types between spruce-fir and deciduous forest in the GSMNP. Observed from a distance, the transition between deciduous and subalpine coniferous forest appears to be unusually abrupt. This impression is exaggerated, in part, by the difference in physiognomy of the dominants. Yet, a mixture of the two growth forms is evident for very short distances down the slopes.

Schofield (1960) investigated whether the transition is actually as abrupt as it appears to be from a distance and, in turn, if it is truly abrupt, what factors contribute to the sharp transition. Schofield's study of the ecotonal forest was planned to include both its lower altitudinal and its southern latitudinal limits, but questions remain about the causes of altitudinal limits of the forests in the GSMNP. Schofield commented (personal communication) that, in retrospect, the study could have been planned or designed better and analyzed differently. Additional data on ecotones in the GSMNP are needed, and there is lack of research on birds in ecotones (W.B. Schofield, personal communication).

Changes in Spruce-Fir Avifauna

High elevation conifer forests in the Southern Appalachians are one of the rarest and most endangered forest types in the eastern United States, encompassing only ca. 100 km2, of which 75% is contained within GSMNP (Saunders 1979; White et al. 1993).

These ecosystems, dominated by red spruce and Fraser fir, have been impacted by a number of human actions in recent decades, the most serious of which has been the introduction of the balsam woolly adelgid in the 1950s. Adelgid-caused mortality of mature Fraser firs has surpassed 90% on some mountains (e.g., Mount Mitchell and Mount Collins; Eagar 1984; Busing et al. 1988; Smith and Nicholas 1999), and the wave of tree deaths has, in turn, affected avifaunal communities (e.g., Alsop and Laughlin 1991; Rabenold et al. 1998).

Analysis of breeding bird populations in montane systems such as the Great Smoky Mountains is of special interest because of the relationships of these populations to the mosaic of vegetation types and to variations in climate and physical conditions (Kendeigh and Fawver 1981). Also, the protection of natural areas is of fundamental importance for the maintenance of biological diversity (Wilson 1988). Breeding migratory birds are sensitive to a variety of factors that can affect biodiversity (Temple and Wiens 1989), including changes in competitive relationships, adaptation to a changing environment, and the loss, alteration, or fragmentation of habitats. The proposed research is intended to help the National Park Service since the GSMNP is being designated as a natural control site for understanding the conservation of Neotropical migratory birds in the Southern Appalachians. Furthermore, Neotropical land bird populations form a significant component of the wildlife resources in the GSMNP.

Although considerable information about birds and vegetation in the GSMNP has accumulated since Tanner (1955) and Whittaker (1956), topological and ecological relationships of bird composition, abundance, and species richness in ecotones and spruce fir forests have not been studied. Thus, first I propose to investigate topological and ecological relationships of Neotropical migratory birds of the deciduous-coniferous ecotone (DCE) on Mount LeConte, GSMNP, in a landscape study of spatial and habitat patterns. To accomplish this, I will collect the following information:

1. Point-counts of species in the bird community at the DCE,
2. Landscape structural and functional characteristics of the DCE,
3. Physical (elevation, slope, and aspect) and habitat gradients of the DCE,
4. Remotely sensed data for vegetation classification, and
5. Field-based descriptions of vegetation physiognomy and floristics.

Then I will examine DCE patterns through the use of multi-scale remotely sensed data and imagery purchased from USGS Eros Data Center (Allen and Kupfer 2000) and a geographic information system. The DCE form has not been well documented, thus the first objective of this research will be to provide a thorough investigation of structural patterns of these ecotones. Malanson (1997a) has noted that the form/pattern of at least one ecotone (alpine treeline) may have important functional roles. An analysis of DCE form/patchiness is thus of interest because the coupling between pattern and process is especially tight at ecotones. Weinstein (1992) maintained that any of three ecological processes maintain ecotones: disturbance, stress, or competition.

Further, if remote-sensing techniques are to be used to detect changes in location of ecotones, it is critical to understand how using T-CAP digital image analysis with sensor resolution may affect interpretation of ecotonal location and consequently of bird diversity.

Study Area

The GSMNP, located in eastern Tennessee and western North Carolina (approximately 83 degrees 30' W longitude, 35 degrees 45' N latitude), contains large areas of undisturbed and little disturbed temperate forests. General descriptions of the physiography, climate, flora, general vegetation, and land-use history are available elsewhere (Cain 1931, 1935, 1945; King and Stupka 1950; Whittaker 1956, 1966; Hoffman 1964; Golden 1974; Frome 1996).

Whittaker's (1956) monograph is the most comprehensive treatment of the general vegetation pattern. He provided a direct gradient analysis that related populations of plant species to, and subjectively defined community types based on, elevation and a qualitative moisture "complex-gradient" based on topographic characteristics. His study was an integration of several multivariate techniques, now more widely used. His focus was on the middle elevation forests of the central portion of the park.

My study site was an approximately 15 x 15 km area centered on Mount LeConte on the Tennessee side of the GSMNP (Fig. 1.1). This site was chosen for many reasons. First, Mount LeConte (2009 m) is the third highest peak within the park and among the highest peaks in the eastern United States. Because of its elevation, it possesses a comparatively extensive spruce-fir zone. Second, vehicular access to field sites is comparatively easy because of the location to US Highway 441 and numerous hiking trails (including the Appalachian Trail) provide easy access by foot. Third, Mount LeConte has a recording weather station near its summit, which will help minimize errors in estimating climatic parameters. Fourth, images and digital elevation models are available for the area. Finally, and most important ecologically, Mount LeConte is

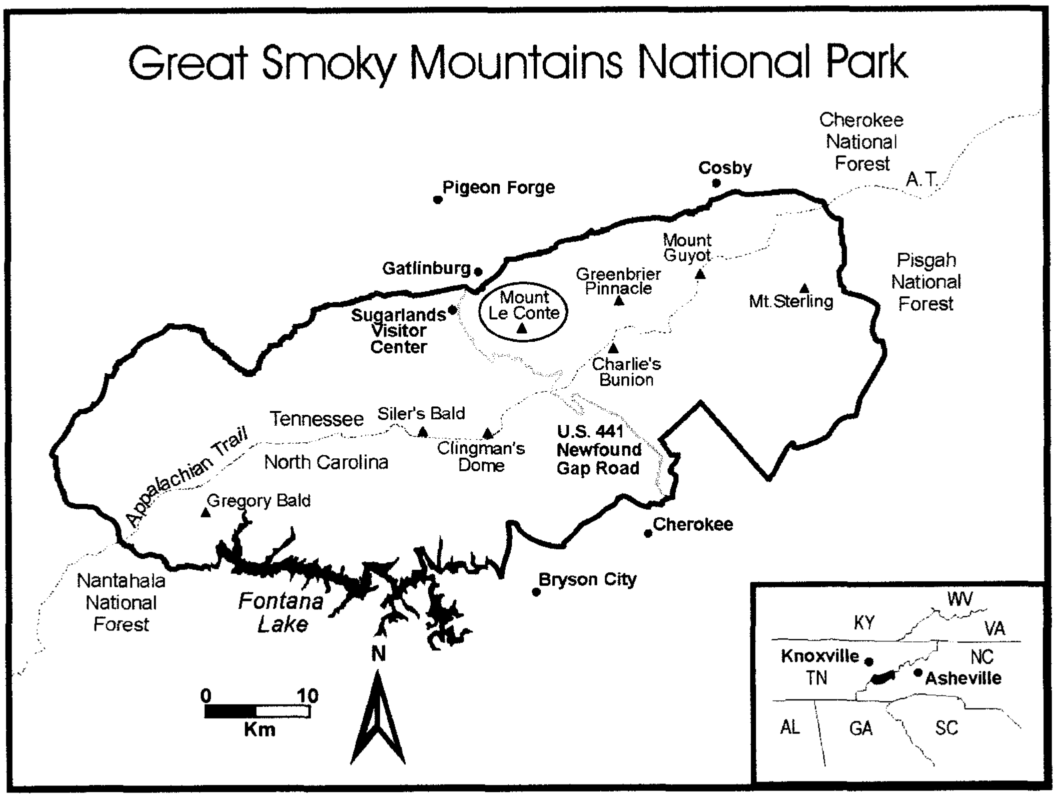

Fig. 1.1 Map of Great Smoky Mountains National Park, Tennessee, showing the location of the study area Mount LeConte, in the north-cental region.

typical of the Smokies in that its slopes are heavily forested, mostly in virgin forest, and the forest changes from oak-chestnut at the lower elevations to spruce-fir at the summit.

Mount LeConte (described in Tanner 1955) rises higher above its base than almost any other mountain in eastern North America. On its northwestern side is a valley containing LeConte Creek. This valley is fairly broad and slopes gently from Gatlinburg up to an elevation of about 790 m above sea level where a large orchard, Cherokee Orchard, spreads. From here the valley narrows and steepens, ascending to the top of Mount LeConte at 2009 m. Above Cherokee Orchard the valley is damp and cool and little undergrowth is present except on some ridges with nearly impenetrable stands of rhododendron. This mixed forest changes to one of yellow birch, spruce, and hemlock a little above 1220 m. At higher elevations the forest on both sides of the valley contains birch, spruce, and fir, with the two evergreens becoming more abundant near the top.

Statistical analysis

In addition to descriptive statistics, my analyses used both parametric and non-parametric tests and univariate and multivariate statistics.

Conservative non-parametric statistical analysis for ANOVA, correlations, and regression were used due to the following reasons: (1) the data were not normally distributed and were not consistently independent, (2) more points were censused on some trails than others, therefore creating unbalanced data, and (3) replication of some points was limited because of difficulties associated with weather. In these analyses, I avoided pseudoreplication by using the trail point as the sampling unit, with relative abundance at each trail point as the dependent variable, and vegetation and topographic factors as the explanatory variables.

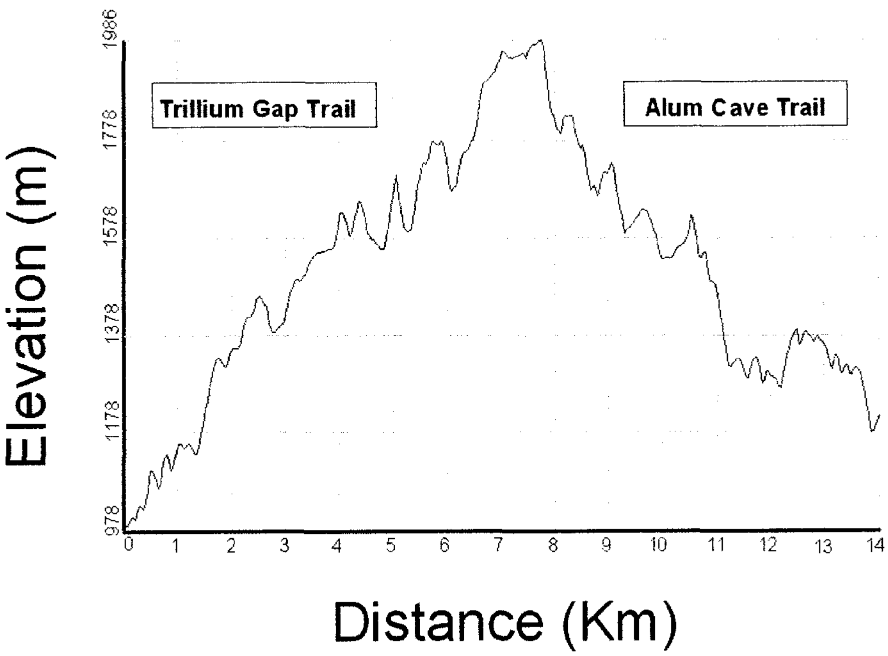

Fig. 1.2 Topographic profiles of two trails on Mount LeConte, Great Smoky Mountains National Park (GSMNP).

I developed a flow chart for data analysis (Fig. 1.3) that would meet the objectives (for the next three chapters) of describing my sample points and relating elevation, vegetation composition, and structure to site selection by (and abundance of) birds, and the response of birds to spatial patterns at the deciduous-coniferous ecotone.

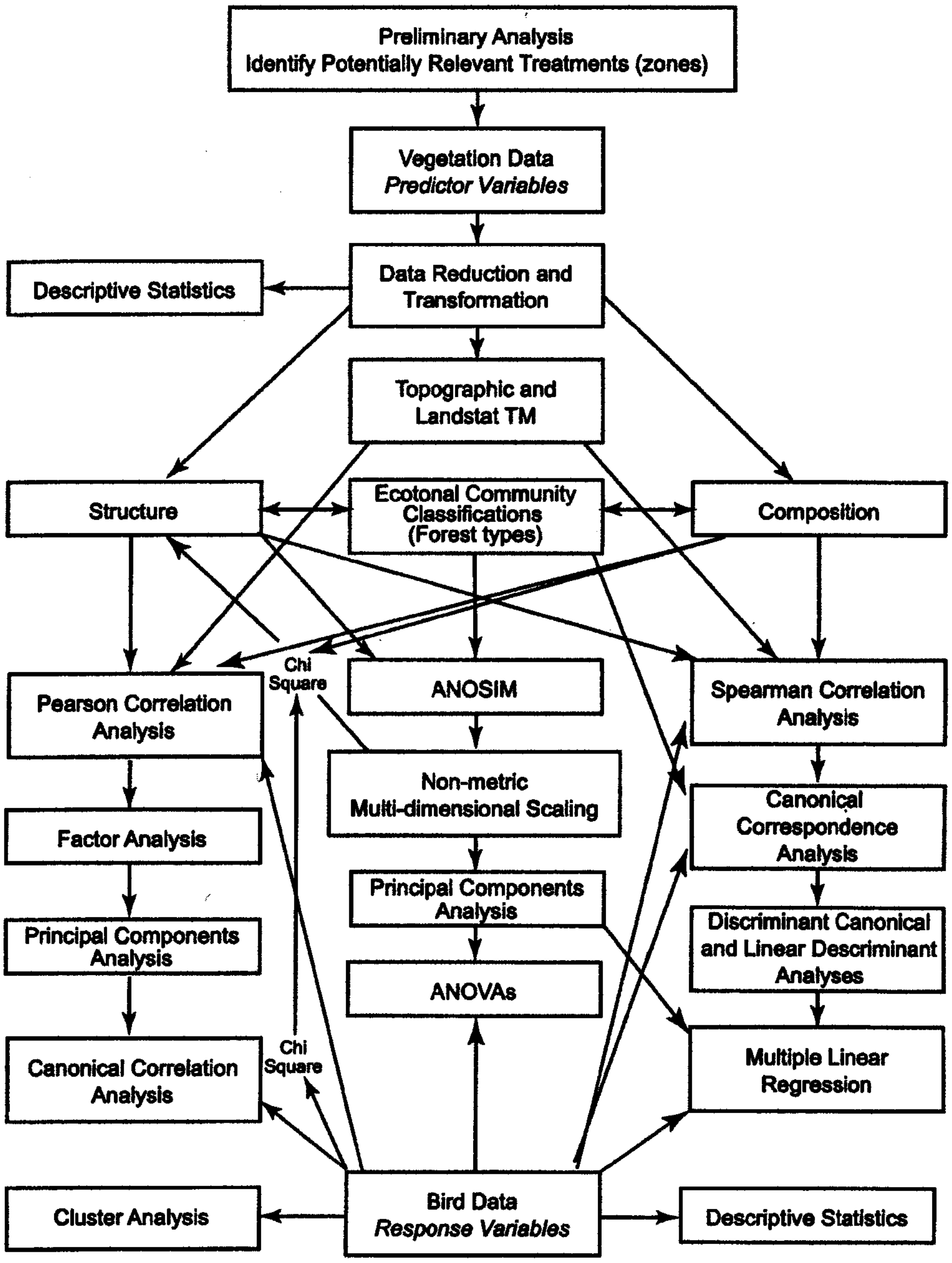

Fig. 1.3 Flowchart of statistical tests used to analyze variables of vegetation and bird data.

CHAPTER II

ECOLOGICAL DETERMINANTS OF BIRD DISTRIBUTIONS IN GREAT SMOKY MOUNTAIN FORESTS

Introduction

Elevation

Studies of species distributions along environmental gradients have made important contributions to our understanding of natural communities, particularly plant communities (Whittaker 1967). This approach has also been applied to birds in the New World tropics (Terborgh 1971) and New Guinea (Diamond 1973). These studies have used gradients of elevation because mountains often encompass a large range of environmental change over a small distance. Regardless of the type of gradient, the distribution of species with respect to each other and in relation to the habitat can be used to evaluate the roles of competition and habitat selection in structuring communities. Detailed gradient studies of vegetation have been done mostly in temperate or arid regions, whereas similar studies of birds have been done primarily in the wet tropics. My study examined breeding birds in a montane temperate location.

Such potentially important factors as vegetation composition, vegetation structure, and slope vary with elevation. Able and Noon (1976) present an analysis of breeding bird communities on elevational gradients on four mountains in northeastern United States. Theirs was the first detailed study of bird community structure on elevational gradients in temperate forests. It provides a basis for comparing forest bird communities on similar gradients in temperate and tropical areas, and permits comparison with vegetation gradient analyses on some of the mountains. However, the relationships and responses of birds to the vegetation and gradients were not investigated.

Despite Gleason's (1926) individualistic concept and Whittaker's (1967) gradient analysis approach, we have little empirical data to evaluate why some species overlap more than others along complex environmental gradients.

Physiognomy and Floristics

Freemark et al. (1995) highlight key concepts of landscape ecology important to the research, conservation, and management of Neotropical migratory birds. They review empirical studies related to the landscape ecology of Neotropical migratory birds in forests, farmland, wetlands, riparian habitats, and urban habitats of temperate breeding areas, and to a more limited extent, on migration stopover areas and over-wintering areas. Research, conservation, and management implications for Neotropical migratory birds arising from a landscape perspective are also discussed.

Landscape studies of wildlife examine patterns in the mosaic of habitat patches in the landscape and how they influence the distribution and dynamics of individuals, populations, and communities (Kotliar and Wiens 1990; Barrett 1992). The size of a landscape and the way its spatial heterogeneity is perceived (i.e. how a patch is defined) vary among organisms (Turner 1989; Wiens 198; Karr 1994; Pearson et al. 1995). For Neotropical migratory birds, landscapes occupy the spatial scales intermediate between an individual's territory or home range (typically one to a few hundred hectares), and the distribution of a species over large areas (e.g., a physiographic region). Species need to be examined individually and in different regions of their geographic range in order to understand habitat requirements (Noon et al. 1980), but they also need to be considered in the context of other species with which they can coexist (Martin 1992). Increased landscape diversity (greater interspersion and numbers of landscape elements) can increase the numbers of species coexisting in the landscape (Johnston 1947; Johnston and Odum 1956; Crawford et al. 1981). In addition, interspersion of vegetation or "cover" types is also associated with increased population sizes of some species. Nevertheless, although increased landscape diversity may result in increased plant and animal diversity locally, it may have detrimental effects on habitat suitability for individual species (defined by fitness within the habitats; Fretwell 1972; Van Horne 1983) and therefore can affect regional diversity (Martin 1992).

It is well known that species richness, composition, and abundance of Neotropical migratory birds vary among habitat types (Keast and Morton 1980; DeGraaf and Rudis 1986; Verner et al. 1986; DaGraaf et al. 1992, 1993; Hagan and Johnston 1992; Rodenhouse et al. 1993). The composition and spatial configuration of a landscape can independently, or in combination, affect ecological processes including distributions and biotic interactions of species (Dunning et al. 1992). Landscape composition includes the variety and abundance of patch types within a landscape, but not the location or relative placement of patches within the mosaic.

The nature of structural or functional boundaries created by the juxtaposition of different patch types is also important (Hansen and diCastri 1992). The presence of corridors may facilitate the movement of organisms across boundaries or through intervening inhospitable patches. However, the conservation value of corridors, although pondered (Simberloff et al. 1992), has not been well studied for Neotropical migratory birds.

Vegetation complexity is clearly associated with the complexity of the avian community. Foliage height profile can be correlated with bird species diversity, both within a series of similar habitats (MacArthur and MacArthur 1961; MacArthur 1964) and in gradients of dissimilar vegetation types (MacArthur 1964; Karr 1968; Karr and Roth 1971). As species are added (or subtracted) with changes in vegetation, it is unclear whether ecological relationships of members of the same or different guilds change or if the width of habitat associated with other ecological characteristics of any species is altered.

The vegetation structure of a habitat has been recognized as one of the principal determinants of the avian community breeding in that habitat (MacArthur et al. 1962; Cody 1968; Orians 1969; Wiens 1969; Zimmerman 1971). MacArthur and MacArthur (1961) found that species diversity of a breeding bird community could be predicted from the measurement of the proportional distribution of foliage layers (foliage height diversity). Other studies in which vegetation structure in the breeding territories of birds has been measured have shown that each species is distributed according to specific habitat variables (James 1971; Shugart and Patten 1972; Anderson and Shugart 1974; Willson 1974; Smith 1977). James (1971) used the term “niche-gestalt” to refer to these habitat configurations as components of the niche.

Previous studies of avian community organization often have focused on homogeneous forest (James 1971; Anderson and Shugart 1974; Smith 1977) or grassland habitat (Cody 1968; Wiens 1969), where species coexist at relatively low densities and in moderate diversity. Several workers (Root 1967; Karr and Roth 1971; Willson 1974) have suggested that high density and high diversity of species that exploit the same food source in a similar foraging manner may cause a narrowing of niche breadth through greater selectivity in habitat requirements or food preference.

Ecotones provide a natural experiment for testing the effect of high density on bird distributions. Distributional limits are determined by habitat discontinuities (ecotones). If the spread of a population is blocked by habitat discontinuities, there will usually be massive faunal turnover at ecotones (Terborgh 1971). I do not know of anyone who has measured this turnover in the last 30 years.

Busing et al. (1993) investigated old-growth spruce-fir vegetation using 1930s and 1980s plot data from the Great Smoky Mountains. Changes in forest composition and position of the ecotone with the deciduous forest were identified using canonical correspondence analysis (CCA) and spruce-fir vegetation response to climate change was evaluated. The data were subsequently stratified into three elevational classes and ordinated separately using CCA to identify gradients at the three elevations. However, the relationships and responses of birds to vegetational and environmental gradients were not investigated.

Thus, my objectives were to determine (1) which landscape elements (i.e. topography and habitat; described or explained by forest composition and structure) influence bird assemblage diversity and abundance of individual bird species, (2) how much variation in use of sites by birds is explained by the effects of habitat mosaic patterns, and (3) how forest composition and structure in ecotones influence habitat selection patterns by birds. Specifically, I determined species richness and relative abundance of individual bird species on sites of varying topographical and habitat diversity, and whether species richness of bird assemblages and frequency and abundance of individual bird species were related to forest composition and landscape structure characteristics. Three potentially underlying mechanisms responsible for landscape associations or relationships with birds were investigated:

(1) I sought to determine whether an elevational gradient was correlated significantly with species frequency, and whether elevational distributions of species were correlated significantly with such environmental factors as slope and aspect.

(2) I studied variation in community type, vegetation structure (physiognomy), and composition (floristics) with distance and elevation to see whether bird species abundance and richness were correlated significantly with structural characteristics or factors of the forest, such as vegetation dbh, density of canopy cover, cover class, foliage height diversity, disturbance, forest opening, logs, snags, and composition of the vegetation.

(3) I documented how landbird species use montane forested landscapes by comparing habitat variables and breeding bird communities among three zones (ecotone, below and above) and relating abundance of breeding birds in these zones to forest characteristics and community types ranging from lower elevational deciduous to high elevational Fraser fir (*Abies fraseri*).

Methods

On Mount LeConte, I selected six already established trails, called gradsects (gradient-oriented transects), on which to sample the vegetation and corresponding bird communities: Alum Cave Trail (ACT), Bull Head Trail (BHT), Rainbow Falls Trail

(RFT), Trillium Gap Trail (TGT), Boulevard Trail (BVT), and Brushy Mountain Trail (BMT). A thorough description of the trails on Mount LeConte is in Wise and Peterson (1998).

Bird censuses were conducted using a variable circular plot method (Reynolds et al. 1980). Vegetation was sampled at each census point. Vegetation sampling included a randomized sampling of trees, an estimate of cover for canopy, subcanopy, tall shrub/sapling, low shrub/seedling, and herbaceous layers, and a record of the predominant species in the canopy, subcanopy, and tall shrub/sapling layers.

Establishment of Census Points

Point-count censuses were conducted in ten major community types staggered to reduce temporal bias and to avoid confounding space and time in spruce fir, northern hardwood, cove hardwood, mesic oak, mixed mesic hardwood, tulip poplar, xeric oak, pine oak, and pine forest community types. Although most points were sited along trails, some were off the trail in order to fulfill stratification by groups of topographic quadrangles and vegetation types. Points were spaced a minimum of 200 m apart. Exceptions were made if significant land features (boulders) were present such that bird observations resulted in an overlap of distance between points. To determine how the gradual transition within the spruce-fir forest is related to decreased elevation, a number of gradsects were placed from the ridge-top down the slopes (Fig. 2.1). Sampling areas were selected by walking down slopes until the lower end of the spruce-fir forest was reached. Because the objective was to determine populations of specific bird communities for comparative purposes, it seemed desirable to select uniform, albeit small, areas rather than diverse large ones. Because the period of observation was the

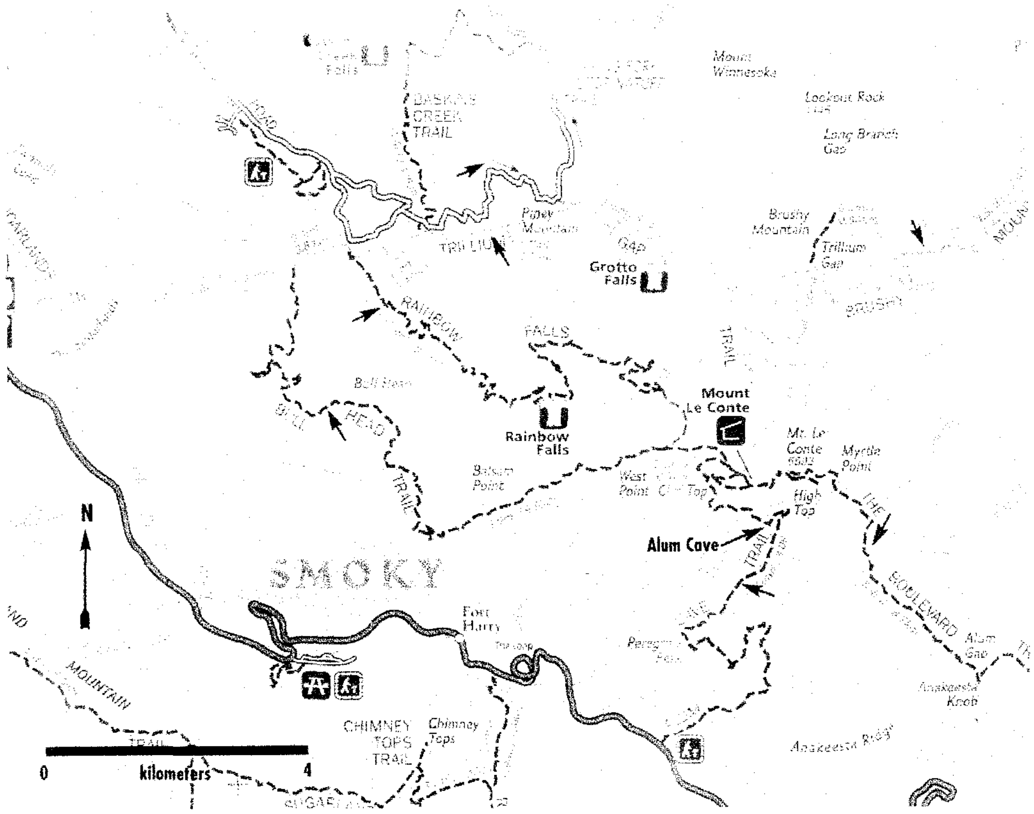

Fig. 2.1 Map of region in which study was conducted showing the trails, here called gradsects. Alum Cave Trail, Bull Head Trail, Rainbow Falls Trail and Trillium Gap Trail were used in the study. (Great Smoky Mountains National Park 1991)

breeding season, data collected on the same site in different years are considered to be independent. These transects, placed at right angles to the ridge-top, varied depending on the extent of the spruce-fir forest and length of the trails.

Community Vegetation Classifications and Habitat Coverages

MacKenzie (1993) used Landsat imagery to develop a vegetation map of GSMNP based on 13 major habitat types. The Nature Conservancy (1999), in cooperation with the National Park Service, is currently conducting a study to develop a new vegetation classification scheme and map for the Park.

The 36-level TNC classification system provided more association or stand types than I could sample effectively. I determined and assigned coverages (percentages) of 21 forest community types describing the study site centered on Mount LeConte into 10 Ecotonal Community Classifications (ECC) and Ecotonal Landscape Classifications by using Arc View 3.2. Therefore, I simplified that system and created a habitat superclass system, or community classification, composed of 10 community types (Appendix A, C). This system contained four coniferous and two hemlock forest types. Each sampling station was redefined as one of 10 superclass community types. Vegetation types were classified into 10 groups [pine, xeric oak, tulip poplar (mixed mesic hardwood), mesic oak, hemlock hardwood, cover hardwood, northern hardwood, spruce northern hardwood, spruce-fir, and fir] based on MacKenzie (1993) and the dominant canopy species present (yellow birch, yellow buckeye, Fraser fir, eastern hemlock, northern red oak, chestnut oak, white oak, Carolina silver bell, red spruce, table mountain pine, Virginia pine, and tulip poplar; Appendix A).

These community vegetation types, used on the vegetation data sheet (Appendix

C) to describe each census point, were also grouped into broader habitat superclasses. For the preliminary analyses, I hypothetically defined ecotonal zones as treatments on each gradsect using ECCs (Appendix A). The community types on the Alum Cave Trail (ACT) gradsect were delineated into zones because of the differential distribution in ECC patterns.

Vegetation evaluated at each point censused for birds was sampled primarily during June and July to ensure that cover estimates and characteristics/features were those present during the breeding season. Vegetation was sampled using each bird census point as the center of an 11.3-m radius circular plot. In general, three sets of data were collected: (1) a random sample of trees, (2) coverage estimates for canopy, subcanopy, tall shrub/sapling, low shrub/seedling, and herbaceous layers, and (3) composition of the canopy, subcanopy, and tall shrub/sapling layers. In addition, The Nature Conservancy (TNC) vegetation associations and Ecotonal Community Classifications (ECCs) were assigned to each bird census point (TNC associations are described in detail in the TNC Report (1999) and ECCs are defined in Appendix A). Qualitative information on site disturbances and heterogeneity were also recorded. All data were recorded on standardized data sheets (See Appendix B, C).

Vegetation Patterns and Avian Distribution

The variety of ways in which bird species were dispersed within the study area required determining whether vegetation heterogeneity in combination with habitat selectivity were important in the distribution patterns of birds. To test the hypothesis that individual male birds settled randomly with respect to vegetation, I first characterized the vegetation along all transects. Next, I summarized the vegetation characteristics of the subset of plots occupied by each bird species and evaluated whether this subset was a random set of available plots.

I analyzed ACT separately from the others because the trend or change in forest communities up the trail was different from the other trails. I had a prior knowledge of these and other unique differences as described in Wise and Peterson (1998), but the differences became more apparent in analysing the results. The community types on the ACT gradsect were defined or delineated into zones separately because of the differential distribution or difference in pattern of forest types. This difference in forest community pattern is a result of several factors. The forest cover along the lower stretch of the trail is called a "hemlock-birch association" and is typical of those found on the mountainsides up the Appalachian chain to central New York and beyond. In addition to the hemlock and birch, these stands include maple, beech, buckeye, silverbell, and an occasional magnolia. Hemlock stands appear in sites which are somewhat less mesic than those of the cove forests, whether on open valley flats at middle elevations or slopes above the valleys at high elevations (Whittaker 1956). These stands are also suspected of being segregated by thin soils (Cain 1937).

Another interesting botanical phenomenon was observed along this lower stretch of trail. In the larger birch trees, where wide crotches are common between the trunks and major limbs or where upper portions of the trunks have been broken off by lightening or wind, small hemlocks, rhododendron, dog-hobble, and ferns can be seen growing up to thirty feet above the ground. Much more common, and also worthy of inspection, are the hundreds of "downed trees" along the trail. Most of these are hemlocks, but some are birch and a few remnant chestnuts that have fallen and decayed. Along the stretch above

Arch Rock, the ACT trail passes through a grove of large hardwood trees, mostly oak and buckeye, with some maple and a few hemlocks. This type of forest is called mixed mesophytic and is typical of those farther north in the Appalachians. The hemlocks and hardwoods maintain a good balance along this ridge, though the red spruce displaces some of the more prevalent species. The two species can be further distinguished by luxuriant lichen growth that appears on the spruce trees but not on the firs.

Censusing Birds: Censusing Techniques and Avian Variables

Initial trail points were established at a random distance from the start of the trailhead, with subsequent points spaced a minimum of 200 m apart. Sections of trails along "loud" streams were not censused due to limited auditory detectability. All birds detected were recorded according to the protocol for censusing of birds, which was consistent with most of the recommendations for point-count methodology listed in the U.S. Department of Agriculture's General Technical Report No. PSWGTR-149 *Monitoring Bird Populations by Point Counts* (Ralph et al. 1995). These recommendations are an attempt to standardize point-count methodology. Observation of birds during point counts was influenced by many factors (e.g., behavior of species, characteristics of vegetation, weather conditions, or observer; Ralph et al. 1995). All counts were conducted by two birders (one the author), both of whom are familiar with the vocalizations and plumages of birds in Appalachian forest communities. In designing a sampling scheme, I had to choose between sampling fewer territories in great detail or sampling more territories less precisely. I chose the latter because I was concerned with the pattern of (male bird) distribution of territories over a relatively large area.

Because differences in habitat occupancy may be a function of year-to-year variation (Wiens 1981a), an effort was made to census as many sites as possible within one breeding season. In 2000, I repeated the same bird census procedures at the same stations used in 1999, with the same level of effort in the same (breeding) seasonal time. The order in which the trails were censused was reversed every time a census was made so that all stations on the trails had equal opportunity to be sampled during the early morning peak in bird activity, in order to increase the likelihood of observing rare, inconspicuous, or previously undetected birds.

Using a modification of the variable-circular plot method, an experienced observer and I conducted audio-visual censuses of diurnal birds (Emlen 1956; Franzreb 1976; Reynolds et al. 1980; Hutto et al. 1986; Ralph et al. 1993; Hamel et al. 1996). I established 212 census points on six trails, or gradsects. I censused/counted birds at each station except during periods of rain or high winds (>13 km/hour; Robbins 1981b; Skirvin 1981) at approximately equal intervals three times per year, June through mid-July 1999 and 2000. Censuses/counts were begun at 6:00 a.m. and were completed by 11:00 a.m. (except during periods of rain or high winds). I recorded all birds seen (1) vocalizing, (2) foraging, or (3) engaging in behavior during the first two minutes, the next three minutes, and final five minutes after one minute of acclimation. At each point, I identified all vocal and visual detections to bird species and recorded each distance as <50 m or >50 m. Birds flying above the canopy and obviously non-territorial birds were recorded but not included in the analyses. I assumed that any bias in bird detection among points was minimal because vegetation characteristics did not differ among gradsects.

I considered bird count data to be estimates of relative bird abundance, which is an index of the density of each species based on a constant but unknown proportion of the population of that species (Bull 1981). Abundance was reported as birds/0.79 ha, the area of a 50-m radius plot. I averaged the high count for each species over all census points to get an index of relative abundance of birds at each forest site (Blondel and Frochot 1981; Blake and Karr 1987). At each point, temperature, wind, and stream noise were recorded on a scale of 1-5 and cloud cover on a score of 1-4. Birds detected were stratified according to time period and location.

The order of surveys within "sub-routes" (½ gradsect) was alternated between time blocks to reduce the effect of time-of-day. The time/order of visits to starting points each morning was standardized. When an individual bird was detected, I recorded species and estimated its distance from the observation point.

To minimize bias, all observers were trained intensively in the study area by highly experienced supervisors for two weeks before the first day each season. The same two observers worked together over both years of study. I compared bird counts within the census plots with various habitat coverages in the surrounding landscape. Bird survey data collected in 1999 were compared with habitat coverages in 1999, and 2000 survey data were compared with 2000 coverages. Abundances of bird species and habitat coverages were not statistically different between years, so I pooled data from 1999 and 2000 to improve statistical power (Snedecor and Cochran 1989).

Vegetation Sampling Techniques and Habitat Variables

The 0.04-ha circle technique, designed to determine the life form of vegetation in bird breeding territories (James 1971), applies an individualistic approach to the distribution of organisms (Gleason 1926), in which populations are treated independently.

The technique permits analysis of the habitats of individual species and then enables comparisons among species not necessarily on the same plot.

I measured habitat characteristics on 120 0.04-ha circular plots (Lindsey et al. 1958; James and Shugart 1970; James 1978; Noon 1981) at each vegetation sampling station on the six gradsects. Vegetation sampling was also conducted so that characteristics/features corresponded to those present during the breeding season. This 0.04-ha plot is small enough to be contained within the individual's territory, but large enough (diameter 22.5 m) to contain an adequate sample of vegetation (see James and Shugart 1970 for additional details). I sampled vegetation using stratified random sample technique.

Data collection included a sample of trees using a wedge prism (Husch et al. 1982). All trees detected within the limits of the wedge prism were identified to species and recorded within dbh range. Six dbh ranges were used: 0-10 cm, 11-25 cm, 26-50 cm, 50-75 cm, 76-100 cm, and >100 cm. Analysis of previous wedge prism data revealed that these dbh ranges are sufficient to distinguish between old-growth and second-growth stands (Simons et al. 1995). I ocularly measured and recorded cover by tree species for overstory (tree canopy), understory (subcanopy), tall shrub/sapling (>1 and <10 cm dbh), and low shrub/seedling coverage on a range from 1 to 10 with 10 being the highest percent coverage: <0.1, >0.1-1, >1-2, >2-5, >5-10, >10-25, >25-50, >50-75, >75-95, and >95% (Mueller-Dombois and Ellenberg 1974). Percent canopy cover was visually estimated using the Cornell Laboratory of Ornithology canopy chart.

At each bird census point, I ocularly estimated the presence of each of five vegetation layers (canopy, subcanopy, tall shrub/sapling, low shrub/seedling, and ground or herbaceous including ground cover) and, using a clinometer, I estimated forest cover class and tree height range of each layer present. The herbaceous layers, including ground cover, were determined to be forb, evergreen, fern, moss, grass, or a combination of these types. I determined species composition of woody components by identifying dominant species in each layer using Radford et al. (1968). The species of each canopy tree was also recorded to verify the forest cover type (deciduous, coniferous, hemlock) of the plot. The vegetation classification of MacKenzie (1993) was used to define forest types occupied by birds, which were described by the dominant species, canopy closure, and height for shrub communities. Abiotic features that influence bird habitat use were assumed to be strongly related to plant community structure and composition. Twenty-seven structural habitat variables were either directly measured or derived. I also tallied such special habitat features as disturbances, forest openings, logs, and snags at each census point.

Environmental Measurements and Variables

The GPS coordinates for each bird census point were determined and registered by a Leica GS50 GPS/GIS receiver, and later differentially corrected. In the GIS laboratory, I derived elevation, slope, direction, and aspect from all 212 geo-referenced points and added the data into the GIS environment for use in statistical analyses. The geo-reference plot locations were overlaid with GSMNP-TNC vegetation coverage associations to accurately assess/compare vegetation classifications and forest types. All data and information from sources in this project were stored in Arc View and GIS operated on PC workstations in the Laboratory for Remote Sensing and Environment (LaRSEA) at Old Dominion University.

Analysis of Vegetation and Habitat Data

Three measurements for each of 35 habitat variables (characteristics) were averaged within each site. Based on correlation analyses, highly correlated ($P<0.01$) variables were excluded from analyses. Differences in the remaining 17 variables were tested among three elevational zones, which I defined as below the deciduous-coniferous ecotone (DCE; zone 1), DCE (zone 2), and above DCE (zone 3), and gradsects using 1-factor ANOVAs and Kruskal-Wallis tests. Experiment-wise error rate was controlled at the 0.05 level using the Bonferroni method of adjusting the nominal alpha level by the number of tests performed.

I also determined mean and total dbh and density for tree species along the gradsects by averaging census-point data for each variable. I subjected each habitat variable to a 2-way analysis of variance (ANOVA; 3 zones by 6 gradsects; $n=18$). I used SAS general linear models (GLM) procedure for all ANOVA tests and comparisons (SAS Institute 2000).

Vegetation composition along gradsects in each of the three zones varied, whereas vegetation composition within the three zones was relatively homogenous, constituting three different classes. I examined the statistical relationships among the above community-level and species-level response variables and the following predictor variables: percent canopy cover, tree canopy density, tree subcanopy density, tree dbh, and canopy height diversity to understand ecological determinants of bird species and their importance in GSMNP.

Using ANOVA, Tukey's HSD test, and multiple comparison procedures, I compared the mean density and mean diameters of canopy trees for each census point and for each gradsect. Multivariate methods, however, elicit comparisons of habitat structure among sites by incorporating all variables into one analysis. Therefore, habitat structure for the 112 plots (plots with values of zero due to balds were eliminated from the analysis) on the 6 gradsects was analyzed by principal factor analysis (PFA) from a correlation matrix (standardized data) of the habitat variables. These statistics were considered significant at $P<0.05$.

Analysis of Bird Data

I determined the abundance of each bird species along each gradsect by summing the number of individual detections during three visits for each year to each census point. Total bird abundance (total detections), species richness (total species), and species abundance were used as independent response variables. I eliminated from the analysis any species having fewer than 20 detections in 1999 and 2000 combined.

I summed bird abundance data over the three visits per census point and averaged over the three visits in each year to produce one measure of abundance for each species per site per year. I examined between-year differences in bird abundance using an ANOVA test (SAS Institute 2000) and because no differences were detected between years, I then averaged the abundance data for the two years. I calculated species richness at each census point for all species combined. I checked abundance and species richness data for normality and homogeneous variances and then used the GLM, which is an extension of traditional general linear models. GLMs are broad classes of models for continuous and categorical variables that use maximum likelihood estimation (Wald X) for model-fitting; McCullagh and Nelder 1989. Logistic regression of binary presence-absence data was used for most individual species, whereas normal linear regression was used for guilds, common species, and species richness data.

I summed numbers of bird species and guilds over the three point counts per census and averaged over the three visits each year to obtain a measure of relative abundance for each guild and species per census point per year. I classified bird species into 12 guilds (3 habitat, 3 migratory, and 6 nesting), based on criteria of Ehrlich et al. (1988) and Brooks and Cronquist (1990; Table 2.1). The 29 most common species in each zone were included in the analyses of species (55 species over both years). I tested for zone and year differences in species richness, total abundance of all species combined, abundances of guilds, and abundances of species using ANOVA. If these bird variables did not differ between years, data were averaged. I considered bird count data to be an estimate of relative bird abundance, which is an index of the density of each species based on a constant but unknown proportion of the population of that species (Bull 1981). I used Kruskal-Wallis tests for point-count comparisons; whenever I rejected the null hypothesis, I applied the mean comparison procedures suggested by Dunn (1964) with a 0.1 experiment-wise error rate.

I used factor analysis (FA) with Varimax rotation and Kaiser normalization (Norusis 1985) to identify principal components of the variance in our data that might reflect important ecological gradients in my study area. I used Varimax rotation (maximizing the variance of squared loadings for each factor), because it is purported to give a clearer separation of factors than other methods (Kim and Mueller 1978). Nichols (1977) suggested that interpretation of factors should be limited to the first three or four factors. Factors with eigenvalues >1 were extracted and a scree plot was used to set the number of factors to include in our model (Norusis 1985). Factor analysis of structural

Table 2.1 Names, status, codes, and guild classifications for the 29 bird species analyzed in this study.

Common name	Scientific name	Status	Alpha code	Habitat	Migratory	Nesting
Acadian Flycatcher	*Empidonax virescens (NM)*	CS*	ACFL	F	NM	SC
American Crow	*Corvus brachyrhynchos (PR)*	CR*	AMCR	F	PR	C
Black-capped Chickadee	*Poecile atricopillus (PR)*	FR* he	BCCH	F	PR	SN
Blue-headed Vireo	*Vireo solitarius (NM)*	CS* he	BHVI	F	NM^1/TM	SC
Blue Jay	*Cyanocitta cristata (PR)*	CR*	BLJA	F	PR	C/SC
Brown Creeper	*Certhia americana (PR)*	FR* he	BRCR	F/OT	PR	SN
Black-throated Blue Warbler	*Dendroica caerulescens (NM)*	CS* he	BTBW	F	NM	SC/SH
Black-throated Green Warbler	*Dendroica virens (NM)*	CS*	BTNW	F	NM	C/SC
Carolina Wren	*Thryothorus ludovicianus (PR)*	CR*	CARW	F	PR	GEN
Canada Warbler	*Wilsonia canadensis (NM)*	CS* he	CAWA	SH	NM	GR
Chestnut-sided Warbler	*Dendroica pensylvanica (NM)*	CS* he	CSWA	SH	NM	SH
Dark-eyed Junco	*Junco hyemalis (PR)*	AR* he	DEJU	F - GR	PR	GR
Eastern Towhee	*Pipilo erythrophthalmus (PR)*	CR*	EATO	SH/GR	PR	SH/GR
Golden-crowned Kinglet	*Regulus satrapa (PR)*	FR*	GCKI	SF	PR	C
Gray Catbird	*Dumetella carolinensus (NM)*	FS,* OW	GRCA	SH	NM^2/TM	SH
Hairy Woodpecker	*Picoides villosus (PR)*	FR*	HAWO	F	PR	SN
Hermit Thrush	*Catharus quttatus (TM)*	FW, US(*?)	HETH	F - GR	TM	SH/GR
Hooded Warbler	*Wilsonia citrina (NM)*	CS*	HOWA	SC	NM	SH
Indigo Bunting	*Passerina amoena (NM)*	C-AS*	INBU	SH	NM^3	SH
Northern Parula	*Parula americana (NM)*	FS*	NOPA	F	NM^4	SC/SH
Ovenbird	*Seiurus aurocapillus (NM)*	CS*	OVEN	F - GR	NM^5	GR
Pileated Woodpecker	*Dryocopus pileatus (PR)*	FR*	PIWO	F	PR	SN
Red-breasted Nuthatch	*Sitta canadensis (PR)*	FR* he	RBNU	SF	PR	C/SC
Red-eyed Vireo	*Vireo olivaceus (NM)*	AS*	REVI	C	NM	SC
Scarlet Tanager	*Piranga olivacea* (NM)	CS*	SCTA	C	NM	SC
Veery	*Catharus fuscescens (NM)*	CS* he	VEER	F - GR	NM	SH/GR
White-breasted Nuthatch	*Sitta carolinensis (PR)*	FR*	WBNU	F	PR	F
Winter Wren	*Troglodytes troglodytes (PR)*	CR* he	WIWR	SC	PR	SC
Wood Thrush	*Hylocichia mustelina (NM)*	CS*	WOTH	F - GR	NM	C/SC

Table 2.1 Continued

Habitat guild
F = forest(in general)
C = canopy
SC = subcanopy
SH = shrub
GR =ground
SF = Spruce-Fir
F-GR= forest ground
OT = old trees

Migratory guild
PR = permanent resident
TM = temperate or short distance migrant
NM = neotropical or long distance migrant

Nesting guild
C = canopy
SC = subcanopy
SH = shrub
GR = ground
SN = snag
GEN =forest edge or opening

STATUS CODE
A = abundant; over 25 seen on a given day in proper habitat/season
C = common; 5-25 seen per day in proper habitat/season
F = fairly common; at least one individual per day in proper habitat/season
U = uncommon; at least one seen per season of occurrence or several seen per year
O = occasional; one seen per year or less
X = rare; has been observed at least once, but is not to be expected
R = permanent resident
W = winter resident
S = summer resident
M = migrant

SPECIAL NOTATIONS
* = considered to breed within the park
* ? = suspected to breed within the park
he = high elevation

Alpha Code - pneumonic assigned by the American Ornithologists' Union (1957).

[1] Note: Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD?

[2] Note: Most GRCA winter in Central America some in South Florida and Gulf Coastal Plains

[3] Note: Many INBU winter on Coastal Plain of Gulf States and South Florida

[4] Note: Many NOPA winter on Coastal Plain of Gulf States and South Florida

[5] Note: Many OVEN winter on Coastal Plain of Gulf States and South Florida

variables generally produced four interpretable factors. Because factor analysis uses only shared variance (whereas principal component analysis uses the variance of all observed variables), variance due to error and variance unique to each variable is eliminated. Exploratory factor analysis summarizes data by grouping together variables that are correlated.

I used principal factor analysis (PFA), with the Varimax procedure to examine relationships among all study sites based on habitat and topographic characteristics. My approach was statistically to screen a large set of potentially important predictor ("independent") variables in an effort to quantify their individual and combined effects on community-level response variables which included measures of bird diversity, species abundance, species richness, and total species abundance.

I used Tukey's "Honestly Significant Difference" (HSD) test criterion to make pair-wise comparisons among means when the ANOVA was significant ($P<0.10$). To reduce the Type II error rate, which was more important because of the inherent variability in natural systems, I used $\alpha=0.10$ (Type I error rate) rather than the conventional 0.05.

Bird Assemblages and Zone Variation; Correlation Analysis

I applied Pearson and Spearman correlations to compare relative abundances of breeding birds and vegetation variables with elevation. Associations among the 33 habitat variables and the 29 bird species ($n=62$) were examined. Unless stated otherwise, all correlations between habitat and avian variables were based on $r>0.75$, $P<0.05$. To determine if distributional patterns of bird species corresponded to zones of habitat structure, I performed a cluster analysis on species abundances. Groups of plots were formed using the means of centroid and K-means procedures of amalgamating cases, based on the arithmetic mean of the Euclidean distances between pairs of abundances in different clusters (Dufrene and Legendre 1991; Finch 1991; Murray and Stauffer 1995).

Habitat structures were categorized into three zones (Finch 1989): (1) deciduous and hemlock sites (D or H; 700 to 1200 m), (2) hemlock, deciduous, and coniferous sites (H, D, or C; 1200 to 2000 m), and (3) mixed spruce-fir sites (SF; 2000 to 3000 m). To verify habitat variation among elevational zones or DCE (deciduous-coniferous ecotone) zones, a 2-factor ANOVA was performed on 19 habitat attributes to determine and adjust for the effects of census point variation before evaluating zone variation. Using census points as replicates within zones, I used ANOVA to determine if zones differed in overall habitat structure. To determine if patterns of species distribution were related to breaks in plant communities, I assessed overall and pairwise differences in mean counts among zones by a one-way ANOVA and Tukey's HSD test.

Correlation coefficients were calculated for all possible combinations of the 62 variables (29 birds plus 23 vegetation variables). Variables highly correlated with other variables ($r>0.7$), as well as those with F-statistics (from ANOVA) with an associated $P<0.05$ were removed before entry into the multivariate analyses. Relations between two sets of variables were tested using Pearson product moment correlation and Spearman correlation coefficients, whereas comparisons between means were made using the Kruskal-Wallis test (Sokal and Rohlf 1995). The latter two tests require neither assumption of homogeneity of variance nor equal sample sizes. The 33 vegetation variables produced by the modified James and Shugart (1970) method were reduced to 19 variables (Table 2.2) by eliminating redundant variables, using a >0.7 criterion (Noon

1981). Any remaining variables that were not normally distributed were either $\log_{10}$ or square-root transformed.

Cluster Analysis

An integrated sequence of multivariate procedures, involving both classification and ordination, was used to explore the vegetative and environmental relationships among the bird and vegetative communities. The sequencing and integration of the procedures are illustrated in Fig. 2.2.

Canonical analysis (CA) essentially provides an ordination of groups or community types in a space defined so as to best separate the groups (Cooley and Johnes, 1971). Cluster analysis searches for "natural" groupings within a collection of individuals. It does not, however, readily display the relationships among individuals and groups. This is better accomplished by ordination, a technique first used by Bray and Curtis (1957) to study stands of vegetation.

I used the centroid linkage method and the Chi-square distance measure (SAS Institute 2000) cluster analysis (Digby and Kempton 1987), based on relative abundances at census points, to identify bird species with similar distributions among the 212 census points. I assumed these species to be similar in their use of habitat and grouped them to form an assemblage, defined here as being a group of species using similar habitats. Distribution patterns in relation to community types were analyzed through Cluster Analysis using squared Euclidean distance (Digby and Kempton 1987).

Factor Analysis; Canonical Correlation Analysis

An ordination of the plots was constructed by a principal axis factor analysis (FA) of the habitat variables with a varimax rotation (Greig-Smith 1964; Overall and Klett

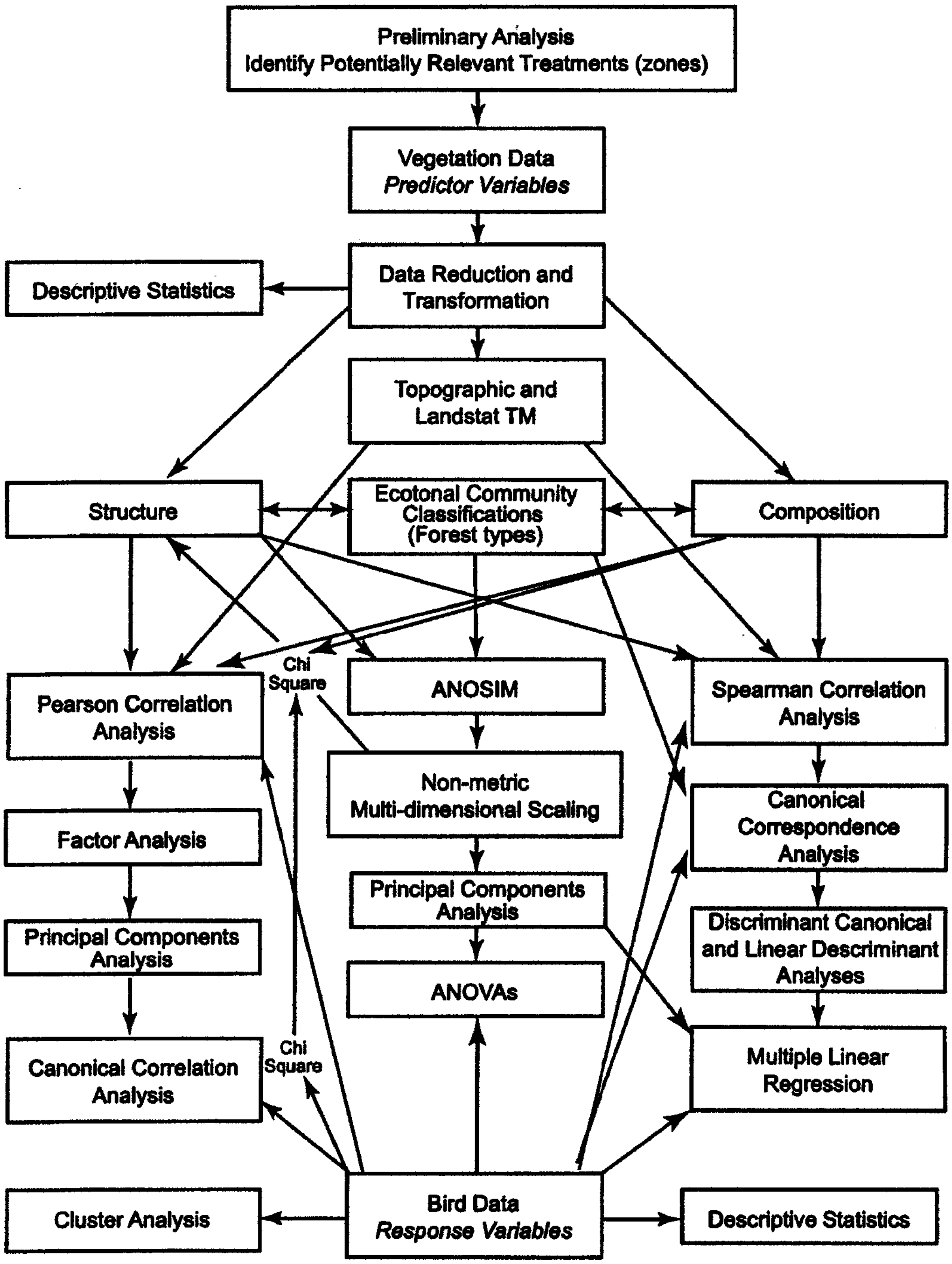

Fig. 2.2 Flowchart of statistical tests used to analyze variables of vegetation and birds.

Table 2.2 Habitat measures and environmental parameters used as independent variables in statistical analyses on Mount LeConte, GSMNP, 2000.[1]

Abbreviation	Variable/Parameter	Description/Explanation
$\bar{x}$DBH	Average or Mean Diameter at Breast Height	Mean diameter at breast height (cm) for each tree. *I took the midpoint for each category* (i.e. if the category is 0-10, then I used 5) and I multiplied that by the number in that category for that species and that point. I then added all those numbers together for all those categories for a particular species point. That gave me a total dbh for that species at that point. The "average" is because I then averaged it over the species and trailpoint, in case there was more than one visit. If there was only one visit, then the average is a misnomer and it is actually the total dbh. So, for example, for yellow birch at ACT 10, if there were 6 counts in dbh 0-10 and 4 counts in dbh 26-50, then the total dbh would be 6 * 5 + 4 * 37.5 = 180. I could then take the 180 and divide it by the counts to get an average dbh for yellow birch for ACT 10 of 18.
TTLDBH	Total Diameter Breast Height	Mean total diameter at breast height (cm) all diameters of trees within a 0.04 ha plot were summed. This is an estimate of quantity of wood and therefore clutter at the site.
DBH_CAN	Diameter at Breast Height of canopy trees	Mean diameter breast height for canopy trees (cm).
DBH_SUB	Diameter at Breast Height of subcanopy trees	Mean diameter breast height for subcanopy trees (cm).
$\bar{x}$SPDENS	Mean Species Density	TTL species density (N/.04 ha) by adding up all the tree counts (stems) in the 6 dbh categories by each species and trailpoint. The average species density is just the average of the species density – total number of trees within each plot.
DEN_CAN	Density of canopy trees	Density (N/.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species.
DEN_SUB	Density of subcanopy trees	Density (N/.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species
CANCLS	CANOPY CLASS	Mean canopy cover of canopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .

Table 2.2 Continued.

Abbreviation	Variable/Parameter	Description/Explanation
SUBCLS	SUBCLASS	Mean canopy cover of subcanopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .7
TALLCLS	TALL CLASS	Mean canopy cover of tall shrubs and saplings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
LOWCLS	LOW CLASS	Mean canopy cover of low shrubs and seedlings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
CANCC	Tree Canopy Cover Class at each site	Mean cover (%) of tree (tall) canopy trees measured at 4 cardinal directions with convex densiometer at each site.[2]
SUBCC	Subcanopy Cover Class	Subcanopy trees
TSHBCC	Tall Shrub Cover Class	Tall shrubs, saplings
LSHBCC	Low Shrub Cover Class	Low shrubs, seedlings
GRNDCC	Ground Cover Class	Ground vegetation
TCANHR	Foliage Height Range of Tree Canopy	Mean height (m) of tree canopy trees. Estimate from 4 samples measured with clinometer at each site.
SUBCHR	Foliage Height Range of Subcanopy	Mean height (m) of subcanopy trees. Estimate from 4 samples measured with clinometer at each site.
TSHBHR	Foliage Height Range of Tall Shrub	Mean height (m) of tall shrubs, saplings. Estimate from 4 samples measured with clinometer at each site.
LSHBHR	Foliage Height Range of Low Shrub	Mean height (m) of low shrub, seedlings. Estimate from 4 samples measured with clinometer at each site.

Table 2.2 Continued.

Abbreviation	Variable/Parameter	Description/Explanation
GHR	Ground Cover Height Range of Foliage	Mean height (m) of ground vegetation. Estimate from 4 samples measured with clinometer at each site.
TCAP_B	T-CAP – Brightness	Positive or negative values.
TCAP_G	T-CAP – Greenness	Positive or negative values.
TCAP_W	T-CAP – Wetness	Positive or negative values.
% C, D, H	Tree composition of canopy	Coniferous, deciduous, hemlock
% C, D, H	Tree composition of subcanopy	Coniferous, deciduous, hemlock
ELEV.	Elevation (m)	m, as determined by Arc View Spatial Analyst
SLOPE	Slope	Degrees, as determined by Arc View Spatial Analyst
ASPECT	Aspect	N, NE, E, SE, as determined by Arc View Spatial Analyst S, SW, W, NW
DIST.	Disturbance	Defined by trees felled by windthrow or man
FO	Forest opening	Presence or absence of a significant opening in the forest, such as those resulting from a tree fall within the 0.04 ha sampling plot
LOGS	Logs (>10 cm dbh)	Presence or absence of logs in the forest, such as those resulting from a tree fall within the 0.04 ha sampling plot
SNAGS	Snags (>10 cm dbh)	Presence or absence of standing dead trees within the 0.04 ha sampling plot

[1] Several parameters describing vegetational structure were derived from vegetation sub-samples. These included mean dbh, total dbh, mean species density, tree composition of canopy, tree composition of subcanopy, dbh of canopy trees, dbh of subcanopy trees, density of canopy trees, and density of subcanopy trees. Floristic information was not included in the analysis, except for the species of dominant tree(s) in the canopy..

[2] The arithmetic mean or average was the sum of the measures of canopy cover by species at the sampling station divided by number of measures. Example: 1=class value: 0.1=numeric value.

of the habitat variables with a varimax rotation (Greig-Smith 1964; Overall and Klett 1972; Barr et al. 1976).

Factor analysis, a common technique for data reduction, orthogonalization, and hypothesis testing, was applied to the problem of identifying suites of patterns and environmental variables that are "linked". In GLMs, the problem of collinearity, often encountered, is overcome through factor analysis and the use of orthogonal variables [e.g., principal components analysis (PCA); Kleinbaum et al. 1988]. In order to relate multiple dimensions of ecotone structure to multiple bird and vegetation variables, correlations among the dependent and independent variables were examined. The primary method was canonical correlation analysis (CANCOR).

One recommended procedure before canonical analysis is the use of either orthogonalized variables (derived from a linear combination of other variables and uncorrelated with fellow orthogonal variables) or surrogates (Bernstein 1988). However, canonical analyses are easily abused and often degenerate into "fishing expeditions" when investigators fail to consider the theoretical aspects of variables. Further, inclusion of correlated dependent or independent variables may lead to misinterpretation of relationships in canonical analyses (Dillon and Goldstein 1984). For this reason, factor analysis was used to quantify the groupings of bird and vegetation variables (i.e. to confirm which variables were related as sets). Ideally, separate factors of bird abundance and vegetation variables would then be used on CANCOR. If factor analysis models proved difficult to interpret, backup methods included correlation analysis and the use of surrogate variables in CANCOR.

A review of the factor analysis literature indicated that iterative analyses (repeated factor generation with different variable combinations) and comparisons would yield the most reliable results (Dillon and Goldstein 1984; Hair et al. 1987; Bernstein 1988). Parameters of selected factor analyses included orthogonal axes, varimax rotation of axes, and Pearson correlation matrices for eigenanalyses. For vegetation variables, the five hypothesized "groups" of variables followed those of the prior ANOVA analysis: 1) coverage, 2) horizontal structure, and 3) vertical structure. It was hypothesized that the input variables (a subset of the entire set of pattern metrics) would form axes representing these factors. Although a confirmatory factor analysis was considered, a qualitative assessment of the hypothesized variable groups was sufficient, because variable loadings on output axes could be interpreted through eigenvectors. Eigenvalues (also expressed as percent of total variance explained) and scree plots were used to determine the best factor model. Rotated factor axes were interpreted using eigenvectors and a specified threshold (1.0) value for inclusion in a set of potential loading variables. Initial factor names were assigned from the input variables with the highest loadings. If a factor was otherwise poorly interpretable, such a variable served as a potential surrogate.

Factor analysis of terrain variables included tests of both common factor models and principal components analysis (PCA). It was hypothesized that 23 vegetation variables (disturbance, elevation, forest opening, slope, snags, DBH_CAN, DBH_SUB, DEN_CAN, DEN_SUB, CANCC, SUBCC, TSHBCC, LSHBCC, GRNDCC, CANCLS, SUBCLS, TALLCLS, LOWCLS, CANHR, SUBCHR, TSHBHR, LSHBHR, and GHR; Table 2.2) would be summarized by four to six axes. Five topographic variables were input to the factor model algorithms, including the vegetation gradients. Eigen-analysis for the factor and PCA model was based on the Pearson correlation matrix, varimax rotation, and 10 iterations. This was performed for scenarios of three, four, and five factors (scree plots of eigenvectors fell off rapidly beyond five factors). Eigenvectors were analyzed as in the pattern factor model.

Principal factor analysis describes bird distribution objectively as ordinations of continuously varying phenomena along gradients of vegetation structure. Factor analysis is similar to PCA in that each test reduces the habitat variables in a multidimensional space to a linear component. PCA scales the variables so that the sum of the squares for the element in each vector equals one. When this is done, the associated eigenvalue (characteristic root) is interpreted as the variance along the principal component axis. Vectors in factor analysis are scaled so that the coefficients are the correlation coefficients with the original measurements.

Species-Habitat Relationships/Associations

I applied principal factor analysis with varimax rotation to the matrix of 112 samples by 33 habitat variables to determine trends in plant community structure. High correlations of habitat variables with the principal factor scores from the reduced set of PCs were used to interpret each component. To determine if abundances of different bird species varied with specific habitat axes, simple correlations were calculated between the factor scores of each component (eigenvalues >1.0) averaged by census point.

Because of the high number of habitat variables (n=33), I reduced vegetation variables to 23 composite variables representing specific habitat attributes. I first separated variables describing over- and understory tree layers and conducted principal factor analyses (Digby and Kempton 1987) on these two group variables. I removed species with low importance values (factor loadings <absolute value 0.45 and 0.40 for

over- and understory variables, respectively) in the first four components from further analysis. I submitted variables retained in analysis in each group to a second principal factor analysis. Variables correlated with the first four components with absolute values <0.5 were removed as in the previous step. I then conducted principal factor analysis on the remaining habitat variables. I combined habitat variables with similar factor loadings on any of the first seven components. I assumed that variables with similar scores on components represented similar habitat characteristics.

The 23 habitat variables that were included in the factor analysis (PCA; PROC PRINCOMP; SAS Institute 2000) were: DBH_CAN, DBH_SUB, DEN_CAN, DEN_SUB, CANCC, SUBCC, TSHBCC, LSHBCC, GRNDCC, CANCLS, SUBCLS, TALLCLS, LOWCLS, TCANHR, SUBCHR, TSHBHR, LSHBHR, and GHR (Table 2.2). This approach was taken because it minimized the number of vegetation variables; thus, it simplified interpretation, yet provided measures of structure for 5 primary habitat layers and included 2 variables (DBH_CAN, DEN_CAN) commonly inventoried by forest managers. For inclusion in analyses of bird-habitat relationships, I selected only those principal components with eigenvalues >1.0. The original variables (tree species dbh, percent canopy cover, site percent canopy cover class, and foliage height diversity) and the principal components scores (PC1 and PC2) were compared among zones with ANOVA.

Canonical Correlation Analysis

Canonical correlations were run on appropriate samples of the data set with the CANCOR procedure of SAS (Barr et al. 1976). I shall refer to a linear compound variable of original variables produced by the procedure CANCORR as a canonical variate, and coefficients of the variates associated with each original variable as factors. In two-group canonical analysis, pairs of canonical variates are produced, each of which contains one variate of bird factors and one variate of environmental (habitat and/or topographic) factors. The first pair has a maximum possible correlation. The second pair is maximally correlated, given that each is orthogonal to its corresponding variate in the first pair, and so on. Usually, only the "significant" correlations and their corresponding variate pairs are considered in evaluation of the relationships. In the usual approach to canonical analysis, the observations are plotted in variate space using either set of variates, and these observations are then clustered to look for relationships among the observations in the variate space. Thus, variates are used to establish relationships among observations, and canonical correlations are used to measure how well the two sets of variates provide the same set of relationships among observations. The interpretation of each variate is usually accomplished by considering simple correlations of each of the variables with the variate.

In my study, emphasis was on the bird community rather than on individual observations; thus, I chose canonical correlation as the technique of classification based directly on relationships of the bird species to environmental variables rather than indirectly through "association" or "distance" relationships among birds themselves. Consequently, rather than group observations based on variate factors (as is normally done), I sought to group species of birds based on their simple correlations with the variates, using the variates as a means of establishing structural relationships between birds and zonal environmental variables.

For inclusion in the Canonical Correlation Analysis of bird-habitat relationships, I selected only those PCs from FA and PCA with eigenvalues >1.0. The original variables in the FA and the principal factor scores (PC1 and PC2) were compared among DCE zones with ANOVA.

Results

In analyzing the vegetation data I found that only four of the six gradsects sampled (ACT, BHT, RFT, and TGT) traversed and included low, mid, and high elevations of forest communities. In addition, these four trails also contained more complete elevation and vegetation characteristics up the gradients than the BVT and BMT gradsects. Therefore, I omitted the latter two trails from all further analyses.

Community and Classification Composition

The study area was mapped in GIS according to forest type (TNC), by Aerial Information Services on behalf of TNC and NPS (Fig. 2.3). The basic unit of the mapping system was the forest association, an area of forest that is represented by roughly homogeneous composition of tree species, forest types.

Vegetational Characteristics and Differences among Zones

Dbh of canopy trees differed significantly among three zones (below DCE, DCE, above DCE) in all classes except >100 cm; this size class was not able to be analyzed due to low sample size (three trees total; Table 2.3). Cover of tall shrubs and saplings of tree species (TALL-CLS) in the canopy and subcanopy differed significantly ($\chi2 = 10.61$, df = 2, $P<0.005$) among zones, but only cover of subcanopy tree species (SUB-CLS) differed significantly ($\chi2 = 9.6$, df = 2, $P<0.01$; Table 2.3). Canopy cover of tall shrubs and saplings (TSCC) and subcanopy trees (SCCC) were highest below the DCE, and differed significantly among the zones (all except TSCC subcanopy of $P=0.23$,

Fig. 2.3 GIS image of the deciduous-coniferous ecotone and forest communities on Mount LeConte, GSMNP. Numbers represent census points on gradsects. Geo-referenced points identified with The Nature Conservancy (1999) community codes were used to delineate the ecotonal boundaries. Numbers represent census points on gradsects. White lines partition three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above DCE.

Table 2.3 Comparisons of habitat structure and composition (mean/0.04 ha ± SE) among three zones on Mount LeConte, GSMNP. N=657. Abbreviations are defined as follows: Dbh = diameter at breast height; LOW_CL = cover of low shrubs/seedlings of tree species, class; TALL_CL = cover of tall shrubs/ saplings of tree species, class; SUB_CLS = cover of subcanopy tree species, class; CAN_CLS = cover of canopy tree species, class; GCC = canopy cover of ground vegetation; LSCC = canopy cover of low shrub/seedling trees; TSCC = canopy cover of tall shrub/sapling trees; SCCC = canopy cover of subcanopy trees; TSCC = canopy cover of canopy trees; GHR = height range of ground vegetation; LSHR = height range of low shrubs/seedling trees; TSHR = height range of tall shrubs/sapling trees; SCHR = height range of subcanopy trees; TCHR = height range of canopy trees.

	Below DCE Elevation Zone 1		DCE Elevation Zone		Above DCE Elevation Zone 3		Test Statistic	
Variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Features of Forest Structure								
Dbh 0-10								
Canopy	5.3	0.7	3.8	0.3	11.5	1.4	47.23	<0.0001
Subcanopy	2.0	0.3	2.1	0.3	3.4	0.7	5.33	0.068
Dbh 11-25								
Canopy	2.8	0.4	1.5	0.2	12.9	2.4	88.22	<0.0001
Subcanopy	2.2	0.2	1.5	0.2	3.3	0.5	12.18	0.0023
Dbh 26-50								
Canopy	1.8	0.2	1.7	0.1	2.1	0.2	2.56	<0.0001
Subcanopy	0.6	0.1	0.6	0.1	1.4	0.4	2.32	0.313
Dbh 51-75								
Canopy	1.3	0.2	0.7	0.1	0.4	0.1	16.54	0.0003
Subcanopy	0.1	0.0	0.1	0.0	0.2	0.1	6.62	0.047
Dbh 76-100								
Canopy	0.3	0.1	0.4	0.0	0.0	0.0	43.26	<0.0001
Subcanopy	0.0	0.0	0.0	0.0	0.1	0.0	15.37	0.0005
Dbh >100								
Canopy	0.0	0.0	0.0	0.0	0.0	0.0	–	–
Subcanopy	0.0	0.0	0.0	0.0	0.0	0.0	–	–
Features of Canopy Coverage of Tree Species								
LOW_CLS								
Canopy	0	0	3.46	0.312	3.38	0.22	0.0069	0.9337
Subcanopy	0.2	0.1	0.2	0.0	0.1	0.0	4.5	0.03
TALL_CLS								
Canopy	4.15	0.174	4.3	0.126	5.6	0.15	55.45	<0.0001
Subcanopy	3.3	0.146	4.127	0.238	4.285	0.32	10.61	0.005
SUB_CLS								
Canopy	4.85	0.24	5.21	0.15	5.5	0.369	2.77	0.25
Subcanopy	3.78	0.15	4.66	0.28	4.74	0.23	9.6	0.0082
CAN_CLS								
Canopy	7.07	0.2	7.27	0.125	6.83	0.138	5.26	0.0719
Subcanopy	5.5	0.866	6.4	0.6	7	0.1	7.94	0.0189

Table 2.3 Continued

Variable	Below DCE Elevation Zone 1		DCE Elevation Zone		Above DCE Elevation Zone 3		Test Statistic	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Features of the Forest Type								
TCCC								
Canopy	7.49	0.1	7.56	0.09	6.87	0.11	25.49	<0.0001
Subcanopy	7.39	0.1	6.97	0.19	6.96	0.21	1.61	0.4453
GHR								
Canopy	0.374	0.05	0.458	0.025	0.233	0.005	40.65	<0.0001
Subcanopy	0.389	0.038	0.381	0.014	0.254	0.007	22.7	<0.0001
LSHR								
Canopy	1.18	0.048	1.647	0.065	1.57	0.03	81.83	<0.0001
Subcanopy	1.15	0.029	1.622	0.03	1.568	0.26	171.89	<0.0001
TSHR								
Canopy	4.58	0.04	4.997	4.997	4.74	0.12	0.5512	0.7591
Subcanopy	4.52	0.029	4.997	4.997	4.778	0.09	3.45	0.1778
SCHR								
Canopy	16.062	0.388	16.4	0.24	12.79	0.379	56.55	<0.0001
Subcanopy	15.7	0.23	15.47	0.23	13.22	0.279	55.25	<0.0001
TCHR								
Canopy	20.757	0.398	22.95	0.267	17.272	0.378	113.52	<0.0001
Subcanopy	20.8	0.244	21.11	0.28	17.668	0.281	113.76	<0.0001
Composition % Conifer								
ACT	0.0	0.0	14.5	0.74	19.97	1.37	80.84	<0.0001
BHT	0.0	0.0	7.43	1.16	15.17	1.17	84.52	<0.0001
BMT	0.89	0.36	1.56	0.56	–	–	1.43	0.2316
BVT	–	–	68.33	4.87	67	0.0	1.20	0.2729
RFT	0.0	0.0	2.85	0.5	15.61	1.23	92.5	<0.0001
TGT	0.0	0.0	4.56	0.51	18.8	1.08	174.79	<0.0001
ALL	5.89	0.53	11.39	0.62	15.76	0.65	142.38	<0.0001
% Deciduous								
ACT	91.97	1.23	85.5	0.74	80.03	1.37	31.23	<0.0001
BHT	83.77	1.27	85.8	1.37	92.73	0.9	7.87	0.0195
BMT	94.25	0.88	89.06	1.41	–	–	10.21	0.0014
BVT	–	–	23.13	4.35	33	–	3.11	0.0776
RFT	95.94	0.56	91.45	0.79	84.39	1.23	16.53	0.0003
TGT	95.13	0.47	86.84	0.8	81.2	1.08	55.57	<0.0001
ALL							60.01	<0.0001
% Hemlock								
ACT	8.03	1.23	0.0	0.0	0.0	0.0	210.19	<0.0001
BHT	1.06	0.27	6.78	0.47	7.27	0.9	97.94	<0.0001
BMT	4.86	0.68	9.38	1.2	–	–	12.61	0.0004
BVT	–	–	8.54	3.1	0.0	0.0	0.276	0.5995
RFT	4.06	0.56	5.7	0.52	0.0	0.0	107.93	<0.0001
TGT	4.87	0.47	8.6	0.42	0.0	0.0	234.44	<0.0001
ALL	3.72	0.26	5.47	0.28	1.02	0.15	198.65	<0.0001

Table 2.4 Topographic and ecotonal community vegetation associations for trail point data: Alum Cave Trail (ACT), Bullhead Trail (BHT), Rainbow Falls Trail (RFT), Trillium Gap Trail (TGT); length 7.88 km., elevational gain 831 m. ECC = ecotonal community classification, abbreviations are defined in Appendix A. Three zones identified by gradsect or transition with hard boundary = **, all other transitions are soft boundaries = *. BHT Trail points were sampled from highest to lowest elevation.

Ecotonal Zone	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
1	ACT 01	7861	1171	6.20	SW	HH
1	ACT 02	7861	1183	9.97	NW	HH
1	ACT 03	7861	1232	4.39	SW	HH
1	ACT 04	7861	1214	3.64	SW	HH
1	ACT 05	7861	1232	4.26	SW	HH
1	ACT 06	7861	1255	8.11	S	HH
1	ACT 07	7861	1191	5.05	SW	HH
1	ACT 08	7861	1182	9.74	NW	HH
1	ACT 09**	7861	1170	6.28	NW	HH
2	ACT 10	114	1370	22.75	SE	SNH
2	ACT 11	114	1398	25.60	E	SNH
2	ACT 12**	6272	1408	30.78	E	SF
2	ACT 13	3814	1433	18.77	S	B
2	ACT 14	3814	1479	37.32	SW	B
2	ACT 15	114	1496	40.15	SS	NH
2	ACT 16	114	1530	29.94	SS	NH
2	ACT 17	112	1570	37.87	W	SF
2	ACT 18	112	1594	32.81	NW	SF
2	ACT 19	114	1587	22.65	NS	NH
2	ACT 20	112	1575	8.64	W	SF
2	ACT 21	112	1591	32.45	SE	SF
2	ACT 22	112	1626	35.59	S	SF
2	ACT 23	112	1654	32.96	SE	SF
2	ACT 24	112	1712	41.51	SE	SF
2	ACT 25	114	1740	40.57	S	SNH
2	ACT 26**	112	1791	37.80	SE	SF
3	ACT 27	6049	1827	34.81	SW	F
3	ACT 28	6049	1844	34.11	SE	F
3	ACT 29	112	1879	22.60	SS	F
3	ACT 30	7876	1880	39.02	SW	B
3	ACT 31	112	1946	29.14	SW	SF
3	ACT 32	6049	1939	19.52	NW	F
3	ACT 33	6049	1938	15.80	NE	F
3	ACT 34	6049	1941	11.80	NE	F
3	ACT 35	6049	1949	7.83	N	F
3	ACT 36	6049	1979	10.60	W	F
3	ACT 37	6049	1999	10.11	SW	F
3	ACT 38	6049	2002	10.74	N	F
1	BHT 34	6192	787	18.75	S	MO
1	BHT 33	6271	807	14.54	N	XO
1	BHT 32	6271	844	7.91	N	XO
1	BHT 31	6271	886	21.01	N	XO
1	BHT 30	6271	920	33.55	W	XO

Table 2.4 Continued

Ecotonal Zone	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
1	BHT 29	6286	970	35.81	NE	MO
1	BHT 28	6271	995	35.66	W	XO
1	BHT 27**	312	1007	35.43	W	CH
1	BHT 26	312	1087	30.43	N	CH
1	BHT 25	312	1074	22.20	NE	CH
1	BHT 24	6271	1102	37.38	NW	XO
1	BHT 23	7861	1147	38.63	N	HH
1	BHT 22	7861	1186	25.75	SW	HH
2	BHT 21	6271	1225	29.21	SW	XO
2	BHT 20	7097	1249	22.01	S	P
2	BHT 19	7097	1257	24.46	N	P
2	BHT 18	4973	1294	23.27	W	NH
2	BHT 17	7861	1323	24.83	N	HH
2	BHT 16	4973	1350	28.80	NW	NH
2	BHT 15	7861	1433	40.39	SW	HH
2	BHT 14	3814	1462	45.04	NW	B
2	BHT 13**	114	1488	36.24	W	SNH
2	BHT 12	114	1522	20.15	SW	SNH
2	BHT 11	7285	1564	33.21	W	NH
2	BHT 10	114	1608	28.77	S	SNH
2	BHT 09	114	1632	29.90	S	SNH
2	BHT 08	112	1668	24.28	S	SF
3	BHT 07	114	1710	23.67	S	SNH
3	BHT 06	114	1733	25.13	S	SNH
3	BHT 05	114	1737	36.25	NW	SNH
3	BHT 04	6124	1755	29.17	NW	NH
3	BHT 03**	112	1759	32.11	NE	SF
3	BHT 02	6124	1790	31.14	N	NH
3	BHT 01	112	1798	35.62	NW	SF
1	RFT 01	7543 (7219*)	818	8.61	NW	CH
1	RFT 02	7543 (7219*)	858	10.21	NW	CH
1	RFT 03**	7543 (7219*)	892	14.60	W	CH
1	RFT 04	6271	926	11.39	NW	XO
1	RFT 05	7693 (6271*)	937	13.25	W	CH
1	RFT 06	6271	999	16.41	W	XO
1	RFT 07	6271 (7097*)	1023	25.35	SW	XO
1	RFT 08	6271	1076	21.19	W	XO
1	RFT 09	6192 (6271*)	1091	19.73	SW	MO
1	RFT 10**	6271	1122	21.64	SW	XO
2	RFT 11	7861 (132*)	1134	13.96	NW	HH
2	RFT 12	6192	1167	23.03	N	MO
2	RFT 13	7693	1207	28.51	W	CH
2	RFT 14	7693	1228	30.76	NE	CH
2	RFT 15	7861	1344	28.46	NW	HH
2	RFT 16	4982	1350	23.20	NW	NH
2	RFT 17	4982	1495	30.76	W	NH
2	RFT 18	4982	1544	33.39	N	NH
2	RFT 19	7861 (7285*)	1389	30.48	N	HH

Table 2.4 Continued

Ecotonal Zone	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
2	RFT 20	7285	1412	32.50	SW	NH
2	RFT 21	6192	1444	32.53	SW	MO
2	RFT 22	7285	1468	33.12	SW	NH
2	RFT 23	7119 (4973*)	1484	43.58	NW	P
2	RFT 24	4973	1523	31.05	N	NH
2	RFT 25	7861 (4973*)	1550	29.81	N	HH
2	RFT 26	7285	1574	34.73	N	NH
2	RFT 27**	7285	1584	34.50	N	NH
3	RFT 28	6124	1610	34.89	NW	NH
3	RFT 29	114	1636	27.09	N	SNH
3	RFT 30	114	1662	35.64	N	SNH
3	RFT 31	112	1677	16.91	W	SF
3	RFT 32	114	1680	32.49	SW	SNH
3	RFT 33	112 (114*)	1737	16.36	SW	SF
3	RFT 34	112	1756	18.48	SW	SF
3	RFT 35	114	1785	11.65	NW	SNH
3	RFT 36	6049	1803	22.94	N	F
3	RFT 37	112 (114*)	1832	29.03	N	SF
3	RFT 38	6049	1866	28.26	N	F
3	RFT 39	112	1901	18.44	N	SF
3	RFT 40	6049	1936	15.57	NE	F
1	TGT 01	7219	797	11.97	N	TP
1	TGT 02**	7230	821	9.37	NW	MO
1	TGT 03	6271 (6286*)	839	10.10	W	XO
1	TGT 04	6271	884	18.80	W	XO
1	TGT 05	6271	887	11.08	N	XO
1	TGT 06	6192	898	12.45	N	MO
1	TGT 07	6192	930	25.63	W	MO
1	TGT 08	6271	954	34.40	W	XO
1	TGT 09	312 (7693*)	954	26.60	NE	CH
1	TGT 10**	6271	952	23.37	N	XO
2	TGT 11	7693	984	11.65	N	CH
2	TGT 12	7693	992	20.24	NE	CH
2	TGT 13	7693	1010	30.75	NE	CH
2	TGT 14	7693	1048	30.66	NE	CH
2	TGT 15	7693	1072	31.29	NE	CH
2	TGT 16	7693	1108	15.64	N	CH
2	TGT 17	7861	1120	25.99	NE	HH
2	TGT 18	7861	1128	14.62	N	HH
2	TGT 19	7861	1176	22.43	NW	HH
2	TGT 20	7693	1202	29.56	N	CH
2	TGT 21	7693	1259	25.18	NE	CH
2	TGT 22	7693	1274	19.29	N	CH
2	TGT 23	7861 (4973*)	1314	21.75	N	HH
2	TGT 24	4973	1322	28.95	NE	NH
2	TGT 25	7861	1333	32.60	NE	HH
2	TGT 26	4973	1380	26.81	W	NH

Table 2.4 Continued

Ecotonal Zone**	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
2	TGT 27	7861 (4973*)	1415	18.88	NW	HH
2	TGT 28	7285	1434	5.40	N	NH
2	TGT 29	7861 (4973*)	1465	24.70	NW	HH
2	TGT 30	6272	1504	29.60	W	SF
2	TGT 31	7861 (6272*)	1518	33.06	W	HH
2	TGT 32	6272	1533	28.05	N	SF
2	RFT 23	7119 (4973*)	1484	43.58	NW	P
2	RFT 24	4973	1523	31.05	N	NH
2	TGT 33	7861 (6272*)	1552	29.85	NE	HH
2	TGT 34**	7861	1548	30.96	N	HH
3	TGT 35	114 (7285*)	1576	28.86	W	SNH
3	TGT 36	114	1583	39.41	SW	SNH
3	TGT 37	114	1590	41.04	W	SNH
3	TGT 38	114	1629	36.34	W	SNH
3	TGT 39	114	1636	10.03	N	SNH
3	TGT 40	7285	1666	39.24	N	NH
3	TGT 41	114 (7285*)	1687	33.76	N	SNH
3	TGT 42	114	1705	28.21	NW	SNH
3	TGT 43	112 (7285*)	1714	34.87	SE	SF
3	TGT 44	114	1774	32.36	E	SNH
3	TGT 45	114 (7285*)	1790	29.15	E	SNH
3	TGT 46	114	1810	23.49	N	SNH
3	TGT 47	112 (114*)	1841	16.18	NW	SF
3	TGT 48	114	1839	31.58	N	SNH
3	TGT 49	6049 (114*)	1896	12.81	NW	F

$P<0.0001$). Foliage height range of ground cover (GHR), low shrubs and seedlings (LSHR), subcanopy trees (SCHR), and canopy trees (TCHR) were highest in the hypothesized ecotone, and all differed significantly ($P<0.0001$). In general, percent compositions of coniferous, deciduous and hemlock trees all differed significantly among zones (Tall $P<0.0001$). Percent conifer was greatest on the four primary trails above the DCE, whereas percent deciduous was greatest below the DCE. Percent hemlock was greatest in the DCE.

