To the Graduate Council:

I am submitting herewith a dissertation written by Kimberly C. Norris entitled "Guidelines for the Use of Hyperdiverse Taxa in Biological Monitoring: Change Through Time in Southern Appalachian Spider Assemblages." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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GUIDELINES FOR THE USE OF HYPERDIVERSE TAXA IN BIOLOGICAL MONITORING:

CHANGE THROUGH TIME IN A SOUTHERN APPALACHIAN SPIDER ASSEMBLAGE

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Kimberly Carol Norris

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DEDICATION

I dedicate this dissertation to my parents, Stuart and Carol Norris. For their continuous support and encouragement, and their ability to make me believe that I can change the world, I cannot thank them enough. Without their persistent and stubborn belief in me, I may have never had the faith or the motivation to keep going through the rough times.

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ABSTRACT

This dissertation addresses issues surrounding the inclusion of terrestrial arthropods in conservation planning. There are potentially disastrous consequences of basing all of our conservation priorities and strategies on what we know of the ecology of a minority of species (vertebrates). Vertebrate species do not provide enough information to be good indicators of ecosystem health, particularly if we are interested in those ecosystem processes which involve invertebrates. We need to learn more about those organisms which comprise the bulk of biodiversity (arthropods) and develop methods which facilitate the inclusion of terrestrial arthropods (or other hyperdiverse groups) in conservation planning. In this dissertation, I begin the process of developing analytical tools appropriate to a representative arthropod group, the spiders (Order Araneae). Spiders were chosen in part because they show particular promise as an indicator group.

One of the difficulties associated with studying a hyperdiverse taxonomic group is ensuring accurate and timely species identification. Using technology similar to that employed in handwriting analysis and/or face recognition, I present an automated species identification system which makes use of neural networks. This technology, once perfected, will increase the accuracy of identifications by non-specialists and thereby reduce the need to burden systematists with routine identifications of ecological collections. This technology could also be used to catalog species which have yet to be identified or even described (morphospecies), thus allowing accurate ecological studies to take place prior to naming all the component species in the assemblage.

Using data collected in the Southern Appalachians, I review and evaluate some commonly used analytical techniques in biodiversity studies: rarefaction (scaling down all samples to the size of the smallest), diversity indices, and extrapolation (estimating the

total richness of a site based on a sample taken from the site). Rarefaction was essential to correct for differences in samples size between samples, particularly when using indices calculated using only presence/absence data. The diversity indices, Shannon-Weiner and Simpson's, were surprisingly robust to differences in sample size and they detected both successional and disturbance-induced changes in spider assemblages. Directional trends in the diversity indices through time proved to be most informative in conjunction with pair-wise statistical tests. My results suggest, however, that extrapolation techniques should be used cautiously, as they were sensitive to differences in sample size and yielded very different richness estimates for surveys taken at the same sites.

Using the same datasets, I identify and discuss potential sources of error which are characteristic of studies involving hyperdiverse taxa and make recommendations for eliminating or reducing this error. I find that collector bias is a significant problem, in that each collector is not sampling a statistically random subset of the community. But, as expected, some collection techniques are more subject to this kind of bias than others. I recommend that if turnover of collectors is likely, methods such as pitfall traps, litter samples, and vegetation beating/sweeping should be emphasized. Also, inclusion of juveniles in diversity estimates and analysis should be avoided as much as possible as their presence appears to obscure ecological trends.

I used the datasets to investigate the intra-annual (early vs. late summer) and inter-annual (yearly vs. decadal) variability of spider assemblages in six Southern Appalachian habitats. Spider assemblages show greater seasonal variation than yearly variation. The diversity and variability of the spider assemblages I studied were closely tied to gross habitat structure.

In conclusion, terrestrial arthropods can and should be included in conservation planning and/or community-level analyses. Techniques exist and are currently being perfected, which address the peculiarities and difficulties associated with working with such hyperdiverse groups.

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PART I: INTRODUCTION

STATEMENT OF PROBLEM

The conservation of biological diversity is intricately tied to the preservation of community structure. Due to the extent of inter-species interactions, loss of species changes community structure. This may, in turn, lead to a destabilized ecosystem in which more species become extinct and further losses of biodiversity occur. Terrestrial arthropods constitute between 79 and 90% of global biodiversity (Pimm *et al.* 1995) and comprise the bulk of biomass in many ecosystems (Kim 1993). They are critical to ecosystem function through their roles as pollinators, decomposers, predators, parasites, and consumers. Thus, the preservation of biological diversity necessitates the conservation of terrestrial arthropods. Studies which improve our knowledge of the ecology of terrestrial arthropods will facilitate their incorporation into current conservation strategies, as well as yielding insight into their use as indicators of community health. Before this can be done, we need to know how quickly and to what extent species assemblages change through time in relatively undisturbed habitats. Without such knowledge, we will be unable to separate natural, stochastic change of the assemblage from change resulting from anthropogenic stress. Knowledge of the variability of arthropod assemblages will also allow evaluation of their potential use as indicators. In this study, I examine how a number of arthropod assemblages change through time over intervals both less than (3 months), similar to (1 to 2 years), and significantly longer than (19-21 years) the life spans of the individuals. Spiders (Order Araneae) possess many of the attributes recommended for an indicator assemblage. I evaluate the variability of various spider assemblages using a number of indices which compare the fauna of recent and historic surveys. In addition, data are presented on the effects of vegetation type and disturbance on spider assemblage dynamics. Lastly, I use

these data to identify and discuss the implications of various sources of error that will adversely affect the accuracy and efficiency of a monitoring protocol involving spiders or any other highly taxonomically diverse (henceforth 'hyperdiverse') group.

BACKGROUND

Importance of Terrestrial Arthropods

Whether you choose to count species, individuals, or biomass, arthropods are the dominant group in terrestrial ecosystems (Kremen *et al.* 1993). As herbivores, they consume as much as or more than vertebrates in most ecosystems (Janzen 1981; Thorton 1985). As pollinators, they are required for successful reproduction of most plant species. For example, Euglossine bees are the only pollinators for many orchid species and are also needed for successful reproduction by 30 or more plant families. Lovejoy *et al.* (1986) have shown that nearby deforestation results in lower and more variable visitation rates by these bees and, lower visitation means lower levels of pollination and seed output for plant species (Aizen and Feinsinger 1994). Terrestrial arthropods are critical as decomposers and the disruption of this activity has been shown to result in decreases in nutrient cycling, leaching of nutrients from the soil, and an accumulation of litter (Rapport *et al.* 1985). As predators and parasitoids, they also play an important role in the regulation of insect populations. Parasitoids of the genus *Aphytis* suppress outbreaks of diaspidid scale insects, which otherwise would over-exploit their plant resources (Samways 1993). Spider assemblages greatly reduce plant damage by insect herbivores in agricultural systems by reducing their population numbers through predation (Riechert and Bishop 1990) or altering their behavior (Young 1999). Monoculture plantations of tree stands suffer 30% more damage due to herbivory than old-growth stands which support a greater variety of herbivores and (most importantly here) arthropod predators

(Schowalter 1990). Bird species which depend on the swarming activity of army ant colonies in Amazonian forests have been shown to disappear when forest fragments become too small to support sufficient colonies of ants (Lovejoy *et al.* 1986). When army ants were intentionally brought back to these forest fragments, these extinction-prone birds returned in significant numbers (Lovejoy *et al.* 1986). These are just a few examples meant to illustrate the importance of arthropods in terrestrial ecosystems. We can conclude that the disappearance of any one species often has the potential to disrupt important ecosystem processes. To quote Myers (1986, p. 40) "If a keystone mutualist is eliminated as a result of human disturbance of forest ecosystems, the extinction of several other species will follow, inevitably. Still more to the point, these additional losses may, in certain circumstances, trigger a cascade of linked extinctions. Eventually a series of forest food webs can become unraveled, with shatter effects throughout their ecosystems."

Conservation of Ecosystems

Due to the hyperdiverse nature of arthropod communities, the lack of either taxonomic or ecological information on most species, and the rate of habitat alteration and/or destruction, traditional management is not feasible for single species. Our options seem to be limited to the 'quick and dirty' conservation technique described by Ehrlich (1992) of evaluating ecosystems, designating reserves to protect 'valuable' habitats, and monitoring the success of those reserves. Most conservation biologists, along with government agencies, have been busy focusing on the first two of these objectives (Soulé and Simberloff 1986). Recently, as more land is set aside for conservation, attention has turned to methods of monitoring the success of these reserves. What are the signs of ecological 'stress' in an ecosystem? Rapport *et al.* (1985) lists the following symptoms of stress: changes in nutrient cycling, changes in primary productivity, changes in species

diversity, retrogression (large fluctuations in populations that reproduce rapidly), changes in the size distribution of species, and changes in the amplitude of fluctuations in component populations. Many of these indices are difficult/costly to measure. Even simply looking at species diversity of the entire community would be an enormous task and could yield ambiguous results (some disturbed ecosystems have higher taxonomic degrees of richness than when they were undisturbed). Rapport *et al.* (1985) state that the earliest indications of ecosystem response to disturbance are abnormal fluctuations in sensitive populations. If we can identify 'sensitive' species which can be used as indicators, we can detect ecological stress in the community (assuming we know the background rate of change). If the goal of the particular conservation project is to conserve a certain species or set of species, it would be beneficial to identify a species or assemblage which is more sensitive to disturbance than the one we are trying to conserve. This will allow for early detection and mitigation before the species/assemblage of interest is greatly affected. The indicator species/assemblage should also have the ability to rebound quickly following disturbance, hence making continued monitoring possible.

Choosing an Indicator Group

When the goal of a conservation effort is to maintain biodiversity, indicator *assemblages* are preferable to indicator *species*. Fry *et al.* (1986), in their examination of the U.S. Fish and Wildlife Service's Habitat Evaluation Procedures (HEP), found that the number of species selected to represent a given habitat type was inversely proportional to the maximum percent error in the sample mean for the Habitat Suitability Index (HSI). Put simply, using more species to classify a habitat type results in less error when predicting the presence of a target species. They recommended that habitat evaluation include as many species as allowed by budget constraints. Choosing a suite of species also broadens the scope of environmental change that can be detected (Kremen 1992,

1993; Block *et al.* 1986). The kinds of changes in a community that we need to detect include the biotic effects of pollution, chemical spills, habitat fragmentation, species invasion, and climate change.

Brown (1991) lists the characters that are desirable in such an indicator group (Table 1). Most other workers require a subset of these criteria (e.g., Noss 1990). Pearson and Cassola (1992) suggest that one might select indicator assemblages based on a) the time required to locate 90% of the species in the field, b) the ease of training non-specialists to collect specimens, and c) the ability of the group to maintain viable populations in small patches of habitat. This last criterion is important given the frequently small size of habitat reserves and the number of habitats that have already experienced extensive disturbance. For example, the Atlantic forest of South America totals less than 8-14% of its original area (Thomas *et al.* 1998) with very few reserves larger than 40,000 ha and most less than 400 ha. The indicator assemblage should also be a group that is resilient and can, therefore, effectively track K (the carrying capacity of the system). Even though such groups will undoubtedly vary from year to year due to stochastic variations in K (e.g., changes in rainfall affects insect abundance which, in turn affects predator levels (Turelli 1978)), these changes should be of a different amplitude than those due to disturbance. The increase in sensitivity outweighs the increase in variability. More explicitly, any group which closely tracks K will be more useful as an indicator because it will respond immediately to changes in K due to disturbance. These species are more likely annual species whose populations will adjust to the new K on a yearly basis. Organisms which do not have the ability to track K closely will, of course, have lower levels of annual change, but will also not be as sensitive a tool to detect ecological stress in the system.

Table 1. Desirable characteristics of indicator assemblages

Usefulness	Ease of Analysis	Group Characteristics
*Responsive to disturbance	*Abundant, non-furtive target individuals	*Taxonomically diverse
*Correlated with other groups and resources	*Easy to find	*Ecologically diverse
*Functionally important to ecosystem	*Taxonomically well known	*Relatively sedentary
*Exhibits damped fluctuations (not stochastic fluctuation)	*Easily identifiable/well studied	*Endemic or well differentiated
	*Easy to obtain large, random samples of species	

* attributes which apply to spiders

One objection to the use of arthropods as indicators is the assumption that their populations, and consequently their communities, are too temporally variable to be of use in monitoring programs (Ward 1978). Landres *et al.* (1988), however, in their critique of criteria used to select indicators, found virtually no data to substantiate this assumption. Indeed Bengtsson (1994), in a review of the predictability of forest soil communities found that not only were these communities highly predictable (in terms of species presence/absence as well as relative abundances), but that the degree of predictability did not increase with increasing body size.

To summarize, a useful indicator will be a group of species which meets the characteristics identified in Table 1 and which, in addition, is both time- and cost-effective to monitor.

Terrestrial arthropods as indicators

Although the goal of most faunal conservation efforts is to preserve one or more vertebrate species, vertebrates are not good indicators of overall habitat disturbance or of health for the natural community. They are typically furtive and present in few numbers, which limits our ability to efficiently sample them. Furthermore, they have relatively long generation times, which limits how quickly we will detect population response to environmental stress. Finally, Murphy and Wilcox (1986) point out that vertebrates have relatively large geographic ranges, and so may be less responsive to localized and selective loss of habitats which may be important to other groups. For instance, stream invertebrates have been shown to be more sensitive to minor changes in substrate-particle size than fish (Berkman *et al.* 1986). *Euphydryas* butterflies will not persist on a reserve which does not have the appropriate host plant(s) for oviposition *and* the appropriate density of food plants for their larvae, no matter how large the reserve (Ehrlich 1992).

Terrestrial arthropods are ideal subjects for conservation studies because they are numerically abundant in a wide variety of microhabitats and exhibit functional niches at virtually all temporal and spatial scales. Aquatic arthropods such as amphipods and isopods have been used as indicators of water quality since the 1970's (Rosenberg *et al.* 1986). The sampling costs involved for an arthropod inventory are substantially lower than for most vertebrate groups (unless multiple systematists must be hired to identify specimens), and statistically rigorous sample sizes are more easily obtained (Brown 1991; Murphy *et al.* 1990). Terrestrial arthropods are also responsive to habitat fragmentation and to fluctuating environmental conditions but have been underutilized (Kremen *et al.* 1993). The early detection of environmental problems would allow mitigation strategies to be implemented before the vertebrate fauna and plant communities are severely affected.

Picking an assemblage

Identifying a terrestrial arthropod assemblage that is limited enough to enable rapid assessment and quantification, and yet diverse enough to respond to a variety of anthropogenic disturbances, is essential for the success of monitoring techniques. Species in the Order Araneae (spiders) may be suitable based on the criteria outlined in Table 1 (Spiders fit all the starred (*) criteria). They meet 11 of the 13 criteria outlined by Brown (1991) and five of the seven criteria given by Noss (1990)—we do not yet have the data to evaluate whether they do or do not fit the remaining 4 criteria. The number of spider species in 1-ha ranges from approximately 40 to well over 100, depending on the habitat type, allowing high resolution data even for relatively depauperate areas. Spider diversity has repeatedly been shown to be positively correlated with vegetation structural complexity (Dobel *et al.* 1990; Frazer and Frankie 1986; Abraham 1983; Hatley and MacMahon 1980). The taxonomy of spiders is also well known relative to other

arthropod groups. Non-specialists can be trained quickly to collect and sort spiders (Dr. S. Riechert, personal communication). In addition, recent work by Oliver and Beattie (1996) conclude that non-specialists can adequately sort spiders into morphological groupings of species (i.e., morphospecies) which correspond very closely to biological species. Morphospecies can be used as surrogates for taxonomically defined species to measure biodiversity and changes in apparent richness through time in monitoring programs. Further, spiders can be easily distinguished into functional guilds of species based on their prey capture method (web builders, wandering hunters, etc.), a convenient subdivision that allows analysis of the relative species richness of these different groups.

Some work exists on the effects of anthropogenic habitat change and natural disturbance on spider species and guilds. Numerous studies have shown that clear-cutting of forests results in predictable changes in the proportions of spider species in different guilds (e.g., McIver *et al.* 1992; Coyle 1981). Fraser and Frankie (1986) found that proportional differences in guild representation also occurred between urban (backyard) and natural habitats. Webb and Hopkins (1984) found that heathland spiders were sensitive to fragment size across the landscape mosaic, exhibiting lower abundances on small, fragmented habitat patches. Gunnarsson (1988) examined the effect of needle loss in evergreen spruce in SW Sweden caused by air pollution. Generating a fine-grained patchiness of arboreal habitat, needle loss significantly changed the relative abundance of spider species in the boreal forest community. In particular, needle loss caused a decline in the large-bodied members of the spider assemblage. The concern is that the decrease in abundance of large-sized spiders will adversely affect over-wintering passerine birds, as these spiders provide a primary food source (for example, 80% of the diet of Goldcrests). In a similar study, Hatley and MacMahon (1980) artificially altered the foliage of shrubs and found that these extremely local perturbations resulted in changes in the number of

spider species, spider guilds, and importance values for the guilds. Decreases in abundance across all guilds has been shown to occur as a result of frequent tidal flooding in a salt marsh (Dobel *et al.* 1990). Fire frequency has also been shown to affect the species composition and relative abundance of spider species (Aitchison-Benell 1994; Johnson 1995; Koponen 1993; Riechert and Reeder 1970), possibly due to changes in habitat structure of predominate plants. Spiders have been shown to accumulate heavy metals (cadmium, copper, and zinc) from a polluted environment (Larsen *et al.* 1994; Macrzyke *et al.* 1992). The biological implications of such toxic accumulation have not been examined, although these studies report that metal burdens were species-specific and thus could produce measurable changes in community composition if accumulation has an effect on fitness. A long term study conducted in Holland by Deeleman-Reinhold (1989) established that spiders living in an area subject to industrial pollution (a peat-bog 6 km from a 16 km-long region of chemical and petrochemical production plants) showed drastic changes in the relative abundance of the large hunting spiders in the arthropod community. Other studies have demonstrated the deleterious affects of pesticides on non-target arthropods including spiders (Olsza *et al.* 1994; Everts *et al.* 1991; Martinat *et al.* 1993). Unfortunately, responses are not yet predictable for spiders or any arthropod group to *all* types of disturbance (e.g., acid rain and near-future climate change anticipated in a Greenhouse world).

Taken as a whole, spiders show promise as a potential indicator assemblage for use in habitat monitoring programs. To further evaluate their usefulness as indicators, we need to answer the following three questions: 1) Are the dynamics of the spider assemblage predictable enough to separate the effect of disturbance from 'normal' stochastic fluctuation? 2) Do spider assemblages respond predictably to habitat disturbance? 3) Is the response correlated with the response of other organisms in the

arthropod or broader natural community? Question 1 is the first step in evaluating the potential of spiders as an indicator assemblage, as predictability is a necessary criterion. Questions 2 and 3 require manipulative studies which will only be worthwhile if question 1 is answered affirmatively. In this study, I answer the question of predictability by quantifying the magnitude and predictability of change through time in the Araneae. To do this, methods and analytical tools appropriate to quantifying the likely dynamics of this group must be selected.

Quantifying community change

To effectively use spiders (or any other arthropod group) as indicators of community health, it is imperative to understand the issues involved in their community dynamics. Some studies have shown that terrestrial arthropod groups exist as a collection of subpopulations which undergo frequent extinctions and recolonizations (also referred to as a metapopulation). This phenomenon is especially prevalent in fragmented landscapes (Hanski *et al.* 1995, Lande 1979, Slatkin 1977). Murphy *et al.* (1990) predict that species with high reproductive rates, small body sizes, short life-spans, and high habitat specificity likely exist as metapopulations. Note, however, that Hanski and Simberloff (1997) contend that not enough evidence exists for these sorts of generalizations. Nevertheless, spiders fit the Murphy *et al.* criteria. As many of the spider assemblages used in this study are found ins early successional habitat following disturbance, it is possible that they exist as a system of overlapping metapopulations (Harrison 1994b). Due to the fragmented nature of current landscapes, conservation biologists have turned to the study of metapopulation dynamics to assess the viability of threatened species. To assign any predictive power to population viability analysis through the study of a metapopulation (e.g. re-calculation of effective population size using metapopulation models) requires long-term population research on the species in

question (Ehrlich 1992). Although it is beyond the scope of this study to evaluate the status of the 50-100 overlapping metapopulations of spider species that exists in any one of the study sites, I apply some of these ideas to introduce analyses which will help understand how spider communities behave through time and space (i.e., different habitats). For example, consider the simplified case, where there is an arbitrarily selected plot in the midst of a forest (see Figure 1A). In year 1, the plot is sampled and a species list consisting of species A-D is obtained. This plot can be said to include partially overlapping metapopulations of these four species. Because individuals of spiders typically exhibit an annual longevity, each local population (within the metapopulation) faces the possibility of an extinction once the adults have died. Potential recolonization occurs once the spiderlings begin to disperse, beginning the next annual cycle. If the plot is sampled the following year, species D may have disappeared, even if environmental conditions have remained the same due only to stochastic events during dispersal and/or low population sizes (see Figure 1B). If there has been some sort of disturbance (e.g., clear-cutting of a forested stand) in the plot, species A-D may be lost and species E-G gained due to changes in the habitat structure (see Figure 1C). The metapopulations of the lost species have been forced to contract due to the failed recolonization of some of the sub-populations attributed to inappropriate habitat for the dispersing spiders. Even though in this situation the plot is arbitrarily defined, the change in the assemblage can be measured in terms of extinction and colonization of the collection of populations which makes up the species' ranges. The existence of metapopulations predicts that there will be temporal turnover of species in a given area (Russell 1996).

The measurement of temporal turnover was first developed as part of island biogeography theory (MacArthur and Wilson 1967). Even though this idea was developed for island situations, it also seems to be the logical parameter to use for the

Figure 1. The geographic location of the six study areas. (A) Overview map illustrating the placement of the three sites located in the GSMNP and the three sites located in the Nantahala National Forest: 2a corresponds to the approximate location of the Hardwood Forest, 2b to the location of the Meadow Marsh and 2c to the Beech Forest. Circle 1 illustrates the location of all three Macon Co. sites, given scale limitations of the map. (B) A finer scale map of the sites located within the GSMNP ('a','b','c' as described above) and (C) a finer scale map of the three sites in Macon Co. Note that 'hc' marks the location of the Horse Clear-cut and 'ell' marks the location of the Ellicott Forest and the adjacent Ellicott Clear-cut.

Figure 1A: Metapopulations A,B,C,D in Year1

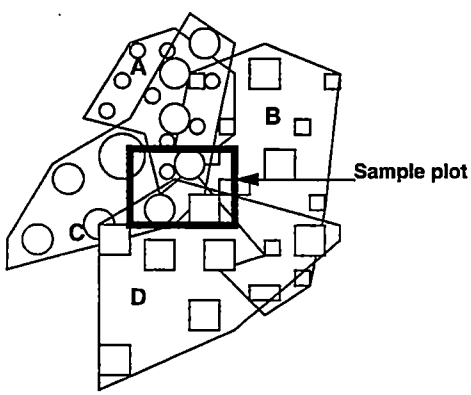


Figure 1C: Metapopulations A,B,C,D,E,F,G in Year 3 (after clearcutting)

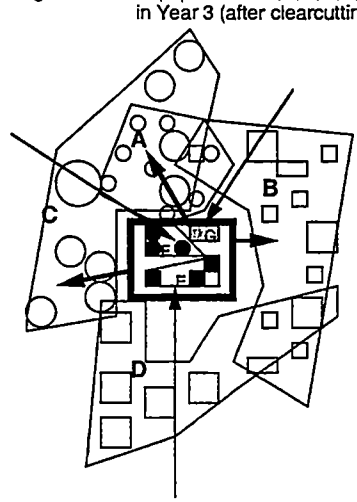
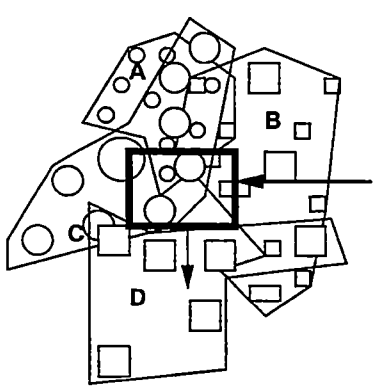


Figure 1B: Metapopulations A,B,C,D in Year 2: (no disturbance)



study of the dynamics of overlapping metapopulations. It is merely a measure of the colonization and extinction of species in a given habitat and thus a measure of community change. In this non-island situation, the degree or rate of turnover will be affected in part by how dynamic the population "islands" are within the species' range, which will depend on the vagility of the study organisms and their degree of dependence on habitat type. Also important may be the type of vegetation present at the site (obstacles or boons to dispersal), the proximity of the site to an ecotone and the sensitivity of the species to environmental changes. Interspecific interactions such as competition and predation may also be important.