These measurements described features that fall into two basic categories: coverage and structure (derived from Table 2.3). "Coverage", simply the percent coverage of various physiognomic classes (low shrubs, seedlings, tall shrubs, saplings, subcanopy and canopy trees), was obtained from the frequency of occurrence of these types at all sample points within a plot. Also included in this category were the total density of all forms and woody vegetation (i.e. shrubs and cacti) and the density of woody plants alone, estimated from the point-quarter method. "Structural" variables had the additional property of "dimension", i.e. variation in a structural index generally associated with spatial variation in either horizontal or vertical plane. "Composition", the percent coniferous (C), deciduous (D), and hemlock (H), was calculated using tree dominance such that if a point had an Eastern hemlock in it, then that record was given a value of H. If that point also had a deciduous tree, then it would have another record with a value of D. To obtain the percent D, C and H for each point, I summed the number of records.

Topographic and Elevational Variables

Elevation, slope, and aspect for each trail are indicated in Table 2.4. I used the geo-referenced points identified with TNC community codes to delineate the ecotonal boundaries (Fig. 2.3).

Relative Bird Abundance and Species Richness

Table 2.5 lists the 29 most commonly observed birds (heard or seen) at the study plots. I compared bird counts within the census plots with the coverages of the communities in the landscape. Bird survey data from 1999 were compared with those from 2000. Abundances of bird species in habitat coverages were not statistically different between years, so I pooled data from 1999 to 2000 to improve statistical power (Snedecor and Cochran 1989).

In 1999 and 2000, I recorded 7,030 observations, which represented 5,707 birds and 63 species. I omitted species with fewer than 20 observations from the analysis, resulting in 29 species. The distributions of these 29 species were subjected to additional statistical analysis (see below). Ten species accounted for nearly 75% of all observations and seven of those most frequent birds were observed at high elevation (>1400 m). Of the 63 species of birds, 15 (51%) were Neotropical (long-distance) migrants, three (1.0%) were temperate (short-distance) migrants, and 13 (44%) were permanent residents. Seventeen of these 63 species were recorded 12 or more times on the four primary gradsects.

Elevational Gradients

Elevational gradients as determinants of bird species distributions were tested using a contingency table Chi-Square analysis. The observed elevational distribution of birds differed significantly from the expected (Table 2.6; $\chi^2 = 34.7$, df=56, $P<0.05$). The null hypothesis predicted one-third in each group (low, middle, high), but more birds than

Table 2.5 Summary statistics for the 29 most frequently observed bird species. Based on 1999 and 2000 data combined.

Bird Species	Total Individuals Detected	Percent of Points Individuals Heard[1]	Total Number Where Heard Species[2]	Percent of Points With Species[3]	Mean Species Detected Per Point[4]
Dark-eyed Junco	703.2	16.7%	161	78.9%	4.4
Veery	407.0	9.7%	129	63.2%	3.2
Winter Wren	404.0	9.6%	138	67.6%	2.9
Blue-headed Vireo	330.8	7.9%	133	65.2%	2.5
Black-throated Blue Warbler	321.9	7.6%	123	60.3%	2.6
Golden-crowned Kinglet	316.2	7.5%	105	51.5%	3
Black-throated Green Warbler	264.1	6.3%	97	47.5%	2.7
Black-capped Chickadee	154.4	3.7%	76	37.3%	2
Red-breasted Nuthatch	147.6	3.5%	88	43.1%	1.7
Canada Warbler	140.3	3.3%	71	34.8%	2
Chestnut-sided Warbler	119.2	2.8%	48	23.5%	2.5
Eastern Towhee	116.6	2.8%	59	28.9%	2
Ovenbird	108.0	2.6%	29	14.2%	3.7
Red-eyed Vireo	87.0	2.1%	32	15.7%	2.7
Brown Creeper	74.8	1.8%	49	24.0%	1.5
Hairy Woodpecker	70.8	1.7%	43	21.1%	1.6
Hermit Thrush	49.2	1.2%	24	11.8%	2
Wood Thrush	48.5	1.2%	19	9.3%	2.6
Scarlet Tanager	48.3	1.1%	27	13.2%	1.8
Hooded Warbler	41.7	1.0%	23	11.3%	1.8
Blue Jay	37.2	0.9%	28	13.7%	1.3
Carolina Wren	34.3	0.8%	26	12.7%	1.3
Acadian Flycatcher	32.5	0.8%	16	7.8%	2
American Crow	31.2	0.7%	23	11.3%	1.4
Northern Parula	28.0	0.7%	18	8.8%	1.6
Indigo Bunting	26.8	0.6%	12	5.9%	2.2
Pileated Woodpecker	26.5	0.6%	19	9.3%	1.4
Gray Catbird	23.5	0.6%	8	3.9%	2.9
White-breasted Nuthatch	19.0	0.5%	12	5.9%	1.6

Note: Total number of points censused = 2,778,
Total number of individuals detected = 30,829

1 (Individuals detected/Total individuals detected) *100
2 Number of points in which each species was detected
3 (Number of points with detections/Total number of points)*100
4 Individuals detected/Number of points with detections

Table 2.6 Comparison of the observed and expected numbers of species in three elevational zones on Mount LeConte, GSMNP. This is a chi square contingency table, not goodness of fit table.

	Elevation					
	Low		Middle		High	
Bird Spp	Observed	Expected	Observed	Expected	Observed	Expected
ACFL	12	3	9	10	0	8
AMCR	0	4	18	13	9	10
BCCH	3	16	47	51	57	40
BHVI	40	32	118	100	51	77
BLJA	3	5	24	15	4	11
BRCR	2	10	28	32	37	25
BTBW	30	31	120	95	50	74
BTNW	47	23	94	72	9	56
CARW	6	5	18	15	7	11
CAWA	0	16	58	51	49	40
CSWA	1	11	16	33	53	26
EATO	9	13	35	41	43	32
GCKI	2	27	85	84	89	65
GRCA	0	2	14	7	0	5
HAWO	6	9	29	29	26	23
HETH	0	6	4	18	33	14
HOWA	14	5	16	14	0	11
INBU	15	3	6	10	0	8
NOPA	2	3	7	10	12	8
OVEN	40	7	4	21	0	16
PIWO	10	4	17	13	0	10
RBNU	2	18	62	56	53	43
REVI	33	7	13	22	0	17
SCTA	21	6	14	19	4	14
UDEJ	34	43	125	133	119	103
VEER	12	33	99	104	107	81
WBNU	7	3	10	8	0	6
WIWR	9	35	101	109	118	84
WOTH	25	5	7	15	0	12
TOTAL	385	384	1198	1198	930	930

Chi-square (calculated) = 640 + 85 + 277 = 1002

df= (29-1)(3-1)=56

Chi-square (table, df=56, alpha=0.05) >34.7 =>highly significant

Table 2.7 Ranges (lowest and highest elevations) for each bird species in this study.
[1] Parentheses indicate elevations at which birds were observed at high numbers per census points (>3).

Species	Lowest elevation (m)	Highest elevation (m)
Acadian Flycatcher	700	1075
American Crow	700	1775
Black - capped Chickadee	730-800 (900)[1]	2000
Blue - headed Vireo	410-490 (610)	2000
Blue Jay	all elevations	all elevations
Brown - Creeper	1200-1500	2000
Black - throated Blue Warbler	640-820 (900)	2000
Black - throated Green Warbler	640-820 (700)	1750
Carolina Wren	700	1000
Canada Warbler	900-975 (1075)	2000
Chestnut - sided Warbler	700-914 (1325)	2000
Dark - eyed Junco	950	2000
Eastern Towhee	950-1075	2000
Golden - crowned Kinglet	1075	2000
Gray Catbird	all elevations	all elevations
Hairy Woodpecker	850-1075	2000
Hermit Thrush	700	1150
Hooded Warbler	700	1220
Indigo Bunting	700	1600
Northern Parula	700	1524
Ovenbird	700	1200-1371
Pileated Woodpecker	all elevations	all elevations
Red - breasted Nuthatch	873-991	2000
Red - eyed Vireo	700	1075-1524
Scarlet Tanager	411-488 (700)	1325
Veery	899-975 (1075)	2000
White - breasted Nuthatch	700	1415-1524
Winter Wren	950-1075 (914)	2000
Wood Thrush	700	1451-1524

expected were found in high elevations and fewer birds in low elevations.

More specifically, comparisons of observed and expected median ranges on the primary trails indicated that the 24 species beginning in the middle bands at all trails (ACT 1370-1791 m above sea level (a.s.l.), BHT 1007-1462 m, BMT 1107-1407, BVT 1497-1636, RFT 1134-1584, TGT 984-1584) had significantly broader elevational ranges than expected (Tables 2.6, 2.7, Fig. 2.4). However, in the lower bands the observed elevational ranges were significantly narrower than expected and a trend of decreasing distributional range with increasing altitude occurred at 672 - 1170 m a.s.l. (Fig. 2.4).

Ecological Correlates

The initial step in evaluating bird/vegetation relationships was to examine the correlation matrix between both sets of variables (Table 2.8). Out of 493 possible correlations, >34% were significant, with 18.25% at $P<0.05$, 11.0% at $P<0.01$, and 5.0% at $P<0.0001$. These percentages of significance strongly suggest that most of the described relationships were not spurious.

Table 2.8 indicates that five measured vegetation variables were significantly associated with the abundance of at least three, and usually seven to ten, bird species. I found no significant correlations between species richness or evenness and any environmental variables.

Bird Species Differences among Zones

Twenty-nine species were recorded in all three zones. Mean species richness (BHT, RFT, TGT trails: $\chi2 = 22.3$, df = 2, $P<0.0001$; ACT trail: $\chi2 = 76.63$, df = 2, $P<0.0001$), and total abundance (BHT, RFT, TGT trails: $\chi2 = 20.99$, df = 2, $P<0.0001$; ACT trail: $\chi2 = 67.99$, df = 2, $P<0.0001$) differed significantly among zones on all

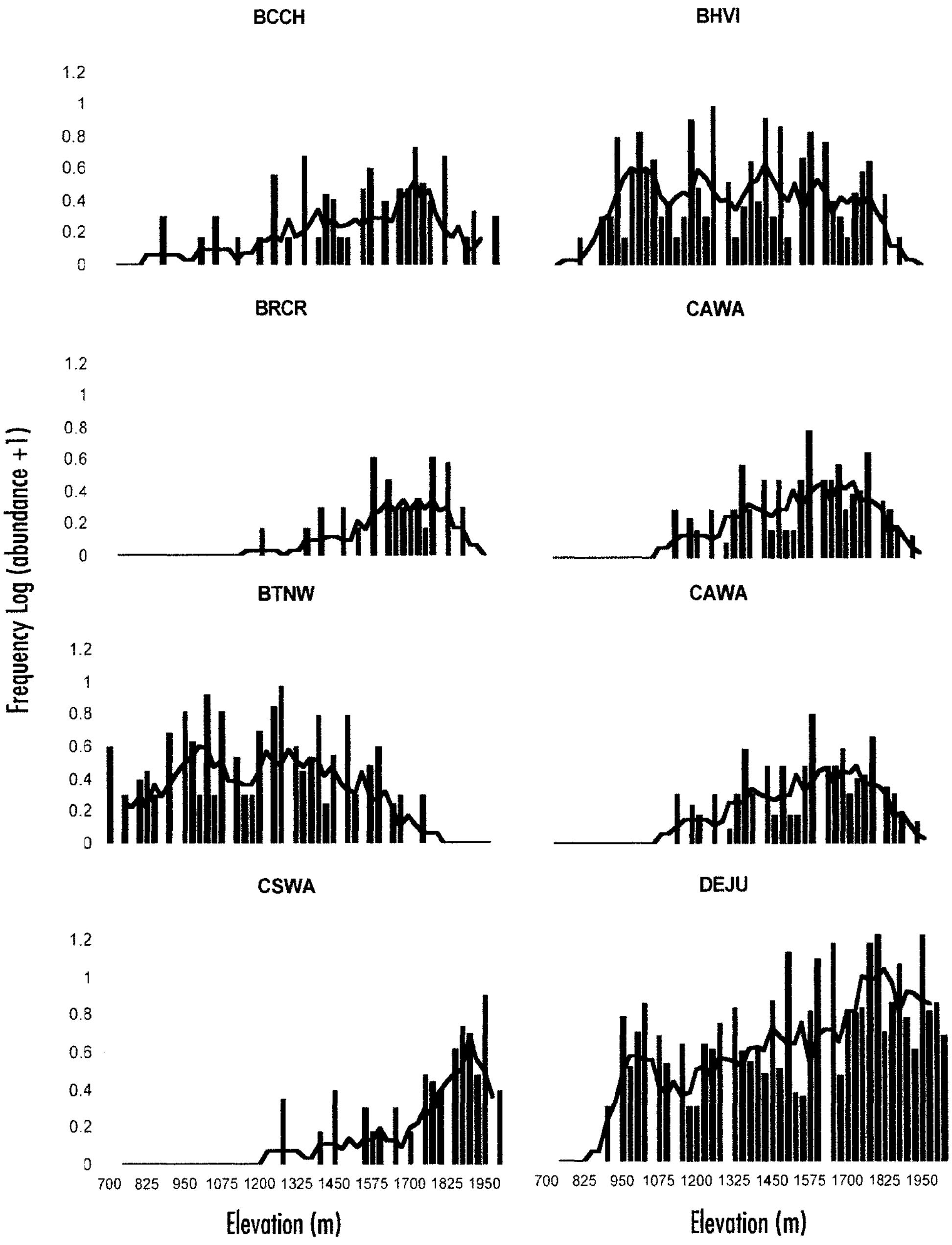

Fig. 2.4 Relative abundances of bird species occurring in relation to elevation at census points on Mount LeConte, GSMNP, 1999-2000. Only relative abundances present on more than 10% of census points were plotted or graphed. Connecting lines represent 3-5 point running averages.

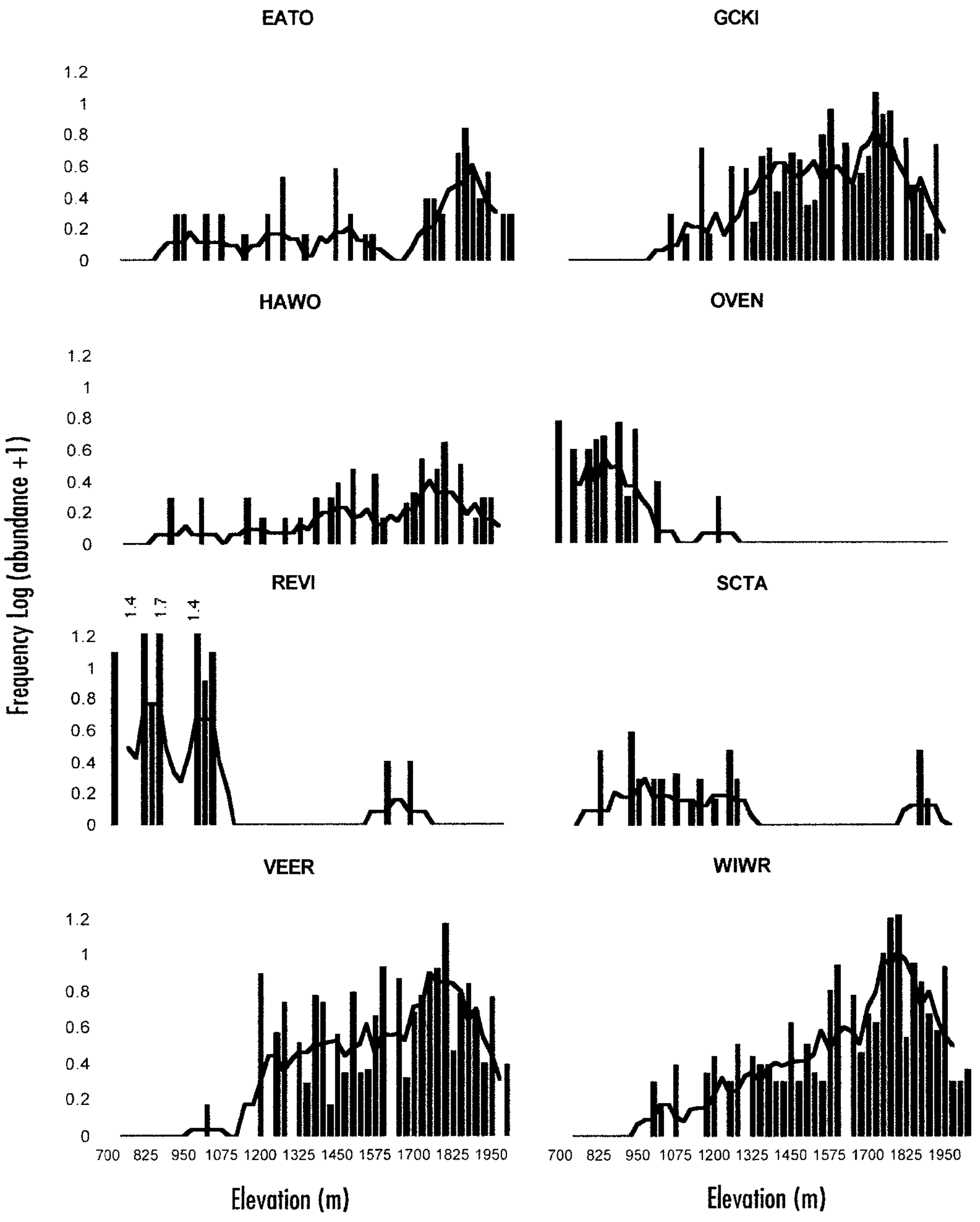

Fig. 2.4 (Continued).

Table 2.8 Significant correlations among bird species abundances and landscape variables. Vegetation structural variables coded as in Table 2.3, * = P<0.05; ** = P<0.01; *** = P<0.0001. – = negative correlation, + = positive correlation

	Spatial				
	Disturbance	Elevation (m)	Forest Opening	Slope (degrees)	Snags
Acadian Flycatcher					+*
American Crow				+**	
Black-capped Chickadee		+*			+*
Blue-headed Vireo	–*	+**			
Blue Jay			+**		+**
Brown Creeper	+*	+*			+*
Black-throated Blue Warbler		+**			
Black-throated Green Warbler	+**		+*		
Carolina Wren			+**		+*
Canada Warbler		+*			
Chestnut-sided Warbler	+*	+*	+*		
Dark-eyed Junco		+*		+*	
Eastern Towhee	+*	+*			+*
Golden-crowned Kinglet				+*	
Gray Catbird		+*		+**	
Hairy Woodpecker					+*
Hermit Thrush			+*		
Hooded Warbler	–*		–*		
Indigo Bunting	–*		–*		
Northern Parula			+*		
Ovenbird		–*	+		
Pileated Woodpecker					+*
Red-breasted Nuthatch		+*			
Red-eyed Vireo	–*	–*			
Scarlet Tanager					
Veery		+*		+*	
White-breasted Nuthatch	+*			–*	–*
Winter Wren	+**	+**		+**	
Wood Thrush			+*		

Table 2.8 Continued

	Vertical Structure					Horizontal Structure (Coverage)				
Species	GHR	LSHR	TSHR	SCHR	TCHR	GCC	LSCC	TSCC	SCCC	TCCC
Acadian Flycatcher	+*	+*	+***			–*	–*		+**	+***
American Crow					+*	–*	–*			+*
Black-capped Chickadee		+***						+***	+***	
Blue-headed Vireo		+**		+*			+*		+**	+*
Blue Jay			+**	+**	+*	–*		+**	+**	+*
Brown Creeper					+**					+**
Black-throated Blue Warbler		+*	+**	+***	+***		+*	+*	+**	
Black-throated Green Warbler	–*				+**	–*		–*	+*	+**
Carolina Wren					–**				+***	
Canada Warbler	+*	+*		+***	+***		+*	–*	+*	+***
Chestnut-sided Warbler	–*	+*	+*	+***	–***	–***	+**	+*	+**	
Dark-eyed Junco	+**		+*			+**				
Eastern Towhee	+*	+**	+*	+**		+*	+*	+*	+**	
Golden-crowned Kinglet			+*		+*	–*	+*	+*		+*
Gray Catbird			+*					+*		–***
Hairy Woodpecker	–*								–*	
Hermit Thrush	+*			–**	–**	+*	+**	–**		
Hooded Warbler	–**		+**				+**	+**		
Indigo Bunting		+**	+*				+**	+*		+*
Northern Parula		+**		+*	–*	–*	+***	+*	+***	–*
Ovenbird	+**		+*	+*	–**	+***				
Pileated Woodpecker	+*	–*			+**			–*		+*
Red-breasted Nuthatch				+*	+*				+*	+*
Red-eyed Vireo	–*		+*		+**				+***	
Scarlet Tanager			+**		+***	–***	+*			
Veery		–*			–*	+*	+**			–**
White-breasted Nuthatch	–*		+**		+**	–*	+***	+***		+***
Winter Wren			+**	+***	–*		+**		+**	
Wood Thrush		+*	+*		+***	+**			+*	

Table 2.8 Continued

Species	Composition		
	% D	% C	% H
Acadian Flycatcher	+*		
American Crow			+*
Black-capped Chickadee	–**	+**	+**
Blue-headed Vireo	–*	+*	+*
Blue Jay	–**	+*	+*
Brown Creeper		+*	
Black-throated Blue Warbler		+*	+*
Black-throated Green Warbler			+*
Carolina Wren		+*	+*
Canada Warbler		+*	
Chestnut-sided Warbler		+**	
Dark-eyed Junco		+*	
Eastern Towhee	+**	+*	+*
Golden-crowned Kinglet	–**	+**	
Gray Catbird	+**		+*
Hairy Woodpecker	+*		+*
Hermit Thrush		+*	
Hooded Warbler	+*		
Indigo Bunting	+*		
Northern Parula	+**		+*
Ovenbird	+*		
Pileated Woodpecker			+*
Red-breasted Nuthatch	+*	+**	+*
Red-eyed Vireo	+**	+*	
Scarlet Tanager	+*		+*
Veery	+*	+*	
White-breasted Nuthatch	+**	+*	
Winter Wren		+**	
Wood Thrush			

Table 2.9 Avian species richness, relative abundances of all bird species combined, and individual guilds among three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) the DCE, and (3) above the DCE on Mount LeConte, GSMNP. ACT = Alum Cave Trail, BHT = Bull Head Trail, RFT = Rainbow Falls Trail, TGT = Trillium Gap Trail. C = canopy, F = forest, GR = ground, SC = subcanopy, SF = spruce-fir, SH = shrub.
[1] = insufficient sample size.

By Variable	Below DCE Zone 1		DCE Zone 2		Above DCE Zone 3			
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Habitat Guilds								
BHT, RFT, TGT								
C	1.98	0.20	1.22	0.10	1.64	0.17	7.57	0.0227
F	1.63	0.07	1.54	0.04	1.27	0.04	12.51	0.0019
GR	2.09	0.11	1.82	0.07	2.28	0.09	17.72	<0.0001
SC	2.07	0.23	1.35	0.06	2.11	0.11	36.60	<0.0001
SF	1.65	0.16	1.51	0.07	1.34	0.05	1.09	0.5786
SH	1.71	0.22	1.18	0.06	1.50	0.09	6.57	0.0373
ACT								
F	2.00	0.14	1.26	0.05	1.08	0.39	42.00	<0.0001
GR	1.73	0.20	2.08	0.14	2.29	0.21	1.14	0.5644
SC	1.08	0.08	1.83	0.14	1.85	0.16	6.57	0.0374
SF	4.25	0.75	1.83	0.14	1.61	0.12	5.52	0.0632
SH	-[1]	-[1]	1.46	0.14	1.75	0.18	3.23	0.1987
Migratory Guild								
BHT, RFT, TGT								
NM	1.92	0.07	1.54	0.03	1.65	0.05	13.25	0.0013
PR	1.76	0.02	1.57	0.04	1.81	0.06	15.32	0.0005
TM	1.28	0.34	1.33	0.33	1.14	0.08	0.57	0.7523
ACT								
NM	1.95	0.11	1.49	0.069	1.57	0.10	18.63	<0.0001
PR	1.50	0.32	1.66	0.07	1.92	0.12	5.86	0.05
TM	-[1]	-[1]	1.50	0.50	1.78	0.40	0.02	0.872

Table 2.9 Continued

By Variable		Below DCE Zone 1		DCE Zone 2		Above DCE Zone 3			
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Nesting Guild									
BHT, RFT, TGT									
	C	1.78	0.11	1.59	0.06	1.33	0.05	8.24	0.102
	F	1.14	0.14	1.12	0.13	-^{1}	-^{1}	0.01	0.9219
	GEN	-^{1}	-^{1}	1.3	0.21	1.04	0.047	0.59	0.7436
	GR	2.08	0.125	1.75	0.06	2.16	0.09	15.54	0.0004
	SC	1.92	0.12	1.48	0.05	1.75	0.07	12.09	0.0024
	SH	1.83	0.14	1.46	0.06	1.46	0.83	2.34	0.3099
	SN	1.28	0.07	1.22	0.06	1.31	0.07	1.35	0.5086
ACT									
	C	1.96	0.29	1.60	0.10	1.53	0.11	2.96	0.2273
	F	-^{1}	-^{1}	-^{1}	-^{1}	-^{1}	-^{1}	-^{1}	-^{1}
	GEN	-^{1}	0.0	^{1}	0.0	-^{1}	-^{1}	-^{1}	-^{1}
	GR	1.73	0.20	1.91	0.11	2.21	0.20	0.59	0.743
	SC	1.77	0.21	0.57	0.09	1.73	0.15	0.96	0.6186
	SH	2.07	0.21	1.42	0.12	1.72	0.17	10.02	0.0066
	SN	-^{1}	-^{1}	1.15	0.63	1.17	0.69	0.35	0.5526
Species Richness									
BHT, RFT, TGT		6.63	0.20	7.73	0.20	9.24	0.20	22.36	<0.0001
ACT Only		4.33	0.30	12.35	0.30	8.41	0.30	76.64	<0.0001
Total Abundance									
BHT, RFT, TGT		10.85	0.50	11.30	0.30	14.88	0.30	21.00	<0.0001
ACT Only		7.53	0.70	16.27	0.70	13.09	0.50	68.00	<0.0001

gradsects (Table 2.9). However, of the migratory guilds, abundances of Neotropical hypothesized ecotone, and all differed significantly ($P<0.0001$).

Bird Species Differences Among Zones

Twenty-nine species were recorded in all three zones. Mean species richness (BHT, RFT, TGT trails: $\chi2 = 22.3$, df = 2, $P<0.0001$; ACT trail: $\chi2 = 76.63$, df = 2, $P<0.0001$), and total abundance (BHT, RFT, TGT trails: $\chi2 = 20.99$, df = 2, $P<0.0001$; ACT trail: $\chi2 = 67.99$, df = 2, $P<0.0001$) differed significantly among zones on all gradsects (Table 2.9). However, of the migratory guilds, abundances of Neotropical migrants and temperate migrants differed significantly among zones on all gradsects (Table 2.10: $\chi2 = 13.25$, df = 2, $P=0.0013$; and Table 2.11: $\chi2 = 18.63$ df = 2, $P<0.0001$). Abundances of Neotropical migrant guilds were greater below the DCE zone and permanent resident guilds were greater above the DCE zone (Table 2.9). Of the nesting guilds, ground was higher above the DCE, subcanopy was higher below the DCE on all trails except ACT, and shrub was higher on ACT (Tables 2.10, 2.11).

The four most common species on four gradsects below the DCE were Acadian Flycatcher, Ovenbird, Red-eyed Vireo, and Wood Thrush, whereas the five predominant species above the DCE were Brown Creeper, Eastern Towhee, Hermit Thrush, Veery, and Winter Wren (Tables 2.10, 2.11). Abundances of Blue-headed Vireo, Black-throated Blue Warbler, Hooded Warbler, and Winter Wren were greater in the DCE zone than the other zones (Table 2.12). On the other hand, Brown Creeper, Eastern Towhee, and Veery were more abundant (20-45%) in Zone 3 compared to Zones 1 and 2 (Table 2.12).

On Alum Cave Trail, below the DCE, only the Black-throated Green Warbler was common ($\chi2 = 4.00$, df = 2, $P=0.05$), whereas the predominant species above the DCE

Table 2.10 Comparative abundances (± SE) and guild classifications in bird species in three zones: (1) below the DCE, (2) at the DCE, and (3) above the DCE, excluding Alum Cave Trail (ACT) on Mount LeConte, GSMNP, 1999-2000. – = insufficient sample size

	Zone 1		Zone 2		Zone 3						
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P	Habitat	Migratory	Nesting
Acadian Flycatcher	2.29	0.61	1.50	0.00	1.00	0.22	7.30	0.026•	F	LD	SC
American Crow	1.37	1.50	2.50	0.28	1.00	0.00	1.27	0.530	F	R	C
Black-capped Chickadee	1.29	0.19	1.49	0.12	1.45	0.12	0.12	0.943	F	R	SN
Blue-headed Vireo	1.10	0.17	1.98	0.10	1.70	0.05	14.35	0.001*	F	LD[1]/SD	SC
Blue Jay	1.20	0.33	1.33	0.12	1.20	1.00	0.61	0.738	F	R	C/SC
Brown Creeper	1.02	0.10	1.22	0.08	1.37	0.12	11.18	0.004•	F-OT	R	SN
Black-throated Blue Warbler	1.26	0.23	1.94	0.09	1.65	0.09	5.87	0.053	F	LD	SC/SH
Black-throated Green Warbler	1.89	0.22	1.89	0.14	1.51	0.20	1.54	0.462	F	LD	C/SC
Carolina Wren	1.00	0.00	1.30	0.21	1.05	0.05	0.59	0.744	F	R	GEN
Canada Warbler	1.16	0.41	1.76	0.07	1.29	0.12	0.51	0.774	SH	LD	GR
Chestnut-sided Warbler	1.30	0.52	1.68	0.20	1.88	0.16	5.57	0.062	SH	LD	SH
Dark-eyed Junco	2.25	0.25	2.46	0.13	2.76	0.20	5.44	0.066	F-GR	R	GR
Eastern Towhee	1.19	0.10	1.59	0.09	1.65	0.14	7.55	0.023	SH/GR	R	SH/GR
Golden-crowned Kinglet	1.38	0.22	1.68	0.12	1.88	0.07	7.52	0.022	SFF	LD[2]/TM	C
Gray Catbird	—[1]	—[1]	0.21	0.21	—[1]	—[1]	—[1]	—[1]	SH	R	SH
Hairy Woodpecker	1.07	0.07	1.37	0.11	1.17	0.13	3.28	0.194	F	SD	SN
Hermit Thrush	1.03	0.34	1.29	0.33	1.45	0.08	6.57	0.050	F-GR	LD	SH/GR
Hooded Warbler	2.10	0.35	2.22	0.02	1.08	0.08	10.38	0.006*	SC	LD[3]	SH
Indigo Bunting	1.53	0.18	1.00	0.00	1.00	0.00	7.03	0.030	SH	LD[4]	SH
Northern Parula	1.43	0.30	1.00	0.00	1.50	0.50	1.26	0.533	F	LD[5]	SC/SH
Ovenbird	3.76	0.25	1.63	0.38	2.06	0.29	10.18	0.006•	F-GR	PR	GR
Pileated Woodpecker	1.00	0.00	1.96	0.10	1.00	0.00	0.82	0.665	F	R	SN
Red-breasted Nuthatch	1.16	0.15	1.29	0.08	1.40	0.09	5.95	0.047	SFF	LD	C/SC
Red-eyed Vireo	2.68	0.27	1.86	0.22	1.66	0.26	11.34	0.003*	C	LD	SC
Scarlet Tanager	1.20	0.14	1.22	0.11	1.13	0.17	1.24	0.570	C	R	SC
Veery	1.55	0.27	2.10	0.07	2.25	0.11	22.79	<0.001*	F-GR	LD	SH/GR
White-breasted Nuthatch	1.14	0.14	1.13	0.13	—[1]	—[1]	0.01	.922	F	R	F
Winter Wren	1.42	0.30	2.42	0.07	2.19	0.11	31.31	<0.001*	SC	R	SC
Wood Thrush	1.86	0.18	1.14	0.00	1.00	0.14	10.28	0.006•	F-GR	LD	C/SC

[1] Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD? – [2] Most GRCA winter in Central America with some in South Florida and Gulf Coast Plains – [3] Many INBU winter on Coastal Plain of Gulf States and South Florida – [4] Many NOPA winter on Coastal Plain of Gulf States and South Florida – [5] Many OVEN winter on Coastal Plain of Gulf States and South Florida; Habitat guild: F=forest (in general), C=canopy, SC=subcanopy, SH=shrub, GR=ground, SF=spruce-fir, F-GR=forest ground; Migratory guild: LD=long distance, SD=short distance, R=resident, PR=permanent resident, TM=temperate migrant, NM=neotropical migrant; Nesting guild: C=canopy, SC=subcanopy, SH=shrub, GR=ground, SN=snag, GEN=forest edge or opening

Table 2.11 Comparative abundances (± SE) and guild classifications in bird species in three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above the DCE, on Alum Cave Trail (ACT) on Mount LeConte, GSMNP, 1999-2000. Acadian Flycatcher was deleted because it was not observed on ACT. [1] = insufficient sample size

	Zone 1		Zone 2		Zone 3						
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P	Habitat	Migratory	Nesting
American Crow			1.00	0.14	0.88	0.00	0.46	0.498	F	R	C
Black-capped Chickadee			1.47	0.16	1.28	0.12	0.31	0.578	F	R	SN
Blue-headed Vireo	1.41	0.30	2.22	0.12	1.00	0.00	9.77	0.008•	F	LD1/SD	SC
Blue Jay			1.33	0.33	1.00	0.00	0.67	0.414	F	R	C/SC
Brown Creeper			1.06	0.03	1.03	0.06	0.27	0.606	F-OT	R	SN
Black-throated Blue Warbler	1.39	0.25	2.09	0.13	1.00	0.00	8.89	0.012	F	LD	SC/SH
Black-throated Green Warbler	1.58	0.13	1.46	0.24			4.01	0.045	F	LD	C/SC
Carolina Wren			1.00	0.00	1.00	0.00	0.00	1.00	F	R	GEN
Canada Warbler			1.38	0.14	0.94	0.06	3.62	0.057	SH	LD	GR
Chestnut-sided Warbler	1.00	0.00	2.00	0.00	1.98	0.19	7.18	0.028	SH	LD	SH
Dark-eyed Junco	1.00	0.00	2.55	0.25	3.64	0.36	19.25	<0.001	SH/GR	R	SH/GR
Eastern Towhee	1.19	0.10	1.59	0.09	1.65	0.14	7.55	0.023	SFF	R	C
Golden-crowned Kinglet	1.81	0.75	3.25	0.19	2.33	0.22	6.75	0.034	SH	LD2/TM	SH
Gray Catbird			2.14	0.51					F	R	SN
Hairy Woodpecker			1.04	0.07	1.00	0.00			F-GR	SD	SH/GR
Hermit Thrush			1.50	0.50	1.79	0.41	4.03	0.049	SC	LD	SH
Hooded Warbler									SH	LD3	SH
Indigo Bunting									F	LD4	SC/SH
Northern Parula	2.00	0.00	1.00	0.00	1.00	0.00	5.00	0.082	F-GR	LD5	GR
Ovenbird									F	PR	SN
Pileated Woodpecker			1.00	0.00					SFF	R	C/SC
Red-breasted Nuthatch			1.11	0.07	1.43	0.12	6.10	0.135	C	LD	SC
Red-eyed Vireo	1.00	0.00	1.00	0.00					C	LD	SC
Scarlet Tanager									F-GR	R	GR
Veery	1.86	0.24	2.10	0.20	1.54	0.16	3.64	0.162	F-GR	LD	SH/GR
White-breasted Nuthatch			1.00	0.00					F	R	F
Winter Wren	1.08	0.08	1.83	0.14	1.85	0.16	6.57	0.037	SC	R	SC
Wood Thrush			1.00	0.00					F-GR	LD	C/SC

[1] Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD? – [2] Most GRCA winter in Central America with some in South Florida and Gulf Coast Plains – [3] Many INBU winter on Coastal Plain of Gulf States and South Florida – [4] Many NOPA winter on Coastal Plain of Gulf States and South Florida – [5] Many OVEN winter on Coastal Plain of Gulf States and South Florida; Habitat guild: F=forest (in general), C=canopy, SC=subcanopy, SH=shrub, GR=ground, SF=spruce-fir, F-GR=forest ground; Migratory guild: LD=long distance, SD=short distance, R=resident, PR=permanent resident, TM=temperate migrant, NM=neotropical migrant; Nesting guild: C=canopy, SC=subcanopy, SH=shrub, GR=ground, SN=snag, GEN=forest edge or opening

Table 2.12 Summary of statistics of the most common species of the gradsects.

Bird species	χ^2 Value	df	P
Below the DCE			
Acadian Flycatcher	7.03	2	0.0298
Ovenbird	10.18	2	0.0062
Red-eyed Vireo	11.34	2	0.0034
Wood Thrush	10.28	2	0.0059
At the DCE			
Blue-headed Vireo	14.35	2	0.0008
Black-throated Blue Warbler	5.87	2	0.0531
Hooded Warbler	10.38	2	0.0056
Winter Wren	31.31	2	<0.0001
Above the DCE			
Brown Creeper	11.19	2	0.0037
Eastern Towhee	7.55	2	0.0229
Hermit Thrush	6.57	2	0.0503
Veery	22.79	2	<0.0001
Winter Wren	31.31	2	<0.0001

were the Winter Wren and the Dark-eyed Junco ($\chi2$ = 19.25, df = 2, P<0.0001), with the latter being more 30% more abundant. Abundances of Blue-headed Vireo, Black-throated Blue Warbler, Chestnut-sided Warbler ($\chi2$ = 7.18, df = 2, P=0.03), Golden-crowned Kinglet ($\chi2$ = 6.75, df = 2, P=0.03), and Veery were greater in the DCE than in the other zones.

Bird Species Diversity among DCE Elevational and Habitat Zones

Species richness and total bird abundance ranged from a low of 4 to 7 nesting species per census point at lower elevations to a high of 10 to 18 nesting species at middle elevations, with intermediate numbers (7-12 species) at high elevations (Fig. 2.5). Elevation of census points accounted for 34% of the variation in mean species richness (of the 29 common species; R=0.52, P<0.0001) and 27% of the variation in total bird abundance (R=0.62, P<0.0001; Tables 2.8, 2.10, and 2.11). Species richness and bird abundance fluctuated markedly and in synchrony at low zonal breaks along the elevational continuum (Fig. 2.6).

The following habitat features explained the breaks among the zones: in Zone 2, a reduction in tree species of 0-10, 11-25, 51-75 cm dbh and an increase in trees of 76-100 cm dbh separated Zones 1 and 3; an increase in tree species cover of canopy trees in Zone 2 resulted in an increase in cover of tall shrubs/saplings and subcanopy trees up the gradsects; an increase in tree canopy cover of census points in Zone 2 was attributable to a reduction in ground cover, low shrub/seedling cover, and subcanopy cover; and a marked increase in foliage height diversity in ground cover, low shrub, seedling, subcanopy and tree canopy characterized or distinguished Zone 2 from the other zones. Generally, mid-elevation locations with hemlock trees separated low elevation locations

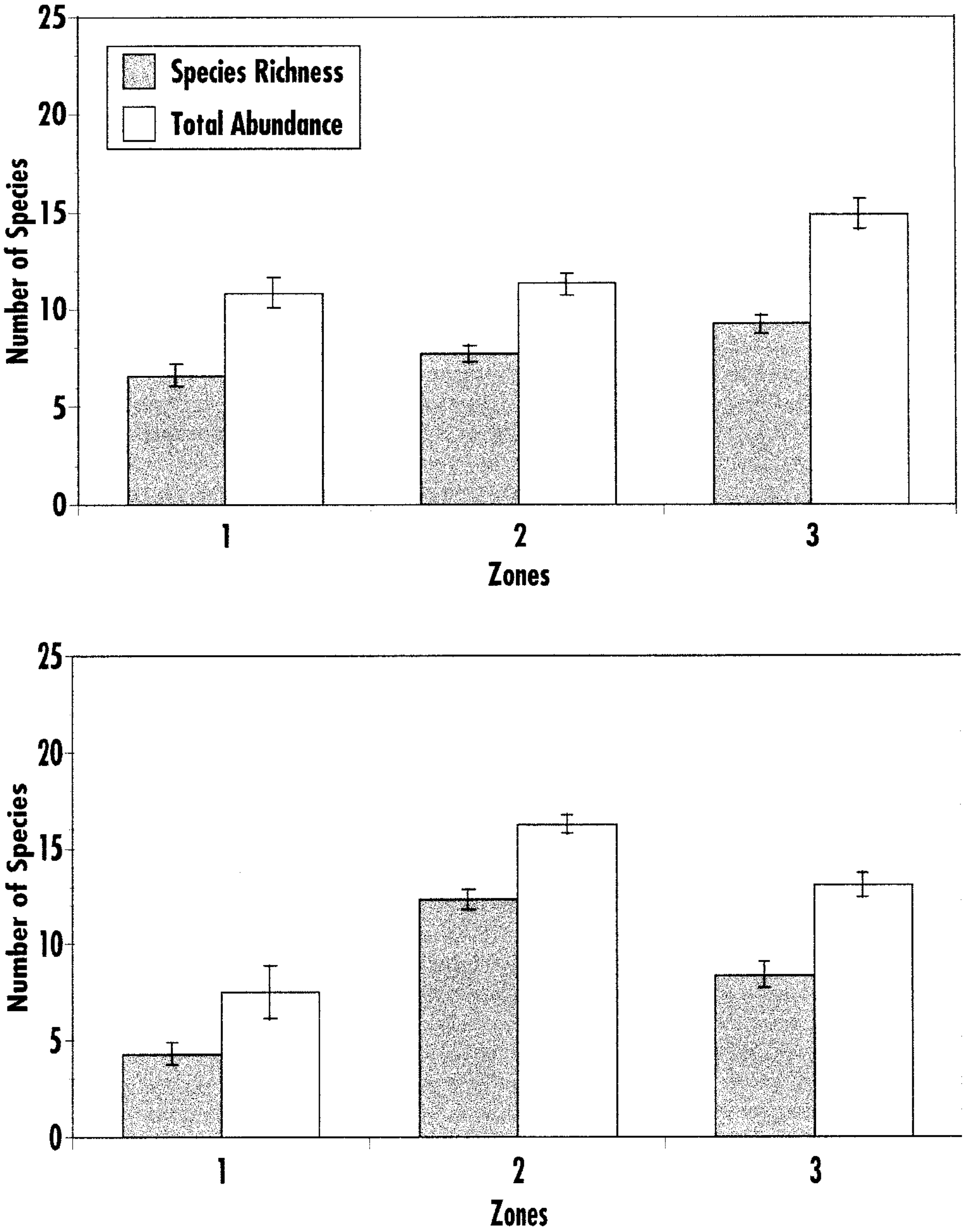

Fig. 2.5 Species richness and total abundance in three zones (mean ± 1 se); 1: below deciduous-coniferous ecotone; 2: ecotone; 3: above deciduous-coniferous ecotone on gradsects. BHT, RFT, and TGT were combined because the trend(s) up their gradients were similar. The trend(s) up the ACT were different. Pairs of bars represent values for a. Bull Head Trail (BHT), Rainbow Falls Trail (RFT), and Trillium Gap Trail (TGT) combined, and b. Alum Cave Trail (ACT).

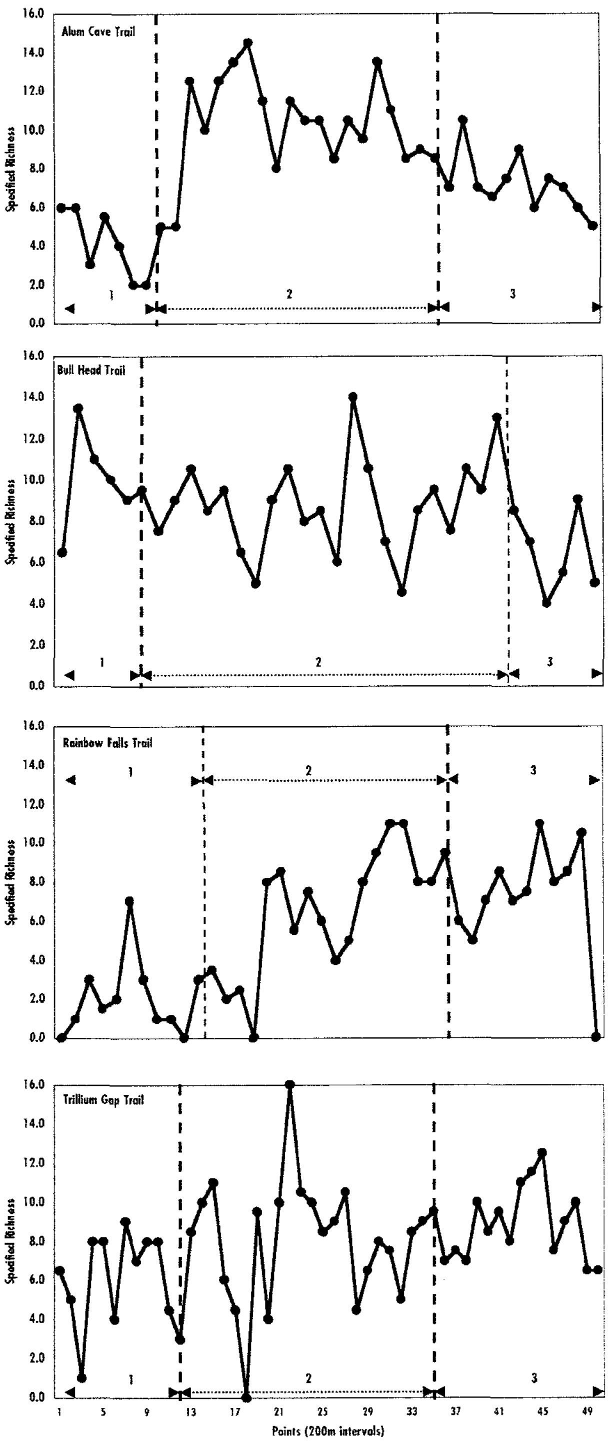

Fig. 2.6 Comparisons in species richness of the ecotone edge among four trails (gradsects) and three zones on Mount LeConte, GSMNP. Species richness is number of birds detected in 50m radius circle per 10 min. Elevation increases along the x-axis. Vertical dashed lines separate the three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE and (3) above the DCE.

with deciduous trees and higher elevational locations with coniferous trees. However, on the ACT trail, mid-elevation locations with spruce-fir trees separated the low-elevation locations with hemlock trees and high elevation locations with Fraser fir trees. In all, 17 habitat features varied among zones after zone-transect variation was adjusted for by means of differential 2-way ANOVA and Kruskal-Wallis Chi-Square tests (Table 2.3). MANOVA indicated that zones differed in overall patterns of vegetation structure (Wilks' $\lambda = 3.7X106$, $P<0.01$).

Habitat Selection and Use

Birds were detected in spruce-fir forests less than expected and in deciduous and hemlock forests more than expected. Golden-crowned Kinglets did not use census points of different forest types according to their availability (Fig. 2.7); this was true for all trails (excluding ACT: Table 2.10, $\chi2 = 3.02$, df = 2, P=0.22; ACT: Table 2.11, $\chi2 = 6.74$, df = 2, P=0.03). Ovenbirds were detected in mid-elevation locations and deciduous-hemlock forests less than expected and in deciduous sites (pine and oak) more than expected. Red-breasted Nuthatches were detected within spruce-fir forests less than expected (Fig. 2.7, Tables 2.10, 2.11), but in higher elevation locations (Zone 3) as expected. Acadian Flycatchers used lower elevational locations and were detected at points within deciduous and hemlock forests as expected (Fig. 2.7) but were detected at mid-elevation locations (in the ecotone) more than expected.

On gradsects excluding ACT, Acadian Flycatchers, Indigo Buntings, Ovenbirds, Red-eyed Vireos, and Wood Thrushes were present in highest numbers at lower elevations in mainly deciduous and only hemlock (ACT) forests (Tables 2.10, 2.11, Fig. 2.7). Blue-headed Vireos, Black-throated Blue Warblers, and Winter Wrens on all

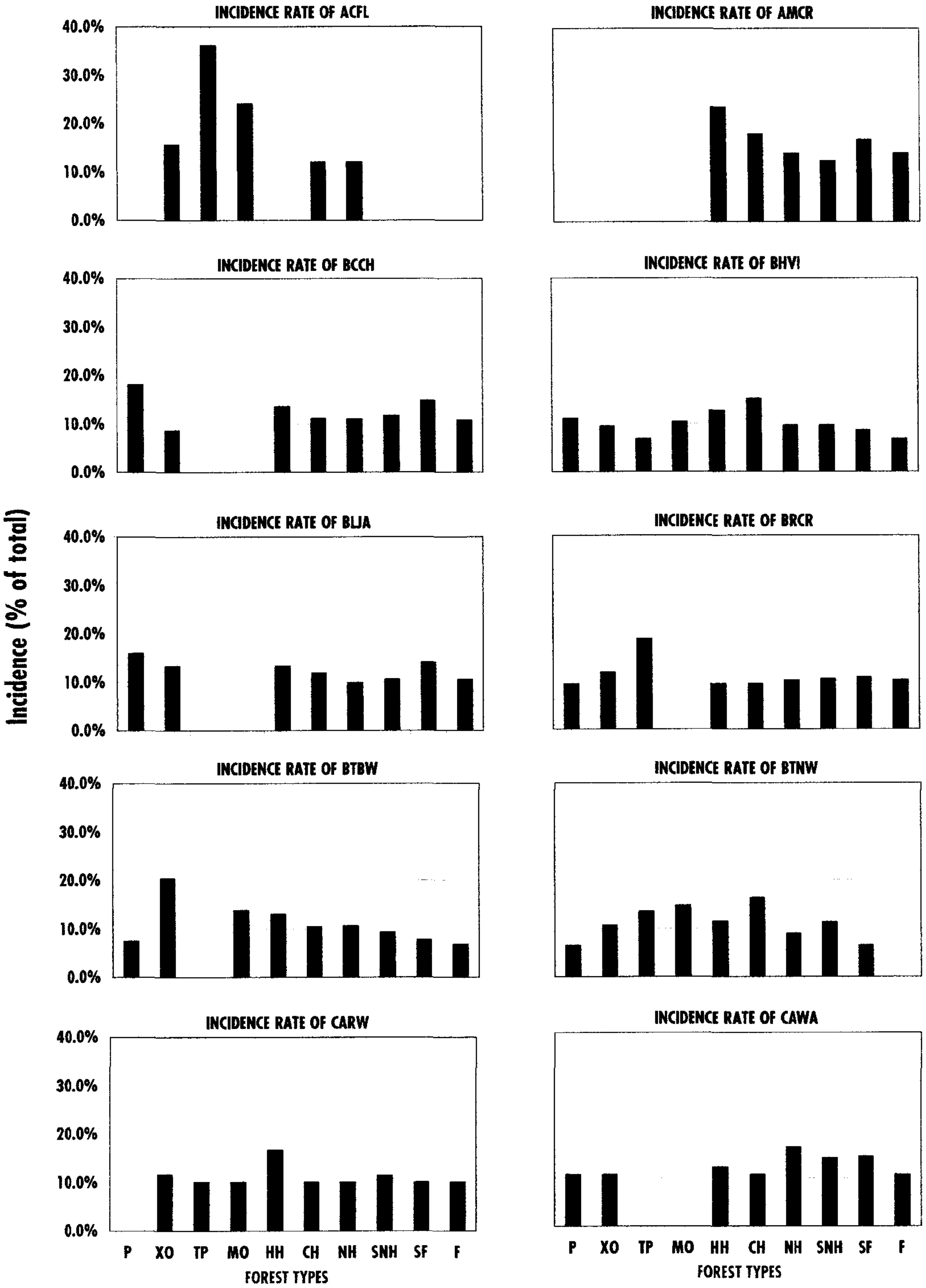

Fig. 2.7 Patterns of incidence of birds detected by forest community classification. Forest types: P=pine, XO=xeric oak, TP=tulip poplar, MO=mesic oak, HH=hemlock hardwood, CH=cove hardwood, NH=northern hardwood, SNH=spruce northern hardwood, SF=spruce fir, F=fir.

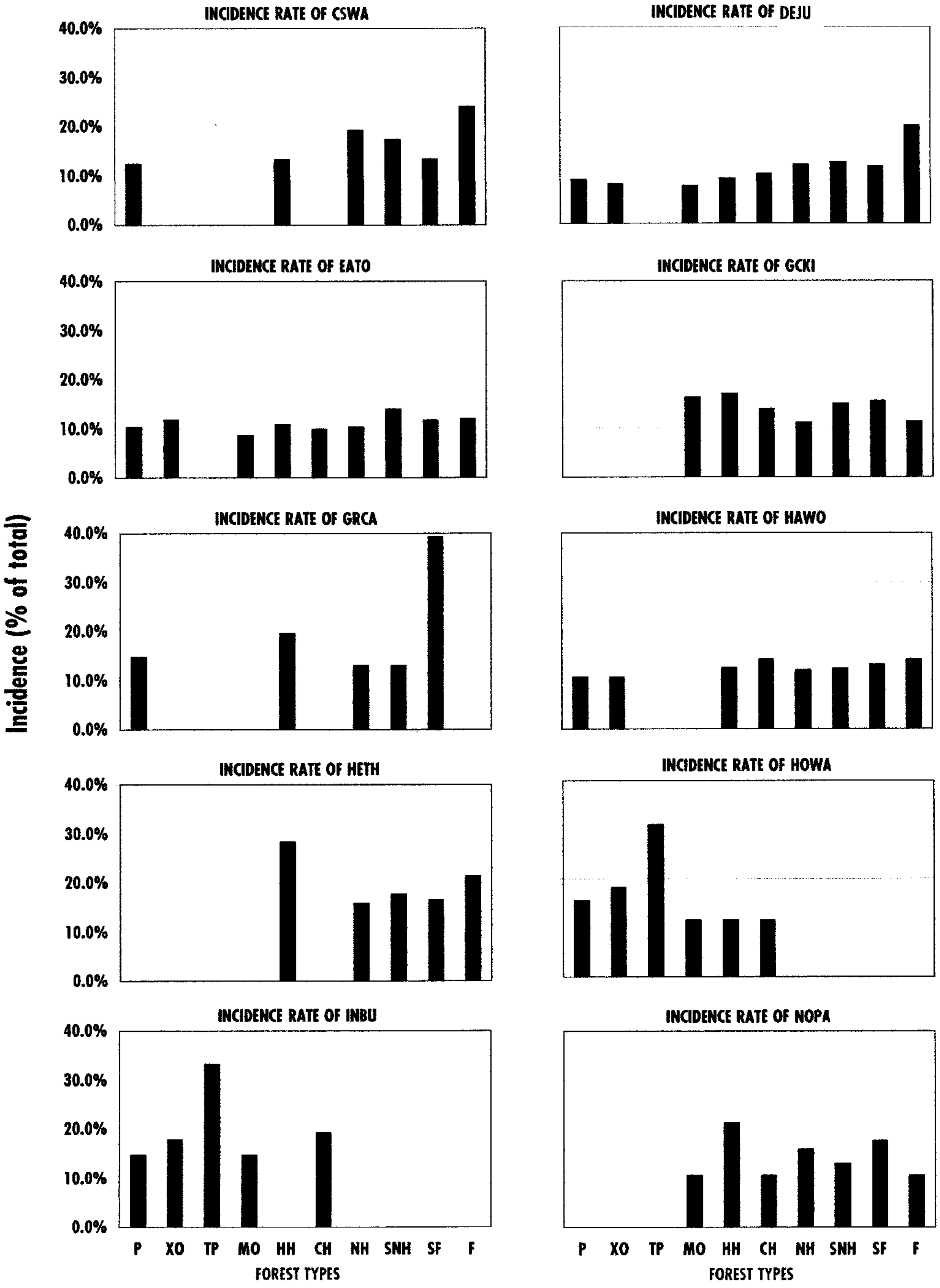

Fig. 2.7 (Continued).

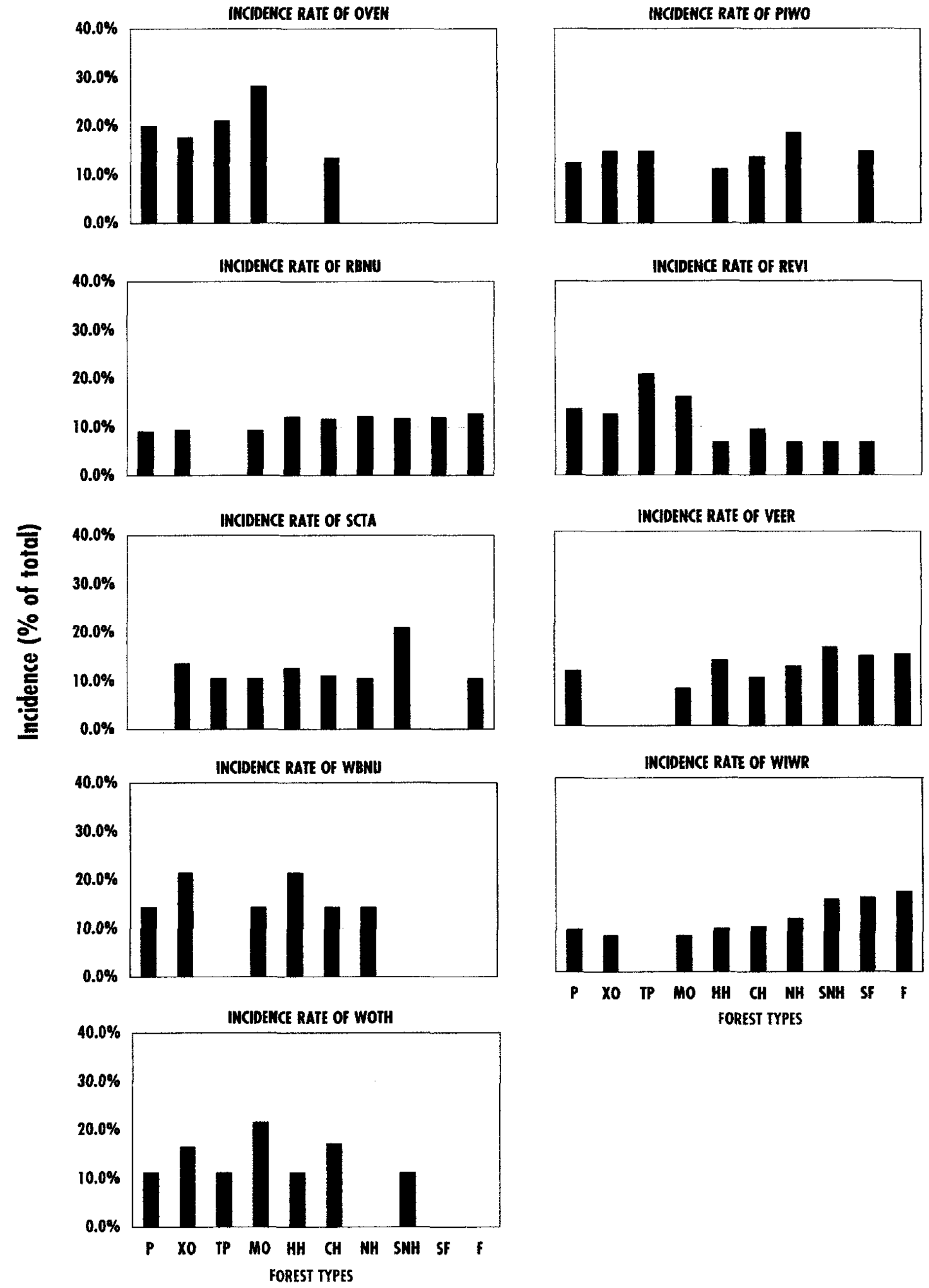

Fig. 2.7 (Continued).

gradsects, and Hooded Warblers on trails excluding ACT, were recorded in greater abundances at mid-elevations in mixed deciduous and hemlock forests (Fig. 2.7). Brown Creeper, Eastern Towhee, Hermit Thrush, Red-breasted Nuthatch, and Veery, on gradsects excluding ACT, Dark-eyed Junco only on ACT, were recorded in greater abundances at higher elevation locations with spruce-fir or fir. The Black-throated Green Warbler, Chestnut-sided Warbler, and Golden-crowned Kinglet differed among distances on gradsects but not in a manner attributable to elevation effect.

Bird Species Distributions at Habitat Breaks

Of the 29 species analyzed, the abundance levels of 13 varied among zones ($P<0.05$; Table 2.13). Pairwise differences in species counts of birds on gradsects with no significant interaction were identified using Tukey's HSD pairwise comparison tests. Hairy Woodpecker, Wood Thrush, Blue-headed Vireo, Black-throated Blue Warbler, and Northern Parula, observed primarily in lower elevations, differed in abundance between the low and mid-elevation zones, and between the lower and higher elevation zones. Most frequent in mid-elevation habitat areas, Veery, Chestnut-sided Warbler, Golden-crowned Kinglet, and Red-breasted Nuthatch varied in abundance between the middle zone and the higher zone(s). The Ovenbird and Red-eyed Vireo, species absent from high elevation locations, had disparate counts among the three zones. Common inhabitants of high elevation areas, the Eastern Towhee and Dark-eyed Junco, also differed in abundance between high elevation forests and those of lower zones.

ECCs (habitat types) had a significant influence on the abundance of birds (Table 2.14). All species combined, as well as all common species, exhibited distributions that were not expected by chance (One-way ANOVA, $P<0.001$ for all comparisons).

Table 2.13 Significant differences in counts of 29 bird species across three forest zones, based on results of ANOVA and pair-wise comparison tests.

a. Three gradsects = BHT, RFT, TGT, significant ANOVA, no significant gradsect interaction,

b. ACT only, significant ANOVA, also no significant gradsect interaction.

PR = Permanent Resident; NM = Neotropical Migrant

a/b	Species Common Name	Migratory Guild	P	Comparisons
a	Eastern Towhee	*PR*	0.0017	b, c
a	Hairy Woodpecker	*PR*	0.0083	a, c
a	Ovenbird	*NM*	0.0185	b, c
a	Red-eyed Vireo	*NM*	0.022	a
a	Veery	*NM*	0.0001	a, b
a	Wood Thrush	*NM*	0.0328	a, c
b	Blue-headed Vireo	*NM*	0.0047	a, c
b	Black-throated Blue Warbler	*NM*	0.0081	a, c
b	Chestnut-sided Warbler	*NM*	0.0122	b
b	Dark-eyed Junco	*PR*	0.0005	b, c
b	Golden-crowned Kinglet	*PR*	0.0096	b
b	Northern Parula	*NM*	<0.0001	a, c
b	Red-breasted Nuthatch	*PR*	0.017	b

NOTE: Pairwise comparisons were computed using the least significant difference range test. Significant differences ($P<0.05$) among two elevational zones are indicated as follows: a. zone 1 vs. zone 2; b, zone 2 vs. zone 3; c, zone 1 vs. zone 3.

Table 2.14 Results of one-way ANOVAs comparing mean bird abundances across ecotonal community classifications (forest types) on Mount LeConte, GSMNP. ANOVA on bird abundance by zone (below DCE, in DCE, above DCE) and gradsect, with three gradsects, BHT, RFT, TGT, and then by ACT only. Bird codes are defined in Table 2.1. a. All three gradsects but ACT. b. ANOVA on ACT only

a/b	Bird species	SS	MS	MSE	F	P
a	BHVI	38.8	3.53	0.58	6.03	<0.0001
a	BTBW	36.7	4.08	0.59	6.96	<0.0001
a	EATO	7.4	0.74	0.22	3.41	0.002
a	HOWA	7.7	1.92	0.44	4.35	0.008
a	OVEN	22.5	5.62	1.67	3.36	0.019
a	REVI	14.9	2.99	0.97	3.09	0.022
a	UDEJ	53.8	4.48	2.12	2.11	0.018
a	VEER	22.6	3.22	0.72	4.48	<0.0001
a	WIWR	44.4	4.44	0.71	6.21	<0.0001
a	WOTH	6.40	1.07	0.38	2.80	0.033
b	BHVI	8.80	4.40	0.73	5.99	0.005
b	BTBW	6.70	3.40	0.63	5.34	0.008
b	CSWA	4.10	2.10	0.36	5.69	0.012
b	GCKI	10.8	5.40	1.04	5.16	0.01
b	RBNU	0.90	0.90	0.14	6.28	0.017
b	UDEJ	38.3	19.2	2.21	8.66	0.001

Post-hoc comparisons revealed that several of the most common species showed significant positive responses to elevation zones (Table 2.15). The remainder of the common species showed significant positive responses primarily to foliage height diversity. Some of these species were associated with areas of forests that were frequently wet or moist.

Zonal differences in bird species richness and bird abundances were related to patterns of species responses to the two ecotonal breaks in plant communities. Based on cluster analysis, I identified 3-5 groups exhibiting similar distributions among the 212 census points (Fig. 2.8). Because species within an assemblage may use habitat differently, each assemblage was not assumed to represent a separate niche, as guilds often are defined; rather, assemblages were groups of species using similar habitats. I named assemblages (Fig. 2.8) on the basis of elevational and forest characteristics. The higher elevation assemblages (3), comprising of birds from Black-capped Chickadee to Winter Wren, were distinct from the lower elevation species groups, which were more similar to each other than to the higher elevation assemblages. Group I (below dashed line) contained 17 species and represented birds in deciduous and hemlock habitats at lower elevation. Of these species, Black-throated Green Warblers and Eastern Towhees were the most common. The four species in Group II occur primarily in middle elevation containing ecotonal (DCE) vegetation. The seven species that prefer higher elevations, (above DCE) and spruce-fir habitats made up Groups IV and V.

Kruskal-Wallis test results were qualitatively similar to ANOVA tests, both in level of significance (at which the null hypothesis of equality of species' means was rejected) and in the variables, indicating that the non-normality of some of the variables

Table 2.15 Results of post-hoc comparisons of density by zones below the deciduous-coniferous ecotone (DCE), at the DCE, and above the DCE. Treatment types with the same letter were not significantly (P<0.05) different using Tukey's Honestly Significant Difference. Bird codes are defined in Table 2.1. a. ANOVA by zone and transect, non-significant interaction effects, all transects by ACT. b. ANOVA by zone and transection, non-significant interactions effects, ACT only.

a/b	Bird Species	Below DCE	DCE	Above DCE
a	EATO	A	A	B
a	HOWA	A	B	B
a	OVEN	A	A	B
a	REVI	A	B	AB
a	VEER	A	B	A
a	WOTH	A	B	B
b	BHVI	A	B	B
b	BTBW	A	B	B
b	CSWA	AB	A	B
b	GCKI	A	B	B
b	NOPA	A	B	B
b	RBNU	No obs in trt 1	A	B
b	DEJU	A	A	B

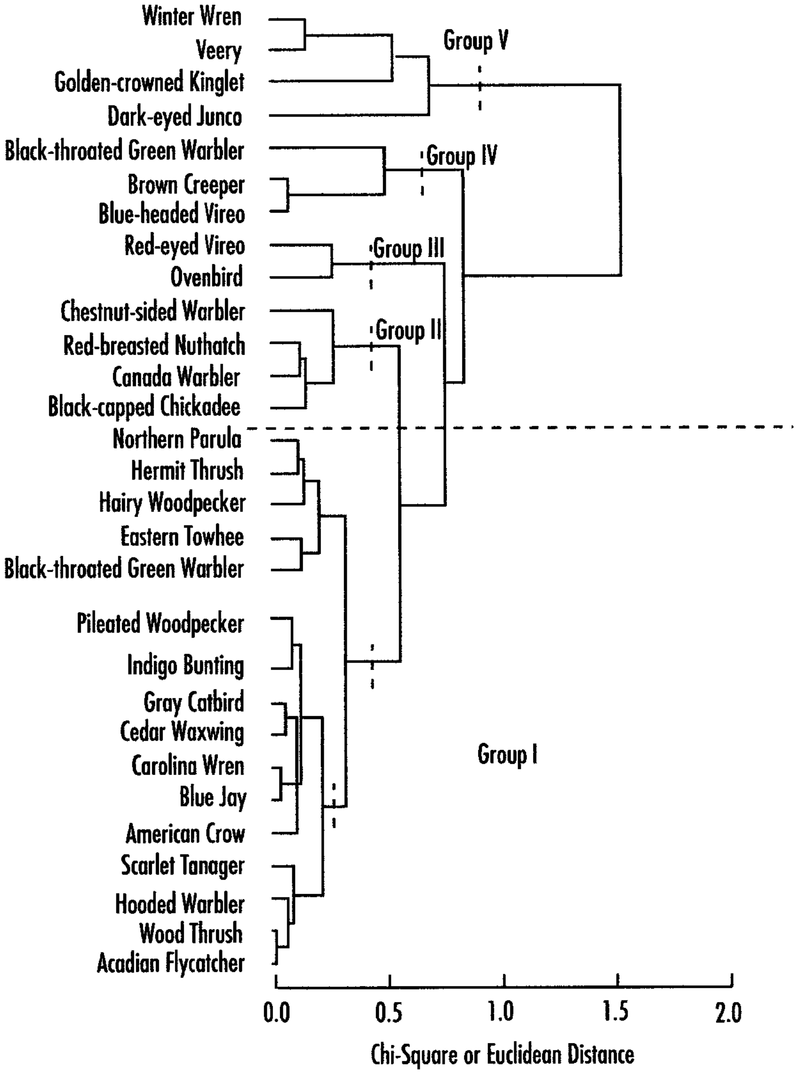

Fig. 2.8 Dendogram of 29 bird species on Mount LeConte, GSMNP, 1999-2000, identifying five assemblages. Assemblages (Groups) were named on the basis of ecotonal habitat characteristics. The vertical dashed lines indicate the division of assemblages. Horizontal dashed line indicates the degree of similarity between clusters or species on the basis of Chi Square measure of similarity. Birds near or at the top of the list were found at high elevations.

did not greatly affect the outcome of the ANOVA tests. For continuity with subsequent multivariate analyses, all succeeding statistical analyses were conducted using parametric tests (cf. Dueser and Shugart 1978).

Factor Analysis and Principal Components Analysis of Bird Habitat Relationships

An ordination of the plots was first constructed by a principal axis factor analysis (FA) of the habitat variables with a varimax rotation. The factor scores for the variables on Table 2.16 allow the selection of the most significant variables.

A factor matrix of rotated loadings showed the sorted eigenvalues with communality estimates of the input variables (Table 2.16). Low communality indicated the amount of common variance a variable shares. Low shrub cover, ground cover, and ground foliage height range showed the lowest communality. An examination of the loading of the first factor showed that it represented foliage height range with a strong positive correlation with subcanopy height range and canopy height range. Sorted eigenvalues showed that the first factor explained the most variance (20.4%) and loaded on several foliage height range metrics. Subcanopy foliage height range had the highest loaded variable on factor 1. The second factor, representing the effect of subcanopy development, had a high positive correlation with the density and dbh of subcanopy trees. The second factor accounted for 14.27% of the variance and loaded on subcanopy dbh and density. The third factor (12.4%) loaded highly on foliage height range of low shrubs and seedlings and represented foliage height range of the shrub and seedling component of the vegetation. The fourth factor (9.6%) loaded on canopy cover, and the fifth factor (9.38%) loaded on, or represented, the dbh and density of the canopy. These loadings on rotated factors showed a tight grouping of variables as hypothesized. Using

Table 2.16 Principal analysis of vegetation characteristics using VARIMAX rotation (total variance explained 63%). Significant factor loading of vegetation principal factors are in bold type. Only values that were significantly correlated ($P<0.05$) with a component are shown; only factors with eigenvalues >1 are shown. Variables defined as follows: DBH canopy = diameter breast height of canopy, DBH subcanopy = diameter breast height of subcanopy, DEN canopy =density of canopy, DEN subcanopy = density of subcanopy, LSHBCC = low shrub/ seedling canopy cover class, SUBCC = subcanopy cover class, CANCC= canopy cover class, TSHBCC - tall shrub/sapling canopy cover class, GRNDCC = ground canopy cover class, SUBC = subclass, TSUBC = tall shrub class, LSUBC = low shrub class, CANC = canopy class, GHR = ground height range, LSHBHR = low shrub height range, SUBCHR - subcanopy height range, TSHBHR = tall shrub height range, TCANHR = tree canopy height range. ^{1} = site specific variables, ^{2}= species specific variables

	Principal Components					
Variables	I	II	III	IV	V	Communality
COVERAGE^{2}						
DBH CANOPY	0.272	-0.098	-0.029	0.361	**0.813**	0.954
DBH SUBCANOPY	0.438	**0.844**	-0.065	0.030	0.031	0.907
DEN CANOPY	-0.027	0.063	-0.056	0.166	**0.911**	0.846
DEN SUBCANOPY	0.161	**0.924**	0.181	0.099	0.095	0.972
STRUCTURAL-HORIZONTAL						
LSHBCC^{1}	-0.010	0.161	0.575	0.057	-0.013	0.352
SUBCC^{1}	0.669	0.229	0.214	-0.042	0.138	0.463
CANCC^{1}	0.435	0.014	0.248	**0.721**	0.089	0.992
TSHBCC^{1}	0.275	0.146	0.424	-0.158	0.198	0.260
GRNDCC^{1}	0.001	0.151	0.142	0.452	0.082	0.125
SUBC^{2}	0.278	0.577	0.104	0.017	-0.131	0.424
TSUBC^{2}	-0.128	0.507	0.464	0.120	0.080	0.458
LSUBC^{2}	-0.261	0.052	-0.077	0.315	0.094	0.034
CANC^{2}	0.397	-0.203	0.252	**0.717**	0.150	0.816
STRUCTURAL-VERTICAL						
GHR^{1}	0.098	-0.019	0.445	0.234	-0.029	0.230
LSHBHR^{1}	0.346	-0.036	**0.707**	0.056	0.013	0.584
SUBCHR^{1}	**0.852**	0.205	0.190	0.199	0.143	0.935
TSHBHR^{1}	0.608	0.125	0.634	0.074	-0.009	0.767
TCANHR^{1}	**0.836**	0.120	0.321	0.227	0.095	0.941
Eigenvalues	3.68	2.57	2.24	1.73	1.69	11.91
Percentage of variance	20.44	14.27	12.44	9.6	9.38	62.7

Table 2.17 Principal component analysis of vegetation variable loadings and eigenvalues (total variance explained = 77%). Significant factor loading of vegetation Principal factors are in bold type. Only values were significantly correlated ($P<0.05$) with a component are shown; only factors with eigenvalues >1 are shown. Variables defined as follows: DBH canopy - diameter breast height of canopy, DBH subcanopy = diameter breast height of subcanopy, DEN canopy = density of canopy, DEN subcanopy = density of subcanopy, LSHBCC = low shrub/seedling canopy cover class, SUBCC = subcanopy cover class, CANCC = canopy cover class, TSHBCC = tall shrub/sapling canopy cover class, GRNDCC = ground cover canopy cover class, SUBC = subclass, TSUBC = tall shrub class, LSUBC = low shrub class, CANC = canopy class, GHR = ground height range, LSHBHR = low shrub height range, SUBCHR = subcanopy height range, TSHBHR = tall shrub height range, TCANHR = tree canopy range. ^{1} = site specific variables, ^{2} = species specific variables

			Principal Components		
Variables	I	II	III	IV	V
COVERAGE^2					
DBH CANOPY	0.152	-0.403	**0.427**	-0.018	-0.224
DBH SUBCANOPY	0.196	**0.407**	0.298	-0.136	0.008
DEN CANOPY	0.100	0.292	**0.503**	0.196	-0.318
DEN SUBCANOPY	0.199	**0.417**	0.313	0.157	0.004
STRUCTURAL-HORIZONTAL					
LSHBCC^1	0.279	-0.041	-0.237	0.150	-0.146
SUBCC^1	**0.327**	-0.021	-0.028	-0.162	-0.056
CANCC^1	**0.331**	0.163	0.016	-0.083	0.027
TSHBCC^1	0.292	-0.009	-0.116	-0.018	-0.135
GRNDCC^1	0.225	0.095	0.049	**0.325**	0.195
SUBC^2	0.159	**0.409**	0.114	-0.142	0.065
TSUBC^2	0.135	-0.253	0.129	**0.532**	-0.077
LSUBC^2	0.031	0.118	0.231	0.118	**0.847**
CANC^2	0.211	**0.336**	0.010	-0.076	0.162
STRUCTURAL-VERTICAL					
GHR^1	0.151	0.096	-0.236	**0.450**	0.042
LSHBHR^1	0.237	0.058	-0.325	0.193	-0.006
SUBCHR^1	0.307	0.016	0.044	-0.332	0.083
TSHBHR^1	0.305	-0.023	-0.237	-0.019	-0.014
TCANHR^1	**0.321**	0.053	-0.052	-0.289	0.071
Eigenvalues	7.47	2.33	1.80	1.23	0.98
Percentage of variance	41.50	12.94	10.00	6.83	5.44

the highest loading variables, these five factors were interpreted as the following: 1) subcanopy height range, 2) subcanopy density, 3) low shrub/seedling height range, 4) canopy cover, and 5) canopy density. The loadings of the factor analysis were inversely correlated with elevation. The combined orthogonal factors (communality) accounted for a clear majority of vegetation variance (62.7%). Results of factor analysis of vegetation variables revealed that four to six axes were derived for nineteen input variables. Total variance explained in the five-factor model was 62.7%.

After trial runs of four to six components, a five-component PCA was assessed for its interpretation of orthogonal vegetation variables. Tables 2.17 and 2.18 show resulting loadings and eigenvalues for five vegetation- and topographic-related components. Five principal components (PC1-PC5) explained 77% of the structural variation in habitats (Table 2.18). PC1 represented a gradient of increasing cover for the subcanopy and canopy and increasing foliage height range for subcanopy with an increase in elevation (Table 2.19). The first three dimensions derived in the analysis accounted for over two-thirds of the variation present in the original data (Table 2.17). The first component loaded highest on subcanopy (SUBCC), canopy cover (CANCC), and subcanopy height range (SUBCHR), while coefficients of variation for canopy density contributed less variance. The first component accounted for 41.5% of total variance and represented a gradient from habitats with low tree cover and height to habitats with higher tree cover and greater horizontal and vertical heterogeneity in foliage height. The second component (12.94%) loaded on variables describing greater subcanopy tree dbh, density, and cover. The second component contrasted plots that displayed volume of tree species and high coverage of subcanopy trees distributed in a

Table 2.18 Topographic and spatial variable PCA loadings and eigenvalues (total variance explained = 75%). Significant loadings are in bold type.

	Factor		
Variables	I	II	III
Disturbance	0.452	-0.606	0.136
Elevation (m)	**0.622**	-0.210	0.065
Forest Opening	**0.512**	0.288	-0.078
Slope (Degrees)	0.196	**0.545**	**0.751**
Snags	0.329	0.456	-0.638
Eigenvalues	1.673	1.102	0.948
Percentage of variance	33.46	22.04	18.96

Table 2.19 Principal components analyses (PCA) of 23 landscape variables, resulting in seven significant components describing trends in habitat structure and topography across the sampling sites.
a. = Principal Components Analysis (PCA) of 5 topographic variables
b. = Principal Components Analysis (PCA) of 18 vegetation variables

Principal Components	Eigenvalue	Percentage of Variance	Interpretation of trend toward positive extreme
a.			
1	1.673	33.5	Higher elevation
2	2.568	12.9	Greater subcanopy tree dbh, density, and cover
b.			
1	3.684	41.5	Greater subcanopy and canopy cover; higher subcanopy and canopy height
2	2.568	12.9	Greater subcanopy tree dbh, density, and cover
3	2.244	10.0	Greater canopy tree dbh and density
4	1.731	6.9	Greater tall shrub/sapling cover
5	1.690	5.4	Greater low shrub/seedling cover

horizontally patchy fashion. The third component (10.0%) clearly loaded on dbh and density of canopy trees, the fourth component (6.8%) loaded on cover of tall shrubs, tree saplings (SUBC), and the fifth component (5.44%) loaded primarily on the coefficient of variation of cover of low shrubs and tree seedlings. This PCA resulted in five meaningful vegetation variables describing major gradients and coverage, and horizontal and vertical structural heterogeneity patterns (using varimax rotation to describe loadings). Overall, five components explaining 76.7% of the structural variation in habitats were found, of which the first two accounted for approximately 54% of the total variance. The third component accounted for 10.0% of the variance, and the fourth and fifth components explained 6.89% and 5.4% of the total variance, respectively. In consideration of the potentially disparate relationships among vegetation or FA, PCA, and bird abundance factors, I retained the highest loading variables on each component for use as possible surrogate variables in CANCOR.