Spiders and turnover calculations

Species turnover in spider communities has been examined by Toft and Schoener (1983), Schoener and Spiller (1987) and Simberloff and Wilson (1969, 1970—as a subset of the arthropod community). The extremely high estimates given by Toft and Schoener (1983) of 34–59% turnover represent averages over 106 small islands (~0.01 ha to 0.9 ha) in an archipelago. Small, near islands are expected to have higher turnover rates than large, far islands (MacArthur and Wilson 1967), which may partly explain these high values. In addition, Toft and Schoener used an assemblage of only four large and visually obvious orb-weaving species that arrive and depart islands by ballooning. This could inflate the turnover rates if other, more sedentary species were also present on the islands. Schoener and Spiller (1987), using the same techniques but including eight species, estimated a mean multiple-island turnover of 34%. The turnover of such small, select assemblages cannot be extrapolated to other areas.

In another study involving spiders, Simberloff and Wilson (1970) surveyed arthropod communities for two consecutive years on four small mangrove islands, but did not calculate turnover. Using Simberloff and Wilson's data from those islands, Schoener

(1983) calculated one year turnover for spiders at 39.9%, though his methods were not explicit. Unfortunately, this estimate is again for very small islands and for only two years of data (yielding one measure of yearly turnover). Due to the limitations of these studies, and of the lack of other turnover data for arthropod groups, we have no good indication of whether the turnover of spiders will be high or low compared to that of vertebrates. Bird communities on islands off the coast of Great Britain have been shown to have a one year turnover ranging from 7% to 19% (Russell *et al.* 1995). In a review, Schoener (1983) concludes that turnover is greater in 'lower' (evolutionarily more primitive) organisms, but his assumption of a linear relationship between turnover and census interval renders his comparisons suspect.

Of course, turnover is only one way of quantifying change in an assemblage through time. One can also look at similarity/predictability indices and/or a time series of diversity indices. As turnover uses just presence/absence data on species, some important information is lost. Most models of community similarity (such as 'Bray-Curtis' (Bray and Curtis 1957)) and predictability make use of abundance data. Bengtsson (1994) in a review of forest soil communities (where spiders are a major component) found that these fine-scale, edaphic communities are highly predictable from year to year. He used Kendall's coefficient of concordance which uses ranked abundances of the component species.

OBJECTIVES

In this study, using ecological measures for turnover, similarity, and diversity indices, I quantify the variability of spider assemblages in three forest sites by comparing spider species composition from historical surveys with three consecutive years of recent survey data. In addition, I quantify the seasonal and yearly variability of spider

assemblages in two additional forest sites and one grassland site using data from three consecutive years of recent survey data. Both the sites chosen and the time scale involved can be considered in the microscale domain (1yr to 500yr; $1m^2$ to 10^6m^2) outlined by Delcourt and Delcourt (1988). The following three primary objectives are addressed in this dissertation:

I. To quantify the degree of variability of spider assemblages through time and how this variability is affected by vegetation structure and its recovery following recent events of disturbance. Also to determine the importance of dispersal method and guild membership within the spider assemblage on the amount of variability exhibited.

II. To evaluate the appropriateness for ecological measures of turnover, similarity and diversity indices and tools such as rarefaction and extrapolation for use in biological monitoring protocols, using the ecological data collected in this study as a test case.

III. To uncover and test the effects of potential sources of error likely to be encountered by managers who implement a biological monitoring protocol developed for any hyperdiverse taxon, again using the survey data collected here as a case study; and consequently to make recommendations which will help to alleviate these potential problems.

RATIONALE FOR STUDY

Up to this point, in terrestrial systems, indicator assemblages have been used primarily to compare taxonomic and functional-guild richness and biological diversity between sites. Sometimes the purpose is to measure the effect of a known disturbance at one or more of the sites, or to decide which of a series of candidate sites would be the best to conserve. The presence or absence of a set of species may be used to indicate either that a habitat is relatively sheltered, or free of disturbance, or that it is in a

'disturbed' state of recolonization and of recovery. Fewer studies have actually tried to measure the change in an assemblage through time at a series of sites to see how the assemblage naturally fluctuates or how these fluctuations might be affected by a disturbance (Spellerberg 1991). Yet maintenance of diversity on protected land often relies on this type of monitoring program. Implementation of a monitoring protocol *before* problems arise allows comparison between 'normal' fluctuations and those which may indicate an unwanted structural change in the assemblage. The methodology used in a monitoring regime will depend on the assemblage being measured. Preferably, the natural community dynamics of the group chosen should be known to a certain degree, to better set guidelines for sampling intensity and the frequency of sampling. It would be best to have some prior indication of what potential problems and sources of error there may be in the monitoring process. That way, time and resources will not be wasted collecting unusable data, or biological data which may not answer the ecological or conservation questions being asked.

HOW THIS DISSERTATION IS ORGANIZED

Using one type of data, consisting of species lists and abundances of spiders collected at various temporal intervals, I ask two types of questions. The first is methodological, and concerns spiders as indicators in general. Questions addressed under this heading include how, when and where to census, what indices to use, how to treat the data (i.e., what to do with juveniles, morphospecies, etc.), what are the consequences of likely sources of error, etc. The second is ecological: for the spider assemblages existing at these sites, what causes the observed community dynamics?

A full methodological study of "arthropods as indicators" would require other taxa, other sites, and be outside the scope of a Ph.D. dissertation. The present study is put

forward as a piece in a larger puzzle. Ecological questions arise naturally out of the data, but the data were not collected primarily in order to answer those questions. The rest of this dissertation is organized by methodological categories. Within each part, a number of ecological patterns are presented. In the final part (Part VII), I bring together the ecological results.

Appendix 1 is a published paper, but is attached as an appendix rather than included as a Part because many of the analyses contained in it have been elaborated on and expanded throughout the many chapters of this dissertation. It contains somewhat of an overview of the analyses presented in Parts IV, V, and VI. Organizationally, it made more sense to split up the published paper into multiple Parts with expanded analyses than to continue to add multiple addenda to a very large Part.

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PART II: SAMPLING PROTOCOLS AND STUDY SITES

INTRODUCTION

A community can simply be defined as the collection of populations of species which exist in the same 'home' place or landscape at the same time (Begon *et al.* 1990). Many ecologists use the term *community* loosely to describe a particular group, or subset, of species occurring in the same area. However, if the biological group is defined by their similar taxonomic classification, the more precise term to use is an *assemblage* (Fauth *et al.* 1996). The majority of analyses presented in the following chapters deal with the contemporary spider assemblages of six terrestrial sites in the Southern Appalachian Mountains. In designing an analysis, it is essential to have estimates of some of the basic attributes of the assemblages under study. The most basic attribute is merely how many species make up the assemblage at a particular place and time. Whether attempting to assess the conservation importance, the degree of disturbance and site history of disturbance, or character of a study site for comparison with another, the first step is invariably to assess the number of species present. The taxonomic inventory provides the biological baseline. In many studies of biological diversity, determining the species richness of a site may be the ultimate goal, or at least the first step towards assessing the relative biodiversity value of a selected area (alpha diversity *sensu* Whittaker 1975). Although seemingly straightforward to measure (how many species are there?), species richness is often difficult to determine exactly because many species are rare, and so may be missed in a preliminary census. This is especially true for species-rich groups like terrestrial arthropods. So the number of species found is often related to the number of individual specimens collected, with more individuals usually yielding more species. When trying to compare between sites or between collections at the same site (beta diversity *sensu* Whittaker 1975), the research question then becomes 'how many species

are tabulated for a given amount of sampling effort or sample size?'. Alternatively, the question may be 'can we extrapolate the true taxonomic richness of a site based on our limited sample?'. There are a variety of indices and techniques available to help the investigator to do just that (Magurran 1988, Chazdon *et al.* 1995).

Determining or estimating the number of species (taxonomic richness) in an assemblage is only one way of characterizing biodiversity at a site. Perhaps of more significance is the distribution of individuals in populations among the species, or the equitability of the assemblage. I define equitability to mean degree to which individuals are spread evenly across species (Magurran 1988). In an assemblage which is highly equitable (i.e., most species are represented by similar numbers of individuals), resources are shared more equally between the species present. We assume that no single species is monopolizing all the space or food or other resource in the habitat, because no single species is numerically dominant. Making this assumption (i.e., that numerical dominance is related to dominance of critical resources), we can better understand the underlying distribution of resources in an assemblage by measuring equitability. Also provided is information that can be used to discriminate between sites of similar richness. Richness and the relative abundance of species can either be combined into a diversity index or can be plotted as species abundance distributions. There are many different diversity indices that give different weights to equitability and to species number. Species abundance distributions are frequently plotted as rank/abundance distributions and are 'fitted' or compared with a particular statistical model, such as the common log series, log normal, geometric series, or broken-stick model (Magurran 1988). Each of these models represents a particular point along a continuum, representing the progression from an assemblage with few common and many rare species, to an assemblage in which the species are almost equally abundant.

Another important reason to look at species abundance distributions and their derivatives or components (e.g., species accumulation curves and the numbers of rare species) is that they can tell you something about the statistical adequacy, or completeness of the sample at a given site (Magurran 1988). For example, given the same sampling effort by the researcher, one species-rich site may be undersampled with respect to the target group, while another species-depauperate site may be adequately sampled. This would obviously be important from a biodiversity standpoint if comparisons were being made between these two sites in terms of apparent equitability and/or taxonomic richness. In addition, comparisons made between these sites in terms of the dynamics of a particular assemblage would also be affected by differences in sampling adequacy. The undersampled site might appear to be more variable from sample to sample, due to the artifact of stochastic sampling effects. Such confounding effects should be taken into consideration when using assemblage data both to discriminate between sites and to examine the seasonal and annual variability within a site.

In this chapter, I describe the selection of study sites, the sampling methods and sampling design I employed, and the kinds of spider species collected. In addition, I compare the biodiversity (taxonomic richness and equitability) of the sites as measured by a variety of techniques. Using this information, I also investigate which of the sites were the most and least adequately sampled with respect to taxonomic richness.

METHODS

Site Selection

My study areas were chosen from prospective sites in the Southern Appalachian Mountains with the criterion that a survey of the spider fauna had been completed at least ten but not more than fifty years ago. I selected study sites that satisfied four

requirements beyond this initial criterion: 1) the previous spider census included species abundance data; 2) the survey was completed over a period of at least one to two months, or preferably included data collected over an entire season; 3) the survey area was relatively small, enabling me to re-sample completely; and 4) the survey was completed by a competent arachnologist who could provide detailed site descriptions and specific locations. Three sites satisfied all four criteria. In order to increase the number of sites included in this study, I broadened my search to include sites sampled within the last ten years. Three additional sites were selected. As a Professor of Biology at Western Carolina University, Dr. Frederick Coyle had sampled the spider fauna at the three selected sites in Macon County, NC in the summer of 1976 (Coyle 1981). He also inventoried the three additionally selected sites in the Great Smoky Mountains National Park (GSMNP) twice yearly between 1995 and 1997. These studies are part of his broader career objective to regionally inventory spider diversity across the Southern Appalachians (Gove 1997).

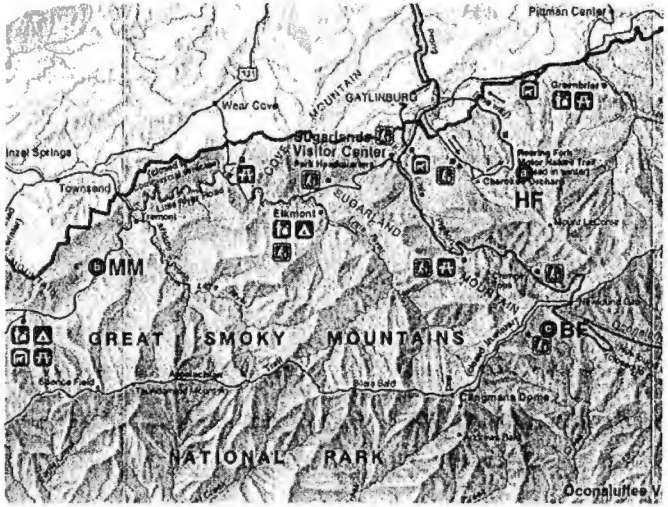
GSMNP. The three sites located in the Great Smoky Mountain National Park (see Figure 1A,B) include a mature beech gap forest (henceforth, Beech Forest) in Swain Co., NC, a mature hemlock/hardwood cove forest (henceforth, Hardwood Forest) in Sevier Co., TN, and a grassy marsh/meadow called Meadow Branch (henceforth, Meadow Marsh) in Blount Co., TN (Table 1). The Beech Forest site has nearly 100% beech in the forest canopy and is classified by The Nature Conservancy as a "*Fagus grandifolia / Ageratina altissima* var. *roanensis*" Forest (TNC's element code CEGL006246) in their national classification (Keith Langdon, written communication, 1999). It is an old growth forest which has never been logged, but is currently being altered by the beech scale insect and a fungus that invades the trees through wounds caused by the insect (Fred Coyle, written communication, 1998). This invasion has resulted in a number of canopy

Figure 1. The geographic location of the six study areas. (A) Overview map illustrating the placement of the three sites located in the GSMNP and the three sites located in the Nantahala National Forest: 2a corresponds to the approximate location of the Hardwood Forest, 2b to the location of the Meadow Marsh and 2c to the Beech Forest. Circle 1 illustrates the location of all three Macon Co. sites, given scale limitations of the map. (B) A finer scale map of the sites located within the GSMNP ('a','b','c' as described above) and (C) a finer scale map of the three sites in Macon Co. Note that 'hc' marks the location of the Horse Clear-cut and 'ell' marks the location of the Ellicott Forest and the adjacent Ellicott Clear-cut.

A


Western
North Carolina

B


Pittman Center
GATLINBURG
Wear Cove
Sugarlands
Visitor Center
Townsend
Elkmont
SUGARLAND
HF
MM
OBF
GREAT SMOKY MOUNTAINS
NATIONAL PARK
Clingmans Dome
Oconaluftee V

C

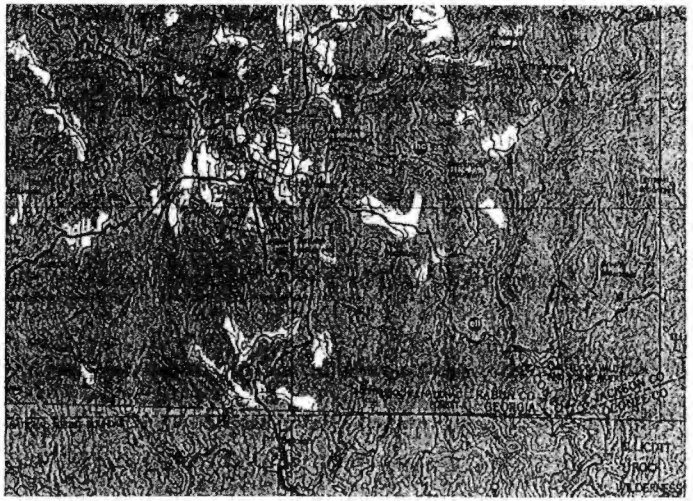


Table 1. General characteristics of the study sites

Sites	Year cut	Size	Slope	Elevation	UTM Grid Location	*Lat./Long. Coordinates
Great Smoky Mtn. National Park						
Hemlock/Hardwood Cove	Natural old growth (uncut)	3 ha	0°-30°	940m	E2772, N39512	35.6814°N, -83.4619°W
Meadow Marsh	Natural (undisturbed)	0.5 ha	0°	530m	E2526, N39470	35.6380°N, -83.7320°W
Beech Gap Forest	Natural old growth (uncut)	3 ha	10°-40°	1640m	E2786, N39433	35.6108°N, -83.4442°W
Macon County, NC.						
Ellicott Rock Forest	Natural old growth (uncut)	8 ha	5°-20°	860m	E3058, N38762	35.0771°N, -83.1281°W
Ellicott Rock Clear-cut	1974	8 ha	5°-12°	880m	E3058, N38762	35.0771°N, -83.1281°W
Horse Cove Clear-cut	1971	16 ha	2°-10°	950m	E3037, N38804	35.0530°N, -83.152°W

* Because the site locations were estimated using topographic maps only (and not using GPS), the latitude/longitude seconds should be viewed as merely an approximation determined using the site locations and a website called Topozone (http://www.topozone.com).

Notes: A site designated as 'natural' means that the site has not been logged in the last hundred years and records prior to that are not available. In Macon co., the size of the clear-cut sites refers to the entire area that was cut, while the size of the old growth site refers to the area across which sampling took place during this study (i.e. Ellicott Rock Forest extends beyond the 8-ha sampled). In the forested sites in the GSMNP, sampling covered an area of approximately 1 ha, while the entire habitat patch measured approximately 3 ha. The marsh site was a 0.5-ha habitat island surrounded by forest, and the entire patch was sampled. The UTM (1000-meter Universal Transverse Mercator grid ticks, zone 17) grid coordinates and the latitude/longitude coordinates were estimated using 7.5' USGS topographic maps.

openings, producing significant amounts of ground-level vegetation that otherwise would not be present in a forest of this type.

The Hardwood Forest site has a mixed, old-growth stand of rich cove hardwood which has not been logged. Its TNC classification is a *"Tsuga canadensis - Liriodendron tulipifera* " type with lesser amounts of understory *Rhododendron* (TNC element code of CEGL007543) (Keith. Langdon, written communication, 1999).

The Meadow Marsh site is a montane wetland along Meadow Branch, consisting of an alluvial glade dominated by wet-meadow grasses and herbs and surrounded by forest. It has not been officially classified yet, but this wetland is not dominated by ferns, *Rubus, Carex,* or *Impatiens*, etc. (Keith Langdon, written communication, 1999).

Macon County. The three sites in Macon County, NC, include one mature (at least 100 years old) forest (Ellicott Rock Forest, henceforth just Ellicott Forest), an adjacent young forest plot last cut in 1974 (Ellicott Rock Clear-cut, henceforth just Ellicott Clear-cut), and another young forest plot last cut in 1971 (Horse Cove Clear-cut, henceforth just Horse Clear-cut) (Table 1). All three of these sites are located in the Highlands Ranger District of the Nantahala National Forest in the mountains of southwestern North Carolina (see Figure 1A,C). The sites were originally selected by Fred Coyle in 1976 as part of a study investigating the effects of clear-cutting on spider communities. Some general characteristics of these sites can be found in Table 1. Coyle (1981) reported that the mature forest at the Ellicott site predominantly consisted of a mature pine-hardwood community, bisected by a narrow, weakly developed cove forest community along a small stream. The dominant tree species in the pine-hardwood community (listed in order of decreasing importance values based upon relative frequency and relative dominance values obtained by the point quarter method) were white pine (*Pinus strobus*), white oak (*Quercus alba*), sourwood (*Oxydendrum*

arboreum), black oak (*Quercus velutina*), red maple (*Acer rubrum*), and scarlet oak (*Quercus coccinea*). The moderately dense understory of the pine-hardwood community contained dogwood (*Cornus florida*), numerous seedlings of the canopy species, and shrubs such as huckleberry (*Gaylussacia ursina*), scattered mountain laurel (*Kalmia latifolia*), and scattered *Rhododendron maximum*. The cove forest community had decreasing importance values for red maple, eastern hemlock (*Tsuga canadensis*), sourwood, black gum (*Nyssa sylvatica*), white pine, tulip poplar (*Liriodendron tulipifera*), white oak, and holly (*Ilex opaca*). Dense stands of *R. maximum* dominate the cove forest understory. Leaf litter depth throughout both forest types ranged from 1 to 15 cm, with a mean depth of 6.5 cm. Based on the pre-logging vegetation data available for the clear-cut sites, Coyle concluded that the Ellicott Clear-cut was botanically very similar to the adjacent Ellicott Forest prior to logging. Horse Clear-cut was markedly different. Unfortunately, I was unable to locate detailed vegetation information for Horse Clear-cut prior to clear-cutting. The limited information I have gives the dominant tree species as *Pinus strobus*, *Quercus prinus*, *Quercus alba*, and *Quercus rubra*. Vegetation surveys within 5 years of clear-cutting indicate that for woody plants over 0.5-m tall, Ellicott Clear-cut was dominated in order of decreasing importance value by huckleberry, red maple, sourwood, greenbriar (*Smilax rotundifolia*), and pignut hickory (*Carya ovalus*). Horse Clear-cut was dominated by blackberry (*Rubus allegheniensis*), huckleberry, tulup tree, mountain laurel, and spicebush (*Claycanthus floridus*) (Coyle 1981).

Sampling Design

The sites in the GSMNP were sampled to prepare an extensive species list as a part of the All Taxa Biodiversity Inventory currently taking place in the Park. Because the goal of that study was initially to systematically sample the spider fauna, the

Coddington Protocol (Coddington *et al.* 1991) was followed (described in detail below). The specific sampling effort at each of these sites was determined after an initial survey had been conducted in the summer of 1995. Using the computer program EstimateS (R.K. Colwell, unpubl.), Coyle determined roughly how close the 'real' species richness was to the first survey and used this information to determine approximately how much sampling effort was necessary to capture the majority of the species at each site. I chose these three sites specifically from a pool of sites at which spider surveys were conducted by Fred Coyle because they had been sampled for three consecutive summers.

All three sites in Macon County were sampled in order to compare modern surveys with the historical survey conducted by Fred Coyle in 1976. Therefore, as a minimum, I duplicated Coyle's sampling protocol as closely as possible during my re-surveys in the summer of 1995, 1996, and 1997. In the second and third years of my study, four transects were set up at the Ellicott sites and additional sampling was conducted at each of nine nodes along the transects. The transects were instituted only at Ellicott because here the clear-cut and old growth forest were adjacent to each other and the data from the transects helped track the changes in the spider assemblage as one moved from one mature-forested site and through a transition zone into the other with young forest. In addition, the transects provided spatially consistent sampling units of one-hr of hand collection, one sweep net sample, and one pitfall trap (consisting of the catch over five weeks of a 24oz trap). These data were used to construct species accumulation curves at each of these two sites. These sampling methods are described in detail in a later section.

The details of the sampling completed at each site are described below for each study area.

Macon County, NC.

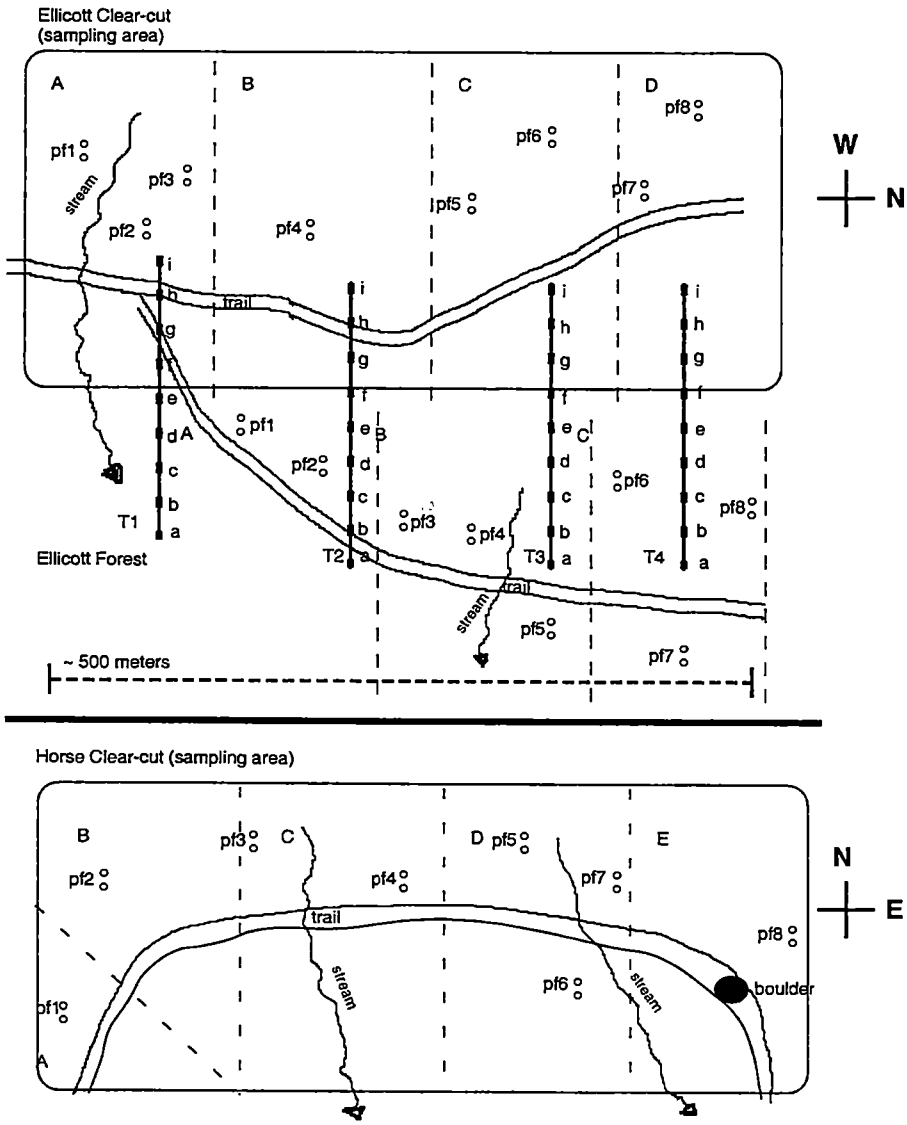
As the modern sampling protocol was meant to duplicate as closely as possible Coyle's methods, I begin by detailing Coyle's sampling design. Afterwards, I give some additional details and clarifications of the study methods and a description of modifications that were made for my surveys. Fred Coyle's sampling protocol was as follows:

> "Four different collecting techniques were used to sample the spider populations at these study sites during the summer of 1976. An attempt was made to distribute the samples evenly over each site and to sample from each type of microhabitat at each site. No samples were collected within 20 m of the edge of any study site. Eight 73 mm diameter sheltered pitfall traps containing an ethylene glycol-detergent mixture were set on each study site on June 25 and were then emptied and reset at three week intervals during the following 15 weeks. Ten 0.25m^2 samples of leaf litter (down to the mineral soil) were collected from each study site at fairly regular intervals between June 16 and August 20 and were processed in large Tullgren funnels. Eight daytime sweep net samples of 50 sweeps apiece were obtained from vegetation between 0.2 m and 2.0 m above ground level at each site between June 29 and July 2. Four hours of intensive daytime hand collecting was performed at each site between June 22 and July 9, with an additional 30 minutes of intensive daytime hand collecting at each site on October 2. Search time was divided equally between the ground stratum and the aerial stratum (branches with leaves above the ground). Ground and aerial spiders were placed in separate collecting vials." (Coyle 1981, p.287).

For my surveys, sampling began in each of the three years (1995, 1996 and 1997) at the end of June/beginning of July with the placement of pitfall traps. Pitfall traps consisted of a 24 oz plastic cup buried so that the rim was flush with the soil surface and a cap made of aluminum flashing as a rain shelter placed approximately three inches above the rim. An internal cup was filled about 1/4 full with Ethanol (70%) to prevent spider cannibalism in the traps and to preserve the specimens. I chose not to use ethylene

glycol as Coyle did because it tends to attract wildlife due to its sweet smell and taste and is frequently lethal to mammals which ingest it. Due to time constraints, I was only able to leave my traps in for five weeks. Ideally, I would have been able to extract just five weeks of pitfall data from Coyle's samples for comparison with my five week samples. Unfortunately, the datasheets from Coyle's study lumped all the pitfall data into one total for each study area. Therefore, to partially compensate for the difference in trap duration, I doubled the number of traps to 16. The total number of individuals collected (and the species composition for the old growth site) in the pitfall traps was very similar for my 16 traps and Coyle's 8 traps, in spite of the difference in sampling duration. For example, in the mature forest site Coyle collected 123 individuals, including 48 adults 1976. In 1995, I collected 115 individuals, including 37 adults, in 1996, 108 individuals with 69 adults, and in 1997, 75 individuals with 58 adults. Using Coyle's field maps, I attempted to place the traps in approximately the same locations as he did, only with two traps (1-meter apart) at each sampling node instead of one. In 1996 and 1997, I placed an additional 36 pitfall traps along four, 90 meter transects running across the boundary between the mature forest and the adjacent clear-cut. The transects were laid out such that three nodes were located within the old clear-cut (Ellicott Clear-cut), three in the transition between Ellicott Clear-cut and Ellicott Forest and three completely in Ellicott Forest. Once marked, the transects were maintained in the same location for the 1996 and 1997 surveys. See Figure 2 for a map of the placement of all pitfall traps in all three of the Macon County sites. The traps were checked and re-set weekly (providing five collection dates as in Coyle's study). In 1995 and 1996, collections from the pitfall traps other than the traps along the transects were pooled as they were collected. In 1997 collections from all pitfall traps were kept in individual vials to enable assessment of spatial variability in yield (number of specimens collected per trap).

Figure 2. Schematic diagram of the three study sites in Macon County, showing the placement of the pitfall traps and the small paths leading through the sites. T1-T4 illustrate the four transects put in place in 1996; A pitfall trap was placed at each node. Capital letters illustrate sampling areas designating locations of hand collection, sweep netting and litter collection. The thick black line under the diagram of Ellicott Forest designates that Horse Cove is not adjacent to the Ellicott sites but rather is located 5-6 kilometers to the northeast. The Ellicott sites are surrounded by continuous forest, while Horse Cove is bordered by a tree plantation, a bog, and land under development.



Elaborating on Coyle's description, litter processing involved collection of litter, and later in the lab, the placement of the litter on sire screens with mesh grid of six to eight mm secured inside the Tullgren funnels (about 10 cm from the top). In the laboratory, a domed cover with an attached 60 watt bulb for heat was then placed on top of the funnel and the litter was left to dry for two to three days or until it was completely dry. I would periodically check the litter manually to see if it had dried sufficiently. A cup containing 70% ethanol was placed at the base of the funnel to collect the spiders. For a second sampling technique, I used sweep netting with a canvas net on a pole to sweep over the vegetation on the ground up to about knee level. Spiders are removed from the canvas net using an aspirator. Aerial sampling involves searching anything found above the knee of the collector up to the maximum reach of the collector including leaves, branches, tree trunks, and spaces in between. Ground collection involves searching vegetation and objects found below knee level, including leaf litter, logs, rocks, and herbaceous plants. Coyle had collected for four and one half hours. As my capture results were initially slightly lower than Coyle's, I collected for five hours. All spiders encountered were taken. Although not explicitly marked, sampling occurred over an area of approximately 10-meters by 10-meters for each hour of sampling or sweep-net sample. All samples were kept separate and the date and location of the collection recorded. All hand collection and sweep netting was completed between 8am and 2pm. Following Coyle's survey, no attempt was made to sample at night or from the forest canopy.

In addition to the minimum amount of collecting required for comparison with the historic survey, in 1996 and 1997, I expanded my sampling program with the help of an undergraduate assistant. I added an additional one hour of hand collection and one sweep net sample from each node of the transects. This added a total of 31 hours of hand

collection and 28 sweep net samples to the total collected (see Table 2 for summary of collection effort).

Seasonal effects. As most arthropod groups are known to exhibit seasonal fluctuations, the timing of sampling can drastically effect the kinds of species present as well as the relative abundance of species in a habitat. As I will show later, samples from the GSMNP sites taken in May differed markedly from those taken in August. In order to limit the impact of seasonality on the following analyses (i.e., limit the inflation of yearly turnover estimates due to seasonal effects), care was taken to sample at the same time each year. Although the exact timing of the surveys in Macon County did vary by a week or two from year to year, all surveys took place between the last week of June and the last week in July. According to a detailed study of spider seasonality conducted in the area by L. Bishop, this is the time of year when the spider communities are the most stable (Bishop 1989).

GSMNP

The sampling protocol used for these sites is a modified version of the one developed by Coddington *et al.* (1991) used to study spider biodiversity in tropical forests. This Coddington Protocol consists of four collection methods: aerial hand collection, ground hand collection, litter extraction with Tullgren funnels, and vegetation beating. The fourth method of vegetation beating involves striking vegetation (usually branches) with a 1m long stick. The falling spiders are collected on a canvas sheet held horizontally below the vegetation. As the exact number of hours and dates (month) of sampling varied from site to site and year to year, the details of sampling are summarized in Table 3.

Hardwood Forest. This hemlock/hardwood site was sampled in June and August, 1995 and in May and August, 1996 and 1997. In June 1995, three collectors completed

Table 2. Sampling effort for sites in Macon County, NC

Site	Sample date	#Collectors	#hand collection hours	#sweeping hours	litter samples (#hour equiv.)	pitfall traps (#hour equiv.)	Total sampling hours
Ellicott	J/Ju '76	1	4.5	2	2.5	*11	20
Forest	Ju '95	1	5	2	2.5	11	20.5
	J/Ju '96	2	12	3	2.5	21	38.5
	J/Ju '97	2	12	3	2.5	21	38.5
Subtotal			33.5	10	10	64	117.5
Ellicott	J/Ju '76	1	4.5	2	2.5	11	20
Clear-cut	Ju '95	1	5	2	2.5	11	20.5
	J/Ju '96	2	12	3	2.5	21	38.5
	J/Ju '97	2	12	3	2.5	21	38.5
Subtotal			33.5	10	10	64	117.5
**Ellicott	J/Ju '96	2	12	3	--	10	25
Transition	J/Ju '97	2	12	3	--	10	25
Subtotal			24	6	0	20	50
Horse	J/Ju '76	1	4.5	2	2.5	11	20
Clear-cut	Ju '95	1	5	2	2.5	11	20.5
	J/Ju '96	2	5	2	2.5	11	20.5
	J/Ju '97	2	5	2	2.5	11	20.5
Subtotal			19.5	8	10	44	81.5
TOTAL			110.5	34	30	192	366.5

*As Coyle (in 1976) had only 8 traps at each site and checked them only once monthly for 15 weeks, I estimated that he probably spent approximately the same number of man-hours as I did checking 16 traps once a week for five weeks, although this is only a rough guess

** Ellicott Transition refers to the nodes on the transects which spread across the 'transition zone' between Ellicott Forest and Ellicott Clear-cut (see text for detailed discussion of these transects).

Notes. At these sites, only hand collection (aerial plus ground) was originally measured in man-hours. All other methods were quantified by other means, e.g., number of traps or number of samples. In order to make this table comparable with the data presented in Table 3, I converted the other sampling techniques into equivalent man-hours. As each sweep-net sample of 50 sweeps takes approximately 15 minutes to complete, I determined that four sweep-net samples are equivalent to one man-hour of sampling. Following Table 3, as each 1-m^2 litter sample was considered (in the GSMNP surveys) equivalent to one man-hour of sampling, I estimated that four 0.25-m^2 litter sample was roughly equivalent to one man-hour. Determining man-hour equivalencies for pitfall traps proved more difficult. Using field notes from the 1995 to 1997 surveys, I estimated the time necessary to install, empty once a week for 5 weeks, and remove a set of 16 pitfall traps from one site as eleven hours. For the additional 12 pitfall traps installed in 1996 and 1997, I added another 10 hours to the total. Sampling was completed between 8am and 4pm. See text for detailed descriptions of sampling methods.

Table 3. Sampling effort for sites in GSMNP

Site	Sample date	#Collectors	#aerial collection hours	#ground collection hours	#beating hours	litter samples (#hour equiv.)	Total sampling hours
Hardwood	6/13/95	3	2	2	2	2	8
Forest	8/11/95	3	2	2	2	1	7
	5/23/96	3	8	8	8	6	30
	8/1/96	4	8	8	8	6	30
	5/19/97	4	8	8	8	6	30
	8/4/97	4	8	8	8	6	30
Subtotal			36	36	36	27	135
Beech	7/12/95	3	3	3	3	2	11
Forest	6/14/96	4	4	4	4	3	15
	8/15/96	4	4	4	4	3	15
	6/10/97	4	4	4	4	3	15
	8/13/97	4	4	4	4	3	15
Subtotal			19	19	19	14	71
*Meadow	6/30/95	2	1	2	2	2	7
Marsh	5/23/96	3	2	4	3	3	12
	8/1/96	4	2	3	3	3	11
	5/15/97	4	2	3	3	2	10
	7/17/97	4	2	3	3	2	10
Subtotal			9	15	14	12	50
TOTAL			64	70	69	53	256

* sweep netting replaced beating at this site due to its grassy vegetation (beating would be impossible at this site due to the lack of trees or bushes).

Notes. Litter samples are measured spatially and each 1-m^2 sample is considered equivalent to one hour's collection effort for the purposes of this study. Sampling effort was spread evenly across collectors where possible (see text for details). Sampling was completed between 8am and 4pm on the dates given.

two hours each of aerial and of ground hand collection and two hours of vegetation beating, for a total of six, one-hour samples. Two, 1-m^2 litter samples were also taken and processed. In August 1995, only one litter sample was collected. During each of the remaining surveys, four collectors completed 24 1-hour samples distributed evenly among hand collection and beating and collected six, 1-m^2 litter samples.

Beech Forest. The beech gap forest was sampled in July of 1995, and then in June and August in 1996 and 1997. The smallest sample was again in 1995 with three collectors completing nine, 1-hour samples distributed evenly among ground and aerial hand collection and vegetation beating and two, 1-m^2 litter samples. In all subsequent surveys, four collectors completed 12, 1-hour samples and collected three 1-m^2 litter samples.

Meadow Marsh. The Meadow Marsh was sampled in June 1995, and then in May and August 1996 and May and July in 1997. Because of the low, grassy vegetation, sweep netting was substituted for vegetation beating in all samples. In June 1995, two collectors completed two hours of ground hand collection, one hour of aerial hand collection, two hours of sweep netting, and collected two 1-m^2 litter samples. In May 1996, four collectors completed two hours of aerial hand collection, three hours of sweep netting, four hours of ground hand collection and collected three 1-m^2 litter samples. In August 1996, four collectors completed two hours of aerial hand collection, three hours of sweep netting, three hours of ground hand collection and collected three 1-m^2 litter samples. In May and July 1997, four collectors completed two hours of aerial hand collection, three hours of sweep netting, three hours of ground hand collection and collected two 1-m^2 litter samples.

Identification

Following Coyle, for the Macon County sites all specimens, including juveniles were identified to species where possible. If a species name could not be assigned to an adult specimen, that specimen would be assigned a morphospecies designation which would be kept constant throughout the survey to allow comparisons between years. Juveniles which could not be confidently assigned to species were typically identified to genus. If a genus designation (for a juvenile) was not possible, the specimen was dropped from the analyses and not included in any of the specimen tallies.

For the sites in the GSMNP, Fred Coyle completed all the spider identifications. I worked with Dr. Coyle to ensure consistency with my identifications for all the sites. He did not attempt to identify juvenile specimens from the 1995 surveys, but did in all subsequent surveys from 1996 and 1997. Juveniles were assigned to spider species only if this could be done with complete confidence. Otherwise, juveniles were not further considered and were not used in any statistical or biodiversity analyses. As I have done with my collections, Coyle assigned morphospecies designations to those adult specimens which could not be assigned a species name and were kept consistent for all samples.

RESULTS

The number of individuals, species, and genera collected at each site during each survey are reported in Table 4. A complete list of all species, broken down by site and collecting method is given in Tables 5A through 10A. Summaries including the numbers of species and genera collected by each sampling method are given in Tables 5B through 10B. To compare yields obtained from each site over the course of the three sampling years, I plotted the number of individuals collected versus the total number of species for

Table 4. Complete collection results

A. Macon County

		1976	1995	1996	1997	Site Total
Ellicott Forest	#individuals (*)	583(217)	387(215)	828(272)	708(387)	2506(1091)
	#species (#morph.)	60(8)	57(3)	60(2)	70(4)	109(11)
	#genera	55	48	58	58	82
Ellicott Clear-cut	#individuals (*)	284(131)	463(212)	793(236)	613(302)	2153(881)
	#species (#morph.)	50(3)	49(1)	56(2)	59(1)	100(4)
	#genera	51	49	52	56	88
Horse Clear-cut	#individuals (*)	378(184)	219(127)	358(158)	456(225)	1411(694)
	#species (#morph.)	70(4)	45(1)	51(1)	55(3)	107(8)
	#genera	60	40	47	48	83
Grand Total	#individuals (*)					6070(2666)
Macon Co.	#species (#morph.)					164(18)
	#genera					114

* Number of adult specimens in collection

B. GSMNP

		*E1995	L1995	E1996	L1996	E1997	L1997	Site Total
Beech Forest	#individuals (*)	---	252(252)	669(491)	855(464)	662(390)	702(356)	3140(1953)
	#species (#morph.)	---	22	35(1)	32	36(1)	36	58(1)
	#genera	---	20	31	28	30	31	50
Hardwood Forest	#individuals (*)	113(112)	116(114)	983(707)	813(229)	1835(988)	1566(411)	5426(2561)
	#species (#morph.)	30(1)	29(1)	62(3)	62(2)	72(5)	57(1)	104(7)
	#genera	26	28	46	51	55	47	73
Meadow Marsh	#individuals(*)	163(160)	---	353(257)	264(130)	421(292)	313(214)	1514(1053)
	#species (#morph.)	45(1)	---	47	44(1)	52(1)	47(1)	110(4)
	#genera	37	---	39	34	42	37	75
Grand Total GSMNP	#individuals(*)							10080(5567)
	#species (#morph.)							200(12)
	#genera							120

*E and L refer to early and late summer collections

*Number of adult specimens in collection

Note. No attempt was made to identify juveniles from the 1995 surveys

C. Total for Southern Appalachians

Southern Appalachians	#individuals (*)	16,150 (8,233)
	#species (#morph.)	290(28)
	#genera	154

Table 5. Species list and species totals (by method) collected from Ellicott Rock Clear-cut

A. Spider species and their abundances

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Calymmaria cavicola* (Banks)	Ground	1	0	1	0	0	0	0	0
		Pitfall	0	0	0	0	1	0	1	1
	Cicurina arcuata Keyserling	Pitfall	0	0	0	0	3	3	2	2
	Cicurina breviaria Bishop & Crosby	Ground	0	0	0	0	1	1	0	0
		Pitfall	0	0	0	0	1	1	1	1
	Cicurina exlinae Chamberlin&Ivie	Litter	0	0	0	0	1	1	0	0
	Cicurina sp.	Litter	1	0	1	0	6	0	7	0
		Ground	1	0	0	0	1	0	1	0
		Pitfall	0	0	0	0	13	0	4	0
	Coras aerialis Muma	Aerial	0	0	0	0	1	1	0	0
	Coras sp.	Aerial	0	0	0	0	3	0	5	0
		Ground	0	0	0	0	2	0	0	0
		Pitfall	0	0	0	0	1	0	0	0
	Coras taugynus Chamberlin	Ground	0	0	0	0	1	1	0	0
	Cybaeus silicis Barrows	Pitfall	3	2	1	0	5	0	2	0
	Wadotes bimucronatus (Simon)	Ground	1	1	0	0	0	0	0	0
		Pitfall	0	0	1	1	2	2	0	0
	Wadotes hybridus (Emerton)	Litter	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	0	0	3	3
		Pitfall	3	3	5	5	6	6	13	13
	Wadotes sp.	Litter	3	0	19	0	13	0	7	0
		Ground	8	0	1	0	31	0	11	0
		Pitfall	26	0	22	0	52	0	15	0
Amaurobiidae	*Callioplus armipotens* (Bishop & Crosby)	Litter	0	0	27	1	26	6	17	2
		Pitfall	0	0	10	0	9	3	4	1
Antrodiaetidae	*Antrodiaetus unicolor* (Hentz)	Pitfall	2	2	1	0	0	0	1	0
Anyphaenidae	*Anyphaena pectorosa* L. Koch	Aerial	0	0	0	0	1	1	5	4
		Sweep	1	1	1	1	0	0	0	0
	Anyphaena sp.	Aerial	0	0	1	0	0	0	0	0
		Ground	0	0	0	0	1	0	0	0
	Wulfila albens (Hentz)	Aerial	0	0	1	1	2	2	1	1
Araneidae	*Acacesia hamata* (Hentz)	Sweep	1	0	0	0	0	0	0	0
	Araneus marmoreus Clerck	Aerial	0	0	2	1	0	0	0	0
		Ground	0	0	1	0	0	0	0	0
	Araneus sp.	Aerial	0	0	0	0	3	0	2	0
		Ground	0	0	0	0	1	0	0	0
	Cyclosa turbinata (Walckenaer)	Aerial	2	0	0	0	0	0	0	0
		Sweep	1	1	0	0	0	0	0	0
	Eustala sp.	Aerial	0	0	0	0	0	0	1	0
	Mangora maculata (Keyserling)	Aerial	0	0	1	0	0	0	0	0
		Ground	0	0	3	0	1	0	1	0
		Sweep	0	0	4	2	2	0	1	1
	Mangora placida (Hentz)	Aerial	0	0	2	0	1	0	1	0
		Ground	0	0	0	0	0	0	1	1
	Mastophora sp.	Sweep	0	0	0	0	2	0	0	0
	Metepeira labyrinthea (Hentz)	Aerial	3	0	1	0	1	0	1	0

Table 5. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Micrathena gracilis (Walckenaer)	Aerial	0	0	0	0	1	1	0	0
	Micrathena mitrata (Hentz)	Aerial	0	0	11	0	27	0	16	0
		Ground	0	0	5	0	3	0	1	0
		Sweep	0	0	6	0	6	1	2	0
	Neoscona arabesca (Walckenaer)	Aerial	0	0	1	1	0	0	0	0
	Wixia sp.	Aerial	0	0	1	0	3	0	3	0
		Sweep	0	0	1	0	1	0	1	0
Atypidae	*Atypus* sp.	Litter	0	0	0	0	0	0	1	0
Clubionidae	*Agroeca minuta* Banks	Litter	0	0	1	0	1	0	0	0
		Pitfall	0	0	0	0	2	2	2	2
	Castianeira longipalpus (Hentz)	Pitfall	2	2	0	0	0	0	0	0
	Clubiona sp.	Aerial	0	0	2	0	2	0	0	0
		Ground	0	0	1	0	0	0	0	0
		Sweep	0	0	3	0	0	0	0	0
	Clubiona spiralis Emerton	Aerial	0	0	0	0	1	1	0	0
	Clubionoides excepta (L. Koch)	Litter	1	1	0	0	0	0	0	0
		Aerial	0	0	0	0	0	0	2	2
		Sweep	0	0	1	1	0	0	0	0
		Pitfall	1	1	0	0	0	0	2	2
	Clubionoides sp.	Aerial	0	0	0	0	1	0	1	0
		Sweep	0	0	0	0	1	0	1	0
	Liocranoides sp.	Pitfall	1	1	0	0	0	0	0	0
	Phrurotimpus alarius (Hentz)	Litter	4	1	6	1	8	3	5	1
		Ground	0	0	0	0	3	2	5	5
		Pitfall	12	10	13	11	9	8	15	13
	Phrurotimpus borealis (Emerton)	Ground	0	0	0	0	1	1	3	3
		Pitfall	6	6	4	4	5	5	2	2
	Scotinella redempta (Gertsch)	Litter	0	0	1	0	2	1	0	0
		Pitfall	1	1	1	0	1	1	1	1
	Scotinella sp.	Litter	1	0	0	0	0	0	0	0
	Scotinella morphospecies A	Litter	1	1	1	1	3	2	1	1
		Ground	0	0	0	0	0	0	3	3
		Pitfall	3	3	3	3	9	9	4	4
Ctenidae	*Anahita punctulata* (Hentz)	Litter	0	0	2	0	1	0	2	0
		Ground	1	1	3	0	47	0	21	1
		Pitfall	7	2	5	0	63	3	13	7
Dictynidae	*Dictyna sublata* Hentz	Aerial	0	0	1	1	2	1	0	0
		Ground	0	0	0	0	1	1	0	0
Gnaphosidae	*Drassyllus fallens* Chamberlin	Pitfall	0	0	0	0	0	0	1	1
	Drassyllus novus (Banks)	Ground	0	0	0	0	0	0	1	1
	Drassyllus sp.	Litter	0	0	0	0	1	0	0	0
	Zelotes laccus (Barrows)	Litter	1	1	0	0	0	0	0	0
Hahniidae	*Neoantistia* sp.	Ground	1	0	0	0	0	0	0	0
Leptonetidae	*Leptoneta gertschi* Barrows	Litter	4	4	10	10	2	2	3	3
		Pitfall	3	3	2	2	5	5	3	3
	Leptoneta sp.	Litter	8	0	4	0	5	0	5	0
		Ground	1	0	0	0	0	0	0	0
		Pitfall	3	0	0	0	1	0	1	0
Linyphiidae	*Blestia sarcocuon* (Crosby & Bishop)	Litter	0	0	0	0	0	0	2	2
		Pitfall	0	0	0	0	1	1	2	2
	Centromerus denticulatus (Emerton)	Litter	7	2	11	3	3	2	1	1
		Pitfall	0	0	0	0	4	3	1	0
	Ceraticelus carinatus *(Emerton)*	Pitfall	0	0	0	0	0	0	1	1