Canonical Correlations Analysis

CANCOR was undertaken using bird abundances and PCA or FA vegetation variables using canonical methods in SAS software (SAS Institute 2000). The canonical analysis procedures were applied to birds vs. 20 habitat variables.

Variables representing the factored and PCA variables were selected from the eigen analysis for habitat data (Tables 2.17, 2.20). For each factor or component the highest loading variable was selected for use in the CANCOR procedure. These variables were correlated with their respective factors, but provided more clearly interpretable measures than strict linear combination variables. Further, since CANCOR analyzes correlations among composites of variables (here dependent pattern and

Table 2.20 Canonical loadings (correlations between dependent variables and canonical variates or variables) of bird species. Significant loadings are in bold type. n=29 species.

	Canonical Variate Loadings	
Variable	I	II
Acadian Flycatcher	0.020	-0.074
American Crow	0.129	0.098
Black-capped Chickadee	0.156	-0.092
Blue-headed Vireo	0.082	0.118
Blue Jay	0.002	0.169
Brown Creeper	0.094	0.121
Black-throated Blue Warbler	-0.089	0.130
Black-throated Green Warbler	**-0.299**	-0.084
Carolina Wren	-0.045	0.011
Canada Warbler	-0.006	0.058
Chestnut-sided Warbler	0.044	-0.138
Dark-eyed Junco	0.149	0.216
Eastern Towhee	0.102	0.105
Golden-crowned Kinglet	0.143	0.206
Gray Catbird	0.088	-0.155
Hairy Woodpecker	0.090	-0.217
Hermit Thrush	0.090	0.004
Hooded Warbler	0.039	0.126
Indigo Bunting	**-0.708**	0.239
Northern Parula	0.129	0.176
Ovenbird	**-0.375**	-0.355
Pileated Woodpecker	0.002	-0.078
Red-breasted Nuthatch	0.108	0.318
Red-eyed Vireo	**-0.525**	-0.398
Scarlet Tanager	-0.118	0.173
Veery	0.135	0.162
White-breasted Nuthatch	-0.132	0.296
Winter Wren	0.172	0.173
Wood Thrush	**-0.314**	0.047

Table 2.21 Habitat parameters (variable) canonical loadings (correlations between independent variables and their independent canonical variates or variables).
Significant loadings are in bold type. AVGTSHR = average tall shrub height range, AVGLSHR = average low shrub height range, CANTTLDBH=total canopy dbh, SCTTLDBH = total subcanopy dbh, CANAVGDBH = average canopy dbh, SCAVGDBH = average subcanopy dbh, CANSPDENAVG = average density of canopy species, SCSPDENAVG = average density of subcanopy species, CANSPDENSUM = sum of density of canopy species, SCSPDENSUM = sum of the density of subcanopy species, AVGSCHR = average subcanopy height range, AVGTCHR = average tree canopy height range, AVGTSCC = average tall shrub canopy cover class (for site), AVGSCCC = average shrub canopy cover class, AVGTCCC = average tree canopy cover class, AVGLSCC = average low shrub cover class, AVGSUBCLS = average subcanopy cover class (for species), AVGTALLCLS = average tall shrub/sapling cover class, AVGLOWCLS = average low shrub/seedling cover class, AVGCANCLS = average canopy cover class.

	Canonical Variate Loadings	
Variable	I	II
AVGTSHR	0.0655	0.1015
AVGLSHR	0.1197	-0.2655
CANTTLDBH	0.3215	0.1678
SCTTLDBH	0.2641	**-0.3076**
CANAVGDBH	**0.5160**	0.1592
SCAVGDBH	**0.4588**	-0.0909
CANSPDENAVG	0.2140	0.1248
SCSPDENAVG	0.2881	-0.1368
CANSPDENSUM	0.0904	-0.0137
SCSPDENSUM	-0.0106	0.0111
AVGSCHR	0.1953	0.1559
AVGTCHR	0.2765	0.2853
AVGTSCC	0.1909	-0.0187
AVGSCCC	0.0128	0.0282
AVGTCCC	**0.3644**	0.0681
AVGLSCC	**0.3089**	**0.4277**
AVGSUBCLS	0.1016	-0.1013
AVGTALLCLS	-0.1311	0.2502
AVGLOWCLS	**0.3710**	0.2946
AVGCANCLS		

independent terrain variables), non-factored metrics were judged more easily interpretable using canonical weights and loadings.

CANCOR procedures were applied to the 29 bird variables and 20 habitat variables. Canonical correlations were generated as well as canonical weights and loadings for individual dependent (Table 2.20) and independent (Table 2.21) variables. The first canonical variate loaded strongly positively lower elevation birds (Table 2.20) and canopy and subcanopy dbh (Table 2.21). The second CANCOR variate also loaded primarily on lower elevation bird variation and low shrub, seedling cover (and negatively on subcanopy total dbh). The Red-breasted Nuthatch loaded negatively with subcanopy total dbh. Generally, low elevation birds loaded opposite to high elevation birds. The second canonical analysis involved birds versus habitat variables. This resulted in three "significant" correlations in which the bird variates explained 24% of the variance in the bird portion of the data set (Table 2.22).

Simple correlations of each bird variable with bird variates were used to determine the coordinates of each species in the correlation space associated with the first two bird variates (Fig. 2.9). This produced six recognizable groups of birds, each consisting of species which were associated with the environmental variables in similar ways (Fig. 2.10).

Discussion

Many ecologists are interested in how organisms are dispersed in space. The answers often provide clues to mechanisms of interaction among individuals and point to factors in the environment that influence their distributions. Organisms can be dispersed in three ways: (1) evenly, in which individuals are more equidistant from each other than

Table 2.22 Canonical correlations and percent variance of bird abundances accounted for by each bird canonical variate.

	Birds vs. Habitat	
Canonical Variate	Eigenvalue Canonical Correlated	Variance (%)
1	0.71	19.00
2	0.63	24.00
		33.35

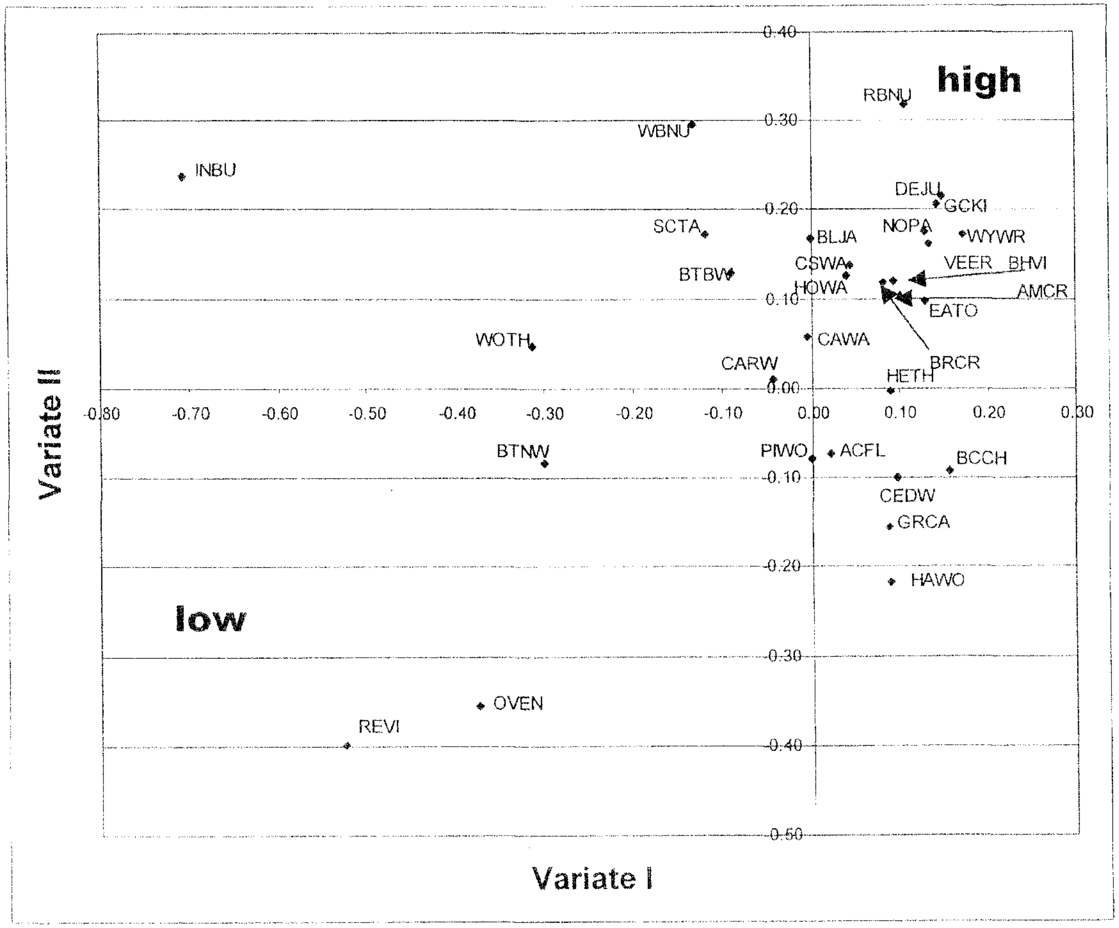

Fig. 2.9 Grouping of bird species resulting from canonical correlation of bird species with the first two canonical variates. Canonical Variate 1= low elevation, Canonical Variate 2 = high elevation.

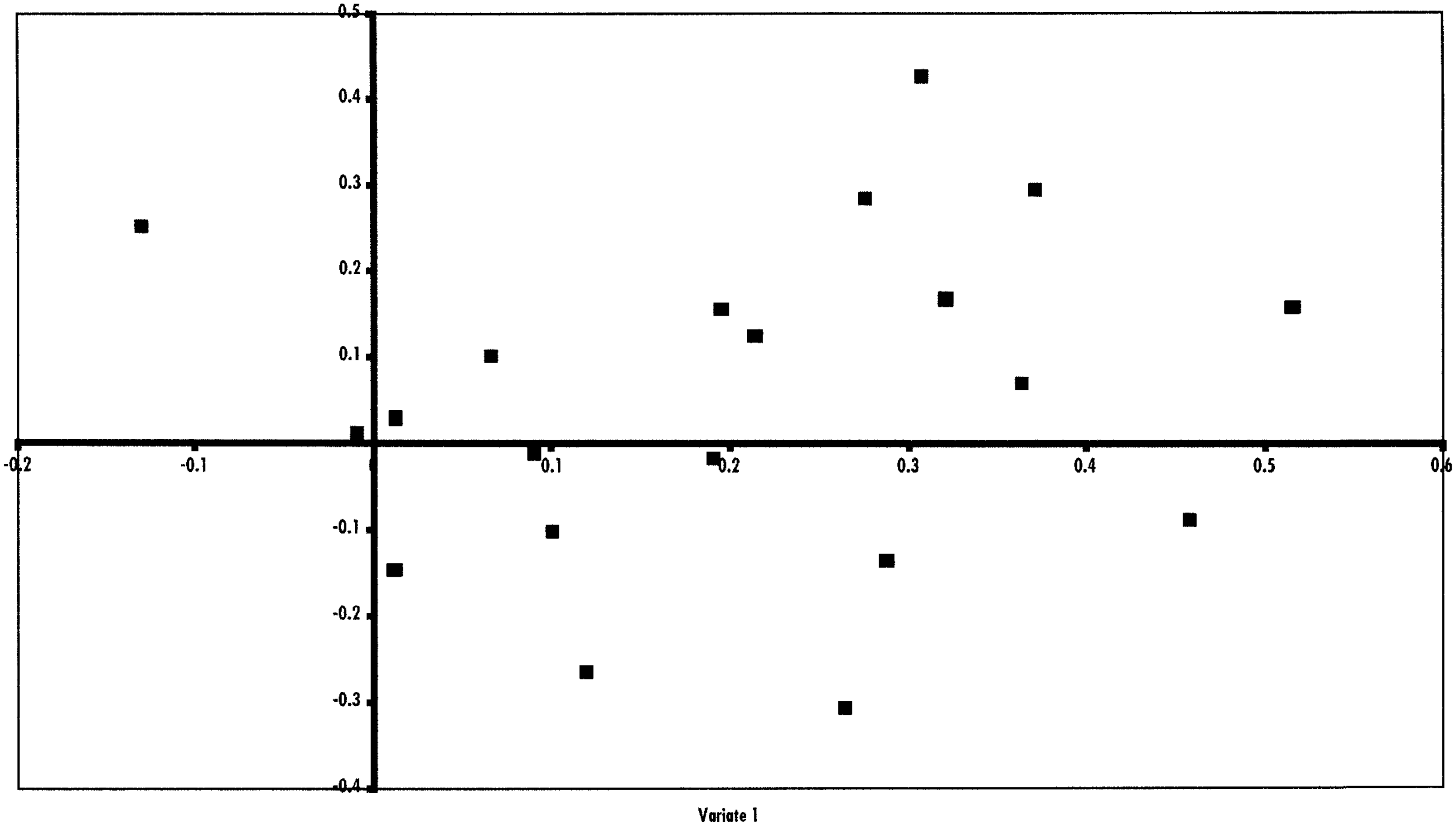

Fig. 2.10 Habitat structure resulting from simple correlation of vegetation variables with the first two vegetative canonical variates. Canonical Variate 1 = average dbh of canopy and subcanopy, average tree canopy cover class; Canonical Variate 2 = low shrub/seedling canopy cover class. Squares refer to habitat variable canonical loadings (correlations between independent variables and their independent canonical variates or variable).

occurs randomly, (2) patchily, in which individuals are closer to each other ("clumped") than occurs at random, or (3) randomly, when the locations of individuals are independent of those of other individuals.

Community Classification and Zonation

To provide a means of standardization in the description of bird distributions, I developed a generalized model of vegetation and bird species distributions along elevational and vegetational gradients on Mount LeConte. Montane spruce-fir was defined as vegetation in which species of spruce and fir contributed over 50 percent of canopy stems. The accelerated vegetation change across the spruce-fir boundaries facilitated my effort to select representative ecotone elevations as a function of the gradsects. The lower ecotone consisted of a relatively rapid shift to dominance by deciduous trees (deciduous/coniferous boundary; on ACT a hemlock/coniferous boundary). The upper ecotone was marked by a reduction in tree height, a subtle shift to spruce-fir (an abrupt shift to fir on ACT), and coverage of more than 50% coniferous forest shrub and tree vegetation (forest boundary).

Site Factors: Topography, Elevational and Vegetational Correlates

The spatial arrangement of range boundaries of plant species on Mount LeConte differed from a random pattern at some elevations. Despite occasional aggregation of boundaries, however, I found little evidence for discrete zones. If discrete zones had existed, transitions between adjacent communities (ecotones) would have been marked by coincidence between the upslope and downslope boundaries. In other words, range endpoints of species in one community (or at least a high proportion of them) and the beginnings in the next higher community would have tended towards aggregation in the same general area.

Coincident aggregation of downslope and upslope boundaries occurred between 672 and 1370 m a.s.l. and higher on the mountain between 1462 and 1827 m (Table 2.3, Fig. 2.4). On ACT, at 1370 m, there appeared to be a rapid or abrupt transition from hemlock-hardwood dominated by eastern hemlock to spruce-northern hardwood forest characterized by red spruce. At 1827 m a.s.l., there was a sharp transition from red spruce ECC to Fraser fir ECC. As mentioned earlier, at the 100-m distance scale, concordant or harmonious merging of upslope and downslope termini at 1370 and 1827 m (ACT), 995 and 1462 m (BHT), 1134 and 1610 m (RFT), and 952 and 1576 m (TGT), was circumspectly or carefully determined because of the probability for downslope aggregation (Table 2.3, Fig. 2.4). However, the fact that clumping of (both) edges at 1370 and 1827 m (ACT), 1134 m (RFT), and 952 and 1576 m (TGT) also appeared at the 50-m scale (at lower probability levels, Table 2.3, Fig. 2.4) and that species turnover (ß-diversity) is greatest in the gradsect belts from ca. 1000 and 1800 m suggests that a discrete ecotone does indeed exist near 1370 and 1827 m on ACT. The other apparently abrupt transition, which will not be discussed further, occurred higher (at 1827 m a.s.l.).

Distributions of mean ranges of species between each elevational contour or at each elevational band provided further evidence for major vegetative transitions at 952 - 1370 m. At lower elevations, the median range of species beginning in each band decreased, with the median range resulting in an upslope boundary from 952 - 1370 m. Thus, plant species that began below 952 m tended to terminate their range in the ecotone.

Discrete transitions also appeared at 1462 and 1827 m at 200-m, but not 100-m scales, although downslope aggregation <1462 m was again statistically questionable (Tables 2.3, 2.4). These scale-dependent differences reflected heterogeneities (subzones) in the transition from deciduous to hemlock to coniferous habitats. It is possible that an abrupt floristic transition occurred at or near the border of a zone, or that replacement of species in an ecotone was only loosely aggregated in space. I tested for these possibilities by relaxing the criterion for discrete transitions by looking for coincidence between adjacent altitudinal bands, i.e. aggregation of upslope boundaries in one band followed by aggregation of downslope boundaries in the next highest band every 200 m.

The absence of coincident community boundaries on Mount LeConte negated the existence of discrete communities, yet the distribution of plant species was clearly not perfectly continuous given the aggregation of dominant species' borders, particularly upslope ones, at some elevations. Similarly, Shipley and Keddy (1987) found aggregation of upslope and downslope boundaries of marsh species but no coincidence in the location of the two types of borders. They cautioned that in testing patterns of species' boundaries along environmental gradients, rejection of the community-unit concept should not imply automatic acceptance of the continuum viewpoint because the two theories do not exhaust all combinations of boundary patterns (Whittaker 1977). In fact, several variants of the continuum concept emerged, each proposing different distribution patterns along gradients (Austin 1985; Austin and Smith 1989). For instance, Gauch and Whittaker (1972) suggested that dominant species should be regularly, and other species independently, distributed along gradients. Because the current analysis was based on presence/absence data and not on estimates of abundance, I was unable to test if distribution patterns differed between dominant and other taxa.

Other studies of vegetation change along elevational gradients have also found no evidence for discrete communities (Whittaker 1956; Hamilton 1975; Enright 1982), although transitional zones or ecotones, such as the ones noted between 952 to 1370 m and 1462 to 1827 m on Mount LeConte, have been investigated in ordination-based studies (e.g., Druitt et al. 1990; Enright and Ogden 1990; Auerbach and Schmida 1993). Ecotones were usually marked by changes in abundance of dominant tree species and were often used to define different plant associations along the gradient. As in the present case, the boundary on the opposite side of the two associations delimiting the ecotone was generally poorly defined. In addition, although dominants in the ecotone changed along its width, distribution of many other species of each association spanned the transition zone. Without an explicit test it was impossible to assess whether there was an unusual number of concordant termini in these ecotones, although I suspected that frequently only a few dominant taxa appeared or disappeared. For example, Ogden and Powell (1979), in their study of vegetation change along altitudinal gradients in Tasmania, noted that "Although three elevational zones can be recognized easily in the forest vegetation of the area studied, there is sufficient continuity between these zones to render sterile any arguments about their precise altitudinal boundaries". Thus, in the absence of sharp edaphic discontinuities, vegetation change along elevational gradients generally appeared to be a subtle, continuous process.

Slope, Exposure, and Moisture

North slopes and coves in the mountains were moist and shady, south slopes were dry and sunny, and east and west slopes were intermediate. BHT, RFT, and TGT were trails with North, West, and Northwest slopes. ACT was a trail with primarily southern slopes. Correlated with changes in habitat was a continuum of plant communities. At low elevations, there was no observable difference between total bird species and number of breeding pairs between cove and hemlock deciduous forests on north slopes and mesic oak (red oak and chestnut oak) on intermediate slopes, but fewer species and smaller populations occurred in pine-oak forests on south slopes. Although the continuum of plant communities in these areas resulted in changes in habitat, at high elevations no observable difference was detectable between total species and number of breeding pairs from red oak forests on intermediate slopes to pine forests on exposed south slopes. Bond (1957), working in southern Wisconsin with a continuum of plant communities in the ecotone between grassland and deciduous forest, found an increase in number of bird species and total populations from moist to intermediate stages and then a decline to the dry end. Individual species varied in their points of greatest abundance along the gradient. Likewise, in a deciduous forest continuum in the Ozark Mountains of Arkansas, Smith (1977) observed three of eight species restricted to the moist end with only one species extending to the extreme dry end. On Mount LeConte, moist soil sites representative of hemlock communities in Zone 1 on ACT and Zone 2 on other trails supported a diverse bird community.

The Wood Thrush and Veery overlapped broadly in vertical distribution and at the census points. The Wood Thrush is a common summer resident in the lower and middle altitudes of the park. This bird occurred in deciduous forests up to the lower limits of the spruce-fir zone. There it made contact with the Veery, which breeds throughout the spruce-fir forests, so there were a number of places in the park between 1070 and 1525 m where both these thrushes were found. The former elevation marked the approximate lowest breeding range of the Veery while the latter marked the upper most breeding extension of the Wood Thrush. The Veery was more likely to “spill over” into the northern hardwood forest just below the high-altitude conifers while the Wood Thrush was apt to penetrate upward into the forests of spruce and fir. The Veery is a common summer resident throughout the higher altitudes, not only in spruce-fir forests in the eastern half of the park but also in the deciduous woodlands west of Clingmans Dome. The unique song of this thrush was confined to the period from the latter part of May to near the end of July.

Red-eyed Vireos, Black-throated Green Warblers, and Blue-headed Vireos were present in deciduous forest communities, and the latter occurred in red oak and chestnut at higher elevations. All were numerous in the cove forest but the Blue-headed Vireos were more abundant in the hemlock forest. The Blue-headed Vireo commonly sang and fed in both deciduous and coniferous trees from 2 to ca. 12 m. By contrast, the Red-eyed Vireo was seldom heard or seen in coniferous trees and never in Fraser fir, while in deciduous trees it conducted its activities from 2 m to the treetops. This agrees in general with observations of the two species in mixed forests in New York State (Kendeigh 1945). The vertical ranges of the two nuthatches broadly overlapped but the White-breasted Nuthatch was largely confined to deciduous sites and the Red-breasted Nuthatch to coniferous ones. The ranges of warbler species from the upper and lower elevations did not overlap except for the Hooded and Canada Warblers in the cove forest.

Species nesting above 2600 m were the Acadian Flycatcher, American Crow, Blue-headed Vireo, Black-throated Blue Warbler, Carolina Wren, Hairy Woodpecker, Blue Jay, Gray Catbird, Cedar Waxwing, Black-throated Green Warbler, and Eastern Towhee. Most of the upper limits of high elevation birds were on the warmer and drier south-facing slope. Some of the lower limits of birds found commonly at high elevations were in lobes and peninsulas of evergreens, usually hemlocks, that extended down the north-facing slope. The Black-throated Blue Warbler provided a good illustration of how the density of a species usually changes toward the limits of its elevational range. This warbler was common from above 1312 m in LeConte Creek Valley; two or more birds were heard singing simultaneously in many places, and singing occurred in almost any area that would attract a pair. Below 1119 m, the species was scarce and the pairs scattered. The pair at the lowest elevation seemed well separated from other Black-throated Blue and Green Warblers, but the male sang regularly and the pair built a nest; they were like pioneers that had pushed ahead into wilderness. After the nesting season, many birds moved up and down the mountain, going well beyond the limits of their nesting range.

Circumstantial evidence indicated that competition as well as changes in vegetation affected vertical limits of some species on Mount LeConte. Upper and lower distributional limits of species coincided with ecotones in vegetation. Able and Noon (1976) found no convincing cases of altitudinal competitive exclusion between communities of species in the temperate mountain forests of New York and Vermont. In the tropical forests of New Guinea, Diamond (1973) believed competition to be more important than changes in vegetation in controlling vertical distribution of bird communities. In the tropical mountains of Peru, Terborgh (1971) believed changes in vegetation account for less than 20% of the altitudinal limits of species, competition for about 33%, and gradually changing physical and other biological conditions for about 50%. Included in the latter category were not only changes in temperature and cloudiness, but also changes in net annual plant productivity, density of insects, and importance of epiphytic plants in the vegetation. If probabilities of occurrence of bird species were the same for all three zones, or at points on each gradsect, then occurrence would not depend on elevation. There was no significant difference between the cumulative frequency distributions of observed and expected downslope boundaries in the 200-m distance elevational bands, but distribution at three zones or upslope boundaries on the six trails differed significantly (Table 2.6, Fig. 2.4). More species than expected ended their range at lower elevation ranges and fewer than expected terminated at the middle and higher elevation ranges. Hence, species beginning low on the mountain tended to have shorter ranges than expected. Thus, many factors potentially contributed to the altitudinal distribution of species of forest birds.

Forest Community Factors: Changes in Composition and Structure

Birds on Mount LeConte actively selected their habitat on the basis of such proximate factors as features of their landscape, terrain, substrate, vegetative structure, or vegetation pattern. Single factors or combinations of factors were important to different bird species. Such factors held for several species of birds in widely separated locales throughout Mount LeConte.

The forest landscape contained both deciduous and coniferous species, in mixed or relatively pure sites, and with physiognomies varying from tall, luxuriant cove forest to short-statured American beech and open pine-heath stands. Relatively high species richness of birds occurred in cove, chestnut oak, red oak and hemlock-deciduous forests.

Likewise, there was similarity between the cove forest avifuana (after those species commonly associated with hemlocks were eliminated) and the pine-oak avifuana. Certain bird species extended widely among these deciduous plant communities although at different population levels. When bird species commonly associated with deciduous trees were excluded from the hemlock-deciduous forest, the remaining "hemlock" avifuana was similar to that of the spruce-fir forest. There was also considerable similarity between avifuanas of spruce-fir forest and high seral stages, even though these plant communities contained different vegetation types.

Species similar in ecological function (= guilds) tended to be dispersed rather than adjacent in distribution. This dispersion indicated resource division among the habitats used by these species. The two largest ecologically similar groups were the thrushes and the warblers. Within both guilds, the member species showed large spatial overlaps. The ground-foraging thrushes were particularly interesting because they were more likely to partition the habitat horizontally than species using higher strata in the forest.

In the Smoky Mountains of Tennessee and North Carolina, Wood Thrush and Veery are Neotropical migrant thrushes and occur in the absence of the other Thrushes or the American Robin. In the Smokies, Wood Thrush and Veery reportedly increase their elevational peaks (amplitudes) and in some instances breed along the entire length of the gradient (Bent 1949; Dilger 1956; American Ornithologists' Union 1957; Stupka 1963; MacArthur 1972). In this study, the Wood Thrush occupied the lower altitudes and its upper elevation coincided with the lower part of the ecotone. However, the Veery did not appear until mid-elevations (though below the lower ecotone) and extended all the way to the upper end of the gradient. The Wood Thrush and Veery had virtually mutually exclusive ranges, with approximately only 400 m of overlap. The Hermit Thrush, a fairly common winter resident, uncommon summer resident, and temperate migrant is the only thrush (excluding Robin and Eastern Bluebird) likely to be encountered in the Great Smoky Mountains between late October and early April. During this study, it was mainly observed at mid-elevation locations including Alum Cave Bluffs on ACT, although the great majority of Hermit Thrushes winter throughout the lower altitudes.

When two or more similar species had similar mean habitat vectors, there was ecological separation and, in my study, vertical separation. This dispersion indicates resource division among the habitats of these species. For example, Red-eyed Vireo, Indigo Bunting, and Wood Thrush had similar mean habitat vectors (as indicated by the closeness of the points, Fig. 2.9), however, the Red-eyed Vireo spent most of its time in the canopy, the Indigo Bunting fed in the subcanopy and understory vegetation, and the Wood Thrush was found on or near the ground. This was the only example of such three-layer vertical separation in this study, but there were several examples of two-layer stratification (e.g., Black-throated Green Warbler and Ovenbird). Any habitat alteration that would move the mean habitat vector (Fig. 2.11) toward a given bird species would be beneficial to that species, since the population would have more area of typical habitat available. Conversely, movement of the vector away from a species could be expected to reduce available habitat.

The Parula Warbler is a fairly common summer resident occurring from the lowest altitudes to approximately 1505 m. This bird was heard singing (by the author) on Bunches Bald (1505 m) where it appears to reach its highest breeding altitude. The Black-throated Blue Warbler is a common summer resident above 854 m. Although

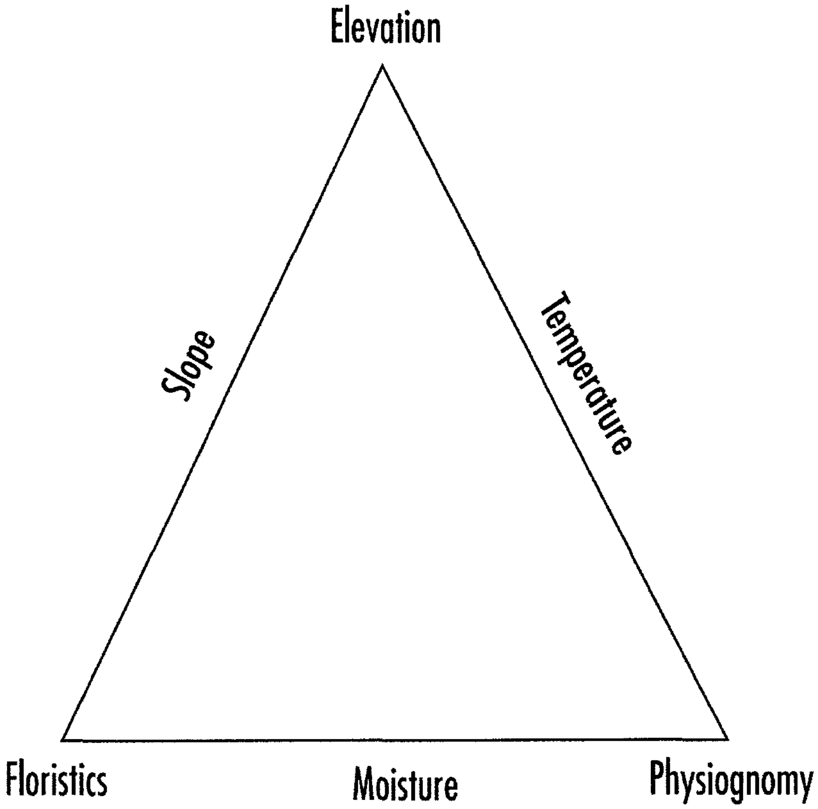

Fig. 2.11 Illustration of contributing factors determining bird distributions in the Great Smoky Mountains. Factors at the points are more important and useful than those between points.

854 m is the approximate low altitude for the nesting of this warbler, it bred down to 732 m. The Black-throated Blue Warbler is one of the most abundant breeding warblers in the higher elevations throughout the Southern Appalachian region. Where the original high-mountain forest is interrupted by heath balds or grass balds, or where it was affected by fires, lumbering, or both, the Chestnut-sided Warbler replaced the Black-throated Blue as the most prevalent breeding warbler. The Black-throated Green Warbler is one of the few summer resident warblers that occurred at all altitudes. At the lower elevations it was common along ravines where hemlocks prevailed, although it occurred in other habitats; in the spruce-fir forests it is a fairly common breeding bird, perhaps the most widespread breeding warbler in the park.

The Chestnut-sided Warbler is a common summer resident 915 m to the summits of the highest mountains. At higher elevations, wherever openings were created in the forest by fire, lumbering, chestnut blight, windthrow, landslide, or by other means, the Chestnut-sided Warbler was one of the most plentiful breeding species. This situation seems to have come about some time after the turn of the century in view of remarks such as Odum's (1945): "The Chestnut-sided Warbler 'push' is especially interesting because it demonstrates how wholesale change in habitat may change the range of species, even though the climate remains the same. Thus, before the blight and lumbering operations by white man, there was probably little suitable habitat for the Chestnut-sided in the Georgia mountains other than the isolated 'balds'. With the destruction of the overstory trees, however, the bush second growth became the dominant habitat, forming a continuous broad highway into formerly unoccupied regions. Birds, of course, are not always able to take advantage of such windfalls, but species that are able to build up large populations and are tolerant of the climatic conditions often do take advantage of such large scale changes as apparently the Chestnut-sided and the Song Sparrow have done."

The Hooded Warbler is a common summer resident in woodland forests at low and middle altitudes, generally below 1220 m. During the breeding season in this study, this bird seldom ascended above 1220 m. The Canada Warbler is a common summer resident up to 1037 m. On Mount LeConte it resided in cool dark tangles of rhododendrons and other shrubs, especially near small watercourses from 1037 m to the top of the mountain.

Bivariate correlations were used to assess the nature of the relationships among topographical, elevational, and vegetational site factors and the breeding bird species. Several patterns emerged from the analyses. For example, there was a clear association between the abundances of Canada Warbler, Chestnut-sided Warbler, Eastern Towhee, Gray Catbird, Hooded Warbler, Indigo Bunting, and Winter Wren (typical forest species) and variables describing subcanopy cover, and tall and low shrub cover (SCCC, TSCC, LSCC; Table 2.8). On the other hand, there were strong negative relationships with GCC, GHR, and several other variables associated with increasing horizontal (TSCC, TCCC) and vertical heterogeneity (TCHR). A typical forest species and PR, Hairy Woodpecker, did not demonstrate these relationships as strongly.

Covarying in a different manner were several of the high altitude species, particularly Black-capped Chickadee, Blue-headed Vireo, Brown Creeper, Black-throated Blue Warbler, Dark-eyed Junco, Red-breasted Nuthatch, Veery, and Winter Wren. These species evidence high positive correlations with canopy and subcanopy coverage values of coniferous trees and with several indices relating to horizontal heterogeneity, but, conspicuously, not with the values of deciduous trees (including shrubs). As shrub coverage increased, the abundances of these species increased.

The correlation matrix of 24 habitat variables (Table 2.8) also indicated that groundcover was negatively correlated with increasing vegetation structure. Some species that showed definite patterns were Black-throated Green Warbler, Chestnut-sided Warbler (both Neotropical migrants), and White-breasted Nuthatch, all with strongly negative relationships to several vertical and horizontal indices (GHR and GCC). Other Neotropical species, however, exhibited less clear patterns. Red-breasted Nuthatch, a high elevation NM preferring spruce-fir forests showed a positive relationship with subcanopy and canopy vertical (height range) and horizontal (coverage) indices or values.

Table 2.8 indicated that every vegetation variable was significantly associated with the abundance of at least three, and usually seven to ten, bird species. The existence of these correlations suggested that, at the least, these variables were important to the relationships and determinants I was investigating. TSHR, SCHR, SCCC, TCHR, TCCC showed perhaps the strongest patterns, serving to separate the responses of most of the Neotropical migrants (more preferred canopy, ground and snag parameters). Another pattern was shown by those species that had forest habitat guilds and were highly correlated with forest openings and snags. They reached their maximum abundances and had positive relationships at the montane sites (Acadian Flycatcher, Black-capped Chickadee, Blue Jay, Black-throated Green Warbler, Carolina Wren, Chestnut-sided Warbler, Eastern Towhee, Hooded Warbler, Hermit Thrush, Northern Parula, Ovenbird, and Wood Thrush). Mountain meadows were often thickly carpeted with wildflowers in the spring, and while these bird species responded to other features of the environment, their association with the forbs was nonetheless significant.

Beyond these relationships of responses of individual species to vegetational habitat parameters, the ecological literature suggests that aspects of overall avian community structure, such as diversity, should be closely related to vegetation structure (MacArthur 1958, 1972; MacArthur and MacArthur 1961). Most causal explanations of this relationship draw attention to the role of environmental complexity, patchiness, or heterogeneity in promoting niche diversification, and thus diversity (Willson 1974; Roth 1976), and in fact such relationships have been explicitly emphasized to explain species numbers in grassland habitats (Cody 1968). As such, heterogeneity was measured in some of the vegetation variables I considered, and I expected to be able to define some key habitat components that enhance diversity in this system. Examining the straightforward bivariate correlations, however, added little to my understanding. Species diversity was significantly more positively correlated with LSHR, TSHR, SCHR, and TCHR then LSCC, TSCC, SCCC, and TCCC (Table 2.8). I found no significant correlations between species richness or evenness considered separately and any environmental variables. These results were similar to Rotenberry and Wiens (1980), who reported that out of 550 correlations, 18.5% were significant at $P<0.05$ or better, 9.6% at $P<0.01$ or better, and 5.5% at $P<0.0005$, for a similar analysis.

The vegetation structure of a habitat was recognized as one of the principal determinants and proximate factors influencing the distribution of the avian community breeding in habitats on Mount LeConte. MacArthur and MacArthur (1961) found that the species diversity of breeding birds in a community could be predicted from a measure of the proportional distribution of foliage layers (foliage height diversity). Other studies in which vegetation structure has been measured in the breeding territories of birds have shown that each species often is distributed according to specific habitat variables (James 1971; Shugart and Patten 1972; Anderson and Shugart 1974; Willson 1974; Smith 1977). James (1971) used the term 'niche-gestalt' to refer to these habitat configurations as components of a species' niche.

The univariate and multivariate orderings of vegetational features and communities documented in this study also permitted an examination of the niche patterns of bird species in this vegetation space. Niche overlap, a measure of the degree to which two species co-occurred in the intervals defined along the communities, was calculated according to the similarity formula presented earlier. An intuitive grasp of the relationships defined thereby can be gained from comparison of species' distributions in Fig. 2.6. For example, Blue-headed Vireos, Dark-eyed Juncos, Red-eyed Vireos, and Winter Wrens were distributed along almost all communities, and their calculated overlap score (9) reflected this. Gray Catbird, however, was distributed along fewer and relatively more disjunct communities and hence had a lower score. Most species lay somewhere between these two extremes. Overlaps calculated in this manner are of course confounded by the spatial co-occurrence of species at sites; such aspects of local and geographic distributions may be at least partially unrelated to the relationships of species on the vegetational gradients I derived.

Of perhaps greater interest was not merely the overlap between two species on one niche dimension but their relationships when several axes were considered simultaneously. Conventional niche theory predicts that species which overlap extensively along one axis should diverge strongly along another in order to permit coexistence (May 1975; Pianka 1975). Because these niche dimensions are truly independent, overall multidimensional overlap is calculated as the product of several separate one-dimensional overlaps (May 1975). However, although two axes were by definition independent from one another, species-pair overlaps on the first axis were highly correlated with overlaps on the second, when the effects of spatial co-occurrence were partialed out ($r = 0.59$, $P<0.0001$). Apparently, then, these species were in fact not independently distributed from one another in the different niche dimensions. The mechanism(s) that would produce this nonrandomness was not detectable with these data; however, I shall offer some speculations concerning its nature in my concluding remarks.

The niche overlaps of all species that occurred at more than one site along the first three vegetation components are graphically summarized in Fig. 2.7. The dendrogram was formed by simple centroid cluster analysis (Sokal and Sneath 1963) of the overlap matrix. Three relatively distinct groups were distinguished at the 0.50-1.0 Chi-square similarity overlap level: birds with affinities for deciduous, hemlock, and coniferous habitats. These groups are not precisely congruent with those I used in earlier zones. For example, Chestnut-sided Warblers, Golden Crowned Kinglets, Red Breasted Nuthatchs, and Winter Wrens demonstrated niche responses more like coniferous species, and Carolina Wrens, Hooded Warblers, and White Breasted Nuthatchs were more closely allied with deciduous species. However, if we choose to define a similarity level for group formation that splits off those seven species (i.e. a group-defining level of 0.60), then Hermit Thrush, an obvious hemlock bird, must be segregated from the shrub-steppe group. Inclusion of all species in construction of the dendrogram serves mainly to increase the within-cluster heterogeneity without altering any of the basic relationships I have already observed. It should be pointed out, too, that this dendrogram represented multidimensional overlap largely independent of spatial co-occurrence, for the correlation between spatial overlap and a matrix of overlaps derived from the dendrogram was only $r = 0.05$ ($P > 0.70$).

Bird Species Differences among Communities and Elevational Zones

Species composition of comparable communities in the three zones was not greatly different, since very few species nest exclusively in only one zone. However, the relative abundance and consequent importance of many species in the three zones was found to be different. In other words, the three zones appeared to differ much more qualitatively than quantitatively. Not all bird guilds differed significantly among zones. Abundance of forest and shrub habitat guilds in general were greater in Zone 1 than ground or subcanopy guilds or gradsects (excluding ACT), but abundance of ground and canopy guilds were greater in Zone 3 compared with forest guilds (in general; Tables 2.10, 2.11).

Observation in the region and results as a whole indicated that White-breasted Nuthatch, American Crow, Carolina Wren, Hermit Thrush, and perhaps Parula Warbler nested largely or entirely in the moist communities of hemlock (CH, HH). All other species commonly found in the hemlock communities were found at least sparingly in the oak-chestnut communities, even though not all were necessarily recorded in the small censused areas. Conversely, the xeric community (XO) had no apparently exclusive species.

Thus, although it was difficult to find differences among species in the two communities, the abundance of many species proved to be different. The Blue-headed

Vireo, found in all 10 forest types (Fig. 2.7), ranked high in forest stages of all three zones. Its abundance, however, was greater in the forest stages of the hemlock community, averaging 2.50 pairs per 0.79 ha for the forest sites of hemlock, and about 1.50 pairs per 0.79 ha for comparable stages in the oak-chestnut series (Tables 2.10, 2.11, Fig. 2.7).

The Black-throated Green Warbler was one of the few species that showed similar abundances in all four communities, averaging 2 pairs per 0.79 ha in each (Tables 2.10, 2.11, Fig. 2.7). This species probably can be considered the second-most common bird of forests in general, although it is outnumbered in one or other of the communities by several species.

In contrast to Canada Warblers, Parula Warblers showed high abundances in hemlock forests but were absent in the xeric communities. Conversely, the Ovenbird and Red-eyed Vireo were important members of the oak-chestnut forests and of minor importance in the hemlock-hardwood forests (Fig. 2.7). These four species were responsible for a large part of the differences in bird populations of the four forest ECC communities.

Bird Species Diversity and Community Changes

Numerical changes in bird populations at the group or guild level explained overall changes in species richness and bird abundance along habitat gradients. Monotonic declines in pooled bird abundances over the elevational gradient paralleled spatial fluctuations in population levels of three numerically dominant species, Dark-eyed Junco, Veery, and Winter Wren. Once their population effects were partialled out, the relationship between overall bird abundance and elevation disappeared. The Black-capped Chickadee, Canada Warbler, Red-breasted Nuthatch, Chestnut-sided Warbler, Blue-headed Vireo, Brown Creeper, Black-throated Blue Warbler, Golden-crowned Kinglet, Veery, and Winter Wren belonged to a cluster of covarying species that crossed zonal boundaries and were identified as habitat generalists. Changes in bird abundance in this dominant group explained 71% of the variation in total bird densities.

In addition, community changes in numbers of bird species at the boundaries of elevational zones corresponded to additions or omissions of sets of species with similar habitat affiliations. Mid-elevation forests had high species richness because multiple sets of covarying species merged together to form the overall bird assemblage, but in spruce-fir and fir forests, species with similar habitat affinities formed an isolated group. Guild responses to three zones of habitat structure resulted in the formation of three general or indistinct bird communities identified by cluster analysis of census point assemblages.

Foliage height diversity was highest (of three zones) in the DCE and significantly different among communities and DCE zones. However, the bird composition of the avifauna at any given position along the elevational gradient did not appear to be dependent on the availability of suitable habitat strata as expected in my study. Species richness and total species abundance generally showed a trend to increase slightly with distance along gradsects. In contrast, on ACT, total bird abundance was highest in the DCE. At the highest elevations, habitats were simple, but supplied suitable resources for more and different species. Generally, communities below DCE contained fewer bird species whereas mid- and higher elevation communities had more species affiliated with hemlock and spruce-fir and contained both shrubs and trees. Similar relationships between habitat complexity and bird species diversity have often been reported (e.g., MacArthur and MacArthur 1961; Karr and Roth 1971; Cody 1974), but few studies relate, as mine has done, changes in bird community structure along steep environmental gradients to numerical shifts in habitat response guilds. The examination of changes in guild composition and abundance was likewise effective in interpreting bird community response to cover type affinities and cover type interactions.

Among the 29 breeding bird species that showed significant differences in their occurrences among forest cover types, 15 occurred in all 8-10 cover types, 10 occurred in over five cover types, and four occurred in only two or three cover types. Only 18 of the 29 species showed significant differences across cover types; some of these included Downy Woodpecker; Blue Jay, Black-capped Chickadee, Red-breasted Nuthatch, Veery, Hermit Thrush, Wood Thrush, Red-eyed Vireo, Northern Parula, Chestnut-sided Warbler, Ovenbird, and Dark-eyed Junco. Occurrences of these species depended in large part on the distribution of cover types. All of these species were clearly predominant in one cover type or group of related types, with the exception of Red-eyed Vireos, Veeries, Wood Thrushes, and Ovenbirds, which were abundant, widely occurring, and likely to respond to other factors. For example, the Veery was most abundant in hemlock and spruce-fir, which were the two wettest types. Also, the Red-eyed Vireo was abundant in the three hardwood types and hemlock; eastern hemlock was commonly associated with both cover types.

Several significant differences in bird species richness were found among cover types. Hemlock and spruce-fir types contained more species (29 and 23, respectively) than did any hardwood type. Although it is frequently reported that coniferous woodlands support fewer bird species than do deciduous woodlands, two important factors contributed to the opposite findings of this study. One was the rich warbler community that bred in the spruce-fir forests of GSMNP. When some cover types are omitted from such analyses, regional differences in the relative importances of forest types can be missed. In the Eastern United States the park is the southernmost extension of the Canadian zone where the Red-breasted Nuthatch, Brown Creeper, Winter Wren, and Golden-crowned Kinglet breed. Here also, the Black-capped Chickadee, Veery, and Dark-eyed Junco were common birds along with the Raven, Canada Warbler, Blackburnian Warbler and others which are ordinarily associated with the forests of northern New England and Canada. The second factor was the nature of the present distribution of cove and hemlock community types. The cove hardwood forests, mostly at altitudes of 1000-1200 m, "are doubtless among the most beautiful deciduous forests in the world" (Whittaker 1956). Here, many of the record-size trees of the park were found, a considerable variety of herbaceous plants carpeted the ground, shrubs and small trees were relatively uncommon, and the main forest species (eastern hemlock, mountain silverbell, yellow buckeye, basswood, sugar maple, yellow birch, yellow-poplar, and American beech) ordinarily grew so tall that bird observation was probably more difficult here than in any other type of forest. At this altitudinal range, however, bird study was of considerable interest for it is here that a number of high-mountain species were at their lowest limits (i.e. Black-capped Chickadee, Black-throated Blue Warbler, and Dark-eyed Junco) while others (i.e. Red-eyed Vireo and Wood Thrush) were at or near their highest penetration.

The relative importance of structure and cover type to bird distributions has been debated for a long time. Many studies have tested this general relationship, however, while some support the importance of stand structure (MacArthur et al. 1962; Karr 1968; Karr and Roth 1971), others have not (Tomoff 1974; Willson 1974). Habitat patchiness, as horizontal diversity is sometimes called, was related to bird species diversity, and forest composition was shown to be important for bird distribution. In this study, bird species diversity was associated with vertical complexity of forest vegetation (the layering and height of vegetation and its density); plant species composition was not shown to be more important than structure in increasing the ability to predict bird species diversity (Tables 2.4, 2.8, 2.17, 2.19, Fig. 2.7). The number of bird species increased faster than the degree of species overlap when cover types changed (Fig. 2.7).

Moisture may be the key to this difference. So much emphasis has been placed on temperature as a controlling factor in the distribution and abundance of birds that the importance of total relative moisture has often been overlooked (Shriner 2001). Since the Smoky Mountains are near the center of an area with one of the highest annual rainfalls (≥ 20 m) in the eastern United States, moisture is an especially important ecological factor at Mount LeConte (Table 2.14). The high total relative moisture index of the forests of the hemlock community could conceivably result in increased populations, both directly by providing more available water and by moderating temperature changes, and indirectly by producing a more luxuriant vegetation with consequent greater variety of niches and, perhaps, a greater amount and variety of foods. At present, there is no way to accurately evaluate these possibilities. Watts (2002) notes that moist soil sites often support a diverse bird community.

Habitat Use and Species Diversity

Within broad limits, diversity studies show that structural aspects of habitats can be used to determine diversity and are at least correlated to features of habitat that the birds themselves use. In general, the number of species that pack into a habitat, defined as diversity, is directly related to structural diversity, and in turn structural diversity is related to either resource diversity or the numbers of ways in which resources are partitioned.

A second component of species diversity is the rate at which species composition changes with changing habitat type (β-diversity), which is directly related to habitat selection. If bird species are narrowly restricted in the range of habitats they occupy along a habitat gradient, then for a given level of diversity, β-diversity will be higher than if species are more broadly distributed over habitats.

I found that the contiguous coniferous spruce-fir (SF) and fir (F) communities more consistently had greater avian abundance and α diversity (diversity within a vegetation type) than the more discontinuous mesic, xeric, and hemlock communities. SF and F communities supported the greater number of birds in both years. In my study, deciduous communities supported the greatest species richness, but SF and F communities together supported the greatest species richness.

The coniferous hemlock (HH) and cove hardwood (CH) communities were the most important streamside vegetation associations in maximizing β-diversity in riparian areas. However, the hemlock communities may be the single most important association in maximizing β-diversity across landscapes (i.e. between riparian areas and adjacent uplands). Hemlock was widespread in all vegetation strata at low and mid-elevations and was the second-most common tree species at Mount LeConte. The continuous hemlock community (HH) supported the greatest number of species exclusive to one vegetation association (27) and the greatest number of species overall. By contrast, only five species were exclusively found in the discontinuous mesic shrub association and only one species in the herbaceous xeric shrub association.

Most habitats occurred as patchworks, as the vegetation maps show (Fig. 2.3), with more or less discontinuity between patches in the form of corridors along ridges or valleys. Both total area of habitat in a region and the frequency distribution of different habitat types helped to determine β-diversity (Cody 1983). In particular, β-diversity increased as the structural differences among >2 habitats increased but was also higher when the areal extents of two similar habitats were high; there were many species differences between common habitat types but fewer between rare and common habitats.

The physiognomy and floristic structure of vegetation and composition present were all features that affected local bird distribution. I also studied the effect on bird distributions due to the change in vegetation structure and composition from deciduous communities to fir communities by censusing birds on gradsects that crossed the ecotone. Habitat heterogeneity was significantly higher in the mixed forest (DCE) ecotone zone than in the adjacent deciduous (below DCE) and spruce-fir (above DCE; Table 2.3). There was a large change in the structure of the bird assemblage coincidental with the vegetation discontinuity (Tables 2.10, 2.11, Fig. 2.5). Although the species richness of birds was relatively constant across the gradsects, the evenness of the diversity of the assemblage (Simpson's Index, Chapter 4) declined across the transition from Zone 3, largely due to the high abundance of Dark-eyed Junco in the spruce-fir and fir communities (SF, F). Simpson's Index is heavily weighted towards the most abundant species in a site while being less sensitive to richness (Magurran 1988). The results suggested that bird assemblage species richness was not determined by spatial heterogeneity of the vegetation structure. The species composition of the zone above DCE was probably related to the historical biogeography of the area (Wise and Peterson 1998), whereas species richness of the DCE zone is probably due to a mass-area or "sink" effect from the adjacent large areas of deciduous and coniferous forests (Forman and Gordon 1986; Forman 1997). However, the evenness, and therefore the diversity, of the assemblage was strongly affected by habitat heterogeneity.

Structural Heterogeneity and Birds of Montane Ecotone Forest

Using multivariate statistical techniques, I quantified habitat relationships among birds to test the assumption that the presence of each species was correlated with a specific configuration of vegetation structure. Multiple statistical methods were used to test for significant differences in the structural habitats of species. Using principal components analysis (PCA) and canonical correlation analysis (CCA), I examined the relationships of species in habitat niche space with each guild member ordinated along several habitat axes. PCA and CCA procedures inferred the significance of specific habitat selection in delimiting the range of a species and in permitting coexistence in areas of overlap. I did not use the reduction of the number of variables to increase the number of canonical variates but used H ($P<0.05$) to test for significance of variates to be included as a canonical variate (Tables 2.21, 2.22). This revealed the most easily interpretable and parsimonious results with $P<0.05$ (D. Wichern, personal communication).

In addition, my study revealed why several species had approximately the same elevational limits, such as their concentration at lower limits at 1000 m and of upper limits between 1100 and 1250 m, and why there were no species with lower limits above 1525 m. It is generally true that closely related species of birds do not occupy the same habitat or elevational range (but see MacArthur 1961). This is illustrated by the elevational separation of the high and low elevational birds (Tables 2.7, 2.8, Fig. 2.4). But some pairs of related species showed elevational overlap: Veery and Wood Thrush, the two Nuthatches, Canada and Hooded Warblers, Blue-headed and Red-eyed Vireos, and Black-throated Blue and Green Warblers.

The predominant factor controlling bird distributions at Mount LeConte was the relationship between bird species and tree dbh, foliage height range, and plant community cover type. Of equal importance were the decrease in moisture gradients from north to south slopes and temperature gradients with elevation (Tables 2.3, 2.10, 2.11, 2.12; Appendix C). Plant communities were identified by life forms of their dominant plant species (deciduous tree, hemlock tree, coniferous tree, shrub), physiognomy (dense, closed forest, open forest cover, foliage height range), location (cove, bald), and species composition. Each plant community, or at least vegetation type, provided a different environment for birds with respect to microclimate (modification of the macroclimate), plant structure (dimensions, branching, leaf size and arrangement), and food supplies (seeds, nuts, fruit foliage, insects and other invertebrates).

Mid- and high-elevation forests were far more heterogeneous in the horizontal plane than were lowland forests. In part, this is an inevitable consequence of mountain topography, with its ridges, slopes, and ravines. The continuity of the forest was frequently interrupted by landslide tracks and deep stream gorges; three heights varied greatly between sheltered ravines and exposed ridgetops. All these irregularities created a variety of "edge" situations that were exploited by Acadian Flycatchers. The thick mats of mosses, lichens, and ferns offered a novel substrate that was exploited by a great array of creeping birds, notably Ovenbirds, Veery, Wood Thrushes, and certain wrens. In addition, the forest harbored a full spectrum of the more conventional types of bark and foliage gleaners that were also prevalent in the lowlands. In sum, the steep terrain, irregular canopy, and an extraordinary variety of arboreal features all contributed to the microspatial heterogeneity of the montane forest.

Conclusions

Of the statistical approaches used to assess spatial pattern and terrain relationships, several were validation procedures rather than direct analytical techniques. Cluster analysis and canonical correlation analysis were the primary methods used to address the questions of the relationships between birds and topographic, elevational, and vegetational factors. Although cluster analysis found significant associations between environmental variables and clusters, it could not describe the nature of these relationships in an explicit fashion. To consider the multiple aspects of ecotone pattern *and* multiple dimensions of environmental processes, a multivariate canonical correlation analysis (CANCOR) was conducted.

My results showed correlations among the abundances of many bird species and elevational, floristic, and physiogonomic features of their habitat, both for univariate and multivariate characters (Fig. 2.11). Although I fully recognized that correlation does not imply causation (habitat selection, in this case), I inferred that birds were distributed by responding either to the variables I have measured or at least to unmeasured features that were strongly associated with those variables. Given that most considerations of the effects of spatial heterogeneity have focused on community structure, I found that individual species responded to patchiness, vegetation structure, and elevation sometimes in a predictable manner. Thus, I came to recognize variation in community structure along such gradients as reflecting higher-level interactions among syntopic birds.

Although my data suggest that intracommunity structure was not a function of close biological relationships among coexisting species, I nevertheless observed clusters of species and communities along my derived zones that appeared to be different. I suspect that most of these species tended to follow more or less independent distributions with respect to one another, but were drawn together by their common responses to similar features of the habitat. Various trends in community composition and structure were followed from one extreme of the moisture gradient to the other. In general, tree coverage and density of the canopy decreased along the moisture gradient from cove forests into pine forests; light penetration to lower strata consequently increased along the gradient (Whittaker 1952). The gradsect data thus suggested that some vegetation types were relatively discontinuous with one another along continuous gradients of "primary" environment, but that many vegetation types existed within a continuum of populations. The broad-scale patterns I saw were modified from the pure Gleasonian individualistic distributions by the very real presence of environmental discontinuities; these were evidenced by the fact that site clusterings were apparent even though PCA and CCA attempted to statistically define continuous gradients in multivariate space.

Breaks in vegetational gradients associated with elevation provided a means of structuring communities of montane birds. If I had used a finer level of resolution (e.g., within a single site or plot), macrohabitat transitions would have been inconspicuous, and patterns in species-habitat associations (if present) would be attributable to heterogeneity in microhabitat resources or other local factors. Macrohabitat differences in species distributions have sometimes been mistakenly ascribed to microhabitat selection, in part because macrohabitats consolidate microhabitat information. Clearly, interpretations of natural phenomena depend on the choice of observational scale (Allen and Starr 1982; Rudd et al. 1984; Maurer 1985). My results supported the idea that suites of species adjusted to different hierarchical levels detected at different spatial scales. Though specialist birds clustered together at subdivisions of the elevational zones, most generalists crossed zonal boundaries, grouping together at a wider level of observation. Further, I found significance tests based on univariate and multivariate statistics useful to detect and delimit ecotonal zones (below DCE, DCE, above DCE). Ecotones were not in any real sense boundaries between communities; they were communities themselves and were often characterized by commodal groupings of different bird species.

Finally, my efforts detected and differentiated three zones based on forest type and tree size class (dbh) related to exposure and elevation. Neither forest type nor tree size class (dbh) was more important to the breeding birds on Mount LeConte, in my judgment; groups of breeding birds likely were associated with either one of the two factors or both. Mature stands supported more species, but such a conclusion is restricted to discussion of one forest type or perhaps a group of similar types. Forest type seemed to be an important factor in whether certain species were present or absent. Thus, both factors and their interactions need to be considered in forest bird habitat management or conservation.

CHAPTER III

RESPONSES OF BREEDING BIRDS TO SPATIAL PATTERNS IN SOUTHERN APPALACHIAN FOREST COMMUNITIES

Introduction

Background

Over the past two decades, there has been an accumulation of literature on principals of landscape ecology and how they have influenced the study of gradients, habitats, landscapes, species, and populations. Principals of landscape-level investigations focus on the dynamics and importance of landscape boundaries (reviewed in Wiens et al. 1985; Holland et al. 1991; Hansen and di Castri 1992), theoretical foundations for understanding boundaries in landscape mosaics (Forman and Moore 1992), habitat edges and edge effects (Palmeirim 1985; Harris 1988; Yahner 1988; Forman 1997; Winter et al. 2000), corridors (Forman and Gordon 1986; Hudson 1991; Forman 1997; Lidicker 1999), functions of corridors in forested landscapes (Gates 1991), and corridors and connectivity (Merriam 1984). Little empirical data exist to assess the value of corridors to birds (MacClintock et al. 1977). Major studies that have influenced landscape-level perspective studies and analysis with Neotropical migratory birds include Kotliar and Wiens (1990); Barrett (1992); Dunning et al. (1992); and Freemark et al. (1995).

Three mechanisms produce vegetation boundaries in the landscape: (1) a patchy physical environment, such as a mosaic of soil types or landforms, (2) natural disturbances, including wildlife and insect infestations, and (3) human activities, such as clearcutting, felling of trees, and development (Forman 1997; R. Forman personal communication). Human activities and natural disturbances promote spatial heterogeneity in forests creating both hard (or sharp) and soft boundaries. The effect of hard and soft boundaries on the delineation of avian territory remains unknown.

Principals explicitly studied in most landscape-level investigations of avian communities focus on (1) arrangement of patch, corridor and matrix elements within landscapes, and spatial heterogeneity (Roth 1976; Turner 1989; Wiens 1989; Karr 1994, Pearson et al. 1995), and (2) patch area and isolation effects on dispersal, colonization, and local extinction (reviewed in Forman 1995). Traditionally, landscape-level studies with birds have examined patterns of habitat occupancy and spatial scale (Wiens et al. 1987), species co-existence (Martin 1992), influence of landscape composition on bird use (Best et al. 2001), effects of landscape structure on breeding bird abundance (Fritz 1979; O'Neill et al. 1989; Turner 1989; Wiens 1989; Turner and Gardner 1991; DeGraaf et al. 1993; Dickson et al. 1993; Freemark et al. 1995; Flather and Sauer 1996) or on nesting songbird distribution in harvested boreal forest (Drolet and Desrochers 1999), landscape influences in hardwood fragments (Kilgo et al. 1997), and responses to landscape pattern changes (Hansen and Urban 1992). Less empirical evidence exists to assess the functional importance of ecotones and the responses of birds to ecotones in spruce-fir forests.

Our knowledge of the way birds utilize landscape is based largely on their selection of habitat for establishing home ranges (Hunter 1991) and satisfying habitat requirements (Noon et al. 1980). For Neotropical migratory birds, landscapes occupy the spatial scales intermediate between the individual's territory or home range (typically one to a few hundred hectares) and the distribution of species over large areas (e.g., a physiographic region). Species need to be examined individually and in different regions of their geographic range to understand habitat requirements (Noon et al. 1980), but they also need to be considered in the context of other species with which they may coexist (Martin 1992). Increased landscape diversity (greater interspersion and numbers of landscape elements) can increase the numbers of species coexisting in the landscape (Johnston 1947; Johnston and Odum 1956; Crawford et al. 1981). In addition, interspersion of vegetation or "cover" types is also associated with increased population sizes of some species. Nevertheless, although increased landscape diversity may result in increased plant and animal diversity locally, it may have detrimental effects on habitat suitability for individual species (defined by fitness within the habitats; Fretwell 1972; Van Horne 1983) and affect regional diversity (Martin 1992).

The composition and spatial configuration of a landscape can independently, or in combination, affect ecological processes, including species' distributions and biotic interactions (Dunning et al. 1992). Landscape composition includes the variety and abundance of patch types within a landscape, but not the location or relative placement of patches within the mosaic. It is well known that species richness, composition, and abundance of Neotropical migratory birds vary among habitat types (Keast and Morton 1980; DeGraaf and Rudis 1986; Verner et al. 1986; DeGraaf et al. 1992, 1993; Hagan and Johnston 1992; Rodenhouse et al. 1993). One aspect of landscape function (Forman and Gordon 1986) is the interaction between the spatial elements, that is, the flow of organisms, among component ecosystems. Under such conditions, the importance of the spatial arrangements of those habitats and their vegetation transition is greatly increased because individual bird species must move between patches to obtain needed resources and satisfy habitat requirements. The role of landscape function in the formation and distribution of assemblages of bird species is also poorly understood. Thus, it is important to obtain good standardized data on what individual birds are doing (J. Rappole, personal communication).

Ecotones and Spatial Patterns in Forests

Interactions, structure, and importance of ecotones are reviewed in Gosz and Sharpe (1989). Ecotones and edges are of interest because they usually show particular properties, such as increases in abundance, diversity, and primary productivity, which are attractive attributes for management purposes. Recently however, with the increase in forest fragmentation the frequency of edges in relation to total length of the edges and ecotones has increased, causing a potential increase in predation, parasitism, and species competition. Impacts of the increase in ecotone length and dynamics and their impacts on biodiversity need to be identified (Fortin 1992). Up to the present, however, mainly qualitative definitions of ecotones, such as "transition zones between communities", are available although some ecotones in the arctic tundra have been quantified by Timoney (1988). Indeed, although most ecotones are found in terrestrial landscapes at several scales of observation, they remain defined both theoretically and operationally.

The term "ecotone" has a long history and is widely used in ecology (e.g., Holland et al. 1991, Schilthuizen 2000), yet its use and definition are imprecise. Clements (1907), first described the junction between two adjacent communities as a stress line or ecotone. More recently, the concept has been broadened to include biotic and abiotic factors at various scales (Holland and Risser 1991; Risser 1995). An ecotone is the zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time and by the strength of interactions between the systems (Holland 1988b; Risser 1993).

To avoid ambiguity by using the terms “edge” and “ecotone” interchangeably (e.g., Clements 1907; Odum 1958; Yahner 1988), I define “edge” as the (two-dimensional) line used to demarcate two adjacent ecosystems, and “ecotone” as the two- or three-dimensional zone of transition between the ecosystems. This transition may be abrupt or gradual (Ratti and Reese 1988; Lennon et al. 1997), extending varying distances on either side of the edge. In practice, both the location of the edge and the extent of the ecotone need to be defined in each case. At one extreme, the boundary between two types of vegetation, such as field and forest, may be relatively abrupt. In this case, the ecotone is narrow and composed mainly of intermixed species from both sides. Sometimes the ecotone is wide, and in it a mosaic of patches of each vegetation type intermingle (Rapoport 1982).

One consequence of ecotones for fauna has been described as the edge effect, first defined by Odum (1958) as the tendency for increased population density and species richness observed at the junction zone between two communities. This definition formalized Leopold’s writings, in which ecotones were presented as beneficial to wildlife (Leopold 1933). The edge effect described by Odum may occur simply because the ecotone contains representatives of species that are characteristic of both the adjacent communities. This view of ecotones is pervasive in the literature, despite the paucity of empirical support for the existence of these sorts of edge effects (Guthery and Bingham 1992). A meta-study by Murcia (1995) concluded that there was no general pattern in the direction of intensity of edge effects in the 24 studies that she reviewed. Odum (1958) suggested that edge effects were especially applicable to bird communities, yet there have been few studies in which bird population density and species richness have been measured across natural habitat edges (see review in Sisk and Margules 1993).

Explicit in Odum's view of the edge effect is the existence of a set of species characteristic of the ecotone. These he defined as primarily or entirely ecotonal species, based on studies (Beecher 1942; Johnston 1947; Johnston and Odum 1956) of the heterogeneity of bird habitat. Once again, many texts and papers use the concept of ecotonal bird species (e.g., Gates and Gysel 1978; Frith 1979; Brewer 1988; Chan 1995; Griggs 1997) despite the few studies specifically designed to test for ecotonal species. Two studies come to opposite conclusions. In Arizona, Laudenslayer and Balda (1976) concluded that none of the 11 bird species breeding in an ecotone between pinyon pine/juniper woodland and ponderosa pine forest were ecotonal. In southeastern Australia, Bramwell et al. (1992) concluded that the Eastern Bristlebird (*Dasyornis brachypeterus*) was ecotonal because they detected significantly more Bristlebirds in the ecotone than in either of the adjacent communities of heathland and woodland. However, this study was confounded by the heterogeneity of the heathwood mosaic and was limited to a single 66-ha site studied during just one spring.

Given the widespread reference to the concepts of ecotone, edge effects, and ecotonal species, and the scarcity of supporting empirical studies, I believed that a replicated and more detailed study was needed. I therefore investigated the patterns in bird community composition and species richness and relative abundance of individual species across naturally occurring deciduous, hemlock and coniferous edges, using replicated sites in a spruce-fir forested landscape.

Objectives

My purpose was to document how landbird species used a spruce-fir forested landscape in the Great Smoky Mountains National Park (GSMNP). With this information, I can make predictions about which species may be vulnerable to disturbances or changes in the ecotone. I relate diversity and abundance of landbird species to habitat types, ranging from deciduous to coniferous community associations. I also relate species abundances to landscape-level parameters. Therefore, my second task sought evidence for differential use by birds of sites within the landscape and of habitats within the ecotone, i.e. I sought to learn how individual bird species and bird assemblages use or respond to the deciduous-coniferous ecotone and spruce-fir community. Specifically, I sought to determine (1) whether there was a difference between the "transitional community" of vegetation and "characteristic assemblage" of birds in the deciduous-coniferous ecotone (DCE), below the DCE, and above the DCE, (2) whether there was a difference between the breeding birds of the DCE and that of the adjacent habitat types, and (3) the details of the relationship between structure and function among deciduous, coniferous and ecotonal communities and how birds use or respond to the DCE.

In order to answer these specific questions regarding avian functional attributes of the DCE and to provide evidence of differential use by birds of habitats between and within the ecotone, I estimated species abundance, total abundance, density, Beta diversity, and total species richness in ecotonal and adjacent habitats, described species composition and vegetation structure in these areas, and combined bird species into assemblages on the basis of their distributions among sampling sites.

Study Area

The GSMNP, located in eastern Tennessee and western North Carolina (approximately 83 degrees 30' W longitude, 35 degrees 45' N latitude), contains large areas of undisturbed and little disturbed temperate forests. General descriptions of the physiography, climate, flora, general vegetation, and land-use history are available elsewhere (Cain 1931, 1937, 1945; King and Stupka 1950; Whittaker 1956, 1966; Hoffman 1964; Golden 1974; Frome 1996).

Whittaker's (1956) monograph is the most comprehensive treatment of the general vegetation pattern. He provided a direct gradient analysis that related populations of plant species, and subjectively defined community types, to elevation and a qualitative moisture "complex-gradient" based on topographic characteristics. His study was an integration of several multivariate techniques, now more widely used. His focus was on the middle elevation forests of the central portion of the park.

My study site was an approximately 15 x 15 km area centered on Mount LeConte on the Tennessee side of the GSMNP (Fig. 3.1). This site was chosen for many reasons. First, Mount LeConte (2009 m) is the third highest peak within the park and among the highest peaks in the eastern United States. Because of its elevation, it possesses a comparatively extensive spruce-fir zone. Second, vehicular access to field sites is comparatively easy because of the location of US Highway 441 and numerous hiking trails (including the Appalachian Trail), which provide easy access by foot. Third, Mount LeConte has a recording weather station near its summit, which will help minimize the errors in estimating climate parameters. Fourth, images and digital elevation models are available for the area. Finally, and most important ecologically, Mount LeConte is

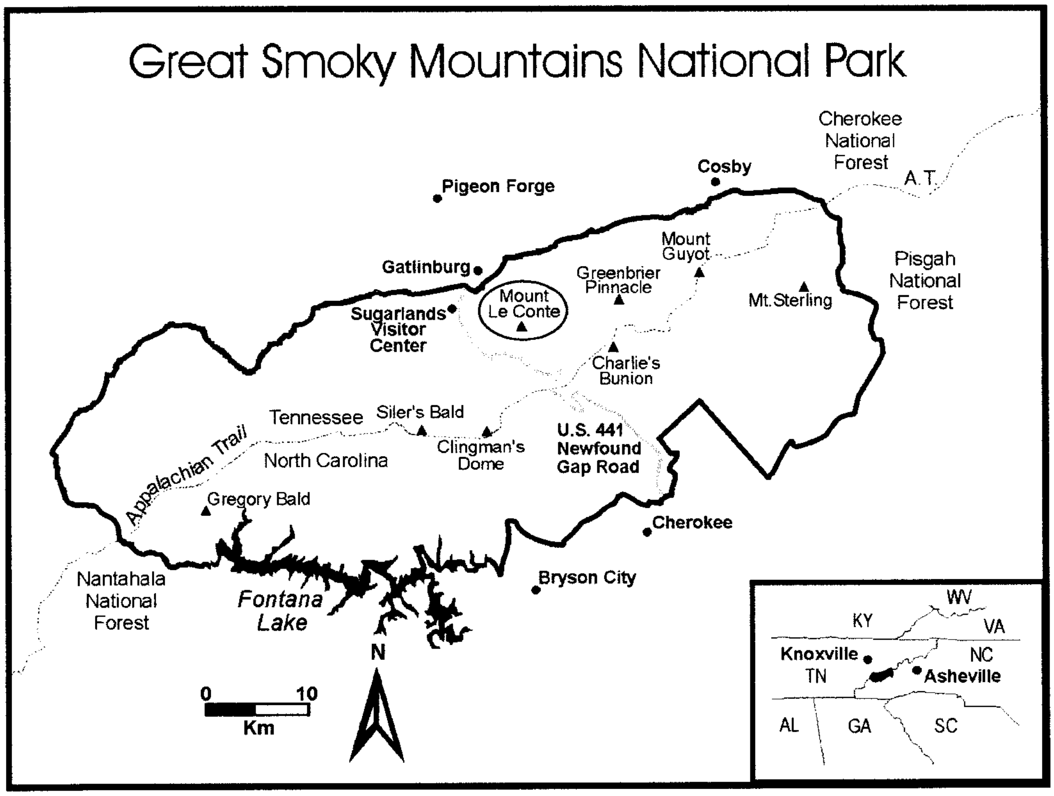

Fig. 3.1 Map of Great Smoky Mountains National Park, Tennessee, showing the location of the study area Mount LeConte, in the north-cental region.

typical of the Smokies in that its slopes are heavily forested, mostly in virgin forest, and the forest changes from oak-chestnut at the lower elevations to spruce-fir at the summit.

Mount LeConte (described in Tanner 1955) rises higher above its base than almost any other mountain in eastern North America. On its northwestern side is a valley containing LeConte Creek. This valley is fairly broad and slopes gently from Gatlinburg up to an elevation of about 790 m above sea level where a large orchard, Cherokee Orchard, spreads. From here the valley narrows and steepens, ascending to the top of Mount LeConte at 2009 m. Above Cherokee Orchard the valley is covered with unbroken forest that is in its primitive condition except for a lower fringe of second growth. Because the axis of the valley is approximately east-west, one slope faces south and is drier and warmer than the opposite north-facing slope. The south-facing slope at lower elevations supports forest of oak and pine, the latter being mostly on the ridge, with heavy undergrowth of laurel and blueberries. This gives way to yellow birch and spruce at an elevation of about 1460 m. On the north-facing slope at low elevations is a deciduous forest with a great variety of trees, such as yellow poplar (or tulip tree), maple, buckeye, and silver bell. Many hemlocks are present too, often in dense stands. Usually damp and cool here, little undergrowth is present except on some ridges with their nearly impenetrable stands of rhododendron. This mixed forest changes to one of yellow birch, spruce, and hemlock a little above 1220 m. At higher elevations the forest on both sides of the valley contains birch, spruce, and fir, the two evergreens becoming more abundant near the top.

Methods

On Mount LeConte, I selected six already established trails, called gradsects (gradient-oriented transects), on which to sample the vegetation and corresponding bird communities: Alum Cave Trail (ACT), Bull Head Trail (BHT), Rainbow Falls Trail (RFT), Trillium Gap Trail (TGT), Boulevard Trail (BVT), and Brushy Mountain Trail (BMT). A thorough description of the trails on Mount LeConte is in Wise and Peterson (1998).

Avian Censusing Techniques and Avian Variables

A total of 212 initial trail points were established at 200 m from the start of the trailheads, with subsequent points spaced a minimum of 200 m apart. Sections of trails along "loud" streams were not censused due to limited detectability of bird song. All birds observed were recorded according to the protocol of bird sampling, consistent with most recommendations for point-count methodology listed in the U.S. Department of Agriculture's General Technical Report No. PSWGTR-149 *Monitoring Bird Populations by Point Counts* (Ralph et al., 1995). These recommendations seek to standardize point-count methodology. Observation of birds during point counts is influenced by many factors (e.g., behavior of species, characteristics of vegetation, weather conditions, or observer; Ralph et al. 1995). If elevation gradients influenced detection probabilities, then differences in results among elevations might simply reflect differences in detection. I had no reason to suspect that such a gradient existed. All counts were conducted by two birders (one the author), both familiar with the vocalizations and plumages of birds in Appalachian forest communities.

Ecologists often ask how individual organisms are distributed or dispersed in space. The answers often provide clues to mechanisms of interaction among individuals and identify factors in the environment that influence distributions. Organisms can be dispersed in three different ways: (1) evenly, in which individuals are more equidistant from each other than occurs randomly; (2) patchily, when individuals are closer to each other ("clumped") than occurs at random; or (3) randomly, in which the locations of individuals are independent of those of other individuals.

In designing a bird censusing scheme, I had to choose between censusing fewer points in great detail or censusing larger areas less precisely. I chose the latter because I was concerned with the pattern of territory (and hence male bird) distribution over a relatively large area. Because differences in habitat occupancy may be a function of year-to-year variation (Wiens 1981b), an effort was made to census as many sites as possible within one breeding season. In June-July 2000, I repeated the same bird-censusing procedures at the same stations used in 1999, with the same level of effort. The order in which the stations were censused was reversed in 2000. For every census, all stations were visited during the early morning peak in bird activity.

The variable-circular plot is an effective technique for estimating bird numbers in rugged terrain (Dawson 1981). Two experienced observers (one the author) conducted audio-visual censuses of diurnal birds using a modification of the variable-circular plot method (following Emlen 1956; Franzreb 1976; Reynolds et al. 1980; Hutto et al. 1986; Ralph et al. 1993; Hamel et al. 1996). I established 212 censusing stations on six trails or "gradsects" (gradient-oriented gradsects, Fig. 3.2). I counted birds at each station at approximately equal intervals three times per year, June through mid-July 1999 and 2000. I began counts at 6:00 a.m., completed them by 11:00 a.m. (Robbins 1981a; Skirvin 1981), and conducted no counts during periods of rain or high winds (>13 km/hour; Robbins 1981b; Skirvin 1981). I recorded all birds seen or heard during the first two

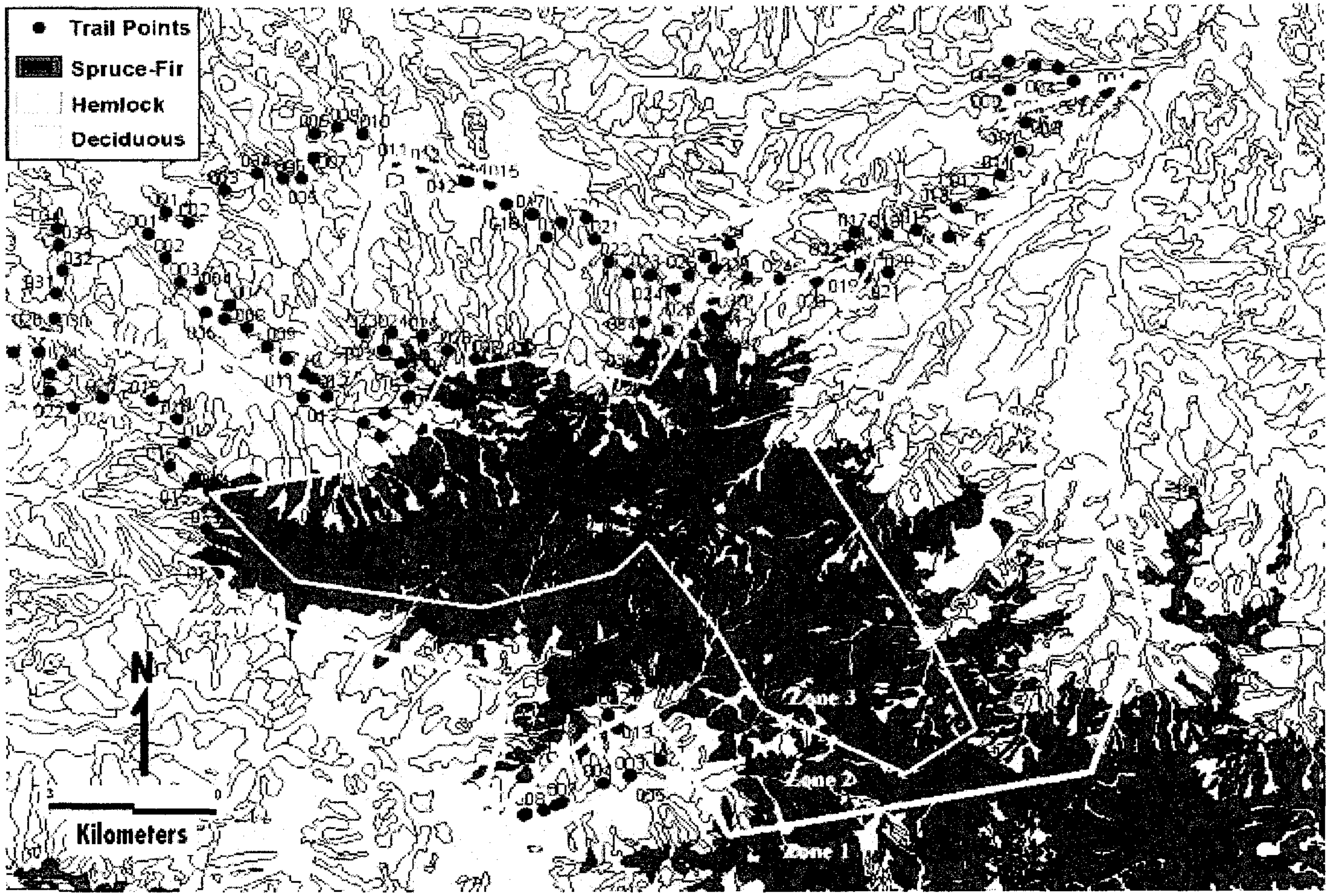

Fig. 3.2 GIS image of the deciduous-coniferous ecotone and forest communities on Mount LeConte, GSMNP. Numbers represent census points on gradsects. Geo-referenced points identified with The Nature Conservancy (1999) community codes were used to delineate the ecotonal boundaries. Numbers represent census points on gradsects. White lines partition three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above DCE.

minutes, next three minutes, and final five minutes following one minute of acclimation. At each station, I identified all vocal and visual evidence of birds and categorized the distance to each bird as <50 m or >50 m. I set temporary flagging at 200-m intervals between census points to assist with distance estimates. Birds flying above the canopy and obviously not using the area being censused were recorded but not included in the analyses. Males and females were combined in this analysis. I calculated the number of individuals of each species within 50 m of each station per visit as an index of relative abundance (birds recorded/point/visit; Lancia et al. 1994). Species observed >50 m were used to measure presence/absence (on the bird data sheet; Appendix B).

I considered bird counts to be estimates of relative bird abundance, which is an index of the density of each species based on a constant but unknown proportion of the population of that species (Bull 1981). Abundance was reported as birds/0.79 ha, the area of a 50-m radius plot. I averaged the high count for each species over listening stations to get an index of relative abundance of birds in each forest community (Blondel and Frochot 1981; Blake and Karr 1987). At each point, temperature, wind, and stream noise were recorded on a scale of 1-5 and cloud cover using a 1-4 score index.

The order of surveys within "sub-routes" (½ trail) was alternated between time blocks to reduce the influence of time-of-day effects. The time/order of visits to starting points each morning was standardized by establishing a pre-set time and census site to start and stop. The gradsect was then walked in the opposite direction to increase the likelihood of observing rare, inconspicuous, or previously undetected birds and of censusing all stations during the early morning peak in bird activity.

To minimize bias, each observer trained intensively in the study area with highly experienced supervisors for two weeks before the first day of each season. I compared bird counts within the census sites with censuses of the communities in the surrounding landscape. Bird survey data collected in 1999 were compared among 1999 habitat coverages (communities), and 2000 survey data were compared with 2000 habitat coverages. Abundances of bird species and habitat coverages were not statistically different between years, so I pooled data from 1999 and 2000 to improve statistical power (Snedecor and Cochran 1989).

Vegetation Sampling Techniques and Habitat Variables

I collected information on spatial distribution of forest communities and habitat (vegetation and topographic) variables for each of the 212 points from May through July 2000 on Mount LeConte, GSMNP. Plants were only studied in 2000. At each point, I measured 30 habitat variables (Table 3.1) for an assessment of each observation point and for estimating important attributes for the spruce-fir bird community. I chose these variables in order to give a good representation of each site regarding the vertical structure and the composition of the habitat. Bird species tend to be associated with habitat type, such as sparse ground cover, dense shrub strata, and closed or open canopy (Smith and Shugart 1987; Steele 1992, 1993); I assumed that canopy habitats were well described by the variables listed in Table 3.1. Vegetation sampling included a randomized sampling of trees by species, an estimate of cover for canopy, subcanopy, tall shrubs/sapling, low shrub/seedling, and herbaceous layers, and a record of the predominate species in the canopy, subcanopy, tall shrubs/sapling layers. Vegetation sampling was conducted during June and July so that the recorded features corresponded to those present during the breeding season. At every second census point, I measured

Table 3.1. Habitat measures and environmental parameters used as independent variables in statistical analyses on Mount LeConte, GSMNP, 2000.[1]

Abbreviation	Variable/Parameter	Description/Explanation
$\bar{x}$DBH	Average or Mean Diameter at Breast Height	Mean diameter at breast height (cm) for each tree. I took the midpoint for each category (i.e. if the category is 0-10, then I used 5) and I multiplied that by the number in that category for that species and that point. I then added all those numbers together for all those categories for a particular species point. That gave me a total dbh for that species at that point. The "average" is because I then averaged it over the species and trailpoint, in case there was more than one visit. If there was only one visit, then the average is a misnomer and it is actually the total dbh. So, for example, for yellow birch at ACT 10, if there were 6 counts in dbh 0-10 and 4 counts in dbh 26-50, then the total dbh would be 6 * 5 + 4 * 37.5 = 180. I could then take the 180 and divide it by the counts to get an average dbh for yellow birch for ACT 10 of 18.
TTLDBH	Total Diameter Breast Height	Mean total diameter at breast height (cm) all diameters of trees within a 0.04 ha plot were summed. This is an estimate of quantity of wood and therefore clutter at the site.
DBH_CAN	Diameter at Breast Height of canopy trees	Mean diameter breast height for canopy trees (cm).
DBH_SUB	Diameter at Breast Height of subcanopy trees	Mean diameter breast height for subcanopy trees (cm).
$\bar{x}$SPDENS	Mean Species Density	TTL species density (N/.04 ha) by adding up all the tree counts (stems) in the 6 dbh categories by each species and trailpoint. The average species density is just the average of the species density – total number of trees within each plot.
DEN_CAN	Density of canopy trees	Density (N/.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species.

Table 3.1 Continued

Abbreviation	Variable/Parameter	Description/Explanation
DEN_SUB	Density of subcanopy trees	Density (N/.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species
CANCLS	CANOPY CLASS	Mean canopy cover of canopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
SUBCLS	SUBCLASS	Mean canopy cover of subcanopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .7
TALLCLS	TALL CLASS	Mean canopy cover of tall shrubs and saplings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
LOWCLS	LOW CLASS	Mean canopy cover of low shrubs and seedlings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
CANCC	Tree Canopy Cover Class at each site	Mean cover (%) of tree (tall) canopy trees measured at 4 cardinal directions with convex densiometer at each site.[2]
SUBCC	Subcanopy Cover Class	Subcanopy trees
TSHBCC	Tall Shrub Cover Class	Tall shrubs, saplings
LSHBCC	Low Shrub Cover Class	Low shrubs, seedlings

Table 3.1 Continued

Abbreviation	Variable/Parameter	Description/Explanation
GRNDCC	Ground Cover Class	Ground vegetation
TCANHR	Foliage Height Range Tree Canopy	Mean height (m) of tree canopy trees. Estimate from 4 samples measured with clinometer at each site.
SUBCHR	Foliage Height Range Subcanopy	Mean height (m) of subcanopy trees. Estimate from 4 samples measured with clinometer at each site.
TSHBHR	Foliage Height Range Tall Shrub	Mean height (m) of tall shrubs, saplings. Estimate from 4 samples measured with clinometer at each site.
LSHBHR	Foliage Height Range Low Shrub	Mean height (m) of low shrub, seedlings. Estimate from 4 samples measured with clinometer at each site.
GHR	Ground of Foliage. Height Range	Mean height (m) of ground vegetation. Estimate from 4 samples measured with clinometer at each site.
TCAP_B	T-CAP – Brightness	Positive or negative values.
TCAP_G	T-CAP – Greenness	Positive or negative values.
TCAP_W	T-CAP – Wetness	Positive or negative values.
% C, D, H	Tree composition of canopy	Coniferous, deciduous, hemlock
% C, D, H	Tree composition of subcanopy	Coniferous, deciduous, hemlock
ELEV.	Elevation (m)	m, as determined by Arc View Spatial Analyst
SLOPE	Slope	Degrees, as determined by Arc View Spatial Analyst
ASPECT	Aspect	N, NE, E, SE, as determined by Arc View Spatial Analyst S, SW, W, NW
DIST.	Disturbance	Defined by trees felled by windthrow or man

Table 3.1 Continued

Abbreviation	Variable/Parameter	Description/Explanation
LOGS	Logs (>10 cm dbh)	Presence or absence of logs in the forest, such as those resulting from a tree fall within the 0.04 ha sampling plot
SNAGS	Snags (>10 cm dbh)	Presence or absence of standing dead trees within the 0.04 ha sampling plot

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[1] Several parameters describing vegetational structure were derived from vegetation sub-samples. These included mean dbh, total dbh, mean species density, tree composition of canopy, tree composition of subcanopy, dbh of canopy trees, dbh of subcanopy trees, density of canopy trees, and density of subcanopy trees. Floristic information was not included in the analysis, except for the species of dominant tree(s) in the canopy..

[2] The arithmetic mean or average was the sum of the measures of canopy cover by species at the sampling station divided by number of measures. Example: 1=class value: 0.1=numeric value.

vegetation variables in the manner described by James and Shugart (1970). For interpretation purposes, variables were classified in three groups, depending on if they primarily defined structure (e.g., cover of vegetation strata), tree composition, or topographical features (e.g., elevation, slope and aspect; Table 3.1).

I measured habitat characteristics on 120 0.04-ha circular plots (Lindsey et al. 1958; James and Shugart 1970; James 1978; Noon 1981), at each census point on the six gradsects. The 0.04-ha circle technique used in breeding territories is designed to determine the life form of vegetation where each species is observed (James 1971). This technique is an application of individualistic approach to the distribution of organisms (Gleason 1926), in which species populations are treated independently. The technique permits analysis of the habitats of individual species and then comparisons among species, not necessarily occurring on the same plot. Each plot was centered at the listening point from where birds were detected and counted. The structural habitat data were obtained by sampling 0.04-ha circular plots centered on the point from which a bird was seen (1) vocalizing, (2) foraging, or (3) engaging in behavior near a nest. The 0.04-ha plot is small enough to be contained within a male's territory, but large enough (diameter 22.5 m) to contain an adequate sample of vegetation (see James and Shugart 1970 for additional details).

Data collection included a sample of trees using a wedge prism (Husch et al. 1982). I identified and tallied overstory and understory tree species >10 cm dbh within the limits of the wedge prism (Husch et al. 1982). Six dbh ranges were established: 0-10 cm, 11-25 cm, 26-50 cm, 50-75 cm, 76-100 cm, and >100 cm. Analysis of wedge prism data revealed that these dbh ranges are sufficient to distinguish between old-growth and second-growth stands (Simons et al. 1995). Using a sighting tube, I ocularly measured and recorded cover by tree species for overstory (tree canopy), understory (subcanopy), tall shrub/sapling (>1 and <10 cm dbh), and low shrub/seedling (<1 cm dbh) coverage in 10 classes with 10 being the highest coverage: <0.1, >0.1-1, >1-2, >2-5, >5-10, >10-25, >25-50, >50-75, >75-95, and >95% (Mueller-Dombois and Ellenberg 1974). Percent canopy cover was visually estimated using the Cornell Laboratory of Ornithology canopy chart. The height range in meters of five vegetation layers (canopy, subcanopy, tall shrubs/sapling, low shrubs/seedling, and ground cover) were also estimated for each point using a clinometer.

I determined species composition of canopy, subcanopy, and tall shrub/sapling layers and low shrub/seedling layers using Radford et al. (1968) and Gleason and Cronquist (1963) by identifying the dominant species in each layer. At each listening station I also tallied presence or absence of such special habitat features as disturbances, forest openings, logs, and snags. The herbaceous layers, including ground cover, were determined to be deciduous, evergreen, fern, moss, grass, or a combination of these types. The species of each canopy tree was recorded to verify forest cover type (deciduous, coniferous, ecotone) of the plot.

The biological measurement of an edge width was very difficult. However, I determined edge width based on vegetative compositional and structural parameter(s) (Table 3.1) and functional use by birds. To facilitate this determination, I took measurements of the spatial distribution of conifers vs. deciduous trees at the ecotone, and, using these data, I arbitrarily established that the edge was X meters wide.

Environmental Measurements and Variables

The GPS locations in Northing and Easting for each station were recorded/registered by a Leica GS50 GPS/GIS receiver, and later differentially corrected. In the laboratory, I determined elevation, slope, and aspect from all 212 geo-referenced points and added those data to the GIS environment. The geo-reference plot locations were overlaid with GSMNP-TNC vegetation coverage associations to accurately compare vegetation classifications. All data and information from sources were stored in Arc View GIS operated on PC workstations in the Laboratory for Remote Sensing and Environmental Analysis (LaRSEA) at Old Dominion University.

Additional data used for this study included U.S. Geological Survey 1:24.000 digital elevation models (DEMs). Maps of independent topographic variables, including elevation, slope angle, and aspect, were derived from the DEMs.

Habitat Superclass Classification and ECCs

I determined and assigned coverages and percentages of composition of 21 forest communities describing the study area centered on Mount LeConte into Ecotonal Community Classifications (ECC) and Ecotonal Landscape Classifications (ELC) by using Arc View 3.2 (Appendix A).

The study area was mapped in 1997 in GIS according to The Nature Conservancy (TNC) forest type by Aerial Information Services on behalf of the National Conservancy and National Park Service. The basic unit of the mapping system was the forest association, i.e. an area of forest represented by roughly homogeneous tree species composition, forest age, and canopy closure. For my study area, each station was given a TNC code that describes its type, age, and crown closure (Table 3.2).

The TNC classification system provided more association types than I could sample effectively. Therefore, I simplified the system and created a habitat superclass system or community classification composed of 10 forest community types (Appendix A). This system contained four deciduous, four coniferous, and two hemlock forest types. Each site was redefined as one of 10 superclasses or community types (Table 3.2). Forest types were classified into 10 groups [pine, xeric oak, tulip poplar (mixed mesic hardwood), mesic oak, hemlock hardwood, cove hardwood, northern hardwood, spruce northern hardwood, spruce-fir, and fir] based on MacKenzie and White (1998) and MacKenzie (1993) and the dominant canopy species present (yellow birch, yellow buckeye, Fraser Fir, eastern hemlock, northern red oak, chestnut oak, white oak, Carolina silverbell, red spruce, table mountain pine, Virginia pine, and tulip poplar; Appendix A). These community types were also grouped into the broader habitat superclasses.

For the preliminary analyses, I hypothetically defined ecotonal zones, below (1), ecotonal (2), and above (3), as treatments on each gradsect using the community classifications, and therefore called these "ecotonal community classifications" (Appendix A). The below, above, and ecotonal zones were determined based on the contiguity of similar vegetation communities (Table 3.2). Forest types on the (ACT) gradsect were defined or delineated into zones separately because of the differential distribution or difference in pattern of the community types. This difference in forest community pattern is a result of several factors. The forest cover along the lower stretch of the trail is called a "hemlock-birch association" and is typical of those found on the mountain sides up the Appalachian chain to central New York and beyond. In addition to the hemlock and birch, these stands include maple, beech, buckeye, silverbell, and an

Table 3.2 Topographic and ecotonal community vegetation associations for trail point data: Alum Cave Trail (ACT), Bullhead Trail (BHT), Rainbow Falls Trail (RFT), Trillium Gap Trail (TGT); length 7.88 km., elevational gain 831 m. ECC = ecotonal community classification, abbreviations are defined in Appendix A. Three zones identified by gradsect or transition with hard boundary = **, all other transitions are soft boundaries = *. BHT Trail points were sampled from highest to lowest elevation.

Ecotonal Zone	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
1	ACT 01	7861	1171	6.20	SW	HH
1	ACT 02	7861	1183	9.97	NW	HH
1	ACT 03	7861	1232	4.39	SW	HH
1	ACT 04	7861	1214	3.64	SW	HH
1	ACT 05	7861	1232	4.26	SW	HH
1	ACT 06	7861	1255	8.11	S	HH
1	ACT 07	7861	1191	5.05	SW	HH
1	ACT 08	7861	1182	9.74	NW	HH
1	ACT 09**	7861	1170	6.28	NW	HH
2	ACT 10	114	1370	22.75	SE	SNH
2	ACT 11	114	1398	25.60	E	SNH
2	ACT 12**	6272	1408	30.78	E	SF
2	ACT 13	3814	1433	18.77	S	B
2	ACT 14	3814	1479	37.32	SW	B
2	ACT 15	114	1496	40.15	SS	NH
2	ACT 16	114	1530	29.94	SS	NH
2	ACT 17	112	1570	37.87	W	SF
2	ACT 18	112	1594	32.81	NW	SF
2	ACT 19	114	1587	22.65	NS	NH
2	ACT 20	112	1575	8.64	W	SF
2	ACT 21	112	1591	32.45	SE	SF
2	ACT 22	112	1626	35.59	S	SF
2	ACT 23	112	1654	32.96	SE	SF
2	ACT 24	112	1712	41.51	SE	SF
2	ACT 25	114	1740	40.57	S	SNH
2	ACT 26**	112	1791	37.80	SE	SF
3	ACT 27	6049	1827	34.81	SW	F
3	ACT 28	6049	1844	34.11	SE	F
3	ACT 29	112	1879	22.60	SS	F
3	ACT 30	7876	1880	39.02	SW	B
3	ACT 31	112	1946	29.14	SW	SF
3	ACT 32	6049	1939	19.52	NW	F
3	ACT 33	6049	1938	15.80	NE	F
3	ACT 34	6049	1941	11.80	NE	F
3	ACT 35	6049	1949	7.83	N	F
3	ACT 36	6049	1979	10.60	W	F
3	ACT 37	6049	1999	10.11	SW	F
3	ACT 38	6049	2002	10.74	N	F

Table 3.2 Continued

Ecotonal Zone	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
1	BHT 34	6192	787	18.75	S	MO
1	BHT 33	6271	807	14.54	N	XO
1	BHT 32	6271	844	7.91	N	XO
1	BHT 31	6271	886	21.01	N	XO
1	BHT 30	6271	920	33.55	W	XO
1	BHT 29	6286	970	35.81	NE	MO
1	BHT 28	6271	995	35.66	W	XO
1	BHT 27**	312	1007	35.43	W	CH
1	BHT 26	312	1087	30.43	N	CH
1	BHT 25	312	1074	22.20	NE	CH
1	BHT 24	6271	1102	37.38	NW	XO
1	BHT 23	7861	1147	38.63	N	HH
1	BHT 22	7861	1186	25.75	SW	HH
2	BHT 21	6271	1225	29.21	SW	XO
2	BHT 20	7097	1249	22.01	S	P
2	BHT 19	7097	1257	24.46	N	P
2	BHT 18	4973	1294	23.27	W	NH
2	BHT 17	7861	1323	24.83	N	HH
2	BHT 16	4973	1350	28.80	NW	NH
2	BHT 15	7861	1433	40.39	SW	HH
2	BHT 14	3814	1462	45.04	NW	B
2	BHT 13**	114	1488	36.24	W	SNH
2	BHT 12	114	1522	20.15	SW	SNH
2	BHT 11	7285	1564	33.21	W	NH
2	BHT 10	114	1608	28.77	S	SNH
2	BHT 09	114	1632	29.90	S	SNH
2	BHT 08	112	1668	24.28	S	SF
3	BHT 07	114	1710	23.67	S	SNH
3	BHT 06	114	1733	25.13	S	SNH
3	BHT 05	114	1737	36.25	NW	SNH
3	BHT 04	6124	1755	29.17	NW	NH
3	BHT 03**	112	1759	32.11	NE	SF
3	BHT 02	6124	1790	31.14	N	NH
3	BHT 01	112	1798	35.62	NW	SF
1	RFT 01	7543 (7219*)	818	8.61	NW	CH
1	RFT 02	7543 (7219*)	858	10.21	NW	CH
1	RFT 03**	7543 (7219*)	892	14.60	W	CH
1	RFT 04	6271	926	11.39	NW	XO
1	RFT 05	7693 (6271*)	937	13.25	W	CH
1	RFT 06	6271	999	16.41	W	XO
1	RFT 07	6271 (7097*)	1023	25.35	SW	XO
1	RFT 08	6271	1076	21.19	W	XO
1	RFT 09	6192 (6271*)	1091	19.73	SW	MO
1	RFT 10**	6271	1122	21.64	SW	XO
2	RFT 11	7861 (132*)	1134	13.96	NW	HH
2	RFT 12	6192	1167	23.03	N	MO
2	RFT 13	7693	1207	28.51	W	CH

Table 3.2 Continued

Ecotonal Zone**	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
2	RFT 14	7693	1228	30.76	NE	CH
2	RFT 15	7861	1344	28.46	NW	HH
2	RFT 16	4982	1350	23.20	NW	NH
2	RFT 17	4982	1495	30.76	W	NH
2	RFT 18	4982	1544	33.39	N	NH
2	RFT 19	7861 (7285*)	1389	30.48	N	HH
2	RFT 20	7285	1412	32.50	SW	NH
2	RFT 21	6192	1444	32.53	SW	MO
2	RFT 22	7285	1468	33.12	SW	NH
2	RFT 23	7119 (4973*)	1484	43.58	NW	P
2	RFT 24	4973	1523	31.05	N	NH
2	RFT 25	7861 (4973*)	1550	29.81	N	HH
2	RFT 26	7285	1574	34.73	N	NH
2	RFT 27**	7285	1584	34.50	N	NH
3	RFT 28	6124	1610	34.89	NW	NH
3	RFT 29	114	1636	27.09	N	SNH
3	RFT 30	114	1662	35.64	N	SNH
3	RFT 31	112	1677	16.91	W	SF
3	RFT 32	114	1680	32.49	SW	SNH
3	RFT 33	112 (114*)	1737	16.36	SW	SF
3	RFT 34	112	1756	18.48	SW	SF
3	RFT 35	114	1785	11.65	NW	SNH
3	RFT 36	6049	1803	22.94	N	F
3	RFT 37	112 (114*)	1832	29.03	N	SF
3	RFT 38	6049	1866	28.26	N	F
3	RFT 39	112	1901	18.44	N	SF
3	RFT 40	6049	1936	15.57	NE	F
1	TGT 01	7219	797	11.97	N	TP
1	TGT 02**	7230	821	9.37	NW	MO
1	TGT 03	6271 (6286*)	839	10.10	W	XO
1	TGT 04	6271	884	18.80	W	XO
1	TGT 05	6271	887	11.08	N	XO
1	TGT 06	6192	898	12.45	N	MO
1	TGT 07	6192	930	25.63	W	MO
1	TGT 08	6271	954	34.40	W	XO
1	TGT 09	312 (7693*)	954	26.60	NE	CH
1	TGT 10**	6271	952	23.37	N	XO
2	TGT 11	7693	984	11.65	N	CH
2	TGT 12	7693	992	20.24	NE	CH
2	TGT 13	7693	1010	30.75	NE	CH
2	TGT 14	7693	1048	30.66	NE	CH
2	TGT 15	7693	1072	31.29	NE	CH
2	TGT 16	7693	1108	15.64	N	CH
2	TGT 17	7861	1120	25.99	NE	HH
2	TGT 18	7861	1128	14.62	N	HH
2	TGT 19	7861	1176	22.43	NW	HH
2	TGT 20	7693	1202	29.56	N	CH
2	TGT 21	7693	1259	25.18	NE	CH

Table 3.2 Continued

Ecotonal Zone**	Trail/Pt	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
2	TGT 22	7693	1274	19.29	N	CH
2	TGT 23	7861 (4973*)	1314	21.75	N	HH
2	TGT 24	4973	1322	28.95	NE	NH
2	TGT 25	7861	1333	32.60	NE	HH
2	TGT 26	4973	1380	26.81	W	NH
2	TGT 27	7861 (4973*)	1415	18.88	NW	HH
2	TGT 28	7285	1434	5.40	N	NH
2	TGT 29	7861 (4973*)	1465	24.70	NW	HH
2	TGT 30	6272	1504	29.60	W	SF
2	TGT 31	7861 (6272*)	1518	33.06	W	HH
2	TGT 32	6272	1533	28.05	N	SF
2	RFT 23	7119 (4973*)	1484	43.58	NW	P
2	RFT 24	4973	1523	31.05	N	NH
2	TGT 33	7861 (6272*)	1552	29.85	NE	HH
2	TGT 34**	7861	1548	30.96	N	HH
3	TGT 35	114 (7285*)	1576	28.86	W	SNH
3	TGT 36	114	1583	39.41	SW	SNH
3	TGT 37	114	1590	41.04	W	SNH
3	TGT 38	114	1629	36.34	W	SNH
3	TGT 39	114	1636	10.03	N	SNH
3	TGT 40	7285	1666	39.24	N	NH
3	TGT 41	114 (7285*)	1687	33.76	N	SNH
3	TGT 42	114	1705	28.21	NW	SNH
3	TGT 43	112 (7285*)	1714	34.87	SE	SF
3	TGT 44	114	1774	32.36	E	SNH
3	TGT 45	114 (7285*)	1790	29.15	E	SNH
3	TGT 46	114	1810	23.49	N	SNH
3	TGT 47	112 (114*)	1841	16.18	NW	SF
3	TGT 48	114	1839	31.58	N	SNH
3	TGT 49	6049 (114*)	1896	12.81	NW	F

occasional magnolia. Hemlock stands appear in sites which are somewhat less mesic than those of the cove forests, whether on open valley flats at middle elevations or slopes above the valleys at high elevations (Whittaker 1956). These stands are also suspected of being segregated by thin soils (Cain 1937).

Another interesting botanical phenomenon was observed along this lower stretch of the ACT. In the larger birch trees, where wide crotches are common between the trunks and major limbs or where the upper portion of the trees have been broken off by lightening or wind, small hemlocks, rhododendron, dog-hobble, and ferns can be seen growing up to thirty feet above the ground. Much more common, and also worthy of inspection, are the hundreds of "nurse logs" along the trail. Most of these are hemlocks, but some are birch and a few remnant chestnuts that have fallen and decayed. Along the stretch above Arch Rock, the ACT passes through a grove of large hardwood trees, mostly oak and buckeye, with some maple and a few hemlocks. This type of forest is called mixed mesophytic and is typical of those farther north in the Appalachians. "Mesophytic" means "middle plants", that is, those of the middle latitudes along the Appalachian chain. Another name for the same forest type is "cove hardwood". Above this point, the ACT continues climbing through cove hardwoods. Within a short distance, the trail climbs to a small rocky spur known as Inspiration Point, where it makes an abrupt right turn. The dominant coniferous trees along the lower elevations are hemlock, which give away to the red spruce about halfway up the gradient. The hemlocks and hardwoods maintain a good balance along this ridge, though the red spruce displaces some of the more prevalent species. As the trail progresses away from Alum Cave and an earth slide scar, Fraser fir begins to appear along the trail. At this elevation, the hemlock has disappeared and the fir emerges in an association with red spruce. The two species can be further distinguished by luxuriant lichen growth that appears on the spruce trees but not on the firs. Further, near the summit of Mount LeConte, widespread death of Fraser fir and increased windthrow of red spruce created obvious changes in vegetation by 1986 (Rabenold et al. 1998). The severity and extent of mortality caused by the introduced insect pest, the woolly adelgid, on most trails, excluding ACT, in addition to the selective retention (at certain distances) of residual trees for trail maintenance on ACT have greatly altered composition and structure along the gradsect. Even after 22 years of adelgid infestation, spruce-fir stands are still in a state of structural and compositional reorganization. In comparison to the zones on Bull Head Trail (BHT), Boulevard Trail (BVT), Brushy Mountain Trail (BMT), Rainbow Falls Trail (RFT), and Trillium Gap Trail (TGT), zone 1 of ACT consists primarily of hemlock forest communities, zone 2 consists primarily of spruce-forest communities, and zone 3 consists primarily of Fraser fir communities (Table 3.2).

Data Analysis: Statistical Methods

Non-parametric multivariate tests were made using PRIMER (Clarke and Warwick 1994; Carr 1996). Initially, I tested whether bird species composition varied with year, using an analysis of similarity (ANOSIM). This was based on a matrix of similarities using the Bray-Curtis Index (Clarke and Warwick 1994). Following the lack of a significant difference between years (Global R = -0.003, P=0.598), years were averaged and all future tests were undertaken on averaged data.

I identified differences in bird assemblages among zones and forest types using a two-factor ANOSIM. A non-metric multidimensional scaling ordination (nMDS) was used to visualize the patterns. I used nMDS to graphically compare similarity in species composition among different forest types. Multidimensional scaling (MDS) is a class of methods in PRIMER that estimates the coordinates of a set of objects in a space of specified dimensionality resulting from data measuring the distances between pairs of objects. Data were analyzed as both presence/absence and untransformed values to investigate whether differences were due to changes in species composition alone (presence/absence) or to changes in abundance of common species (untransformed). Where significant differences were detected, I used the SIMPER module to identify which species were causing differences between each zone and community. To identify species that were characteristic of groups of sites, I chose to measure consistency using the ratio of similarity contribution to standard deviation as described by Clarke and Warwick (1994). I chose an arbitrary value of one for this ratio to denote species that are characteristic of groups of sites, but I also described the range of species that contribute to the average similarity found for that group even when characteristic species were not present.

Two-factor ANOSIMs were used to investigate whether species composition varied with snags or with forest gaps, after accounting for variation due to forest type. SIMPER analysis was conducted for factors that were significantly different.

To investigate the relationship between environmental parameters and bird assemblages, I examined the relationship between the set of environmental parameters at a vegetation sampling station and its bird assemblage, using the BIOENV module in PRIMER. Because environmental data were collected only at every second station, the bird data were analyzed only at those stations where environmental data had been collected. Initially, a PCA analysis with normalized Euclidean distance was produced using 33 environmental parameters (Table 3.1). Draftsman plots and correlation coefficients were used to identify highly correlated variables, which then were excluded from the analysis. I repeated the analysis with elevation excluded because I was trying to understand the effects of other topographical features and vegetation characteristics on bird assemblages. I only used two (out of three possible) tassel cap parameters because the *brightness* index was highly correlated with the *greenness* index.

NMDS was used with Bray-Curtis similarities to compare bird and forest community composition among samples. Stress is a measure of the distortion between rank, similarities, and distances in the ordination plot. The stress value is an estimate of how much compromise the program made to ensure every point was the same relative distance from every other point according to the similarity value it has with each point. The goal of the nMDS algorithm was to construct an ordination configuration that minimized this stress by iteratively converging on the solution that gave the lowest stress values (<D.20). Both PCA and nMDS produced a "map" of the census sites in which the distance between any two census sites represented their dissimilarity based on the area under analysis. PCA is a parametric procedure more appropriate to the variables in the environmental data.

The BIOENV procedure was used to identify those environmental variables that best "explained" the patterns of variation seen in the community data. BIOENV is a non-parametric method that measures correlation between biological and environmental similarity matrices. The similarity matrices were composed of pair-wise comparisons of every census site. For this study, the normalized Euclidean distance matrix for environmental parameters was correlated with the Bray-Curtis similarity matrix for birds. This procedure identified the set of possible environmental parameters that most closely correlated with the differences among bird assemblages at sites.

BIOENV tested the relationship of community matrix against environmental matrices constructed from different combinations of environmental variables, and combinations giving the highest correlation coefficients are reported. Essentially, BIOENV compared a chosen biological similarity matrix with a number of different environmental similarities matrices. Different combinations of environmental variables were used to find the set that yielded a similarity matrix that closely matched the relative similarities in the bird matrix. If a variable improved the correlation with the bird matrix or suite of birds, it was presumed to have some relationship to the forest community features. If the variables degraded the correlation, then it was omitted from the analysis and likely had little influence on the bird community.

Analysis of Bird Communities

I determined the abundance of each bird species along each gradsect by summing the number of individual observations over the three point counts per census point during three visits for each year and averaged over the two visits in each year to produce one measure of abundance for each species per site per year. Total bird abundance (total individual observations), species richness (total species), and individual species abundance (each species with >20 individual detections during 1999 and 2000 combined) were used as independent response variables. I examined between-year differences in abundance using an ANOVA test (SAS Institute 2000) and because no differences were detected, I averaged the abundance data. I checked abundance and species richness data for normality and homogeneous variances and then used the generalized linear model (GLM), which is an extension of the traditional general linear model. GLMs are a broad class of models for continuous and categorical variables that use maximum likelihood estimation (Wald X) for model-fitting (McCullagh and Nelder 1989). The 29 most common species in each zone (DCE, below and above DCE) were included in the analyses of individual species. I tested for zone and year differences in species richness, total abundance of all species combined, and abundances of individual species using 3-factor ANOVA in time via a stratified design (3 zones X 4 gradsects X 2 years; n=24). All statistical analyses were conducted using SAS software (SAS Institute 2000). I considered bird count data to be estimates of relative bird abundance, which is an index of the density of each species based on a constant, but unknown, proportion of the population of that species (Bull 1981).

Principal factor analysis (PFA) using the Varimax procedure was used to examine relationships among all study sites based on habitat and topographic characteristics. My approach was to screen a large set of potentially important predictor ("independent") variables statistically in an effort to quantify their individual and combined effects on community-level response variables, which included the following measures of bird diversity: individual species abundance, species richness, and total species abundance.

I used Tukey's "Honesty Significant Difference" (HSD) test to make pair-wise comparisons among means when the ANOVA was significant ($P<0.10$). To reduce the Type II error rate, which was more important because of the inherent variability in natural systems, I used $a=0.10$ (Type I error rate) rather than the conventional 0.05.

The multivariate analysis was undertaken using PRIMER (Carr 1996). The abundance of each bird species was determined by the cumulative numbers of observations over the six visits. Differences in the composition of the communities were tested using a two-way ANOSIM with location and distance (either plots or parts of plots) as factors. Similarity among the plots (or between pairs of plots) was determined by ordination, using non-metric multi-dimensional scaling (nNMDS; Kruskal and Wish 1978) and was represented in two dimensions.

Ecotonal Analysis of Individual Species of Birds

The relative abundance of each bird species at each site was expressed as the mean (and standard error) for each site and displayed as a histogram. Based on the intuitive categorization proposed by Sisk and Margules (1993), I sought to determine whether bird species at ecotones could be (1) ecotonally neutral, (2) ecotone-conspicuous, or (3) ecotone-shy, and could be divided further into habitat generalists or specialists of either side of the edge. Species with >75% of detections at the three stations on the deciduous side of the edge were called below-DCE specialists; those with >75% of detections at the three plots on the spruce-fir side of the edge were called above-DCE specialists; the remainder were considered to be DCE "habitat generalists". Species with >50% of detections at the ecotonal stations were called "ecotone-conspicuous", those with <25% of detections at the ecotonal stations were called ecotone-shy, and the remainder were considered to be ecotone neutral. This gave nine hypothetical responses for species abundance across the edge between two habitats. Ecotone-conspicuous birds demonstrate density at the ecotone whereas ecotone-shy birds have decreased density at the ecotone. The density of ecotone-neutral birds is unchanged across the ecotone, except for species that are habitat specialists. Birds that are habitat-specialists but ecotonally neutral have reduced density across the ecotone in relation to the amount of decrease in suitable habitat. A tenth hypothetical response is that of an entirely ecotonal species, which would be expected to have high density at the ecotone and be absent from the habitats on either side.

Rarely detected species (less than 20 detections) were not considered further. For the remaining species, the histogram pattern of variation in bird abundance across the stations from one zone to another, or, for example, from deciduous to hemlock to ecotone to spruce-fir, was used to categorize the bird species into one of the models of ecotone response according to the following decision rules.

Abundance data for each species were analyzed using the same ANOVA design as for the whole-communities analysis previously described. All data were transformed using the square root of (x + 0.375) because the variances were proportional to the means and because some values were small or zero (Zar 1984). Tukey's HSD was used (α=0.05) where ANOVAs revealed significant differences among means.

Results

In analyzing the vegetation data I found that only four of the six gradsects sampled (ACT, BHT, RFT, and TGT) traversed and included low, mid, and high elevations of forest communities. In addition, these four trails also contained more complete elevation and vegetation characteristics up the gradients than the BVT and BMT gradsects. Therefore, I omitted the latter two trails from all further analyses.

Differences among Bird Assemblages Between Zones and Forest/Vegetation Types

The zones below the DCE (Zone 1), DCE (Zone 2), and above the DCE (Zone 3), were determined based on the contiguity of similar forest communities (Table 3.2).

Zones clearly differed in bird species composition, with the ecotone (Zone 2) intermediate between the two main zones (Global R = 0.204, P=0.001, Fig. 3.2a). Forest types also differed in bird species composition (Global R = 0.218, P=0.001, Fig. 3.2b). Similar results were obtained when presence/absence data were used, indicating that main differences between each zone and each vegetation type were the result of changes in species present rather than abundances of particular species (zones: Global R = 0.206, P=0.001; vegetation type: Global R = 0.192, P=0.001). "Rank order information about which samples are most or least similar can say nothing about absolute 'distance apart' of two samples: what can be interpreted is relative distances apart" (Clark and Warwick 1994). The degree of stress (0.17) indicates how well the picture relates to the calculated similarities among sites; the higher the value, the more compromise had to be made - up to 0.2 is an acceptable image.

To investigate which species were different among each zone and vegetation type, results from presence/absence data are presented because these maximally account for rarer species. In Zone 1 (below the DCE), sites varied markedly in composition of bird species, resulting in low similarity among sites (av. similarity = 33.49%) and sites less clustered on the MDS (Fig. 3.3a). No species were identified as typifying sites below the DCE, because no species was consistently seen at the range of sites within this zone. The species that contributed the most to the similarity among sites were three Neotropical migrants: Black-throated Green Warbler (*Dendroica virens*; contributed 20.6% to the av. similarity), Ovenbird (*Seiurus aurocapillus*; 18.4%), and Blue-headed Vireo (*Vireo solitarius*;17.3%).

Above the DCE (Zone 3), sites were more similar in species composition (65.4%)

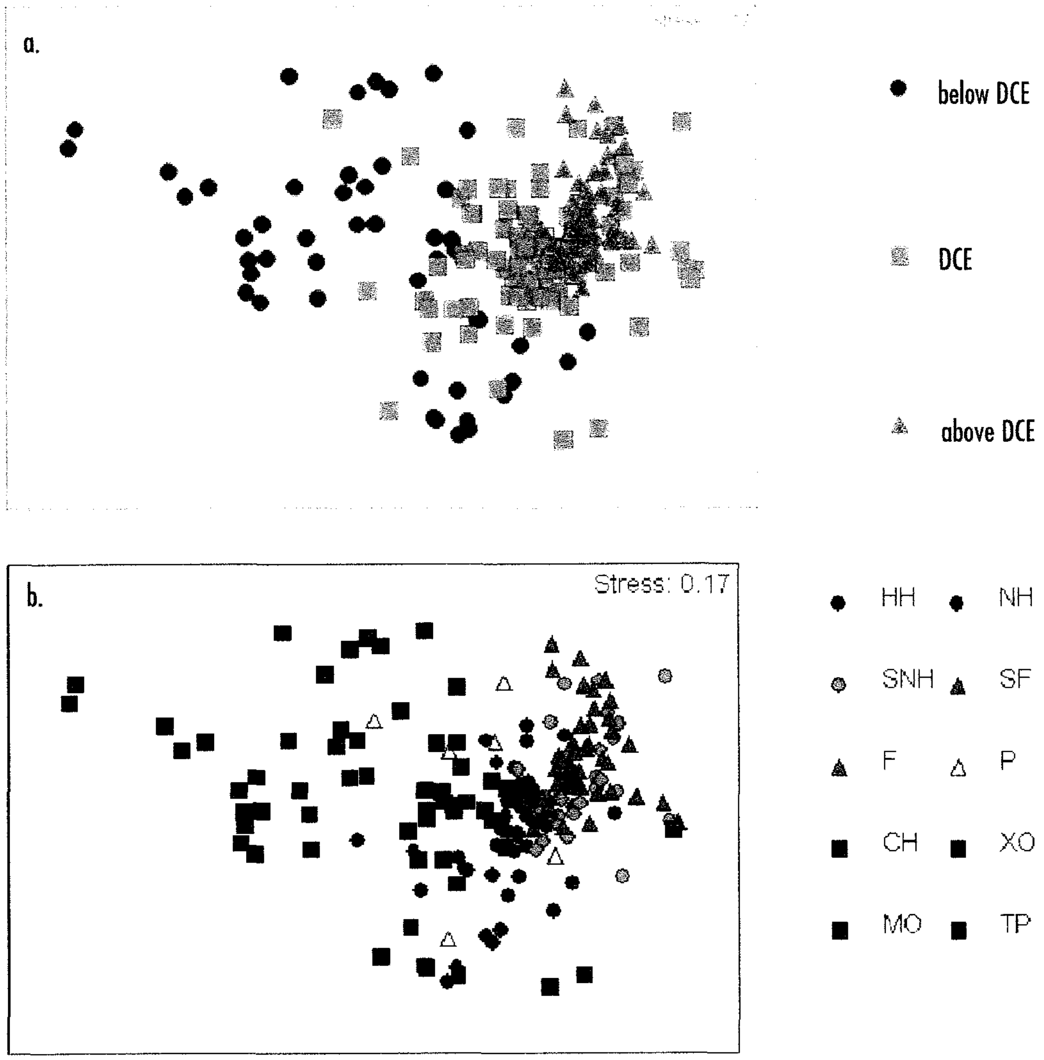


Fig. 3.3 Ordination plot (nMDS) of bird assemblages using untransformed data for a) zone and b) forest type. DCE= deciduous-coniferous ecotone, HH=hemlock/northern hardwood, NH=northern hardwood, XO=xeric oak, MO=mesic oak, TP=tulip/poplar forests. There are no labels for axes because MDS plots can be arbitrary scales, located rotated or inverted.

as indicated by a tighter cluster of points on the MDS (Fig. 3.2a). Four species characterized the bird assemblage in this zone and together contributed to 55% of the average similarity: Winter Wren (*Troglodytes troglodytes*; contributed 16.1% to the av. similarity), Dark-eyed Junco (*Junco hyemalis*; 16.1%), Veery (*Catharus fuscescens*; 13.6%), and Golden-crowned Kinglet (*Regulus satrapa*; 9.4%). Three of these were permanent residents, the Veery being a Neotropical migrant.

The ecotonal sites (Zone 2) also showed highly similarity in bird assemblages (av. similarity = 51.6%). Three species consistently recorded at these sites were characteristic of this zone: Dark-eyed Junco (contributed 18.4% to the av. similarity), Winter Wren (15.0%), and Blue-headed Vireo (12.0%). The latter is a Neotropical migrant, while the others are permanent residents.

Zones 1 and 2 were dissimilar in species composition (av. dissimilarity = 73.7%). Thirteen species contributed up to 70% of the dissimilarity among sites; four of these were good discriminating species, having dissimilarity to standard deviation ratios greater than one (Table 3.3). In general, these discriminating species were more abundant in Zone 2 than Zone 1. Zones 1 and 3 showed a similar pattern of differences, with thirteen species contributing up to 70% of the dissimilarity between zones (Table 3.3). In this comparison most of these species were good discriminating species, with the exception of Ovenbirds, Black-throated Blue Warblers (*Dendroica caerulescens*), and Black-throated Green Warblers, which were more abundant in Zone 3 than Zone 1. The overlap between Zones 2 and 3 was much greater than the overlap between Zones 1 and 2, as indicated by a lower average dissimilarity (46.5%). Twelve species contributed up to 70% of this dissimilarity; however, only two species were good discriminators: Black-throated Blue

Table 3.3 Differences in assemblages among zones based on SIMPER analysis in PRIMER using presence/absence data. The average dissimilarity value, based on Bray-Curtis Indices, for sites within one zone compared to sites in the other zone, are shown together with average abundances of each species for each zone (Av. abundance), the ratio of dissimilarity contribution (for each species) to standard deviation (Diss/SD), and the % contribution of each species to the overall dissimilarity (Contrib %). Only species contributing up to 70% of the average dissimilarity are shown. Cum.% = Cumulative dissimilarity percentage. Species in bold are considered good discriminating species as the ratio Diss/SD is greater than 1. NM=Neotropical migrant, PR=permanent resident, Zone 1=below DCE, Zone 2=DCE, Zone 3=above DCE.

Zones 1 & 2 **Average dissimilarity = 73.72%**	**Zone 1** **Av.Abund**	**Zone 2** **Av.Abund**	**Diss/SD**	**Contrib** **%**	**Cum.** **%**
Winter Wren (PR)	**0.13**	**1.25**	**1.31**	**7.98**	**7.98**
Veery (NM)	**0.26**	**1.19**	**1.20**	**7.10**	**15.08**
Dark-eyed Junco (PR)	0.70	2.09	0.99	6.57	21.65
Golden-crowned Kinglet (PR)	**0.09**	**1.11**	**1.08**	**6.05**	**27.70**
Black-throated Blue Warbler (NM)	0.83	1.13	0.95	5.99	33.69
Ovenbird (NM)	1.38	0.03	0.95	5.87	39.56
Blue-headed Vireo (NM)	0.92	1.21	0.84	5.57	45.13
Black-throated Green Warbler (NM)	1.10	1.10	0.84	5.42	50.55
Red-breasted Nuthatch (PR)	**0.04**	**0.67**	**1.02**	**4.81**	**55.36**
Red-eyed Vireo (NM)	1.00	0.13	0.79	4.61	59.98
Black-capped Chickadee (PR)	0.12	0.53	0.76	3.47	63.45
Canada Warbler (NM)	0.00	0.47	0.77	3.37	66.82
Scarlet Tanager (NM)	0.35	0.15	0.62	3.14	69.96
Zones 1 & 3 **Average dissimilarity = 80.94%**	**Zone 1** **Av.Abund**	**Zone 3** **Av.Abund**	**Diss/SD**	**Contrib** **%**	**Cum.** **%**
Winter Wren (PR)	**0.13**	**2.17**	**2.10**	**7.91**	**7.91**
Veery (NM)	**0.26**	**2.01**	**1.93**	**7.17**	**15.08**
Golden-crowned Kinglet (PR)	**0.09**	**1.31**	**1.80**	**6.52**	**21.60**
Dark-eyed Junco (PR)	**0.70**	**3.18**	**1.11**	**5.54**	**27.14**
Black-capped Chickadee (PR)	**0.12**	**0.95**	**1.31**	**5.43**	**32.58**
Black-throated Green Warbler (NM)	**1.10**	**0.12**	**1.12**	**4.93**	**37.50**
Red-breasted Nuthatch (PR)	**0.04**	**0.75**	**1.08**	**4.80**	**42.30**
Chestnut-sided Warbler (NM)	**0.04**	**1.03**	**1.04**	**4.79**	**47.09**
Ovenbird (NM)	**1.38**	**0.00**	**1.03**	**4.71**	**51.80**
Black-throated Blue Warbler (NM)	**0.83**	**0.77**	**1.02**	**4.71**	**56.50**
Canada Warbler (NM)	**0.00**	**0.79**	**1.11**	**4.65**	**61.16**
Blue-headed Vireo (NM)	0.92	0.80	0.92	4.42	65.58
Eastern Towhee (PR)	0.12	0.67	0.93	4.39	69.97
Zones 2 & 3 **Average dissimilarity = 46.22%**	**Zone 2** **Av.Abund**	**Zone 3** **Av.Abund**	**Diss/SD**	**Contrib** **%**	**Cum.** **%**
Black-throated Green Warbler (NM)	**1.10**	**0.12**	**1.14**	**6.88**	**6.88**
Black-capped Chickadee (PR)	**0.53**	**0.95**	**1.04**	**6.75**	**13.64**
Chestnut-sided Warbler (NM)	0.22	1.03	0.99	6.54	20.18
Canada Warbler (NM)	0.47	0.79	0.98	6.24	26.42
Red-breasted Nuthatch (PR)	0.67	0.75	0.92	6.15	32.56
Eastern Towhee (PR)	0.34	0.67	0.92	6.13	38.70
Brown Creeper (PR)	0.20	0.58	0.95	5.75	44.55
Golden-crowned Kinglet (PR)	1.11	1.31	0.82	5.65	50.10
Blue-headed Vireo (NM)	1.21	0.80	0.82	5.64	55.73
Black-throated Blue Warbler (NM)	1.13	0.78	0.81	5.55	61.28
Hermit Thrush (TM)	0.06	0.47	0.72	4.47	65.84
Hairy Woodpecker (PR)	0.25	0.39	0.77	4.42	70.26

Warblers were more abundant in Zone 2 and Black-capped Chickadees (*Poecile atricapillus*) were more abundant in Zone 3.

For forest types, high similarity among sites was found for northern hardwood forest types (HH, NH, and SNH), and fir forest types (SF and F). These groups were characterized by a range of species (Table 3.4). Low similarity among sites was found within more isolated forest patches, such as pine (P), or protected forest types, including oak (MO and XO) and cove hardwood (CH), and where no characteristic species were identified. The exception was found among tulip-poplar forests (TP), which had high similarity (55.9%) and where Ovenbirds and Red-eyed Vireos (*Vireo olivaceous*) were the characteristic species (Table 3.4).

Multiple comparisons among vegetation types, following ANOSIM analysis, revealed that northern hardwood forests had similar bird assemblages to both spruce/northern hardwood (R=0.006, P=0.450) and northern hardwood/hemlock forests (R=-0.28, P=0.703). Differences among spruce/northern and hemlock/norther hardwood forests (R=0.203, P=0.001) were associated with a greater abundance of Golden-crowned Kinglets and Red-breasted Nuthatches (*Sitta canadensis*), both permanent residents, in spruce/northern hardwood forests, and a greater abundance of Black-throated Green Warblers (a Neotropical migrant) in hemlock/northern hardwood forests.

Forest types with spruce did not differ in bird assemblages (R=0.072, P=0.058); however, fir forests had a different bird assemblage compared to spruce/fir forest (R=0.205, P=0.005). Eastern Towhees (*Pipilo erythrophthalmus*) and Chestnut-sided Warblers (*Dendroica pensylvanica*) were more abundant in fir forests, while Canada Warblers (*Wilsonia canadensis*), Golden-crowned Kinglets, Black-throated Blue

Table 3.4. Species that contribute to similarities among sites for each forest type, based on SIMPER analysis in PRIMER, using Bray-Curtis indices of similarity on presence/absence data. The ratio of similarity contribution (for each species) to standard deviation (Sim/SD) and the % contribution of each species to the overall similarity (Contrib %) are given. Only species contributing over 10% of the average similarity are shown. Cum.% = Cumulative similarity percentage. Species in bold are considered characteristic species of the forest type, as the ratio Sim/SD is greater than 1. NM=Neotropical migrant, PR=permanent resident.

	Sim/SD	Contrib%	Cum.%
Hemlock Northern Hardwood (HH)			
Average similarity: 55.77			
Black-throated Blue Warbler (NM)	**1.72**	**22.64**	**22.64**
Blue-headed Vireo (NM)	**1.51**	**21.11**	**43.75**
Black-throated Green Warbler (NM)	**1.09**	**13.27**	**57.02**
Veery (NM)	0.90	10.88	67.91
Dark-eyed Junco (PR)	0.92	10.07	77.98
Spruce Northern Hardwood (SNH)			
Average similarity: 62.02			
Winter Wren (PR)	**2.47**	**18.11**	**18.11**
Veery (NM)	**2.77**	**17.35**	**35.46**
Dark-eyed Junco (PR)	**2.21**	**16.28**	**51.75**
Golden-crowned Kinglet (PR)	**1.31**	**11.25**	**63.00**
Spruce Fir (SF)			
Average similarity: 63.25			
Winter Wren (PR)	**2.92**	**16.84**	**16.84**
Dark-eyed Junco (PR)	**2.92**	**16.84**	**33.67**
Golden-crowned Kinglet (PR)	**2.43**	**15.06**	**48.74**
Veery (NM)	**1.77**	**12.17**	**60.91**
Fir (F)			
Average similarity: 62.24			
Winter Wren (PR)	**4.14**	**21.47**	**21.47**
Dark-eyed Junco (PR)	**4.14**	**21.47**	**42.95**
Eastern Towhee (PR)	**1.23**	**12.97**	**55.92**
Veery (NM)	**1.25**	**11.94**	**67.86**
Chestnut-sided Warbler (NM)	**1.01**	**10.48**	**78.34**
Northern Hardwood (NH)			
Average similarity: 65.76			
Veery (NM)	**4.80**	**14.79**	**14.79**
Blue-headed Vireo (NM)	**4.80**	**14.79**	**29.58**
Dark-eyed Junco (PR)	**4.80**	**14.79**	**44.37**
Winter Wren (PR)	**1.78**	**11.69**	**56.06**
Pine (P)			
Average similarity: 38.76			
Black-throated Blue Warbler (NM)	**2.27**	**34.51**	**34.51**
Dark-eyed Junco (PR)	**1.20**	**19.20**	**53.71**
Blue-headed Vireo (NM)	0.65	13.53	67.23
Xeric Oak Forest (XO)			
Average similarity: 33.27			
Ovenbird (NM)	0.67	17.85	17.85
Blue-headed Vireo (NM)	0.61	17.20	35.05
Scarlet Tanager (NM)	0.59	12.89	47.94
Dark-eyed Junco (PR)	0.60	12.07	60.01
Black-throated Green Warbler (NM)	0.61	11.98	71.99

Table 3.4. Continued.

	Sim/SD	**Contrib%**	**Cum.%**
Cove Hardwood (CH)			
Average similarity: 35.02			
Black-throated Green Warbler (NM)	0.82	23.57	23.57
Blue-headed Vireo (NM)	0.87	22.07	45.63
Dark-eyed Junco (PR)	0.84	17.01	62.64
Black-throated Blue Warbler (NM)	0.61	13.53	76.17
Mesic Oak Forest (MO)			
Average similarity: 29.30			
Dark-eyed Junco (PR)	0.74	31.04	31.04
Red-eyed Vireo (NM)	0.60	22.30	53.35
Wood Thrush (NM)	0.43	12.67	66.02
Ovenbird (NM)	0.43	11.85	77.87
Black-throated Green Warbler (NM)	0.43	10.24	88.11
Tulip-Poplar Forest (TP)			
Average similarity: 55.94			
Ovenbird (NM)	**4.63**	**36.13**	**36.13**
Red-eyed Vireo (NM)	**1.53**	**22.69**	**58.82**
Black-throated Green Warbler (NM)	**1.53**	**22.69**	**81.51**
Arcadian Flycatcher (NM)	0.60	11.20	92.71

Warblers and Blue-headed Vireos were more abundant in spruce/fir forests. All except Golden-crowned Kinglets were good discriminating species between these two forest types.

Tulip-poplar forests represented one end of a gradient of bird assemblages associated with low-elevation forest types, whereas cove hardwood forests were at the other end of this gradient. Xeric oak, mesic oak, and tulip-poplar forests did not differ in bird assemblages (XO vs. MO: R=0.011, P=0.383; XO vs. TP: R=0.021, P=0.368; MO vs. TP: R=0.074, P=0.188). In general, bird assemblages in cove hardwood also did not differ from these three forest types, although a significant difference was found between tulip poplar and cove hardwood forests (R=0.045, P=0.018). Differences were associated with a greater abundance of Ovenbirds and Red-eyed Vireos in tulip-poplar forest, and Blue-headed Vireos and Dark-eyed Juncos in cove hardwood forest. While bird assemblages in pine forests were indistinguishable from those in the oak and cove hardwood forests, they were significantly different from those in tulip-poplar forests (R=0.705, P=0.028). Ovenbirds, Red-eyed Vireos, Acadian Flycatchers (*Empidonax virescens*), and Black-throated Green Warblers were more abundant in tulip poplar forest, and Blue-headed Vireos and Dark-eyed Juncos were more abundant in pine forest.

Neotropical Migrants and Resident Species

Ordination of Neotropical and resident bird assemblages suggested that Neotropical migrants were largely responsible for patterns seen in the whole bird assemblage because their clustering was similar to that when all birds were considered (Fig. 3.4 vs. Fig. 3.2). With respect to Neotropical birds, the bird community within the DCE was more homogeneous than the community in the deciduous forest below the

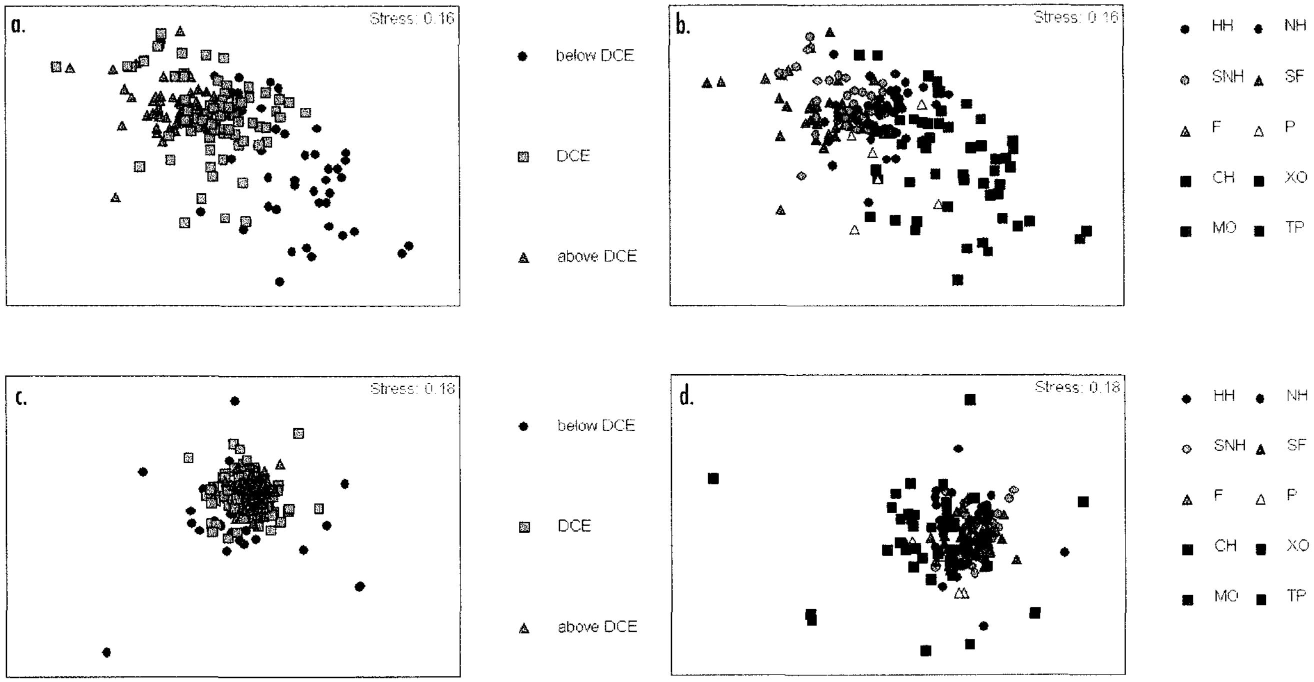


Fig. 3.4 Ordination plots (nMDS) of Neotropical (a and b) and resident (c and d) bird assemblages using untransformed data for zone (a and c) and vegetation type (b and d). DCE=deciduous-coniferous ecotone, HH= hemlock/northern hardwood, NH=northern hardwood, SNH=spruce/northern hardwood, SF=spruce/fir, F=Fir, P=pine, CH=cove hardwood, XO=xeric oak, MO=mesic oak, TP=tulip/poplar forests. There are no labels for axes because "MDS plots can be arbitrarily scales, located rotated or inverted. Rank order information about which samples are most or least similar can say nothing about absolute 'distance apart' of two samples: what can be interpreted is relative distances apart" (from Clarke and Warwick 1994). The degree of stress indicates how well the picture relates to the calculated similarities among sites. The higher the value, the more compromise had to be made; up to 0.2 is a reasonable image.

DCE but less homogeneous than the coniferous forest bird community above the DCE. One can see this by either looking at the similarity values in Table 3.3 or the spread of the points in Fig. 3.4. There is a gradation of "homogeneity" from below the DCE through the DCE to above the DCE.

Neotropical bird assemblages were more similar among sites in northern hardwood and fir forests than in oak, cove hardwood, and pine forests. This was similar to the pattern when all birds were considered (Fig. 3.4a). This pattern was not so obvious for resident birds. Notably, resident birds were more similar among sites in mesic oak forests, fir, and some northern hardwood forests, and less similar in tulip-poplar, xeric oak and hardwood hemlock forests. However, both groups of birds had significant differences in zones (Neotropical migrants: Global R=0.207, P=0.001; residents: Global R=0.130, P=0.006) and in forest types (Neotropical migrants: Global R=0.213, P=0.001; residents: Global R=0.118, P=0.001). The intermediate nature of Zone 2 is more obvious than Zones 1 and 3 in Neotropical assemblages, with a greater difference between Zones 1 and 3 (average dissimilarity: Neotropical = 86.7%, resident = 77.0%). For resident bird assemblages, there was much greater similarity between Zones 2 and 3 (average dissimilarity: Neotropical = 60.7%, resident = 49.0%, Fig. 3.5b) than between Zone 1 and 2.

For Neotropical birds, differences in assemblage composition based on SIMPER analysis, showed a range of species that were good discriminators among habitats.

Diversity and Abundance

Diversity indices are instructive but potentially misleading if high diversity is assumed to be desirable from a conservation perspective. Edges and ecotones tend to

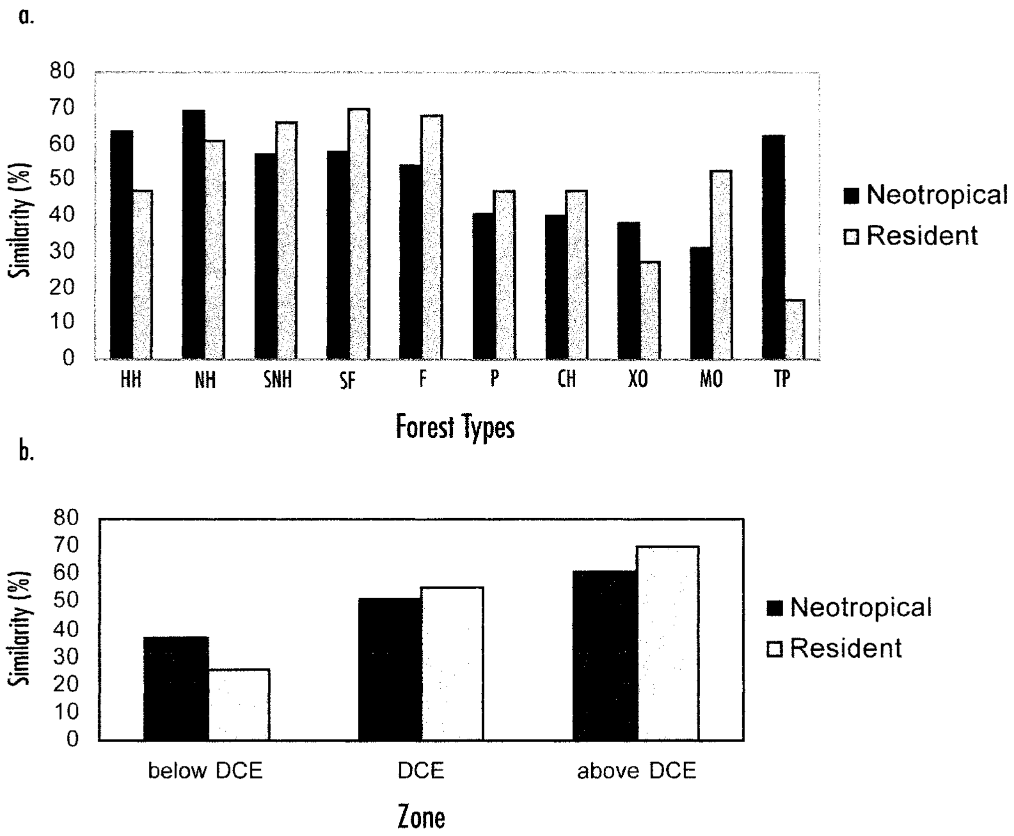
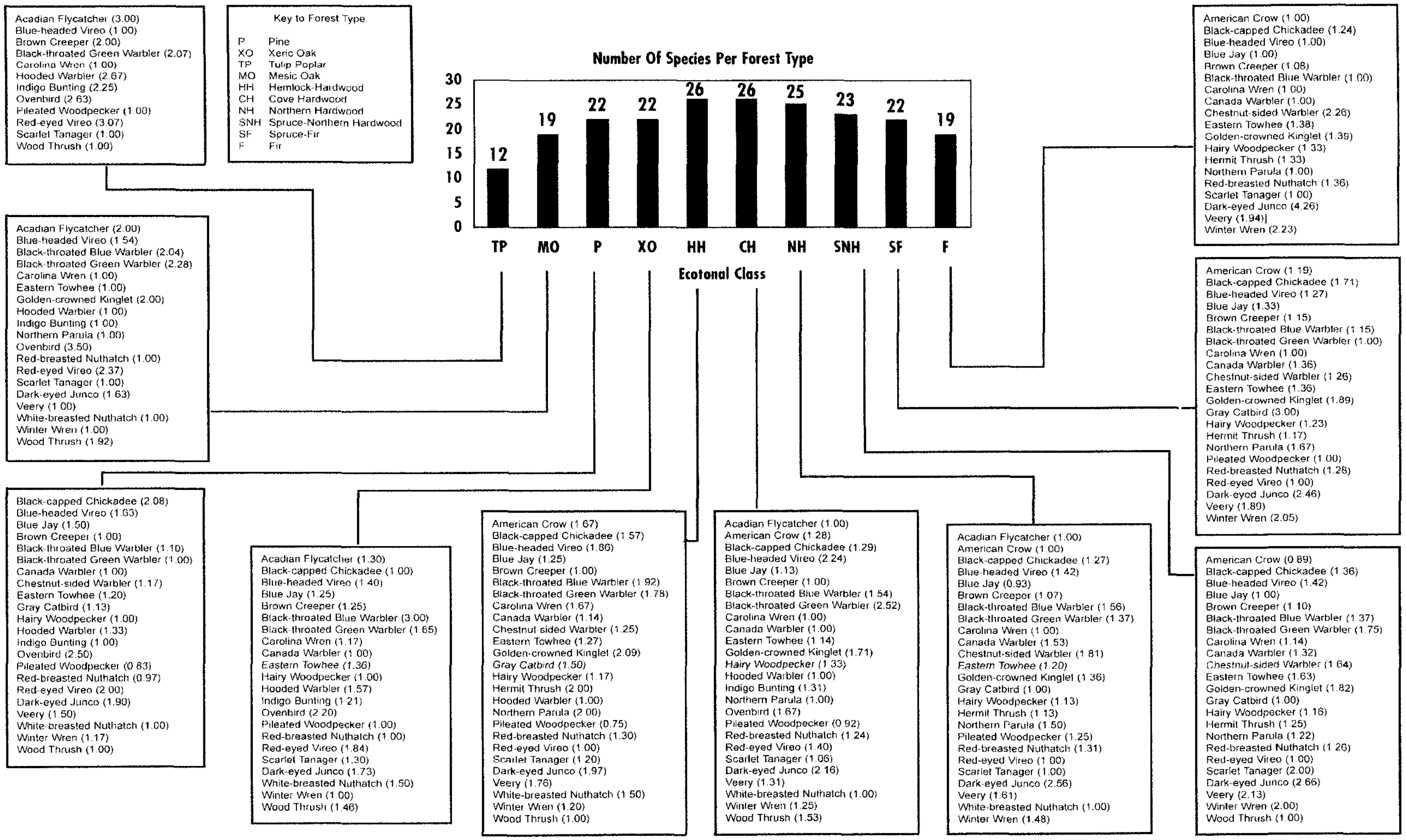


Fig. 3.5 Average similarity for Neotropical and residential bird assemblages in a) vegetation types and b) zones. Acronyms for forest types are given in the legend to Fig. 3.4.



Key to Forest Type

P	Pine
XO	Xeric Oak
TP	Tulip Poplar
MO	Mesic Oak
HH	Hemlock-Hardwood
CH	Cove Hardwood
NH	Northern Hardwood
SNH	Spruce-Northern Hardwood
SF	Spruce-Fir
F	Fir

Acadian Flycatcher (3.00)
Blue-headed Vireo (1.00)
Brown Creeper (2.00)
Black-throated Green Warbler (2.07)
Carolina Wren (1.00)
Hooded Warbler (2.67)
Indigo Bunting (2.25)
Ovenbird (2.63)
Pileated Woodpecker (1.00)
Red-eyed Vireo (3.07)
Scarlet Tanager (1.00)
Wood Thrush (1.00)

Acadian Flycatcher (2.00)
Blue-headed Vireo (1.54)
Black-throated Blue Warbler (2.04)
Black-throated Green Warbler (2.28)
Carolina Wren (1.00)
Eastern Towhee (1.00)
Golden-crowned Kinglet (2.00)
Hooded Warbler (1.00)
Indigo Bunting (1.00)
Northern Parula (1.00)
Ovenbird (3.50)
Red-breasted Nuthatch (1.00)
Red-eyed Vireo (2.37)
Scarlet Tanager (1.00)
Dark-eyed Junco (1.63)
Veery (1.00)
White-breasted Nuthatch (1.00)
Winter Wren (1.00)
Wood Thrush (1.92)

Black-capped Chickadee (2.08)
Blue-headed Vireo (1.63)
Blue Jay (1.50)
Brown Creeper (1.00)
Black-throated Blue Warbler (1.10)
Black-throated Green Warbler (1.00)
Canada Warbler (1.00)
Chestnut-sided Warbler (1.17)
Eastern Towhee (1.20)
Gray Catbird (1.13)
Hairy Woodpecker (1.00)
Hooded Warbler (1.33)
Indigo Bunting (1.00)
Ovenbird (2.50)
Pileated Woodpecker (0.83)
Red-breasted Nuthatch (0.97)
Red-eyed Vireo (2.00)
Dark-eyed Junco (1.90)
Veery (1.50)
White-breasted Nuthatch (1.00)
Winter Wren (1.17)
Wood Thrush (1.00)

Acadian Flycatcher (1.30)
Black-capped Chickadee (1.00)
Blue-headed Vireo (1.40)
Blue Jay (1.25)
Brown Creeper (1.25)
Black-throated Blue Warbler (3.00)
Black-throated Green Warbler (1.65)
Carolina Wren (1.17)
Canada Warbler (1.00)
Eastern Towhee (1.36)
Hairy Woodpecker (1.00)
Hooded Warbler (1.57)
Indigo Bunting (1.21)
Ovenbird (2.20)
Pileated Woodpecker (1.00)
Red-breasted Nuthatch (1.00)
Red-eyed Vireo (1.84)
Scarlet Tanager (1.30)
Dark-eyed Junco (1.73)
White-breasted Nuthatch (1.50)
Winter Wren (1.00)
Wood Thrush (1.46)

American Crow (1.67)
Black-capped Chickadee (1.57)
Blue-headed Vireo (1.86)
Blue Jay (1.25)
Brown Creeper (1.00)
Black-throated Blue Warbler (1.92)
Black-throated Green Warbler (1.78)
Carolina Wren (1.67)
Canada Warbler (1.14)
Chestnut-sided Warbler (1.25)
Eastern Towhee (1.27)
Golden-crowned Kinglet (2.09)
Gray Catbird (1.50)
Hairy Woodpecker (1.17)
Hermit Thrush (2.00)
Hooded Warbler (1.00)
Northern Parula (2.00)
Pileated Woodpecker (0.75)
Red-breasted Nuthatch (1.30)
Red-eyed Vireo (1.00)
Scarlet Tanager (1.20)
Dark-eyed Junco (1.97)
Veery (1.76)
White-breasted Nuthatch (1.50)
Winter Wren (1.20)
Wood Thrush (1.00)

Acadian Flycatcher (1.00)
American Crow (1.28)
Black-capped Chickadee (1.29)
Blue-headed Vireo (2.24)
Blue Jay (1.13)
Brown Creeper (1.00)
Black-throated Blue Warbler (1.54)
Black-throated Green Warbler (2.52)
Carolina Wren (1.00)
Canada Warbler (1.00)
Eastern Towhee (1.14)
Golden-crowned Kinglet (1.71)
Hairy Woodpecker (1.33)
Hooded Warbler (1.00)
Indigo Bunting (1.31)
Northern Parula (1.00)
Ovenbird (1.67)
Pileated Woodpecker (0.92)
Red-breasted Nuthatch (1.24)
Red-eyed Vireo (1.40)
Scarlet Tanager (1.06)
Dark-eyed Junco (2.16)
Veery (1.31)
White-breasted Nuthatch (1.00)
Winter Wren (1.25)
Wood Thrush (1.53)

Acadian Flycatcher (1.00)
American Crow (1.00)
Black-capped Chickadee (1.27)
Blue-headed Vireo (1.42)
Blue Jay (0.93)
Brown Creeper (1.07)
Black-throated Blue Warbler (1.56)
Black-throated Green Warbler (1.37)
Carolina Wren (1.00)
Canada Warbler (1.53)
Chestnut-sided Warbler (1.81)
Eastern Towhee (1.20)
Golden-crowned Kinglet (1.36)
Gray Catbird (1.00)
Hairy Woodpecker (1.13)
Hermit Thrush (1.13)
Northern Parula (1.50)
Pileated Woodpecker (1.25)
Red-breasted Nuthatch (1.31)
Red-eyed Vireo (1.00)
Scarlet Tanager (1.00)
Dark-eyed Junco (2.56)
Veery (1.61)
White-breasted Nuthatch (1.00)
Winter Wren (1.48)

American Crow (0.89)
Black-capped Chickadee (1.36)
Blue-headed Vireo (1.42)
Blue Jay (1.00)
Brown Creeper (1.10)
Black-throated Blue Warbler (1.37)
Black-throated Green Warbler (1.75)
Carolina Wren (1.14)
Canada Warbler (1.32)
Chestnut-sided Warbler (1.64)
Eastern Towhee (1.63)
Golden-crowned Kinglet (1.82)
Gray Catbird (1.00)
Hairy Woodpecker (1.16)
Hermit Thrush (1.25)
Northern Parula (1.22)
Red-breasted Nuthatch (1.26)
Red-eyed Vireo (1.00)
Scarlet Tanager (2.00)
Dark-eyed Junco (2.66)
Veery (2.13)
Winter Wren (2.00)
Wood Thrush (1.00)

American Crow (1.19)
Black-capped Chickadee (1.71)
Blue-headed Vireo (1.27)
Blue Jay (1.33)
Brown Creeper (1.15)
Black-throated Blue Warbler (1.15)
Black-throated Green Warbler (1.00)
Carolina Wren (1.00)
Canada Warbler (1.36)
Chestnut-sided Warbler (1.26)
Eastern Towhee (1.36)
Golden-crowned Kinglet (1.89)
Gray Catbird (3.00)
Hairy Woodpecker (1.23)
Hermit Thrush (1.17)
Northern Parula (1.67)
Pileated Woodpecker (1.00)
Red-breasted Nuthatch (1.28)
Red-eyed Vireo (1.00)
Dark-eyed Junco (2.46)
Veery (1.89)
Winter Wren (2.05)

American Crow (1.00)
Black-capped Chickadee (1.24)
Blue-headed Vireo (1.00)
Blue Jay (1.00)
Brown Creeper (1.08)
Black-throated Blue Warbler (1.00)
Carolina Wren (1.00)
Canada Warbler (1.00)
Chestnut-sided Warbler (2.26)
Eastern Towhee (1.38)
Golden-crowned Kinglet (1.39)
Hairy Woodpecker (1.33)
Hermit Thrush (1.33)
Northern Parula (1.00)
Red-breasted Nuthatch (1.36)
Scarlet Tanager (1.00)
Dark-eyed Junco (4.26)
Veery (1.94)]
Winter Wren (2.23)

Fig. 3.6 Relative abundance (mean detections / 50m radius point count circle) of bird species in each forest type. Species' common names and maximum abundance valules (the mean number of pairs within the area of a 50m radius) are listed with each habitat. Acronyms for forest types are given in Fig. 3.4. Number of bird species in each forest type are shown above bars.

have greater local or alpha diversity than adjacent habitats, but this might come at the expense of landscape-level diversity (ß-diversity). To aid in understanding diversity, I calculated relative abundance indices for each species for each forest type (Fig. 3.6) and thus identified the single habitat in which each species showed its maximum abundance (Fig. 3.7).

More species had their maximum abundances in hemlock-hardwood than in any other forest type. High avian diversity in hemlock-hardwood was positively related to the species that had their maximum abundances in hemlock-hardwood. Twenty-six species showed their maximum abundances in this habitat. In contrast, tulip-popular and fir forests had lower diversity (12 and 19, respectively) but hosted a relatively large number of bird species (five) with maximum abundance values (Fig. 3.7). Of the coniferous forest types, spruce-fir had the most species with maximum abundance scores. Mixed hardwood sites (mesic oak and xeric oak) had higher diversity scores than tulip or fir forests, but each contained only two species with maximum abundances (these species differed between the two community types, Fig. 3.7). This higher species richness may reflect the fact that mixed-wood forest tends to be used by both softwood and hardwood forest specialists, though it may not be their optimal habit. The spatial pattern of this distribution in forest types is presented in Fig. 3.8. The vegetation shows a continuum of change with elevation and slope exposures. For convenience, however, separate plant communities, based on their dominant species, were recognized. Distributional relations of bird species to one another in the landscape were represented by species ordination in relation to the habitat hyperspace.

I generated separate maximum abundance histograms for three groups:

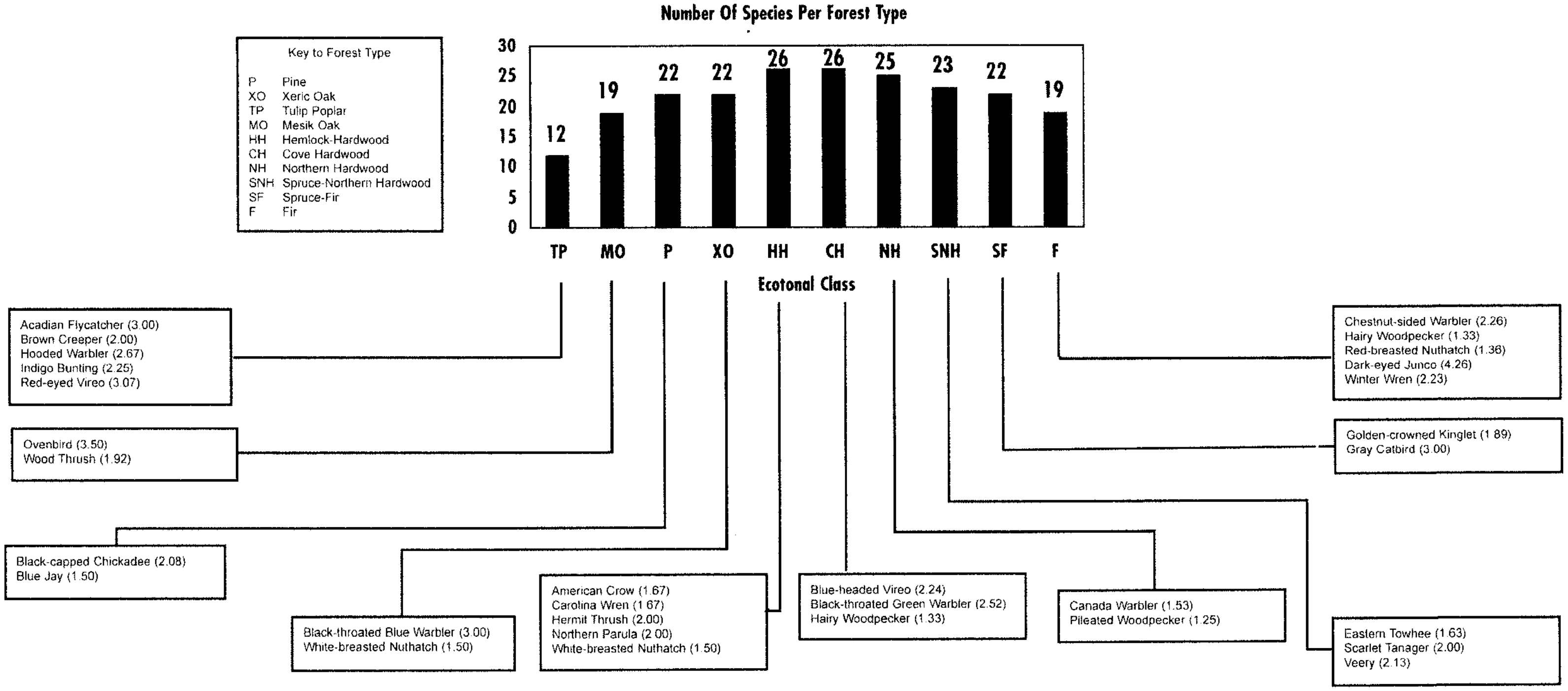


Fig. 3.7 Maximum abundance (mean detections / 50m radius point count circle) of bird species in each forest type. Species' common names and maximum abundance values (the mean number of pairs within the area of a 50m radius) are listed with each habitat. Acronyms for forest types are given in Fig. 3.4. Number of bird species in each forest type are shown above bars.

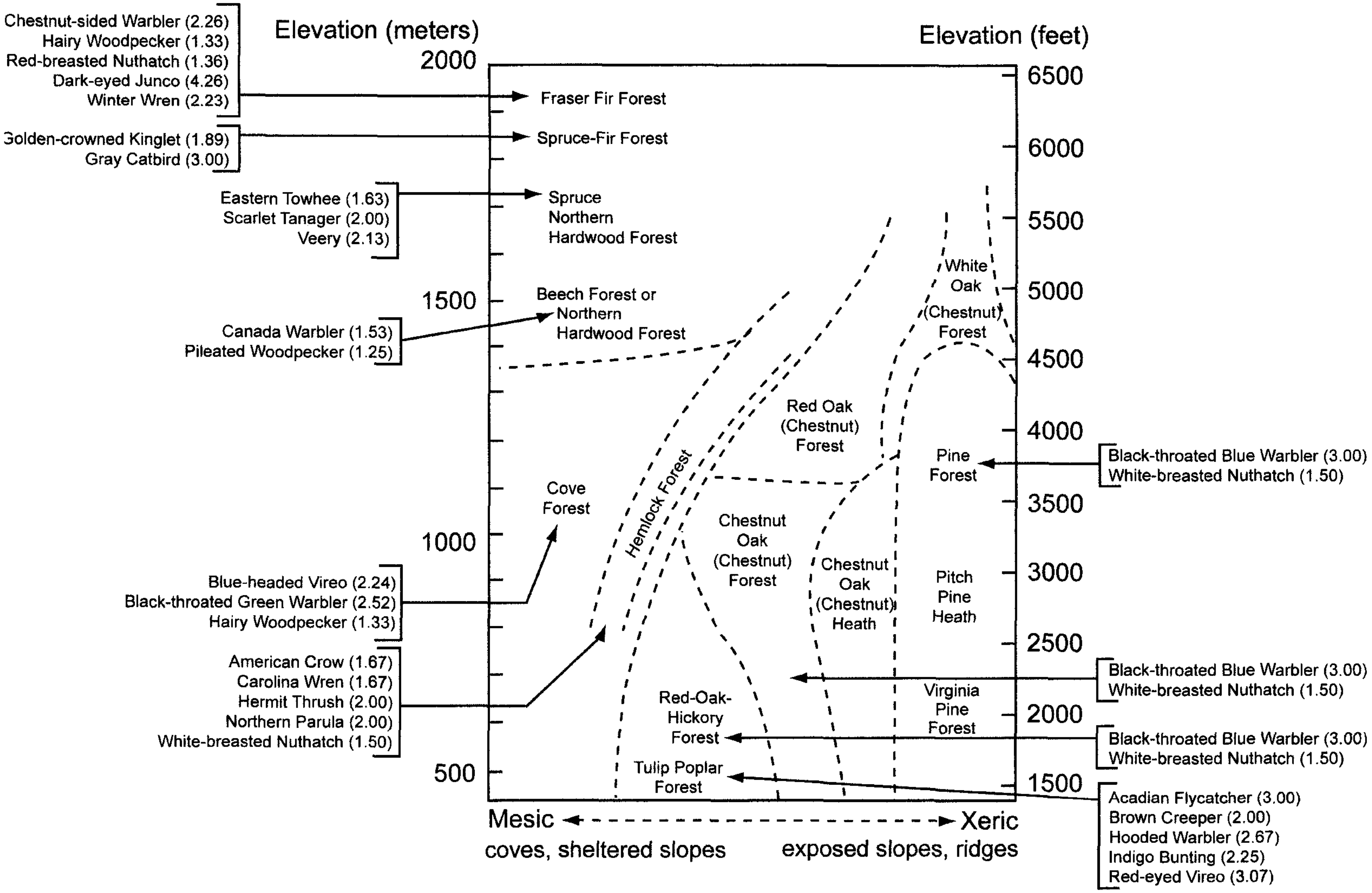


Fig. 3.8 Mosaic of plant and bird communities showing special variations with elevation and slope exposure (modified from Whittaker 1956). (Chestnut) = with dead or snag chestnut. The maximum abundance values (mean number of pairs within a 50m radius circle) are given after each species common name.

Neotropical (or long-distance) migrants, permanent residents, and temperate (or short-distance) migrants (Fig. 3.9). The hemlock habitats (CH, HH) together contained 25 Neotropical migrant species with maximum abundances. Cove hardwood contained the largest number of Neotropical migrant species (13) at their maximum abundances, while Fraser fir forests (SF, F) and tulip-poplar forests had the lowest values. Permanent resident species also tended to show high abundances (13) in cove hardwood habitats. This indicated that an equal proportion of permanent residents and Neotropical migrants use cove hardwood habitats. All the permanent resident species showed equal abundances (13) in cove and hemlock hardwood sites.

There were only a few differences in resident bird assemblages among forest types. Tulip-poplar forests tended to be distinguished from other forest types by the absence of a range of species, notably Dark-eyed Juncos, Winter Wrens, and Eastern Towhees. Spruce communities were distinguishable from oak, cove hardwood, and pine forests due to higher abundances of Winter Wrens, Golden-crowned Kinglets, and Red-breasted Nuthatches. These spruce forests also had fewer Blue Jays and Eastern Towhees than pine forests.