Table 5. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Ceraticelus fissiceps O.P.-Cambridge	Litter	0	0	3	1	1	1	0	0
		Aerial	0	0	1	1	2	1	7	6
		Ground	0	0	3	3	3	2	2	2
		Sweep	14	14	99	93	48	41	69	53
		Pitfall	0	0	0	0	2	1	0	0
	Ceraticelus minutus (Emerton)	Litter	2	2	2	2	0	0	0	0
	Ceratinopsidis formosa (Banks)	Aerial	0	0	0	0	0	0	1	1
	Ceratinopsis interpres (O.P.-Cambridge)	Sweep	1	1	0	0	0	0	0	0
	Ceratinopsis sp.	Aerial	0	0	0	0	2	0	0	0
		Ground	0	0	0	0	1	0	0	0
		Sweep	0	0	0	0	1	0	0	0
	Drapetisca alteranda Chamberlin	Aerial	0	0	0	0	0	0	2	1
	Erigone autumnalis Emerton	Litter	0	0	0	0	0	0	2	2
	Erigone brevidentata Emerton	Litter	1	1	0	0	0	0	0	0
	Floricomus tallulae Chamberlin & Ivie	Litter	0	0	2	2	2	2	0	0
		Ground	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	1	1	1	1
	Florinda coccinea (Hentz)	Aerial	1	0	0	0	0	0	0	0
	Frontinella pyramitela (Walckenaer)	Aerial	5	2	3	1	1	0	4	0
		Ground	7	0	2	1	0	0	0	0
	Grammonota pictilis (O.P.-Cambridge)	Litter	0	0	0	0	0	0	1	1
		Aerial	0	0	1	1	0	0	0	0
	Graphomoa theridiodes Chamberlin	Ground	0	0	14	4	9	2	2	2
	Lepthyphantes sp.	Ground	0	0	0	0	1	0	7	0
		Pitfall	0	0	0	0	0	0	1	0
	Lepthyphantes zebra (Emerton)	Ground	0	0	0	0	2	1	5	1
	Linyphiidae morphospecies A2	Pitfall	0	0	0	0	1	1	0	0
	Linyphiidae morphospecies E	Litter	3	3	0	0	0	0	0	0
	Maso sundevallii (Westring)	Litter	0	0	1	1	2	2	2	2
		Sweep	0	0	0	0	0	0	1	1
	Meioneta micaria (Emerton)	Ground	0	0	0	0	0	0	1	1
	Meioneta sp.	Litter	1	0	0	0	0	0	0	0
	Meioneta unimaculata (Banks)	Litter	1	1	0	0	0	0	0	0
	Neriene clathrata (Sundevall)	Ground	0	0	1	1	0	0	0	0
	Neriene sp.	Aerial	0	0	0	0	1	0	0	0
		Ground	0	0	0	0	1	0	0	0
	Neriene variabilis (Banks)	Aerial	0	0	0	0	1	0	0	0
		Ground	0	0	11	1	6	3	0	0
	Pitiohyphantes costatus (Hentz)	Aerial	0	0	5	0	23	1	25	0
		Ground	0	0	1	0	2	0	1	0
		Sweep	0	0	1	0	1	0	0	0
	Scylaceus pallidus (Emerton)	Litter	0	0	0	0	1	1	0	0
	Walckenaeria directa (O.P.-Cambridge)	Sweep	0	0	1	1	0	0	0	0
	Walckenaeria dixiana (Chamberlin & Ivie)	Litter	0	0	0	0	1	1	0	0
	Walckenaeria sp.	Pitfall	0	0	0	0	1	0	0	0
Lycosidae	*Gladicosa gulosa* (Walckenaer)	Litter	0	0	1	0	0	0	0	0
		Ground	2	1	0	0	7	0	7	0
		Pitfall	8	1	1	0	8	0	3	0
	Pardosa milvina (Hentz)	Ground	16	14	0	0	0	0	0	0
		Pitfall	2	2	0	0	0	0	0	0
	Pardosa saxatilis (Hentz)	Pitfall	1	1	0	0	0	0	0	0
	Pardosa sp.	Ground	1	0	0	0	0	0	0	0
		Pitfall	1	0	0	0	0	0	0	0

Table 5. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Pirata montanus Emerton	Litter	0	0	7	2	4	0	3	2
		Ground	0	0	5	2	27	13	49	28
		Sweep	0	0	0	0	0	0	2	0
		Pitfall	0	0	20	19	47	17	22	17
Oxyopidae	*Oxyopes* sp.	Sweep	0	0	0	0	1	0	0	0
Salticidae	*Eris aurantia* (Lucas)	Aerial	1	0	0	0	0	0	0	0
	Habrocestum parvulum (Banks)	Litter	0	0	5	3	1	0	2	2
		Ground	0	0	0	0	21	11	16	11
		Pitfall	0	0	4	3	29	21	11	10
	Habrocestum pulex (Hentz)	Aerial	0	0	0	0	0	0	2	1
		Ground	3	2	0	0	1	0	2	1
		Pitfall	10	3	0	0	0	0	1	1
	Habrocestum sp.	Litter	0	0	1	0	0	0	0	0
		Pitfall	0	0	0	0	0	0	1	0
	Habronattus viridipes (Hentz)	Pitfall	1	0	0	0	0	0	0	0
	Hentzia mitrata (Hentz)	Sweep	1	1	0	0	0	0	0	0
	Maevia inclemens (Walckenaer)	Litter	3	1	0	0	0	0	0	0
		Aerial	2	1	0	0	5	0	3	1
		Ground	3	1	2	1	22	0	13	3
		Sweep	6	5	8	0	9	0	6	1
		Pitfall	6	5	0	0	3	3	1	0
	Marpissa lineata (C.L. Koch)	Litter	1	1	1	1	0	0	1	1
	Metaphidippus galathea (Walckenaer)	Aerial	1	0	0	0	0	0	0	0
		Sweep	1	1	0	0	0	0	0	0
	Neon nellii Peckham	Pitfall	1	1	0	0	0	0	0	0
	Onondaga lineata (C.L. Koch)	Aerial	1	1	0	0	0	0	0	0
	Phidippus sp.	Ground	1	0	0	0	0	0	0	0
	Salticidae morphospecies B	Sweep	6	0	0	0	0	0	0	0
	Thiodina sylvana (Hentz)	Aerial	0	0	1	0	3	0	0	0
		Ground	0	0	0	0	0	0	1	0
		Sweep	5	3	2	0	2	0	0	0
Tetragnathidae	*Leucauge venusta* (Walckenaer)	Aerial	1	1	7	4	4	4	2	1
		Ground	0	0	1	1	1	1	0	0
		Sweep	0	0	0	0	2	2	1	1
	Tetragnatha elongata Walckenaer	Aerial	2	1	0	0	0	0	0	0
	Tetragnatha sp.	Sweep	0	0	2	0	0	0	0	0
Theridiidae	*Achaearanea rupicola* (Emerton)	Ground	0	0	1	1	0	0	1	1
	Argyrodes trigonum (Hentz)	Aerial	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	0	0	1	1
	Dipoena nigra (Emerton)	Sweep	1	1	0	0	0	0	0	0
	Episinus amoenus Banks	Aerial	0	0	0	0	0	0	1	1
		Sweep	0	0	1	1	0	0	0	0
	Mysmena guttata (Banks)	Litter	1	0	0	0	0	0	0	0
		Ground	0	0	0	0	1	1	0	0
	Pholcomma hirsutum Emerton	Litter	16	7	1	1	7	4	9	8
		Aerial	0	0	0	0	1	1	0	0
		Ground	0	0	0	0	1	1	5	5
		Pitfall	0	0	0	0	1	1	0	0
	Robertus frontatus (Banks)	Litter	1	0	17	9	4	2	26	13
		Pitfall	0	0	0	0	1	0	1	0
	Spintharus flavidus Hentz	Litter	0	0	0	0	0	0	1	0
		Aerial	0	0	0	0	4	0	5	0
		Ground	0	0	1	0	5	0	4	0
		Sweep	0	0	10	0	16	0	5	0

Table 5. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Theridion albidum Banks	Aerial	0	0	0	0	2	2	0	0
		Sweep	1	1	0	0	0	0	0	0
	Theridion differens Emerton	Aerial	0	0	0	0	0	0	1	1
	Theridion flavonotatum Becker	Aerial	0	0	0	0	5	5	12	12
		Ground	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	1	1	0	0
	Theridion lyricum Walckenaer	Aerial	0	0	0	0	1	1	7	7
		Sweep	0	0	0	0	0	0	1	0
	Theridion pennsylvanicum Emerton	Aerial	0	0	0	0	1	1	0	0
	Theridion sp.	Litter	0	0	0	0	1	0	0	0
		Aerial	0	0	0	0	0	0	1	0
		Pitfall	0	0	2	0	0	0	0	0
	Theridula opulenta (Walckenaer)	Ground	0	0	1	1	0	0	0	0
	Ulesanis americana Emerton	Aerial	0	0	1	0	0	0	1	0
Theridiosomatidae	*Theridiosoma gemmosum* (L. Koch)	Ground	0	0	0	0	2	0	2	2
Thomisidae	*Misumenoides formosipes* (Walckenaer)	Sweep	2	0	0	0	0	0	0	0
	Misumenops oblongus (Keyserling)	Sweep	3	1	0	0	0	0	1	1
	Thanatus sp.	Sweep	1	0	0	0	0	0	0	0
	Xysticus sp.	Litter	3	0	1	0	3	0	0	0
		Sweep	1	0	2	0	0	0	1	0
		Pitfall	5	0	0	0	0	0	0	0
Uloboridae	*Hyptiotes cavatus* (Hentz)	Aerial	0	0	0	0	2	0	4	0

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 5. (continued)

B. Summary for Ellicott Rock Clear-cut

	Method	1976	1995	1996	1997	Tot
# Families	All	15	15	18	18	21
# Genera	All	51	49	52	56	88
	Aerial	10	17	23	24	38
	Ground	12	18	25	25	41
	Sweep	16	15	14	13	31
	Pitfall	17	12	23	23	34
	Litter	18	19	21	19	34
# Species (# Morphosp.)	All	50(3)	49(1)	56(2)	59(1)	100(4)
	Aerial	10	15	23	22	41
	Ground	8	17	23	27(1)	40(1)
	Sweep	14(1)	11	9	10	26(1)
	Pitfall	18(1)	14(1)	25(2)	26(1)	35(2)
	Litter	15(2)	18(1)	18(1)	17(1)	33(2)

Table 6. Species list and species totals (by method) collected from Ellicott Rock Forest

A. Spider species and their abundances

Family	*Species*	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Calymmaria cavicola* (Banks)	Pitfall	1	1	0	0	0	0	0	0
	Cicurina arcuata Keyserling	Ground	0	0	0	0	1	1	0	0
		Pitfall	0	0	0	0	2	2	1	1
	Cicurina breviaria Bishop & Crosby	Litter	0	0	0	0	0	0	1	1
		Pitfall	1	1	2	2	4	4	6	6
	Cicurina exlinae Chamberlin & Ivie	Litter	0	0	0	0	0	0	2	2
		Pitfall	0	0	0	0	2	2	1	1
	Cicurina sp.	Litter	6	0	4	0	11	0	1	0
		Ground	0	0	0	0	1	0	0	0
		Pitfall	4	0	0	0	11	0	6	0
	Cicurina morphospecies A (nr.gertshi)	Litter	0	0	1	1	0	0	0	0
		Pitfall	0	0	0	0	0	0	1	1
	Coras sp.	Aerial	0	0	0	0	3	0	1	0
		Ground	3	0	0	0	1	0	0	0
		Pitfall	0	0	0	0	1	0	0	0
	Cybaeus silicis Barrows	Litter	0	0	0	0	0	0	2	0
		Ground	2	0	0	0	0	0	0	0
		Pitfall	3	3	0	0	9	0	5	1
	Wadotes bimucronatus (Simon)	Ground	0	0	2	1	1	1	0	0
		Pitfall	1	1	1	1	6	6	1	1
	Wadotes hybridus (Emerton)	Litter	0	0	1	1	0	0	0	0
		Ground	0	0	0	0	0	0	2	2
		Pitfall	14	14	3	3	3	3	12	12
	Wadotes sp.	Litter	15	0	9	0	16	0	11	0
		Aerial	0	0	0	0	0	0	1	0
		Ground	11	0	2	0	43	0	43	0
		Pitfall	36	0	7	0	58	0	32	0
Amaurobiidae	*Callioplus armipotens* (Bishop & Crosby)	Ground	0	0	0	0	1	0	0	0
		Pitfall	0	0	0	0	3	0	0	0
Antrodiaetidae	*Antrodiaetus unicolor* (Hentz)	Litter	1	0	1	0	0	0	0	0
		Pitfall	2	2	1	0	0	0	0	0
Anyphaenidae	*Anyphaena pectorosa* L. Koch	Aerial	0	0	0	0	3	3	2	2
		Ground	0	0	1	1	0	0	0	0
		Sweep	1	1	0	0	1	1	0	0
	Anyphaena sp.	Aerial	0	0	1	0	1	0	2	0
		Ground	0	0	1	1	0	0	0	0
		Sweep	0	0	1	0	0	0	1	0
	Wulfila albens (Hentz)	Litter	1	0	0	0	0	0	0	0
		Aerial	0	0	1	1	5	5	4	3
		Ground	1	1	0	0	0	0	0	0
		Sweep	2	2	1	1	3	3	3	3
		Pitfall	0	0	0	0	1	1	1	1
Araneidae	*Araneus bicentenarius* (McCook)	Aerial	0	0	1	1	0	0	0	0
	Araneus marmoreus Clerck	Aerial	0	0	1	0	1	0	0	0
	Araneus miniatus (Walckenaer)	Aerial	0	0	1	1	0	0	0	0
	Araneus nordmanni (Thorell)	Aerial	1	1	1	1	1	0	0	0
	Araneus sp.	Aerial	0	0	0	0	3	0	3	0
		Sweep	1	0	0	0	0	0	0	0
	Araniella displicata (Hentz)	Aerial	1	1	0	0	0	0	0	0
	Mangora maculata (Keyserling)	Sweep	0	0	1	1	2	0	0	0
	Mangora placida (Hentz)	Aerial	4	2	1	1	2	2	2	1
		Sweep	0	0	1	0	0	0	0	0

Table 6. (continued)

Family	*Species*	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Mangora sp.	Aerial	0	0	0	0	3	0	1	0
		Ground	0	0	0	0	1	0	0	0
		Sweep	1	0	0	0	0	0	0	0
	Metepeira labyrinthea (Hentz)	Aerial	1	0	0	0	0	0	0	0
	Micrathena gracilis (Walckenaer)	Aerial	0	0	0	0	1	0	0	0
		Ground	0	0	0	0	2	2	0	0
	Micrathena mitrata (Hentz)	Aerial	3	0	14	0	46	0	19	0
		Ground	0	0	9	0	7	0	1	0
		Sweep	12	0	9	0	15	0	3	0
		Pitfall	0	0	0	0	1	0	1	0
	Micrathena sagittata (Walckenaer)	Aerial	0	0	0	0	0	0	1	0
	Neoscona arabesca (Walckenaer)	Aerial	0	0	2	0	0	0	0	0
	Neoscona domiciliorum (Hentz)	Aerial	0	0	1	0	0	0	0	0
	Neoscona Hentzii (Keyserling)	Aerial	0	0	1	0	0	0	0	0
	Wixia sp.	Aerial	0	0	0	0	2	0	2	0
		Sweep	0	0	1	0	0	0	0	0
Atypidae	*Atypus* sp.	Litter	0	0	0	0	1	0	0	0
Clubionidae	*Agroeca minuta Banks*	Litter	0	0	0	0	3	0	1	1
		Pitfall	0	0	1	1	5	2	0	0
	Clubiona kastoni Gertsch	Sweep	0	0	0	0	0	0	1	1
	Clubiona obesa Hentz	Sweep	0	0	0	0	1	1	0	0
	Clubiona sp.	Aerial	0	0	0	0	1	0	2	0
		Ground	0	0	0	0	1	0	2	0
		Sweep	3	0	0	0	1	0	0	0
		Pitfall	1	0	0	0	0	0	0	0
	Clubiona spiralis Emerton	Sweep	0	0	1	1	0	0	0	0
		Pitfall	0	0	0	0	1	1	0	0
	Clubionoides excepta (L. Koch)	Aerial	0	0	0	0	0	0	3	1
		Sweep	0	0	1	0	1	0	0	0
	Phrurotimpus alarius (Hentz)	Litter	7	1	1	0	0	0	6	2
		Ground	0	0	0	0	8	8	12	11
		Pitfall	21	10	10	8	18	18	19	18
	Phrurotimpus borealis (Emerton)	Ground	0	0	0	0	2	2	7	5
		Pitfall	0	0	1	0	2	2	2	2
	Phrurotimpus sp.	Litter	0	0	0	0	0	0	1	0
		Ground	0	0	0	0	1	0	0	0
		Pitfall	0	0	0	0	0	0	1	0
	Scotinella redempta (Gertsch)	Litter	0	0	0	0	1	0	2	0
		Ground	0	0	0	0	0	0	1	1
		Pitfall	1	1	0	0	0	0	1	1
	Scotinella sp.	Litter	4	0	0	0	0	0	0	0
		Pitfall	0	0	0	0	2	0	0	0
	Scotinella morphospecies A	Litter	1	1	6	3	10	5	7	5
		Ground	0	0	0	0	1	1	0	0
		Pitfall	0	0	1	1	6	6	7	7
Ctenidae	*Anahita punctulata* (Hentz)	Litter	4	0	1	0	0	0	0	0
		Ground	1	1	0	0	7	0	0	0
		Pitfall	8	1	1	0	28	1	11	4
Dictynidae	*Dictyna* sp.	Aerial	0	0	0	0	1	0	0	0
	Dictyna sublata (Hentz)	Aerial	1	1	0	0	0	0	0	0
		Aerial	0	0	0	0	0	0	1	1
Gnaphosidae	*Drassyllus fallens* Chamberlin	Pitfall	0	0	0	0	1	1	1	1
	Drassyllus sp.	Litter	0	0	0	0	0	0	2	0
Hypochilidae	*Hypochilus thorelli* Marx	Aerial	1	0	0	0	0	0	0	0

Table 6. (continued)

Family	*Species*	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Leptonetidae	*Leptoneta Gertschi* Barrows	Litter	27	27	8	8	4	4	8	8
		Pitfall	2	2	3	3	5	5	0	0
	Leptoneta sp.	Litter	44	0	16	0	12	0	3	0
		Pitfall	1	0	0	0	0	0	0	0
Linyphiidae	*Bathyphantes* sp.	Ground	0	0	0	0	1	0	0	0
	Bathyphantes morphospecies A	Pitfall	0	0	0	0	0	0	1	1
	Blestia sarcocuon (Crosby & Bishop)	Litter	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	2	2	5	5
	Centromerus denticulatus (Emerton)	Litter	34	7	5	2	5	3	3	1
		Pitfall	0	0	0	0	2	1	3	1
	Ceraticelus carinatus (Emerton)	Litter	0	0	0	0	0	0	2	2
		Ground	0	0	0	0	1	1	0	0
		Pitfall	0	0	1	1	1	1	1	1
	Ceraticelus fissiceps O.P.-Cambridge	Litter	0	0	0	0	0	0	1	1
		Aerial	0	0	3	2	3	2	2	0
		Ground	0	0	2	2	4	3	1	1
		Sweep	48	42	86	83	38	28	59	53
		Pitfall	0	0	0	0	0	0	1	1
	Ceraticelus minutus (Emerton)	Pitfall	0	0	0	0	0	0	1	1
	Ceratinopsidis formosa (Banks)	Aerial	0	0	0	0	2	2	4	2
		Sweep	0	0	1	1	1	1	2	2
	Ceratinopsis sp.	Aerial	0	0	0	0	0	0	3	0
		Sweep	0	0	0	0	1	0	2	0
	Erigone autumnalis Emerton	Litter	0	0	5	5	3	3	9	9
		Sweep	1	1	1	1	0	0	1	1
		Pitfall	0	0	0	0	3	3	4	4
	Erigone brevidentata Emerton	Litter	5	5	0	0	0	0	0	0
	Floricomus tallulae Chamberlin & Ivie	Litter	0	0	0	0	0	0	1	1
	Florinda coccinea (Hentz)	Aerial	0	0	1	0	0	0	0	0
	Frontinella pyramitela (Walckenaer)	Aerial	6	3	3	0	0	0	1	0
	Grammonota pictilis (O.P.-Cambridge)	Aerial	0	0	0	0	2	2	3	3
		Sweep	0	0	0	0	1	1	2	2
	Graphomoa theridiodes Chamberlin	Ground	0	0	7	3	5	2	3	1
		Pitfall	0	0	0	0	1	0	0	0
	Lepthyphantes sabulosa (Keyserling)	Pitfall	0	0	0	0	0	0	1	1
	Lepthyphantes zebra (Emerton)	Aerial	1	1	0	0	0	0	0	0
		Ground	0	0	1	1	25	24	7	5
		Pitfall	2	0	0	0	2	2	1	1
	Linyphiidae morphospecies A1	Aerial	1	1	0	0	0	0	0	0
	Linyphiidae morphospecies A2	Pitfall	0	0	1	1	1	1	1	1
	Linyphiidae morphospecies B	Aerial	1	1	0	0	0	0	0	0
	Linyphiidae morphospecies C	Aerial	1	1	0	0	0	0	0	0
	Linyphiidae morphospecies D	Aerial	1	1	0	0	0	0	0	0
	Maso sundevallii (Westring)	Litter	0	0	0	0	1	1	1	1
		Sweep	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	1	1	0	0
	Meioneta sp.	Sweep	0	0	0	0	1	0	0	0
	Meioneta morphospecies A	Pitfall	2	1	0	0	0	0	0	0
	Meioneta unimaculata (Banks)	Litter	1	0	4	4	0	0	0	0
		Pitfall	0	0	9	9	0	0	1	1
	Microneta sp.	Litter	1	0	0	0	0	0	0	0
	Neriene clathrata (Sundevall)	Aerial	0	0	0	0	0	0	1	1
		Ground	0	0	1	0	0	0	0	0

Table 6. (continued)

Family	*Species*	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Neriene sp.	Ground	0	0	0	0	1	0	0	0
	Neriene variabilis (Banks)	Aerial	0	0	0	0	1	0	0	0
		Ground	0	0	6	0	4	0	1	0
	Pelecopsidis frontalis (Banks)	Litter	1	1	0	0	1	1	0	0
	Pitiohyphantes costatus (Hentz)	Aerial	1	0	7	0	5	0	13	0
		Ground	0	0	2	0	0	0	0	0
	Scylaceus pallidus (Emerton)	Litter	2	2	0	0	0	0	0	0
	Walckenaeria *directa* (O.P.-Cambridge)	Litter	0	0	2	2	0	0	0	0
	Walckenaeria *dixiana* (Chamberlin & Ivie)	Pitfall	0	0	0	0	2	2	1	1
	Walckenaeria *spiralis* (Emerton)	Pitfall	0	0	0	0	0	0	1	1
Lycosidae	*Gladicosa gulosa* (Walckenaer)	Litter	1	0	0	0	1	0	0	0
		Ground	5	0	0	0	1	0	3	0
		Pitfall	8	1	2	0	3	0	3	0
	Pardosa sp.	Ground	9	0	0	0	0	0	0	0
	Pirata montanus Emerton	Litter	0	0	1	0	18	0	0	0
		Aerial	0	0	0	0	0	0	1	0
		Ground	1	1	2	2	76	15	100	73
		Sweep	0	0	0	0	0	0	1	1
		Pitfall	0	0	25	25	53	10	20	14
Mimetidae	*Mimetus interfector* (Hentz)	Aerial	0	0	0	0	1	0	0	0
		Sweep	0	0	0	0	1	0	0	0
Oxyopidae	*Ero* sp.	Ground	0	0	0	0	1	0	0	0
Salticidae	*Habrocestum parvulum* (Banks)	Litter	0	0	3	1	2	2	2	2
		Ground	0	0	0	0	17	9	16	10
		Pitfall	0	0	5	3	26	20	9	7
	Habrocestum pulex (Hentz)	Aerial	0	0	0	0	0	0	1	1
		Ground	1	1	0	0	1	0	1	1
	Habrocestum sp.	Litter	0	0	1	0	0	0	0	0
	Icius morphospecies A	Sweep	1	0	0	0	0	0	0	0
	Maevia inclemens (Walckenaer)	Litter	15	0	0	0	0	0	0	0
		Aerial	0	0	0	0	6	1	11	0
		Ground	2	1	0	0	14	3	19	8
		Sweep	17	2	13	0	25	0	6	1
		Pitfall	0	0	1	0	0	0	2	2
	Marpissa sp.	Litter	0	0	1	0	0	0	0	0
	Metaphidippus flaviceps Kaston	Sweep	1	1	0	0	0	0	0	0
	Salticidae morphospecies A	Litter	3	0	0	0	0	0	0	0
		Ground	4	2	0	0	0	0	0	0
		Pitfall	11	9	0	0	0	0	0	0
	Thiodina sylvana (Hentz)	Aerial	0	0	1	0	2	0	0	0
		Ground	0	0	1	0	0	0	0	0
		Sweep	4	0	6	0	2	0	3	0
	Zygoballus bettini Peckham	Sweep	2	2	0	0	0	0	0	0
Tetragnathidae	*Leucauge venusta* (Walckenaer)	Aerial	7	5	2	2	2	2	4	4
		Ground	0	0	1	1	1	1	0	0
		Sweep	10	7	4	2	3	3	2	2
	Tetragnatha elongata Walckenaer	Aerial	0	0	1	1	0	0	0	0
	Tetragnatha versicolor Walckenaer	Sweep	4	4	0	0	0	0	0	0
Theridiidae	*Achaearanea rupicola* (Emerton)	Ground	1	1	0	0	0	0	1	1
	Argyrodes trigonum (Hentz)	Aerial	5	5	1	1	0	0	1	1
	Crustulina sp.	Ground	0	0	0	0	1	0	0	0
	Episinus amoenus Banks	Ground	0	0	0	0	0	0	1	1
		Sweep	0	0	1	1	0	0	1	1

Table 6. (continued)