Environmental Parameters

Principal components analysis on environmental parameters showed clustering of sites in each zone and vegetation type (Fig. 3.10). ANOSIM on the normalized Euclidean distance matrix identified significant differences in both forest type (Global R=0.151, P=0.008) and zone (Global R=0.272, P=0.001). However, only 36.3% of the variation in the data was explained by the first two axes (47.1% by 3 axes). The first axis was largely associated positively with elevation and negatively with subcanopy height

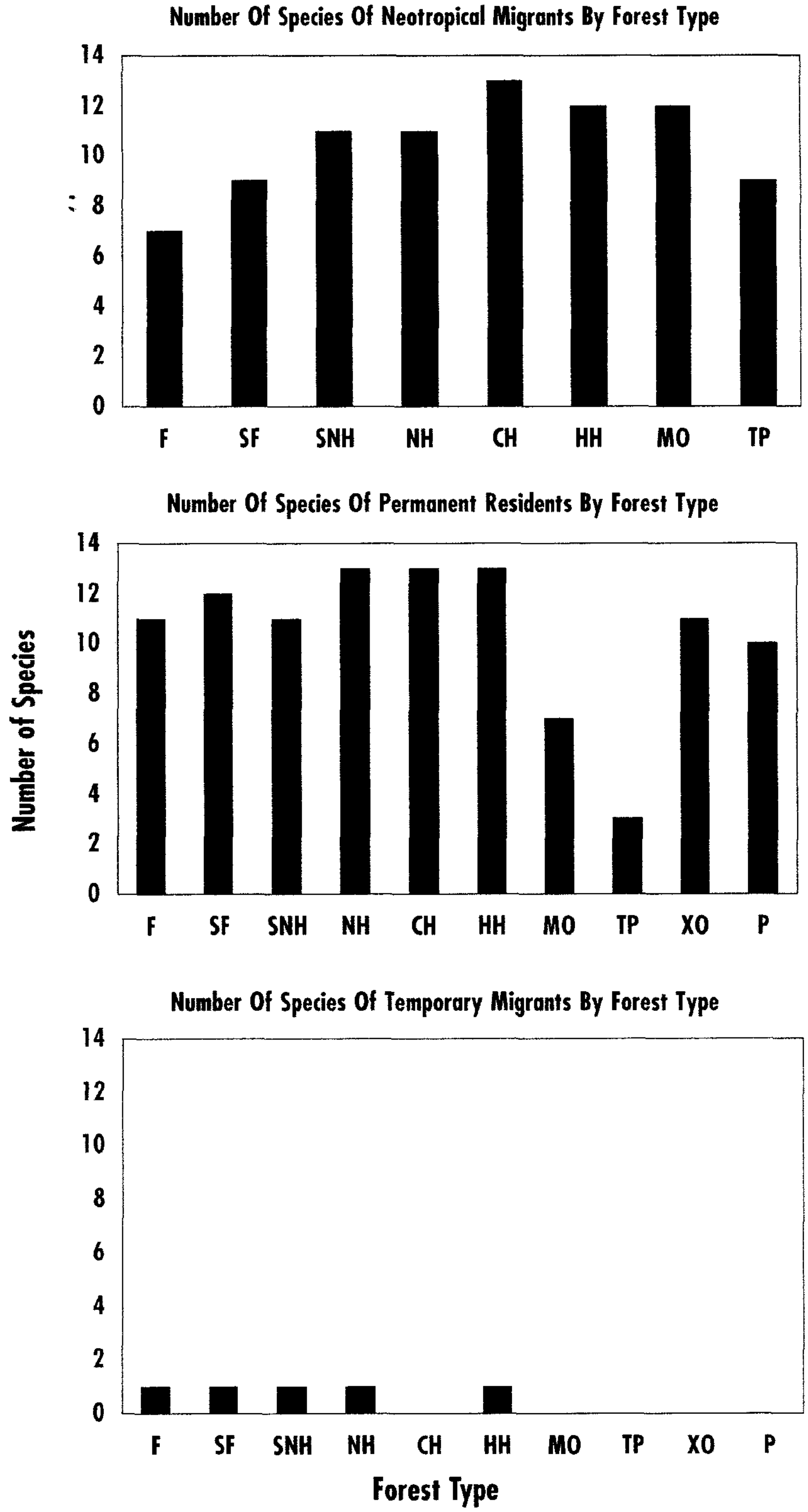


Fig. 3.9 The number of species with maximum abundance in each forest type, separated by migratory status (a. Neotropical migrants, b. Permanent residents, c. Temporary migrants). Acronyms for forest types are defined in legend of Fig. 3.3.

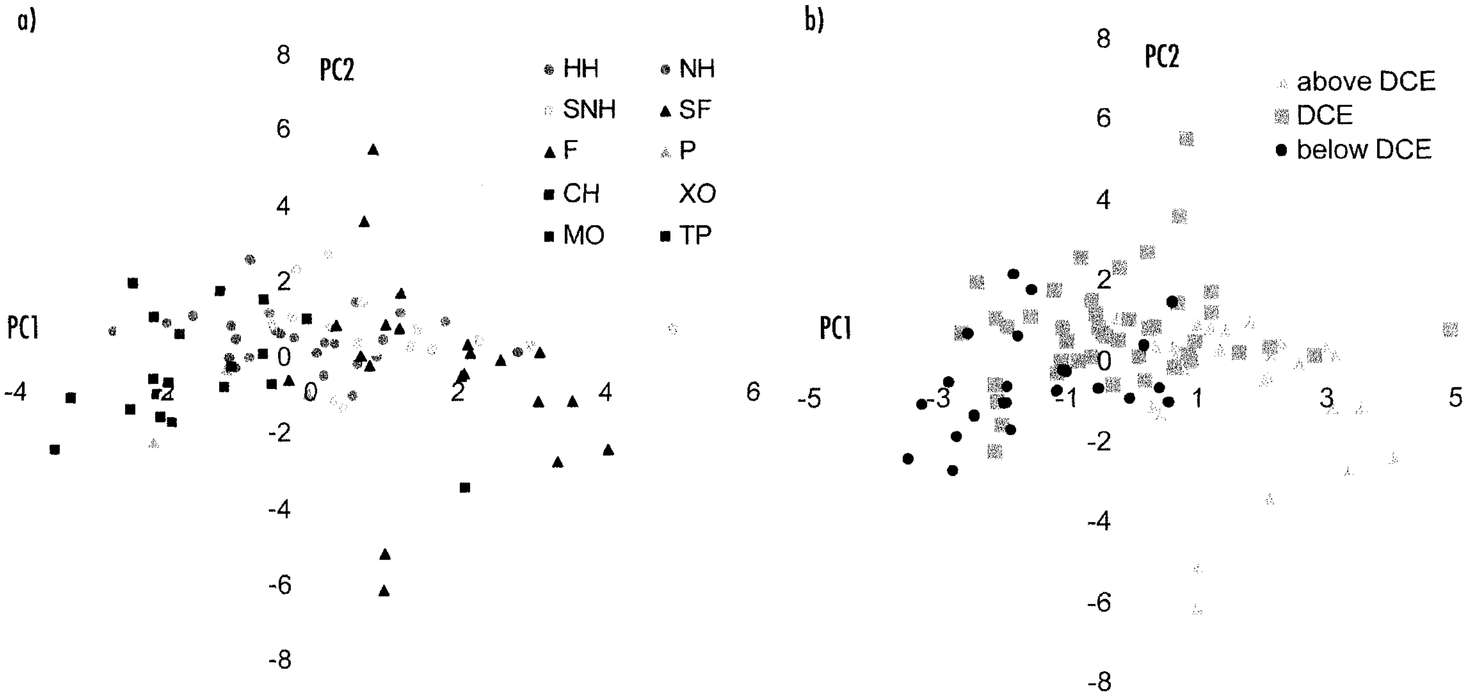


Fig. 3.10 Principal components analysis plot (first and second axes) based on environmental parameters showing a) forest types and b) zones. DCE = deciduous-coniferous ecotone. See the legend to Fig. 3.4 for abbreviations of forest types. The variance in the environmental parameters explained by these axes is 36.2%.

range and tree canopy height range. The second axis was associated with total quality of trunk, density of trees, and height range of tall shrub/saplings. Fir and spruce/fir showed little similarity with the other forest types.

Bird assemblages were (primarily) correlated with elevation (R=0.591). Adding other environmental parameters always decreased the explanatory power of the model. When elevation was excluded, the four environmental parameters that gave the best correlation (R=0.353) were slope, the TM Tasseled Cap Index (*greenness*), total tree density, and height range of subcanopy.

The presence of snags at sites did not influence the bird assemblage when untransformed data were considered (Global R=0.065, P=0.117), but did influence the bird assemblage when presence/absence data were considered (Global R=0.102, P=0.036). This suggests that changes in species composition are masked by abundant species being unaffected by the presence of snags. Sites with snags were characterized by the presence of Winter Wrens, whereas those without snags were characterized by Blue-headed Vireos, Black-throated Blue Warblers, and Dark-eyed Juncos. No species were good discriminators between sites with and without snags.

The presence of forest openings was significant when both untransformed and presence/absence data were analyzed (untransformed: Global R=0.312, P=0.006; presence/absence: Global R=0.323, P=0.004). Using presence/absence data, sites with forest openings were characterized by Winter Wrens, Veerys, Black-throated Blue Warblers, and Dark-eyed Juncos, although Blue-headed Vireos contributed the most to average similarity and presence. However, using untransformed data, the differences between sites with and without forest openings could be discriminated by a decreased abundance in Dark-eyed Juncos, Veerys, Winter Wrens, and Golden-crowned Kinglets (together contributing 31% of the average dissimilarity). Red-breasted Nuthatches and Canada Warblers, also good discriminators, were more abundant in sites with forest openings, but these contributed much less to the overall dissimilarity.

Avian Species Richness

Using the census sites established in the three different zones, mean species richness differed significantly among zones ($F_{2,6}$ = 18.02, df=2, P<0.0001) with a significant gradsect interaction ($F_{2,6}$ = 15.39, df=2, P<0.0001; Tables 3.5, 3.6, Fig. 3.11).

Forest type was much more important than distance or proximity to edge in explaining species richness and total abundance. On ACT, species richness and total bird abundance was greater in the DCE, with mixed habitats of deciduous and hemlock communities (ECCs), than in the relatively more deciduous or spruce-fir communities (Fig. 3.11b). On the other trails, species richness and total abundance differed among zones (Tables 3.5, 3.6, Fig. 3.11a), and I detected no significant zone by gradsect interaction effect for both diversity measures (Tables 3.5, 3.6). Individually, 12 of 29 common bird species were most abundant in either Zone 1 (four species), Zone 2 (three species), or Zone 3 (five species; Tables 3.5, 3.6). Of the four species most abundant below the DCE zones, three species (Ovenbird: F=3.36, P=0.0185; Red-eyed Vireo: F=3.09, P=0.0220; and Wood Thrush: F=2.80, P=0.0328) were most abundant in deciduous communities (TP and MO; Table 3.4, Fig. 3.6). All five of the species that were most abundant above the DCE zone (Dark-eyed Junco: F=2.11, P=0.0177; Eastern Towhee: F=3.41, P=0.0017; Veery: F=4.48, P=0.0001; Winter Wren: F=6.21, P<0.0001; and Red-breasted Nuthatch: F=6.20, P=0.0170) were most abundant in the spruce-fir or

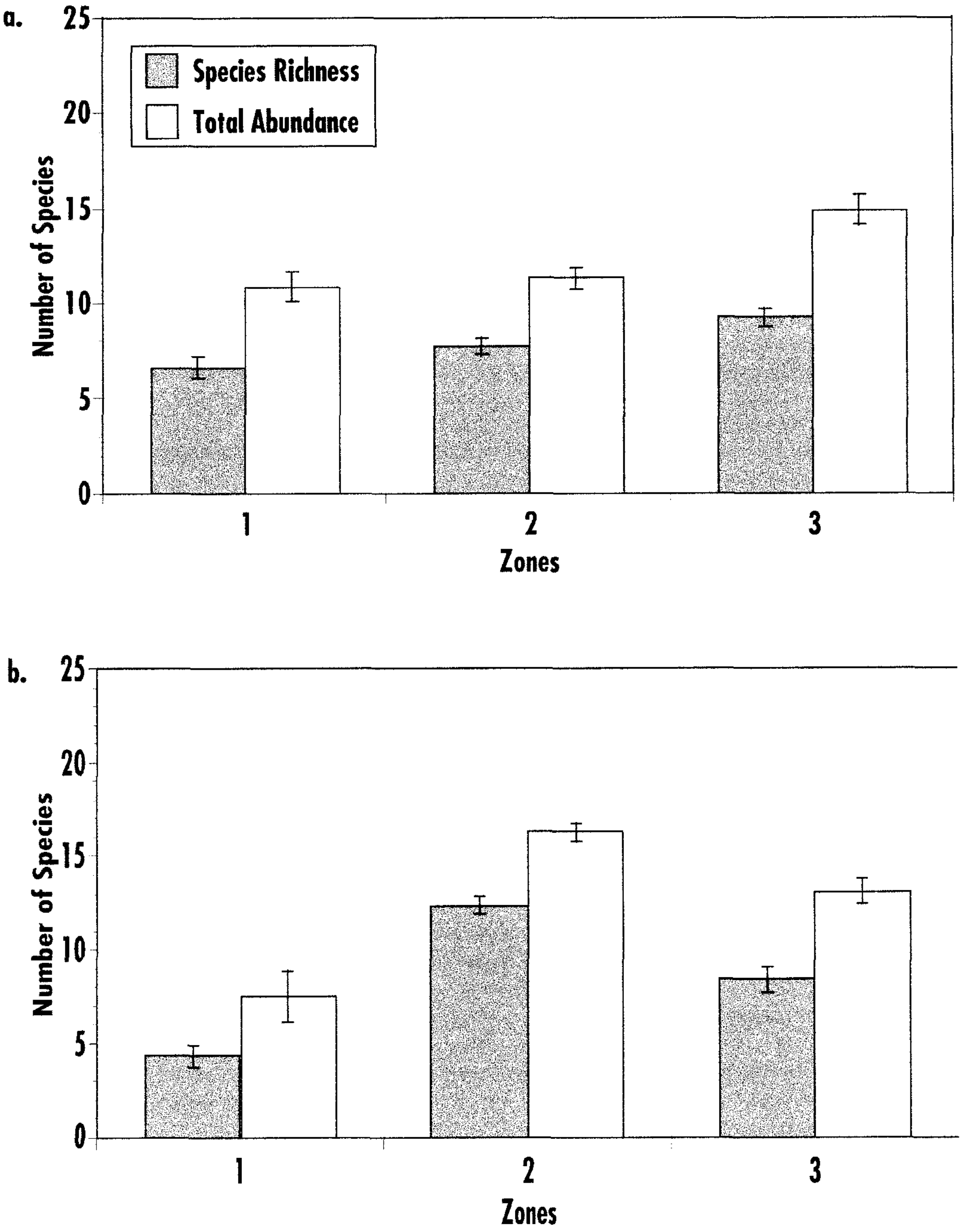


Fig. 3.11 Species richness and total species abundance in three zones (mean ± 1 SE); (1) below deciduous-coniferous ecotone (DCE); (2) at the DCE, (3) above the DCE on gradsects for a) combined BHT, RFT, and TGT and b) ACT. Bull Head Trail (BHT), Rainbow Falls Trail (RFT), and Trillium Gap Trail (TGT) were combined because the trends up their gradients were similar. The trends up the Alum Cave Trail (ACT) were different.

Table 3.5 Breeding birds, species abundance, total bird abundance, and species richness along gradsects characterized by three different elevational and habitat zones of BHT, RFT, and TGT gradsects on Mount LeConte, GSMNP, 1999-2000[a].

								Test Statistic [b]			
	<DCE Zone		DCE Zone		>DCE Zone			Zonal		Overall	
Species	x̄	SE	x̄	SE	x̄	SE	Effect	F	P	F	P
Acadian Flycatcher *(Empidonax virescens)*	2.29	0.61	1.50	0.00	1.00	0.22	N	2.25	0.119	2.25	0.119
American Crow *(Corvus brachyrynchos)*	1.37	1.50	2.50	0.28	1.00	0.00	N	1.64	0.247	1.08	0.422
Black-capped Chickadee *(Poecile atricopillus)*	1.45	0.19	1.49	0.12	1.45	0.12	N	0.13	0.879	0.14	0.997
Blue-headed Vireo *(Vireo solitarius)*	1.68	0.17	**1.71**	0.10	1.10	0.05	(TXZ)Y	16.58	<0.0001	6.03	<0.0001
Blue Jay *(Cyanocitta cristata)*	1.20	0.33	1.33	0.12	1.00	1.00	N	0.14	0.867	0.80	0.580
Brown Creeper *(Certhia americana)*	1.02	0.10	1.07	0.08	1.34	0.12	N	0.65	0.529	1.51	0.197
Black-throated Blue Warbler *(Dendroica caerulescens)*	1.26	0.23	**1.94**	0.09	1.65	0.09	T(T)	2.30	0.104	6.96	<0.0001
Black-throated Green Warbler *(Dendroica virens)*	1.89	0.22	1.89	0.14	1.51	0.20	N	1.29	0.278	1.15	0.329
Carolina Wren *(Thryothorus ludovicianus)*	1.00	0.00	1.30	0.21	1.05	0.05	N	0.49	0.628	0.33	0.927
Canada Warbler *(Wilsonia canadensis)*	1.16	0.41	1.76	0.07	1.29	0.12	N	1.34	0.267	1.31	0.260
Chestnut-sided Warbler *(Dendroica pensylvanica)*	1.30	0.52	1.87	0.20	1.88	0.16	N	1.67	0.201	1.21	0.323
Dark-eyed Junco *(Junco hyemalis)*	2.25	0.25	2.46	0.13	**2.76**	0.20	Y	1.87	0.157	2.11	0.018
Eastern Towhee *(Pipilo erythrophthalmus)*	1.19	0.10	1.29	0.09	**1.65**	0.14	T	3.10	0.053*	3.41	0.002
Golden-crowned Kinglet *(Regulus satrapa)*	1.38	0.22	1.68	0.12	1.88	0.07	Y	2.38	0.097	2.01	0.060
Gray Catbird *(Dumetella carolinensus)*	[d]		1.21	0.21	[d]		N	0.67	0.450	0.67	0.450
Hairy Woodpecker *(Picoides villosus)*	1.07	0.07	1.36	0.11	1.17	0.13	N	1.90	0.166	0.59	0.779
Hermit Thrush *(Catharus guttatus)*	1.15	0.34	1.29	0.33	1.33	0.08	N	7.70	0.041	7.52	0.018
Hooded Warbler *(Wilsonia citrina)*	1.02	0.35	2.10	0.02	1.08	0.08	N	2.90	0.074	4.35	0.008
Indigo Bunting *(Passerina amoena)*	**1.53**	0.18	1.00	0.00	1.00	0.00	N	2.01	0.166	2.28	0.106
Northern Parula *(Parula americana)*	1.43	0.30	1.00	0.00	1.50	0.50	N	0.75	0.401	0.71	0.604
Ovenbird *(Seiurus aurocapillus)*	**3.76**	0.25	1.63	0.38	2.23	0.29	N	7.28	0.010*	3.36	0.018
Pileated Woodpecker *(Dryocopus pileatus)*	1.00	0.00	1.96	0.10	1.00	0.00	N	0.08	0.926	0.09	0.985
Red-breasted Nuthatch *(Sitta canadensis)*	1.16	0.15	1.29	0.08	**1.40**	0.09	N	0.11	0.899	0.40	0.931
Red-eyed Vireo *(Vireo olivaceus)*	**2.68**	0.27	1.86	0.22	1.22	0.26	N	6.93	0.003**	3.09	0.022
Scarlet Tanager *(Piranga olivacea)*	1.20	0.14	1.22	0.11	1.13	0.17	N	1.07	0.358	1.70	0.131
Veery *(Catharus fuscescens)*	1.55	0.27	2.10	0.07	**2.25**	0.11	(Z)Y	12.21	<0.0001***	4.48	<0.0001
White-breasted Nuthatch *(Sitta carolinensis)*	1.14	0.14	1.13	0.13	[d]			0.00	1.000	1.10	0.390
Winter Wren *(Troglodytes troglodytes)*	1.42	0.30	**2.06**	0.07	**2.19**	0.11	Y	1.12	0.328	6.21	<0.0001
Wood Thrush *(Hylocichia mustelina)*	**1.86**	0.18	1.14	0.00	1.00	0.14	Z	2.32	0.120	2.80	0.033

[a] Data represent either species in order of abundance with ≥20 total individual bird detections in 1999 and 2000 combined or community measures for all species with ≥1 detection; all detections ≤50 m from sample points along transects. Significant abundances in zones are bolded. [b] Completely randomized 3 way (factor) ANOVA in time (3 zones X 4 tradsects X 2 yr; n = 24 with transects as the error term to test zonal effect and residual as the error term to test year and zone X transect X year interaction effects).*
[c]T = transect effect; Z = zone effect, Y = year effect, N = no effect; T X Z = transect X zone interaction. [d] = no birds observed.

fir communities. The most abundant species in the mixed forest ecotonal community were Blue-headed Vireo (F=6.03, P<0.0001), Black-throated Blue Warbler (F=6.96, P<0.0001), Hooded Warbler (F=4.83, P=0.0083), and Golden-crowned Kinglet (F=5.16, P=0.0096).

For the analyses on the BHT, RFT, and TGT gradsects, the Eastern Towhee, Veery, and Wood Thrush (*Hylocichia mustelina*) had significant gradsect effects but non-significant interaction effects. For the ACT-only analyses, Blue-headed Vireo, Black-throated Blue Warbler, Chestnut-sided Warbler, Golden-crowned Kinglet, Northern Parula, Red-breasted Nuthatch, Dark-eyed Junco, and White-breasted Nuthatch (*Sitta cvarolinensis*) had significant gradsect effects (Tables 3.5, 3.6).

Seventeen species, including the Acadian Flycatcher, American Crow, Blue Jay, Carolina Wren, and Pileated Woodpecker, did not differ in abundance among forest types or zones. These 17 species occurred in all three zones, except the White-breasted Nuthatch, which was not detected in the forests above the DCE. Five species, the Blue-headed Vireo, Dark-eyed Junco, Golden-crowned Kinglet, Veery, and Winter Wren, all ecotone-conspicuous species, increased in abundance from 1999 to 2000 (Tables 3.5, 3.6). ANOVAs for ACT-only revealed that for Black-headed Vireo, Black-throated Blue Warbler, Golden-crowned Kinglet, and Northern Parula, zone 1 was significantly different from zones 2 and 3, but zone 2 was not significantly different from zone 3. For Chestnut-sided Warbler, zone 2 was significantly different from zone 3; but zone 1 was not significantly different from zones 2 or 3. For Red-breasted Nuthatch zone 2 was significantly different from zone 3. For Dark-eyed Junco, zone 3 was significantly different from zones 1 and 2, and zones 1 and 2 were not significantly different. White-breasted Nuthatch only had values on zones 1 and 2 and these did not differ significantly.

Table 3.6 Breeding birds, species abundance, total bird abundance, and species richness along gradsects characterized by three different elevational and habitat zones only on the Alum Cave Trail gradsect on Mount LeConte, GSMNP, 1999-2000[a].

								Test Statistic[b]			
	<DCE Zone		DCE Zone		>DCE Zone			Zonal		Overal	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Effect	F	P	F	
Acadian Flycatcher *(Empidonax virescens)*	2.29	0.61	1.50	0.00	1.00	0.22	N	2.25	0.119	2.25	0.119
American Crow *(Corvus brachyrynchos)*	1.37	1.50	2.50	0.28	1.00	0.00	N	1.64	0.247	1.08	0.422
Black-capped Chickadee *(Poecile atricopillus)*	1.49	0.19	1.45	0.12	1.45	0.12	N	0.70	0.413	0.70	0.413
Blue-headed Vireo *(Vireo solitarius)*	1.68	0.17	**1.71**	0.10	1.10	0.05	(TXZ)Y	16.58	<.0001	6.03	<.0001
Blue Jay *(Cyanocitta cristata)*	1.33	0.33	1.20	0.12	1.00	1.00	N	0.60	0.495	0.60	0.495
Brown Creeper *(Certhia americana)*	1.02	0.10	1.07	0.08	1.34	0.12	N	0.65	0.529	1.51	0.197
Black-throated Blue Warbler *(Dendroica caerulescens)*	1.26	0.23	**1.65**	0.09	1.26	0.09	T	5.34	0.008*[1]	5.34	0.008
Black-throated Green Warbler *(Dendroica virens)*	1.89	0.22	1.89	0.14	1.51	0.20	N	0.13	0.725	0.13	0.725
Carolina Wren *(Thryothorus ludovicianus)*	1.00	0.00	1.30	0.21	1.05	0.05	N	0.49	0.628	0.33	0.927
Canada Warbler *(Wilsonia canadensis)*	1.16	0.41	1.76	0.07	1.29	0.12	N	1.34	0.267	1.31	0.260
Chestnut-sided Warbler *(Dendroica pensylvanica)*	1.30	0.52	1.87	0.20	1.88	0.16	N	1.67	0.201	1.21	0.323
Dark-eyed Junco *(Junco hyemalis)*	2.25	0.25	2.46	0.13	**2.76**	0.20	T	8.66	0.005*[4]	8.66	0.005
Eastern Towhee *(Pipilo erythrophthalmus)*	1.19	0.10	1.29	0.09	**1.65**	0.14	N	1.79	0.196	1.79	0.196
Golden-crowned Kinglet *(Regulus satrapa)*	1.38	0.22	1.88	0.12	1.68	0.07	T	5.16	0.100	5.16	0.010
Hairy Woodpecker *(Picoides villosus)*	1.07	0.07	1.36	0.11	1.17	0.13	N	1.90	0.166	0.59	0.779
Hermit Thrush *(Catharus guttatus)*	1.15	0.34	1.29	0.33	1.33	0.08	N	7.70	0.041	7.52	0.018
Hooded Warbler *(Wilsonia citrina)*	1.02	0.35	2.10	0.02	1.08	0.08	N	2.90	0.074	4.35	0.008
Indigo Bunting *(Passerina amoena)*	**1.53**	0.18	1.00	0.00	1.00	0.00	N	2.01	0.166	2.28	0.106
Northern Parula *(Parula americana)*	1.43	0.30	**1.50**	0.00	1.00	0.50	T	12.03	<.0001***[1]	7.33	<.0001
Ovenbird *(Seiurus aurocapillus)*	**3.76**	0.25	1.63	0.38	2.23	0.29	N	7.28	0.010*	3.36	0.018
Pileated Woodpecker *(Dryocopus pileatus)*	1.00	0.00	1.96	0.10	1.00	0.00	N	0.08	0.926	0.09	0.985
Red-breasted Nuthatch *(Sitta canadensis)*	1.16	0.15	1.29	0.08	**1.40**	0.09	T	6.28	0.017*[3]	6.28	0.017
Red-eyed Vireo *(Vireo olivaceus)*	**2.68**	0.27	1.86	0.22	1.22	0.26	N	6.93	0.003**	3.09	0.022
Scarlet Tanager *(Piranga olivacea)*	1.20	0.14	1.22	0.11	1.13	0.17	N	1.07	0.358	1.70	0.131
Veery *(Catharus fuscescens)*	1.55	0.27	2.10	0.07	**2.25**	0.11	(Z)Y	12.21	<0.0001***	4.48	<0.0001
White-breasted Nuthatch *(Sitta carolinensis)*	1.14	0.14	1.13	0.13			N	0.00	1.000	1.10	0.390
Winter Wren *(Troglodytes troglodytes)*	1.42	0.30	**2.06**	0.07	**2.19**	0.11	Z	2.83	0.068	2.83	0.068
Wood Thrush *(Hylocichia mustelina)*	**1.86**	0.18	1.14	0.00	1.00	0.14		2.32	0.120	2.80	0.033

[a] Data represent either species in order of abundance with ≥20 total individual bird detections in 1999 and 2000 combined or community measures for all species with ≥1 detection; all detections ≤50 m from sample points along transects. Significant abundances in zones are bolded. [b] Completely randomized 3 way (factor) ANOVA in time (3 zones X 4 tradsects X 2 yr; n = 24 with transects as the error term to test zonal effect and residual as the error term to test year and zone X transect X year interaction effects).* [c]T = transect effect; Z = zone effect, Y = year effect, N = no effect; T X Z = transect X zone interaction. [d] = no birds observed.

Species richness and total abundance in the zones clearly separated the ecotone community from the other two community types. For ACT-only, there were nearly one-third more species, by 4-7 species, in the DCE than above the DCE (Table 3.7, Fig. 3.11b). However, for BHT, RFT, and TGT combined, species richness and total abundance were higher, by 3-4 species, above the DCE than in the DCE (Table 3.7, Fig. 3.11a). The three coniferous communities (SNH, SF, and F), with 23, 22, and 19 species, had approximately ten more species than the deciduous forests below the DCE (Table 3.7, Fig. 3.6).

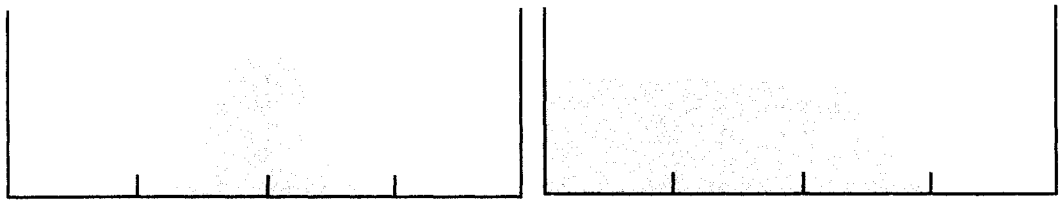
Responses of Species across Deciduous-Coniferous Edges

Of the 55 bird species recorded in the study, 29 were present in sufficient numbers to be categorized into one of the models of ecotone response (Fig. 3.12). Five species [American Crow (*Corvus brachyrynchos*), Blue-headed Vireo, Blue Jay, Black-throated Green Warbler, and Pileated Woodpecker (*Dryocopus pileatus*)] were considered to be habitat-generalists. Twelve of the 29 species were categorized as ecotone-neutral, but showed a marked change in abundance across the DCE edges. Of these, seven species were below-DCE specialists/ecotone-neutral and four were above-DCE specialists/ecotone-neutral. Only the White-breasted Nuthatch was exclusively a below-DCE specialist.

Seventeen species (Tables 3.5, 3.6, Fig. 3.12) were categorized as ecotone-conspicuous and were therefore potentially ecotonal species. However, 16 of these speices were also found in zones below and above the DCE; hence, one was entirely ecotonal. One species, the Gray Catbird (*Dumetella carolinensus*), was significantly ecotone-conspicuous, whereas two were ecotone-shy. No species was categorized as

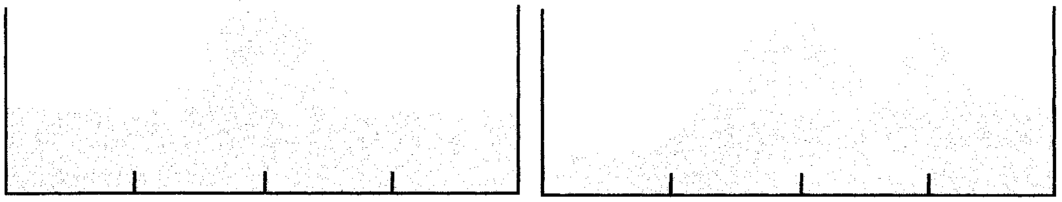
Table 3.7 Comparison of species richness and total abundance in three zones on Mount LeConte GSMNP. ACT = Alum Cave Trail, BHT = Bull Head Trail, RFT = Rainbow Falls Trail, TGT = Trillium Gap Trail.

	Below DCE		DCE		Above DCE				
	Zone 1		Zone 2		Zone 3		Test Statistic		
Measure of Diversity	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	df	P
Species Richness									
BHT, RFT, TGT	6.63	0.20	7.73	0.2	9.24	0.2	22.3604	2	<0.0001
ACT	4.33	0.3	12.35	0.3	8.41	0.3	76.6367	2	<0.0001
Total Abundance									
BHT, RFT, TGT	10.85	0.5	11.30	0.3	14.88	0.3	20.9972	2	<0.0001
ACT	7.53	0.7	16.27	0.7	13.09	0.5	67.9939	2	<0.0001



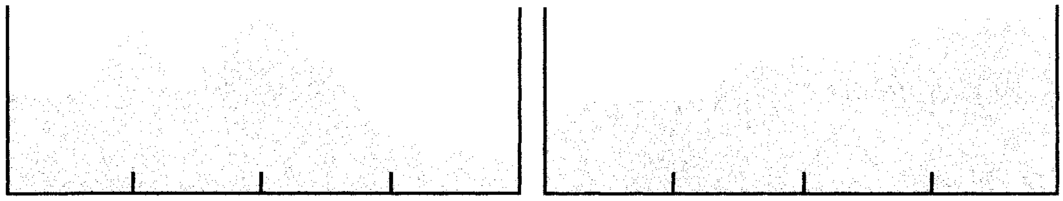
Ecotone conspicuous:
GRCA

Below DCE specialist-above DCE shy-ecotone neutral:
WBNU



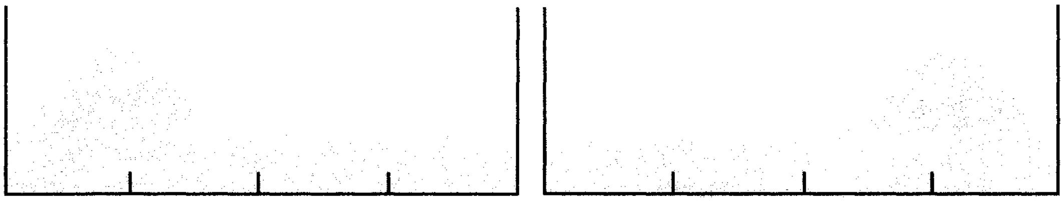
Habitat generalist-ecotone conspicuous
AMCR, BHVI, BLJA, BTBW, (CARW), PIWO

Above DCE specialist-ecotone conspicuous:
CARW, CAWA, DEJU, GCKI, HAWO, RBNU,VEER, WIWR



Below DCE specialist-ecotone conspicuous:
BTNW, HOWA

Above DCE specialist-ecotone neutral:
CSWA, EATO, HETH, VEER



Below DCE specialist-ecotone neutral:
ACFL, INBU, NOPA, OVEN, REVI, SCTA, WOTH

Above DCE specialist-ecotone shy:
BCCH, BRCR

Fig. 3.12 Models of response for birds across ecotone edges and between two forest types, adapted from Sisk and Margules (1993), and examples applying the models to species using frequency of detections (Table 3.8). Definitions of bird abbreviations are given in Table 2.1. DCE = Deciduous Coniferous Ecotone.

DCE specialist ecotone-conspicuous, or entirely ecotonal.

The Canada Warbler was detected at all sites in the three zones, with 65% of the records at the ecotone, 10% below, and 25% above the DCE (Fig. 3.12). This density pattern is not consistent with an entirely ecotonal species. Although the decision rules categorized it as an ecotone-conspicuous species, the ANOVAs did not show a significant effect of distance. At each location, the Canada Warbler and Hermit Thrush (*Catharus guttatus*) were detected in zones below, above, and in the ecotone, although, among locations, there was variation in abundance on either side of the edge and the ANOVAs showed a significant zonal effect ($F_{2,30} = 5.45\text{-}6.39$, $P<0.001$). These species had histograms most like the ecotonal species model, although neither showed a significant effect of distance in the ANOVAs ($P>0.1$) below or above the ecotone and the results were variable among those sites.

Discussion

Spatial Distribution of Birds and Forest Types

Odum (1958) suggested that, in terrestrial communities, the concept of the edge effect was especially applicable to bird communities. However, in the present study, evidence for the traditionally held concept of increased abundance and species richness at the edge was limited to results on ACT, i.e. no appreciable edge effect was detected in the other three gradsects. Multivariate analysis of the bird communities across the DCE edge indicated that, in general, bird community composition at the ecotone was intermediate between the communities above and below the ecotone, not unique from them.

When the ecotone was analyzed at a 200-m wide distance interval spanning both sides of the DCE edge, there was no evidence for greater bird abundance or species richness at the ecotone. Rather, the ecotone edge and the edge on the coniferous side of the ecotone (above the DCE) were similar in most cases, and had twice the bird density and richness as the deciduous side (below the DCE). This result highlights the importance of comparing the ecotone community, and its width, with the communities in both adjacent ecosystems. Had I compared only the bird community below the DCE to that at the deciduous-coniferous edge, I may have falsely concluded that there was a strong edge effect.

When the ecotone was analyzed using 400-m wide zones, one on either side of the edge, there was some evidence for an edge effect. Using the census sites spanning the edge, there was an underlying pattern, namely that relative abundance and species richness were greatest at the coniferous side of the edge, whereas abundance and richness were lower below the DCE. This pattern was statistically significant on all four gradsects; bird abundance on the coniferous side of the ecotone was greater than in the 400 m below the DCE, and the trend was consistent across four gradsects. This was the strongest evidence for the traditional view of an edge effect. However, this pattern is largely explained by the relative abundance patterns of only eight species: Chestnut-sided Warbler, Dark-eyed Junco, Red-breasted Nuthatch, Veery, Winter Wren, Eastern Towhee, Hairy Woodpecker, and Ovenbird (Fig.s 3.5, 3.6). The first five were found at higher elevations.

Ecologically this edge effect may indicate that the coniferous side of the ecotone is a particularly important habitat because it accommodates an increased abundance of some species of birds. However, an insight counters this explanation, namely, that at the edge there is greater visibility than in the adjacent woods and the birds may be both easier to detect and more readily observable. Hence, some of the apparent higher density may be an artifact of censusing.

Three other studies of natural edges, each from a different continent, also reported no support for increased diversity at the ecotone. Laudenslayer and Balda (1976) concluded that bird diversity in the ecotone between pinyon pine/juniper woodland and ponderosa pine forest in Arizona was no greater than that in either adjacent habitat, Terborgh et al. (1990) found no evidence for increased species richness at ecotones in forests in Peru, and Luck et al. (1999) concluded that the bird diversity at the ecotone between mallee and shrubland in south-central Australia was not generally greater than in the mallee. Comparisons with studies involving anthropogenic forest edges provide little additional support for the concept of edge effect. For example, in a regrowth forest in Uganda, Dale et al. (2000) found no change in the abundance of understory birds moving from the edge of a 15-ha clearing to 500 m into the forest. However, they did find a significant increase in species richness, with fewer more-common species near the edge and more less-common species in the forest interior.

In my study, models of avian response to ecotones were useful for describing the community abundance patterns of 29 bird species, although the statistical evidence for associating species with particular models was definitive only for the Blue-headed Vireo, Black-throated Blue Warbler, Carolina Wren (on the ACT gradsect), and Golden-crowned Kinglet (on ACT); all were DCE specialists or more ecotone-conspicuous species. For the generalist-specialist dichotomy, 68% of the species were community specialists of either deciduous or coniferous communities. At the ecotone, the abundance of 25% of species was reduced. Of the habitat generalists but slight ecotone-conspicuous species, all five of the coniferous specialists and two of the seven habitat generalists showed relatively high abundances only on the coniferous side of the ecotone and might be better described as conspicuous at the coniferous side of the ecotone, as exemplified by the Dark-eyed Junco, Eastern Towhee, and Red-breasted Nuthatch (Table 3.4, Fig. 3.12). Only three birds were observed in significant numbers among the species categorized as ecotone-conspicuous and either deciduous specialists (Hooded Warbler) or habitat generalists (Black-throated Blue Warbler, Blue-headed Vireo). Six deciduous specialists (Acadian Flycatcher, Indigo Bunting, Ovenbird, Red-eyed Vireo, White-breasted Nuthatch, and Wood Thrush) were mostly detected in deciduous sites (Table 3.4, Fig. 3.12). Hence, the deciduous specialists contributed little to bird species richness at the ecotone. However, the intermediate or transitional nature of the ecotonal bird community and higher species abundances above DCE revealed by the multivariate analysis, were almost entirely due to the habitat generalists and coniferous specialist species.

Results from my study were comparable to those of Sisk and Margules (1993), who could definitively assign few species to their models on the basis of unambiguously different mean bird densities across an edge. Nevertheless, both studies identified several species that were neutral or conspicuous at the ecotone, fewer species that were ecotone-shy, and some species that were omitted from the categorization (Table 3.8). In particular, I found 35% of species to be ecotone-conspicuous, whereas Sisk and Margules (1993) categorized ~50% of species as ecotone exploiters. Both my results and those of Sisk and Margules (1993) are comparable to Odum's (1958) estimate that 40% of the regionally common birds in Georgia were ecotonal. However, all three studies (including mine) measured the pattern of bird density rather than the functional use of ecotones by birds. Hence, all three studies have detected about the same percentage of ecotone-conspicuous bird species, but none has measured how these species might be exploiting the ecotone.

None of the seven ecotone-conspicuous species (Acadian Flycatcher, American Crow, Blue-headed Vireo, Blue Jay, Black-throated Blue Warbler, Carolina Wren, and Pileated Woodpecker) investigated on the four gradsects showed strong evidence of being entirely ecotonal. The Black-throated Blue Warbler, Carolina Wren, Golden-crowned Kinglet, and Hermit Thrush were community generalists, with twice as many records in the approximately 2-km wide DCE as in the adjacent communities. In a similar study, Bramwell et al. (1992) made 52% of 132 detections in a 40-m wide ecotone, with the remaining 48% of detections in the adjacent woodland and heathland.

I found no entirely ecotonal species. There are several possible explanations for this including the degree of vegetation connectivity or contiguity, soft vegetation boundaries, and little overlap in zones. Other studies have similarly failed to find strictly ecotonal species. McFarland (1988) reported no species (of 54) restricted to the ecotone between wet and dry heathland in southeastern Queensland, Australia. Chapman and Harrington (1997) reported no species (of 16) restricted to the west sclerophyll-rainforest ecotone in northeastern Queensland, Australia. For 88 bird species at montane rain forest and cloud forest ecotones in the Andes, Terborgh (1985) found that ecotones limited the distribution of some bird species but reported no evidence of any purely or strictly ecotonal species. In the northeastern United States, Able and Noon (1976) found that of

Table 3.8 Summary of results compared to Sisk and Margules (1993) and Baker et al. (2002) showing the percentage of bird species in each of three categories of response to the ecotone.

Study and Response	No. Species Studied	No. Species Categorized	Percentage of Species
Present study	55	29	
Ecotone-neutral			40
Ecotone-conspicuous			55
Ecotone-shy			5
Baket et al. (2002)			
Ecotone-neutral	86	31	55
Ecotone-conspicuous			35
Ecotone-shy			10
Sisk and Margules (1993)			
Hard edge	38	26	
No response			35
Edge exploiter			54
Edge avoider			12
Soft edge	36	24	
No response			33
Edge exploiter			46
Edge avoider			21

40 bird species, half had their altitudinal limits coinciding with three ecotones, but they noted no ecotonal species. Sisk and Margules (1993) reported no species (of ≥ 38) restricted to the oak woodland ecotones in central-coastal California. And finally, Laudenslayer and Balda (1976), who tested specifically for ecotonal species in the southwestern United States, found none.

Multivariate Analysis of the Bird Communities

The two-dimensional ordination for censuses confirmed that bird community composition at the ecotone was intermediate between that of the deciduous and coniferous zones (Fig. 3.3a). The ordination for censuses showed that community composition at the deciduous side of the DCE was intermediate between that of the deciduous community and the spruce-fir community that merged with the coniferous side of the DCE edge (Fig. 3.3b). Both ordinations had low stress values (0.17 and 0.16, respectively), which give good two-dimensional representations of the spread of objects. The ordinations also demonstrate that these patterns were consistent among censuses. Similarity indices for censuses were high (47-65%) within all three zones and between the above-DCE (spruce-fir) and the ecotone (50-75%) zones and the ecotone and below-DCE (deciduous or hemlock) zones, and low (25-50%) between deciduous and spruce-fir zones (Fig. 3.5).

Contributions of Neotropical Migrants and Resident Species to Zonal Patterns

With respect to Neotropical birds, the bird community in the ecotonal habitat (DCE) was more homogeneous than the community in the deciduous forest (below DCE) but less homogeneous than the coniferous forest bird community (above DCE). One could see this by either looking at the similarity values in Table 3.3 or the spread of the points in Fig. 3.3. There was a gradation of "homogeneity" from below the DCE to the DCE to above the DCE. This meant that the bird communities were becoming more similar with higher elevation. However, the ACT gradsect had fewer bird species at higher elevations.

Resident species had less of an impact than Neotropical species in determining the spatial pattern of bird distributions. Resident bird species showed no differences in composition among zones, whereas the Neotropical species had a pattern of distribution that was similar to that shown by all bird species (Fig. 3.5). This suggests that differences in bird composition were largely caused by changes in Neotropical migrants rather than resident birds.

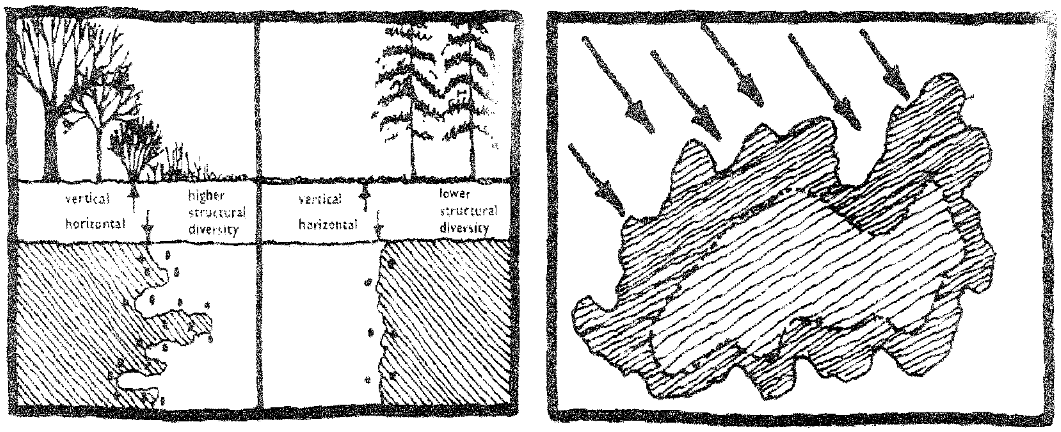
Neotropical birds were more widely distributed among the zones and forest communities (types) than resident bird species. But, within the zones of forest communities, they formed a more homogeneous unit and distribution. Neotropical birds were more homogeneous from site to site within any zone, but were more distinct from one zone to the next than resident species (Tables 3.3, 3.4, Fig.s 3.3, 3.4).

Responses of Birds to DCE Edges and Gradients

The spatial distributions of bird species exhibited complex patterns. At one extreme, the boundary between two types of vegetation, such as hemlock and spruce, was relatively abrupt. In this example, the ecotone was narrow and composed mainly of a mixture of species from both sides. However, sometimes ecotones can be wide and composed of a mosaic of patches of each vegetation type (Rapoport 1982). In my study, this was exemplified by forests such as xeric oak, cove hardwood, hemlock/hardwood, spruce fir and fir. A sharp contrast in plant community composition was observed between deciduous and spruce-fir communities, in which ecotonal forest contained much higher densities of hemlock subcanopy and canopy trees and shrubs and somewhat lower densities of deciduous trees. The higher elevational edge between forest types was not as abrupt as between lower elevational edge, but typically the overlap extended only 200-400 meters.

An "ecotone" traditionally refers to the overlap or transition zone between two plant or animal communities. Often contrasted with a gradient, the ecotone concept emphasizes a sharp change in distributions of species, or a congruity in the distributional limits of species. Species present in the DCE were shown to be intermixed subsets from the adjacent communities (Tables 3.2, 3.3, Fig.s 3.2, 3.10).

Boundaries of ecotones are sometimes differentiated as being hard or soft. A straight border with high contrast, such as that between deciduous (MO, XO) and coniferous (SF, F) communities, best illustrated the hard boundary (Table 3.2). The soft boundary had varying degrees of softness, from single and double-sided patchiness to curvaceous, as between cove and hemlock hardwood (CH, H). Few studies have directly compared the ecological roles of hard and soft boundaries. To evaluate the relative penetration of species between deciduous-coniferous communities in GSMNP, I compared hard boundaries with soft boundaries. The latter are perhaps best described as single-sided mosaics (Fig. 3.13). Bird species crossed the soft and convoluted boundaries of forest types in greater numbers than the abrupt or hard boundaries (Tables 3.2, 3.3). With soft boundaries, the species also penetrated farther into the ecotone. Observations in other landscapes suggest similar results (Harris and McElveen 1981; Stamps et al. 1987; Wunderle et al. 1987; Naiman et al. 1988; Forman and Moore 1992).

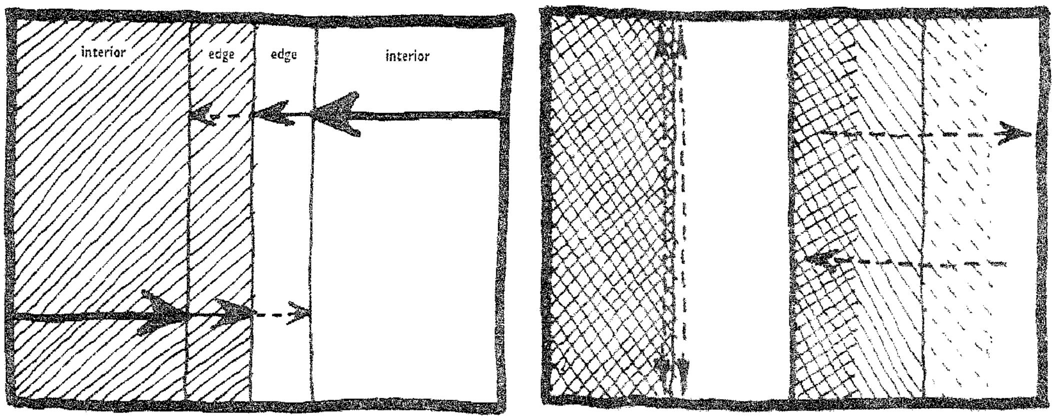


a) Edge structural diversity

b) Edge width

Vegetative edges with a high structural diversity, vertically or horizontally, are richer in animal species.

Edge width differs around a patch, with wider edges on sides facing the predominant wind direction and solar exposure.



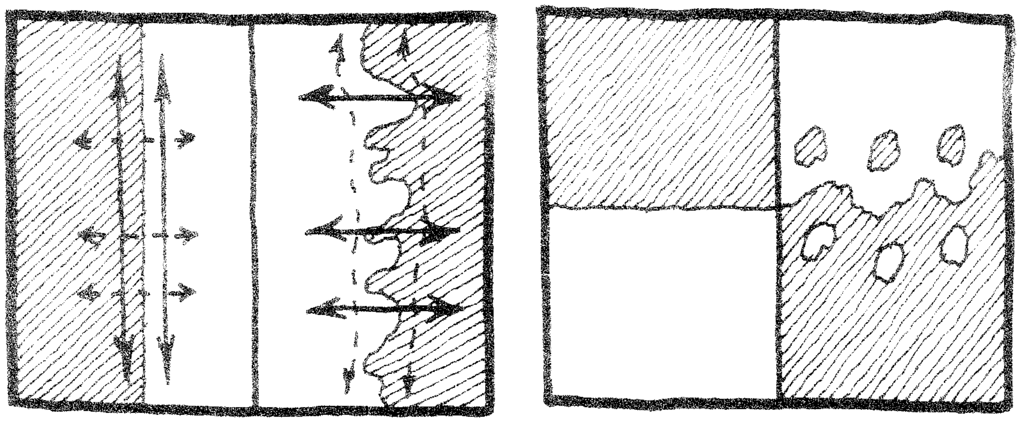
c) Edge as filter

d) Edge abruptness

Patch edges normally function as filters, which dampen influences of the surroundings on the patch interior.

Increased edge abruptness (left panel) tends to increase movement along an edge, whereas less edge abruptness (right panel) favors movement across an edge.

Fig. 3.13 **Landscape ecology principals functioning or operating on Mount LeConte forest communities. (Adapted from Dramstad et al. 1996 with permission)**

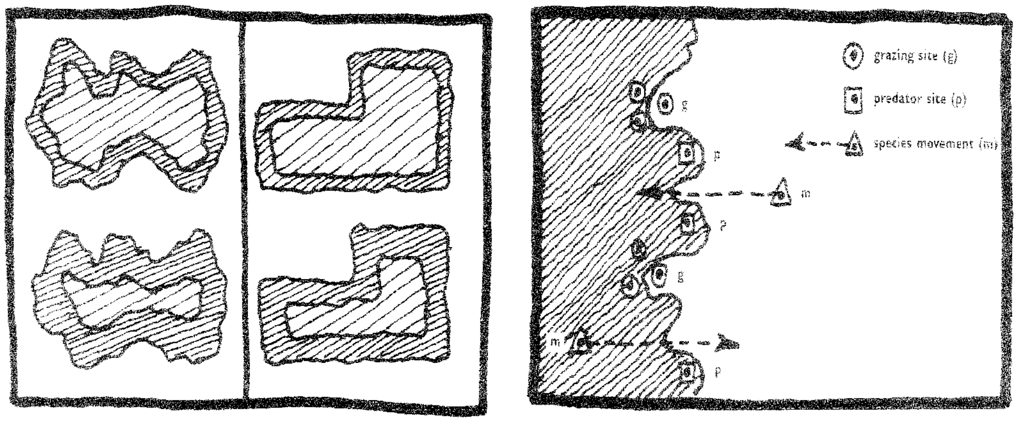


e) Straight and curvilinear boundaries

A straight boundary tends to have more species movement along it (left panel), whereas a convoluted boundary is more likely to have movement across it (right panel).

f) Hard and soft boundaries

A "tiny-patch" boundary may provide a number of ecological benefits, including less soil erosion and greater wildlife usage.



g) Edge curvilinearity and width

Curvilinearity and width of an edge combine to determine the total amount of edge habitat within a landscape.

h) Coves and lobes

The presence of coves and lobes along an edge provides greater habitat diversity than along a straight edge, therby encouraging higher species diversity.

Fig. 3.13 (Continued).

Compared with a gradient between ecosystems, an abrupt edge was shown to have a greater density of edge species present. Hard edges have more of such species than soft edges (Fig. 3.13d, Thomas 1979; Harris 1988). Edge species were observed by the author to penetrate adjacent ecosystems, or affect the movement of other species between forest communities. Three dimensions of an ecotonal edge, as well as a boundary, were important for understanding both its anatomy and functioning in GSMNP vegetation transitions. Edge dimensions were "width" between the border and ecotone interior (Fig. 3.13b), "vertical" foliage height and stratification, and "length" along the ecotone boundary (Table 3.2, white lines in Fig. 3.1). Length included the overall curvilinearity (Fig. 3.13g) as well as the arrangement of forest lobes, coves (CH), and other boundary surfaces along the border (Table 3.2, Fig. 3.13h).

This study focused on two of the three edge dimensions, namely width and curvilinearity or "interdigitation of habitats" (T. Allen, personal communication). Edge width was analyzed from the perspective of what determines it. The curvilinearity was examined primarily to see how boundaries affected bird movements. Different species of birds responded differently to edge width. I determined the width based on physical, structural, and compositional vegetative parameter(s), and on some functional use of the edge by birds. I also took measurements of the spatial distribution of coniferous vs. deciduous trees at the ecotone and, after censusing the birds and estimating the extent of their territories, I determined that the edge was X meters wide.

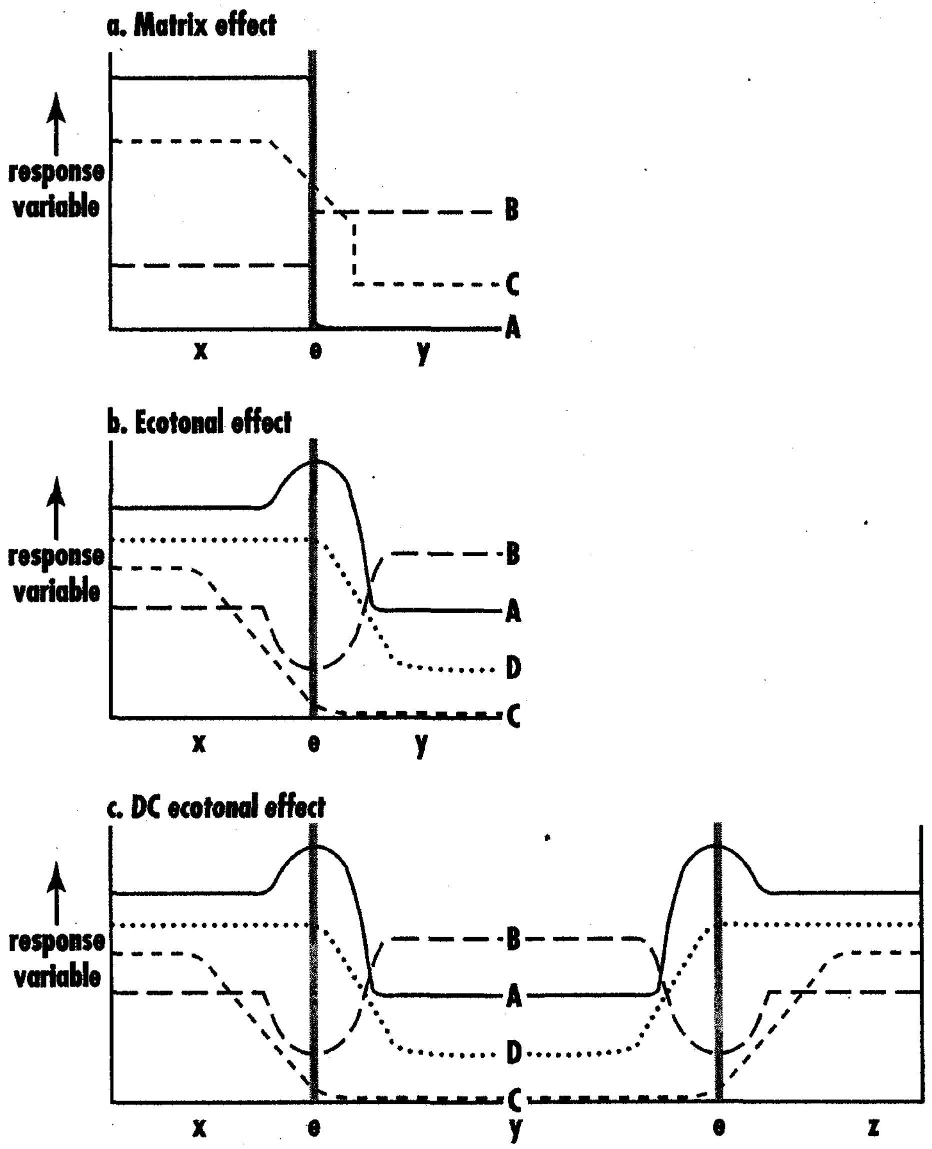
Formally, habitat edges are discontinuities in habitat features as perceived by a focal individual or species, and that in turn affects the performance of a species in some way. This view of habitat edges generates several important corollaries (Lidicker 1999).

(1) Habitat edges separate two or more different habitat types. (2) Habitat edges will be species-specific, and possibly sex- and age-specific as well. (3) Human observers may not be able to recognize a habitat edge without careful study. (4) In fact, it will likewise be difficult to measure the length of a habitat edge.

A fundamental property of habitat edges is whether they generate emergent response properties in birds, i.e. properties occurring as a consequence or result of the edge. Such a criterion, related directly to the performance of birds relative to edges, would, in turn, lead to a mechanistic understanding of edge-related behaviors. A two-part classification based on this idea is illustrated in Lidicker and Peterson (1999) and modified here (Fig. 3.14a,b). Lidicker and Peterson (1999) measured performance in behavioral, physiological, or demographic terms; perhaps some useful refinements in this classification could be based on these different criteria. In this study, a three-parted ecotonal classification was detected on Mount LeConte (Fig. 3.14c).

One class of edge was characterized by the absence of emergent properties with respect to target species. The response of organisms at an edge was explained strictly by the response pattern of the organism to two adjacent habitat types (Fig. 3.14a). This type of edge effect is called a “matrix effect” (Lidicker and Peterson 1999). It is characterized by an abrupt change in some response variable as the edge is crossed (“A” and “B” in Fig. 3.14a). If the edge was not sharp, because of a blending of the two habitat types, the edge response by birds was not abrupt (Tables 3.2, 3.3, 3.4, Fig. 3.11), but reflected the mixing of the two habitat types on the border (“C” in Fig. 3.14a). The diagnostic criterion is that the response pattern corresponds to the degree of habitat mixing.

The second type of edge effect was characterized by the presence of emergent



a. Matrix effect

b. Ecotonal effect

c. DC ecotonal effect

Fig. 3.14 Idealized representations of three fundamental kinds of edge effects: a.) Matrix effect, i.e. without emergent properties, b.) Ecotonal effect, and c.) montane or DC (deciduous-coniferous) ecotonal effect, i.e. with the presence of emergent properties. X, y, and z are three juxtaposed habitat-types, e is the edge between them, and A-D are response variables. Modified from Fig. 1 in Lidicker and Peterson, 1999.

properties, that is, organisms' responses werere not explained by their behavior in the two habitat types. Moreover, it was not possible to predict the nature of these new properties simply by observing the performance of organisms in a single habitat type. This category of edge influence has been termed an "ecotonal effect" (Fig. 3.14b, Lidicker and Peterson 1999). Emergent properties produced an enhancement of function on or near the edge (Tables 3.3, 3.4, Fig.s 3.5b, 3.6, 3.12a,b), a diminution of the response variable (Fig. 3.14b), or an asymmetrical response not directly attributable to the mixing of habitat types ("C" and "D" in Fig. 3.14b).

Distinguishing these two categories of edge effects was often difficult. For example, there were instances in which response patterns, such as "C" in Fig. 3.14a and 3.12b,c,d looked similar. Operationally the matrix effect was the null hypothesis because it was possible to make a clear prediction of the edge response based on the values of variables in each habitat type separately and the degree of blending on the edge. Any significant deviation from this prediction of a matrix effect represented ecotonal effects. For example, a brood parasite may invade a habitat patch from an adjacent patch for some distance beyond the actual edge. Or, an interior species might use the border of an adjacent patch even though it would not be able to live solely in that habitat. In such instances, ecotone edges could be sources of invasive species and the adjacent habitat could be the sink into which these species move.

As patches of deciduous or coniferous communities increased in size, so did the number of edge species (Tables 3.2, 3.4, Fig. 3.12). Several categories of edge species, independent of taxonomic group, were recognized. In addition to residents, edge often contained multihabitat species, i.e. those requiring or frequently using two or more habitat types. These species capitalize on the complementarity of resources provided by the boundary between two plant communities.

Edge species were differentiated from patch and ecotone-interior species (Fig. 3.11a,b). Because a species often behaves differently throughout the year and in different parts of its geographic range, edge and interior species are best categorized locally. Thus, edge species were those found primarily, or only, near the border of a zone, and interior species were primarily, or only, observed distant from a border (Table 3.5, 3.6, Fig. 3.12). Determining which Neotropical migrants are edge species was confounded by the fact that different species responded to edges in different ways (e.g., Canada Warbler, Chestnut-sided Warbler, Grey Catbird, and Indigo Bunting). Some migrants were purely edge species, occurring only where two forest types came together. The analysis of abundance patterns (Tables 3.5, 3.6, Fig. 3.12) showed that Neotropical migratory species responded in a variety of ways to forest edge. Some species were more abundant near edges (e.g., Black-throated Blue Warbler, Black-throated Green Warbler, Blue-headed Vireo, Northern Parula, and Scarlet Tanager), some were less abundant (e.g., Red-eyed Vireo, Hooded Warbler, Acadian Flycatcher, Wood Thrush), and others were unaffected (e.g., Ovenbird).

In summary, the edge effect reflected the *habitat* function of a boundary. The primary significance of shape in determining the nature of patches of communities in the landscape appeared to be related to the edge effect. Wider edges were expected where the patch and matrix differed more in vertical structure. To a lesser extent, this was the case for differences in species composition. Within the Mount LeConte landscape, edge species were those only, or primarily, near the margins of forest types or the DCE, and interior species were those located only, or primarily, away from the periphery.

In reference to the *filter* function (Fig. 3.13a,c), this study found no evidence for absolute barriers or boundaries, only filters (Tables 3.5, 3.6, Fig.s 3.5, 3.10). A major recent development in studying landscape boundaries is understanding their filter function, i.e. how boundaries affect the rates of movement and flow between communities or ecosystems. This effect on rate of exchange is a key role of boundaries. In this study, some boundaries had differential permeability with species passing readily among the forest types, but others scarcely moving at all. Basic floristic and physiognomic characteristics of the forest communities largely determined the filter function. The key function revealed among the forest communities and zones was a differentially permeable filter, i.e. one permitting certain birds through but not others. Different birds crossed at different communities and elevations; single birds (warblers) crossed in passive diffusion, and flocks of birds (Red Crossbills) crossed in "bulk transfers".

Conclusions

Habitat edges (ecotones) have been a part of mainstream ecology for almost a century, although animal ecologists seem to have been slower than their plant-oriented colleagues to incorporate, at least explicitly, edge phenomena into their thinking. In wildlife management, edges are seen as management tools for enhancing populations of game species (Leopold 1933). The recent surge of interest in landscape ecology has heightened the critical examination of ecotones, returning them to the arena of active research. Furthermore, they are a central tenet of modern conservation biology.

The discontinuities and vegetation transitions in habitat features were revealed for breeding birds on Mount LeConte. I determined whether, as predicted, species expanded or contracted their distributions in localities where the homogenous ecotone was displaced upward or downward in elevation relative to its location on Mount LeConte. Where the ecotone was displaced away from centers of species distributions [e.g., downward for species whose lower limits coincided with the ecotone on the Alum Cave Trail gradsect (Fig. 3.3)], 34% of species expanded their distributions. This result supports the view of the ecotone as a distributional barrier to these species in forest communities.

Combining the results reported here with those presented in previous publications, I conclude that direct and diffuse competitive exclusion account for about two-thirds of the distributional limits of Mount LeConte birds, and ecotones for about one-fifth. Terborgh (1985) reported similar results, with ecotones accounting for less than 20% of the distributional limits, competitive exclusion for about one-third, and gradually changing conditions along the gradient for about one-half of the limits.

Generally, distributional changes or limits were determined by habitat discontinuities (ecotones), and the ecological amplitudes of species inhabiting the gradients were expressed in terms of some convenient unit, e.g., bird abundance per length of gradient or meters of elevation of spatial distribution (density) of coniferous vs. deciduous trees at the ecotone. When distributions of all the species in a group were known, their ecological amplitudes were plotted as frequencies or histograms. The extent to which any species became specialized or generalized with respect to any one gradient, however, was dependent on the vegetational and topographic variables. Specialization that led to a low(er) amplitude would expose the extreme specialist to the risk of facing endangerment or extinction. The extreme generalist, for example, American Crow, Blue-headed Vireo, Blue Jay, Black-throated Blue Warbler, Carolina Wren, and Pleated Woodpecker were found at the opposite end of the adaptational spectrum, provided that successful existence at different points on the vegetational and elevational gradients required some degree of divergent adaptation.

Along gradsects, ecotones between community types were perceived by many bird species as significant discontinuities. In fact, they were not. Indeed, habitat types corresponded more frequently to forest types or communities. Thus, in my study, spatial fluctuations in counts of individual bird species were, in general, related to zonal transitions in plant communities. Breeding bird diversity was correlated with the abundance and connectivity of suitable habitat in Southern Appalachian landscapes (Fig. 3.6). The spatial patterning of individual species and species assemblages along forest edges resulted from the configuration of patch types within the landscape. The avian communities across deciduous-coniferous transitions and edges on Mount LeConte provided little support for Odum's (1958) views of distinct edge effects and of ecotonal species. Other bird studies that I reviewed also failed to give strong support to these theories.

The strongest pattern of the communities I studied was that bird abundance and species richness in the coniferous community were generally greater than those of the deciduous community, except on ACT, where ecotonal communities were displaced and abundance and richness were greater in the DCE, a predominantly spruce-fir community. Communities above the DCE, on gradsects BHT, RFT, TGT, and in the DCE, on ACT, had more horizontal vegetation coverage and foliage height diversity and a correspondingly more diverse bird community than the community below the DCE. This finding supports MacArthur and MacArthur's (1961) habitat complexity theory.

Birdwatchers find that many species are more conspicuous at edges (Griggs 1997). However, being conspicuous at an edge does not make a species ecotonal or an ecotone-exploiter. These terms imply some habitat function, beyond simple observation of their presence, as evidence of a pattern of occurrence. The distinction is important for two reasons: it clarifies the difference between pattern and ecological process and it cautions against describing or managing birds as ecotonal species in landscapes that are becoming increasingly fragmented and often, increasingly ecotonal.

CHAPTER IV

ECOLOGICAL APPLICATION OF LANDSAT TASSELED CAP INDICES TO THE ANALYSIS OF BIRD HABITATS IN SPRUCE-FIR FORESTS

Introduction

The growing need to develop quantitative methods to assess wildlife habitat was specifically mandated by the Resources Planning Act (Mead et al. 1981). Remote sensing, an important tool for holistic landscape evaluation (Naveh and Lieberman 1984), has provided the means for mapping land-cover/vegetation over large areas for use in wildlife habitat management (Pengelly 1978). However, the maps themselves supply only part of the inventory data needed by wildlife biologists. The analysis and interpretation of characteristics of the landscape and their associated wildlife can provide many insights for sound management decisions. This paper presents a method to analyze and interpret land-cover maps that produces spatially defined data for managing wildlife habitat. Remote sensing also has potential for ecotone detection and has been used to track the location of the ecotone between desert and arable land in the Sahara (Tucker et al. 1985) and the southwestern United States (Mohler et al. 1986). However, remotely sensed images provide information about the entire landscape, not just ecotones, thus, GIS techniques are needed to extract information about ecotones from the entire image.

GIS, Satellite Imagery, and Spatial Analysis of the Landscape

The most important limitation of a habitat evaluation model based on Landsat imagery is that it can only include variables that can be directly detected and measured on the imagery or easily included as digital ancillary data. The imagery is, however, particularly suited for modeling using spatial components of the habitat and closely correlated variables. Forest edges are a good example. They can be accurately mapped and are closely associated with a denser understory. Forest edges are, therefore, an important element in this habitat study.

Mapping and evaluation of habitat using Landsat Thematic Mapper (TM) satellite imagery and spatial modeling were used by Palmeirim (1985) to determine the locations of release sites for Ruffed Grouse. The imagery was digitally processed to produce a habitat classification in a study area in northeastern Kansas. In addition, bird counts were subsequently conducted throughout the study area in order to determine the effectiveness of their introduction. The two databases were then combined to obtain habitat suitability estimates and to produce maps of the habitat needs of Ruffed Grouse. This processing considered not only the types of habitat in which grouse were present but also the spatial characteristics of their habitats. Using this approach, it was possible to generate distribution, suitability, and density maps for Ruffed Grouse in Kansas.

Remote sensing is a powerful tool, and when it is combined with extensive ground censusing it can provide estimates of habitat distribution and rates of change that are useful for determining the (conservation) status of certain birds. Remote-sensing technology is a feasible way to examine the abundance of available habitat and the influence of habitat change on migratory bird populations (Green et al. 1987; Sader et al. 1991; Powell et al. 1992). Rappole et al. (1994) used remote sensing to assess the availability of tropical habitats for a Nearctic migrant, the Wood Thrush (*Hylocichia mustelina*). They analyzed vegetation cover information from satellite imagery and then examined the winter habitats the Wood Thrush actually uses. Their objective was to determine if remote-sensing technology could be used to identify thrush habitats. Their study generated a land-cover classification from Landsat TM imagery. The resulting habitat map was input into a geographic information system (GIS) and bird survey data were input in a cartographic format. Landsat TM imagery was used as the only source of information on the available habitat. This information was processed with the GIS to obtain habitat suitability estimates and to generate cartographic features that the Wood Thrush seemingly required. This processing takes into consideration not only the types of habitat present (e.g., forest or rangeland) but also the spatial characteristics of the habitat of the Wood Thrush (e.g., minimal habitat patch size and distance to edge). Based on these analyses, and as verified during field surveys, the TM process is quite accurate in identifying major habitat types used by the Wood Thrush (Rappole et al. 1994).

The ecological interpretation of satellite imagery with special reference to bird habitats was first reported by Griffiths et al. (1993). They contend that there is a requirement to develop methodologies for rapid, cost-effective mapping and monitoring of extensive areas of land to determine their conservation value. The possibility of rapidly classifying extensive areas of land from digital satellite imagery provides, for certain types of landscapes and species, increased opportunities to develop quantitative models for the relationship between land cover and both species diversity and abundance. The large number of samples that can be extracted from satellite imagery provides a rigorous basis for the development and testing of statistical, ecological models. Results of such models can then be applied to broad areas covered by satellite images (e.g., SPOT satellite images with a scene coverage of 60 X 60 km and Landsat images with a scene coverage of 185 X 185 km).

In a study of bird distributions in relation to area and distribution of xeric and mesic forests and farmland, Palmeirim (1988) used classified Landsat TM data to produce probability maps depicting the likelihood of occurrence of select species and incorporated spatial factors into the analysis. For example, it was known that the Red-eyed Vireos (*Vireo olivaceous*) avoid forest edges. The Landsat-derived probability map was reprocessed using GIS software to show a decreased probability of finding this species near the edge of mapped woodland areas. Studies of breeding Red-eyed Vireos indicated that the whole territory must be within a continuous forest canopy, suggesting a reluctance to fly into open spaces. Because the territory of each male is known to be about 1 ha, all woodlots <1 ha could be eliminated from the habitat suitability map. Habitat suitability maps for different species can thus be generated using GIS systems in conjunction with sets of rules about habitat preferences. These maps can depict areas of high abundance and diversity of species and the relative ecological value of habitat patches for a species.

Avery and Haines-Young (1990) used Landsat Multispectral Scanner (MSS) imagery to predict Dunlin (*Calidris alpine*) numbers in the Flow country of northern Scotland. MSS imagery projects soil and vegetation information into a single plane in multispectral data space, a plane in which the major spectral components (axes of maximum variance) of an agricultural scene are displayed in two dimensions. The application of habitat parameters and the rules to derive and present ecological maps have merit, but the digital nature of thematic land cover maps derived from classified satellite imagery is also well suited to the analysis of the spatial pattern and relationships between wildlife and habitat. The techniques for analyzing spatial relationships using raster images are well developed (e.g. Joyce-Loebl 1985) and a number of researchers have applied them to classified image data (e.g. Janssens and Gunlick 1988; Griffiths and Wooding 1989).

GIS for Spatial and Temporal Analyses of the Landscape

Many ecological questions that require the understanding of spatial heterogeneity and methods for spatio-temporal analyses are now becoming increasingly important for ecological studies. For example, Turner (1990) described a grid cell-based spatial analysis program (SPAN) and presented results of landscape pattern analysis using SPAN. Several ecological topics in which GIS can play important roles, such as landscape pattern analysis, neutral models of pattern and process, and extrapolation across special scales, are reviewed by Turner (1990). To study the relationship between observed landscape patterns and ecological processes, he recommends a neutral-model approach in which the expected patterns of the spread of disturbance across a landscape can be generated and then tested using actual landscape data stored in a GIS. Because observed spatial or temporal patterns in ecological data are influenced by scale, the creation of a spatial database frequently requires integrating data at different scales. Spatial scale influences pattern analysis, but extrapolation of data across spatial scales may be possible if the grain and extent of the data are specified. The expected patterns of a variety of ecological phenomena (e.g., spatial distribution of species) can also be studied using a neutral model approach. Thus, the suitability of a landscape for a particular species (see Palmeirim 1988) can be predicted.

Pulliam et al. (1992), who studied how animal populations can be modeled in changing landscapes, suggest that the initial landscape can usually be based on a GIS representation of the habitat configuration. Information about the size, shape, condition, and location of each habitat patch is preserved in the simulations. Habitat-specific demographic parameters, such as reproductive success or survival probability, may be functions of management attributes, such as the number of years since a patch was last burned or the basal area of canopy trees remaining after thinning. In brief, information on the degree of interspersion of cover types, relative value of each edge type, and the importance of spatial diversity, relative to each wildlife species or group of species of interest, can be used to compute an index of habitat spatial diversity for each parcel of land (or any desired area). In turn, this information can be used to assess which vegetation and land-cover patterns are important to manage effectively.

Gap Analysis (Scott et al. 1987), an important wildlife technique, seeks to identify vegetation types and species that are not adequately represented in the current network of special management areas. These are the "gaps" in the present-day overall mix of conservation lands and conservation activities. This information is intended to be used by decision makers for proactive land management planning, which will hopefully lead to fewer species becoming endangered, and thus reduce the number of future conflicts regarding natural resource issues. Gap Analysis is intended to complement, not replace, the species-by-species approach to preserving biodiversity that is so critical to the survival of species facing endangerment. The main goal of Gap Analysis is to prevent additional species from being listed as threatened or endangered.

The intent of the Gap Analysis Program (GAP) is to provide focus and direction for proactive, rather than reactive, land management at the community and landscape levels. For example, GAP provides an ecological context for a hierarchical approach to land management leading to more detailed and relevant ecological studies in the future. I believe that GAP is one step in comprehensive land management planning.

Scott et al. (1987) contend that Gap Analysis, which uses GIS technology, offers a new opportunity to analyze species richness. GIS systems were developed to assemble and analyze diverse data pertaining to specific geographic areas, with spatial locations of the data serving as the basis for the information system. By having data referenced by spatial or geographic coordinates (Estes 1987) as the primary source of input, GIS can assemble, store, retrieve, and manipulate data on the distributions of species. These data can be used to present information to a resource manager in an easily understood form. The straightforward process of plotting species richness or habitat types with overlays of land ownership and management practices into a GIS can provide a relatively inexpensive but powerful land-use planning tool. Raw data required for a GAP can include range maps for well-documented species, vegetation maps, land ownership maps, and boundaries of existing preserves, among others.

The Tasseled-CAP

Remotely sensed images consist of pixels that contain data in numerous bands on the electromagnetic spectral properties of a ground scene. Image data that evaluate pixels irrespective of their neighbors operate solely in the spectral domain. Spectral domain is the analysis of multispectral images using statistics-based decision rules for determining the identity, with respect to forest stand characteristics of interest, of each pixel in the image (Cohen 1994). Excluding radiometric and geometric preprocessing considerations, the common choice for such analyses is to either use the unprocessed band data or first create one or more vegetation indices (Perry and Lautenschlager 1984; Cohen 1991a).

Although the normalized difference vegetation index (NDVI) is by far the most commonly used, it does not take full advantage of the Landsat Thematic Mapper data (it uses only two spectral bands).

Some indices from the early days of digital image analysis are still used. Perhaps the most important of these are T-CAP *brightness* and *greenness* (Kauth and Thomas 1976). The T-CAP was adapted to TM data by Crist and Cicone (1984a), and an additional index or axis, *wetness*, was defined by Crist et al. (1986).

Brightness is a weighted sum of six reflectance bands of the TM imagery defined by the direction of the principal variation in soil reflectance. *Greenness*, orthogonal to *brightness*, is a contrast between the near-infrared band (TM4) and the three visible bands (TM1, TM2, and TM3) and is strongly related to the amount of green vegetation in the scene. Use of the terms *brightness* and *greenness* is well accepted within the remote-sensing community, and a substantial body of literature suggests that the names of these spectral features of TM data are consistent with the information they represent. *Wetness*, a contrast of the mid-infrared bands (TM5 and TM7) with four other bands, has been shown to correlate with the amount of moisture in a scene (Crist et al. 1986; Musick and Pelletier 1988; Cohen 1991a; Lillesand and Kiefer 1994). Despite its potential usefulness as a measurable environmental variable, *wetness* has received little attention in an image-processing framework (Cohen 1994). At present, there is no way to accurately evaluate the importance of these possibilities.

The original "T-CAP" transformation (Kauth and Tomas 1976) is a linear transformation of Landsat MSS data. Although defined initially for MSS data, subsequent research (Crist and Cicone 1984b) has extended the concept to the six nonthermal bands of the TM. The TM T-CAP indices were designed to take optimal advantage of the original six TM bands, and together the first three axes account for as much as 85% or more of the spectral information of a vegetated TM scene. The transformation consists of linear combinations of the four MSS bands to produce a set of four new variables: TC1, TC2, TC3, and TC4 (Cohen 1994). Although these four new bands do not directly match observable spectral bands, they do carry specific information concerning landscape scenes.

Kauth and Thomas (1976) interpret TC1 as *greenness*, a band that conveys information concerning abundance and vigor of living vegetation. It can be considered analogous to the *soil brightness* (TC2) information, as defined by Richardson and Wiegand (1977). TC3 depicts *yellowness*, a new dimension to the scene not identified by Richardson and Wiegand. The first two bands (TC1 and TC2, *greenness* and *soil brightness*) convey almost all the information in an agricultural scene, often 95% or more. Kauth and Thomas (1976) developed the T-CAP as a fertile source of ideas for processing techniques. Examples include a linear preprocessing transformation that isolates green development, yellow development, and *soil brightness*. The transformed components of the Kauth-Thomas T-CAP Model are important vegetation indices (Zhao 1998).

The TM T-CAP transformation provides a convenient method for reorienting TM data such that vegetation and soil information can be more easily extracted, displayed, and understood (Crist and Cicone 1984b). The transformation applied to many temperate climate scenes will produce invariant features that can be directly compared (e.g., between scenes or sensors), thereby simplifying the development of automatic signalprocessing algorithms and minimizing the need for recalibration of either algorithms or expectations (e.g., of human interpreters).

In a study of bird populations of the Highlands Plateau, North Carolina, in relation to plant succession and bird invasion, study plots using percentage differences showed that moisture may separate species (Odum 1950). According to Beals (1969), moisture is probably the overriding factor influencing altitudinal zonation. So much emphasis has been placed on temperature as a factor controlling distribution and abundance of birds, that the importance of water has often been overlooked. Since the Highlands Plateau is near the center of an area with the highest annual rainfall in the eastern United States (80 in.), moisture is an especially important ecological factor. The high water content of the forests of the hemlock sere could conceivably result in increased bird populations both directly, by providing more available water and moderating temperature changes, and indirectly, by producing a more luxuriant vegetation with a consequently greater variety of niches and perhaps greater amounts of food.

TM T-CAP principals implicitly addressed in landscape-level investigations focus on (1) responses of vegetation indices to changes in three measures of canopy leaf water stress (Cohen 1991b) and (2) responses of spectral indices to variations in vegetation cover and soil background (Campbell 1996; Todd and Hoffer 1998). The only published use of T-CAP indices (*brightness, greenness,* and *wetness*) in Great Smoky Mountain National Park (GSMNP) focused on (1) applying spherical statistics to study change vector analysis (CVA) of Landsat data in southern Appalachian spruce-fir forests (Allen and Kupfer 2001) and (2) spectral response and spatial pattern of Fraser fir mortality and regeneration (Allen and Kupfer 2001). To test their hypotheses, Allen and Kupfer analyzed spectral reflectance from Landsat TM images. They first related T-CAP measures of reflectance (*brightness, greenness, wetness*) from 192 forest plots to vegetation associations of two TNC community types, levels of canopy closure and understory composition. Once they established that T-CAP values could be tied to differences in overstory and understory condition, they tested for statistical relationships between T-CAP indices and species diversity in an effort to better understand their prediction or inferential powers. As part of the analysis, they applied this technique to test the magnitude of change in, and utility of, tasseled indices as a "pattern recognition tool" based on prior fieldwork.

No empirical evidence exists with which to assess the application of T-CAP vegetation indices to the analysis of changes or disturbances in bird habitats on a landscape level. Paradoxically, ecologists have virtually ignored the implication of these T-CAP indices for assessing habitats, components of spatial diversity, and relationships between bird species diversity and T-CAP indices in spruce-fir forests. One objective of my study was to develop such a pattern recognition tool for measuring the spatial and species diversity components of bird habitat from vegetation maps.

Disturbances in the Spruce-Fir Zone

High elevation coniferous forests in the Southern Appalachians are one of the rarest and most endangered forest types in the eastern United States, encompassing only ca. 100 km^2, of which 75% is contained within the GSMNP (Saunders 1979; White et al. 1993). These ecosystems, which are dominated by red spruce and Fraser fir, have been adversely affected by a number of human actions in recent decades, the most serious of which has been the introduction of an insect, the balsam woolly adelgid (*Adelges piceae*), in the 1950s. Widespread death of Fraser fir and increased windthrow of red spruce created obvious changes in the vegetation by 1986 (Rabenold et al. 1998). Near the summit of Mount LeConte, GSMNP, permanent plots were first established in 1979 to assess changes in spruce-fir stands resulting from overstory mortality caused by balsam woolly adelgid. The severity and extent of mortality caused by the adelgid have greatly altered composition and structure, and even after 22 years, the stand is still in a state of structural and compositional reorganization [Jenkins 2003; refer to differences on ACT in Chapter II, and its description in Wise and Peterson (1998)]. Adelgid-caused mortality of mature Fraser firs has surpassed 90% on some mountains (e.g., Mount Mitchell and Mount Collins; Eagar 1984; Busing et al. 1988; Smith and Nicholas 1999), and the wave of tree deaths has in turn affected bird communities (e.g., Alsop and Laughlin 1991; Rabenold et al. 1998).

Researchers (e.g., Sharp and Keddy 1986) have recently suggested use of vegetational changes as indicators of change in environmental conditions. Indeed, given the availability of aerial photographs and remotely sensed images of vegetation types, more researchers would like to use automated techniques to detect ecotones and their movement. Wiens et al. (1985) studied factors that influence the location of vegetation boundaries and concluded that edaphic factors are the most important. However, as Johnston and Naiman (1987) showed, changes in edaphic variables are not always reflected by changes in the vegetation composition or abundance. Hence, it is not always true that vegetation patterns respond to environmental change. Therefore, depending on the purpose of the study, it would be necessary to analyze more than just the canopy structure (Turner 1990).

Neotropical landbird populations form a significant component of the wildlife resources of many protected areas in the Southeast United States, including GSMNP, where the need for baseline inventories and population monitoring has been identified as a high priority in the Park's resource management plan. Among the most immediate threats the Park faces are the effects of air pollution, the introduction of exotic insect species, and habitat fragmentation on the periphery. The severity of future changes in the high-elevation avifauna will depend on the ability of both Fraser fir and red spruce to regenerate and upon the degree to which dispersal of birds from other forest types can repopulate the spruce-fir zone. The effects of introduced pathogens, pollutants, and disturbances by exotic insects will hamper this process in those forests. This has led to development of a strategy to monitor biodiversity at hierarchical scales, namely species, community, ecosystem, and landscape. My study seeks to determine if the sensitivity of individual species and the stability of the community can point to, or be detected by, general principals of bird responses to vegetation transitions and habitat disturbance.

Landscape determinants and ecological relationships of bird diversity indices in ecotones have been little studied. Bird species and their habitats have one common characteristic: They are distributed over some part of the landscape (Udvardy 1969) and remote sensing offers methods to assess wildlife habitat at large spatial scales. The linkage of remote sensing, GIS, and bird distributions is both important and necessary to this study. Landscape-scale monitoring will be accomplished primarily by remote sensing to analyze data that I will use to predict the consequences of current trends in habitat disturbances (Green et al. 1987; Sader et al. 1991; Powell et al. 1992).

Landscape Change and Disturbance Influences on Species Diversity

There is a growing literature on the role of ecotones in influencing ecological flow processes (e.g., energy, resources, information and biodiversity, and changes in the global environment; Hansen et al. 1988). Questions have been posed with respect to current interest in the suitability of ecotones as detectors of climate change (cf. Kupfer and Cairns 1996). Geographers, ecologists and other scientists have been interested in ecotones for longer periods and for more reasons (e.g., papers in Holland et al. 1991 and Hansen and di Castri 1992). Ecotones, defined as transition zones or tension zones between two or more distinct communities, can be sensitive indicators of change and of interactions of climate, topography, and biota. The structural features of fine-scale ecotones (sometimes extending hundreds of meters) are likely determined by site-specific characteristics such as fine-scale vegetation, soil discontinuities, edge, and even fire. At one extreme, the boundary between two types of vegetation, such as field and forest, may be relatively abrupt. In this case, the ecotone is narrow and composed mainly of a mixture of species from both sides. Sometimes the overlap zone is wide, with a mosaic of patches of vegetation (Rapoport 1982).

Ecotones have provided excellent opportunities to test hypotheses concerning interactions and distributions of species. They are important agents for controlling fluxes of matter, energy, and species because of their position at the intersection of two dissimilar habitats or between two different ecosystems. Yet, with only a few exceptions (e.g. forest-river ecotones: Peterjohn and Correl 1984; Kupfer and Malanson 1993; forest-field ecotones: Ranney 1977; Kupfer 1996; plus numerous other papers for each), knowledge of ecotone processes is lacking. I believe that a study that can couple the strengths of remote-sensing techniques with field studies and the use of holistic models has potential to reveal dominant processes shaping the deciduous-coniferous ecotone (DCE) and provide a view of how the ecotone's, and its associated species', response to disturbances or changes are realized or revealed.

The ecotone located between high-elevation hardwood and coniferous ecosystems has been studied throughout the Appalachian Mountains, including the southern Appalachians (Schofield 1960; Busing et al. 1993). The ecotone transition has been described as narrow (spanning 100 to 300 m), although species follow the continuum model of distribution (White et al. 1993). In the southern Appalachians, northern hardwoods are dominant up to approximately 1500 m. High-altitude hardwood communities generally include a large number of species, including sugar maple, American beech, yellow birch, yellow buckeye and oak species (Cain 1935; Brown 1941; Whittaker 1956; Busing et al. 1993; White et al. 1993). Composition of both overstory and understory in the deciduous hardwood forest zone shows a great deal of variability due to topographic and edaphic factors (e.g. cove forest, beech gaps), aspect (e.g. north vs. south-facing sites), and disturbance (e.g. logging; Whittaker 1956; Golden 1981; Busing et al. 1993). Stands from 1500-1800 m are dominated by red spruce (relative basal area 30-90%, relative density 10-50%) and Fraser fir (relative basal area 10-70%, relative density 20-90%), with yellow birch (*Betula lutea*) as a minor canopy tree (Busing et al. 1988). Above 1800 m, red spruce diminishes, and forests are composed almost entirely of Fraser fir (White et al. 1993).

Most of the vegetative pattern of the Great Smoky Mountains is one of continuous gradation; but certain relative discontinuities in the pattern can also be recognized

(Whittaker 1956). As observed by Schofield (1960), from a distance the transition between the subalpine conifer forest and the deciduous forest appears to be unusually abrupt. This impression is exaggerated, in part, by the difference in physiognomy of the dominants. Although the DCE itself has been described as a relatively smooth transition from dominance over the face of a mountain (Allen and Kupfer 2001), at finer scales, it exhibits patchiness in response to variations in environmental conditions (e.g., topography, soil textures, aspect, slope). Empirical studies quantifying ecotones using GIS (Johnston and Bonde 1989) and digital image analysis for gradient-oriented transect data (Ludwig and Cornelius 1987; Wierenga et al. 1987; Johnston and Bonde 1989) are well documented. GIS also has been used to assess potential impacts of disturbances (Turner et al. 1989; Barrett and Nodvim 1993) and to characterize the form of the DCE (Malanson 1997b; Allen and Kupfer 2000, 2001). An analysis of the patchiness of the DCE would thus be of interest because the coupling between pattern and process is especially tight at ecotones (Allen and Kupfer 2001). At this time, I am unaware of any study that directly examines questions concerning DCE form, structure, and function as evidence of environmental changes and consequently indicators of changes in bird communities.

Therefore, my third and final task was to test whether T-CAP indices can be used as a "pattern recognition tool" for predicting vegetation diversity, bird species richness, and abundance of breeding birds. Specifically, I identified T-CAP indices, *brightness*, *greenness*, and *wetness*, which represent (reflect) habitat or community types and hence represent species richness and relative abundance of bird species. I then related these indices to particular species and their responses to changes in landscape structure and function due to the destructive disturbances by wooly adelgid in spruce-fir forests. Based on statistical analysis and pattern recognition, I developed three quantitative models to study these relationships:

(1) Forest types are a function of the T-CAP indices *brightness*, *greenness*, and *wetness*.

(2) Species richness and abundance of breeding birds are functions of patterns of T-CAP indices.

(3) Species richness of breeding birds is a function of spatial changes in T-CAP indices.

Methods

The form of the decidous-coniferous ecotone (DCE) was not well documented, so my first objective was to provide a thorough investigation of ecotone patterns. Methods used in this project included (1) image classification, (2) polygon creation, (3) accuracy assessment of habitat characteristics, (4) censuses and distributions of birds, and (5) mapping male bird territories by habitat (Udvardy 1981).

Study Components: Digital Data, Remote Sensing, and Field Work

I examined patterns of the DCE using remotely sensed data (Landsat TM, color infrared photography), and a GIS. The Landsat TM data were preprocessed and classified, and their accuracy assessed using two scenes (18 August 1988 and 15 September 1998). The majority of the area of GSMNP (90%) falls within one Landsat-5 TM scene: All of the Park is in one scene; some is within the second scene to the east (Fig. 4.1). Landsat TM-based coverage of vegetation types in the study area was obtained from the Tennessee Valley Authority (TVA). This coverage was produced

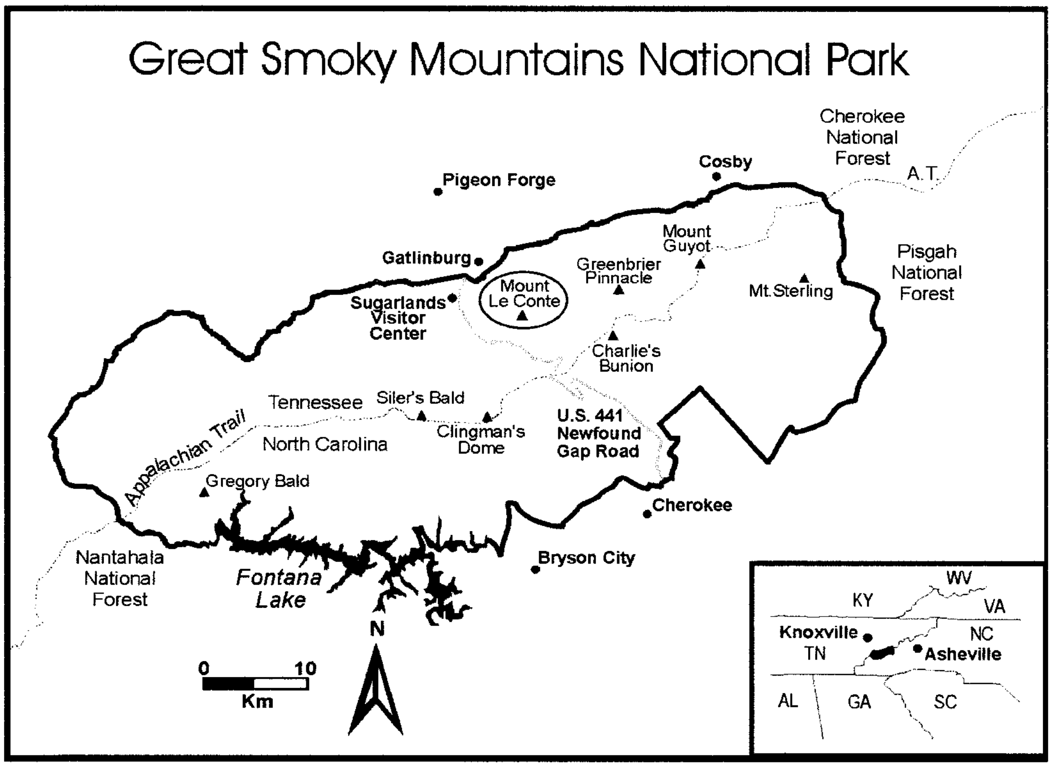


Fig. 4.1 Map of Great Smoky Mountains National Park, Tennessee, showing the location of the study area, including the focal point of the study, Mount LeConte, in the north-central region.

using TM data from 1989-1992. Earth Resources Data Analysis System Production Services performed the land-cover classification for the TVA using both spectral (combining supervised and unsupervised classification methods) and manual interpretation methods.

Landsat TM data were preprocessed and classified, and their accuracy assessed with new, cloud-free 1998 imagery used for land-cover mapping in association with the vegetation map of MacKenzie and White (1998) and the National Park Service vegetation survey and map. The anniversary dates and temporal separation are important to consider for replication of illumination conditions and sufficient time of forest change. Imagery acquired after the onset of foliage change would threaten the accuracy of change detection. Thus, summer was selected as the optimal season for data acquisition owing to the least amount of seasonal precipitation and possible cloud cover and optimum time for vegetation sampling and bird censusing. The high-elevation area and temperate rainforest conditions of the Smoky Mountains seriously restrict the availability of cloud-free imagery. Late summer (mid-August to mid-September) was the most opportune time for image acquisition with the additional benefit that understory vegetation, ground cover, and subcanopy foliage may have less spectral influence than in fall or winter (Ekstrand 1989). Digital orthophotographs in 1-m pixels dated March 1994 were also used.

GIS coverages and Geospatial data in GIS format were obtained from the Inventory and Mapping Program of the GSMNP Twin Creeks Natural Resource Center. These coverages included fire and logging history, geology, and topography. A color plot/map of USGS/NPS Vegetation was provided by Aerial Information Systems (2000).

These data included maps of vegetation type classified from 1988/89 Landsat TM data, Digital Elevation Models (DEMs) and disturbance history (after Pyle 1985).

DEMs consist of a regular array of elevations referenced horizontally in the UTM (Universal Transverse Mercator) coordinate system. The 7.5' 1:24,000 DEMs for GSMNP were obtained from the National Park Service (Great Smoky Mountains National Park, 1991). These models provide elevations at a 30-m pixel size and height (m) corresponding to the 200-foot contour interval of each quadrangle.

Field Work: Bird Communities

Bird audio-visual censuses were performed using a form of the variable circular plot method (Reynolds et al. 1980; Ralph et al. 1993). Along four trails (Fig. 4.2), Alum Cave Trail (ACT), Bull Head (BHT), Rainbow Falls (RFT), and Trillium Gap (TGT), called “gradsects” (gradient-oriented transects), 212 bird census points and vegetation sampling plots were established in three zones: (1) the deciduous zone downslope of the deciduous-coniferous ecotone (DCE), (2) the DCE itself, and (3) the spruce-fir zone above the DCE. Because of forest declines due to the balsam wooly adelgid (Busing et al. 1988), some of the points/plots in the spruce-fir zone were taken from adelgid-impacted areas to provide reflectance values for these areas. Locations were registered by GIS, and their slope angles and aspects were derived using Arc View Spatial Analyst. Once registered, the locations were downloaded to a GIS and overlaid with the Landsat coverage to verify points/plots with respect to the imagery. The reciprocal of Simpson’s Index ($1/\Sigma pi^2$, where pi = the proportion of the total sample in the *ith* group) was used to express niche breadth (i.e., the generality of resource use) across resource categories (Whittaker and Levin 1975:169; Best et al. 1979). Index values were calculated

Fig. 4.2 GIS image of the deciduous-coniferous ecotone and forest communities on Mount LeConte, GSMNP. Numbers represent census points on gradsects. Geo-referenced points identified with The Nature Conservancy (1999) community codes were used to delineate the ecotonal boundaries. Numbers represent census points on gradsects. White lines partition three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above DCE.

for habitat selection of 29 species based on their frequencies of observation in the 10 forest types. Species with broader niches (higher index values) were assumed more tolerant of habitats that are more diverse. Herein the index is referred to as the tolerance index.

Field Work: Plant Communities

I sampled vegetation during June and July so that cover estimates corresponded to those features present during the breeding season of birds. Vegetation was sampled using each census point as the center of an 11.3-m radius plot delimited with a laser rangefinder. Estimates of vegetation composition and structure were obtained using the 0.04 ha (100 m^2 or 5.64 m radius) method (Lindsay et al. 1958; James and Shugart 1970; James 1978). At each census point the following data were collected: (1) diameter at breast height (dbh) of trees >10 cm; (2) forest cover class and tree height range of five vegetation layers, canopy, subcanopy, tall shrub/sapling, low shrub/seedling, and herbaceous categories; (3) species composition of canopy, subcanopy, tall shrub/sapling layers, and low shrub/seedling layers; and (4) percent cover by species for tree canopy, subcanopy, saplings, seedlings, tall/low shrubs, and herbaceous layers.

GPS locations for each site were recorded using a Leica GS50 GPS/GIS receiver and later differentially corrected. The 212 census points were determined from differentially corrected GPS positions using maps, image, and shape-file coordinations. GPS rover positions were taken using the Leica hand-held receiver. I determined elevation, slope, and aspect from the 212 geo-referenced points and added the data into the GIS environment. Once registered, the locations were input to the GIS and overlaid with Landsat coverage to verify their positions. All dated information from sources in this project was stored in ESRI (1997) Arc View and GIS operated on a PC workstation in the Laboratory for Remote Sensing and Environmental Analysis at Old Dominion University. The georeferenced point/plot locations were overlaid with GSMNP-TNC vegetation coverage associations to accurately compare vegetation associations and classifications. I developed a usable geographic database by recording geographic features using (UTM) real-world coordinates and storing related coverages in one common coordinate system. For each coverage, I spatially referenced its features against those of associated coverages to make certain that new coverages were concordant.

Community Classifications and Vegetational Characteristics

I determined and assigned coverage and percentages of composition of 21 communities for the area centered on Mount LeConte into Ecotonal Community Classifications (ECC) and Ecotonal Landscape Classifications (ELC) using Arc View 3.2 (Appendix A).

I mapped the study area in GIS according to The Nature Conservancy (TNC) forest type by Aerial Information Services on behalf of TNC and National Park Service (Fig. 4.2). The basic unit of the mapping system was the forest association and area of forest that is represented by a roughly homogeneous composition of tree species, forest age, and canopy closure. For our study area, each census point was given a TNC code describing its type, age, and crown closure (Table 4.1).

The 36-level TNC classification system provided more forest associations or types than I could sample effectively. Therefore, I simplified that system and created a habitat superclass system or community classification composed of 10 community types (Appendix A, C). This system contained four deciduous, four coniferous, and two

Table 4.1 Comparisons of habitat structure and composition (mean/0.04 ha ± SE) among three zones on Mount LeConte, GSMNP. N=657. Abbreviations are defined as follows: Dbh = diameter at breast height; LOW_CL = cover of low shrubs/seedlings of tree species, class; TALL_CL = cover of tall shrubs/ saplings of tree species, class; SUB_CLS = cover of subcanopy tree species, class; CAN_CLS = cover of canopy tree species, class; GCC = canopy cover of ground vegetation; LSCC = canopy cover of low shrub/seedling trees; TSCC = canopy cover of tall shrub/sapling trees; SCCC = canopy cover of subcanopy trees; TSCC = canopy cover of canopy trees; GHR = height range of ground vegetation; LSHR = height range of low shrubs/seedling trees; TSHR = height range of tall shrubs/sapling trees; SCHR = height range of subcanopy trees; TCHR = height range of canopy trees.

Variable	Below DCE Elevation Zone 1		DCE Elevation Zone		Above DCE Elevation Zone 3		Test Statistic	P
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	
Features of Forest Structure								
Dbh 0-10								
Canopy	5.3	0.7	3.8	0.3	11.5	1.4	47.23	<0.0001
Subcanopy	2.0	0.3	2.1	0.3	3.4	0.7	5.33	0.068
Dbh 11-25								
Canopy	2.8	0.4	1.5	0.2	12.9	2.4	88.22	<0.0001
Subcanopy	2.2	0.2	1.5	0.2	3.3	0.5	12.18	0.0023
Dbh 26-50								
Canopy	1.8	0.2	1.7	0.1	2.1	0.2	2.56	<0.0001
Subcanopy	0.6	0.1	0.6	0.1	1.4	0.4	2.32	0.313
Dbh 51-75								
Canopy	1.3	0.2	0.7	0.1	0.4	0.1	16.54	0.0003
Subcanopy	0.1	0.0	0.1	0.0	0.2	0.1	6.62	0.047
Dbh 76-100								
Canopy	0.3	0.1	0.4	0.0	0.0	0.0	43.26	<0.0001
Subcanopy	0.0	0.0	0.0	0.0	0.1	0.0	15.37	0.0005
Dbh >100								
Canopy	0.0	0.0	0.0	0.0	0.0	0.0	–	–
Subcanopy	0.0	0.0	0.0	0.0	0.0	0.0	–	–
Features of Canopy Coverage of Tree Species								
LOW_CLS								
Canopy	0	0	3.46	0.312	3.38	0.22	0.0069	0.9337
Subcanopy	0.2	0.1	0.2	0.0	0.1	0.0	4.5	0.03
TALL_CLS								
Canopy	4.15	0.174	4.3	0.126	5.6	0.15	55.45	<0.0001
Subcanopy	3.3	0.146	4.127	0.238	4.285	0.32	10.61	0.005
SUB_CLS								
Canopy	4.85	0.24	5.21	0.15	5.5	0.369	2.77	0.25
Subcanopy	3.78	0.15	4.66	0.28	4.74	0.23	9.6	0.0082
CAN_CLS								
Canopy	7.07	0.2	7.27	0.125	6.83	0.138	5.26	0.0719
Subcanopy	5.5	0.866	6.4	0.6	7	0.1	7.94	0.0189

Table 4.1 Continued

	Below DCE Elevation Zone 1		DCE Elevation Zone		Above DCE Elevation Zone 3		Test Statistic	
Variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	χ^2	P
Features of the Forest Type								
TCCC								
Canopy	7.49	0.1	7.56	0.09	6.87	0.11	25.49	<0.0001
Subcanopy	7.39	0.1	6.97	0.19	6.96	0.21	1.61	0.4453
GHR								
Canopy	0.374	0.05	0.458	0.025	0.233	0.005	40.65	<0.0001
Subcanopy	0.389	0.038	0.381	0.014	0.254	0.007	22.7	<0.0001
LSHR								
Canopy	1.18	0.048	1.647	0.065	1.57	0.03	81.83	<0.0001
Subcanopy	1.15	0.029	1.622	0.03	1.568	0.26	171.89	<0.0001
TSHR								
Canopy	4.58	0.04	4.997	4.997	4.74	0.12	0.5512	0.7591
Subcanopy	4.52	0.029	4.997	4.997	4.778	0.09	3.45	0.1778
SCHR								
Canopy	16.062	0.388	16.4	0.24	12.79	0.379	56.55	<0.0001
Subcanopy	15.7	0.23	15.47	0.23	13.22	0.279	55.25	<0.0001
TCHR								
Canopy	20.757	0.398	22.95	0.267	17.272	0.378	113.52	<0.0001
Subcanopy	20.8	0.244	21.11	0.28	17.668	0.281	113.76	<0.0001
Composition % Conifer								
ACT	0.0	0.0	14.5	0.74	19.97	1.37	80.84	<0.0001
BHT	0.0	0.0	7.43	1.16	15.17	1.17	84.52	<0.0001
BMT	0.89	0.36	1.56	0.56	–	–	1.43	0.2316
BVT	–	–	68.33	4.87	67	0.0	1.20	0.2729
RFT	0.0	0.0	2.85	0.5	15.61	1.23	92.5	<0.0001
TGT	0.0	0.0	4.56	0.51	18.8	1.08	174.79	<0.0001
ALL	5.89	0.53	11.39	0.62	15.76	0.65	142.38	<0.0001
% Deciduous								
ACT	91.97	1.23	85.5	0.74	80.03	1.37	31.23	<0.0001
BHT	83.77	1.27	85.8	1.37	92.73	0.9	7.87	0.0195
BMT	94.25	0.88	89.06	1.41	–	–	10.21	0.0014
BVT	–	–	23.13	4.35	33	–	3.11	0.0776
RFT	95.94	0.56	91.45	0.79	84.39	1.23	16.53	0.0003
TGT	95.13	0.47	86.84	0.8	81.2	1.08	55.57	<0.0001
ALL							60.01	<0.0001
% Hemlock								
ACT	8.03	1.23	0.0	0.0	0.0	0.0	210.19	<0.0001
BHT	1.06	0.27	6.78	0.47	7.27	0.9	97.94	<0.0001
BMT	4.86	0.68	9.38	1.2	–	–	12.61	0.0004
BVT	–	–	8.54	3.1	0.0	0.0	0.276	0.5995
RFT	4.06	0.56	5.7	0.52	0.0	0.0	107.93	<0.0001
TGT	4.87	0.47	8.6	0.42	0.0	0.0	234.44	<0.0001
ALL	3.72	0.26	5.47	0.28	1.02	0.15	198.65	<0.0001

hemlock forest types. Each census point was redefined as belonging to one of 10 forest types. Vegetation types were classified into 10 groups [pine, xeric oak, tulip poplar (mixed mesic hardwood), mesic oak, hemlock hardwood, cove hardwood, northern hardwood, spruce northern hardwood, spruce fir, and fir] based on MacKenzie (1993) and the dominant canopy species (yellow birch, yellow buckeye, Fraser fir, eastern hemlock, northern red oak, chestnut oak, white oak, Carolina silver bell, red spruce, table mountain pine, Virginia pine, and yellow tulip poplar; Appendix A). These community vegetation types, used on the vegetation data sheet (Appendix C) to describe each census point, were also grouped into, or assigned, broader habitat superclasses or forest community classes.

For the preliminary analyses, I defined ecotonal transitions as zones or treatments on each gradsect using the forest community classifications ECCs (Appendix A). The forest types on the ACT gradsect were defined or delineated into zones separately because of the differential distribution in pattern of their ECCs. (Refer to Chapter II for why ACT deserves to be analyzed separately from the other gradsects and Wise and Peterson 1998).

From the vegetation images in Biological Resources Discipline (BRD)-NPS vegetation mapping program (The Nature Conservancy 1999), the communities at the 212 census points, representing a variety of deciduous and coniferous canopy conditions, were analyzed (Fig. 4.2). Those points corresponding to the ground locations of each site were extracted from the images. Field data collected from these sites (Table 4.2) were used to calculate a number of attribute values each census point regarding mean tree size (dbh), tree density, and five newly developed categories of canopy and subcanopy

Table 4.2 Habitat measures and environmental parameters used as independent variables in statistical analyses on Mount LeConte, GSMNP 2000.[1]

Mnemonic	Variable/Parameter	Description/Explanation
x̄DBH	Average or Mean Diameter at Breast Height	Mean diameter at breast height (cm) for each tree. I took the midpoint for each category (i.e., if the category is 0-10, then I used 5) and I multiplied that by the number in that category for that species and that point. I then added all those numbers together for all those categories for a particular species point. That gave me a total dbh for that species at that point. The "average" is because I then averaged it over the species and trailpoint, in case there was more than one visit. If there was only one visit, then the average is a misnomer and it is actually the total dbh. So, for example, for yellow birch at ACT 10, if there were 6 counts in dbh 0-10 and 4 counts in dbh 26-50, then the total dbh would be 6 * 5 + 4 * 37.5 = 180. I could then take the 180 and divide it by the counts to get an average dbh for yellow birch for ACT 10 of 18.
TTLDBH	Total Diameter Breast Height	Mean total diameter at breast height (cm) all diameters of trees within a 0.04 ha plot were summed. This is an estimate of quantity of wood and therefore clutter at the site.
DBH_CAN	Diameter at Breast Height of canopy trees	Mean diameter breast height for canopy trees (cm).
DBH_SUB	Diameter at Breast Height of subcanopy trees	Mean diameter breast height for subcanopy trees (cm).
x̄SPDENS	Mean Species Density	TTL species density (N/0.04 ha) by adding up all the tree counts (stems) in the 6 dbh categories by each species and trailpoint. The average species density is just the average of the species density – total number of trees within each plot.
DEN_CAN	Density of canopy trees	Density (N/0.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species.
DEN_SUB	Density of subcanopy trees	Density (N/0.04 ha) of tree stems. Estimate from 3 11.4-m radius plots – average density of that particular species
CANCLS	CANOPY CLASS	Mean canopy cover of canopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .

Table 4.2 Continued.

Mnemonic	Variable/Parameter	Description/Explanation
SUBCLS	SUBCLASS	Mean canopy cover of subcanopy trees by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .7
TALLCLS	TALL CLASS	Mean canopy cover of tall shrubs and saplings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
LOWCLS	LOW CLASS	Mean canopy cover of low shrubs and seedlings by species (%). Subtract the lower value from the upper value and then divide by 2. I will then take the value and add it to the lower value to get the average. If the class value is: the numeric value will be: 1 : 0.1; 2 : 0.5; 3 : 1.5; 4 : 2.5; 5 : 7.5; 6 : 17.5; 7 : 37.5; 8 : 62.5; 9 : 85; 10 : 97.5 .
CANCC	Tree Canopy Cover Class at each site	Mean cover (%) of tree (tall) canopy trees measured at 4 cardinal directions with convex densiometer at each site.[2]
SUBCC	Subcanopy Cover Class	Subcanopy trees
TSHBCC	Tall Shrub Cover Class	Tall shrubs, saplings
LSHBCC	Low Shrub Cover Class	Low shrubs, seedlings
GRNDCC	Ground Cover Class	Ground vegetation
TCANHR	Tree Canopy Foliage Height Range	Mean height (m) of tree canopy trees. Estimate from 4 samples measured with clinometer at each site.
SUBCHR	Subcanopy Foliage Height Range	Mean height (m) of subcanopy trees. Estimate from 4 samples measured with clinometer at each site.
TSHBHR	Tall Shrub Foliage Height Range	Mean height (m) of tall shrubs, saplings. Estimate from 4 samples measured with clinometer at each site.
LSHBHR	Low Shrub Foliage Height Range	Mean height (m) of low shrub, seedlings. Estimate from 4 samples measured with clinometer at each site.

Table 4.2 Continued.

Mnemonic	Variable/Parameter	Description/Explanation
GHR	Ground Foliage Height Range	Mean height (m) of ground vegetation. Estimate from 4 samples measured with clinometer at each site.
TCAP_B	Tasseled Cap – Brightness	Positive or negative values.
TCAP_G	Tasseled Cap – Greenness	Positive or negative values.
TCAP_W	Tasseled Cap – Wetness	Positive or negative values.
% C, D, H	Tree composition of canopy	Coniferous, deciduous, hemlock
% C, D, H	Tree composition of subcanopy	Coniferous, deciduous, hemlock
ELEV.	Elevation (m)	m, as determined by Arc View Spatial Analyst
SLOPE	Slope	Degrees, as determined by Arc View Spatial Analyst
ASPECT	Aspect	N, NE, E, SE, as determined by Arc View Spatial Analyst S, SW, W, NW
DIST.	Disturbance	Defined by trees felled by windthrow or man
FO	Forest opening	Presence or absence of a significant opening in the forest, such as those resulting from a tree fall within the 0.04 ha sampling plot
LOGS	Logs (>10 cm dbh)	Presence or absence of logs in the forest, such as those resulting from a tree fall within the 0.04 ha sampling plot
SNAGS	Snags (>10 cm dbh)	Presence or absence of standing dead trees within the 0.04 ha sampling plot

[1] Several parameters describing vegetational structure were derived from vegetation sub-samples. These included mean dbh, total dbh, mean species density, tree composition of canopy, tree composition of subcanopy, dbh of canopy trees, dbh of subcanopy trees, density of canopy trees, and density of subcanopy trees. Floristic information was not included in the analysis, except for the species of dominant tree(s) in the canopy..

[2] The arithmetic mean or average was the sum of the measures of canopy cover by species at the sampling station divided by number of measures. Example: 1=class value: 0.1=numeric value.

structural indices: canopy and subcanopy dbh, density, cover, and foliage height range (FHR). FHR is based on theoretical concepts that describe the relative volume of "ecological space" occupied by trees at a site.

Derivation of T-CAP Indices and Terrain Variables: T-CAP Transformation

The only use of T-CAP indices in the GSMNP is in the application of spherical statistics to study change vector analysis (CVA) of landsat data in southern Appalachian spruce-fir forests (Allen and Kupfer 2000). Drawing from methods in spherical statistics, the extended CVA technique measures absolute angular changes and total magnitude of T-CAP indices (*brightness, greenness,* and *wetness*). Polar plots and spherical statistics summarize change vectors to quantify and visualize both magnitude and direction of change. Results separate vectors for forest stands by extent and time interval since adelgid infestation, along the crest of Smokies Range. Changes in the *greenness-wetness* plane improve prediction of fir class more than *brightness-greenness* change. The two Landsat TM scenes used in this study were the same and those used in the TM analysis of Allen and Kupfer (2000), where they are described in detail. Additional data used for this study included USGS 1:24.000 DEMs. Maps of independent topographic variables, including elevation, slope angle, and aspect, were derived from the DEMs.

Statistical Methodology

The relationships between two sets of variables were tested using Spearman and product-moment and Pearson correlation coefficients. Comparisons between means were made using ANOVA with general linear models (PROC SLM, SAS Institute 2000), which requires no assumption of homogeneity of variances nor equal sample sizes.

Canonical correspondence analysis (CCA), a constrained ordination technique, was performed with CANOCO (Ter Braak 1986, 1987) using forest types, topographic features, and T-CAP indices. Direct gradient analysis with CCA was appropriate for testing hypotheses concerning the effects of environmental gradients on vegetation (Gauch 1982; Ter Braak and Prentice 1988). CCA scores along axes 1 and 2 were compared with those from unconstrained ordinations to ensure that the environmental variables in the CCAs sufficiently explained compositional variation (Ter Braak 1986; Allen and Peet 1990). Fifteen environmental variables were included in the CCA: elevation, slope, 10 forest types, and three T-CAP indices.

"Pattern recognition," an activity or process that assigns meaning to one's experiences (i.e., classifies them), can be subdivided into three distinct steps: (1) perception, (2) interpretation, and (3) decision-making. These are the same fundamental steps a biologist uses when he/she assesses habitat and, as such, was the basis of my approach to habitat assessment. I used SAS General Linear Models (GLM) procedure for ANOVA and Tukey's HSD mean comparison procedure to compare vegetation and T-CAP (T-CAP) variables for census points, forest types, and zones. I used Kruskal-Wallis tests (χ^2 values presented) for point-count comparisons.

Development of Ecological Regression Models

Two different approaches were used to model the relationships between habitat data derived from the classified satellite imagery and bird census data. I used stepwise linear regression (Draper and Smith 1981) to generate equations relating community or species-level responses of birds to structural and floristic aspects of forest composition by zone as determined by T-CAP indices. The computed equations included all predictor variables that showed statistically significant partial correlations with the response variable being tested or examined. The stepwise method begins with the predictor variable that is most highly correlated with the response variable, and then successively adds the remaining predictor variables in decreasing order of their ability to reduce "unexplained" variation in the response variable. This stepwise procedure was ended when additional predictor variables failed to cause a statistically significant ($P<0.05$) reduction in unexplained variance.

I used multiple regression to select the optimal set of predictor variables, i.e., the fewest variables to explain as much of the observed variation in species richness and total abundance as possible. The forward selection procedure in this model was used to select a single variable and then add variables (including T-CAP indices) one at a time until the addition of further variables failed to produce an appreciable increase in the coefficient of determination. The "goodness of fit" could reflect the power of the pattern-recognition tool or process to assess DCE forest patterns, habitat changes, disturbances, and, therefore, changes in species richness.

Multi-collinearity analyses were performed on independent variables ($n=33$); those variables accounting for the highest degree of multi-collinearity were removed. One member of a pair of highly correlated ($r>0.8$) habitat variables was removed from consideration for inclusion in the regression procedure in order to select the optimum set of predictor variables. The variable in the correlated pair that was retained was the one judged more biologically meaningful and easier to measure. Most pairs of variables had either high (>0.8) or low (<0.5) r-values. Thus, my original set of 33 variables was reduced to 18 variables with low intercorrelations. Furthermore, the lowest two height intervals of foliage volume (<5 and 5-10 m) were combined to simplify the analysis.

Basal areas were removed from further analysis because of high correlations with other variables, e.g. dbh.

I set the significance value necessary for an independent variable to enter (P-to-enter) in the stepwise procedure at <0.15 so as not to exclude any variable that might be biologically important to the species. The final regression model was determined, however, by examining the change in the adjusted R (Norusis 1985) after each step in the procedure; a variable was included in the final model if it was accompanied by significant (P<0.1) change in the F-value associated with overall regression.

Stepwise multiple linear regression (Draper and Smith 1981) was used to develop equations, for each bird species, predicting bird abundances from habitat variables and relating community- or species-level responses of birds to structural and floristic aspects of forest composition. The stepwise procedure was used to identify a subset of habitat variables that accounted for the majority of explainable variation in the bird abundance data. If there was a prevalence of zero values, all variables either were transformed (variable + 1) prior to statistical analysis or logistic regression was used. All calculations were performed using GLM in the SAS statistical package (SAS Institute 2000). Plots of residuals and box plots were examined to check for homogeneity of variances and possible outliers. This procedure included the F-Max test for homogeneity of variances. I used PROCARIMA to test for independence. These analyses represent tests of the hypothesis that habitat characteristics recorded at census points influence the relative abundances of birds. Model building in this manner assumes that there is no variation in bird abundances between years. I tested this requirement with ANOVA, using years as the main effect and habitat variables as covariates; the dependent variables were assemblage measures and relative abundance of birds.

I also used stepwise-multiple regression analyses (PROC REG, SAS Institute 2000) to investigate the relationship among habitat variables and abundances for each of the 12 guilds and 10 most common species (>1 mean detection per visit or >20 detections for the study area). Before analyses, landscape and habitat variables were transformed (e.g. log or square root) if necessary, to meet assumptions of normality and homogeneity of variances, and then screened for multi-colinearity using correlation analysis, variation-inflation proportions, and condition indices (Neter et al. 1996). Several correlated or collinear variables were combined into the following new variables: species-specific variables for canopy and subcanopy trees, and densities of canopy and subcanopy trees; site variables for canopy, subcanopy, low shrub, and ground foliage height diversity (FHD). Because the number of snags and percent cover for ground cover were highly correlated with other values (>0.7 correlation coefficients) and because slope, forest opening, The Nature Conservancy (TNC) vegetation codes, and temperature (except fog) showed multi-collinearity problems, I removed these variables from analyses. I also removed temperature and cloud cover after analysis revealed little variation in these variables among zones and gradsects. Twelve variables remained in my data set for stepwise multiple regression analyses. At each step in the analysis, an F-statistic was calculated for each independent variable in the model. Only full models with $P<0.05$ were considered significant. Individual variables having a significance level of $P<0.15$ were allowed to enter the model initially but were later removed if P changed to >0.10 after the inclusion of other variables.

If the generated T-CAP Indices represented habitat characteristics that were biologically meaningful to birds, then, as these characteristics varied across study sites, I expected bird abundances to vary correspondingly. I tested this hypothesis with stepwise multiple linear regression using bird assemblage indices and species abundance indices as dependent variables and habitat measures and indices as predictors (Myers 1986; SAS Institute 2000).

To reduce the Type II error rate, which I was more concerned about due to the inherent variability in natural systems, I used $\alpha = 0.10$ (Type I error rate) rather than the conventional 0.05.

Results

Bird Species Abundances and Environmental Relationships

Table 4.3 lists the 29 most comomonly observed birds (heard or seen) at the census points. Table 4.4 indicates the status, alpha code, and guilds for species analyzed in this study. Within the census plots I compared bird counts with vegetation coverages of the forest community. Bird survey data from 1999 were compared with those from 2000. Because abundances of birds in habitats were not statistically different between Years, I pooled data from 1999 and 2000 to improve statistical power (Snedecor and Cochran 1989).

In 1999 and 2000 combined, I recorded 7,030 observations, which represented 5,707 birds and 63 species. I excluded species with fewer than 20 observations as well as species flying above the canopy, resulting in 29 species used in the following analysis. Ten species accounted for nearly 75% of all bird observations and seven of these were observed at high elevations (>1400 m). Of the 29 species of birds observed during morning censuses 15 (51%) were Neotropical migrants (long-distance migrants), one

Table 4.3 Summary statistics for the 29 most frequently observed bird species. Based on 1999 and 2000 combined data.

Bird Species	Total Individuals Detected	Percent of Points Individuals Heard[1]	Total Number Where Heard Species[2]	Percent of Points With Species[3]	Mean Species Detected Per Point[4]
Dark-eyed Junco	703.2	16.70%	161	78.90%	4.4
Veery	407	9.70%	129	63.20%	3.2
Winter Wren	404	9.60%	138	67.60%	2.9
Blue-headed Vireo	330.8	7.90%	133	65.20%	2.5
Black-throated Blue Warbler	321.9	7.60%	123	60.30%	2.6
Golden-crowned Kinglet	316.2	7.50%	105	51.50%	3
Black-throated Green Warbler	264.1	6.30%	97	47.50%	2.7
Black-capped Chickadee	154.4	3.70%	76	37.30%	2
Red-breasted Nuthatch	147.6	3.50%	88	43.10%	1.7
Canada Warbler	140.3	3.30%	71	34.80%	2
Chestnut-sided Warbler	119.2	2.80%	48	23.50%	2.5
Eastern Towhee	116.6	2.80%	59	28.90%	2
Ovenbird	108	2.60%	29	14.20%	3.7
Red-eyed Vireo	87	2.10%	32	15.70%	2.7
Brown Creeper	74.8	1.80%	49	24.00%	1.5
Hairy Woodpecker	70.8	1.70%	43	21.10%	1.6
Hermit Thrush	49.2	1.20%	24	11.80%	2
Wood Thrush	48.5	1.20%	19	9.30%	2.6
Scarlet Tanager	48.3	1.10%	27	13.20%	1.8
Hooded Warbler	41.7	1.00%	23	11.30%	1.8
Blue Jay	37.2	0.90%	28	13.70%	1.3
Carolina Wren	34.3	0.80%	26	12.70%	1.3
Acadian Flycatcher	32.5	0.80%	16	7.80%	2
American Crow	31.2	0.70%	23	11.30%	1.4
Northern Parula	28	0.70%	18	8.80%	1.6
Indigo Bunting	26.8	0.60%	12	5.90%	2.2
Pileated Woodpecker	26.5	0.60%	19	9.30%	1.4
Gray Catbird	23.5	0.60%	8	3.90%	2.9
White-breasted Nuthatch	19	0.50%	12	5.90%	1.6

Note: Total number of points censused = 2,778,
Total number of individuals detected = 30,829

[1] (Individuals detected/Total individuals detected) *100

[2] Number of points in which each species was detected

[3] (Number of points with detections/Total number of points)*100

[4] Individuals detected/Number of points with detections

Table 4.4 Names, status, codes, and guild classifications for the 29 bird species analyzed in this study. *Definitions are given in footnotes at bottom of table (next page).

Common name	Scientific name	Status	Alpha code	Guild Habitat	 Migratory	 Nesting
Acadian Flycatcher	*Empidonax virescens (NM)*	CS*	ACFL	F	NM	SC
American Crow	*Corvus brachyrhynchos (PR)*	CR*	AMCR	F	PR	C
Black-capped Chickadee	*Poecile atricopillus (PR)*	FR* he	BCCH	F	PR	SN
Blue-headed Vireo	*Vireo solitarius (NM)*	CS* he	BHVI	F	NM^1/TM	SC
Blue Jay	*Cyanocitta cristata (PR)*	CR*	BLJA	F	PR	C/SC
Brown Creeper	*Certhia americana (PR)*	FR* he	BRCR	F - OT	PR	SN
Black-throated Blue Warbler	*Dendroica caerulescens (NM)*	CS* he	BTBW	F	NM	SC/SH
Black-throated Green Warbler	*Dendroica virens (NM)*	CS*	BTNW	F	NM	C/SC
Carolina Wren	*Thryothorus ludovicianus (PR)*	CR*	CARW	F	PR	GEN
Canada Warbler	*Wilsonia canadensis (NM)*	CS* he	CAWA	SH	NM	GR
Chestnut-sided Warbler	*Dendroica pensylvanica (NM)*	CS* he	CSWA	SH	NM	SH
Dark-eyed Junco	*Junco hyemalis (PR)*	AR* he	DEJU	F - GR	PR	GR
Eastern Towhee	*Pipilo erythrophthalmus (PR)*	CR*	EATO	SH/GR	PR	SH/GR
Golden-crowned Kinglet	*Regulus satrapa (PR)*	FR*	GCKI	SF	PR	C
Gray Catbird	*Dumetella carolinensus (NM)*	FS,* OW	GRCA	SH	NM^2/TM	SH
Hairy Woodpecker	*Picoides villosus (PR)*	FR*	HAWO	F	PR	SN
Hermit Thrush	*Catharus quttatus (TM)*	FW, US(*?)	HETH	F - GR	TM	SH/GR
Hooded Warbler	*Wilsonia citrina (NM)*	CS*	HOWA	SC	NM	SH
Indigo Bunting	*Passerina amoena (NM)*	C-AS*	INBU	SH	NM^3	SH
Northern Parula	*Parula americana (NM)*	FS*	NOPA	F	NM^4	SC/SH
Ovenbird	*Seiurus aurocapillus (NM)*	CS*	OVEN	F - GR	NM^5	GR
Pileated Woodpecker	*Dryocopus pileatus (PR)*	FR*	PIWO	F	PR	SN
Red-breasted Nuthatch	*Sitta canadensis (PR)*	FR* he	RBNU	SF	PR	C/SC
Red-eyed Vireo	*Vireo olivaceus (NM)*	AS*	REVI	C	NM	SC
Scarlet Tanager	*Piranga olivacea* (NM)	CS*	SCTA	C	NM	SC
Veery	*Catharus fuscescens (NM)*	CS* he	VEER	F - GR	NM	SH/GR
White-breasted Nuthatch	*Sitta carolinensis (PR)*	FR*	WBNU	F	PR	F
Winter Wren	*Troglodytes troglodytes (PR)*	CR* he	WIWR	SC	PR	SC
Wood Thrush	*Hylocichia mustelina (NM)*	CS*	WOTH	F - GR	NM	C/SC

Table 4.4 Continued

Habitat guild	**Migratory guild**	Nesting guild
F = forest(in general)	PR = permanent resident	C = canopy
C = canopy	TM = temperate or short distance migrant	SC = subcanopy
SC = subcanopy	NM = neotropical or long distance migrant	SH = shrub
SH = shrub		GR = ground
GR =ground		SN = snag
SF = Spruce-Fir		GEN =forest edge or opening
F-GR= forest ground		
OT = old trees		

STATUS CODE

A = abundant; over 25 seen on a given day in proper habitat/season
C = common; 5-25 seen per day in proper habitat/season
F = fairly common; at least one individual per day in proper habitat/season
U = uncommon; at least one seen per season of occurrence or several seen per year
O = occasional; one seen per year or less
X = rare; has been observed at least once, but is not to be expected
R = permanent resident
W = winter resident
S = summer resident

SPECIAL NOTATIONS

* = considered to breed within the park
* ? = suspected to breed within the park
he = high elevation

Alpha Code - pneumonic assigned by the American Ornithologists' Union (1957).

[1]Note: Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD?
[2]Note: Most GRCA winter in Central America some in South Florida and Gulf Coastal Plains
[3]Note: Many INBU winter on Coastal Plain of Gulf States and South Florida
[4]Note: Many NOPA winter on Coastal Plain of Gulf States and South Florida

(1.0%) was temperate (short-distance migrants), and 13 (44%) were permanent residents. I recorded 17 of these 29 species 12 or more times on the four primary gradsects (see Chapter II, Results, for explanation of fifth and sixth gradsect). Distributions of the 29 species were subjected to additional statistical analysis.

The initial step in evaluating bird, vegetation, and T-CAP relationships was to examine the correlation matrix between both sets of variables (Table 4.5). Out of 493 possible correlations, >34% were significant: 18.25% at $P<0.05$, an additional 11.0% at $P<0.01$, and a further 6.5% at $P<0.0001$ (Table 4.5). These percentages of significance strongly suggest that most of the described relationships are not spurious. Table 4.5 indicates that five measured vegetation variables were significantly associated with the abundance of at least three, and usually seven to ten bird species. These findings are similar to those of Cohen and Spies's (1990) correlation coefficients for the relationships between structural attributes and variables derived from satellite data and TM T-CAP *brightness*, *greenness*, and *wetness* axes. He reported 18.5%, 9.6% and 5.5% for these values, respectively.

To evaluate vegetation factors and T-CAP relationships, I analyzed spectral reflectance from Landsat Thematic Mapper images. I first related T-CAP measures of reflectance (*brightness, greenness, wetness*) from 212 census points to TNC vegetation associations, two forest types, levels of canopy closure, and understory composition. Once I established that T-CAP values could be tied to differences in overstory and understory conditions, I tested for statistical relationships between T-CAP indices and species diversity in an effort to better understand their predictive or inferential powers. As part of the analysis, I applied this technique to test the magnitude of change in

Table 4.5 Significant correlations among bird species abundances and landscape variables. Vegetation structural variables coded as follows: LSHR = height range of low shrubs/seedling trees; TSHR = height range of tall shrubs/sapling trees; SCHR = height range of subcanopy trees; TCHR = height range of canopy trees; GCC = canopy cover of ground vegetation; LSCC = canopy cover of low shrub/seedling trees; TSCC = canopy cover of tall shrub/sapling trees; SCCC = canopy cover of subcanopy trees; TCCC = canopy cover of canopy trees;. * = P <0.05; ** = P <0.01; *** = P <0.0001. – = negative correlation, + = positive correlation.

	Spatial				
	Disturbance	Elevation (m)	Forest Opening	Slope (degrees)	Snags
Acadian Flycatcher					+*
American Crow				+**	
Black-capped Chickadee		+*			+*
Blue-headed Vireo	–*	+**			
Blue Jay			+**		+**
Brown Creeper	+*	+*			+*
Black-throated Blue Warbler		+**			
Black-throated Green Warbler	+**		+*		
Carolina Wren			+**		+*
Canada Warbler		+*			
Chestnut-sided Warbler	+*	+*	+*		
Dark-eyed Junco		+*		+*	
Eastern Towhee	+*	+*			+*
Golden-crowned Kinglet				+*	
Gray Catbird		+*		+**	
Hairy Woodpecker					+*
Hermit Thrush			+*		
Hooded Warbler	–*		–*		
Indigo Bunting	–*		–*		
Northern Parula			+*		
Ovenbird		–*	+		
Pileated Woodpecker					+*
Red-breasted Nuthatch		+*			
Red-eyed Vireo	–*	–*			
Scarlet Tanager					
Veery		+*		+*	
White-breasted Nuthatch	+*			–*	–*
Winter Wren	+**	+**		+**	
Wood Thrush			+*		

Table 4.5 Continued

	Vertical Structure					Horizontal Structure (Coverage)				
	GHR	LSHR	TSHR	SCHR	TCHR	GCC	LSCC	TSCC	SCCC	TCCC
Acadian Flycatcher	+*	+*	+***			–*	–*		+**	+***
American Crow					+*	–*	–*			+*
Black-capped Chickadee		+***						+***	+***	
Blue-headed Vireo		+**		+*			+*		+**	+*
Blue Jay			+**	+**	+*	–*		+**	+**	+*
Brown Creeper					+**					+**
Black-throated Blue Warbler		+*	+**	+***	+***		+*	+*	+**	
Black-throated Green Warbler	–*				+**	–*		–*	+*	+**
Carolina Wren					–**				+***	
Canada Warbler	+*	+*		+***	+***		+*	–*	+*	+***
Chestnut-sided Warbler	–*	+*	+*	+***	–***	–***	+**	+*	+**	
Dark-eyed Junco	+**		+*			+**				
Eastern Towhee	+*	+**	+*	+**		+*	+*	+*	+**	
Golden-crowned Kinglet			+*		+*	–*	+*	+*		+*
Gray Catbird			+*					+*		–***
Hairy Woodpecker	–*								–*	
Hermit Thrush	+*			–**	–**	+*	+**	–**		
Hooded Warbler	–**		+**				+**	+**		
Indigo Bunting		+**	+*				+**	+*		+*
Northern Parula		+**		+*	–*	–*	+***	+*	+***	–*
Ovenbird	+**		+*	+*	–**	+***				
Pileated Woodpecker	+*	–*			+**			–*		+*
Red-breasted Nuthatch				+*	+*				+*	+*
Red-eyed Vireo	–*		+*		+**				+***	
Scarlet Tanager			+**		+***	–***	+*			
Veery		–*			–*	+*	+**			–**
White-breasted Nuthatch	–*		+**		+**	–*	+***	+***		+***
Winter Wren			+**	+***	–*		+**		+**	
Wood Thrush		+*	+*		+***	+**			+*	

Table 4.5 Continued

	Tasseled Cap Indices						Composition		
	1988			1998					
	TCAPB	TCAPG	TCAPW	TCAPB	TCAPG	TCAPW	% D	% C	% H
Acadian Flycatcher	+***	+***		+***	+***		+*		
American Crow				_*	_*				+*
Black-capped Chickadee							_**	+**	+**
Blue-headed Vireo				+*	+*	+**	_*	+**	+*
Blue Jay	+***	+**	_***	+**	+**	_***	_**	+*	+*
Brown Creeper						+**		+*	
Black-throated Blue Warbler	_*	_*		_*	_*	+*		+*	+*
Black-throated Green Warbler	+*			+*	+*				+*
Carolina Wren								+*	+*
Canada Warbler								+*	
Chestnut-sided Warbler						_*		+**	
Dark-eyed Junco								+*	
Eastern Towhee					+**	_*	+**	+*	+*
Golden-crowned Kinglet							_**	+**	
Gray Catbird	_*		+*	_*	_*	+*	+**		+*
Hairy Woodpecker				+*	+*		+*		+*
Hermit Thrush								+*	
Hooded Warbler					+*		+*		
Indigo Bunting				+*	+*	_*	+*		
Northern Parula						+*	+**	+*	
Ovenbird				+**		_*	+*		
Pileated Woodpecker						+***		+*	
Red-breasted Nuthatch							+*	+**	+*
Red-eyed Vireo					+**	+*	+**	+*	
Scarlet Tanager						+*	+*	+*	
Veery				_*	_*		+*	+*	
White-breasted Nuthatch					_*	+*	+**	+*	
Winter Wren				+*	+**	+*		+**	
Wood Thrush									

tasseled indices as a "pattern recognition tool" based on prior fieldwork.

Results of Spearman correlations indicated that 12 vegetation characteristics were weakly (r <0.50), but significantly (P<0.10), correlated with T-CAP variables (Tables 4.4, 4.5). These included subcanopy development, and canopy and subcanopy foliage height range, which were proximate and prominent factors influencing bird distributions. An important finding was that *brightness* and *greenness* variable relationships were significantly (P<0.10), and moderately (0.50) to strongly (0.80), correlated with ECCs or forest type when the dominant and codominant trees were considered.

Bird Species and Environmental Gradients

Redundancy analysis (RDA) and canonical correspondence analysis (CCA) relate species data to explanatory variables of interest using direct gradient analysis and ordination. Both make assumptions about the distributions of species' response curves in relation to compound (linearly combined) environmental gradients; RDA assumes species have linear responses to ecological gradients and CCA assumes species have symmetric, unimodal responses to ecological gradients. I compared these two ordination methods using bird community and vegetation data collected along gradients of elevation in the GSMNP. I explored how each analytical technique treats species with distribution curves that do not fit well with the model. The findings suggest that RDA performed poorly with species distributions that do not fit the assumption of linearity, whereas CCA performed relatively well when the data do not completely satisfy the unimodal assumption (Table 4.7).

CCA is an eigenvector ordination technique that also produces a multivariate direct gradient analysis (Ter Braak, 1986). CCA can reveal a pattern of community

Table 4.6 Significant Spearman correlations of T-Cap indices with measures of forest vegetation parameters as predictors/indicators of bird abundance. T-CAP_B = T-CAP *brightness*, T-CAP_G = T-CAP *greenness*, T-CAP_W = T-CAP *wetness*.

	Tasseled Cap Indices		
Vegetation Variables	TCAP_B	TCAP_G	TCAP_W
DBH_Subcanopy Dbh of subcanopy (DBH_SUB)	0.33**	0.36**	0.38**
Density_Subcanopy Density of subcanopy (DEN_SUB)		0.33**	
Subcanopy Cover Class (SCCC)		0.34**	
Mean canopy cover of canopy trees by species (%) (SUBCLS)	0.31**	0.33**	
Subcanopy Foliage Height Range (SCHR)	0.41**	0.48**	
Tree Canopy Foliage Height Range (TCHR)	0.39**	0.44**	
Ecotonal Community Classification (ECC)	0.56** 0.33**	0.57** 0.36**	0.28** 0.38**

n=113

Table 4.7 Comparison of the ordinations by canonical correspondence analysis (CCA), detrended canonical correspondence (DCCA), and redundancy analysis (RDA) of bird and vegetation data; eigenvalues and species-environment correlation coefficients for the first three axes.

	Axis			
	1	2	3	4
		Eigenvalues		
CCA	0.185	0.104	0.060	0.050
DCCA	0.185	0.095	0.050	0.036
RDA	0.115	0.039	0.025	0.018
		Correlation coefficients		
CCA	0.793	0.104	0.060	0.050
DCCA	0.818	0.705	0.695	0.696
RDA	0.831	0.729	0.644	0.605

Table 4.8 Comparison of the ordinations by canonical correspondence analysis (CCA), detrended canonical correspondence analysis (DCCA), partial CCA and partial DCCA, of bird and vegetation data; eigenvalues and species-environment correlation coefficients for the first three axes.

	Axis			
	1	2	3	4
		Eigenvalues		
CCA	0.471	0.142	0.079	0.052
DCCA	0.482	0.103	0.054	0.036
		Correlation coefficients		
CCA	0.934	0.782	0.671	0.719
DCCA	0.962	0.855	0.709	0.648
		Eigenvalues		
CCA	0.490	0.12	0.610	0.031
Partial CCA	0.170	0.061	0.031	0.026
DCCA	0.490	0.064	0.038	0.029
Partial DCCA	0.170	0.135	0.094	0.074
		Correlation coefficients		
CCA	0.923	0.717	0.589	0.532
Partial CCA	0.719	0.589	0.532	0.435
DCCA	0.945	0.883	0.637	0.655
Partial DCCA	0.719	0.719	0.712	0.692

variation, as in standard ordination, and the main features of species' distributions across an environmental gradient. The ordinations by CCA, DCCA (detrended canonical correspondence analysis), and RDA were similar for these data (Table 4.8).

The second axis of the CCA showed a contrast among sites, with a high cover of tulip poplar, mesic or xeric oak (Table 4.9). When the tree data were stratified into three elevational classes, the relative importance of environmental variables changed. For example, the influence of topographic variable slope increased with elevation. Variables clearly decreasing in importance with elevation included aspect and potential solar radiation.

Responses of tree species to environmental variables also differed among CCAs stratified by elevation. For example, Fraser fir was often associated with high topographic positions and variables (ridgetops and convex slopes). It was also associated with cove sites, although primarily at low elevations (<1450 m). An additional contrast was the positive association of red spruce with steep, concave slopes rather than ridges in the high elevational class.

The CCA ordination diagram displays forest types, bird species, and environmental variables (Fig. 4.3), represented by arrows. Loosely speaking, the arrow for an environmental variable points in the direction of maximum change for that environmental variable across the diagram, and its length is proportional to the rate of change in this direction. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and thus more closely related to the pattern of community variation shown in the ordination diagram.

The most convenient rule for quantitative interpretation of the CCA biplot (Ter

Table 4.9 Canonical coefficients and correlations coefficients of environmental variables with the first two axes of canonical correspondence analysis (CCA). The environmental variables were standardized to unit variance after log-transformation. For abundance data and definitions of variables, see Fig. 4.3. Significant loadings are in bold type. [1] = sites contrasted, correlated negatively or inverse relationship; [2] = correlated positively

	Canonical Coefficients		**Correlation Coefficients**	
Axis Variable	1	2	1	2
Elevation	0.8189	-0.2546	**0.928**[2]	-0.362
SPRUCEF	-0.2012	-0.178	**0.382**[2]	**-0.438**
SPRUCENH	-0.1708	-0.1312	**0.346**	-0.152
COVEH	-0.0435	-0.0686	**-0.203**[1]	0.323
BALD	-0.0594	-0.0733	0.074	0.046
NHARD	-0.059	-0.0518	0.081	0.186
MESICO	-0.2102	-0.2179	**-0.356**[1]	-0.215
XERICO	-0.2092	-0.2049	**-0.474**[1]	0.035
PINE9_10	-0.059	-0.0912	-0.104	-0.033
TULIP	-0.3112	-0.2831	**0.550**[1]	**-0.388**
HEMHARD	0	0	0.037	**0.550**
Slope	0.0814	0.1172	**0.319**[2]	**0.317**
TCAP98 G	0.0296	0.0545	**-0.571**[1]	**0.252**
TCAP98 W	-0.0398	-0.0155	**0.267**[2]	**-0.236**

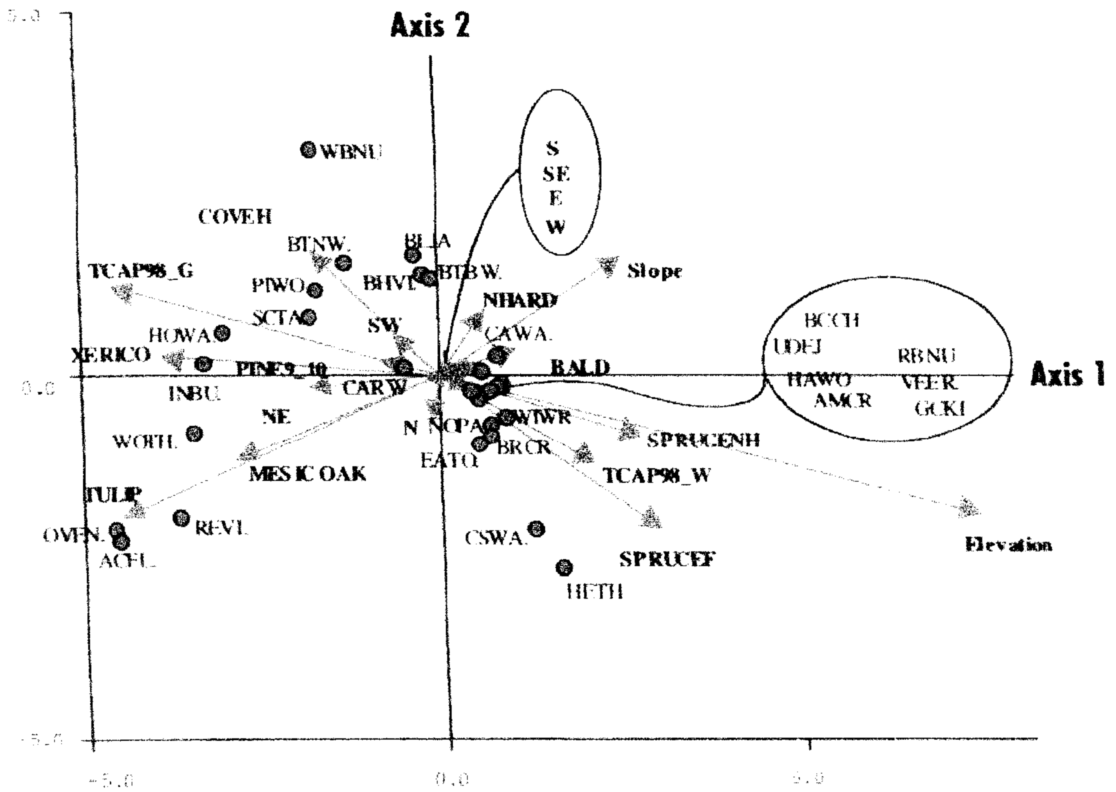


Fig. 4.3 Canonical Correspondence Analysis ordination diagram with birds (dots) showing the relationship among birds, ecotonal classes, topographic and vegetation variables (in bold letters) with the omission of highly correlated variables. Definitions of bird acronyms are given in legend to Table 4.3. N, S, E, W, NE, NW, SE, SW = directon of aspect; SPRUCENH = spruce nothern hardwood, SPRUCEF = spruce fir, XERICO = xeric oak, COVEH = cove hardwood, TCAP98_G = tasseled cap greenness, TCAP98_W = wetness.

Braak 1986) is therefore as follows: each arrow representing an environmental variable determines a direction or 'axis' in the diagram, and species points can be projected onto this axis (Fig. 4.3). The order of the projection points corresponds approximately to the ranking of the weighted averages of the species with respect to that environmental variable. The weighted average indicates the position for a species' distribution along an environmental variable, and thus the projection point of a species also indicates this position, although approximately.

Finally, the length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the biplot, and is therefore a measure of how much a species' distribution differs along that environmental variable. Important environmental variables, therefore, tend to be represented by longer arrows than less important ones.

From the CCA correlations (Table 4.9), I infer that the first axis is an elevation gradient on which high elevation census points have a high percentage of spruce-fir or spruce northern hardwood. The second axis is for mesic hardwood communities. The correlations show a contrast among sites with high cover of tulip poplar and mesic or xeric oak that separate hemlock hardwood forest from spruce-fir forests at higher elevations. This can be seen also from the CCA ordination diagram (Fig. 4.3).

The most important environmental gradients identified with CCA were elevation slope, T-CAP greenness, and mixed mesic hardwood communities (Fig. 4.3). An inverse relationship existed between elevation, spruce-fir, and T-CAP_W gradients, and cove hardwood, xeric oak, and T-CAP_G gradients. This was expected because northerly aspects (with low potential solar radiation values) had high aspect values.

Fraser fir and mountain ash were at the high end of the elevation gradient. Yellow buckeye and yellow birch were at the high end of the aspect gradient, indicating an affinity for north-facing slopes with presumably cool-mesic conditions. By contrast, yellow birch was at the low end of the aspect gradient. The high elevational dominants, spruce-fir and Fraser fir, tended to be at intermediate positions on the aspect gradient. Yellow birch and yellow buckeye were at the low end of the topographic position gradient, indicating an affinity for coves (or ravines) rather than ridges.

When the tree data were stratified into three elevational classes, the relative importance of environmental variables changed. For example, the influence of topographic position increased with elevation. Variables clearly decreasing in importance with elevation included aspect and potential solar radiation.

Responses of bird species to environmental variables also differed among CCAs stratified by elevation (Table 4.10, Fig. 4.3). For example, Chestnut-sided Warblers, Hairy Woodpeckers, Red-breasted Nuthatches, Dark-eyed Juncos, and Winter Wrens were often associated with Fraser-fir and high topographic positions (ridgetops and convex slopes). An additional contrast was the positive association of Golden-crowned Kinglets and Gray Catbirds with red spruce on steep, concave slopes rather than ridges in the high elevational class. In some cases, habitats were associated with particular bird species (Fig. 4.3). For example, the Black-throated Green Warbler, Blue-headed Vireo, and White-breasted Nuthatch were mainly found in habitats with higher percentages of hemlock. By contrast, the Acadian Flycatcher, Red-eyed Vireo, Ovenbird, Wood Thrush, and Indigo Bunting were found in habitats with mesic oak and tulip poplar trees. The Canada Warbler, found in northern hardwood, was the only species influenced

Table 4.10 Canonical correspondence analysis scores for bird species. Gray Catbird was excluded due to low sample size. Significant loadings are in bold.

Name	Environmental Factor 1
Acadian Flycatcher	-4.447
American Crow	**0.821**
Black-capped Chickadee	**0.639**
Black-throated Blue Warbler	-0.141
Black-throated Green Warbler	-1.294
Bluejay	-0.450
Blue-headed Vireo	-0.223
Brown Creeper	**0.671**
Canada Warbler	**0.850**
Carolina Wren	-0.523
Chestnut-sided Warbler	1.415
Eastern Towhee	**0.512**
Golden-crowned Kinglet	**0.875**
Hairy Woodpecker	**0.534**
Hermit Thrush	1.723
Hooded Warbler	-3.131
Indigo Bunting	-3.188
Northern Parula	**0.587**
Ovenbird	-4.289
Pileated Woodpecker	-1.785
Red-breasted Nuthatch	**0.785**
Red-eyed Vireo	-3.782
Scarlet Tanager	-1.903
Dark-eyed Junco	**0.503**
Veery	**0.903**
White-breasted Nuthatch	-1.610
Winter Wren	**0.976**
Wood Thrush	-3.537
Eigenvalue	0.490

by slope.

Site Characteristics of the Ecotone

The transition from deciduous and hemlock - deciduous forest to spruce-fir forest occurred in the 1000-1500 m elevation interval and was strongly associated with elevation. The fact that a substantial proportion (24%) of the samples containing red spruce or Fraser fir were 30-70% spruce-fir by dbh suggested that the ecotone was not abrupt. In comparison, predominantly deciduous forests (<30% spruce-fir by dbh) comprised 30% of the census points, and predominantly coniferous forests (>70% spruce-fir by dbh) comprised 46% of the census points (Table 2.3 Chapter II).

My results indicated hemlock was widespread in all vegetation strata at low to mid-elevations and is the second most common tree species in the park. Hemlock presence is significantly associated with elevation, total relative moisture index represented by T-CAP_W, disturbance history, vegetation type, and bedrock geology (Table 4.9). Sixteen of 29 breeding bird species showed significant correlations with hemlock presence. In the eastern United States, invasion of hemlock wooly adelgid (*Homoptera: Adelgidae: Adelges tsugae*) is transforming species composition of native forests by causing extensive mortality in eastern hemlock populations.

When considered across all census sites, the elevation of the ecotone varied widely (Fig. 4.2). Across the study area, plots dominated by spruce-fir occurred as low as 1300 m elevation. However, while forest plots lacking both red spruce and Fraser fir occasionally occurred in the 1300-1500 m range, they were rare above 1600 m. Strong effects of other variables on the elevation of ecotones were not apparent. The ecotone was not markedly lower on northerly slopes (Table 2.3 Chapter II).

Site Selection and Vegetational Classification Using T-CAP indices

T-CAP *greenness* and *wetness* indices were represented by axes in CCA and principal component analysis. T-CAP indices correlated with measures of vegetation that are indicators/predictors of bird abundance (Tables 4.4, 4.10, Fig. 4.3). A three component PCA was assessed for interpretation of T-CAP variables. Table 4.11 shows the resultant loadings and eigenvalues for three T-CAP and topographic-related components. Three principal components (PCI-PC3) explained 87% of the topographic and remotely sensed variation. The T-CAP scores for PC1 *greenness* and *brightness* were inversely correlated with elevation. PC1 represented a gradient of (increasing) *greenness* and PC2 represented a gradient of *wetness*. The first two dimensions accounted for over two-thirds of the variation present in the T-CAP data. The first component loaded highest on T-CAP *greenness* (*greenness* and *brightness* were correlated) and explained 51.6% of the variation. The second component explained 22.4% of total variance and loaded on T-CAP *wetness*. The third component contained 12.6% of total variance and clearly loaded on slope (Table 4.11).

I estimated composition and percent cover (0-100%) for overstory and understory vegetation. Results of Kruskal-Wallis nonparametric Chi-Square (χ^2 values presented and used because T-CAP data failed tests for normality and equality of variances among forest classes) indicated significant differences in mean values of all three T-CAP indices for the three types of vegetation composition (Tables 4.11, 4.12).

Community vegetation types determined and classified by MacKenzie (1993) were grouped into broader "habitat super classes" or ECCs to delineate the ecotone boundary. An ANOVA using T-CAP_*Wetness* and the new ECCs revealed significant

Table 4.11 T-CAP principal component analysis loadings and eigenvalues (total variance explained = 87%). Significant loadings are in bold.

Variables	PC1	PC2	PC3
Elevation	-0.3523	-0.396	0.034
Slope	0.0201	-0.117	**0.973**
TCAP88_B	0.472	-0.090	-0.040
TCAP88_G	**0.451**	-0.029	**0.019**
TCAP88_W	-0.049	**0.620**	0.216
TCAP98_B	**0.473**	-0.069	-0.009
TCAP98_G	**0.469**	0.017	-0.020
TCAP98_W	-0.040	**0.657**	-0.057
Sum of Squares Eigenvalue	4.127	1.79	1.01
Percentage of Variance	52.2	22.4	12.6

Table 4.12 Tukey's HSD and LS means for TCAP_W comparisons among ECCs with means in increasing order for 1988 and 1998 presented two different ways, a. Conclusions are often shown diagrammatically by underlining the means that are not significantly different. Based upon the results of the multiple comparison procedures, an underline can be placed under the treatment means that are not significantly different from one another. [1]In the D-H comparison, since D and H are not significantly different from one another, they are underlined. [2]In the D-C and H-C comparisons, D and C, and H and C are significantly different from one another. [3]In 1998 comparisons, D, H, and C are all significantly different from each other. D = deciduous, H = hemlock, C = coniferous forest types

TCAP Data				
TC1 vs. TC2	TC2 vs. TC3	TC3 vs. TC1		
D	H	C	Comparison	P
8.63	8.96	10.03		
1988				
————	————	————	D-H[1]	
————		————	D-C[2]	<0.0001
	————	————	H-C[2]	<0.0001
1998[3]				
————	————		D-H	<0.0001
————		————	D-C	<0.0001
	————	————	H-C	<0.0001

(P<0.0001) results for twelve comparisons between years and among habitat super classes or ECCs (Table 4.13). I ran the ANOVA using GLM and determined both Tukey's HSD and least square (LS) means; Tukey's HSD only shows differences between means, while LS means shows the mean values themselves. I grouped the ECCs as follows: H was HH; C included SF, F, and SNH; and D included all the rest (CH, MO, NH, P. TP, and XO; Appendix A). Highest to lowest values were determined from Tukey's HSD and LS means (Tables 4.11, 4.12). *Greenness* values differentiated deciduous canopy values and *wetness* values differentiated spruce-fir from all other classes.

Results for the t-test on T-CAP_*Wetness* for the two years showed that the variances were not equal. Therefore, I used Satterhwaite t-test, which showed a significant difference between the two years ($t_s = 2.98$, $P < 0.005$; $t_{.01[400]} = 2.5$). I then determined how one separation differed from the others. In 1988, T-CAP_W values for deciduous (D) and hemlock (H) forest types did not differ in *wetness* but T-CAP_W values for D and H differed significantly from coniferous (C) T-CAP_W values (Tables 4.11, 4.12). This concurs with the CCA plot (Fig. 4.3). Likewise, when D and C were compared, values of D (1) differed significantly from C (3; P<0.001) and when H (2) and C were compared, values of H differed significantly from C (P<0.0001; Tables 4.11, 4.12).

Gradsect Comparison of Plant and Bird Communities

Despite dramatic changes, the red spruce on Alum Cave Trail (ACT) in Zones 2 and 3 were significantly larger in diameter than at sites located on the other gradsects (Fig. 4.4; $_{F3.67}$=15.2, P<0.001); spruce was rare in Zones 1 and 2 on Bull Head Trail

Table 4.13 Tukey's HSD and LS means for TCAP_W comparisons among ECCs with means in increasing order for 1988 and 1998 presented two different ways, b. Significance values (P) for comparing TCAP data among ECCs. * = <0.05, ** = <0.01, *** = <0.0001. D = deciduous, H = hemlock, C = coniferous forest types

TCAP Data	TC1 vs. TC2	TC2 vs. TC3	TC3 vs. TC1
Difference	-8.63	-8.96	-10.03
1988			
D-H P Value	n.s	n.s	*
D-C P Value	*	**	***
H-C P Value	*	***	***
1988			
D-H P Value	*	*	*
D-C P Value	**	*	***
H-C P Value	*	***	***

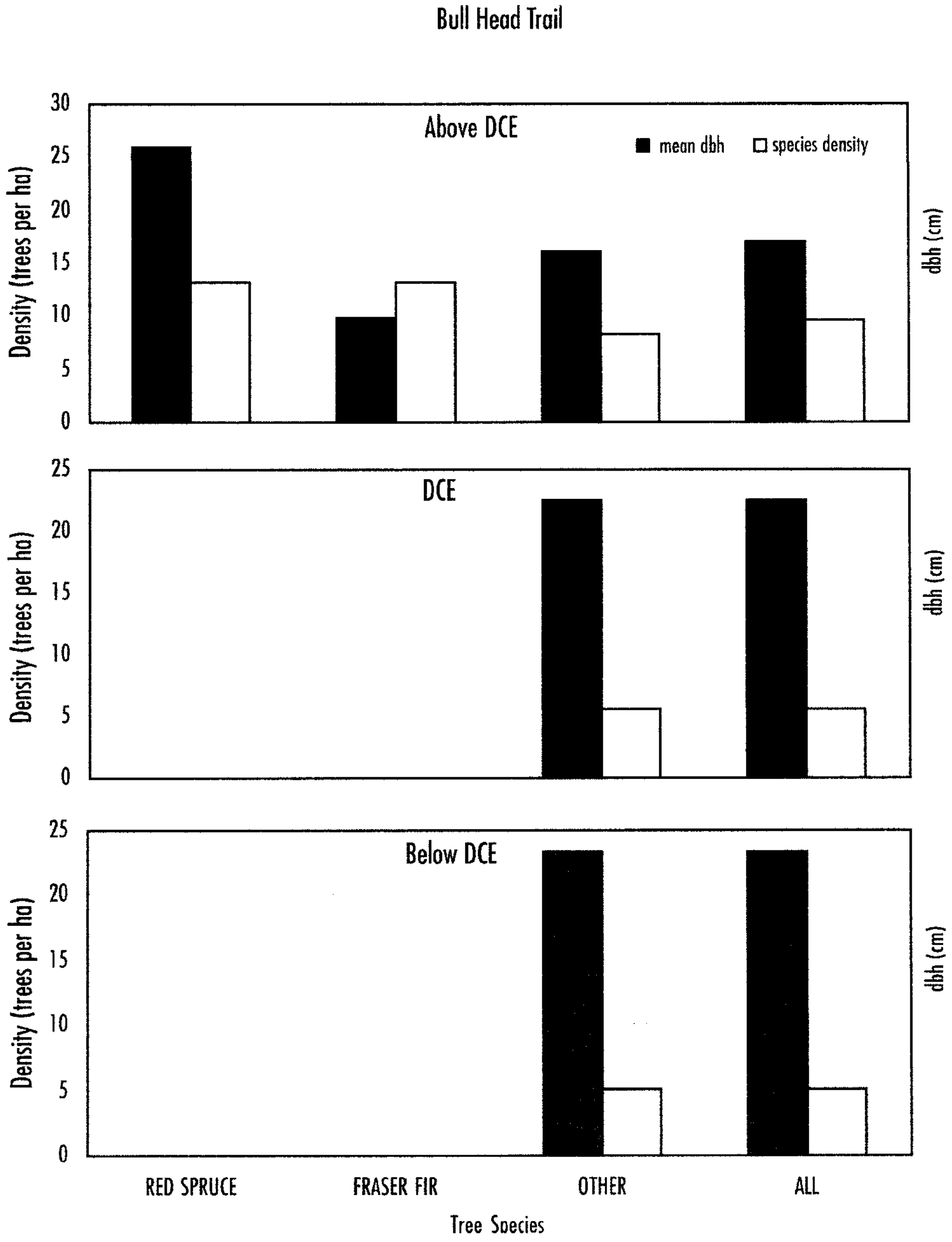


Fig. 4.4a Density and mean dbh of canopy trees (>10cm dbh 1.5m above ground) at the high-elevation study sites on Mount LeConte, GSMNP in 2000 on Bull Head Trail (BHT). Estimates are based on 0.04-ha circular plots.

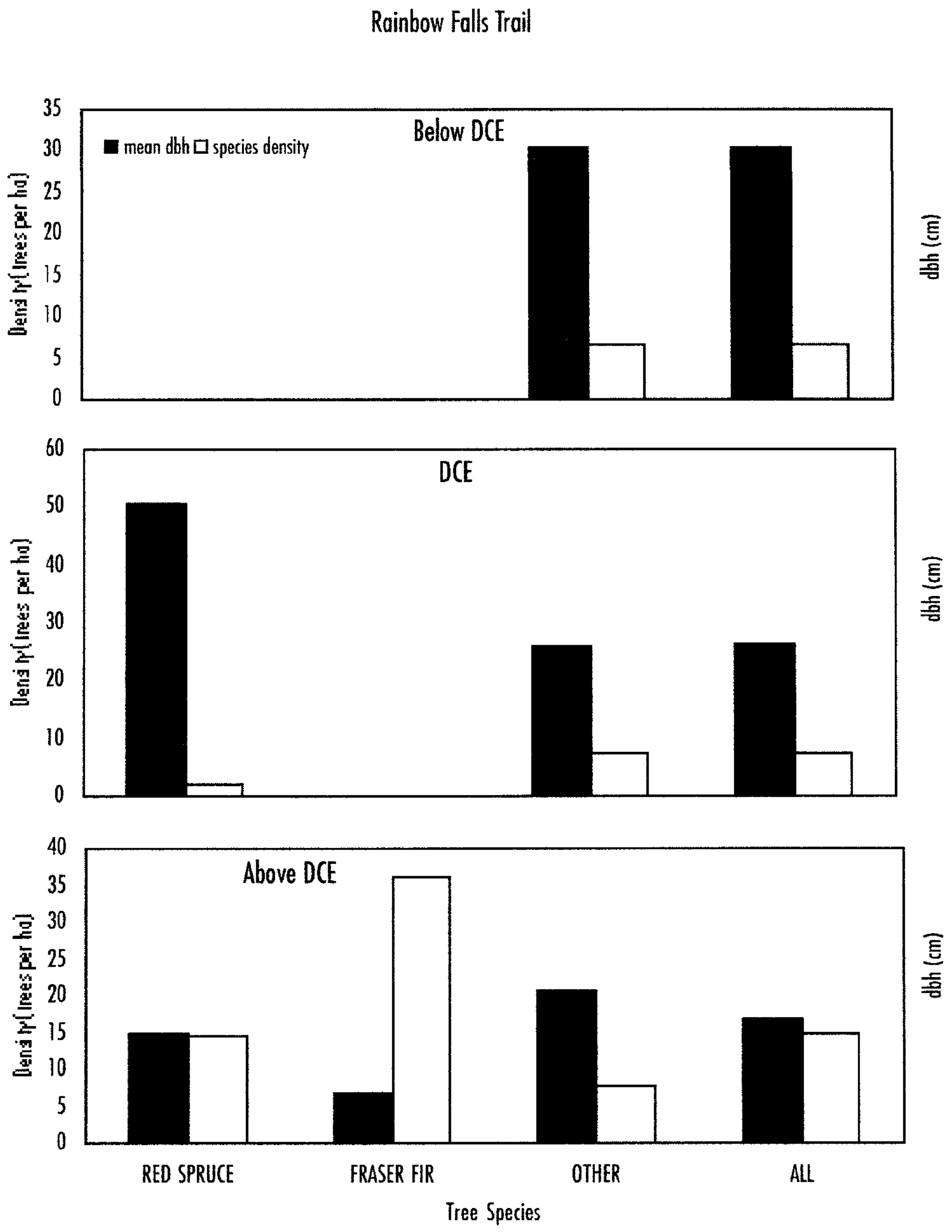


Fig. 4.4b Density and mean dbh of canopy trees (>10cm dbh 1.5m above ground) at the high-elevation study sites on Mount LeConte, GSMNP in 2000 on Rainbow Falls Trail (RFT). Estimates are based on 0.04-ha circular plots.