Family	*Species*	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Euryopis funebris (Hentz)	Ground	0	0	0	0	1	1	0	0
	Mysmena guttata (Banks)	Litter	0	0	0	0	0	0	1	0
		Pitfall	2	1	0	0	0	0	0	0
	Pholcomma hirsutum Emerton	Litter	68	18	4	2	5	4	13	8
		Aerial	1	1	0	0	0	0	0	0
		Ground	0	0	0	0	1	1	4	3
		Sweep	2	2	0	0	0	0	2	2
		Pitfall	0	0	0	0	1	1	0	0
	Robertus frontatus (Banks)	Litter	14	2	8	7	11	7	5	5
	Spintharus flavidus Hentz	Aerial	0	0	0	0	2	0	7	0
		Ground	0	0	2	0	0	0	2	0
		Sweep	0	0	8	0	7	0	14	0
	Theridion albidum Banks	Aerial	0	0	1	1	0	0	2	2
		Sweep	1	1	1	1	2	2	1	1
	Theridion flavonotatum Becker	Aerial	2	2	1	1	5	5	9	9
		Ground	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	1	1	0	0
	Theridion glaucescens Becker	Aerial	0	0	0	0	0	0	1	1
	Theridion lyricum Walckenaer	Aerial	2	2	0	0	0	0	0	0
		Ground	0	0	1	1	0	0	0	0
		Sweep	0	0	2	2	0	0	2	2
	Thymoites unimaculatum (Emerton)	Aerial	0	0	0	0	1	1	2	2
		Sweep	1	1	1	1	0	0	1	1
	Ulesanis americana Emerton	Aerial	0	0	0	0	0	0	1	0
Theridiosomatidae	*Theridiosoma gemmosum* (L. Koch)	Ground	0	0	0	0	2	2	1	0
		Sweep	1	1	0	0	0	0	0	0
		Pitfall	1	0	0	0	0	0	1	0
Thomisidae	*Misumenops oblongus* (Keyserling)	Aerial	0	0	1	0	0	0	0	0
		Sweep	1	0	0	0	1	0	0	0
	Philodromus placidus Banks	Aerial	0	0	0	0	1	1	0	0
		Sweep	1	1	0	0	0	0	0	0
	Philodromus rufus Walckenaer	Sweep	1	1	0	0	0	0	0	0
	Philodromus sp.	Sweep	0	0	1	0	0	0	1	0
	Xysticus elegans Keyserling	Litter	0	0	0	0	0	0	1	1
	Xysticus fraternus Banks	Ground	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	0	0	1	1
	Xysticus sp.	Litter	1	0	1	0	1	0	0	0
		Ground	0	0	0	0	1	0	0	0
		Sweep	2	0	0	0	0	0	0	0
		Pitfall	1	0	0	0	1	0	0	0
Uloboridae	*Hyptiotes cavatus* (Hentz)	Aerial	1	0	0	0	3	0	2	0
		Ground	0	0	0	0	1	0	0	0
		Sweep	3	0	0	0	0	0	0	0
	Uloborus glomosus (Walckenaer)	Aerial	0	0	0	0	0	0	1	1

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 6. (continued)

B. Summary for Ellicott Rock Forest

	Method	1976	1995	1996	1997	Tot
# Families	All	17	13	20	16	22
# Genera	All	55	48	58	58	82
	Aerial	16	16	23	29	42
	Ground	12	13	27	20	38
	Sweep	23	18	18	21	34
	Pitfall	17	15	28	24	36
	Litter	20	17	16	19	33
# Species (# Morphosp.)	All	60(8)	57(3)	60(2)	70(4)	109(11)
	Aerial	20(4)	21	21	26	52(4)
	Ground	9(1)	14	24(1)	21	39(2)
	Sweep	20(1)	17	17	19	36(1)
	Pitfall	16(2)	17(2)	30(2)	34(4)	46(6)
	Litter	16(2)	15(2)	13(1)	20(1)	34(3)

Table 7. Species list and species totals (by method) collected from Horse Cove Clear-cut

A. Spider species and their abundances

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Agelenopsis utahana* (Chamberlin & Ivie)	Aerial	0	0	3	0	0	0	1	1
		Ground	0	0	0	0	1	0	1	0
		Sweep	0	0	2	0	0	0	0	0
	Calymmaria cavicola (Banks)	Pitfall	2	2	0	0	0	0	0	0
	Cicurina arcuata Keyserling	Pitfall	1	1	0	0	1	1	1	1
	Cicurina sp.	Litter	6	0	0	0	3	0	0	0
		Pitfall	1	0	0	0	3	0	0	0
	Coras sp.	Aerial	1	0	1	0	1	0	0	0
		Ground	1	0	0	0	0	0	0	0
	Coras taugynus Chamberlin	Pitfall	1	1	0	0	0	0	0	0
	Cybaeus silicis Barrows	Litter	1	0	0	0	0	0	0	0
		Pitfall	8	6	6	6	4	2	5	1
	Wadotes bimucronatus (Simon)	Pitfall	3	3	1	1	0	0	0	0
	Wadotes hybridus (Emerton)	Pitfall	22	22	2	2	0	0	2	2
	Wadotes sp.	Litter	9	0	0	0	4	0	9	0
		Ground	0	0	0	0	5	0	3	0
		Pitfall	27	0	6	0	13	0	10	0
Amaurobiidae	*Callioplus armipotens* (Bishop & Crosby)	Litter	15	1	10	2	19	4	53	10
		Ground	0	0	0	0	1	0	0	0
	Callioplus armipotens (Bishop & Crosby)	Pitfall	2	0	12	5	22	2	19	4
Antrodiaetidae	*Antrodiaetus unicolor* (Hentz)	Pitfall	4	4	0	0	0	0	0	0
Anyphaenidae	*Anyphaena pectorosa* L. Koch	Aerial	0	0	3	3	1	1	1	1
		Sweep	0	0	1	1	0	0	0	0
	Wulfila albens (Hentz)	Aerial	0	0	4	4	2	2	2	2
		Sweep	0	0	0	0	1	1	2	2
	Wulfila saltabunda (Hentz)	Sweep	1	1	0	0	0	0	0	0
Araneidae	*Araneus marmoreus* Clerck	Aerial	0	0	1	0	0	0	1	0
		Ground	0	0	0	0	1	0	0	0
	Araneus marmoreus Clerck	Pitfall	1	0	0	0	0	0	0	0
	Araneus niveus (Hentz)	Ground	0	0	0	0	0	0	1	1
	Araneus nordmanni (Thorell)	Aerial	0	0	0	0	0	0	1	1
	Cyclosa turbinata (Walckenaer)	Aerial	4	1	0	0	0	0	0	0
	Mangora maculata (Keyserling)	Ground	0	0	1	0	2	0	0	0
		Sweep	0	0	0	0	3	0	1	0
	Mangora placida (Hentz)	Aerial	0	0	0	0	4	0	0	0
	Metepeira labyrinthea (Hentz)	Aerial	1	0	0	0	0	0	0	0
	Micrathena mitrata (Hentz)	Aerial	0	0	1	0	6	0	1	0
		Ground	0	0	0	0	2	0	0	0
		Sweep	0	0	0	0	1	0	0	0
	Neoscona arabesca (Walckenaer)	Aerial	0	0	0	0	1	1	0	0
	Neoscona hentzii (Keyserling)	Aerial	0	0	0	0	1	0	0	0
Clubionidae	*Agroeca minuta* Banks	Pitfall	0	0	0	0	0	0	5	3
	Castianeira cingulata (C.L. Koch)	Ground	1	0	0	0	0	0	0	0
	Castianeira longipalpus (Hentz)	Pitfall	4	2	0	0	0	0	0	0
	Chiracanthium inclusum (Hentz)	Sweep	1	0	0	0	0	0	0	0
	Clubiona sp.	Litter	2	0	0	0	0	0	0	0
		Sweep	1	0	1	0	0	0	0	0
		Pitfall	0	0	1	0	0	0	0	0
	Clubionoides excepta (L. Koch)	Ground	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	1	0	0	0
		Pitfall	0	0	1	1	1	1	0	0

Table 7. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Liocranoides sp.	Pitfall	1	1	0	0	0	0	0	0
	Phrurotimpus alarius (Hentz)	Litter	9	2	2	0	2	1	7	3
		Ground	1	1	0	0	4	3	4	4
		Pitfall	37	35	15	12	40	39	52	51
	Phrurotimpus borealis (Emerton)	Ground	0	0	0	0	0	0	6	6
		Pitfall	13	7	2	2	0	0	5	5
	Phrurotimpus sp.	Litter	0	0	1	0	0	0	0	0
	Scotinella redempta (Gertsch)	Litter	1	1	8	5	0	0	3	1
		Ground	0	0	0	0	1	1	6	4
		Pitfall	3	3	4	4	10	9	14	14
	Scotinella morphospecies A	Litter	0	0	1	1	0	0	0	0
Ctenidae	*Anahita punctulata* (Hentz)	Litter	0	0	0	0	1	1	0	0
		Ground	0	0	0	0	0	0	1	0
		Pitfall	0	0	0	0	1	0	0	0
Dictynidae	*Lathys pallida* Marx	Litter	0	0	0	0	0	0	1	1
Gnaphosidae	*Cesonia bilineata* (Hentz)	Pitfall	1	0	0	0	0	0	0	0
	Drassyllus fallens Chamberlin	Pitfall	1	1	0	0	1	1	1	1
	Drassyllus sp.	Litter	2	0	0	0	1	0	0	0
	Micaria aurata (Hentz)	Sweep	2	0	0	0	0	0	0	0
	Micaria longipes Emerton	Pitfall	1	1	0	0	0	0	0	0
	Zelotes duplex Chamberlin	Pitfall	5	4	0	0	0	0	0	0
	Zelotes hentzi Barrows	Pitfall	1	1	0	0	0	0	0	0
Hahniidae	*Neoantistea agilis* (Keyserling)	Litter	1	0	0	0	0	0	0	0
		Sweep	0	0	0	0	0	0	1	0
	Neoantistia sp.	Ground	1	0	0	0	0	0	0	0
Hypochilidae	*Hypochilus thorelli* Marx	Aerial	2	0	0	0	0	0	0	0
Leptonetidae	*Leptoneta gertschi* Barrows	Litter	1	1	1	1	1	1	2	2
		Pitfall	0	0	0	0	1	1	1	1
	Leptoneta sp.	Litter	7	0	0	0	0	0	2	0
Linyphiidae	*Bathyphantes* morphospecies A	Litter	0	0	0	0	1	1	1	1
		Ground	0	0	0	0	1	1	0	0
	Blestia sarcocuon (Crosby & Bishop)	Litter	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	0	0	3	3
	Ceraticelus carinatus (Emerton)	Litter	0	0	7	7	2	2	1	1
		Pitfall	0	0	1	1	2	1	1	1
	Ceraticelus fissiceps O.P.-Cambridge	Litter	0	0	1	1	1	1	1	1
		Ground	0	0	3	3	0	0	0	0
		Sweep	10	10	4	4	14	12	15	14
	Ceraticelus minutus (Emerton)	Litter	2	2	2	2	2	2	0	0
	Ceratinopsidis formosa (Banks)	Aerial	0	0	5	5	2	2	3	2
		Ground	0	0	2	2	1	1	0	0
		Sweep	0	0	4	2	1	1	4	3
	Ceratinopsis interpres (O.P.-Cambridge)	Aerial	2	2	0	0	0	0	0	0
		Ground	1	1	0	0	0	0	0	0
		Sweep	9	9	0	0	2	2	0	0
	Frontinella pyramitela (Walckenaer)	Aerial	7	2	3	3	0	0	1	0
	Graphomoa theridiodes Chamberlin	Ground	0	0	1	1	1	0	0	0
	Lepthyphantes morphospecies A	Litter	0	0	0	0	0	0	1	1
	Lepthyphantes zebra (Emerton)	Litter	15	0	0	0	0	0	0	0
		Ground	0	0	2	2	9	9	10	10
		Pitfall	1	0	1	1	3	3	4	4

Table 7. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Maso sundevallii (Westring)	Litter	0	0	2	2	3	3	1	1
		Ground	0	0	0	0	0	0	1	1
	Meioneta angulata (Emerton)	Litter	0	0	0	0	0	0	1	1
		Aerial	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	0	0	3	3
	Meioneta morphospecies B1	Pitfall	2	2	0	0	0	0	0	0
	Meioneta morphospecies B2	Ground	0	0	0	0	0	0	1	1
	Meioneta morphospecies C	Litter	1	1	0	0	0	0	0	0
	Meioneta unimaculata (Banks)	Aerial	0	0	1	1	0	0	0	0
		Ground	0	0	0	0	0	0	2	2
		Pitfall	0	0	1	1	2	2	1	1
	Neriene clathrata (Sundevall)	Ground	0	0	2	2	0	0	0	0
	Neriene variabilis (Banks)	Litter	0	0	0	0	1	0	0	0
		Aerial	0	0	1	0	0	0	0	0
		Ground	0	0	1	0	9	1	0	0
	Pelecopsis moestum (Banks)	Litter	1	1	0	0	1	1	1	1
		Pitfall	0	0	0	0	2	2	8	8
	Pitiohyphantes costatus (Hentz)	Litter	0	0	1	0	0	0	0	0
		Aerial	0	0	0	0	1	0	14	0
		Sweep	0	0	0	0	0	0	2	0
	Walckenaeria directa (O.P.-Cambridge)	Litter	0	0	0	0	1	1	0	0
		Sweep	1	1	0	0	0	0	0	0
Lycosidae	*Gladicosa gulosa* (Walckenaer)	Litter	0	0	1	0	3	0	4	0
		Ground	0	0	5	0	5	0	14	0
		Pitfall	3	0	18	0	15	1	14	1
	Pardosa milvina (Hentz)	Ground	3	2	0	0	0	0	0	0
	Pardosa saxatilis (Hentz)	Ground	3	3	0	0	0	0	0	0
	Pirata minutus Emerton	Ground	1	1	0	0	0	0	0	0
	Pirata montanus Emerton	Litter	10	3	0	0	0	0	4	1
		Ground	0	0	6	3	18	7	12	6
		Pitfall	4	1	1	1	2	0	8	5
	Pirata sp.	Sweep	1	0	0	0	0	0	0	0
	Schizocosa ocreata (Hentz)	Pitfall	1	1	2	2	0	0	0	0
Mimetidae	*Mimetus interfector* (Hentz)	Aerial	0	0	0	0	0	0	1	0
Nesticidae	*Nesticus sheari* Gertsch	Litter	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	1	1	2	2
Pisauridae	*Dolomedes* sp.	Ground	0	0	0	0	0	0	1	0
		Sweep	0	0	0	0	0	0	2	0
	Pisaurina mira (Walckenaer)	Aerial	1	0	0	0	0	0	0	0
		Sweep	0	0	0	0	0	0	1	0
Salticidae	*Agassa cerulea* (Walckenaer)	Sweep	1	0	0	0	0	0	0	0
	Eris aurantia (Lucas)	Sweep	1	0	0	0	0	0	0	0
	Eris morphospecies A	Sweep	7	0	0	0	0	0	0	0
	Habrocestum pulex (Hentz)	Litter	1	1	0	0	0	0	0	0
		Ground	1	1	0	0	0	0	0	0
		Pitfall	3	0	0	0	0	0	0	0
	Hentzia mitrata (Hentz)	Aerial	0	0	0	0	0	0	1	1
	Icius elegans (Hentz)	Sweep	1	0	0	0	0	0	0	0
	Maevia inclemens (Walckenaer)	Litter	4	0	0	0	1	0	0	0
		Aerial	1	0	0	0	1	0	3	1
		Ground	1	0	0	0	1	1	2	1
		Sweep	2	1	2	0	2	0	0	0

Table 7. (continued) .

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Metaphidippus canadensis (Banks)	Litter	3	0	0	0	3	0	2	1
		Ground	0	0	1	1	1	0	0	0
		Pitfall	0	0	2	1	1	1	1	0
	Metaphidippus galathea (Walckenaer)	Sweep	3	3	0	0	0	0	0	0
	Metaphidippus sp.	Pitfall	0	0	0	0	0	0	1	0
	Neon nellii Peckham	Litter	1	1	0	0	1	1	0	0
		Pitfall	1	1	0	0	0	0	0	0
	Phidippus princeps (Peckham)	Aerial	1	1	0	0	0	0	0	0
		Sweep	1	1	0	0	0	0	0	0
	Salticidae morphospecies B	Sweep	7	0	0	0	0	0	0	0
	Sitticus floridanus Gertsch & Mulaik	Litter	1	1	0	0	0	0	0	0
	Thiodina sylvana (Hentz)	Aerial	0	0	1	0	0	0	0	0
		Sweep	4	3	1	0	3	1	2	0
	Zygoballus bettini Peckham	Litter	1	1	0	0	0	0	0	0
		Sweep	3	2	0	0	0	0	0	0
Tetragnathidae	*Leucauge venusta* (Walckenaer)	Aerial	4	4	3	3	1	1	0	0
		Ground	0	0	1	1	0	0	0	0
		Sweep	0	0	4	4	1	1	0	0
	Tetragnatha elongata Walckenaer	Aerial	1	1	0	0	0	0	0	0
	Tetragnatha seneca Seeley	Aerial	2	1	0	0	0	0	0	0
		Pitfall	0	0	1	1	0	0	0	0
	Tetragnatha versicolor Walckenaer	Aerial	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	0	0	1	1
Theridiidae	*Achaearanea rupicola* (Emerton)	Ground	0	0	2	2	0	0	0	0
	Argyrodes trigonum (Hentz)	Aerial	2	2	0	0	2	2	1	1
		Sweep	1	1	0	0	0	0	0	0
	Episinus amoenus Banks	Ground	0	0	0	0	1	1	0	0
		Sweep	1	1	2	2	0	0	1	1
	Mysmena guttata (Banks)	Litter	3	1	0	0	0	0	0	0
		Ground	0	0	0	0	2	2	0	0
		Pitfall	2	0	0	0	0	0	0	0
	Pholcomma hirsutum Emerton	Litter	9	5	4	4	6	5	3	2
		Ground	0	0	0	0	2	2	0	0
		Sweep	0	0	0	0	0	0	1	1
		Pitfall	0	0	0	0	2	2	1	1
	Spintharus flavidus Hentz	Aerial	0	0	1	0	5	0	5	0
		Ground	0	0	0	0	6	0	3	0
		Sweep	0	0	3	0	25	0	38	0
	Theridion albidum Banks	Aerial	0	0	0	0	1	1	0	0
		Sweep	0	0	0	0	0	0	1	1
	Theridion flavonotatum Becker	Aerial	1	1	1	1	4	4	4	4
		Ground	0	0	1	1	0	0	0	0
		Sweep	1	1	1	1	0	0	1	1
	Theridion lyricum Walckenaer	Aerial	0	0	1	1	1	1	3	3
		Pitfall	0	0	0	0	1	1	0	0
	Theridion sp.	Litter	0	0	0	0	2	0	0	0
		Aerial	0	0	0	0	1	0	0	0
	Theridula opulenta (Walckenaer)	Aerial	0	0	1	1	1	1	0	0
		Sweep	0	0	4	3	1	0	0	0
Theridioso-matidae	*Theridiosoma gemmosum* (L. Koch)	Litter	0	0	1	1	0	0	2	1
		Aerial	2	2	0	0	0	0	0	0
		Ground	0	0	3	2	2	1	1	1
		Sweep	0	0	1	1	0	0	0	0

Table 7. (continued)

Family	Species	Method	1976		1995		1996		1997	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Thomisidae	*Misumenoides formosipes* (Walckenaer)	Aerial	1	1	0	0	0	0	0	0
		Sweep	2	0	0	0	0	0	0	0
	Misumenops oblongus (Keyserling)	Aerial	2	0	0	0	0	0	0	0
		Sweep	2	1	0	0	0	0	0	0
	Xysticus pellax O.P.-Cambridge	Pitfall	1	1	0	0	0	0	0	0
	Xysticus sp.	Sweep	2	0	0	0	0	0	1	0
Uloboridae	*Hyptiotes cavatus* (Hentz)	Aerial	1	0	8	0	4	0	3	0

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 7. (continued)

B. Summary for Horse Cove Clear-cut

	Method	1976	1995	1996	1997	Tot
# Families	All	19	13	16	21	23
# Genera	All	60	40	47	48	83
	Aerial	17	16	15	17	33
	Ground	9	13	22	16	37
	Sweep	23	13	12	15	39
	Pitfall	25	15	20	19	38
	Litter	23	10	19	19	35
# Species (# Morphosp.)	All	70(4)	45(1)	51(1)	55(3)	107(8)
	Aerial	17	16	17	19	39
	Ground	8	14	21(1)	17(1)	40(2)
	Sweep	21(2)	12	12	14	38(2)
	Pitfall	27(1)	16	19	21	41(1)
	Litter	19(1)	13(1)	17(1)	19(2)	35(4)

Table 8. Species list and species totals (by method) collected from Beech Gap Forest

A. Spider species and their abundances

Family	Species	Method	6/95		6/96		8/96		6/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Agelenopsis utahana* (Chamberlin & Ivie)	Beating	0	0	0	0	6	2	0	0	5	1
		Aerial	1	1	0	0	5	2	0	0	15	14
		Ground	0	0	0	0	10	4	5	0	5	5
	Cicurina arcuata Keyserling	Ground	0	0	0	0	0	0	1	1	0	0
	Cicurina breviaria Bishop & Crosby	Ground	0	0	0	0	0	0	1	1	0	0
	Coras montanus (Emerton)	Aerial	1	1	4	0	5	2	11	0	1	1
		Ground	0	0	0	0	0	0	3	0	1	0
	Cybaeus patritus Crosby & Bishop	Litter	0	0	1	0	0	0	0	0	0	0
		Ground	0	0	1	0	2	1	0	0	1	0
	Wadotes tennesseensis Gertsch	Litter	2	2	4	1	35	6	21	4	24	5
		Ground	2	2	33	2	20	10	6	0	33	19
Amaurobiid-ae	*Callioplus pantoplus* Bishop & Crosby	Litter	0	0	2	2	0	0	0	0	4	4
	Callobius bennetti (Blackwall)	Aerial	0	0	2	1	1	0	9	1	3	2
		Ground	0	0	1	0	1	0	2	0	0	0
Antrodiaetid-ae	*Antrodiaetus unicolor* (Hentz)	Litter	0	0	3	0	1	0	2	0	4	0
		Ground	0	0	1	0	0	0	2	0	0	0
Araneidae	*Araneus marmoreus* Clerck	Beating	0	0	31	0	30	4	41	0	38	3
		Aerial	0	0	23	0	53	5	47	0	94	34
		Ground	0	0	2	0	12	0	14	5	26	4
	Araneus nordmanni (Thorell)	Beating	0	0	11	0	44	0	0	0	31	0
		Aerial	0	0	11	0	14	9	0	0	5	0
		Ground	0	0	2	0	2	0	1	1	2	0
	Araniella displicata (Hentz)	Beating	0	0	0	0	1	0	0	0	0	0
	Cyclosa turbinata (Walckenaer)	Beating	0	0	0	0	0	0	0	0	1	1
		Aerial	0	0	0	0	0	0	0	0	2	2
	Larinioides patagiata (Clerck)	Aerial	0	0	1	1	0	0	0	0	0	0
	Micrathena gracilis (Walckenaer)	Aerial	0	0	0	0	1	0	0	0	0	0
	Neoscona arabesca (Walckenaer)	Beating	0	0	0	0	0	0	0	0	1	0
		Aerial	0	0	0	0	0	0	0	0	2	2
Clubionidae	*Clubiona canadensis* Emerton	Litter	0	0	0	0	0	0	1	1	0	0
		Beating	0	0	0	0	44	1	13	12	2	2
		Aerial	0	0	0	0	0	0	2	2	2	0
		Ground	0	0	0	0	1	0	1	1	0	0
	Clubiona rhododendri Barrows	Litter	0	0	0	0	0	0	4	4	0	0
		Beating	8	8	8	8	38	4	3	3	8	8
		Aerial	0	0	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	1	0	0	0	1	1
Dictynidae	Dictyna maxima *Banks*	Beating	0	0	0	0	0	0	4	4	0	0
		Aerial	0	0	0	0	0	0	2	2	0	0
		Ground	0	0	0	0	0	0	1	1	0	0
Hahniidae	*Cryphoeca montana* Emerton	Aerial	0	0	2	1	0	0	2	2	1	1
	Neoantistea magna (Keyserling)	Litter	0	0	7	0	5	5	11	3	9	4
		Ground	1	1	13	1	7	7	1	0	0	0
Linyphiidae	*Bathyphantes bishopi* Ivie	Litter	0	0	0	0	0	0	1	1	0	0
		Beating	0	0	0	0	0	0	1	1	0	0
		Ground	3	3	13	9	1	1	24	12	6	4
	Centromerus denticulatus (Emerton)	Litter	0	0	0	0	0	0	1	1	0	0

Table 8. (continued)