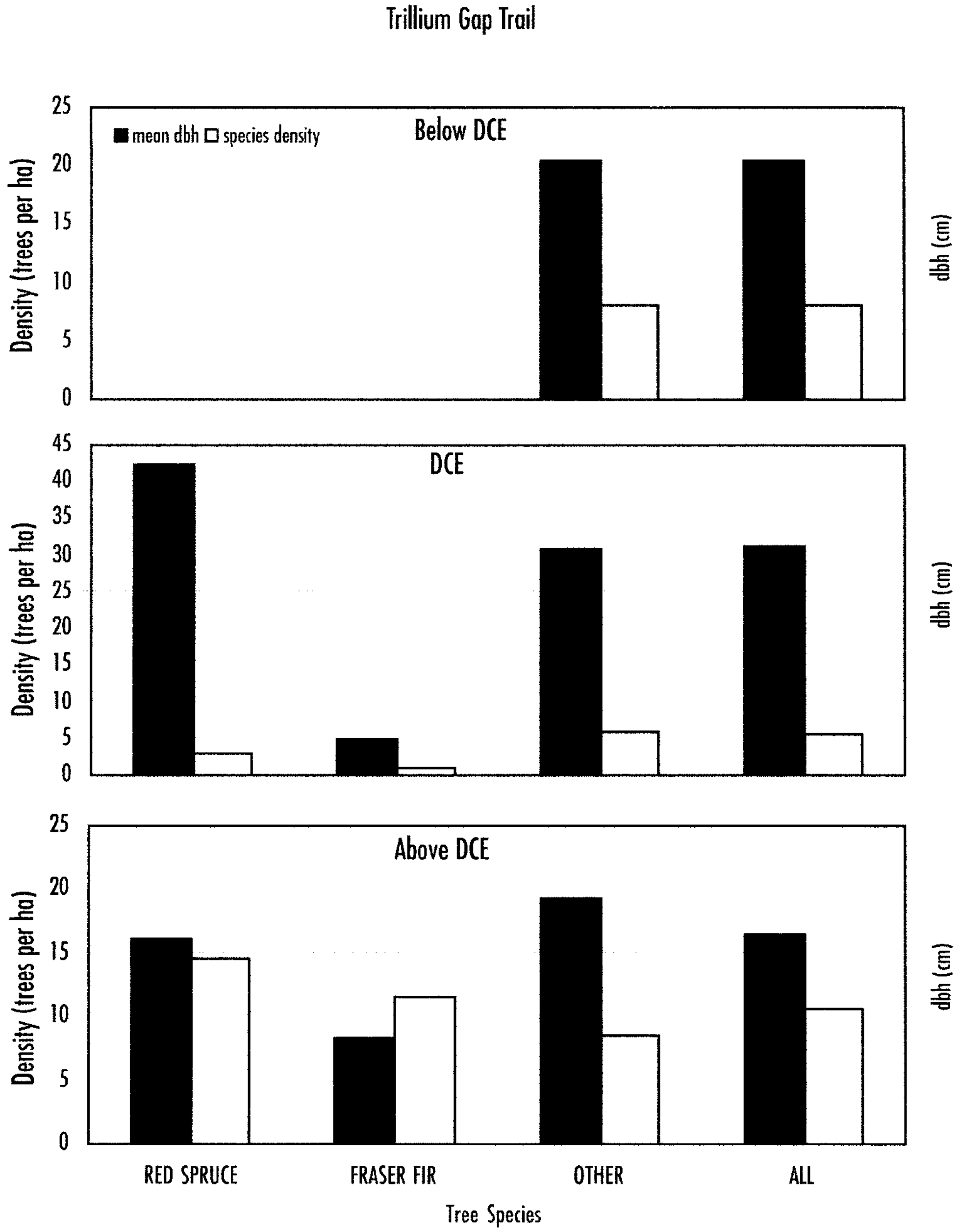


Fig. 4.4c Density and mean dbh of canopy trees (>10cm dbh 1.5m above ground) at the high-elevation study sites on Mount LeConte, GSMNP in 2000 on Trilium Gap Trail (TGT). Estimates are based on 0.04-ha circular plots.

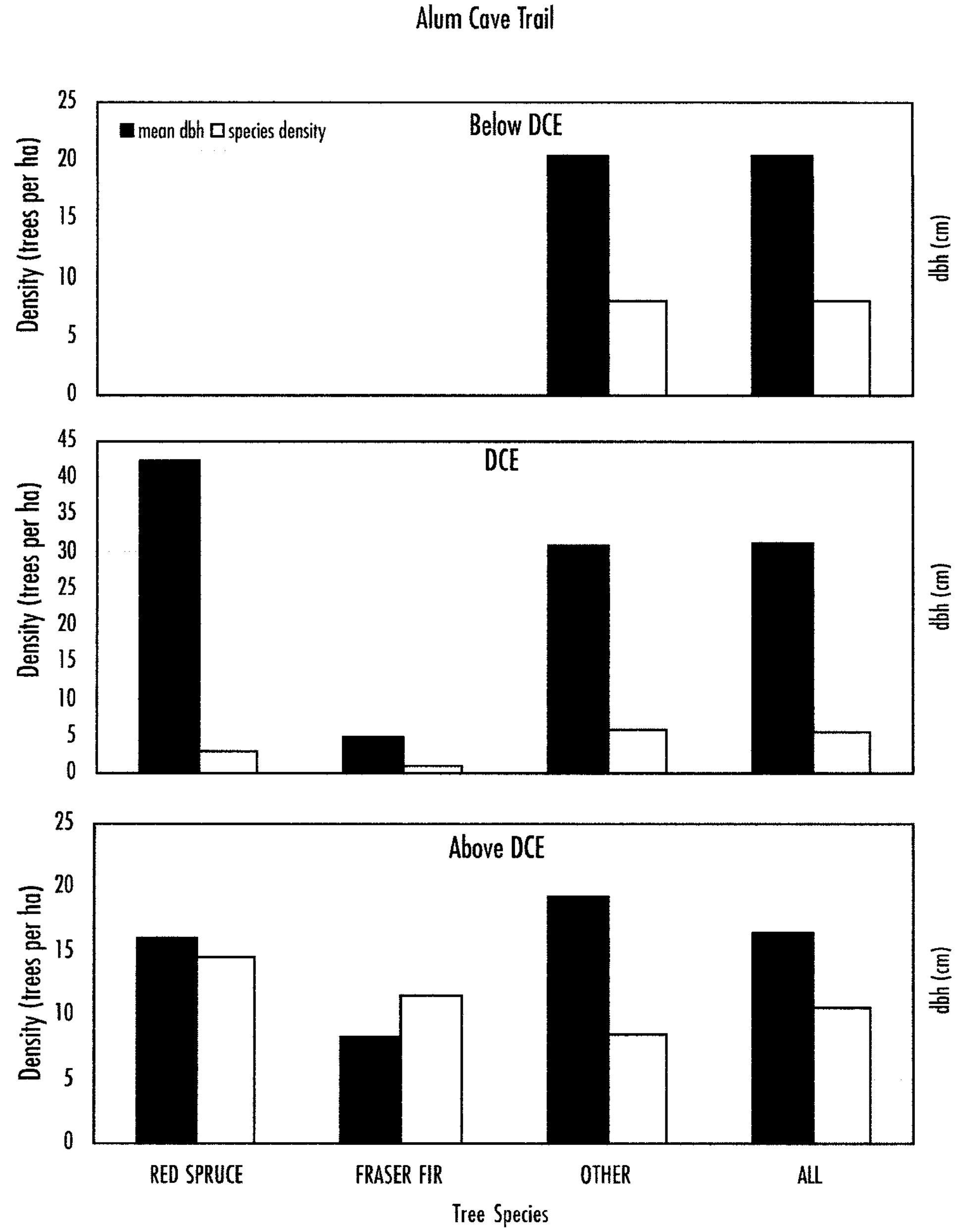


Fig. 4.4d Density and mean dbh of canopy trees (>10cm dbh 1.5m above ground) at the high-elevation study sites on Mount LeConte, GSMNP in 2000 on Alum Cave Trail (ACT). Estimates are based on 0.04-ha circular plots.

Table 4.14 Comparative abundances (± SE) and guild classifications in bird species in three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above the DCE, on BHT, RFT, TGT (excluding Alum Cave Trail) on Mount LeConte, GSMNP, 1999-2000. ^{1} = insufficient sample size

Species	Zone 1		Zone 2		Zone 3						
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	X^2	*P*	Habitat	Migratory	Nesting
Acadian Flycatcher *(Empidonax virescens)*	2.29	0.61	1.50	0.00	1.00	0.22	7.30	0.026•	F	LD	SC
American Crow *(Corvus brachynchos)*	1.37	1.50	2.50	0.28	1.00	0.00	1.27	0.530	F	R	C
Black-capped Chickadee *(Poecile atricopillus)*	1.29	0.19	1.49	0.12	1.45	0.12	0.12	0.943	F	R	SN
Blue-headed Vireo *(Vireo solitarius)*	1.10	0.17	1.98	0.10	1.70	0.05	14.35	0.008*	F	LD^1/SD	SC
Blue Jay *(Cyanocitta cristata)*	1.20	0.33	1.33	0.12	1.20	1.00	0.61	0.738	F	R	C/SC
Brown Creeper *(Certhia americana)*	1.02	0.10	1.22	0.08	1.37	0.12	11.18	0.004•	F-OT	R	SN
Black-throated Blue Warbler *(Dendroica caerulescens)*	1.26	0.23	1.94	0.09	1.65	0.09	5.87	0.053	F	LD	SC/SH
Black-throated Green Warbler *(Dendroica virens)*	1.89	0.22	1.89	0.14	1.51	0.20	1.54	0.462	F	LD	C/SC
Carolina Wren *(Thryothorus ludovicianus)*	1.00	0.00	1.30	0.21	1.05	0.05	0.59	0.744	F	R	GEN
Canada Warbler *(Wilsonia canadensis)*	1.16	0.41	1.76	0.07	1.29	0.12	0.51	0.774	SH	LD	GR
Chestnut-sided Warbler *(Dendroica pensylvanica)*	1.30	0.52	1.68	0.20	1.88	0.16	5.57	0.062	SH	LD	SH
Dark-eyed Junco *(Junco hyemalis)*	2.25	0.25	2.46	0.13	2.76	0.20	5.44	0.066	F-GR	R	GR
Eastern Towhee *(Pipilo erythrophthalmus)*	1.19	0.10	1.59	0.09	1.65	0.14	7.55	0.023	SH/GR	R	SH/GR
Golden-crowned Kinglet *(Regulus satrapa)*	1.38	0.22	1.68	0.12	1.88	0.07	7.52	0.022	SFF	LD^2/TM	C
Gray Catbird *(Dumetella carolinensus)*	—^{1}	—^{1}	1.21	0.21	—^{1}	—^{1}	—^{1}	—^{1}	SH	R	SH
Hairy Woodpecker *(Picoides villosus)*	1.07	0.07	1.37	0.11	1.17	0.13	3.28	0.194	F	SD	SN
Hermit Thrush *(Catharus quttatus)*	1.03	0.34	1.29	0.33	1.45	0.08	6.57	0.050	F-GR	LD	SH/GR
Hooded Warbler *(Wilsonia citrina)*	2.10	0.35	2.22	0.02	1.08	0.08	10.38	0.006*	SC	LD^3	SH
Indigo Bunting *(Passerina amoena)*	1.53	0.18	1.00	0.00	1.00	0.00	7.03	0.030	SH	LD^4	SH
Northern Parula *(Parula americana)*	1.43	0.30	1.00	0.00	1.50	0.50	1.26	0.533	F	LD^5	SC/SH
Ovenbird *(Seiurus aurocapillus)*	3.76	0.25	1.63	0.38	2.06	0.29	10.18	0.006•	F-GR	PR	GR
Pileated Woodpecker *(Dryocopus pileatus)*	1.00	0.00	1.96	0.10	1.00	0.00	0.82	0.665	F	R	SN
Red-breasted Nuthatch *(Sitta canadensis)*	1.16	0.15	1.29	0.08	1.40	0.09	5.95	0.047	SFF	LD	C/SC
Red-eyed Vireo *(Vireo olivaceus)*	2.68	0.27	1.86	0.22	1.66	0.26	11.34	0.003*	C	LD	SC
Scarlet Tanager (Piranga olivacea)	1.20	0.14	1.22	0.11	1.13	0.17	1.24	0.570	C	R	SC
Veery (Catharus fuscescens)	1.55	0.27	2.10	0.07	2.25	0.11	22.79	<0.0001*	F-GR	LD	SH/GR
White-breasted Nuthatch (Sitta carolinensis)	1.14	0.14	1.13	0.13	—^{1}	—^{1}	0.01	0.922	F	R	F
Winter Wren (Troglodytes troglodytes)	1.42	0.30	2.42	0.07	2.19	0.11	31.31	<0.0001*	SC	R	SC
Wood Thrush (Hylocichia mustelina)	1.86	0.18	1.14	0.00	1.00	0.14	10.28	0.006•	F-GR	LD	C/SC

[1] Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD? – [2] Most GRCA winter in Central America some in South Florida and Gulf Coast Plains --[3] Many INBU winter on Coastal Plain of Gulf States and South Florida – [4] Many NOPA winter on Coastal Plain of Gulf States and South Florida – [5] Many OVEN winter on Coastal Plain of Gulf States and South Florida Habitat guild: F=forest (in general), C=canopy, SC=subcanopy, SH=shrub, GR=ground, SF=spruce-fir, F-GR=forest ground.

Migratory guild: LD=long distance, SD=short distance, R=resident, PR=permanent resident, TM=temperate migrant, NM=neotropical migrant.

Nesting guild: C=canopy, SC=subcanopy, SH=shrub, GR=ground, SN=snag, GEN=forest edge or opening

(BHT). The canopy before the adelgid invasion most resembled the relative diversity values (Rabenold et al. 1998) for spruce, fir, and birch currently on ACT.

I focused my statistical analyses on 10 species of birds common to spruce-fir sites in all three zones on the four gradsects (Fig. 4.5). Golden-crowned Kinglets were significantly more abundant on ACT (sites least affected by the adelgid) than at the other sites (χ^2=7.52, $P<0.05$; Tables 4.13, 4.14, Fig. 4.5), possibly because of the high percentage of spruce-fir trees at those sites (r^2=0.68, P=0.02; Table 4.16). Gray Catbirds were rare throughout and Hairy Woodpeckers were marginally recorded. Veerys and Winter Wrens were most abundant on BHT, RFT, and TGT, where, in spite of the decline in spruce-fir, some of the largest trees remain (Tables 4.13, 4.14, Fig.s 4.4, 4.5; Veery: χ^2=22.79, P=0.0001; Winter Wren: χ^2=31.31, $P<0.0001$). Abundance of both species combined regressed negatively against T-CAP *greenness* and positively against forest opening (Veery: r^2=0.56; Winter Wren: r^2=0.74; combined: r^2=0.85, P=0.003). Eastern Towhees were significantly more abundant at BHT, RFT, and TGT than at ACT (χ^2=7.55, P=0.0229; Tables 4.13, 4.14, Fig. 4.5).

Species that did not seem as sensitive to adelgid damage on ACT also varied less in distribution among zones. Veerys were significantly more abundant and varied less on ACT (χ^2 = 3.64, P=0.162) than at the other sites (χ^2=22.79, $P<0.001$). Dark-eyed Juncos were relatively equal in abundance among gradsects but differed significantly in distribution on ACT compared to the other three heavily affected gradsects (ACT: χ^2 = 19.25, $P<0.0001$; BHT, RFT, TGT: χ^2 = 5.44, P= 0.06; Tables 4.13, 4.14, Fig. 4.5). The invasion of bird species not characteristic of spruce-fir forests, e.g. the Chestnut-sided Warbler and Eastern Towhee, showed patterns across sites consistent with trends or

Table 4.15 Comparative abundances (± SE) and guild classifications in bird species in three zones: (1) below the deciduous-coniferous ecotone (DCE), (2) at the DCE, and (3) above the DCE, on Alum Cave Trail (ACT) on Mount LeConte, GSMNP, 1999-2000. Acadian Flycatcher was deleted because it was not observed on ACT. [1] = insufficient sample size

	Zone 1		Zone 2		Zone 3						
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	X^2	*P*	Habitat	Migratory	Nesting
American Crow *(Corvus brachynchos)*			1.00	0.14	0.88	0.00	0.459	0.498	F	R	C
Black-capped Chickadee *(Poecile atricopillus)*			1.47	0.16	1.28	0.12	0.309	0.578	F	R	SN
Blue-headed Vireo *(Vireo solitarius)*	1.41	0.30	2.22	0.12	1.00	0.00	9.771	0.008•	F	LD[1]/SD	SC
Blue Jay *(Cyanocitta cristata)*			1.33	0.33	1.00	0.00	0.667	0.414	F	R	C/SC
Brown Creeper *(Certhia americana)*			1.06	0.03	1.03	0.06	0.266	0.606	F-OT	R	SN
Black-throated Blue Warbler *(Dendroica caerulescens)*	1.39	0.25	2.09	0.13	1.00	0.00	8.886	0.012	F	LD	SC/SH
Black-throated Green Warbler *(Dendroica virens)*	1.58	0.13	1.46	0.24			4.008	0.045	F	LD	C/SC
Carolina Wren *(Thryothorus ludovicianus)*			1.00	0.00	1.00	0.00	0.000	1.000	F	R	GEN
Canada Warbler *(Wilsonia canadensis)*			1.38	0.14	0.94	0.06	3.617	0.057	SH	LD	GR
Chestnut-sided Warbler *(Dendroica pensylvanica)*	1.00	0.00	2.00	0.00	1.98	0.19	7.181	0.028	SH	LD	SH
Dark-eyed Junco *(Junco hyemalis)*	1.00	0.00	2.55	0.25	3.64	0.36	19.249	<0.0001	SH/GR	R	SH/GR
Eastern Towhee *(Pipilo erythrophthalmus)*	1.19	0.10	1.59	0.09	1.65	0.14	7.550	0.023	SFF	R	C
Golden-crowned Kinglet *(Regulus satrapa)*	1.81	0.75	3.25	0.19	2.33	0.22	6.747	0.034	SH	LD[2]/TM	SH
Gray Catbird *(Dumetella carolinensus)*			2.14	0.51					F	R	SN
Hairy Woodpecker *(Picoides villosus)*			1.04	0.07	1.00	0.00			F-GR	SD	SH/GR
Hermit Thrush *(Catharus quttatus)*			1.50	0.50	1.79	0.41	4.026	0.049	SC	LD	SH
Hooded Warbler *(Wilsonia citrine)*									SH	LD[3]	SH
Indigo Bunting *(Passerina amoena)*									F	LD[4]	SC/SH
Northern Parula *(Parula Americana)*	2.00	0.00	1.00	0.00	1.00	0.00	5.000	0.082	F-GR	LD[5]	GR
Ovenbird *(Seiurus aurocapillus)*									F	PR	SN
Pileated Woodpecker *(Dryocopus pileatus)*			1.00	0.00					SFF	R	C/SC
Red-breasted Nuthatch *(Sitta canadensis)*			1.11	0.07	1.43	0.12	6.097	0.135	C	LD	SC
Red-eyed Vireo *(Vireo olivaceus)*	1.00	0.00	1.00	0.00					C	LD	SC
Scarlet Tanager (Piranga olivacea)									F-GR	R	GR
Veery (Catharus fuscescens)	1.86	0.24	2.10	0.20	1.54	0.16	3.639	0.162	F-GR	LD	SH/GR
White-breasted Nuthatch (Sitta carolinensis)			1.00	0.00					F	R	F
Winter Wren (Troglodytes troglodytes)	1.08	0.08	1.83	0.14	1.85	0.16	6.575	0.037	SC	R	SC
Wood Thrush (Hylocichia mustelina)			1.00	0.00					F-GR	LD	C/SC

[1]Some BHVI winter in South Florida and along U.S. Gulf Coast - may be this population. Perhaps SD/LD? – [2]Most GRCA winter in Central America some in South Florida and Gulf Coast Plains --[3]Many INBU winter on Coastal Plain of Gulf States and South Florida – [4]Many NOPA winter on Coastal Plain of Gulf States and South Florida – [5]Many OVEN winter on Coastal Plain of Gulf States and South Florida Habitat guild: F=forest (in general), C=canopy, SC=subcanopy, SH=shrub, GR=ground, SF=spruce-fir, F-GR=forest ground

Migratory guild: LD=long distance, SD=short distance, R=resident, PR=permanent resident, TM=temperate migrant, NM=neotropical migrant

Nesting guild: C=canopy, SC=subcanopy, SH=shrub, GR=ground, SN=snag, GEN=forest edge or opening

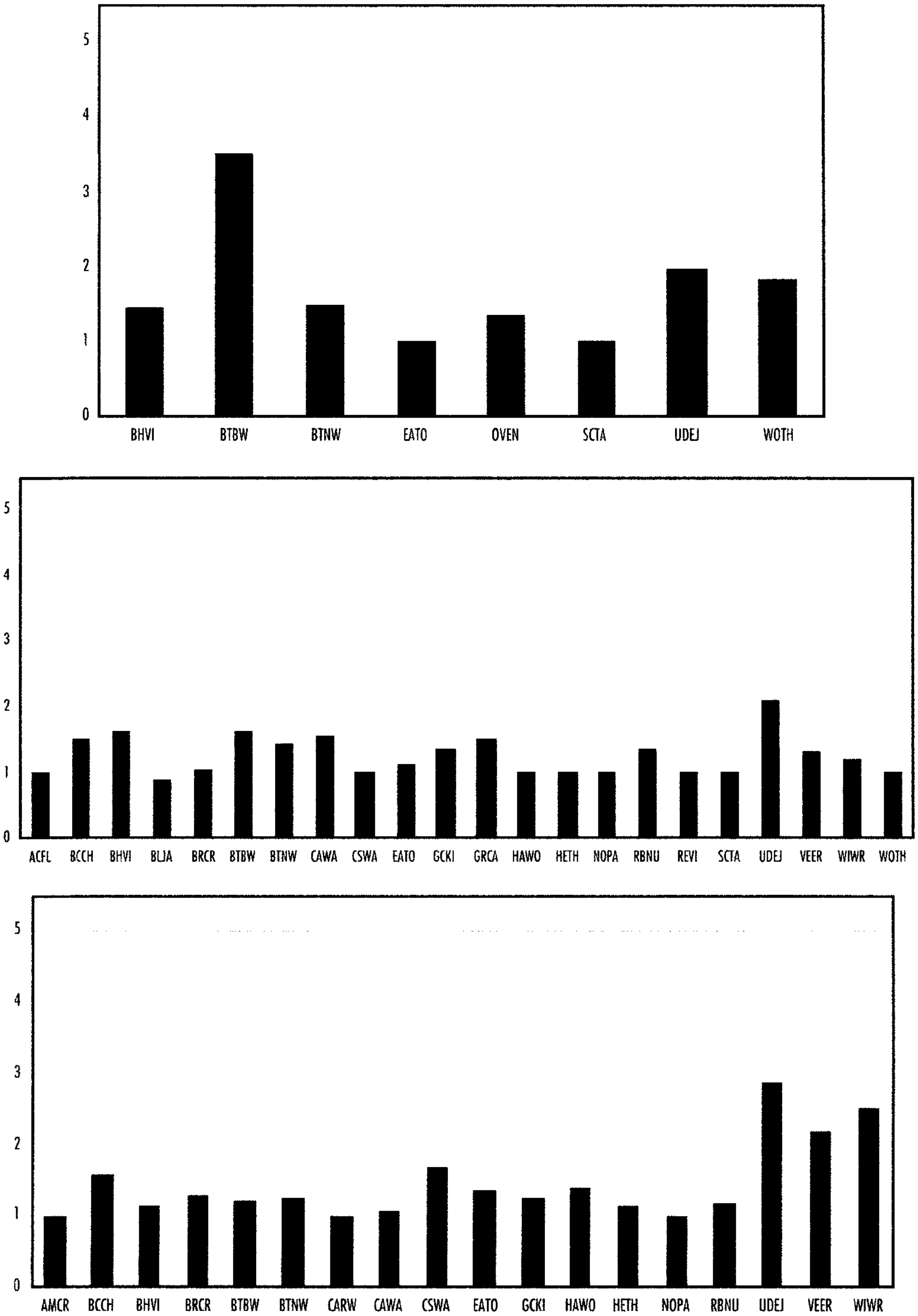


Fig. 4.5a Mean abundance of bird species in three zones at the southern Appalachian study sites from 1999-2000 on Bull Head Trail (BHT) gradsect. Data are mean detection rates from 10-minute, fixed radius (50-m) point counts (based on the mean number of detections for each point replicated three times during each breeding season). Diversity measures (D) are inverse Simpson's.

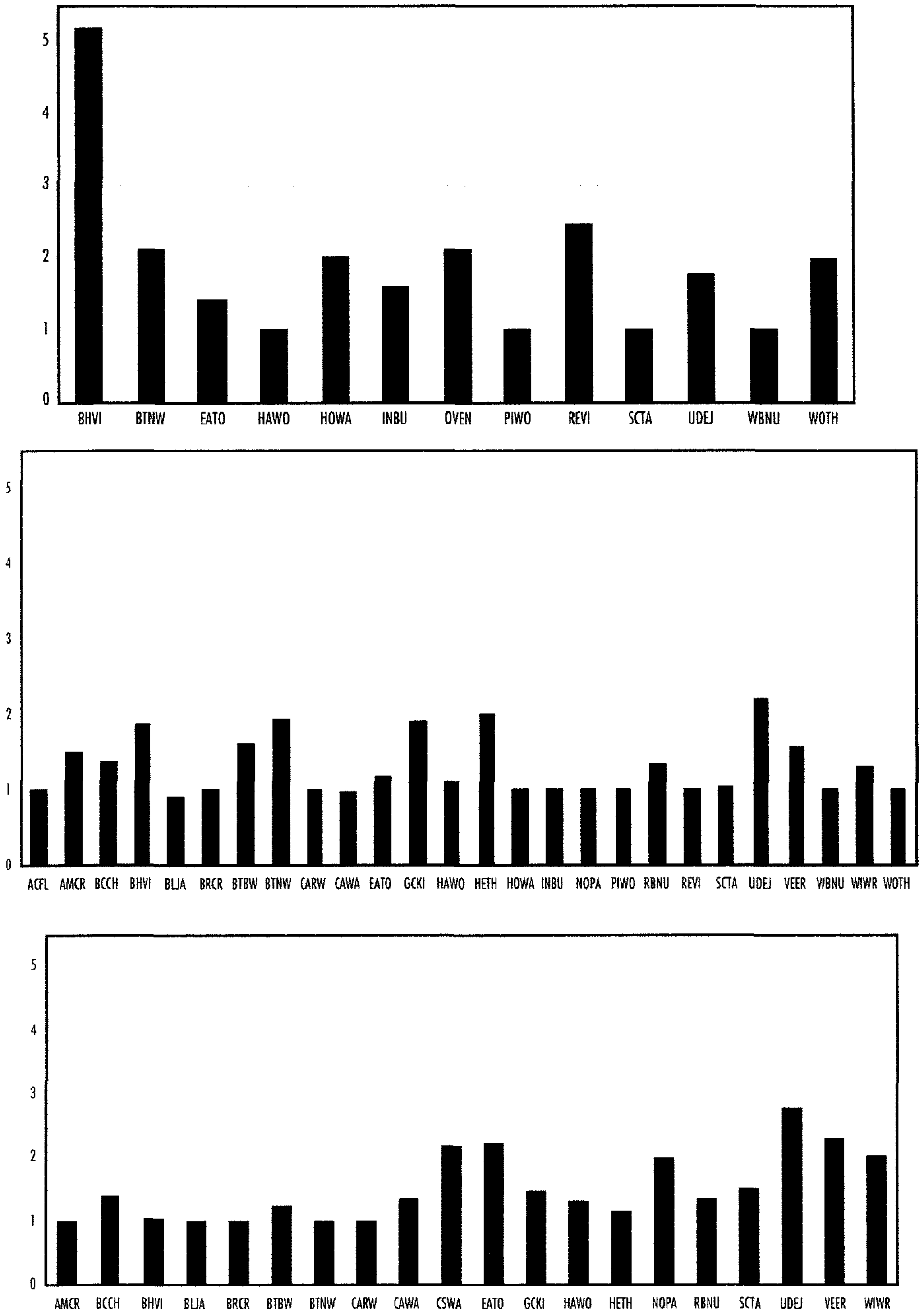


Fig. 4.5b Mean abundance of bird species in three zones at the southern Appalachian study sites from 1999-2000 on Rainbow Falls Trail (RFT) gradsect. Data are mean detection rates from 10-minute, fixed radius (50-m) point counts (based on the mean number of detections for each point replicated three times during each breeding season). Diversity measures (D) are inverse Simpson's.

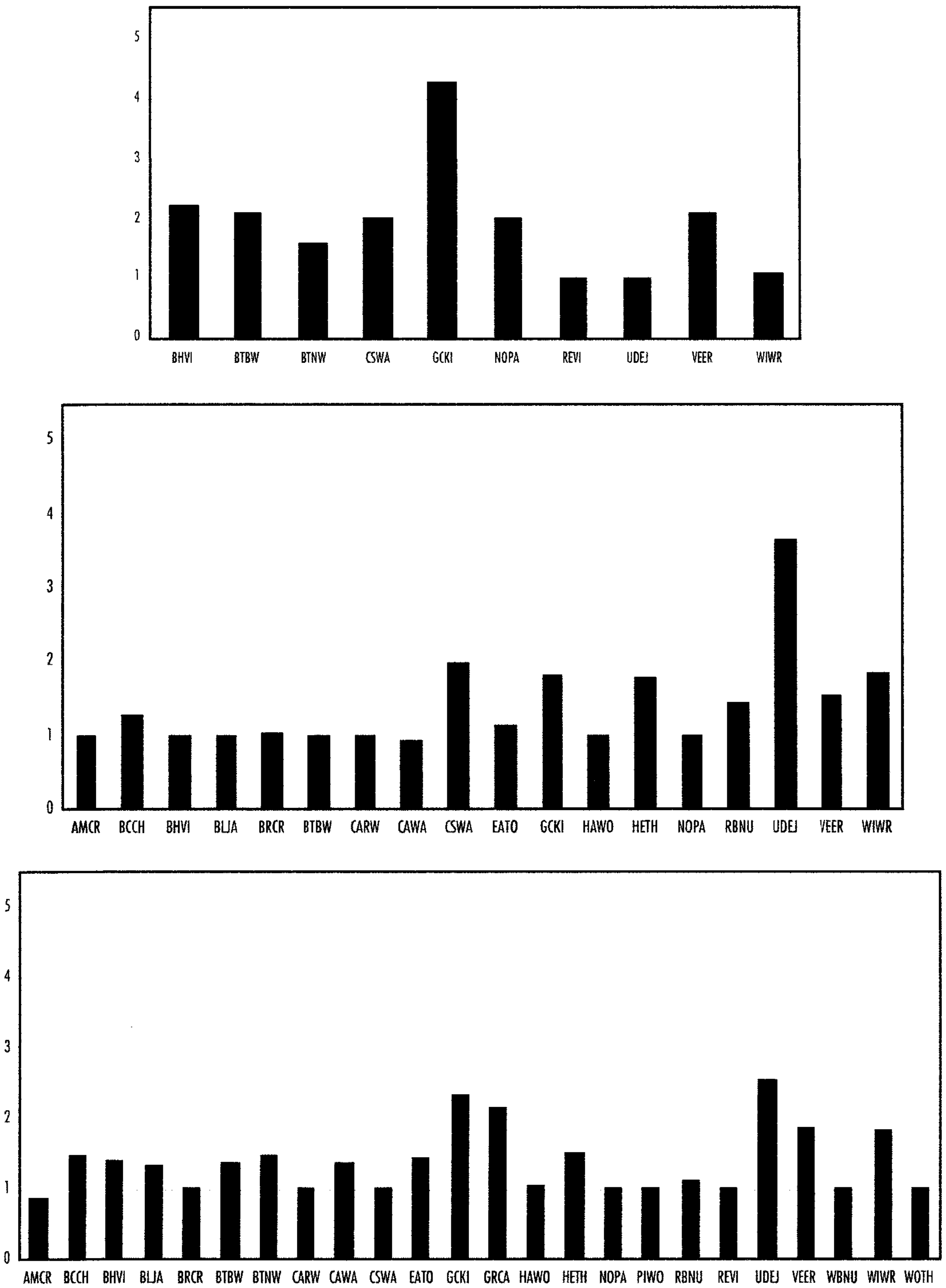


Fig. 4.5c Mean abundance of bird species in three zones at the southern Appalachian study sites from 1999-2000 on Trillium Gap Trail (TGT) gradsect. Data are mean detection rates from 10-minute, fixed radius (50-m) point counts (based on the mean number of detections for each point replicated three times during each breeding season). Diversity measures (D) are inverse Simpson's.

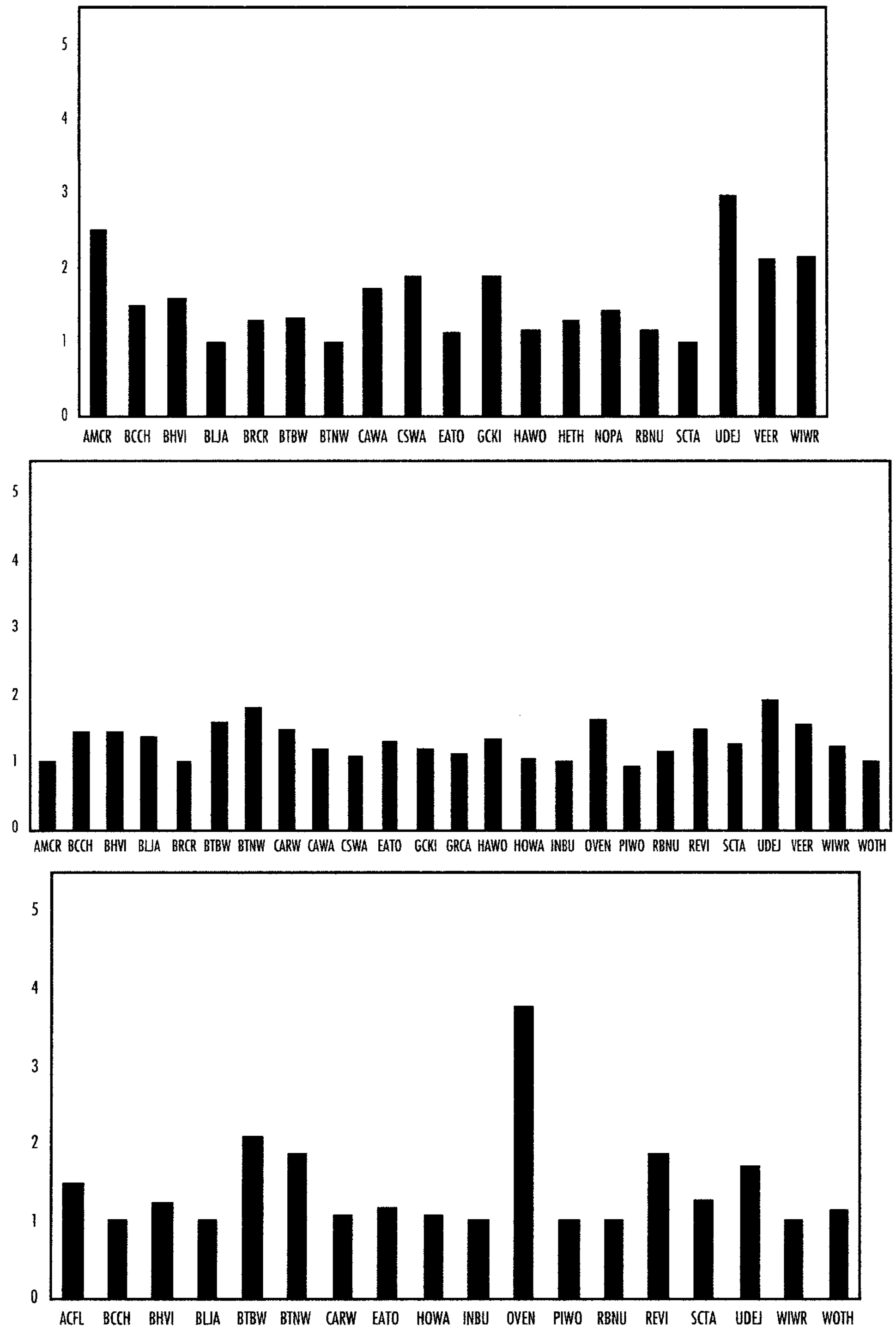


Fig. 4.5d Mean abundance of bird species in three zones at the southern Appalachian study sites from 1999-2000 on Alum Cave Trail (ACT) gradsect. Data are mean detection rates from 10-minute, fixed radius (50-m) point counts (based on the mean number of detections for each point replicated three times during each breeding season). Diversity measures (D) are inverse Simpson's.

Table 4.16 Multiple regression models (stepwise inclusion of variables) predicting bird abundance, based on bird-habitat and TCAP parameters and TCAP relationships for birds breeding at Mount LeConte, GSMNP. Mnemonics for vegetation and other variables are in Table 4.5. Cp statistic was used as a criterion for discriminating between models. One then favors the candidate model with the smallest Cp value of a model is Cp=p, a value that suggests that the model contains no estimated bias. PRESS residuals gave separate measures of the stability of the regression and helped to identify which data points or observations had a sizable influence on the outcome of the regression. TTLABUND = Total Abundance; SPPRICH = Species Richness; FINALGHR = Gound Height Range; FINALLSHR = Final Low Shrub/Tree Seedling Range; FINALTSHR = Final Tall Shrub/Tree Sapling Range; FINALSCHR = Final Subcanopy Height Range; FINALTCHR = Final Tall Shrub/Tree Sapling Range; Other abbreviations are described in Tables 4.2, 4.5 and 4.6. Models for Carolina Wren, Gray Catbird and Hermit Thrush were not developed due to insufficient usable detections.

Bird Species	Model	Cp^{1}	P^{3}	PRESS^{2}	R-SQUARE
Acadian Flycatcher	+ 2.21021(FINALGHR) + 0.02319(TALLCLS)	0.000	2.000	1.256	0.917
American Crow	+ 0.15437(TTLABUND) - 0.06698(TCAP88_B) + 0.02528(TSCC) - 0.01288(TCCC)	0.000	4.000	0.319	0.992
Black-capped Chickadee	- 0.08655(FINALSCHR) - 0.06937(TCAP98_W) + 0.07569(PCTH) - 1.03881(FINALGHR) + 0.11107 (TTLABUND) + 2.28282(FINALLSHR)	8.623	6.000	58.661	0.535
Blue-headed Vireo	- 0.01277(LSCC) + 0.14446(TTLABUND) + 0.00968(TCAP98_B) + 0.00675(TCCC) + 0.01994(PCTD) - 0.20399(SPPRICH) + 0.02005(SLOPE_DEGREES) - -0.76409(DISTURBANCE)	8.044	8.000	188.485	0.486
Blue Jay	- 0.5747(GCC)	0.000	1.000	0.000	1.000
Brown Creeper	- 0.05079(TCAP98_W) + 0.32089(FINALGHR) + 0.00024956(SLOPE_DEGREES)	4.000	3.000	14.753	0.362
Black-throated Blue Warbler	+ 0.03144(FINALTCHR) + 0.11740(FINALTSHR) - 0.11775(SPPRICH) + 0.02407(SCCC) - 0.03108(PCTH) - 0.02925(TALLCLS) - 0.24485(SNAGS)	3.114	7.000	67.722	0.329
Black-throated Green Warbler	+ 1.44614(DISTURBANCE) + 0.00913(GCC) + 0.03172(PCTH) - 0.05552(TCAP88_G) + 0.15596(TCAP98_W) + 0.20374(TTLABUND) + 0.08029(TCAP98_G) - 0.00679(TSCC) + 0.12086(TCAP88_W) - 0.00326(TCCC)	22.284	10.000	78.214	0.824
Canada Warbler	+ 0.06271(TTLABUND) + 0.08448(FINALSCHR) + 0.01033(TALLCLS) - 0.00352 (SCAVGDBH) + 0.00407(CANAVGDBH)	5.326	5.000	10.787	0.744
Chestnut-sided Warbler	+ 0.00112(ELEVATION_M) - 0.08892(FINALTCHR) + 0.93969(FORESTOPENING) - 0.06416(TCAP88_W)	2.958	4.000	25.725	0.660
Eastern Towhee	+ 0.01222(SCCC) - 0.02631(TTLABUND) - 0.03665(SLOPE_DEGREES) + 0.60715(FORESTOPENING) + 0.00884(CANSPDENAVG) - 0.01208(CANSPDENSUM) - 0.02356(SCSPDENSUM) + 0.00051031(CANTTLDBH)	9.000	8.000	4.966	0.764
Golden-crowned Kinglet	+ 0.01053(GCC) - 0.22072(SPPRICH) + 0.08915(TTLABUND) + 0.04831(PCTH) + 0.1827(PCTC) + 0.40129(FORESTOPENING) - 0.00919(TSCC) - 0.00694(SCAVGDBH)	9.000	8.000	51.954	0.687

Table 4.16 Continued.

Bird Species	Model	Cp[1]	P[3]	PRESS[2]	R-SQUARE
Hairy Woodpecker	- 0.01472(TCAP88_G) - 0.01282(GCC) - 0.01567(PCTH) - 0.01488(CANSPDENAVG) + 0.00073675(ELEVATION_M) - 0.00668(SCCC) + 0.00580(SCAVGDBH) - 0.043(SCSPDENAVG)	9.000	8.000	3.903	0.739
Hooded Warbler	-0.05686 (SLOPE_DEGREES) + 0.25116 (FINALTSHR) + 0.03483 (PCTH) - 0.00651 (SCAVGDBH)	5.000	4.000	0.085	
Indigo Bunting	+ 0.00865 (GCC) + 0.14158 (CANSPDENAVG)	3.000	2.000	7.183	
Northern Parula	- 0.03395(TCCC) + 0.90680(FORESTOPENING)	3.000	2.000	3.040	0.869
Ovenbird	- 0.12685(CANSPDENAVG) + 0.10291(FINALSCHR) - 0.02550(SCSPDENSUM) + 0.05109(TCAP88_B) + 0.11906(TTLABUND) - 0.63207(SNAGS)	7.000	6.000	35.825	0.822
Pileated Woodpecker	+ 0.13032(TCAP88_W) - 0.00523(TSCC)	3.000	2.000	0.319	0.806
Red-breasted Nuthatch	+ 0.03901(TCAP98_W) + 0.02003(SCSPDENSUM) + 0.00051905(CANAVGDBH)	65.400	3.000	30.999	0.228
Red-eyed Vireo	- 0.00133(CANTTLDBH) + 0.90404(FINALTSHR) + 0.06826(SCCC) + 0.06672(CANSPDENSUM)	5.000	4.000	9.876	0.801
Scarlet Tanager	+ 0.07277(GCC) - 0.17556(SPPRICH)	3.000	2.000	1.303	0.950
Dark-eyed Junco	-1.3316 + 0.09918(TTLABUND) - 0.00507(CANAVGDBH) + 0.64126(FINALGHR) - 0.06318(PCTH) - 0.03307(TCAP98_B + 0.00055854(SLOPE_DEGREES) + 0.03085(TCAP88_B) + 0.29704(FINALTSHR) + 0.01953(PCTD) + 0.10858 (CANSPDENAVT) -0.05282(CANSPDENSUM) - 0.02178(SCSPDENSUM) +0.00369(CANTTLDBH)	14.000	13.000	375.318	0.057
Veery	0.01336(PCTC) - 0.003(SLOPE+DEGREES) - 0.05956(TCAP88_B) +0.07975(TCAP98_B) - 0.06938(TCAP98_G) + 0.10001(TTLABUND) + 0.02126(PCTH) - 0.53204(FINALLSHR) + 0.4751(FINALGHR) + 0.4751(FINALGHR) + 0.00915(SUBCLS) + 0.70631(FORESTOPENING) + 0.00936(TSCC)	11.491	12.000	61.445	0.567
White-breasted Nuthatch	- 0.01453(TCAP98_G) - 0.000579(CANTTLDBH) + 0.00251(SCAVGDBH) - 0.03247(SLOPE_DEGREES)	5.000	4.000	3.534	0.736
Winter Wren	+ 0.00165(ELEVATION_M) - 0.02166(PCTD) - 0.04399(TCAP88_G) + 0.027772(TCAP98_B) + 0.03272(TALLCLS) + 0.42651(FORESTOPENING) + 0.00927(SCCC) - 0.42131(FINALTSHR) - 0.01092(CANSPDENSUM) - 0.0029(SCAVGDBH)	6.140	10.000	13.149	0.744
Wood Thrush	- 0.23154(FINALTCHR) - 0.00637(LSCC) - 0.19339(SCSPDENAVG)	4.000	3.000	0.801	0.970

changes on the gradsects. Both of these species showed significantly higher densities at the most heavily affected sites on BHT, RFT, and TGT than at the other sites (Chestnut-sided Warbler: $\chi^2=7.18$, $P<0.0276$; Eastern Towhee: $\chi^2=7.55$, $P=0.0229$; Fig. 4.5). The same was true for the Canada Warbler ($\chi^2=3.61$, $P<0.05$; Fig. 4.5). These two species responded to changes in the understory as the canopy opened; density of invading species combined regressed positively with forest openings (Tables 4.13, 4.14: $r^2=0.66$, $r^2=0.76$, $P=0.021$). I also found a positive relationship between forest openings at a site and abundance of Solitary Vireos ($r^2=0.77$, $P=0.03$). Blue-headed Vireos and Black-throated Blue Warblers were abundant on all gradsects and significantly different among zones in spite of the disparate patterns in coniferous, deciduous, and hemlock communities [Blue-headed Vireo: $\chi^2=14.35$, $P=0.008$ (ACT only: $\chi^2=9.77$, $P=0.008$); Black-throated Blue Warbler: $\chi^2=5.07$, $P=0.05$ (ACT only: $\chi^2=8.88$, $P=0.012$); Tables 4.13, 4.14, Fig. 4.5].

Relationships among Birds, Habitat Measures, and T-CAP Indices

Twenty-six bird species were modeled using stepwise multiple linear regression (Table 4.16). The bird species were diverse in that they included bark foragers (gleaners and drillers), salliers, foliage gleaners, and ground foragers; except for the Dark-eyed Junco, the most numerous species were foliage gleaners. The (adjusted) coefficient of multiple determination (R^2) was lowest in the Red-breasted Nuthatch (0.228) and highest in the American Crow (0.99). In most species, R^2 ranged from 0.05 to 0.99 (Table 4.16). Prediction errors were small (i.e., 10.0% for all species except the Black-throated Green Warbler, Red-breasted Nuthatch, and Veery; Table 4.16). Dbh, density, T-CAP *greenness*, T-CAP *wetness*, and percent hemlock were the most commonly selected predictor variables (Table 4.16). Two of the 15 cover-type variables (TCCL and GCL) were not selected as significant predictors of species abundance in any stepwise multiple regression model.

As structural features of vegetation, dbh and density of canopy and subcanopy trees were selected most often as significant predictors of bird species abundance, each appearing in seven of 26 species models developed using multiple regression (Table 4.16). Species abundance was positively related to the DBH_CAN variable in all of the models in which it appeared. Species abundance was positively related to DBH_DENS in four of seven models in which it appeared. DBH and DENS of the subcanopy appeared in 11 of 26 species models and were negatively related to species abundance in seven of these.

The standardized regression coefficients that comprised the final regression models indicated the relative importance of each variable to the model. For example, abundance of Golden-crowned Kinglets increased with an increasing volume and number of coniferous trees (spruce-fir), but decreased with an increase in subcanopy development (Table 4.16). Also, abundance of Black-throated Blue Warblers increased with an increase in cover and height range of tall shrubs (saplings and subcanopy trees, but decreased with an increase in ground cover. Therefore, the habitat-relationships for each species can be deciphered in a similar manner.

T-CAP *greenness* and *wetness* appeared as predictor variables for 15 birds (Table 4.16). For example, the abundance of Blue Jays increased with an increasing number of deciduous trees and *greenness*; abundances of Red-breasted Nuthatch and Warblers were associated with increasing *wetness*; and abundance of Veerys was associated with an increasing number of coniferous (including hemlock) trees but decreased with an increase

Table 4.17 Comparison of Inverse Simpson diversity indices among zones and trails (gradsects). Gradsect means were obtained by averaging the means for all three zones to get one mean.

Variable Trail	Zone 1		Zone 2		Zone 3		Averaged Gradsect Mean
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	
ACT	7.79	0.16	12.69	0.14	8.60	0.27	9.69
BHT	9.95	0.15	12.64	0.28	11.09	0.71	11.22
BMT	13.46	1.08	9.19	0.55	–	–	
BVT	–	–	8.05	0.32	1.97	0.00	
RFT	4.07	0.36	9.97	0.25	9.97	0.15	8.00
TGT	8.39	0.28	11.60	0.22	9.04	0.18	9.67
Canopy	8.011	0.42	10.49	0.22	9.57	0.27	
Subcanopy	9.28	0.26	11.61	0.12	9.50		0.16

in sites representing *greenness* and *brightness*.

Species Diversity and T-CAP among Zones and Gradsects

Composite measures of relative abundance showed clear patterns across zones and gradsects. I averaged the means for all zones to obtain one mean for each gradsect. Species diversity was highest on BHT (D=11.22 according to inverse Simpson's index of diversity, D-1/Σpi^2, where *pi* is the proportion of all birds belonging to species *i*, expressing diversity as the equivalent number of equally represented species; Peet 1974; Fig. 4.5). Greatest diversity occurred on BHT and compared to ACT and TGT, dominance of invading species (those not characteristic of the zone/gradsect) was not pronounced (Fig. 4.5). Except for the high values on BHT, diversity indices followed by ranking of intensity of disturbance, with ACT ($\bar{x}$=9.69, D=5.94) and TGT ($\bar{x}$=9.67, D=9.67) more diverse than RFT ($\bar{x}$=8.00, D=7.68; Tables 4.16, 4.17).

Patterns of species richness on ACT, BHT, RFT, and TGT are shown in Fig. 4.6. Patterns of relationships among species diversity measures and T-CAP indices on the gradsects are shown in Fig.s 4.7 and 4.8. On ACT, Zone 1 was significantly different (lower) than Zones 2 and 3; *greenness* values decreased from Zone 1 to Zone 3 (Fig. 4.7), with Zone 3 having the lowest value, whereas *wetness* increased from Zone 1 to Zone 3 (Fig. 4.8). BHT showed an increase in species richness from Zone 1 to Zone 3 and *greenness* also increased from 1 to 3. For both RFT and TGT, species richness increased when *greenness* and *wetness* decreased.

Four general levels of tolerance to habitat alterations were identified based upon the relationship between birds and their distributions in the ten forest community habitat categories (Table 4.19). Species with low tolerance indices were restricted to few

Table 4.18 Species richness and total abundance in forest community types on Mount LeConte, GSMNP. Definition of forest types are found in Appendix A.

Ecotonal Community Classification	**Species Richness**	**Total Abundance**
CH	8.66	10.52
F	8.83	14.29
HH	8.07	10.91
MO	7.03	9.63
NH	12	13.72
P	6.55	11.45
SF	9.28	13.25
SNH	10.58	13.36
TP	6.57	13.79
XO	6.68	9.52

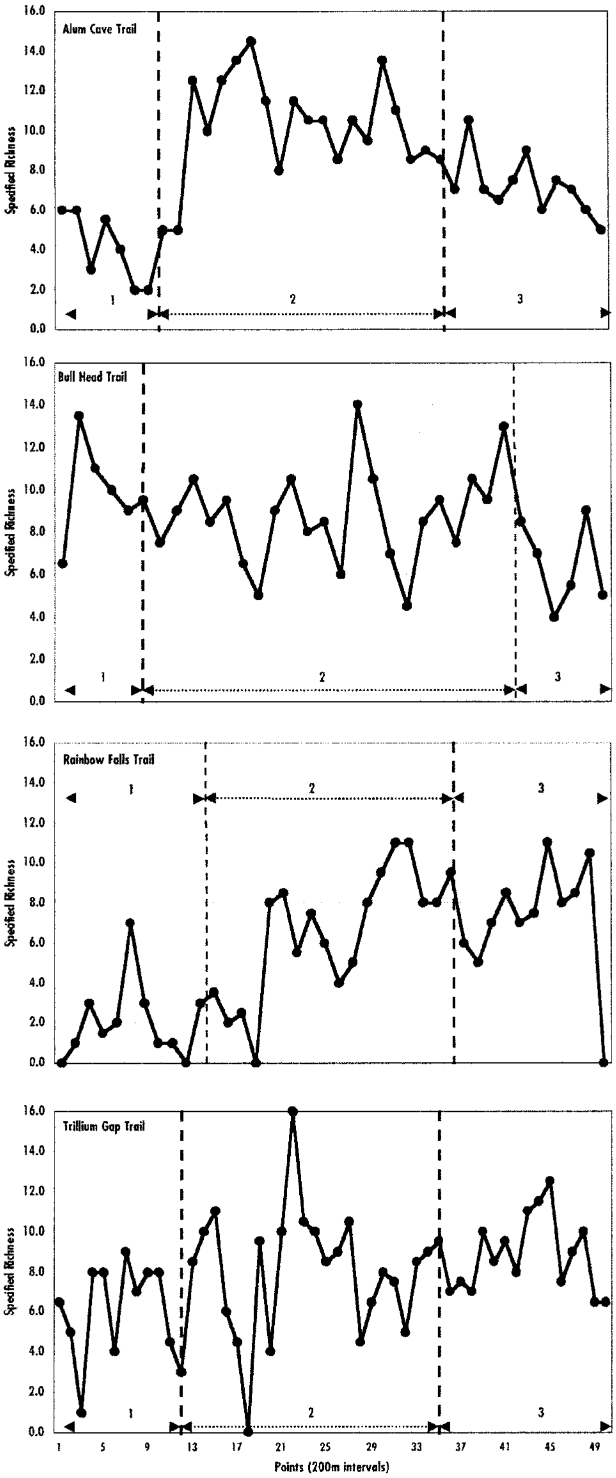


Fig. 4.6 Comparisons in species richness on four elevational gradsects (trails) on census points at 200m distance intervals. Elevation increases along the x-axis. Vertical lines define ecotonal boundaries in species richness. Dashed lines define zones 1, 2, and 3.

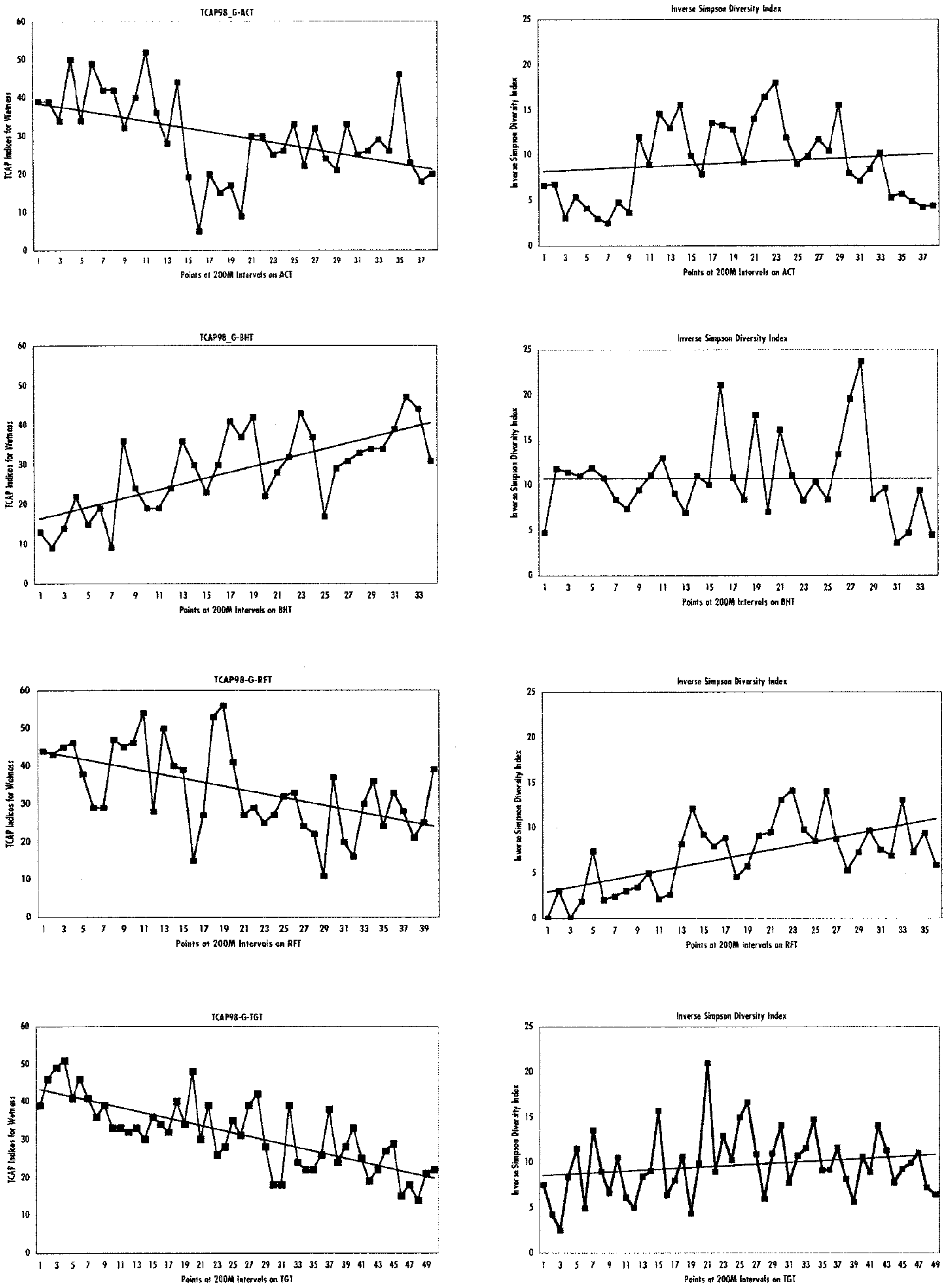


Fig. 4.7 Comparison between T-CAP Greenness Indices and Inverse Simpson Diversity Indices on four elevational gradsects (ACT, BHT, RFT, TGT) at trailpoints of 200-m intervals on Mount LeConte, GSMNP. Elevation increases with trail points along the x-axis, except for BHT where elevation decreases. Bold straight lines indicate trend patterns.

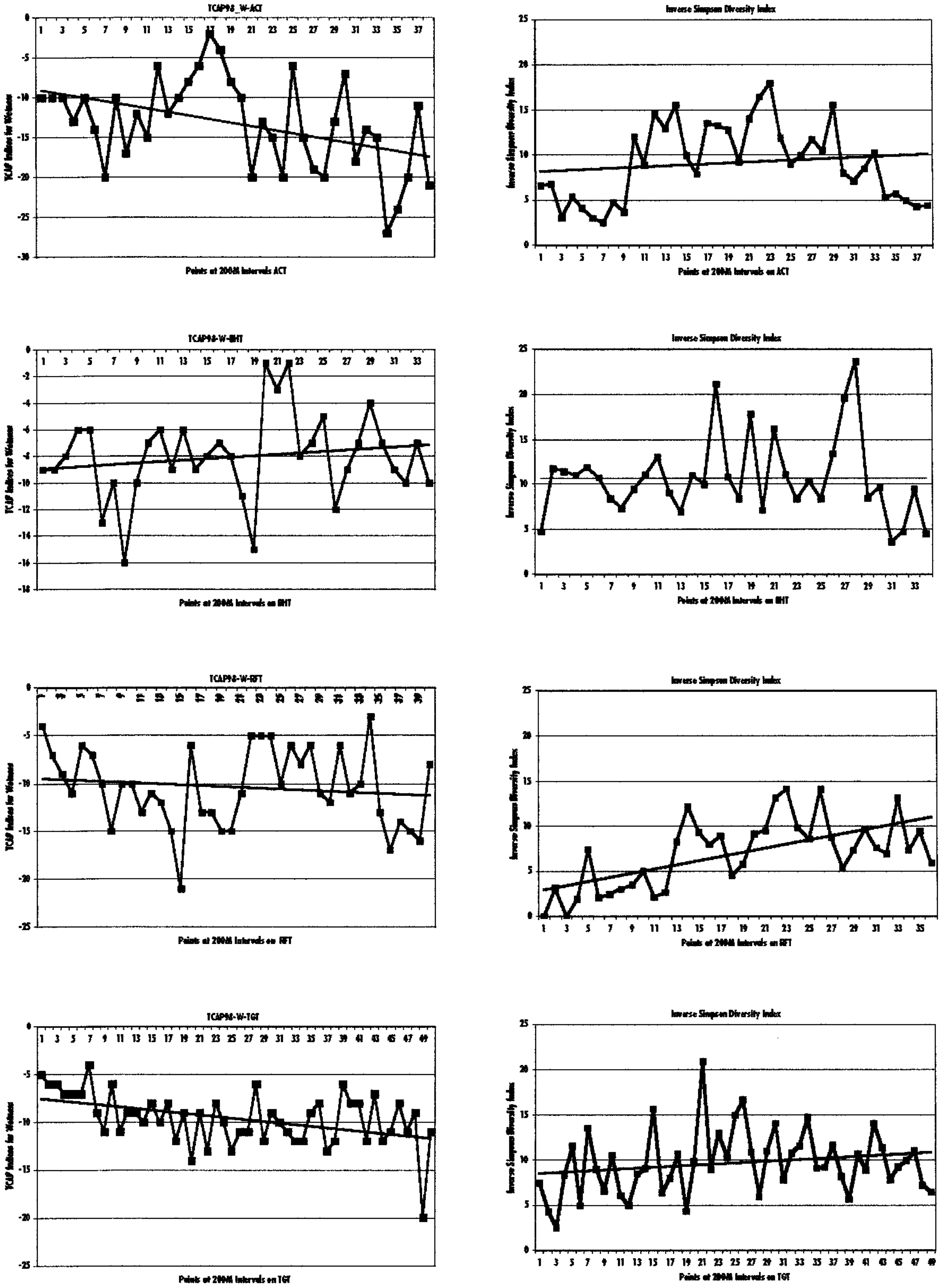


Fig. 4.8 Comparison between TCAP Wetness Indices and Inverse Simpson Diversity Indices on four elevational gradsects at points (distance) at 200-meter intervals on Mount LeConte (GSMNP). Elevation increases along the x-axis. Bold straight lines indicate trend patterns.

habitats or used their habitats more unevenly. Such species would be affected most adversely by loss of their preferred habitats.

Results of Kruskal-Wallis nonparametric ANOVAs (used because T-CAP data failed tests of normality and equality of variances among forest classes) indicated significant differences in mean values of all three T-CAP indices for coniferous, deciduous, and hemlock classifications and thinned overstory classifications. Pairwise Tukey's HSD tests delineated a decreasing gradient of brightness values from forest openings to closed-canopy deciduous sites, with other classes having intermediate values in 1998 (Tables 4.8, 4.10, 4.12; Fig. 4.7). *Greenness* values also differentiated closed canopy fir stands from all other classes. *Wetness* distinguished deciduous sites from coniferous sites, with higher values associated with wetter conditions. Zone 1 on ACT which had exclusive hemlock sites, rendered *greenness* values.

Spatio-Temporal Variation in T-CAP Topographic Variable Relationships

After defining the spectral differences among 10 forest classes, I explored the relationships among T-CAP indices, environmental variables, and bird diversity measures to reveal how remote-sensing techniques could be used to study and monitor spatial and temporal patterns of changes in bird diversity. This analysis benefitted from the zonal and elevational gradients of Mount LeConte.

Regressions of bird diversity measurements using T-CAP indices as predictor variables, revealed *brightness* and *greenness* were correlated in significantly linear relationships (Table 4.15, Fig. 4.9). Patterns of T-CAP values, however, suggested that bird diversity measures, in most cases, were inversely related to *greenness* and *wetness* (Fig. 4.9).

Table 4.19 Relative abundance of bird species (n=15,893) among the forest types (expressed as the number of observations per hectare per 12 censuses) and the (hypothesized) relative tolerance of each species to habitat alteration, including deterioration (due to destruction of conifers by the balsam woolly adelgid). Tolerance index was the reciprocal of Simpson's Index (1/Σpi2, where pi=the proportion of the total sample in the ith group) calculated for habitat selection of 29 species on the basis of their relative abundance in the 10 forest types.

	General Habitat Type										
Species	CH	F	HH	MO	NH	P	SF	SNH	TP	XO	Tolerance Index
Low Tolerance Species											
Gray Catbird			1.5		1	1.1	3	1			4
Acadian Flycatcher	1			2	1				3	1.3	4.1
Indigo Bunting	1.3			1		1			2.3	1.2	4.4
Ovenbird	1.7			3.5		2.5			2.6	2.2	4.7
Hermit Thrush		1.5	2		1.1		1.2	1.3			4.8
Wood Thrush	1.5		1	1.9		1		1	1	1.5	6.5
Eastern Towhee	1.1	1.4	1.3	1	1.2	1.2	1.4	1.7	1.4		8.8
Moderate Tolerance Species											
Hooded Warbler	1		1	1		1.3			2.7	1.6	5.1
Chestnut-sided Warbler		2.3	1.3		1.9	1.2	1.3	1.6			5.7
American Crow	1.3	1	1.7		1		1.2	0.9			5.7
White-breasted Nuthatch	1		1.5	1	1	1				1.5	5.8
Tolerant Species											
Northern Parula	1	1	2	1	1.5		1.7	1.2			6.5
Pileated Woodpecker	0.9		0.8		1.3	0.8	1		1	1	6.8
Golden-crowned Kinglet	1.7	1.4	2.1	2	1.4		1.9	1.8			6.9
Scarlet Tanager	1.1	1	1.2	1	1			2	1	1.3	7.5
Red-eyed Vireo	1.4		1	2.4	1	2	1	1	3.1	1.8	7.6
Black-capped Chickadee	1.3	1.2	1.6		1.3	2.1	1.7	1.4		1	7.6
Veery	1.3	1.9	1.8	1	1.6	1.5	1.9	2.1			7.7

Table 4.19 Continued

	General Habitat Type										
Species	CH	F	HH	MO	NH	P	SF	SNH	TP	XO	Tolerance Index
Tolerant Species											
Canada Warbler	1	1	1.1		1.5	1	1.4	1.3	1	7.8	
Blue Jay	1.1	1	1.3		0.9	1.5	1.3	1		1.3	7.8
Hairy Woodpecker	1.3	1.3	1.2		1.1	1	1.2	1.2		1	7.9
Black-throated Blue Warbler	1.5	1	1.9	2	1.6	1.1	1.2	1.4		3	8
Winter Wren	1.3	2.2	1.2	1	1.5	1.2	2.1	2		1	8.3
Black-throated Green Warbler	2.5		1.8	2.3	1.4	1		1.8	2.1	1.7	8.3
Brown Creeper	1	1.1	1		1.1	1	1.2	1.1	2	1.3	8.5
Carolina Wren	1	1	1.7	1	1		1	1.1	1	1.2	8.7

Although Lansat TM data were not topographically corrected (apart from the correlations with elevation), T-CAP values were significantly related to few of the topographic variables. On Mount LeConte, elevation was significantly related to T-CAP *brightness* and *greenness* in both years as well as *wetness* in 1998. In 1988, when fir mortality was peaking at Mount LeConte, T-CAP *brightness, greenness,* and *wetness* were significantly associated with slope, suggesting that forest community distribution at this time was structured by steepness of slope.

Discussion

One purpose of this study was to develop and test bird habitat models (with multiple linear regression and multivariate analyses) that describe the ability of T-CAP variables to predict species abundance and richness and to detect changes in communities that have deteriorated due to balsam woolly adelgid infestations.

Analyses of Bird Habitat Relationships

Correlation analysis initially provided a relatively straightforward technique for coupling bird abundance estimates with numerous measurable habitat variables. The existence of significant correlations suggests that, at the least, these variables are relevant to the sorts of questions I am asking. Several patterns emerged as a result. For example, there was a clear association between the abundances of Canada Warbler, Chestnut-sided Warbler, Eastern Towhee, Gray Catbird, Hooded Warbler, Indigo Bunting, and Winter Wren (typical forest species) and variables describing subcanopy, tall, and low shrub cover (SCC, TSCC, LSCC). On the other hand, there were strong negative relationships with GCC and several other variables associated with increasing vertical heterogeneity (GHR and TCHR). Carolina Wren and Hairy Woodpecker, both forest-dwelling

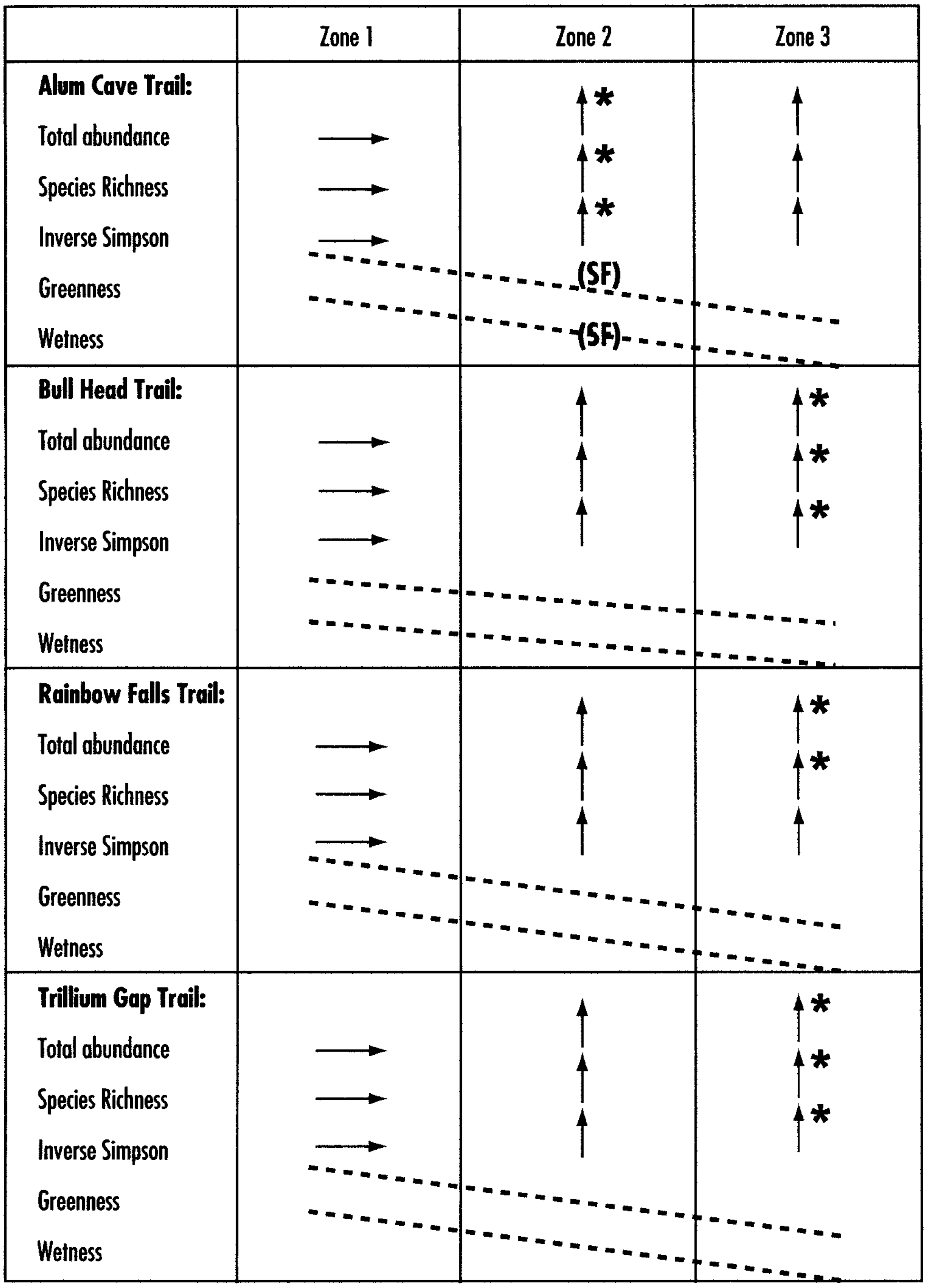


Fig. 4.9 Pattern recognition by author using total abundance, species richness, Inverse Simpson Diversity Index, and T-CAP greenness and wetness among gradsects to predict trends in forest communities. *Indicates highest values, dashed line indicates trend, right arrow indicates beginning values, upward arrow indicates increasing values, and downward arrow indicates decreasing values.

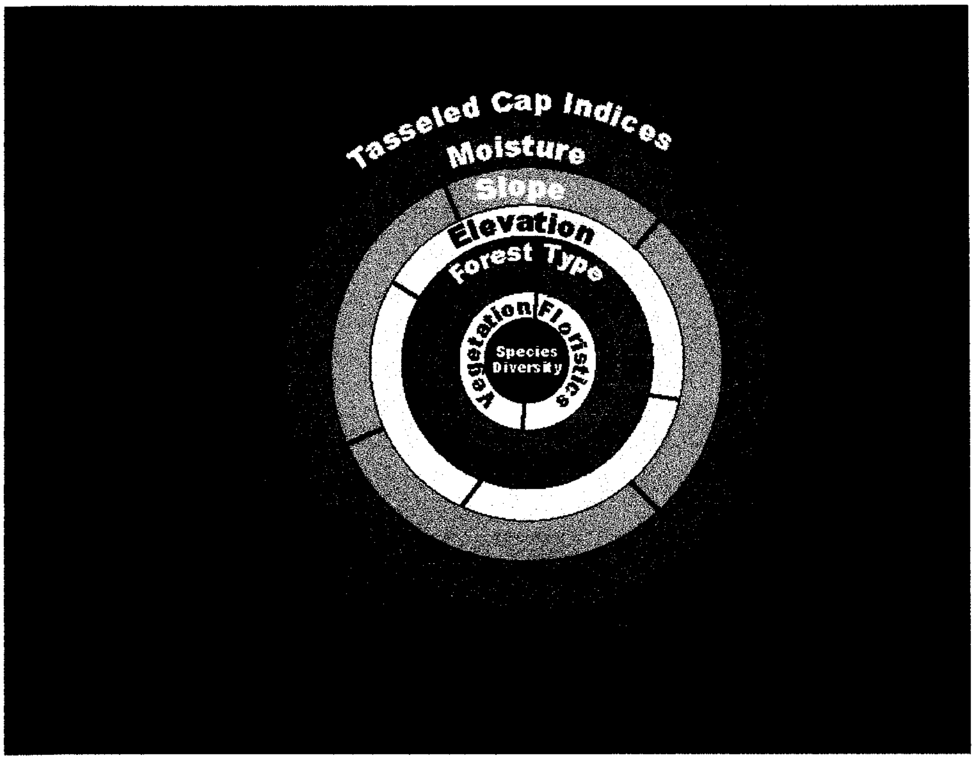


Fig. 4.10 Illustration of factors that can be used to predict species richness. Rotation of each factor changes the relationship among factors. Such changes may result in the correct configuration alignment to predict species diversity.

permanent residents, PR, did not demonstrate such strong relationships.

Covarying in a different manner, were several of the high elevational species, particularly Black-capped Chickadee, Blue-headed Vireo, Brown Creeper, Black-throated Blue Warbler, Dark-eyed Junco, Red-breasted Nuthatch, Veery, and Winter Wren. These species had high positive correlations with canopy and subcanopy coverage values of coniferous trees and with several indices relating to horizontal heterogeneity, but, conspicuously, not with values of deciduous trees and shrubs. As shrub coverage increased, the abundance of these species increased.

Black-throated Green Warbler, Chestnut-sided Warbler, and White-breasted Nuthatch, showed definite patterns with strongly negative relationships to both several vertical (GHR) and horizontal indices (GCC). Although both the Black-throated Green Warbler and Chestnut-sided Warbler are Neotropical migrants, the other Neotropical species exhibited less clear patterns. Red-breasted Nuthatch, a high elevation Neotropical migrant (NM) preferring spruce-fir forests or coniferous sites, showed a positive relationship with the vertical height range of subcanopy and canopy and horizontal coverage values.

TSHR, SCHR, SCCC, TCHR, and TCCC showed perhaps the strongest patterns, serving to separate the responses of most of the NM species (which preferred shrub and subcanopy parameters) from those of the permanent resident species (which preferred canopy, ground, and snag parameters). In addition, forest opening and snags were highly correlated with birds of forest habitat guilds. The birds that reached their maximum abundances and had significant relationships with these landscape variables were the Acadian Flycatcher, Black-capped Chickadee, Blue Jay, Black-throated Green Warbler, Carolina Wren, Chestnut-sided Warbler, Eastern Towhee, Hooded Warbler, Hermit Thrush, Northern Parula, Ovenbird, and Wood Thrush. Montane meadows are often thickly carpeted with wildflowers in the spring, and while these bird species may be responding to other features of the environment, their association with the forbs is nonetheless significant. A greater number of bird species associated with community size, canopy volume (summed dbh), and trees per hectare (density), whereas relatively few species were associated with features such as trunk height, logs, or snags; mortality of Balsam Fir in GSMNP apparently left many snags that have attracted certain birds into the area.

Two levels of habitat variables can be distinguished among those commonly used by biologists. First, major features of the habitat, such as habitat size, distance to the edge, canopy volume, dbh, tree density, and forest types (ECC), that are correlated with many bird species. Such variables represent broad or "macro" habitat features and are associated with the community as a whole. Second, features, such as snags and logs, that are associated with some bird species but were not useful as predictors for large number of species in my study. This "micro" level is associated with features that could potentially be correlated with individual species.

When collecting data in the field, I sampled macro features on a micro level, such as by viewing the canopy through a camera on a tripod to measure openness or ocularly determining the presence or absence of ground cover. This approach provided useful data; however, when macro information may be the only data required, aerial photography is a quicker and cheaper method than tedious on-site sampling. At the macro level, several patterns emerged using variables describing dbh subcanopy, density subcanopy, subcanopy cover class, species specific subcanopy cover, subcanopy foliage height range, tree canopy foliage height range, and ecotonal community classification (Table 4.6). For example, in interpreting the two characteristics of the Pearson correlation coefficient, the signs of the coefficient indicated significant positive relationships between T-CAP indices and forest vegetation parameters. Another important characteristic of a correlation coefficient is its size: the greater the absolute value of a correlation coefficient the stronger the correlation (e.g. ± 0.00 = no correlation vs. ± 1.00 = perfect correlation). Relationships of the T-CAP indices (*brightness* and *greenness*) with variables describing dbh subcanopy, subcanopy foliage height range, and tree canopy foliage height range ("micro"-level features) were significant, but weakly to moderately correlated (0.31-0.48; Table 4.6). This means only 31-48% of the variation in the data can be (was) explained by T-CAP indices. The correlation between *brightness* and *greenness* with forest type or ecotonal community classification was stronger (0.56 and 0.57, respectively). I explained more variation using this ("macro"-level) feature than with the "micro"-level features. This could mean that I have less (little) confidence in using T-CAP indices, and more confidence in using forest type, to predict bird abundance or species diversity. Overall, as this was an initial investigation, the results were adequate in describing preliminary T-CAP-habitat-bird relationships.

The coefficients of multiple determination (R^2) from regression analyses indicated that the vegetation variables I used accounted for a high amount of the variation in bird abundance; in contrast, Cp values that suggest the model contains no estimated bias, were generally low. My results indicated that variables describing the size (dbh or height) of trees by species, the foliage volume in the subcanopy (i.e. taller ht intervals), and forest openings were important predictors of bird abundance. In a related study, Morrison et al. (1987) found that tree size and subcanopy development were important components of the habitat of many forest birds, as well as seasonal variation in habitat use. I concluded that final models presented herein (Table 4.15) successfully predicted presence or absence of bird species (except for several species that were less common in my study area).

Exploratory models that search for general bird-habitat relationships and those that sought only presence absence resolution were probably adequate in the initial investigation. For example, Black-throated Blue Warblers nested and foraged in the shrub and subcanopy layers of the forest. Their distribution was associated with subcanopy and tall shrub cover. Pearson correlation analysis correlated them with shrub height and density in coniferous forests. Multiple regressions (Table 4.15) demonstrated that Black-throated Blue Warblers occurred on sites with more substantial subcanopy and shrub cover. Thus, subcanopy, shrub cover, and height range seemed to influence Black-throated Blue Warbler density. Its distribution, then, was affected by vegetation structure and not by distribution of any plant species. In forests on Mount LeConte, presence of coniferous trees affected Golden-crowned Kinglet and Veery distributions. In addition, some bird species foraged in hemlock trees, suggesting that the spatial distribution of tree species could affect bird distribution.

The Mount LeConte bird community, then, consisted of birds that are affected by tree species composition and distribution as well as birds that were influenced by vegetation structure. Thus, understanding patterns of bird species' co-occurrence will result from both detailed studies of the features that affect individual species distributions, and analyses that compare the bird community as a whole to structural or floristic characteristics of the habitat.

Site Characteristics and Comparisons

Canonical correspondence analysis showed that elevation played a role in the importance of high elevation dominants, namely Fraser fir, red spruce, and yellow birch, and their associated bird species. Fraser fir was often associated with ridgetops, particularly at the highest elevational sites; comparatively high disturbance frequency on such sites is one reason for its prevalence. Red spruce, at the highest elevational sites, tended to occur in sheltered coves rather than on ridges, whereas at the lower ends of its elevational range, it often occurred with hemlock on ridges. Yellow birch often dominated cove sites at comparable (lower) elevations and red spruce was less important in the coves than on ridges at these lower elevations. Golden (1981) also notes that red spruce is more prominent on upper slopes and ridges at the lower end of its elevation range.

These observations indicate that topographic position was a key factor in determining ecotone position of the montane spruce-fir forest. For Fraser fir, there did not appear to be an effect of topographic position at the lower end of its elevation range, but, in this case, it grew at minimal elevations on lower slopes and in coves, not ridges. From these patterns, I conclude that (1) topography, slope, aspect, and potential solar radiation did not play a strong role in determining the lower elevational limits of the spruce-fir zone, and (2) factors determining the lower limits of red spruce differed from those determining the lower limits of Fraser fir.

Inferences on movement of the ecotone over time were made by comparing bird populations and the size-class structures of red spruce and Fraser fir across elevational zones. Data from 1935 (Cain 1935) indicate a lack of very large red spruce trees on northerly slopes in the lower transition zone (<1450 m). According to Leak and Graber (1974), red spruce appears to be advancing downslope rather than retreating upslope. However, based on my study, the evidence for such a trend regarding red spruce was weak. In contrast, the evidence for Fraser fir was somewhat stronger. For example, large Fraser fir trees were not abundant below 1450 m and were absent on southerly slopes near the lower end of its elevational range. Thus, Fraser fir also appeared to be advancing downslope rather than retreating upslope. By contrast, Leak and Graber (1974) found evidence to suggest that red spruce and Fraser fir were retreating upslope ca. 1970 in northern Appalachian forests. Although the 1930s data base on red spruce and Fraser fir is limited, the continuous expanses of primeval forest across the ecotone in the southern Appalachians are ideal for the study of forest migration and their associated bird species. Further, population studies with more extensive vegetation sampling within the transition zone may help resolve current and future ecotone dynamics in the southern Appalachians.

Unlike many other spruce-fir areas in the southern Appalachians, forests near the summit of Mount LeConte were never commercially logged (Nichols 1977). However, with the establishment of LeConte Lodge near the summit in 1926, trees were cut to provide fuel and construction materials (Nichols 1977). After creation of GSMNP in 1934, salvage cutting of downed and damaged trees became common maintenance practice. When woodcutting was banned in 1976, approximately 3.6 ha near the summit had sustained severe windthrow and less intensive salvage cutting and another 4.4 ha received partial windthrow and less intensive salvage cutting (Nichols 1977). This situation occurred on ACT above the DCE and resulted in Fraser fir trees spaced further apart. Consequently, tree proximity determined spread of the adelgid and subsequent tree mortality; longer distances retarded infestation and spread. Sites above DCE that are south of the summit are more protected and have fir stands where average dbh is 40 cm. In addition to descriptions of ACT and differences discussed in Chapters II, III, and Wise and Peterson (1998), all the aforementioned effects further explain the differential distribution of fir or presence of fir in Zone 3 (Jenkins 2003).