Family	Species	Method	6/95		6/96		8/96		6/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Ceraticelus alticeps (Fox)	Litter	0	0	4	3	1	1	7	7	3	3
		Beating	138	138	140	140	279	279	81	81	64	64
		Aerial	3	3	23	23	2	2	4	4	0	0
		Ground	1	1	11	11	3	3	5	5	2	2
	Ceraticelus carinatus (Emerton)	Litter	8	8	9	9	32	32	13	13	20	20
		Ground	0	0	0	0	3	3	2	2	0	0
	Ceratinella brunnea Emerton	Beating	0	0	0	0	0	0	1	1	0	0
	Ceratinops carolinus (Banks)	Litter	0	0	0	0	0	0	2	2	0	0
	Collinsia oxypaederotipus (Crosby)	Litter	7	7	33	33	7	7	29	29	6	6
		Ground	0	0	1	1	0	0	1	1	0	0
	Eperigone entomologica (Emerton)	Litter	0	0	2	2	0	0	0	0	0	0
	Eperigone maculata (Banks)	Litter	4	4	13	13	0	0	41	41	13	13
		Ground	0	0	3	3	0	0	2	2	0	0
	Erigone autumnalis Emerton	Litter	0	0	0	0	0	0	1	1	0	0
		Beating	0	0	1	1	2	2	1	1	0	0
		Aerial	0	0	0	0	0	0	1	1	0	0
	Erigoninae morphospecies C1	Litter	0	0	2	2	0	0	2	2	0	0
	Estrandia grandaeva (Keyserling)	Beating	0	0	1	1	0	0	0	0	0	0
	Florinda coccinea (Hentz)	Beating	2	2	0	0	0	0	0	0	0	0
	Frontinella pyramitela (Walckenaer)	Beating	0	0	0	0	0	0	0	0	2	2
		Aerial	0	0	0	0	1	1	0	0	0	0
		Ground	0	0	0	0	0	0	0	0	2	2
	Gonatium crassipalpum Bryant	Beating	1	1	0	0	4	4	0	0	0	0
	Grammonota pictilis (O.P.-Cambridge)	Beating	0	0	3	3	0	0	10	10	0	0
	Helophora insignis (Blackwall)	Beating	0	0	0	0	6	0	0	0	16	0
		Ground	0	0	0	0	1	0	0	0	5	0
	Horcotes uncinatus Barrows	Litter	0	0	9	9	0	0	0	0	2	2
	Lepthyphantes zebra (Emerton)	Litter	0	0	0	0	1	0	5	5	1	1
		Beating	1	1	0	0	0	0	0	0	5	0
		Aerial	1	1	0	0	0	0	0	0	0	0
		Ground	2	2	9	9	0	0	8	8	36	0
	Meioneta micaria (Emerton)	Litter	0	0	0	0	0	0	1	1	0	0
		Beating	1	1	2	2	0	0	0	0	0	0
		Aerial	0	0	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	0	0	3	3	0	0
	Neriene radiata (Walckenaer)	Beating	0	0	0	0	1	0	0	0	0	0
		Aerial	2	2	1	1	0	0	0	0	0	0
		Ground	1	1	1	1	0	0	0	0	1	1
	Pitiohyphantes costatus (Hentz)	Beating	1	1	1	1	20	0	3	2	6	1
		Aerial	0	0	4	4	2	0	0	0	0	0
		Ground	0	0	0	0	4	0	1	1	0	0
	Pocadicnemis americana Millidge	Beating	8	8	10	10	0	0	7	7	0	0
		Aerial	0	0	1	1	0	0	0	0	0	0
	Walckenaeria *directa* (O.P.-Cambridge)	Beating	0	0	0	0	1	1	0	0	0	0
Salticidae	*Habrocestum pulex* (Hentz)	Aerial	0	0	1	1	0	0	0	0	0	0
	Neon nellii Peckham	Litter	0	0	0	0	2	1	4	3	18	3
		Beating	2	2	2	2	0	0	1	1	1	1
		Aerial	0	0	0	0	0	0	1	1	0	0
		Ground	0	0	1	1	0	0	0	0	0	0
	Pelegrina montanus Emerton	Beating	0	0	0	0	0	0	24	10	3	3
		Aerial	0	0	0	0	0	0	2	2	0	0

Table 8. (continued)

Family	Species	Method	6/95		6/96		8/96		6/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Pelegrina proterva (Walckenaer)	Litter	0	0	0	0	0	0	1	1	0	0
		Beating	0	0	0	0	20	0	0	0	0	0
Tetragnathi-dae	*Glenognatha foxi* (McCook)	Beating	0	0	0	0	0	0	1	1	0	0
	Leucauge venusta (Walckenaer)	Beating	4	4	0	0	0	0	0	0	0	0
		Aerial	1	1	2	0	0	0	0	0	0	0
		Ground	2	2	1	0	0	0	0	0	3	2
	Tetragnatha versicolor Walckenaer	Beating	0	0	1	1	11	0	0	0	4	0
		Aerial	0	0	0	0	0	0	1	0	0	0
Theridiidae	*Robertus frontatus* (Banks)	Litter	6	6	4	4	2	2	0	0	11	11
	Theridion albidum Banks	Beating	0	0	0	0	0	0	0	0	2	2
		Ground	0	0	0	0	0	0	0	0	1	1
	Theridion aurantium Emerton	Litter	0	0	0	0	2	0	4	3	1	0
		Beating	23	23	157	156	67	33	79	48	61	59
		Aerial	3	3	2	2	7	7	1	1	2	2
		Ground	5	5	15	15	29	18	53	26	75	29
	Theridion frondeum (Hentz)	Litter	0	0	0	0	0	0	1	0	0	0
		Beating	4	4	23	0	2	2	15	0	1	1
		Aerial	2	2	0	0	2	2	2	0	3	3
		Ground	1	1	0	0	0	0	3	0	2	2
	Theridula opulenta (Walckenaer)	Beating	0	0	0	0	1	1	0	0	0	0
Thomisidae	*Misumenops asperatus* (Hentz)	Beating	0	0	0	0	0	0	0	0	1	1

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 8. (continued)

B. Summary for Beech Gap Forest

	Method	1995	1995	1996	1996	1997	1997	Tot
# Families	All	--	7	10	10	11	11	12
# Genera	All	--	20	31	28	30	31	50
	Aerial	--	7	12	9	12	10	25
	Ground	--	8	15	12	18	14	24
	Beating	--	11	12	15	14	15	31
	Litter	--	5	11	9	17	12	21
# Species (# Morphosp.)	All	--	22	35(1)	32	36(1)	36	58(1)
	Aerial	--	8	13	11	13	43	28
	Ground	--	9	16	15	22	17	30
	Beating	--	12	14	18	16	19	36
	Litter	--	5	13	10	20	13	25

Table 9. Species list and species totals (by method) collected from Meadow Branch Marsh/Meadow

A. Spider species and their abundances

Family	*Species*	Method	6/95		5/96		8/96		5/97		7/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Cicurina arcuata* Keyserling	Litter	2	2	0	0	0	0	0	0	0	0
Antrodiaetidae	*Antrodiaetus unicolor* (Hentz)	Litter	0	0	0	0	1	1	0	0	0	0
Anyphaenidae	*Anyphaena pectorosa* L. Koch	Sweep	0	0	0	0	1	1	0	0	0	0
	Teudis mordax (O.P.-Cambridge)	Aerial	0	0	0	0	0	0	0	0	1	1
Araneidae	*Acanthepeira cherokee* Levi	Aerial	0	0	0	0	0	0	1	1	0	0
		Ground	0	0	0	0	0	0	0	0	4	1
		Sweep	0	0	0	0	0	0	1	1	0	0
	Araneus bicentenarius (McCook)	Aerial	1	1	0	0	0	0	0	0	4	4
	Araneus iviei (Archer)	Aerial	0	0	1	0	0	0	0	0	0	0
		Ground	0	0	1	0	0	0	1	0	0	0
		Sweep	1	1	5	0	0	0	2	0	0	0
	Araneus marmoreus Clerck	Aerial	0	0	0	0	1	0	0	0	2	0
		Ground	0	0	0	0	0	0	0	0	1	0
		Sweep	0	0	0	0	1	0	0	0	1	0
	Araneus miniatus (Walckenaer)	Aerial	0	0	0	0	0	0	2	2	0	0
	Araneus nordmanni (Thorell)	Sweep	0	0	1	0	0	0	0	0	0	0
	Araneus pratensis (Emerton)	Sweep	0	0	0	0	0	0	1	1	0	0
	Araniella diplicata (Hentz)	Sweep	0	0	0	0	0	0	1	1	0	0
	Arctosa virgo (Chamberlin)	Ground	0	0	2	2	0	0	0	0	0	0
	Argiope aurantia Lucas	Aerial	0	0	0	0	2	1	0	0	0	0
	Cyclosa turbinata (Walckenaer)	Aerial	0	0	0	0	0	0	2	2	0	0
	Eustala anastera (Walckenaer)	Aerial	1	1	0	0	0	0	0	0	0	0
	Gea heptagon (Hentz)	Ground	1	1	0	0	0	0	1	1	0	0
		Sweep	0	0	0	0	0	0	1	1	0	0
	Mangora maculata (Keyserling)	Aerial	0	0	0	0	3	3	0	0	0	0
		Ground	0	0	0	0	0	0	0	0	1	0
		Sweep	0	0	0	0	12	12	0	0	2	0
	Mangora placida (Hentz)	Aerial	0	0	3	3	0	0	6	6	0	0
		Ground	0	0	0	0	0	0	1	1	0	0
		Sweep	0	0	1	1	2	2	4	3	0	0
	Micrathena gracilis (Walckenaer)	Aerial	0	0	0	0	2	2	0	0	0	0
	Micrathena mitrata (Hentz)	Aerial	0	0	0	0	7	0	0	0	0	0
		Sweep	0	0	0	0	2	0	0	0	0	0
Clubionidae	*Clubiona abbotii* L. Koch	Ground	0	0	0	0	1	1	0	0	0	0
		Litter	2	2	0	0	0	0	0	0	0	0
		Sweep	3	3	2	2	7	7	3	3	9	9
	Clubiona obesa Hentz	Sweep	0	0	0	0	0	0	3	3	0	0
	Trechelas similis F.O.P.-Cambridge	Aerial	0	0	0	0	0	0	1	1	0	0
Ctenidae	*Anahita punctulata* (Hentz)	Ground	0	0	1	1	9	0	5	5	0	0
		Litter	0	0	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	0	0	0	0	1	1
Dictynidae	*Dictyna roscida* Hentz	Aerial	0	0	1	1	0	0	0	0	0	0
		Sweep	0	0	0	0	0	0	1	1	0	0
Gnaphosidae	*Castianeira longipalpus* (Hentz)	Ground	0	0	1	1	0	0	0	0	0	0
	Drassyllus eremitus Chamberlin	Litter	0	0	0	0	0	0	1	1	0	0
	Drassyllus novus (Banks)	Ground	0	0	1	1	0	0	2	2	0	0
	Drasyllus fallens Chamberlin	Litter	1	1	0	0	0	0	0	0	0	0
	Gnaphosa fontinalis Keyserling	Litter	0	0	0	0	0	0	1	1	0	0
Hahniidae	*Neoantistea agilis* (Keyserling)	Ground	0	0	11	11	0	0	7	7	0	0
Linyphiidae	*Bathyphantes pallidus* (Banks)	Ground	2	2	0	0	3	3	2	2	3	3
		Sweep	0	0	0	0	0	0	0	0	1	1
	Centromerus denticulatus (Emerton)	Litter	2	2	0	0	0	0	0	0	0	0

Table 9. (continued)

Family	*Species*	Method	6/95		5/96		8/96		5/97		7/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Ceraticelus fastidiosus Crosby & Bishop	Ground	1	1	0	0	1	1	1	1	1	1
		Litter	2	2	2	2	2	2	0	0	6	6
		Sweep	11	11	31	31	13	13	2	2	66	66
	Eperigone maculata (Banks)	Litter	0	0	2	2	1	1	0	0	0	0
	Erigone autumnalis Emerton	Sweep	0	0	0	0	1	1	0	0	0	0
	Erigoninae morphospecies L	Litter	0	0	0	0	0	0	0	0	3	3
	Erigoninae morphospecies M	Ground	0	0	0	0	1	1	0	0	0	0
	Floricomus nr. praedesignatus Bishop&Crosby	Litter	6	6	0	0	0	0	0	0	0	0
	Frontinella pyramitela (Walckenaer)	Aerial	0	0	0	0	1	0	3	3	3	2
		Ground	0	0	0	0	0	0	0	0	1	1
		Sweep	0	0	0	0	0	0	1	1	0	0
	Graphomoa theridioides Chamberlin	Ground	1	1	0	0	2	2	0	0	4	4
	Lepthyphantes zebra (Emerton)	Litter	1	1	0	0	0	0	0	0	0	0
	Meioneta angulata (Emerton)	Litter	5	5	0	0	0	0	0	0	0	0
	Meioneta micaria (Emerton)	Ground	0	0	1	1	3	3	1	1	0	0
		Sweep	0	0	0	0	0	0	1	1	0	0
	Neriene clathrata (Sundevall)	Ground	1	1	3	1	10	4	11	9	4	3
		Sweep	0	0	1	1	0	0	0	0	0	0
	Neriene redacta Chamberlin	Ground	1	1	0	0	0	0	0	0	0	0
	Neriene variabilis (Banks)	Ground	2	2	4	2	6	3	1	1	13	0
		Sweep	0	0	3	2	1	1	0	0	2	2
	Pitiohyphantes costatus (Hentz)	Aerial	0	0	1	1	0	0	0	0	0	0
	Walckenaer*ia pallida* (Emerton)	Ground	1	1	0	0	0	0	0	0	0	0
Liocranidae	*Phrurotimpus alarius* (Hentz)	Ground	0	0	3	3	2	2	0	0	1	1
		Litter	1	1	3	3	0	0	3	3	0	0
	Phrurotimpus borealis (Emerton)	Ground	4	4	2	2	2	2	0	0	0	0
		Litter	1	1	0	0	0	0	0	0	0	0
Lycosidae	*Hogna helluo* (Walckenaer)	Ground	0	0	1	1	0	0	0	0	0	0
	Hogna punctulata (Hentz)	Ground	0	0	1	1	0	0	1	0	0	0
	Hogna sp.	Ground	0	0	0	0	0	0	0	0	1	1
	Pardosa milvina (Hentz)	Ground	0	0	0	0	1	1	14	9	1	1
	Pardosa saxatilis (Hentz)	Ground	0	0	0	0	0	0	1	1	0	0
	Pirata insularis Emerton	Ground	28	28	11	11	14	14	66	38	38	30
		Litter	2	2	0	0	0	0	0	0	0	0
	Rabidosa rabida (Walckenaer)	Ground	1	1	0	0	0	0	0	0	1	0
	Schizocosa ocreata (Hentz)	Ground	2	2	13	13	7	7	14	10	1	1
		Litter	1	1	0	0	0	0	0	0	0	0
		Sweep	0	0	0	0	1	1	0	0	1	1
	Schizocosa saltatrix (Hentz)	Ground	0	0	0	0	0	0	0	0	1	1
	Trabeops aurantiaca (Emerton)	Ground	0	0	9	9	1	1	4	4	4	4
		Litter	4	4	0	0	0	0	0	0	0	0
	Varacosa avara (Keyserling)	Sweep	0	0	1	1	0	0	0	0	0	0
	Oxyopes aglossus Chamberlin	Sweep	4	4	0	0	0	0	1	1	0	0
Oxyopidae		Sweep	0	0	1	1	0	0	0	0	0	0
	Oxyopes salticus Hentz	Sweep	2	2	0	0	0	0	0	0	0	0
Philodromidae	*Philodromus minutus* Banks	Aerial	0	0	1	1	0	0	0	0	0	0
Pisauridae	*Dolomedes vittatus* Walckenaer	Ground	1	0	0	0	0	0	1	0	1	1
	Pisaurina mira (Walckenaer)	Aerial	1	1	3	0	0	0	0	0	7	2
		Ground	2	2	6	3	6	0	6	1	0	0
		Sweep	1	1	43	1	54	2	44	1	45	2

Table 9. (continued)

Family	*Species*	Method	6/95		5/96		8/96		5/97		7/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Salticidae	*Eris aurantia* (Lucas)	Sweep	2	2	0	0	0	0	0	0	0	0
	Eris marginata (Walckenaer)	Aerial	0	0	0	0	0	0	1	1	0	0
		Sweep	0	0	0	0	0	0	1	1	0	0
	Habrocestum parvulum (Banks)	Ground	0	0	2	2	2	2	0	0	0	0
		Litter	0	0	1	1	0	0	1	1	2	2
		Sweep	0	0	0	0	0	0	0	0	1	1
	Habrocestum pulex (Hentz)	Sweep	1	1	0	0	0	0	0	0	0	0
	Maevia inclemens (Walckenaer)	Ground	0	0	0	0	1	0	1	1	0	0
		Litter	0	0	0	0	0	0	1	1	2	2
		Sweep	7	6	7	7	15	4	14	14	10	7
	Marpissa formosa (Banks)	Sweep	0	0	0	0	0	0	0	0	1	1
	Neon nellii Peckham	Litter	0	0	1	1	0	0	0	0	0	0
	Pelegrina exigua (Banks)	Sweep	0	0	0	0	0	0	6	4	1	1
	Pelegrina galathea (Walckenaer)	Sweep	0	0	0	0	0	0	1	1	0	0
	Pelegrina proterva (Walckenaer)	Sweep	3	3	2	2	1	1	3	3	1	1
	Pelegrina morphospecies A	Sweep	0	0	0	0	1	1	0	0	0	0
	Phidippus insignarius C.L. Koch	Ground	1	1	0	0	0	0	0	0	0	0
	Phidippus princeps (Peckham)	Aerial	1	1	0	0	0	0	0	0	0	0
		Ground	1	1	0	0	0	0	0	0	0	0
		Sweep	4	4	1	1	0	0	0	0	1	1
	Phidippus whitmani Peckham & Peckham	Sweep	0	0	0	0	0	0	0	0	1	1
	Salticidae sp. A	Litter	1	1	0	0	0	0	0	0	0	0
	Sitticus palustris (Peckham & Peckham)	Litter	1	1	0	0	0	0	0	0	0	0
		Sweep	0	0	0	0	0	0	0	0	1	1
	Thiodina sylvana (Hentz)	Aerial	0	0	0	0	1	0	0	0	0	0
		Ground	0	0	0	0	1	0	0	0	0	0
		Sweep	0	0	7	7	19	0	6	6	0	0
	Zygoballus bettini Peckham	Ground	1	1	2	2	1	1	1	1	0	0
		Litter	0	0	1	1	0	0	0	0	0	0
		Sweep	9	8	62	61	7	7	26	26	9	9
Segestriidae	*Ariadna bicolor* (Hentz)	Aerial	0	0	1	1	0	0	0	0	1	0
Tetragnathidae	*Leucauge venusta* (Walckenaer)	Aerial	0	0	8	1	0	0	10	0	6	6
		Ground	1	1	1	0	0	0	1	1	1	1
		Sweep	0	0	5	2	0	0	7	0	0	0
	Tetragnatha elongata Walckenaer	Aerial	0	0	0	0	0	0	0	0	1	0
	Tetragnatha laboriosa Hentz	Sweep	0	0	0	0	0	0	2	2	1	0
	Tetragnatha straminea Emerton	Aerial	1	1	0	0	0	0	0	0	1	1
		Ground	2	2	0	0	4	0	0	0	6	3
		Sweep	4	4	27	23	3	0	53	45	3	2
	Tetragnatha versicolor Walckenaer	Aerial	0	0	0	0	0	0	3	2	0	0
		Ground	0	0	0	0	0	0	2	2	4	0
		Sweep	0	0	2	2	2	0	44	38	0	0
Theridiidae	*Pholcomma hirsutum* Emerton	Litter	5	5	0	0	0	0	0	0	1	1
	Theridion albidum Banks	Aerial	0	0	0	0	0	0	0	0	1	1
		Ground	2	2	2	0	3	3	0	0	2	2
		Sweep	7	7	13	0	2	2	0	0	3	3
	Theridion cheimatos Gertsch & Archer	Sweep	0	0	0	0	1	1	0	0	0	0
	Theridion flavonotatum Becker	Aerial	1	1	13	13	1	1	2	2	1	1
	Theridion lyricum Walckenaer	Aerial	0	0	0	0	1	0	0	0	0	0
		Sweep	0	0	0	0	0	0	0	0	1	0
	Theridion neshamini Levi	Aerial	0	0	1	1	0	0	0	0	0	0
		Ground	0	0	1	0	0	0	0	0	0	0

Table 9. (continued)

Family	*Species*	Method	6/95		5/96		8/96		5/97		7/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Theridion pennsylvanicum Emerton	Ground	0	0	2	0	0	0	0	0	0	0
		Litter	1	1	0	0	0	0	0	0	0	0
		Sweep	0	0	1	0	0	0	0	0	0	0
	Theridula opulenta (Walckenaer)	Ground	0	0	0	0	1	1	0	0	1	1
		Sweep	2	2	4	4	7	7	1	1	7	5
	Thymoites unimaculatum (Emerton)	Aerial	0	0	0	0	0	0	1	1	0	0
		Sweep	0	0	0	0	0	0	1	1	0	0
Theridiosomatidae	*Theridiosoma gemmosum* (L. Koch)	Ground	0	0	0	0	0	0	1	0	0	0
		Sweep	0	0	5	5	0	0	1	0	0	0
Thomisidae	*Misumenoides formosipes* (Walckenaer)	Sweep	0	0	0	0	2	0	0	0	0	0
	Misumenops oblongus (Keyserling)	Sweep	0	0	0	0	1	1	0	0	0	0
	Tmarus angulatus (Walckenaer)	Sweep	0	0	0	0	0	0	0	0	1	1
	Xysticus elegans Keyserling	Sweep	0	0	0	0	1	1	0	0	0	0
	Xysticus ferox Hentz	Ground	0	0	2	2	1	1	1	1	0	0
		Litter	0	0	1	1	0	0	0	0	0	0
		Sweep	0	0	0	0	1	1	1	1	4	4
	Xysticus fraternus Banks	Ground	1	1	0	0	0	0	1	1	0	0
		Sweep	1	1	0	0	0	0	0	0	0	0
Uloboridae	*Uloborus glomosus* (Walckenaer)	Ground	0	0	0	0	0	0	0	0	1	1
		Sweep	0	0	1	1	0	0	0	0	0	0
Zoridae	*Zora pumila* (Hentz)	Ground	0	0	0	0	0	0	1	1	0	0

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 9. (continued)

B. Summary for Meadow Branch Marsh/Meadow

	Method	1995	1995	1996	1996	1997	1997	Tot
# Families	All	13	--	18	13	16	14	22
# Genera	All	37	--	39	34	42	37	75
	Aerial	6	--	9	7	11	8	22
	Ground	18	--	19	22	24	21	40
	Sweep	15	--	22	20	24	21	41
	Litter	16	--	7	3	5	6	27
# Species (# Morphosp.)	All	45(1)	--	47	44(1)	52(1)	47(1)	110 (4)
	Aerial	6	--	10	9	11	11	32
	Ground	21	--	24	24	27(1)	24	54(1)
	Sweep	16	--	27	25(1)	29	25	61(1)
	Litter	17(1)	--	7	3	5	6(1)	28(2)

Table 10. Species list and species totals (by method) collected from Hemlock/Hardwood Cove Forest

A. Spider species and their abundances

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Agelenidae	*Agelenopsis utahana* (Chamberlin & Ivie)	Aerial	0	0	7	7	1	0	9	4	2	0	46	27
		Beating	0	0	1	1	0	0	13	5	2	0	57	7
		Ground	0	0	0	0	16	0	5	0	38	0	26	2
	Cicurina arcuata Keyserling	Litter	0	0	0	0	3	3	0	0	1	1	0	0
	Cicurina breviaria Bishop & Crosby	Ground	1	1	0	0	1	1	1	1	0	0	0	0
		Litter	0	0	0	0	0	0	1	1	1	1	1	1
	Cicurina brevis (Emerton)	Ground	0	0	0	0	0	0	1	1	0	0	1	1
		Litter	1	1	0	0	0	0	0	0	0	0	0	0
	Cicurina bryantae Exline	Ground	0	0	1	1	4	4	0	0	1	1	3	3
	Cicurina placida Banks	Ground	0	0	0	0	0	0	0	0	1	1	0	0
	Coras aerialis Muma	Aerial	0	0	0	0	0	0	0	0	1	1	0	0
	Coras montanus (Emerton)	Aerial	0	0	1	1	23	0	5	5	21	1	12	7
		Ground	0	0	0	0	0	0	0	0	0	0	3	2
	Cybaeus patritus Crosby & Bishop	Aerial	0	0	1	1	0	0	0	0	0	0	0	0
		Ground	0	0	1	1	0	0	3	2	0	0	11	8
	Wadotes tennesseensis Gertsch	Aerial	0	0	0	0	0	0	0	0	1	1	0	0
		Ground	1	1	2	2	2	2	2	2	6	6	3	3
		Litter	0	0	1	1	0	0	1	1	1	1	8	6
Amaurobii-dae	*Callioplus pantoplus* Bishop & Crosby	Litter	6	6	0	0	67	67	11	11	53	53	37	37
	Callobius bennetti (Blackwall)	Aerial	1	1	2	0	16	7	24	0	30	13	22	2
		Ground	0	0	0	0	1	1	6	1	8	2	5	3
Antrodiaeti-dae	*Antrodiaetus unicolor* (Hentz)	Ground	0	0	0	0	0	0	0	0	2	0	0	0
		Litter	1	0	0	0	0	0	0	0	5	4	0	0
Araneidae	*Araneus marmoreus* Clerck	Beating	0	0	0	0	1	0	0	0	0	0	0	0
	Araneus miniatus (Walckenaer)	Aerial	0	0	0	0	1	1	4	0	0	0	0	0
		Beating	0	0	0	0	3	3	5	0	8	5	2	0
	Araneus nordmanni (Thorell)	Aerial	0	0	3	3	5	0	3	1	17	5	38	25
		Beating	0	0	5	5	13	0	40	2	47	0	93	12
		Ground	0	0	0	0	0	0	0	0	4	0	4	2
	Cyclosa conica (Pallas)	Aerial	0	0	0	0	2	1	3	0	29	27	1	0
		Beating	0	0	0	0	5	4	8	0	36	30	8	0
		Ground	0	0	0	0	1	0	0	0	0	0	0	0
	Hyposinga rubens (Hentz)	Beating	0	0	0	0	0	0	0	0	1	1	0	0
	Mangora placida (Hentz)	Aerial	0	0	0	0	0	0	0	0	1	1	0	0
		Beating	0	0	0	0	0	0	0	0	5	5	0	0
	Metepeira labyrinthea (Hentz)	Aerial	0	0	0	0	0	0	1	0	0	0	0	0
		Beating	0	0	0	0	0	0	0	0	0	0	1	1
	Micrathena gracilis (Walckenaer)	Aerial	0	0	1	1	0	0	0	0	0	0	0	0
	Micrathena mitrata (Hentz)	Aerial	0	0	0	0	0	0	1	0	0	0	1	0
		Beating	0	0	0	0	0	0	1	0	0	0	0	0
	Ocrepeira ectypa (Walckenaer)	Beating	0	0	0	0	0	0	2	0	2	0	0	0

Table 10. (continued)

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Clubionidae	*Clubiona canadensis* Emerton	Aerial	0	0	0	0	1	1	0	0	0	0	0	0
		Beating	0	0	0	0	2	2	0	0	3	2	0	0
	Clubiona rhododendri Barrows	Beating	2	2	1	1	4	4	1	1	0	0	0	0
	Clubiona spiralis Emerton	Beating	0	0	0	0	7	7	1	1	0	0	0	0
	Clubionoides excepta (L. Koch)	Beating	0	0	0	0	0	0	0	0	2	1	0	0
		Ground	0	0	0	0	0	0	0	0	1	1	0	0
Dictyindae	*Lathys immaculata* Chamberlin & Ivie	Litter	1	1	0	0	1	1	1	1	0	0	0	0
	Dictyna maxima Banks	Aerial	0	0	0	0	0	0	0	0	1	1	1	1
		Beating	0	0	0	0	17	17	35	0	38	21	25	0
		Ground	0	0	0	0	0	0	0	0	1	1	0	0
		Litter	0	0	0	0	0	0	0	0	1	1	0	0
Gnaphosidae	*Herpyllus ecclesiasticus* Hentz	Ground	0	0	0	0	0	0	0	0	1	1	0	0
Hahniidae	*Calymmaria persica* (Hentz)	Ground	0	0	0	0	3	3	3	3	5	5	0	0
	Calymmaria morphospecies A	Ground	0	0	3	3	0	0	0	0	0	0	0	0
	Cryphoeca montana Emerton	Ground	0	0	0	0	1	1	0	0	0	0	1	1
	Neoantistea magna (Keyserling)	Ground	0	0	0	0	0	0	0	0	0	0	2	2
		Litter	1	1	0	0	2	2	1	1	2	2	1	1
Hypochilidae	*Hypochilus pococki* Platnick	Aerial	0	0	0	0	1	0	7	0	1	0	9	1
		Ground	0	0	1	1	3	0	6	2	3	0	20	9
Leptonetidae	*Leptoneta coma* Barrows	Litter	0	0	0	0	1	1	1	1	1	1	4	4
	Leptoneta silvicultrix Crosby & Bishop	Ground	0	0	0	0	1	1	0	0	0	0	0	0
		Litter	6	6	0	0	9	9	11	11	7	7	5	5
	Leptoneta morphospecies A	Litter	0	0	0	0	13	13	18	18	4	4	0	0
Linyphiidae	*Bathyphantes bishopi* Ivie	Aerial	0	0	0	0	0	0	1	1	0	0	0	0
		Beating	0	0	0	0	1	1	0	0	0	0	0	0
		Ground	0	0	2	2	13	13	7	7	8	8	3	3
		Litter	0	0	0	0	1	1	0	0	0	0	0	0
	Centromerus denticulatus (Emerton)	Litter	0	0	0	0	38	38	0	0	2	2	8	8
	Centromerus tennapax (Barrows)	Ground	0	0	0	0	1	1	0	0	0	0	0	0
		Litter	0	0	1	1	1	1	1	1	0	0	0	0
	Ceraticelus alticeps (Fox)	Beating	0	0	0	0	1	1	1	1	1	1	1	1
	Ceraticelus carinatus (Emerton)	Litter	1	1	0	0	5	5	4	4	3	3	14	14
	Ceraticelus Emertoni (O.P.-Cambridge)	Beating	0	0	0	0	0	0	0	0	1	1	0	0
	Ceratinops carolinus (Banks)	Litter	0	0	0	0	0	0	0	0	3	3	1	1
	Ceratinopsidis formosa (Banks)	Beating	0	0	1	1	0	0	0	0	0	0	0	0
	Collinsia oxypaederotipus (Crosby)	Aerial	0	0	0	0	1	1	0	0	0	0	0	0
		Ground	0	0	0	0	0	0	0	0	1	1	0	0
		Litter	21	21	0	0	158	158	9	9	231	231	8	8

Table 10. (continued)

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Erigone autumnalis Emerton	Beating	0	0	0	0	0	0	1	1	0	0	0	0
	Erigone maculata (Banks)	Litter	1	1	0	0	0	0	0	0	0	0	0	0
	Erigoninae morphospecies X	Litter	0	0	0	0	0	0	0	0	1	1	0	0
	Erigoninae morphospecies Y	Litter	0	0	0	0	0	0	0	0	1	1	0	0
	Floricomus tallulae Chamberlin & Ivie	Litter	2	2	0	0	0	0	0	0	0	0	0	0
	Frontinella pyramitela (Walckenaer)	Aerial	0	0	0	0	0	0	1	1	0	0	0	0
	Grammonota pictilis (O.P.-Cambridge)	Aerial	0	0	0	0	0	0	0	0	1	1	0	0
		Beating	2	2	0	0	28	28	4	1	60	54	1	1
		Ground	0	0	0	0	1	1	0	0	0	0	0	0
	Horcotes uncinatus Barrows	Litter	0	0	0	0	0	0	1	1	0	0	0	0
	Lepthyphantes turbatrix (O.P.-Cambridge)	Aerial	0	0	1	1	0	0	4	4	0	0	3	2
	Lepthyphantes zebra (Emerton)	Aerial	0	0	0	0	0	0	1	1	0	0	0	0
		Ground	0	0	1	1	14	14	3	2	8	8	2	2
		Litter	0	0	0	0	1	1	0	0	2	2	1	1
	Maso sundevallii (Westring)	Litter	0	0	0	0	0	0	0	0	3	3	0	0
	Meioneta micaria (Emerton)	Beating	0	0	0	0	0	0	0	0	1	1	0	0
	Meioneta morphospecies A	Litter	1	1	0	0	2	2	0	0	3	3	0	0
	Neriene radiata (Walckenaer)	Aerial	12	12	3	3	45	18	25	8	162	9	48	29
		Beating	3	3	1	1	20	7	34	3	140	20	153	16
		Ground	2	2	1	1	45	13	50	10	138	22	46	29
	Pitiohyphantes costatus (Hentz)	Aerial	3	3	0	0	23	22	19	0	84	84	34	0
		Beating	1	1	0	0	19	19	59	0	81	79	152	1
		Ground	0	0	0	0	6	6	2	1	29	29	0	0
	Pocadicnemis americana Millidge	Beating	0	0	0	0	1	1	0	0	0	0	0	0
		Litter	0	0	0	0	1	1	0	0	2	2	0	0
	Tapinopa bilineata Banks	Ground	0	0	1	1	0	0	0	0	0	0	0	0
	Taranucnus ornithes (Barrows)	Aerial	0	0	0	0	0	0	1	1	0	0	0	0
		Ground	0	0	0	0	3	3	1	1	1	1	1	1
		Litter	0	0	0	0	1	1	0	0	0	0	0	0
	Walckenaeria *spiralis* (Emerton)	Litter	2	2	0	0	0	0	0	0	0	0	0	0

Table 10. (continued)

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Liocranidae	*Phrurotimpus borealis* (Emerton)	Aerial	0	0	0	0	0	0	1	1	0	0	0	0
		Ground	0	0	0	0	1	1	0	0	0	0	0	0
		Litter	0	0	0	0	0	0	0	0	7	7	0	0
	Scotinella redempta (Gertsch)	Beating	0	0	0	0	0	0	0	0	0	0	1	1
		Ground	0	0	0	0	0	0	1	1	0	0	0	0
		Litter	0	0	1	1	3	3	3	3	12	12	13	9
Lycosidae	*Pirata montanus* Emerton	Aerial	0	0	0	0	1	1	0	0	0	0	0	0
		Ground	2	2	1	1	69	69	5	5	116	116	11	11
		Litter	0	0	0	0	6	6	2	2	7	7	2	2
Miturgidae	*Strotarchus piscatorius* (Hentz)	Aerial	0	0	0	0	0	0	0	0	1	0	0	0
Nesticidae	*Nesticus reclusus* Gertsch	Ground	4	4	4	4	1	1	1	1	1	1	1	1
		Litter	0	0	0	0	0	0	0	0	1	1	2	2
Philodromi-dae	*Philodromus montanus* Bryant	Beating	0	0	0	0	0	0	0	0	1	1	0	0
	Philodromus rufus Walckenaer	Aerial	0	0	0	0	0	0	0	0	0	0	1	1
		Beating	4	4	0	0	3	2	59	5	27	0	8	5
Salticidae	*Habrocestum parvulum* (Banks)	Ground	0	0	1	1	3	3	1	1	4	4	0	0
		Litter	0	0	1	1	1	1	3	3	0	0	1	1
	Habrocestum pulex (Hentz)	Aerial	0	0	0	0	2	2	0	0	1	1	0	0
		Beating	0	0	0	0	1	1	0	0	0	0	0	0
		Ground	0	0	0	0	2	2	0	0	1	1	0	0
	Hentzia *mitrata* (Hentz)	Beating	0	0	0	0	0	0	0	0	5	1	0	0
	Maevia inclemens (Walckenaer)	Beating	0	0	0	0	0	0	1	0	0	0	0	0
	Metaphidippus canadensis (Banks)	Litter	0	0	0	0	0	0	0	0	0	0	5	5
	Neon nellii Peckham	Litter	0	0	0	0	5	5	0	0	1	1	1	1
	Pelegrina flavipedes (Peckham & Peckham)	Beating	1	1	8	8	22	22	18	5	26	26	5	5
	Pelegrina proterva (Walckenaer)	Beating	0	0	0	0	0	0	0	0	1	1	0	0
Segestriidae	*Ariadna bicolor* (Hentz)	Aerial	0	0	1	1	1	1	0	0	6	1	2	0

Table 10. (continued)

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
Tetragnathidae	*Leucauge venusta* (Walckenaer)	Aerial	1	1	5	5	9	0	2	2	16	0	8	7
		Beating	4	4	0	0	5	0	3	3	20	0	1	1
		Ground	1	1	1	1	1	0	1	1	4	0	2	2
	Meta menardi (Latreille)	Aerial	0	0	0	0	10	0	0	0	1	0	1	1
		Beating	0	0	0	0	0	0	0	0	7	0	0	0
		Ground	0	0	1	1	29	0	9	2	33	0	30	2
	Tetragnatha versicolor Walckenaer	Aerial	0	0	0	0	1	0	2	0	4	0	1	0
		Beating	0	0	0	0	18	8	33	0	58	1	67	3
		Ground	0	0	0	0	0	0	1	0	1	0	0	0
	Tetragnatha viridis Walckenaer	Beating	0	0	0	0	1	1	1	0	0	0	3	1
Theridiidae	*Achaearanea rupicola* (Emerton)	Aerial	0	0	0	0	0	0	4	4	0	0	3	3
		Ground	0	0	0	0	0	0	5	5	0	0	7	7
	Argyrodes trigonum (Hentz)	Aerial	0	0	1	1	0	0	7	7	0	0	2	2
		Beating	1	1	1	1	2	0	2	2	6	0	1	1
		Ground	0	0	0	0	1	1	4	2	0	0	0	0
	Episinus amoenus Banks	Beating	0	0	0	0	3	3	0	0	3	0	0	0
		Ground	0	0	0	0	0	0	0	0	2	0	0	0
	Pholcomma barnesi Levi	Litter	0	0	0	0	2	2	0	0	5	5	1	1
	Pholcomma hirsutum Emerton	Litter	0	0	0	0	2	2	1	1	0	0	0	0
	Phoroncidia americana (Emerton)	Ground	0	0	0	0	0	0	1	1	0	0	0	0
	Robertus frontatus (Banks)	Ground	0	0	0	0	0	0	0	0	1	1	0	0
		Litter	0	0	0	0	12	12	0	0	3	3	13	13
	Spintharus flavidus Hentz	Aerial	0	0	0	0	0	0	1	0	0	0	1	0
		Beating	0	0	1	1	0	0	11	0	0	0	17	0
		Ground	0	0	0	0	0	0	0	0	0	0	1	0
	Theridiidae morphospecies A2	Litter	0	0	0	0	0	0	1	1	0	0	0	0
	Theridiidae morphospecies A1	Litter	0	0	0	0	9	9	0	0	1	1	3	3
	Theridion albidum Banks	Aerial	0	0	0	0	0	0	1	1	1	0	0	0
		Beating	2	2	0	0	1	1	1	1	2	0	0	0
	Theridion differens Emerton	Aerial	0	0	0	0	0	0	1	1	1	0	1	1
		Beating	1	1	0	0	7	0	1	1	4	0	6	6
		Ground	0	0	0	0	0	0	0	0	2	1	0	0

Table 10. (continued)

Family	Species	Method	6/95		8/95		5/96		8/96		5/97		8/97	
			Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad	Tot	Ad
	Theridion frondeum (Hentz)	Aerial	0	0	0	0	1	1	0	0	0	0	2	1
		Beating	2	2	0	0	20	0	1	1	21	0	2	2
		Ground	0	0	0	0	0	0	0	0	1	0	1	1
	Theridion glaucescens Becker	Beating	1	1	0	0	0	0	0	0	0	0	0	0
	Theridion lyricum Walckenaer	Aerial	0	0	0	0	2	2	1	0	0	0	0	0
		Beating	0	0	0	0	5	0	3	2	1	0	0	0
	Theridion neshamini Levi	Beating	0	0	0	0	0	0	0	0	0	0	1	0
Theridiosomatidae	*Theridiosoma gemmosum* (L. Koch)	Aerial	2	2	0	0	6	4	1	1	4	2	1	1
		Beating	7	7	0	0	16	11	1	1	7	1	6	6
		Ground	8	8	0	0	38	17	12	6	46	14	14	12
Uloboridae	*Hyptiotes cavatus* (Hentz)	Aerial	0	0	8	8	0	0	30	1	0	0	51	0
		Beating	0	0	37	37	0	0	107	20	0	0	337	0
		Ground	0	0	1	1	0	0	5	1	0	0	2	0

Notes. Specimens which are named 'Genus sp.' refer to juvenile specimens which could not be assigned to species. Specimens which are named 'Genus morphospecies X' refer to adult individuals for which a species designation could not be found.

Table 10. (continued)

B. Summary for Hemlock/Hardwood Cove Forest

	Method	1995	1995	1996	1996	1997	1997	Tot
# Families	All	15	15	19	19	21	18	23
# Genera	All	26	28	46	51	55	47	73
	Aerial	5	12	18	23	20	22	36
	Ground	7	15	24	24	27	23	43
	Beating	10	9	19	22	24	19	35
	Litter	12	4	20	15	24	19	33
# Species (# Morphosp.)	All	30(1)	29(1)	62(3)	62(2)	72(5)	57(1)	104(7)
	Aerial	5	12	20	27	22	23	43
	Ground	7	15(1)	26	25	30	24	49(1)
	Beating	13	9	27	28	31	24	48
	Litter	12(1)	4	24(3)	17(2)	28(5)	20(1)	41(6)

1995, 1996, and 1997 (Figures 3, 5). Although the shape of the curves varied between sites, most sites showed consistent patterns of yields for all three years. Minor differences in results probably reflected differing weather conditions and their influence upon spider mobility. Note, however, that the Hardwood Forest site (Figure 5) displays yields that varied greatly from year to year. In order to see if the curves reached an asymptote after all the collection had been completed, I did the same plots, only with all collecting years combined (Figures 4, 6). The only sites appearing to approach an asymptote are Beech Forest and Hardwood Forest.

Abundance Distributions

All the collection data indicated somewhat skewed distributional species abundance, with few common species and many rare species. See Figure 7 for representative plots of abundance vs. number of species. This graphed pattern is typical for most animal groups (Williams 1964). To more accurately compare the abundance distributions of the sites, both with each other and with existing abundance models, I made rank abundance plots with abundance expressed as a percentage of the yearly site total (Figure 8 and Figure 9). I compared these plots with the typical shape expected for the four types of species abundance: geometric series, log series, log normal and broken stick models (Figure 10). These statistical models represent points along a continuum from one extreme situation in which few species dominate and have pre-empted a large portion of the available niche "space" (Southwood 1978), graded toward another extreme in which resources are quite equally (equably) divided among the species in the assemblage. Therefore, an assemblage resembling the geometric series distribution will have very low evenness or equitability, while an assemblage resembling the broken stick model will have a high degree of evenness (Figure 10).

Figure 3. Total number of individuals versus cumulative number of species after randomization of samples using the program EstimateS (Colwell, unpublished) for the 1996 surveys (squares) in Macon County. Data from 1995 and 1997 are plotted similarly and are represented by circles and diamonds, respectively. All three Macon Co. sites are represented in (A) Ellicott Clear-cut, (B) Horse Clear-cut and (C) Ellicott Forest. In (A) and (C), 1996 and 1997 had a more intensive sampling regime than in 1995 and therefore more individuals were collected.

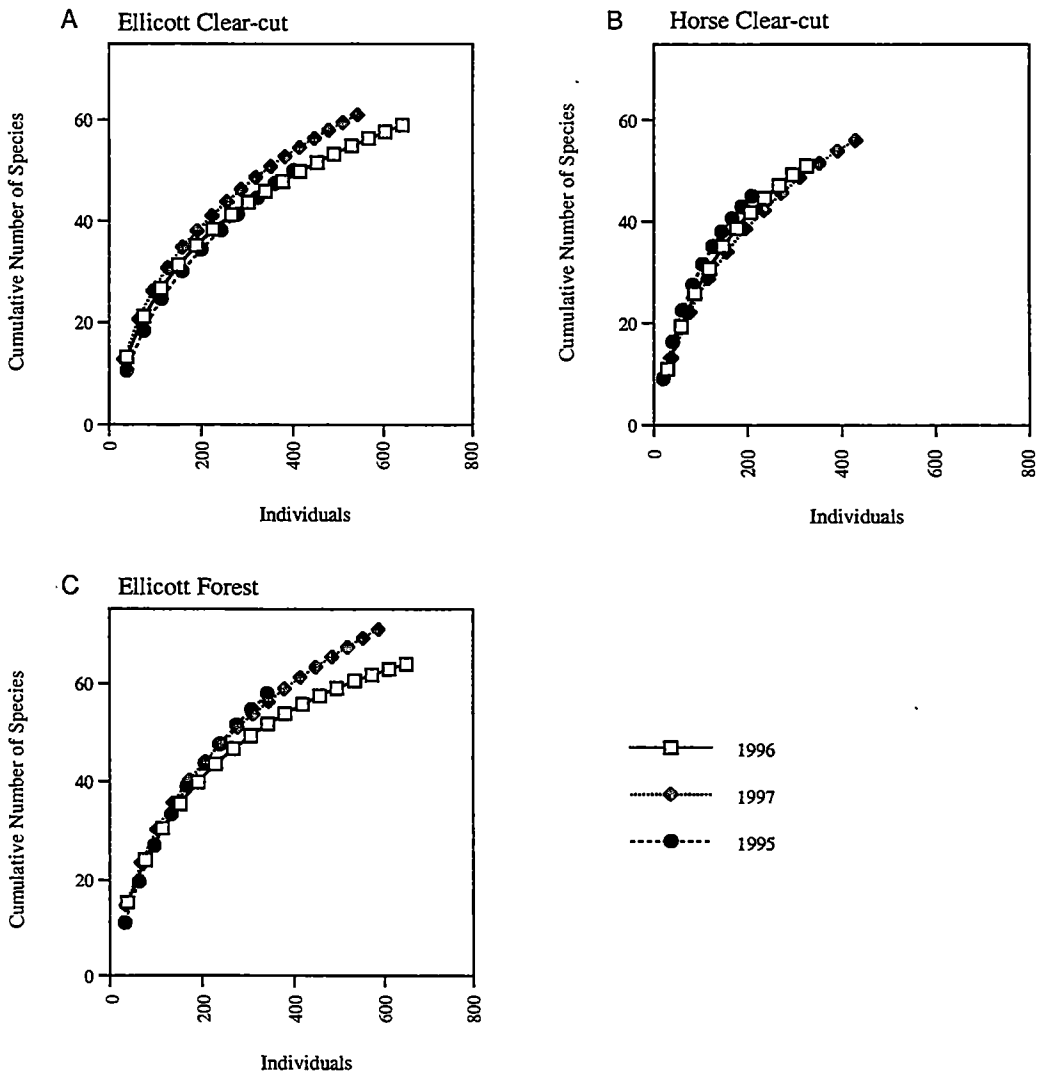


Figure 4. Mean number of observed species versus cumulative number of individuals, after randomization of samples using the program EstimateS (Colwell, unpublished) for sites in Macon County. In (A) Ellicott Clear-cut and (B) Horse Clear-cut, data from the modern surveys (1995-1997) were pooled. Data from 1976 were not included in the sample, as these sites have undergone drastic changes in vegetation structure since that time due to secondary succession. Therefore, pooling of data from these sites was deemed inappropriate, as many of the species which existed in 1976 could no longer exist in the altered habitat. In (C), data from all surveys (1976; 1995-1997) were pooled.

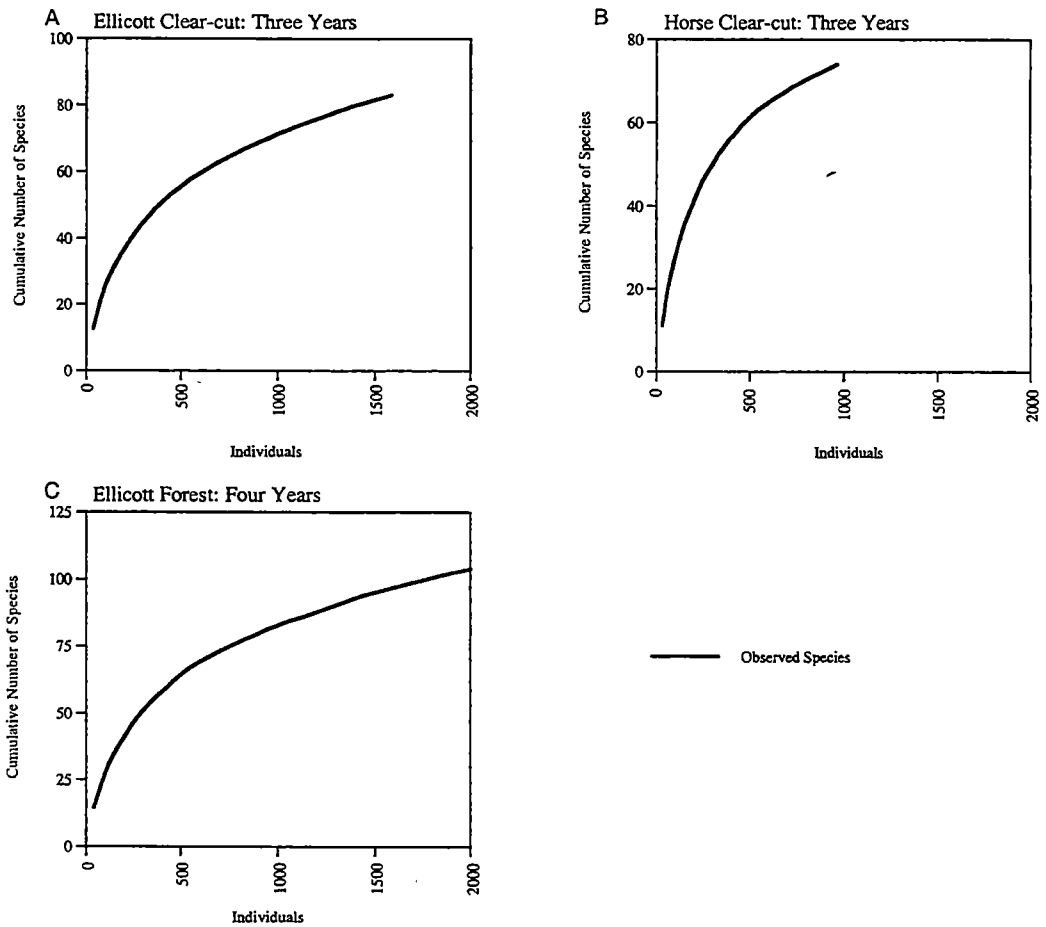


Figure 5. Mean number of individuals collected versus cumulative number of species, after randomization of samples using the program EstimateS (Colwell, unpublished) for sites in the GSMNP. For (A) and (B), squares represent data from the early summer collection of 1996, diamonds represent data from the early summer collection of 1997, circles represent data from the late summer collection of 1996 and triangles represent data from the late summer collection of 1997. In (C), squares and triangles represent data from the early summer collections of 1997 and 1996, respectively. Diamonds and circles represent data from the late summer collections of 1996 and 1997, respectively.