Comparison of Spruce-Fir Communities

Studies at the ecotone sites on all gradsects confirmed that many birds characteristic of spruce-fir forests also were common in nearby mixed spruce and northern deciduous forests. For instance, two species that had lower abundances in Zone 3 on BHT, RFT, and TGT (Black-capped Chicakadee and Golden-crowned Kinglet) were common in Zone 2 (Fig. 4.6), an ecotone habitat 200 m lower in elevation then the previous census point on the gradsect. In the Great Smoky Mountains, these same species also declined dramatically in spruce-fir forests but remained common in mixed spruce-hardwood forests (Rabenold et al. 1998). Although many of the birds found in spruce-fir forests may have historically been more numerous there, all spill over into downslope forests (Stupka 1963; Alsop 1991; Simons et al. 1995). Across all of the spruce-fir sites in my study, I also found higher densities of sensitive or low tolerant species and lower densities of invading species (those not characteristic of spruce-fir), especially where fir was less affected by the adelgid and the density of trees remained high (particularly true on ACT).

Habitat Use

Total abundances and species richness of breeding birds increased from deciduous to mixed hemlock, hardwood, and coniferous forest types (Table 4.17, Table 4.18). Deciduous study plots supported a maximum of 10 species, compared to 14 for coniferous habitats. Thus, although hemlock and conifer habitats were similar in species richness, the latter was more important in terms of the total abundance of supported species.

Three general levels of tolerance to habitat deterioration were identified, based upon the distribution of bird observations in the 10 forest categories (Table 4.19). Species with low tolerance indices were restricted to few habitats or used their selected habitats more unevenly. Such species would be affected most adversely by loss of their preferred habitats.

Habitat features selected or used within habitats in general by each species (as indicated by significant correlations and regression coefficients, $P<0.01$) were also identified (Table 4.15). The relationship between density of cavity-nesters and snags most likely represented a direct response to use of snags as nesting and foraging locations. For other species, relationships were indirect and represented selection of habitat characteristics that were associated with snag size (i.e., a dying tree often creates an opening in the woodland that promotes dense growth of shrubs and forbs). For example, Johnston (1947) found that Indigo Buntings are attracted to openings created by snags. Presence (or absence) of particular vegetation strata was shown to be important to specific bird species and to composition of the avian community in that zone. Of the measured sapling/tree characteristics, dbh was much more frequently associated with bird species abundances than with density.

Expected Impacts of Habitat Alterations

Knowledge of the relationships of species to T-CAP indices, forest types, general habitat, and vegetation characteristics (Tables 4.5, 4.14) were used to identify the habitat needs of each species. This information can then be used to predict the effects of habitat alterations, including deterioration due to destruction of conifers by the balsam wooly adelgid (or hemlock wooly adelgid) on the species (Table 4.19). My results indicated hemlock was widespread in all vegetation strata at low and mid elevations and was the second most common tree species in the park. In the eastern U.S., invasion of hemlock wooly adelgid (*Homoptera: Adelgidae: Adelges tsugae*) is also transforming species composition of native forests by causing extensive mortality in eastern hemlock (*Tsuga canadensis*) populations. Shriner (2001) assesses the potential effects of hemlock loss in GSMNP by evaluating current hemlock distribution and abundance patterns and identifying environmental correlates of hemlock presence. She investigates potential effects of hemlock mortality on the park's avifuana by identifying bird species associated with hemlock. She found hemlock presence to be significantly associated with elevation, total relative moisture index, disturbance history, vegetation type, and bedrock geology. In my study, 16 of 30 common breeding bird species showed significant correlations with hemlock presence. For species with little data, predictions can be supplemented using information from the published literature.

For any given species, alteration of its preferred habitat (where it occurs in highest numbers) by adelgids would be more detrimental than perturbations of its less desirable habitats. Of the species examined, Dark-eyed Juncos, Blue Jays, and Black-capped

Chickadees have adapted well to more forest types and total population numbers would be least affected by alteration of natural habitats. Bird species diversity was correlated with habitat diversity. Therefore, disturbances increasing a habitat's structural diversity would benefit the greatest number of species or, conversely, could be detrimental to less common species that contribute little to overall diversity.

Analysis of T-CAP Data

The spatial form, or configuration, of bird habitat was analyzed using remotely sensed data. At first, the most direct method of analysis was simply to use bivariate and multivariate correlations to examine relationships between variations in bird species abundances, or bird community attributes, and single habitat features, using bird abundance values, topographic measurements, and T-CAP values for each entire plot. One of the analyses that I conducted was a PCA of the elevation, slope, and T-CAP values obtained at each site. This analysis indicated that variation in *brightness, greenness,* and *wetness* over the range of habitats could be arrayed along three independent dimensions, representing variations in *greenness, wetness,* and slope.

I identified strong relationships between elevation and T-CAP values for Mount LeConte. The lower *wetness* values for high elevation sites were inferred to be the result of a more open canopy. Higher values at low elevations suggested both the increased presence of species other than fir (especially red spruce and yellow birch) as well as a longer period of recovery since adelgid-caused declines in forest quality. Elevation was thus significantly correlated with *brightness* and *greenness* (which primarily separate mature fir stands from other vegetation types) in 1988, when the adelgid was just beginning to affect this area, and dense pure fir stands were limited to the relatively unaffected areas above 1800 m. However, elevation was strongly correlated with *wetness* (and thus openness) by 1998, an indication of the upslope wave of adelgid-caused mortality.

Distributions of several bird species were significantly associated with these factors in a PCA. For instance, species that were normally considered high elevation and spruce-fir birds, such as Chestnut-sided Warblers, Red-breasted Nuthatches, Winter Wrens, and Dark-eyed Juncos, reached their highest abundances on sites that exhibited low *greenness* values and high *wetness* values. Blue Jays and Ovenbirds, more typical of low elevation habitats, showed a similar response to increasing *greenness* values.

The nonlinearity of the relationship between elevation and T-CAP values for some areas (Fig. 4.7) further supports these findings since elevation gradient, forest types, and adelgid dispersal are all interrelated. The parabolic nature of the relationship was especially evident for Mount LeConte on the gradsects and occurred because fir dieback was most recent at the highest elevations.

Prediction of T-CAP Data and Habitat and Species Diversity Patterns

Forest types, characteristics, and topographic data corresponded to the T-CAP data dimensions called *greenness* and *wetness*. Most of the variation in the data was concentrated in four features, directly associated with characteristics of the physical scene (Table 4.11, 4.12, 4.14, Fig. 4.3). The underlying TM data structure, based on the TM scenes as well as simulated data, can be described as the general spectral characteristics of agricultural crops and other scene classes in the transformed data space (Crist et al. 1986). T-CAP application, though, can be extended from agricultural areas to spruce-fir or other forests (T. Lillesand, personal communication).

Such habitat analyses could be presented in ways to make the potential conservation applications (and the need for consideration of single-species conservation) more apparent (Fig. 4.10). Trends in the spatial patterning of individual species, species assemblages, and diversity measures in montane forests appeared to be predictable from T-CAP indices (*greenness* and *wetness*), spectral changes, topographic features (elevation, slope), vegetation characteristics (floristics and physiognomy), and forest types. On Mount LeConte, these factors/predictors can be likened to a roulette wheel (Fig. 4.10). Whenever and wherever these factors may align/converge to reveal resource or habitat requirements, a pattern of bird species diversity can be recognized or predicted. As an example, CCA and PCA can be used to determine habitat gradients and then the plots can be positioned in the PCA-space according to their factor scores. Then, by labeling each plot location with the density of a species, plots having similar densities can be grouped to define isopleths or contours of abundance of a species in the PCA-space. Because each plot is located in the PCA space according to its habitat features, it should be possible to predict how the position of a site might change were the habitat altered in some predictable way. By relating this to the contours of a species' abundance, one might then predict the species' patterns of response to habitat changes. For example, in Fig. 4.3, an alteration that caused the spruce-fir site to move in habitat space (as indicated in Quadrant D) would likely result in an increase in Chestnut-sided Warbler abundance, but a different sort of change (e.g., decline in spruce-fir) would more likely result in a decrease in their abundance. These changes in habitat could be detected by magnitude of change in wetness values.

Because I recorded locations of individual birds at my census points, I could distinguish between census points falling within occupied and unoccupied portions of the forest type (community). This permitted a finer resolution of habitat associations for a particular species since, if not all of the area of a census point was occupied by territories, the average values for habitat features characteristic of species' territories would deviate from those of the forest type as a whole.

It is doubtful that a single derived T-CAP value could predict the relative abundance of individual bird species or that T-CAP indices can be used as surrogates for species richness, but the approach could supply the resolution needed to develop models capable of predicting presence-absence or abundance of birds on a larger scale. However, in general, species diversity increased in locations with a high-habitat diversity, steep topography, and high *wetness* values. This landscape type also had the highest number and quality of habitats important for conservation. Thus, spectral differences of high elevation spruce-fir forest mirrored environmental differences, which, in turn, mirrored differences in habitat diversity and, therefore, overall richness and abundance.

Conclusions

The potential of remote sensing and GIS technology to model and predict spatial patterns in species-level biodiversity has largely been ignored. Remotely sensed information enhanced with GIS data was integrated in complementary ways to assess biodiversity. The use of satellite imagery and GIS to study and predict species richness showed promise for revealing distributional patterns that might not otherwise be apparent. Remote sensing also showed potential for ecotone detection and was used to track the location of the ecotone among three zones. However, remotely sensed images also provided information about the entire landscape, not just the ecotones, therefore GIS techniques were necessary to extract ecotone information from the image as a whole.

When using satellite imagery as the source of data for a habitat map, some uncertainties are expected. To improve the habitat classification, I used aerial photographs and NPS satellite imagery. Areas requiring data that are more detailed could be selected based on topography and fragmentation of habitats.

The use of T-CAP, Geographic Information (GI), ecological data, and associated GIS techniques (Fig. 4.10), as a surrogate for richness patterns of bird species included some shortcomings of which users should be aware. However, the T-CAP-GIS approach also offers many advantages. One of the most important is that with GIS and T-CAP transformation techniques, it is easy to rapidly obtain approximate predictions of the locations of ecologically valuable sites for birds over extensive areas, a feature particularly valuable in land-use planning with limited resources for field inventories. In fact, since I was able to detect strong relationships between species richness and spatial variables derived from satellite imagery, regression model predictions should be able to efficiently direct field surveys.

I believe my results demonstrated that environmental variables derived from Landsat TM images and digital elevation models can be used as surrogates of habitat and bird diversity in montane areas. These results suggest that satellite data can predict patterns of species richness on regional scales in mesoscale resolution. Satellite images and GIS provided a cost-effective method to estimate the biodiversity status of wide areas on a broad scale. I believe that the modeling techniques and the GIS-T-CAP approach used in the present paper deserve further attention in conservation biology and land use planning.

My project showed that by T-CAP transformations could detect canopy and structural changes. Such habitat changes as thinning, extensive canopy mortality, and differential regeneration of canopy and subcanopy species could be distinguished, whereas covertype changes required more careful interpretation. However, more extensive application in more rugged areas is limited by topographic bias on steep slopes having differential illumination. The use of Landsat TM T-CAP transformations also facilitated the understanding of changes occurring in canopy and understory cover within the high-elevation spruce-fir zone.

There were many potential shortcomings in using satellite imagery, topographic, and other kinds of (GI) data as a surrogate for species richness, including the appropriate collection of source data for modeling, technique problems in processing satellite imagery, and methodological pitfalls in regression models, among others. The results of predictive models should be applied with caution, extrapolations should be critically evaluated before use, and a good ornithological and biological knowledge of the study area is crucial to understanding the interplay among these features.

CHAPTER V

SUMMARY AND MANAGEMENT IMPLICATIONS

The main goal of my study was to evaluate the potential of landscape and habitat variables derived from remotely sensed and topographic data as cost-effective surrogates for evaluating patterns of total bird abundance and species richness. However, I also sought to examine which landscape and habitat variables strongly correlated with patterns of bird species richness, and how well regression models developed from field data and Landsat TM imagery could predict richness patterns across forest types at Mount LeConte, GSMNP.

The ability to rapidly predict species occurrences is often crucial for managers and conservation biologists with limited time and funds. I used associations of T-CAP indices with landscape patterns to build accurate, predictive habitat models that were quickly and easily applied (i.e. required no additional collection of field data to make predictions). I concluded that associations of T-CAP values with landscape patterns could be used to build relatively accurate and easy to use predictive models for some species and species diversity. My results stress, however, that both selecting the proper scale at which to assess landscape associations and empirically testing the models derived from those associations are crucial for building useful predictive models. My objective was to use associations with landscape patterns to build predictive habitat models that were accurate, general, and easy to apply. My approach included a model-building phase followed by field testing at different, but stratified, locations. To build the models, I censused birds at 212 field points. At sites centered on these census points, I also measured several aspects of habitat and landscape patterns.

Vegetation and land cover patterns affect the quality of habitat available for wildlife. Given the degree of interspersion of cover types, relative values of each edge type, and the importance of spatial diversity, an index of habitat spatial diversity was computed for each site relative to each bird species or group of species (guild). The spatial coverage of habitat complexity scores allowed a variety of additional "spatial" habitat variables to be predicted. For example, within forest landscapes, unoccupied or blow-down areas of lower quality provided temporary, suitable habitats inside dense forest mosaics.

The strength of my approach is that the input data on habitat complexity can be derived as part of a standard forest-mapping program with the addition of remotely sensed spatial imagery. Species' habitat relationships were developed via field observations and examined spatially using the developed spatial relationships. Structural features of the ecotone were determined by site-specific characteristics, e.g., vegetation discontinuities, such as edge and forest openings. The potential utility of this relationship was demonstrated by my results, which found distinct contrasts between zones. The effect of boundary abruptness on flow rates between spatial elements may be a curvilinear relationship, but apparently this has not been studied in landscapes. The effect of various soft and hard boundaries on rates of movement could be important, for instance, in park and wildlife management.

I applied "The T-CAP," a graphic description of the spectral-temporal development of locations to analyze bird-habitat relationships in spruce-fir forests. Responses of spectral indices to variations in vegetation cover and topography examined the degree to which the *brightness*, *greenness*, and *wetness* plane varied with vegetation characteristics such as dbh and percent canopy cover. Sequential data from remote sensing, combined with field sampling at sites (selected preferably stratified, based on remote sensing images) made it possible to detect spatial changes and vegetation analyses visible by extrapolation and prediction.

The technology of remote sensing provided the means to predict bird diversity associated with land cover and vegetation over large areas (15 x 15 km) for habitat analysis. However, maps themselves supply only part of the inventory data needed by biologists who must analyze the data and manage the wildlife. The maps must be analyzed and interpreted to enhance the various characteristics of the landscape, which have a bearing on management decisions. In short, the T-CAP indices are a source of information that could be helpful in making management decisions even in spruce-fir forests.

REFERENCES

Able KP, Noon BR (1976) Avian community structure along elevational gradients in the northeastern United States. Oecologia 26:275-94

Aerial Information Systems (2000) Great Smoky Mountains National Park, Cades Cove and Mount LeConte, USGS/NPS Vegetation and Inventory Mapping Program, Final Project Report. Environmental Systems Research Institute, Redlands

Allen RB, Peet RK (1990) Gradient analysis of forest of the Sangre de Cristo Range, Colorado. Can J Bot 68:193-201

Allen TFH (1987) Hierarchal complexity in ecology: a moneuclidean conception of the data space. Vegetatio 69:17-25

Allen TFH, Starr TB (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago

Allen TR, Kupfer JA (2000) Application of spherical statistics to study change vector analysis of Landsat data in southern Appalachian spruce-fir forests. Remote Sens Environ 74:482-493

Allen TR, Kupfer JA (2001) Spectral response and spatial pattern of Fraser fir mortality and regeneration, Great Smoky Mountains, USA. Plant Ecology 156:59-74

Alsop FJ III (1991) Birds of the Smokies. Great Smoky Mountains Natural History Association, Gatlinburg

Alsop FJ III, Laughlin TF (1991) Changes in the spruce-fir avifauna of Mount Guyot, Tennessee, 1967-1985. J Tennessee Acad Sci 66:207-210

American Ornithologists' Union (1957) Check-list of North American birds. 5th ed. American Ornithologists' Union, Baltimore

Amman GD, Speers CF (1965) Balsam wooly aphid in the southern Appalachians. J For 63:18-20

Anderson SH, Shugart HH (1974) Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55:828-837

Auerbach M, Shmida A (1993) Vegetation change along an altitudinal gradient on Mount Hermon, Israel - no evidence for discrete communities. Ecology 81:25-33

Austin MP (1985) Continuum concept, ordination methods, and niche theory. Ann Rev Ecol Syst, 16:39-61

Austin MP, Smith TM (1989) A new model for the continuum concept. Vegetatio 83:35-47

Avery MI, Haines-Young RH (1990) Population estimates for the Dunlin (*Calidris alpina*) derived from remotely sensed satellite imagery of the Flow Country of northern Scotland. Nature 322:860-862

Baker J, French K, Whelan, R (2002) The edge effect and ecotonal species:bird communities across a natural edge in Southeastern Australia. Ecology 83(1):3048-3059

Barr AJ, Goodnight JH, Sal JP, Helwig JT (1976) A user's guide to SAS76. SAS Institute, Cary

Barrett G (1992) Landscape ecology: Designing sustainable agricultural landscapes. J Sustainable Agr 2:83-103

Barrett HR, Nodvim SC (1993) Using GIS to assess potential impacts of gypsy moth infestations at Great Smoky Mountain National Park. Park Science 13(2):26-27

Beals EW (1969) Vegetational change along altitudinal gradients. Science 165:981-985

Beecher WH (1942) Nesting birds and the vegetation substrate. Chicago Ornithol Soc, Chicago

Bennett AF (1991) Roads, roadsides, and wildlife conservation: a review. In: Saunders DA, Hobbs RJ (eds) Nature conservation 2: The role of corridors, Surrey Beatty, Chipping Norton, Australia, pp 99-117

Bent AC (1949) Life histories of North American thrushes, kinglets, and their allies. U S Nat Mus Bull 196. Smithsonian Institution, Washington, DC

Bernstein I (1988) Applied multivariate analysis. Springer-Verlag, New York

Best LB, Bergin TM, Freemark KE (2001) Influence of landscape composition on bird use of rowcrop fields. J Wildl Manage 65:442-449

Best LB, Stauffer DF, Grier AR (1979) Evaluating the effects of habitat alteration on birds and small mammals occupying riparian communities. In: Stauffer DF, Best LB (eds) Proceedings of the symposium on strategies for protection and management of flood plain wetlands and other riparian ecosystems. U S Dep Agric For Serv Gen Tech Rep WO-12. U S Dep Agric, Washington DC, pp 117-124

Blake JG, Karr JR (1987) Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724-1734

Blondel J, Frochot B (1981) How to determine the duration of observation in station counts. In: Ralph CJ, Scott JM (eds) Estimating the numbers of terrestrial birds. Stud Avian Biol 6, pp 585

Bond RR (1957) Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol Monogr 27:351-384

Botkin DF, Estes JE, MacDonald RM, Wilson MV (1984) Studying the earth's vegetation from space. Bioscience 34:508-514

Bramwell MG, Pyke G, Adams C, Coontz P (1992) Habitat utilization by eastern bristlebirds at Barren Grounds Nature Reserve. Emu 92:117-121

Braun EL (1967) Deciduous forests of eastern North America. Hainer Publishing Company, New York

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325-349

Brewer R (1988) The science of ecology. Saunders, New York

Brittingham MC, Temple SA (1983) Have cowbirds caused forest songbirds to decline? Bioscience 33:31-35

Brooks RB, Cronquist MJ (1990) Wetland, habitat, and trophic response guilds for wildlife species in Pennsylvania. J Penn Acad Sci 64:93-102

Brown DM (1941) Vegetation of Roan Mountain: a phytosociological and successional study. Ecol Monogr 11:61-97

Brubaker LB (1986) Response of tree population to climatic change. Vegetatio 67:119-130

Bull EL (1981) Indirect estimates of abundance of birds. Stud Avian Biol 6:76-80

Busing RT, Clebsch EEC (1988) Fraser fir mortality and dynamics of a Great Smoky Mountains fir-spruce stand. Castanea 53:177-182

Busing RT, Clebsch EEC, Eagar CC, Pauley EF (1988) Two decades of change in a Great Smoky Mountains spruce-fir forest. Bull Torrey Bot Club 115:25-31

Busing RT, White PS, MacKenzie MD (1993) Gradient analysis of old spruce-fir forests of the Great Smoky Mountains, circa 1935. Can J Botany 71:951-958

Cain SA (1931) Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee 1. Soil reaction and plant distribution. Bot Gaz 91:22-41

Cain SA (1935) Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee II The quadrat method applied to sampling spruce and fir forest types. Am Midl Nat 16:566-584

Cain SA (1937) A preliminary guide to the Greenbrier-Brushy Mountain Nature Trail, the Great Smoky Mountains National Park. University of Tenn, Knoxville

Cain SA (1945) A biological spectrum of the flora of the Great Smoky Mountains National Park. Butler University Bot Stud 7:1-14

Campbell JB (1996) Introduction to remote sensing, 2nd ed. Guilford Press, New York

Carr MR (1996) PRIMER 4.0 beta. Plymouth Marine Laboratory, Plymouth

Chan K (1995) Bird community patterns in fragmented vegetation zones around steambeds of the Northern Tablelands, New South Wales. Australian Bird Watcher 16:11-20

Chapman A, Harrington GN (1997) Responses by birds to fire regime and vegetation at the wet sclerophyll/tropical rainforest boundary. Pac Cons Biol 3:213-220

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth

Clements FC (1897) Peculiar zonal formations of the Great Plains. Am Nat 31:968

Clements FC (1905) Research methods in ecology. University Publishing Co., Lincoln

Clements FC (1907) Plant physiology and ecology. Henry Holt, New York

Cody ML (1968) On the methods of resource division in grassland bird communities. Am Nat 102:107-147

Cody ML (1974) Competition and the structure of bird communities. Monogr Pop Biol 7:1-318

Cody ML (1983) Continental diversity patterns and convergent evolution in bird communities. In: Kruger FJ, Mitchel DT, Jarvis JUM (eds) Mediterranean-type ecosystems vol. 43. Springer-Verlag, Berlin and New York, pp 357-402

Cohen WB (1991a) Response of vegetation indices to changes in three measures of leaf water stress. Photogram Eng Remote Sens 57:195-202.

Cohen WB (1991b) Chaparral vegetation reflectance and its potential utility for assessment of fire hazard. Photogram Eng Remote Sens 57:203-207

Cohen WB (1994) GIS applications perspective: current research on remote sensing of forest structure. In: Sample V (ed) Remote sensing and GIS in ecosystem management, Island Press, Washington DC, pp 107-137

Cohen WB, Spies TA (1990) Remote sensing of canopy structure in the Pacific Northwest Environ. J Remote Sens 6:415-418

Cooley WH, Johnes PR (1971) Multivariate data analysis. Wiley, New York

Crawford HS, Hooper RG, Titterington RW (1981) Songbird population response to silvicultural practices in central Appalachian hardwoods. J Wildl Manage 45:680-692

Crist EP, Cicone RC (1984a) A physically based transformation of thematic mapper data-the tasseled cap. IEEE Trans Geosci Rem Sens 22:256-263

Crist EP, Cicone RC (1984b) Application of the tasseled cap concept to simulated thematic mapper data. Photogram Eng Remote Sens 50(3):343-352

Crist EP, Laurin R, Ciccone RC (1986) Vegetation and soils information contained in transformed thematic mapper data. In: Christ EP, Cicone RC (eds) Proceedings, IGARSS '86 Symposium, Zurich, Switzerland, 8-11 September 1986. ESA Publ. Division 254:1465-1470

Dale S, Mork K, Solvang R, Plumptre AJ (2000) Edge effects on the understory bird community in a logged forest in Uganda. Conserv Biol 14:265-276

Dawson DK (1981) Sampling in rugged terrain in estimating numbers of terrestrial birds. Stud Avian Biol 6:311-315

DeGraaf RM, Rudis DD (1986) New England wildlife: habitat, natural history, and distribution. U S Dep Agric For Serv Gen Tech Rep NE-108, Northeastern Forest Exp Sta, Broomall

DeGraaf RM, Yamasaki M, Leak WB (1993) Management of New England northern hardwoods, spruce-fir and eastern white pine for neotropical migratory birds. In: Finch DM, Stangel PW (eds) Status and management of neotropical migratory birds. U S Dep Agric Forest Serv Gen Tech Rep RM-229, Rocky Mount Forest Range Exp Station, Fort Collins, Colorado, pp 363-373

DeGraaf RM, Yamasaki M, Leak WB, Lanier JW (1992) New England wildlife: management of forested habitats. U S Dep Agric For Serv Gen Tech Rep NE-144, Northeastern Forest Exp Sta Radnor, Pennsylvania

Delcourt PA, Delcourt HR (1992) Ecotone dynamics in space and time. In: Hansen AJ, diCastri F (eds) Landscape boundaries: consequences for biotic diversity and landscape flows. Ecol Studies 92. Springer Verlag, New York, pp 19-54

Diamond JM (1973) Distributional ecology of New Guinea birds. Science 179:759-769

Dickson JG, Thompson FR III, Conner RN, Franzreb KE (1993) Effects of silviculture on neotropical migratory birds in central and southeastern oak pine forests. In: Finch DM, Stangel PW (eds) Status and management of neotropical migratory birds. U S Dep Agric For Serv Gen Tech Rep RM-229, Rocky Mount Forest Range Exp Station, Fort Collins, Colorado, pp 374-385

Digby PGN, Kempton RA (1987) Multivariate analysis of ecological communities. Chapman and Hall, New York

Dilger WC (1956) The hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla.* Auk 73:313-353

Dillon WR, Goldstein M (1984) Multivariate analysis: methods and applications, Wiley and Sons, New York

Dramstad WE, Olsen JD, Forman RTT (1996) Landscape ecology: principles in landscape architecture and land-use planning. Island Press, Washington DC

Draper NR, Smith H (1981) Applied regression analysis, 2nd ed. Wiley and Sons, New York

Drolet B, Desrochers A (1999) Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. Condor 101:699-704

Druitt DG, Enright NJ, Ogden J (1990) Altitudinal zonation in the mountain forests of Mount Hauhungatahi, North Island, New Zealand. J Biogeogr 17:205-220

Dueser, RD, Shugart HH Jr. (1978) Microhabitats in a forest-floor small mammal fauna. Ecology 59:89-98

Dufrene M, Legendre P (1991) Geographic structure and potential ecological factors in Belgium. J Biogeogr 18:257-266

Dunn OJ (1964) Multiple comparisons using rank sums. Technometrics 6:241-252

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169-175

Eagar C (1984) Review of the biology and ecology of the balsam woolly aphid in southern Appalachian spruce-fir forests. In: White PS (ed) The southern Appalachian spruce-fir ecosystem its biology and threats. Research management report SER-71. U S Nat Park Serv, Atlanta, pp 36-50

Ehrlich PR, Dobkin DS, Wheye D (1988) The birder's handbook: a field guide to the natural history of North American birds. Simon and Shuster, New York

Ekstrand S (1989) The possibilities of assessing moderate damages on Norway spruce using Landsat TM data and ancillary stand information in a GIS environment. In: Ekstrand S (ed) Proceedings, IGARSS '89 Symposium. Int Geoscience and Remote Sensing Symposium,Vancouver pp 1553-1557

Elton CS (1966) The pattern of animal communities. Methuen and Co. Ltd, London

Emlen JT Jr (1956) A method for describing and comparing avian habitats. Ibis 98:565-576

Enright NJ (1982) The ecology of *Araucaria* species in New Guinea, I Ordination studies of forest types and environments. Aust J Ecol 7:23-38

Enright NJ, Ogden J (1990) Altitudinal zonation in the mountain forests of Mt. Hauhungatahi, North Island, New Zealand. J Biogeogr 17(2): 205-220

ESRI (1997) ARC/INFO Version 7.11. Environmental Systems Research Institute, Inc. Redlands

Estes JE (1987) A perspective on the use of geographic information systems for environmental protection. In: Scott JM, Estes JE (eds) Proceedings of the January 1986 Environmental Protection Agency workshops on GIS for environmental protection. U S Environmental Protection Agency, Las Vegas pp 137-153

Ferson S (1988) Are competition communities stable assemblages? (Ph.D Dissertation) Stony Brook State University of New York, New York

Finch DM (1989) Positive associations among riparian bird species correspond to elevational changes in plant communities. Can J Zool 69:951-963

Finch DM (1991) Population ecology, habitat requirements and conservation of neotropical migratory birds. U S Dep Agric For Serv Gen Tech Rep RM-205, Rocky Mountain Forest and Range Exp Sta, Fort Collins

Flather CH, Sauer JR (1996) Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77:28-35

Forman RTT (1983) Corridors in a landscape: their ecological structure and function. Ekologia (CSSR) 2:375-387

Forman RTT (1995) Some general principles of landscape and regional ecology. Landscape Ecol 10:133-142

Forman RTT (1997) Land mosaics: The ecology of landscapes and regions. Cambridge University Press, New York

Forman RTT, Gordon M (1986) Landscape ecology. Wiley and Sons, New York

Forman RTT, Moore PN (1992) Theoretical foundations for understanding boundaries in landscape mosaics. In: Hansen AJ, diCastri F (eds) Landscape boundaries: consequences for biotic diversity and ecological flows, Ecol Studies 92. Springer-Verlag, New York, pp 236-58

Fortin MJ (1992) Detection of ecotones: definition and scaling factors (Ph.D Dissertation) Stony Brook State University of New York, New York

Franzreb KE (1976) Comparison of variable strip transect and spot map methods for censusing avian populations in a mixed coniferous forest. Condor 78(2): 260-262

Freemark KE, Dunning JB, Hejl SJ, Probst JR (1995) A landscape ecology perspective for research, conservation and management. In: Martin TE, Finch DM (eds) Ecology and management of neotropical migratory birds, A synthesis and review of critical issues. Oxford University Press, New York, pp 381-427

Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton

Frith HJ (1979) Wildlife conservation. Angus and Robertson, Sydney

Fritz RS (1979) Consequences of insular population structure: distribution and extinction of spruce grouse populations. Oecologia 42:57-65

Frome M (1996) The unofficial guide to the Great Smoky and Blue Ridge Mountains. University of Tennessee Press, Knoxville

Gates JE (1991) Powerline corridors, edge effects, and wildlife in forested landscapes of the Central Appalachians. In: Rodick JE, Bolen EG (eds) Wildlife and habitats in managed landscapes. Island Press, Washington DC, pp 13-32

Gates JE, Gysel LW (1978) Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883

Gates JE, Mosher JA (1981) A functional approach to estimating habitat edge width for birds. Am Midl Nat 105:189-192

Gauch HG (1982) Multivariate analysis in community ecology. Cambridge University Press, New York

Gauch HG, Whittaker RH (1972) Coenocline simulation. Ecology 53:446- 451

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7-26

Gleason HA, Cronquist A (1963) Manual of vascular plants of northeastern United States and adjacent Canada. D van Nostrand, New York

Golden MS (1974) Forest vegetation and site relationships in the central portion of the Great Smoky Mountains National Park. (Ph.D Dissertation) University of Tennessee, Knoxville

Golden MS (1981) An integrated multivariate analysis of forest communities of the central Great Smoky Mountains. Am Midl Nat 106:37-53

Gosz JR (1992) Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In Hansen AJ, diCastri F (eds) Landscape boundaries; consequences for biotic diversity and ecological flows, Ecol Studies 92. Springer-Verlag, New York pp 55-75

Gosz JR, Sharpe PJH (1989) Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. Landscape Ecol 3:229-43

Great Smoky Mountains National Park (1991) Great Smoky Mountains National Park Tennessee/North Carolina, USA trails illustrated map (topographic map). National Geographic, Evergreen

Green KM, Lynch JF, Sircar J, Greenberg LSZ (1987) Landsat remote sensing to assess habitat for migratory birds in the Yucatan Peninsula, Mexico. Vida Silvestre Neotropical 1:27-38

Greig-Smith P (1964) Quantitative plant ecology. Butterworths, London

Griffiths GH, Wooding MG (1989) Use of satellite data for the preparation of land cover maps and statistics, vol 11, Ecological consequences of land use change. Final Report to the Department of the Environment. TJ Press (Padstow), Oxford

Griffiths GH, Smith JM, Veitch N, Aspinal R (1993) The ecological interpretation of satellite imagery with special reference to bird habitats. In: Haines T Young R, Green D, Cousina S (eds) Landscape ecology and GIS. Taylor and Francis Ltd, TJ Press (Padstow), London pp 255-272

Griggs J (1997) American Bird Conservancy's field guide to all the birds of North America. Harper Collins, New York

Guthery FS, Bingham RL (1992) On Leopold's principle of edge. Wildl Soc Bull 20:340-344

Hagan JM III, Johnston DW (eds) (1992) Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC

Hair JF Jr , Anderson RE, Tatham RL (1987) Multivariate data analysis with readings. Macmillan, New York

Hamel PB, Smith WP, Twedt DJ, Daniel J, Wohr JR, Morris E, Hamilton RB, Cooper RJ (1996) A land manager's guide to pointcounts of birds in the Southeast. Gen Tech Rep SO-120. U S Dep Agric For Serv Southern Res Station, New Orleans

Hamilton AC (1975) A quantitative analysis of altitudinal zonation in Uganda forests. Vegetatio 30:99-106

Hansen AJ, diCastri F (eds) (1992) Landscape boundaries: consequences for biotic diversity and ecological flows, Ecol Studies 92. Springer-Verlag, New York

Hansen AJ, Urban DL (1992) Avian response to landscape pattern: the role of species' life histories. Landscape Ecol 7:163-180

Hansen AJ, diCastri F, Naiman R (1988) Ecotones: what and why? Biol Int 17: 9-46

Hansen AJ, Urban DL, Marks B (1992) Avian community dynamics: the interplay of landscape trajectories and species life histories. In: Hansen AJ, diCastri F, (eds) Landscape boundaries: consequences for biotic diversity and ecological flows. Ecol Studies 92. Springer-Verlag, New York, pp 170-195

Harris LD (1988) Edge effects and conservation of biotic diversity. Conserv Biol 2:330-332

Harris LD, Gallagher PB (1989) New initiatives for wildlife conservation, the need for movement corridors. In: Mackintosh G (ed) Defense of wildlife: preserving communities and corridors. Defenders of Wildlife, Washington DC, pp 11-34

Harris LD, McElveen JD (1981) Effect of forest edges on North Florida breeding birds. IMPAC Report 6(4) School of Forest Resources and Conservation, University of Florida, Gainesville

Hobbs RJ (1990) Remote sensing of spatial and temporal dynamics of vegetation. In: Hobbs RJ, Mooney HA (eds) Remote sensing of biosphere functioning. Springer-Verlag, New York, pp 203-219

Hoffman HL (1964) Checklist of vascular plants of the Great Smoky Mountains. Castanea 29:1-45

Holland MM (1988a) SCOPE/MAB technical consultations on landscape boundaries, report of a SCOPE/MAB workshop on ecotones. Biol Int 17:47-136

Holland MM (1988b) SCOPE/MAB technical consultations on landscape boundaries: Report of a SCOPE/MAB workshop on ecotones. Biol Int 17:107-136

Holland MM, Risser PG (1991) The role of landscape boundaries in the management and restoration of changing environments: introduction. Holland MM, Risser PG, Naiman RJ (eds) Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Routledge, Chapman and Hall, New York, pp 1-7

Holland MM, Risser PG, Naiman RJ (eds) (1991) Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Routledge, Chapman and Hall, New York

Hudson W (ed) (1991) Landscape linkages and biodiversity. Island Press, Washington DC

Hunter ML Jr (1991) Introductory remarks: bird conservation at a landscape called seeing the world from a bird's eye view. In: Bell B, Crosee RO, Flux JEC, Heather BD, Hitchmough RA, Robertson CJR, Williams MJ (eds) Proceedings of Acta XX Congressus Internationalis Ornithologics: 2-9 December 1990. New Zealand Ornithological Congress Trust Board, New Zealand, pp 2223-2225

Husch B, Miller C, Beers T (1982) Forest mensuration, 3rd ed. John Wiley and Sons, New York.

Hutto RL, Pletschet SM, Hendricks P (1986) A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593-602

James FC (1971) Ordinations of habitat relationships among breeding birds. Wilson Bull 83:215-236

James FC (1978) On understanding quantitative surveys of the vegetation. Am Birds 32:18-21

James FC, Shugart HH Jr (1970) A quantitative method of habitat description. Audubon Field Notes 24(6):727-736

Janssens P, Gunlick H (1988) Connectivity, proximity and contiguity in the landscape; interpretation of remote sensing data. In: Janssens P, Gunlick H (eds) Connectivity in landscape ecology, Proc. 2nd International Seminar on the International Association for Landscape Ecology. Kluwer, Munster, Germany, pp 373-397

Jeffers J, Bretschko G, El Daoushi F, Frenald E, Hadley M, Hansen A, Jolankai G, Kharchnko T, Lachvanne JB, Lauga J, Risser P, Shugart HH, Stanford J, Suzuki M, Vervier P, Webber P, Wissmar RC (1989) Theoretical considerations of the ecotone concept. In: Hansen A, Holland M, Shugart HH (eds) Role of landscape/inland water ecotones in landscape management and restoration, proposals for collaborative research. Springer Verlag, Berlin, pp 55-59

Jenkins MA (2003) Impact of the Balsam Woolly Adelgid (*Adelges piceae Ratz.*) on an *Abies fraseri* (Pursh) Poir. dominated stand near the summit of Mount LeConte, Tennessee. Castanea 68:109-118

Johnson AH, Fernandez IJ (1992) Synthesis and conclusions from epidemiological and mechanistic studies of red spruce decline. In: Eagar C, Adams MB (eds) Ecology and decline of red spruce in the eastern United States, Springer-Verlag, New York, pp 905-914

Johnston CA, Bonde JP (1989) Quantitative analysis of ecotones using a geographic information system. Photogram Eng Remote Sens 55:1643-1647

Johnston CA, Naiman RJ (1987) Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecol 1:47-57

Johnston DW, Odum EP (1956) Breeding bird populations in relation to plant succession on the piedmont of Georgia. Ecology 37:50-62

Johnston VR (1947) Breeding birds of the forest edge in east-central Illinois. Condor 49:45-53

Joyce-Loebl (ed) (1985) Image analysis: principles and practice: a technical handbook produced by Joyce-Loebl. Gateshead, United Kingdom

Karr JR (1968) Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70:348-357

Karr JR (1994) Landscapes and management for ecological integrity. In: Kim RC, Weaver RD (eds) Biodiversity and landscape: a paradox for humanity. Cambridge University Press, New York, pp 229-251

Karr JR, Roth RR (1971) Vegetation structure and avian diversity in several new world areas. Am Nat, 105:423-435

Kauth RJ, Thomas GS (1976) The tasseled cap-a graphic description of the spectral-temporal development of agricultural crops as seen by Landsat. In: Cicone RC, Crist EP, Thomas GS (eds) Proc Symp on Machine Processing of Remotely Sensed Data, 6 June-2 July 1976, LARS. Purdue University, West Lafayette, pp 41-51

Keast A, Morton ES (eds) (1980) Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, DC

Kendeigh SC (1945) Community selection by birds on the Helderberg Plateau of New York. Auk 62:418-436

Kendeigh SC, Fawver BJ (1981) Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina. Wilson Bull 93:218-242

Kilgo JC, Sargeant RA, Miller KV, Chapman BR (1997) Landscape influences on breeding bird communities in hardwood fragments in South Carolina. Wildl Soc Bull 25:878-885

Kim J, Mueller CW (1978) Introduction to factor analysis. Sage Publications, Beverly Hills

King PB, Stupka A (1950) The Great Smoky Mountains - their geology and natural history. Sci Monthly 61:31-43

Kleinbaum DG, Kupper LL, Muller KE (1988) Applied regression analysis and other multivariate methods. Duxbury Press, Belmont

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253-260

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage Publications, Beverley Hills

Kupfer JA (1996) Patterns and determinants of edge vegetation of a midwestern forest preserve. Phys Geogr 17:62-76

Kupfer JA, Cairns DM (1996) The suitability of montane ecotones as indicators of global climatic change. Prog Phys Geogr 20:253-72

Kupfer JA, Malanson GP (1993) Observed and modeled directional change in riparian forest composition at a cutbank edge. Landscape Ecol 8:185-199

Lancia RA, Nichols JD, and Pollock KH (1994) Estimating the number of animals in wildlife populations. In: Bookhout TA (ed) Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, pp 215-253

Laudenslayer WF Jr, Balda RP (1976) Breeding bird use of a pinyon-juniper-ponderosa pine ecotone. Auk 93:571-586

Leak WB, Graber RE (1974) A method for detecting migration of forest vegetation, Ecology 55:1425-1427

Lennon JJ, Turner JRG, Connell D (1997) A meta-population model of species boundaries. Oikos 78:486-502

Leopold A (1933) Game management. Charles Scribner and Sons, New York

Leslie M, Jaffe GK, Hardesty JL, Adams DL (1996) Conserving biodiversity on military lands: a handbook for natural resources managers. HQ USAF/CEVP, Directorate of Environment, Office of the Air Force Pentagon, Washington, DC

Lidicker WZ Jr (1988) The synergistic effects of reductionist and holistic approaches in animal ecology. Oikos 53:278-281

Lidicker WZ Jr (1995) The landscape concept: something old, something new. In: Lidicker WZ Jr (ed) Landscape approaches in mammalian ecology and conservation. University of Minnesota Press, Minneapolis, pp 3-19

Lidicker WZ Jr (1999) Responses of mammals to habitat edges: an overview. Landscape Ecol 14:333-343

Lidicker WZ Jr, Peterson JA (1999) Responses of small mammals to habitat edges. In: Barrett GW, Peles JD (eds) Landscape ecology of small mammals. Springer-Verlag, New York, pp 211-277

Likens GE (1992) The ecosystem approach: its use and abuse. Ecology Institute. Oldendorf/Luhe, Germany

Lillesand TM, Kiefer RW (1994) Remote sensing and image interpretation. Wiley and Sons, New York

Lincoln RJ, Boxhall GA, Clark PF (1982) A dictionary of ecology, evolution, and systematics. Cambridge University Press, Cambridge

Lindsey AA, Barton JD, Miles SR (1958) Field efficiencies of forest sampling methods. Ecology 39:428-444

Luck GW, Possingham HP, Paton DC (1999) Bird responses at inherent and induced edges in the Murray Mallee, South Australia 1. Differences in abundance and diversity. Emu 99:157-169

Ludwig JA, Cornelius JM (1987) Locating discontinuities along ecological gradients. Ecology 68:448-450

MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619

MacArthur RH (1964) Environmental factors affecting bird species diversity. Am Nat 98:387-396

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594-598

MacArthur RH, MacArthur JW, Preer J (1962) On bird species diversity II. Prediction of bird census from habitat measurements. Am Nat 96:167-174

MacClintock L, Whitcomb RF, Whitcomb BL (1977) Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. Am Birds 31(1):6-12

MacKenzie MD (1993) The vegetation of Great Smoky Mountains National Park: past, present, and future. (Ph.D Dissertation) University of Tennessee, Knoxville

MacKenzie MD, White PS (1998) Vegetation of Great Smoky Mountains National Park, 1935-1938. Castanea 63:323-336

Magurran AE (1988) Ecological diversity and its measurement. Princeton University Press, Princeton

Malanson GP (1993) Riparian landscapes. Cambridge University Press, Cambridge

Malanson GP (1997a) Simulated responses to hypothetical fundamental niches. J Veg Sci 8:307-316

Malanson GP (1997b) Effects of feedbacks and seed rain on ecotone patterns. Landscape Ecol 12:27-38

Martin TE (1992) Landscape considerations for viable populations and biological diversity. Transactions of the No Am Wildl Natural Resources Conf 52:283-291

May RM (1975) Some notes on estimating the competition matrix, alpha. Ecology 56: 737-741

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London

McFarland DC (1988) The composition, microhabitat use and response to fire of the avifauna of subtropical heathlands in Coloola National Park, Queensland. Emu 88:249-257

Mead RA Sharik TL, Prisley SP, Heinen JT (1981) A computerized spatial analysis system for assessing wildlife habitat from vegetation maps. Can J Rem Sens, 7:34-40

Merriam G (1984) Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt J, Agger P (eds) Methodology in landscape ecological research and planning, vol. 1. Roskilde Universitetsforlag GeoRuc, Roskilde, Denmark, pp 5-15

Mohler RRJ, Wells GL, Hallum CR, Trenchard MH (1986) Monitoring vegetation of drought environments. Bioscience 36:478-483

Morrison ML, Timossi IC, With KA (1987) Development and testing of linear regression models predicting bird-habitat relationships. J Wildl Manage 51:247-253

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. Wiley and Sons, New York

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. TREE 10:58-62

Murray NL, Stauffer DF (1995) Non-game bird use of habitat in central Appalachian riparian forests. Wildl Manage 59:78-88

Musick HB, Pelletier RE (1988) Response to soil moisture of spectral indices derived from bidirectional reflectance in thematic mapper wavebands. Remote Sens Environ 25:167-184

Myers RH (1986) Classical and modern regression with applications. Duxbury Press, Boston

Naiman RJ, Decamps H, Pastor J, Johnston CA (1988) The potential importance of boundaries to fluvial ecosystems. J N Am Benthol Soc 7:289-306

Naveh Z (1982) Landscape ecology as an emerging branch of human ecosystem science. Adv Ecol Res 12:189-237

Naveh Z, Lieberman AS (1984) Landscape ecology: theory and application. Springer-Verlag, New York

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models, 4th ed. WCB McGraw-Hill, Boston

Nichols R (1977) The ecological effects of LeConte Lodge in the Great Smoky Mountains National Park. Uplands Field Research Laboratory, Southeast Region, National Park Service, Atlanta

Nicholas NS, Zedaker SM, Eagar C, Bonner FT (1992) Seedling recruitment and stand regeneration in spruce-fir forests of the Great Smoky Mountains. Bull Torrey Bot Club 119:289-299

Noon RB (1981) The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol Monogr 51:105-124

Noon BR, Dawson DK, Inkley DB, Robbins CS, Anderson SH (1980) Consistency in habitat preference of forest bird species. Transactions of the No Am Wildl Natural Resources Conf 45:226-244

Norusis MJ (1985) SPSSX advanced statistics guide. McGraw-Hill, New York

O'Neill RV, Johnson AR, King AW (1989) Hierarchical framework for analysis of scale. Landscape Ecol 3:193-205

O'Neill RV, DeAgnelis DL, Waide JB, Allen TFH (1986) A hierarchal concept of ecosystems. University of Princeton Press, Princeton

Odum EP (1945) The concept of the biome as applied to the distribution of North American Birds. Wilson Bull 57:191-201

Odum EP (1950) Bird populations of the highlands (North Carolina) plateau in relation to plant succession and avian invasion. Ecology 31:587-605

Odum EP (1958) Fundamentals of ecology, 2nd ed. Saunders, Philadelphia

Ogden J, Powell JA (1979) A quantitative description of the forest vegetation on analtitudinal gradient in the Mount Field National Park, Tasmania, and a discussion of its history and dynamics. Aust J Ecol 4:293-325

Orians GH (1969) The number of bird species in some tropical forests. Ecology 50:783-801

Overall JE, Klett CJ (1972) Applied multivariate analysis. New York, McGraw Hill

Palmeirim JM (1985) Using Landsat TM imagery and spatial modeling. In: Bauer ME, Gregg WW (eds) Automatic habitat evaluation and release site selection for the ruffed grouse (Galliformes: Tetranoidae) Proc. 19th Int. Symp Rem Sens Environ. University of Michigan, Ann Arbor, pp 729-738

Palmeirim JM (1988) Automatic mapping of avian species habitat using satellite imagery. Oikos 52:59-68

Pauley EF, Clebsch EEC (1990) Patterns of *Abies fraseri* regeneration in a Great Smoky Mountains spruce-fir forest. Bull Torrey Bot Club 117:375-381

Pearson SM, Turner MG, Gardner RH, O'Neill RV (1995) An organism based perspective of habitat fragmentation. In: Szaro RC, Johnston DL (eds) Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York pp 77-95

Peart DR, Nicholas NS, Zedaker SM, Miller-Weeks MM, Siccama TG (1992) Condition and recent trends in high elevation red spruce populations. In: Egar C, Adams MB (eds) Ecology and decline of red spruce in the eastern United States. Springer-Verlag, New York, pp 125-191

Peet RK (1974) The measurement of species diversity. Ann Rev Ecol Syst 5:285-307

Pengelly W (1978) The changing history of wildlife management. In: Klaas EE, Anderson WH, Frederick RB (eds) Proceedings of PECORA IV, Symposium on Application of Remote Sensing Data to Wildlife Management, Sioux Falls, South Dakota. National Wildlife Federation, Scientific and Technical Series 3, Reston, pp 1-5

Perry CR, Lautenschlager LF (1984) Functional equivalence of spectral vegetation indices. Rem Sens Environ 14:169-182

Peterjohn WT, Correll DL (1984) Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65:1466-1475

Pianka ER (1975) Niche relations of desert lizards. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap Press, Cambridge pp 292-314

Pickett STA, White PS (eds) (1985) The ecology of natural disturbance and patch dynamics. Academic Press, New York

Pollard E, Hooper MD, Moore NW (1974) Hedges. W Collins, London

Powell GVN, Rappole JH, Sader SA (1992) Neotropical migrant landbird use of lowland Atlantic habitats in Costa Rica: a test of remote sensing for identification of habitat. In: Hagan JM, Johnston DW (eds) Ecology and conservation of neotropical migrant landbirds. Smithsonian Press, Washington DC, pp 287-298

Pulliam HR, Dunning JB Jr, Liu J (1992) Population dynamics in complex landscapes: a case study. Ecol Appl 2:165-172

Pyle C (1984) Pre-park disturbance in the spruce-fir forests of Great Smoky Mountains National Park. In: White PS (ed) The southern Appalachian spruce-fir ecosystem: its biology and threats. Research/Resource Management Report SER-71. U S Dep Int, Nat Park Service, Atlanta pp 115-130

Pyle C (1985) Vegetation disturbance history of Great Smoky Mountains National Park: an analysis of archival maps and records. Research/Resources Management Report SER-77. U S Dep Int, Nat Park Service, Southeast Regional Office, Atlanta

Rabenold KN, Fauth PT, Parker PG (1998) Response of avian communities to disturbance by an exotic insect in spruce-fir forest of the Southern Appalachians. Conserv Biol 12:177-189

Radford AE, Ahles HE, Bell CR (1968) Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, North Carolina

Ralph CJ, Sauer JR, Droege S (1995) Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. U S Dep Agric For Serv, Pacific Southwest Res Sta, Albany, CA

Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF (1993) Handbook of field methods for monitoring landbirds. Gen Tech Rep PSW-GTR-144. U S Dep Agric For Serv, Albany, CA

Ranney JW (1977) Forest island edges - their structure, development, and importance to regional forest ecosystem dynamics. EDFB/IBP-77/1. Oak Ridge National Laboratory, Oak Ridge

Ranney JW, Bruner MC, Levenson JB (1981) The importance of edge in the structure and dynamics of forest islands. In: Burgess RL, Sharpe DM (eds) Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York. pp 67-96

Rapoport EH (1982) Areography: geographical strategies of species. Pergamon Press, New York

Rappole JH, Powell CVN, Sader A (1994) Remote sensing assessment of tropical habitat availability for a nearctic migrant: the wood thrush. In: Miller RI (ed) Mapping the diversity of nature. Chapman and Hall, London, pp 91-103

Ratti JT, Reese KP (1988) Preliminary tests for the ecological trap hypothesis. J Wildl Manage 52:484-491

Reynolds RT, Scott JM, Nussbaum RA (1980) A variable circular-plot method for estimating bird numbers. Condor 82:309-313

Richardson AJ, Wiegand CL (1977) Distinguishing vegetation from soil background. Photogram Eng Rem Sens 43:1541-1552

Risser PG (1990) Landscape pattern and its effect on energy and nutrient distribution. In: Zonneveld IS, Forman RTT (eds) Changing landscapes: an ecological perspective. Springer Verlag, New York, pp 45-56

Risser PG (1993) Ecotones at local to regional scales from around the world. Ecol Appl 3:367-368

Risser PG (1995) The status of the science examining ecotones. Bioscience 45:318-325

Robbins CS (1981a) Effect of time of day on bird activity. Stud Avian Biol 6:275-286

Robbins CS (1981b) Bird activity levels related to weather. Stud Avian Biol 6:301-310

Rodenhouse NL, Best LB, O'Connor RJ, Bollinger K (1993) Effects of temperate agriculture on Neotropical migrant land birds. In: Finch DM, Stangel PW (eds) Neotropical migratory birds. U S Dep Agric For Serv Gen Tech Report RM-229. U S Dep Agric, Rocky Mountain Forest Range Exp Sta, Fort Collins, pp 280–295

Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. Ecol Monogr 37:317-350

Rotenberry JT, Wiens JA (1980) Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228-1250

Roth RR (1976) Spatial heterogeneity and bird species diversity. Ecology 57:773-782

Sader SA, Powell GVN, Rappole JH (1991) Migratory bird habitat monitoring through remote sensing. Int J Rem Sens 12:363-72

SAS Institute (2000) SAS/STAT user's guide, version 8.0. SAS Institute, Cary

Saunders DA, Hobbs RJ (eds) (1991) Nature conservation 2: the role of corridors. Surrey Beatty, Chipping Norton

Saunders PF (1979) The vegetational impact of human disturbance on the spruce-fir forests of the Southern Appalachians (Ph.D Dissertation) Duke University, Durham

Schilthuizen M (2000) Ecotone: speciation-prone. TREE 15:130-131

Schofield WB (1960) The ecotone between spruce-fir and deciduous forest in the Great Smoky Mountains. (Ph.D Dissertation) Duke University, Durham

Scott JM, Csuti B, Jacobi JD, Estes JE (1987) Species richness: A geographic approach to protecting future biological diversity. Bioscience. 37(11):782-788

Sharp MJ, Keddy PA (1986) A quantitative technique for estimating the boundaries of wetlands from vegetation data. Env Manage 10:107-112

Shipley B, Keddy PA (1987) The individualistic and community unit concepts as falsifiable hypotheses. Vegetatio 69:47-55.

Shriner SA (2001) Distribution of breeding birds in Great Smoky Mountains National Park. (Ph.D Dissertation) North Carolina State University, Raleigh

Shugart HH, Patten BC (1972) Niche quantification and the concept of niche pattern. In: Patten BC (ed) Systems analysis and simulation in ecology, vol II. Academic Press, New York, pp 283-327

Siccama TG, Bliss M, Vogelmann HW (1982) Decline of red spruce in the Green Mountains of Vermont. Bull Torrey Bot Club 109:62-168

Simberloff DJ, Farr A, Cox J, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? Biol Conserv 6:493-504

Simons T, Rabenold KN, Farnsworth G (1995) Characterization of deciduous forest breeding bird communities of Great Smoky Mountains National Park, Final Report to National Park Service. U S Dep Int, Nat Park Service, Gatlinburg

Sisk TD, Margules CR (1993) Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. In: Saunders DA, Hobbs RJ, Ehrlich PR (eds) Nature conservation 3: reconstruction of fragmented ecosystems. Surrey Beatty and Sons, Chipping Norton, pp 45-55

Skirvin AA (1981) Effect of time of day and time of season on the number of observations and density estimates of breeding birds. Stud Avian Biol 6:271-274

Smith DG (1977) Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819

Smith GF, Nicholas NS (1999) Post-disturbance spruce-fir forest stand dynamics at seven disjunct sites. Castanea 64:175-186

Smith TM, Shugart HH (1987) Territory size variation in the ovenbird: the role of habitat structure. Ecology 68:695-704

Snedecor GW, Cochran WG (1989) Statistical methods, 8th ed. Iowa State University, Ames

Sokal RR, Sneath PHA (1963) Principles of numerical taxonomy. WH Freeman and Company, San Francisco

Sokal RR, Rohlf FJ (1995) Biometry, 3rd ed. WH Freeman and Company, New York

Speers CF (1958) The balsam woolly aphid in the Southeast J For 56:515-516

Stamps JA, Buechner M, Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am Nat 129:533-52

Steele BB (1992) Habitat selection by breeding Black-throated Blue Warblers at two spatial scales. Ornis Scand 23:33-42

Steele BB (1993) Selection of foraging and nesting sites by black-throated blue warblers: their relative influence on habitat choice. Condor 95:568-579

Stupka A (1963) Notes on the birds of Great Smoky Mountains National Park. University of Tennessee Press, Knoxville

Tanner JT (1955) The altitudinal distribution of birds in a part of the Great Smoky Mountains. Migrant 26:37-40

Temple SA, Wiens JA (1989) Bird populations and environmental change: can birds be bio indicators? Am Birds 43:260-270

Terborgh J (1971) Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 53:23-40

Terborgh J (1985) The role of ecotones in the distribution of Andean Birds. Ecology 66:1237-1246

Terborgh JS, Robinson K, Parker TA III, Munn CA, Pierpont N (1990) Structure and organization of an Amazonian forest bird community. Ecol Monogr 60:213-238

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179

Ter Braak CJF (1987) CANOCO-a FORTRAN program for community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis, V2.1. ITI-TNO, Wageningen the Netherlands

Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271-317

The Nature Conservancy (1999) BRD-NPS vegetation mapping program, vegetation classification of Great Smoky Mountains National Park (Cades Cove and Mount LeConte quadrangles) final report. The Nature Conservancy, Arlington

Thomas JW (ed) (1979) Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. U S Dep Agric For Serv Agric Handb No. 553, Washington DC

Timoney KP (1988) A geobotanical investigation of the sub arctic forest-tundra of the Northwest Territories. (Ph.D Dissertation) University of Alberta, Edmonton

Todd SW, Hoffer RM (1998) Responses of spectral indices to variations in vegetation cover and soil background. Photogram Eng Remote Sens 64 (9):915-921

Tomoff CS (1974) Avian species diversity in desert scrub. Ecology 55:390-403

Troll C (1939) Luftbidplan and ökologische Bodenforschung. Z Ges. Erdkunde:241-98

Tucker CJ, Townshend JRG, Goff TE (1985) African land cover classification using satellite data. Science 227:369-375

Turner MG (1989) Landscape ecology: the effect of pattern on process. Ann Rev Ecol Syst 20:171-197

Turner MG (1990) Spatial and temporal analysis of landscape patterns. Landscape Ecol 4(1):21-30

Turner MG, Gardner RH (eds) (1991) Quantitative methods in landscape ecology. The analysis and interpretation of landscape heterogeneity. Springer-Verlag, New York

Turner MG, Gardner RH, Dale VH, O'Neill RV (1989) Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121-129

Udvardy MDF (1969) Dynamic zoogeography. Van Nostrand Reinhold Co., New York

Udvardy MDF (1981) An overview of grid-based atlas works in ornithology. Stud Avian Biology 6:103-109

Urban DL, O'Neill RV, Shugart HH (1987) Landscape ecology. Bioscience 37:119-127

Van der Maarel E (1976) On the establishment of plant community boundaries. Ber Deutsch Bot Ges 89:415-443

Van der Maarel E (1990) Ecotones and ecoclines are different. J Veg Sci 1:135-138

Van Horne B (1983) Density as a misleading indicator of habitat quality. J Wildl Manage 47:893-901

Verkaar HJ (1988) The possible role of road verges and river dykes as corridors for the exchange of plant species between natural habitats. In: Schrieber KF (ed) Connectivity in landscape ecology, Munstersche Geographische Arbeiten 29. Ferdinand Schoningh, Paderborn, Germany, pp 79-84

Verner JM, Morrison L, Ralph CJ (eds) (1986) Wildlife (2000): modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison

Vogelmann HW, Bliss M, Badger G J, Klein RM (1985) Forest decline on Camels Hump, Vermont. Bull Torrey Bot Club 112:274-287

Watts BD (2002) Winter use of early successional habitats by birds within the Alligator River, NWR and Pocosin Lakes, NWR: Evaluating the benefit of management scenarios. Center for Conservation Biology Technical Report Series. CCBTR-02-07. College of William and Mary, Williamsburg

Weinstein DA (1992) Use of simulation models to evaluate the alteration of ecotones by global carbon dioxide increases. In: Hansen AJ, diCastri F (eds) Landscape boundaries: consequences for biotic diversity and ecological flows, Ecol Studies 92. Springer-Verlag, New York, pp XXX-XX

Westman WE (1987) Monitoring the environment by remote sensing. TREE 2:333-337

White PS, Buckner F, Pitillo JD, Cogbill CV (1993) High elevation forests: spruce-fir forests, northern hardwood forests, and associated communities. In: Martin WH, Boyce SG, Echternacht AC (eds) Biodiversity of the Southeastern United States. Wiley, New York, pp 305-338

Whittaker RH (1952) A study of summer foliate insect communities in the Great Smoky Mountains. Ecol Monogr 22:1-44

Whittaker RH (1956) Vegetation of the Great Smoky Mountains. Ecol Monogr 26:1-80

Whittaker RH (1966) Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121

Whittaker RH (1967) Gradient analysis of vegetation. Bio Rev 42:207-264

Whittaker RH (1977) Communities and ecosystems, 2nd ed. Macmillan, London

Whittaker RH, Levin SA, (eds) (1975) Niche: theory and application. Benchmark Papers in Ecology. Dowden, Hutchinson, and Ross Inc, Stroudsburg

Whitcomb RF, Robbins CS, Lynch JF, Whitcomb BL, Klimkiewicz K, Bystrak D (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess RL, Sharpe DM (eds) Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, pp 125-206

Wiens JA (1969) An approach to the study of ecological relationships among grassland birds. Ornith Monogr 8:1-93.

Wiens JA (1976) Population responses to patchy environments. Ann Rev Ecol Syst 7:81-120

Wiens JA (1981a) Scale problems in avian censusing. In: Ralph CJ, Scott JM (eds) Estimating the numbers of terrestrial birds. Stud Avian Biol, 6:513-521

Wiens JA (1981b) Single-sample surveys of communities: are the revealed patterns real? Am Nat 117:90-98

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385-397

Wiens JA, Crawford CS, Gosz JR (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45:421-427

Wiens JA, Rotenberry JT, Van Horne B (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132-147

Wiens JA, Stenseth NC, Van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369-380

Wierenga PJ, Hendricks JMH, Nash MH, Ludwig JA, Daugherty LA (1987) Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. J Arid Environ 13:53-63

Wilson EO (1988) Biodiversity. National Academy Press, Washington DC

Willson ME (1974) Avian community organization and habitat structure. Ecology 55:1017-1029

Winter M, Johnson DH, Faaborg J (2000) Evidence for edge effects on multiple levels in tall grass prairie. Condor 102:256-266

Wise K, Petersen R (1998) A natural history of Mount LeConte. University of Tennessee Press, Knoxville, Tennessee, 137 pp

Witter JA, Ragenovich IR (1986) Regeneration of fraser fir at Mount Mitchell, North Carolina, after depredations by balsam woolly adegid. For Sci 32:585-594

Wunderle JM, Diaz A, Velazquez I, Schawon R (1987) Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bull 99:22-37

Yahner RH (1988) Changes in wildlife communities near edges. Conserv Biol 2:333- 339

Zar JH (1984) Biostatistical analysis. Prentice-Hall, London

Zhao G (1998) Development and evaluation of spectral transformation algorithms for analysis and characterization of forest vegetation (multivariate clustering, canonical variates, ordination methods). (Ph.D Dissertation) Michigan Technological University, Ann Arbor

Zimmermann JL (1971) The territory and its density-dependent effect in Spiza Americana. Auk 88 591-612

APPENDIX A

DESCRIPTIONS AND DATA ON TNC CODES USED

Frequency and percent of TNC Code Vegetation Descriptions, Community Classifications, and Landscape scale species composition. (C=coniferous, D=deciduous, H=hemlock)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
112	*Picea rubens – (Abies fraseri) / Rhododendron catawbiense, Rhododendron maximum* Forest	Red Spruce – Fraser Fir (Evergreen Shrub Type)	1193	19.8	Spruce Fir 1	SF	C
112	*Picea rubens – (Abies fraseri) /Vaccinuim erythocarpum /Oxalis Montana – Dryopteris campyloptera / Hylocomium splendens* Forest	Red Spruce – Fraser Fir Forest (Deciduous Shrub Type)			Spruce N. Hardwood 1.5	SF	C
114	*Picea rubens – (Betula alleghiensis, Aesculus flava) / Rhododendron (maximum catawbiense)* Forest	Red Spruce – Northern Hardwood Forest (Shrub Type)	929	15.42	Spruce – N. Hardwood 1.5	SNH	C

APPENDIX A (Continued)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
114	*Picea rubens – (Betula alleghiensis Aesculus flava) / Viburn(maximum catawbiense)* Forest	Red Spruce – Northern Hardwood Forest (Herb Type)			Spruce – N. Hardwood 1.5	SNH	C
312	*Aesculus flava – Acer saccharum – (Fraxinus Americana, Tilia Americana) / Hydophyllum canadense – Solidago flexicaulis* Forest	Southern Appalachian/Cove Forest (Rich Montane Type)	141	2.34	Cove Hardwood 3	CH	D
3814	*Kalmia latifolia – Rhodoendron catawbiense – (Gaylussacia baccata, Pieris floribunda, Vaccinium corymbosum)* Shrubland	Southern Appalachian Mountain Laurel Bald	141	2.34	Bald 11	B	B

APPENDIX A (Continued)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
4973	*Aesculus flava – Betula alleghaniensis – Acer spicatum /Caulophyllum thalictroides – Laportea Canadensis* Forest	Southern Appalachian/ Northern Hardwood Forest (Rich Type)	221	3.67	Northern Hardwood 2	NH	D
4982	*Betula allegheniensis / Acer spicatum / Hydrangea arborescens – Ribes cynosbati / Dryopteris marginalis* Forest	Southern Appalachian/ Hardwood Boulderfield Forest (Typic Type)	77	1.28	Northern Hardwood 2	NH	D
6049	*Abies fraseri / Viburmum lantanoides / Dryopteris campyloptera – Oxalis montana / Hyclocomium splendens* Forest	Fraser Fir Forest (Deciduous Shrub Type)	472	7.84	Spruce-Fir 1	F	C
6124	*Betula alleghaniensis / Ribes glandulosum / Polypodium appalachianum* Forest	Southern Appalachian/ Hardwood Boulderfield Forest (Currant and Rockcap Fern Type)	176	2.92	Northern Hardwood 2	NH	D

APPENDIX A (Continued)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
6192	*Quercus rubra – Acer rubrum / Calycanthus floridus – Pyrularia pubera / Thelypteris noveboracensis* Forest	Appalachian Type Oak – Hickory Forest (Red Oak Type)	128	2.12	Mesic Oak 4	MO	D
6271	*(Quercus prinus, Quercus coccinea) / Kalmia latifolia / Galax urceolata* Forest	Chestnut Oak Forest (Xeric Ridge Type)	568	9.43	Xeric Oak 7	XO	D
6272	*Picea rubens – Tsuga Canadensis / Rhododendron maximum* Forests	Red Spruce – Fraser Fir Forest (Hemlock Type)	116	1.93	Spruce-Fir 1	SF	C
6286	*Quercus prinus – Quercus rubra / Rhodendron maximum / Galax urceolata*-Forest	Chestnut Oak Forest (Xeric Ridge Type)	53	0.88	Mesic Oak 4	MO	D
7097	*Pinus purgens – Pinus rigida (Quercus prinus) / Kamia latifola – Vaccinium palladum* Forest	Blud Ridge Table Mountain Pine – Pitch Pine Woodland (Typic Type)	134	2.22	Pine 10	P	C

APPENDIX A (Continued)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
7119	*Pinus virginiana – Pinus (rigida, echinata) – (Quercus prinus) / Vaccinium palladum* Forest	Appalachian Low Elevation Mixed Pine Forest	13	.22	Pine 9	P	C
7219	*Liriodendron tulipifera – Acer rubrum – Robinia pseudoacacia* Forest	Early Successional Appalachian Hardwood	118	1.96	Tulip Poplar 6	TP/MMH	D
7230	*Quercus alba – Quercus (Rubra, prinus) / Rhododendron calendulaceum – Kalmia latifolia – (Gaylussaccia ursine)* Forest	Appalachian Montane Oak Hickory Forest (Typic Acidic Type)	25	.42	Mesic Oak 4	MO	D
7285	*Betula alleghaniensis – Fagus grandifolia – Aesculus flava / Viburnmum lantanoides / Aster chlorolepis – Dryopteris intermedia* Forest	Southern Appalachian Northern Hardwood Forest (Typic Type)	236	3.92	Northern Hardwood 2	NH	D

APPENDIX A (Continued)

TNC CODE	ASSOCIATION	COMMON NAME	Frequency	Percent	Community Type Modified from (McKenzie 1993)	Ecotonal Community Class. (ECC)	Comp.
7543	*Tsuga canadensis / Litriodendron tulipifera / Rhododendron maximum – Tiarella cordifolia* Forest	Southern Appalachian Acid Cove Forest (Typic Type)	42	.07	Cove Hardwood 3	CH	H
7693	*Tsuga canadensis / Halesia tetraptera – (Fagus grandifolia, Magnolia fraseri) / Rhododendron maximum / Dryopteris intermedia* Forest	Southern Appalachian Acid Cove Forest (Silverbell Type)	381	6.32	Cove Hardwood 3	CH	H
7861	*Tsuga canadesis – Betula allegheniesis / Rhodendron maximum / Leucothoe fontanensiana* Forest	Blue Ridge Hemlock – Northern Hardwood Forest	820	13.61	Hemlock Hardwood 3.5	HH	H
7876	*Rhododendron carolinianum – Rhododendron catawbiense – Leiophyllum buxifolium* Shrubland	Southern Appalachian Heath Bald	40	0.66	Bald 11	B	B

APPENDIX B

POINT COUNT SURVEY SHEET

Trail/Transect ☐ Point ☐ Visit ☐ Start time ☐ End time ☐

Date ☐ Temp ☐ Sky cond. Cloud cover ☐ Wind speed ☐ Stream noise ☐ Overall noise ☐

			< 50 m			> 50 m			Flyovers		
SPECIES	**alpha code**	**no.**	**0-3 min**	**4-5 min**	**6-10 min**	**0-3 min**	**4-5 min**	**6-10 min**	**3 min**	**2 min**	**5 min**
Hawks											
Broad-winged	BWHA	343									
Red-tailed	RTHA	337									
Falcons											
Peregrine	PEFA	356									
Grouse											
Ruffed	RUGR	300									
Owls											
Great Horned	GHOW	375									
Barred	*BDOW*	*368*									
Northern Saw-whet	NSWO	372									
Swifts											
Chimney	CHSW	423									
Woodpeckers											
Flicker Intergrade	FLIN	412									
Yellow-bellied Sapsucker	WBSA	402									
Downy	DOWO	394									
Hairy	HAWO	393									
Pileated	PIWO	405									
Flycatchers											
Olive-sided	OSFL	459									
Acadian	ACFL	465									
Eastern Phoebe	EAPH	456									
Vireos											
Blue-headed	BHVI	629									
Red-eyed	REVI	624									
Jays, Crows											
Blue Jay	BLJA	477									
American Crow	AMCR	488									
Common Raven	CORA	486									
Titmice and Chickadees											
E. Tufted Titmouse	ETTI	731									
Black-capped Chickadee	BCCH	735									
Carolina Chickadee	CACH	736									
Brown Creeper	BRCR	726									
Nuthatches											
White-breasted	WBNU	727									
Red-breasted	RBNU	728									
Wrens											
Winter	WIWR	722									
Carolina	CARW	718									
Kinglets											
Golden-crowned	GCKI	748									
Thrushes											
Veery	VEER	756									
Hermit	HETH	759									
Wood	WOTH	755									
American Robin	AMRO	761									

APPENDIX B (Continued)

POINT COUNT SURVEY SHEET

SPECIES	alpha code	no.	< 50 m			> 50 m			Flyovers		
			0-3 min	4-5 min	6-10 min	0-3 min	4-5 min	6-10 min	3 min	2 min	5 min
Mockingbirds, Thrashers											
Gray Catbird	GRCA	704									
Brown Thrasher	BRTH	705									
Warblers											
Northern Parula	NOPA	648									
Chestnut-sided	CSWA	659									
Magnolia	MAWA	657									
Black-and-white	BAWW	636									
Black-throated Blue	BTBW	654									
Cerulean	CERW	658									
Blackburnian	BLBW	662									
Black-throated Green	*BTNW*	*667*									
Kentucky	KEWA	677									
Canada	CAWA	686									
Hooded	HOWA	684									
Ovenbird	OVEN	674									
Louisiana Waterthrush	LOWA	676									
Tanager											
Scarlet	SCTA	608									
Eastern Towhee	EATO	587									
Junco											
Unid. Dark-eyed	UDEJ	567									
Cardinals											
Rose-breasted Grosbeak	RBGR	595									
Northern Cardinal	NOCA	593									
Indigo Bunting	INBU	598									
Blackbirds											
Brown-headed Cowbird	*BHCO*	*495*									
Finches											
Purple	PUFI	517									
Red Crossbill	RECR	521									
Pine Siskin	PISI	533									
American Goldfinch	AMGO	529									
Total birds											
Total species											
GPS location											

Observer ____________________

APPENDIX C

VEGETATION DATA SHEET FOR .04 ha OR 11.3 m (37') RADIUS CIRCULAR PLOT

Name ____________ Date ________ Trail/Transect ☐ Point ☐ GPS location ______________

	Dbh (Trees)						Cover			
Tree Species	**0-10**	**11-25**	**26-50**	**51-75**	**76-100**	**>100**	**Can class**	**Sub class**	**Tall class**	**Low class**
ASH, MOUNTAIN										
ASH, AMER. WHITE										
BASSWOOD, WHITE										
BEECH, AMERICAN										
BIRCH, BLACK OR SWEET										
BIRCH, YELLOW										
BLACKGUM										
BUCKEYE, YELLOW										
CHERRY, BLACK										
CHERRY, PIN OR FIRE										
CHESTNUT, AMERICAN										
CUCUMBERTREE										
DOGWOOD, FLOWERING										
FIR, FRASER										
HEMLOCK, EASTERN										
HOLLY, AMERICAN										
HICKORY, MOCKERNUT										
IRONWOOD/AMER. HORNBEAM										
LOCUST, BLACK										
MAGNOLIA, FRASER										
MAPLE, MOUNTAIN										
MAPLE, RED										
MAPLE, SILVER										
MAPLE, STRIPED										
MAPLE, SUGAR										
OAK, BLACK										
OAK, CHESTNUT										
OAK, NORTHERN RED										
OAK, SCARLET										
OAK, WHITE										
PINE, PITCH										
PINE, SHORT-LEAF										
PINE, TABLE MOUNTAIN										
PINE, VIRGINIA										
PINE, EASTERN WHITE										
SASSAFRAS										
SILVERBELL, CAROLINA										
SOURWOOD										
SPRUCE, RED										
SWEETGUM, RED										
SYCAMORE										
TULIP/YELLOW-POPLAR										
WALNUT, BLACK										
YELLOWWOOD										

Vegetation stratification classes	
Fir mortality-young fir regeneration	A1
Fir mortality-non fir/deciduous regrowth	**A2**
Thinned fir-deciduous understory growth	B1
Thinned fir-young fir regeneration	**B2**
Stable-mature fir stand	C1
Stable-spruce-dominated stand	**C2**
Special habitat features	
Disturbance	
Forest opening	
Logs	
Snags	
TNC vegetation classification: code no.	

Tall class = # of stems tall shrubs/saplings > 1 < 10cm dbh
Low class = # of stems low shrubs/seedling < 1 cm dbh

Topographic features

Elevation m ☐

Slope % ☐

Aspect ☐
N NE E SE S SW W NW

Rainfall ☐

Cover Class/Height Range (m)

Tree canopy	
Subcanopy	
Tall Shrub/ Sapling	
Low Shrub/ Seedling	
Ground or Herbaceous	

Deciduous Evergreen
Ferns Moss

Cover class categories

1	< 0.1
2	> 0.1-1%
3	> 1-2%
4	> 2-5%
5	> 5-10%
6	> 10-25%
7	> 25-50%
8	> 50-75%
9	> 75-95%
10	> 95%

Community type

1. Spruce Fir
1.5. Spruce-Northern Hardwood
2. Northern Hardwood
3. Cove Hardwood
3.5. Hemlock-Hardwood
4. Mesic Oak
5. Mixed Mesic Hardwood
6. Tulip Poplar
7. Xeric Oak
8. Pine Oak
9. Pine
10. Health Bald
11. Grassy Bald
12. Grape Thicket or Treeless

APPENDIX C (Continued)

VEGETATION DATA SHEET FOR .04 ha OR 11.3 m (37') RADIUS CIRCULAR PLOT

	Dbh (Trees)						Cover			
SHRUBS	**0-10**	**11-25**	**26-50**	**51-75**	**76-100**	**>100**	**Can class**	**Sub class**	**Tall class**	**Low class**
Blackberry, Smooth										
Rubus canadensis										
Blueberry										
Vaccinium spp										
Chokeberry, Black										
Aronia melanocarpa										
Cranberry, Mountain										
Vaccinium erythrocarpum										
Dog-hobble										
Leucothae fontanesiana										
Dogwood, Alternate-leaf										
Cornus alternifolia										
Elder, Red-berried										
Sambucus pubens										
Gooseberry, Roundleaf										
Ribes rotundifolium										
Holly, Mountain										
Ilex montana										
Huckleberries										
Gaylussacia spp										
Hydrangea, Wild										
Hydrangea arborescens										
Mountain-laurel										
Kalmia latifolia										
Rhododendron, Catawaba										
Rhododendron catawabensis										
Rhododendron, Rosebay										
Rhododendron maximum										
Serviceberry, Alleghany										
Amelenchier laevis										
Sweetshrub										
Calycanthus floridus										
Viburnum, Maple-leaved										
Viburnum acerifolium										
Witch-hazel										
Hamamelis virginiana										
Witch-hobble										
Viburnum lantanoides										
Witherod										
Viburnum cassinoides										
Wood-aster										
Aster acuminatus										
Wood sorrel										
Oxalis acetosela										

APPENDIX D

DATA ON TRAILS NOT USED IN ANALYSES

Topographic and ecotonal community vegetation associations for Brush Mountain Trail (BMT) point data; length 7.88 km, elevational gain 762 m. ECC=ecotonal community classification, abbreviations are defined in Appendix A. Two zones identified by gradsect =**, transition with hard boundary = *, all other transitions are soft boundaries.

Ecotonal Zone**	Trail / Pt.	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
1	BMT 01	7543	672	16.63	NE	CH
1	BMT 02	7219	697	8.29	NE	TP
1	BMT 03	7219	729	8.98	E	TP
1	BMT 04	6271	736	9.92	E	OX
1	BMT 05	6286	763	8.73	NE	MO
1	BMT 06	7219	793	10.70	NE	TP
1	BMT 07	7219	822	12.77	NE	TP
1	BMT 08	7219	847	26.00	N	TP
1	BMT 09	7219	876	27.88	NE	TP
1	BMT 10	6271	923	20.80	E	XO
1	BMT 11	7097	947	27.44	SE	P
1	BMT 12	6271	992	26.47	SE	XO
1	BMT 13	6271	1022	18.87	E	XO
1	BMT 14	7097	1044	20.45	SE	P
1	BMT 15*	6271	1081	27.49	S	XO
2	BMT 16	7693	1107	30.00	S	CH
2	BMT 17	7097	1157	19.32	SE	P
2	BMT 18	7693	1181	33.35	N	CH
2	BMT 19	7861	1216	31.55	E	HH
2	BMT 20	7861	1241	23.56	NE	HH
2	BMT 21	7861	1239	32.48	N	HH
2	BMT 22	7861	1275	29.33	N	HH
2	BMT 23	4973	1301	32.18	NW	NH
2	BMT 24	7861	1353	35.72	NW	HH
2	BMT 25	7861	1407	30.25	E	HH

APPENDIX D (Continued)

DATA ON TRAILS NOT USED IN ANALYSES

Topographic and ecotonal community vegetation associations for Boulevard Trail (BVT) point data; length 8.53 km, elevational gain 487.6 m. ECC=ecotonal community classification, abbreviations are defined in Appendix A. Two zones identified by gradsect =**, transition with hard boundary = *, all other transitions are soft boundaries.

Ecotonal Zone**	Trail / Pt.	TNC Veg. Code	Elev (m)	Slope (Degrees)	Aspect	ECC
2	BVT 02	114	1947	39.03	N	SNH
2	BVT 03	114	1868	41.91	N	SNH
2	BVT 04	114	1857	46.05	NE	SNH
2	BVT 05	114	1857	33.37	NE	SNH
2	BVT 06	112	1822	23.50	NE	SF
2	BVT 07*	114	1796	9.52	E	SNH
2	BVT 08	114	1778	12.10	E	SNH
2	BVT 09	114	1765	8.76	NE (S)	SNH
2	BVT 10	114	1775	25.82	SE	SNH
2	BVT 11	114	1769	18.24	E	SNH
2	BVT 12	112	1750	34.09	SW	SF
2	BVT 13	114	1743	19.82	SW	SNH
2	BVT 14	114	1769	25.00	SW	SNH
2	BVT 15	112	1798	26.05	SE	SF
2	BVT 16	112	1756	12.10	SE	SF
2	BVT 17*	112	1636	44.25	SW	SF
3	BVT 01	6049	1963	32.74	S	F

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EDUCATION

◆ Old Dominion University, *Norfolk, VA* **Ph.D.** Eocological Sciences	9/1994 –12/2005
◆ Virginia Tech, *Blacksburg, VA* **M.S.** Wildlife Management	9/1970 – 3/1973
◆ Old Dominion University, *Norfolk, VA* **B.S.** Biology; Geology	9/1965 – 6/1970

SKILLS & QUALIFICATIONS

- Certified Wildlife Biologist: The Wildlife Society
- Certified Environmental Specialist: Environment Assessment Association
- Aerial Photo Interpretation: Use of Stereoscope
- Computer Skills & GIS Applications: MS Office, Windows XP and NT, GIS Software: ARC View 3.3, ARC GIS 8.3, ARC View Spatial Analyst, Idrisi 32
- Environmental: Write Phases I & II Environmental Site Assessments, Environmental Assessments (EAs), Environmental Impact Assessments (EISs), HAZWOPER trained & certified (5/2003)
- Professional Photographer: Aerial, Environmental, Outdoor, Wildlife, Digital with GPS
- Scientific Field Sampling: Use of standardized methods
- Measuring & Monitoring of Birds and Mammals: Use of standardized methods

RELATED EXPERIENCE

◆ Environmental Project Manager: Federal Emergency Management Agency (FEMA), *Philadelphia, PA*	9/2003-Present
◆ Ecological Scientist: Baker Engineering & Energy, *Virginia Beach, VA*	4/2003-9/2003
◆ Natural Resource Manager / Environmental Scientist: Langley AFB, *Langley, VA*	4/2002-4/2003
◆ Certified Wildlife Biologist / Environmental Scientist: Damalas Enterprises Inc. & Davis Environmental Consultants Inc., *Virginia Beach, VA*	3/1994-3/2002
◆ Adjunct Instructor: Dept. of Geography, Old Dominion University, *Norfolk, VA*	9/1998-5/1999
◆ Wildlife Biologist / Environmental Scientist: Damalas Enterprises Inc., *Virginia Beach, VA*	1982-1994
◆ Wildlife Biologist / Interpretative Naturalist: Friends of the Earth, *Limassol, Cyprus*	Summers of 1987-1990
◆ Wildlife Biologist / Environmental Scientist: Damalas Environmental Consultants, Inc., *Virginia Beach, VA*	1969-1978
◆ Adjunct Teacher: Dept. of Biological & Health Sciences, Fairleigh Dickenson University, *Madison, NJ*	1974-1975
◆ Conservation Executive & Director of Conservation Education: Boy Scouts of America Headquarters, *Brunswick, NJ*	1973-1976

RESEARCH EXPERIENCE

- Ph.D. Candidate: Conducted over 3000 bird point count censuses & obtained quantitative data on over 1000 samples of vegetation & soil