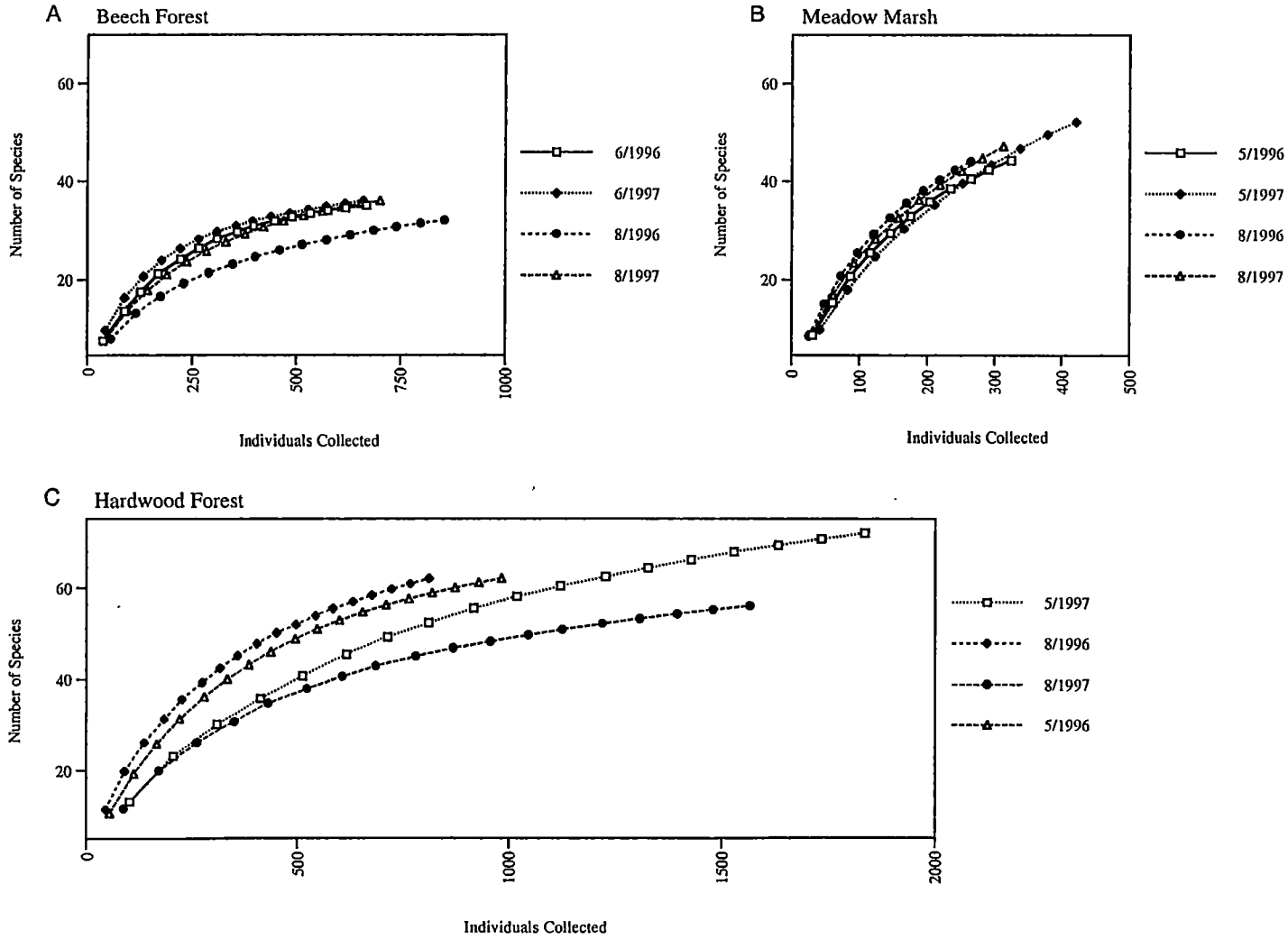

A
Beech Forest
Number of Species
60
40
20
0
250
500
750
1000
Individuals Collected
6/1996
6/1997
8/1996
8/1997
B
Meadow Marsh
Number of Species
60
40
20
0
100
200
300
400
500
Individuals Collected
5/1996
5/1997
8/1996
8/1997
C
Hardwood Forest
Number of Species
60
40
20
0
500
1000
1500
2000
Individuals Collected
5/1997
8/1996
8/1997
5/1996

Figure 6. Mean number of individuals collected versus cumulative number of species, after randomization of all samples (all years) using the program EstimateS (Colwell, unpublished) for sites in the GSMNP. Data from all three years of surveys were pooled prior to randomization for all three sites.

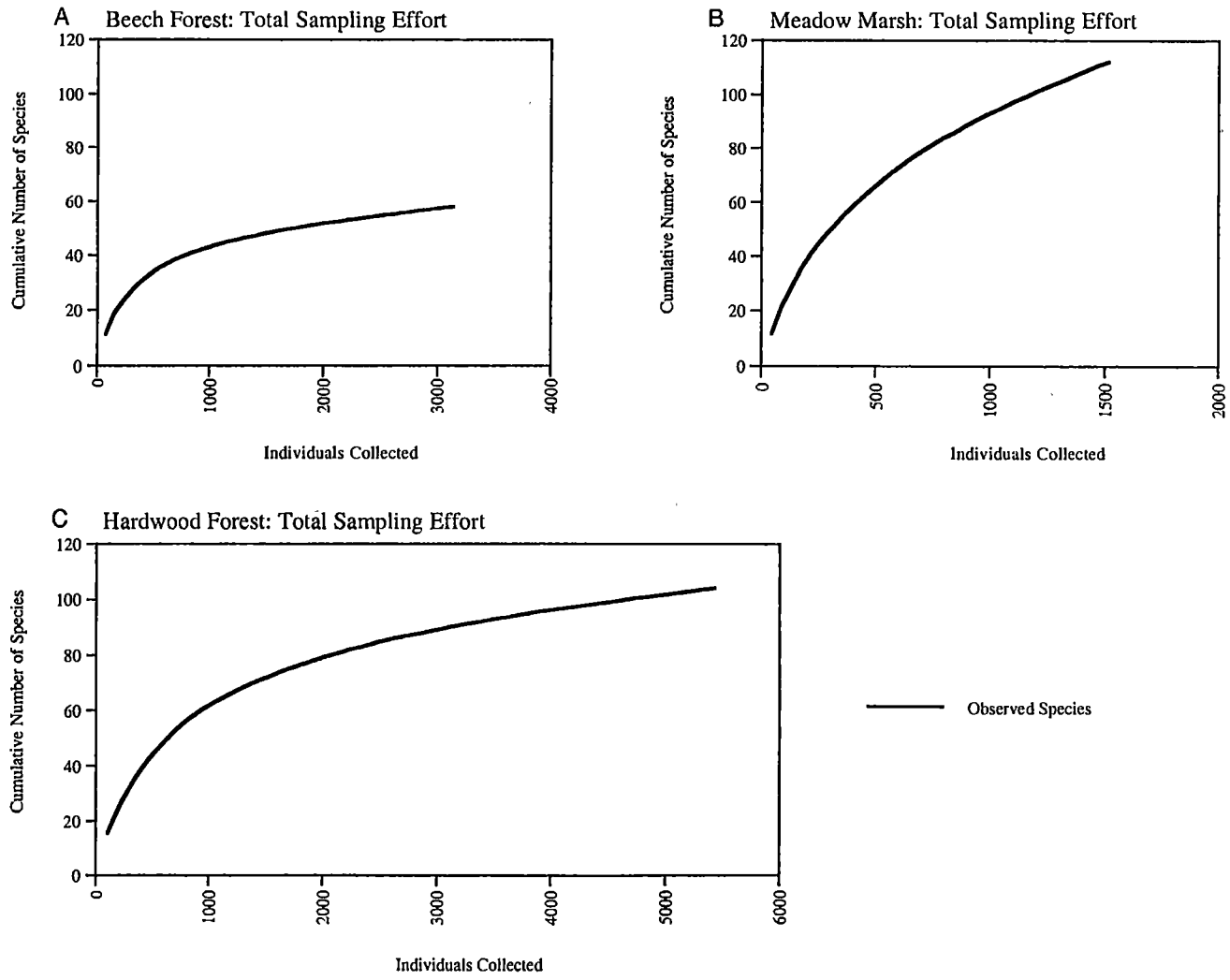
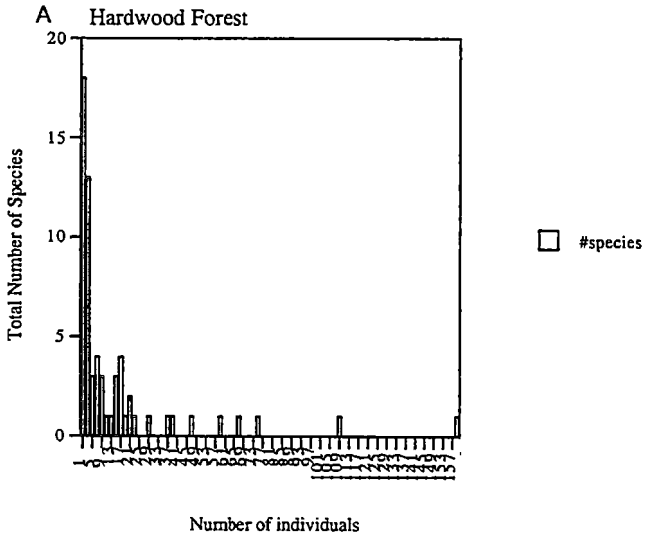

A
Beech Forest: Total Sampling Effort
Cumulative Number of Species
0
20
40
60
80
100
120
0
1000
2000
3000
4000
Individuals Collected
B
Meadow Marsh: Total Sampling Effort
Cumulative Number of Species
0
20
40
60
80
100
120
0
500
1000
1500
2000
Individuals Collected
C
Hardwood Forest: Total Sampling Effort
Cumulative Number of Species
0
20
40
60
80
100
120
0
1000
2000
3000
4000
5000
6000
Individuals Collected
Observed Species

Figure 7. Typical raw abundance plots for each study area (number of species represented by set numbers of individuals). (A) is an abundance plot of the raw data from Hardwood forest. The number of species represented by each category of individuals collected (in this case, 4) is represented by the open bars. (B) is the same, but based on data from Ellicott Forest.



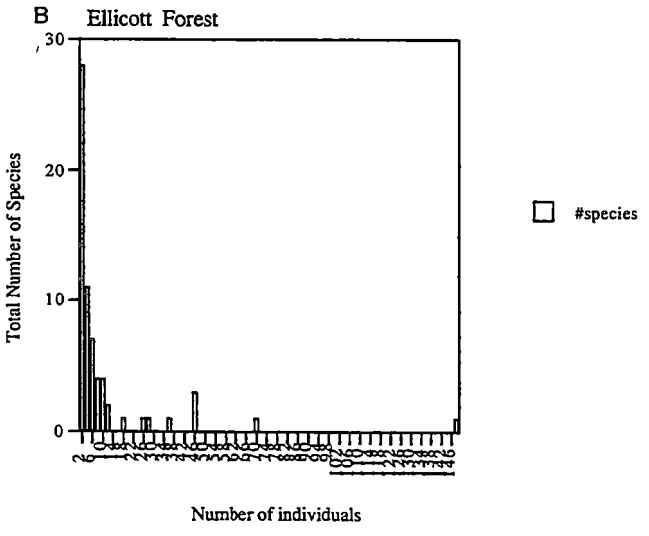


Figure 8. Rank abundance distribution of species collected in 1996 (dashed lines) for Ellicott Forest (A), Ellicott Clear-cut (B), and Horse Clear-cut (C). Solid lines represent the rank abundance distribution of species collected in 1995 for these same sites. The y-axis is the abundance of the species measured as a percent, plotted on a logarithmic scale. The x-axis ranks the species from the most to the least abundant. The least abundant species are always singletons.

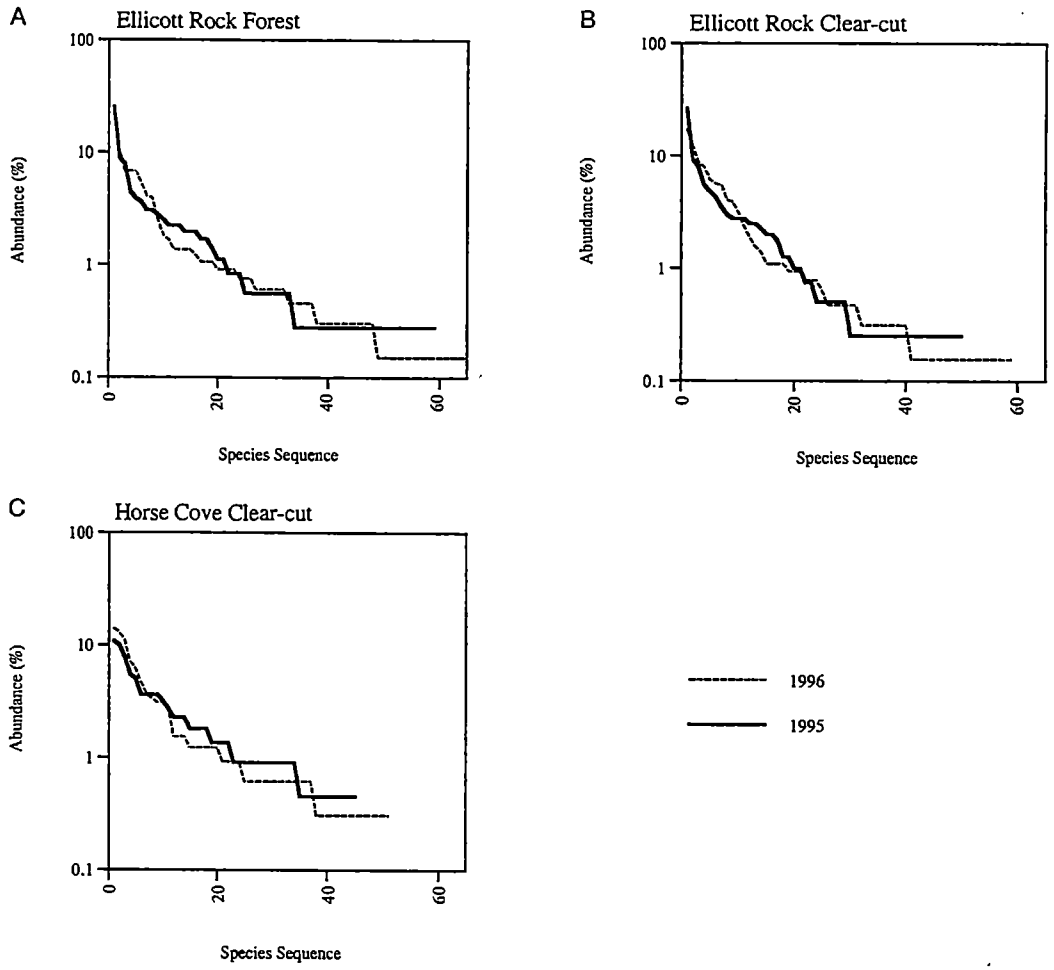


Figure 9. Rank abundance distribution of species collected in 1995 (dashed lines) for Beech Forest (A), Hardwood Forest (B), and Meadow Marsh (C). Solid lines represent the rank abundance distribution of species collected in a larger sample taken in the same month as the 1995 survey, only in 1996 (A) or in 1997 (B and C). The y-axis is the abundance of the species measured as a percent, plotted on a logarithmic scale. The x-axis ranks the species from the most to the least abundant. The least abundant species are always singletons.

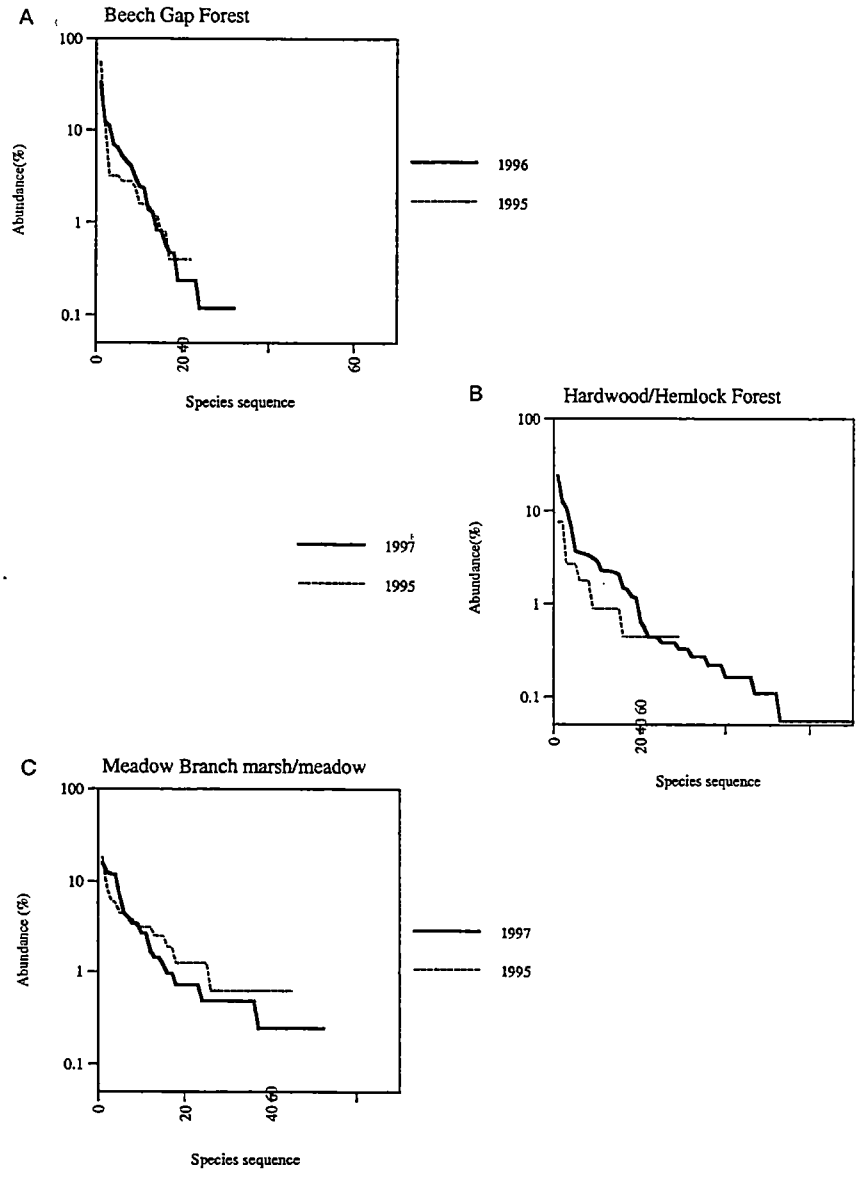
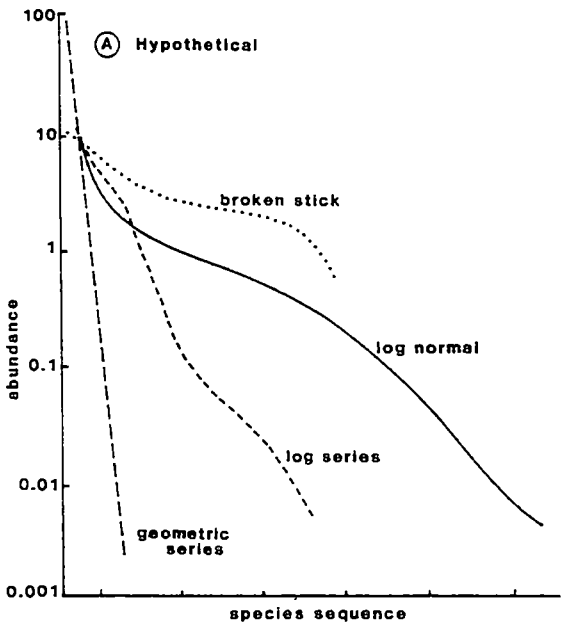


Figure 10. Hypothetical rank abundance distributions, used to illustrated the differences in shape between the four basic models discussed in the text: broken stick, log normal, log series, and geometric series (taken from Magurran 1988). The shape of these distributions can be compared with the curves produced for Figures 8 and 9, as the axes are the same. The y-axis is the abundance of the species measured as a percent, plotted on a logarithmic scale. The x-axis ranks the species from the most to the least abundant.



Visual inspection of the rank abundance plots shows that for the Macon County sites, both Ellicott Forest and Ellicott Clear-cut appear most similar to the log series model distribution shown in Figure 10. Indicating an intermediate level of equitability, the log series model is often cited as the most appropriate fit to empirical arthropod data (Magurran 1988). This is not necessarily the case, however, since small sample sizes may lead to what is called a truncated log normal distribution, which is effectively indistinguishable from the log series (Magurran 1988). What is most interesting is that Horse Clear-cut appears to be most similar to the broken-stick model, indicating that the assemblage is highly equitable in its distribution of resources.

Among the GSMNP sites, Beech Forest has the steepest distribution and is, therefore, most similar to the log-series model. As this site was thoroughly sampled, one might expect it to most likely fit the log series model. Thus it is dominated by a few abundant species, as is the nearly pure stand of beech trees dominating the plant community at this site (Keith Langdon, written communication, 1999). The Hardwood Forest assemblage of spiders appears to best fit the log-normal model. Presumably, resources of shelter and prey availability are divided more equally at this site among the component spider species resulting in the greater number of species exhibiting intermediate levels of abundance. This pattern may also reflect the more complex vegetation at this site as compared with the Beech Forest. The Meadow Marsh has the flattest of the three distributions and is therefore somewhat intermediate between the log-normal and the broken stick.

Species Richness and Diversity

The purpose of this study was not to measure the complete richness of the sites sampled, but rather to compare community structure in samples taken from the same sites at different times. This is most true of the Macon County sites, at which a more limited

sampling regime was conducted over a relatively larger area than at the GSMNP sites. Nonetheless, as the distribution of sampling techniques was consistent within sampling areas (GSMNP and Macon County), richness and diversity estimates are comparable between sites. The number of species for each sample is given in Table 4. To get a more complete picture of the community being measured, it is useful to calculate a diversity index which makes use of both presence/absence and abundance data. The Shannon-Weiner and Simpson Indices are two of the most commonly used in the literature (Magurran 1988). A complete list of Shannon-Weiner and Simpson's Index for each sample at each site is given in Table 11. Of the modern surveys, Ellicott Forest and Hardwood Forest had the most species represented, and therefore the highest apparent richness. Beech Forest and Horse Clear-cut had the lowest values for taxonomic richness. The diversity indices give a somewhat different result, with Horse Clear-cut on average having the highest diversity of Macon County, and Meadow Marsh the highest of the GSMNP. The least diverse site remained the Beech Forest for the GSMNP, while in Macon County, Ellicott Clear-cut had the lowest Shannon value and an intermediate Simpson's value.

Inventory Completeness

Species accumulation curves provide rough estimates of the completeness of a survey attempt (Pielou 1975). We assume that the initial samples taken from a site contain many unique species and that each subsequent sample will yield fewer and fewer unique species until virtually the entire community has been sampled. At this point, the plot of samples vs. cumulative number or species should reach an asymptote. Usually, the order of the samples is randomized and the mean species accumulation curve is plotted to see if an asymptote is evident. I plotted fully randomized species accumulation curves for all date/site combinations. For the GSMNP sites, each sample was equivalent to one hour

Table 11. Diversity indices

Site	Index	S1	S2	S3	S4	S5	S6	mean (range)
Macon Co.								
Ellicott	Shannon	3.11	3.10	3.11	3.28	--	--	3.15 (0.18)
Forest	1/Simpson's	14.7	10.5	11.7	13.7	--	--	12.7 (4.2)
Ellicott	Shannon	3.34	2.97	3.09	3.25	--	--	3.16 (0.37)
Clear-cut	1/Simpson's	22.2	10.2	13.7	16.1	--	--	15.6 (12)
Horse	Shannon	3.56	3.35	3.18	3.07	--	--	3.29 (0.49)
Clear-cut	1/Simpson's	21.7	21.7	15.4	13.0	--	--	18.0 (8.7)
GSMNP								
Beech	Shannon	1.81	--	2.42	2.36	2.72	2.62	2.39 (0.91)
Forest	1/Simpson's	3.0	--	6.4	6.4	9.8	8.5	6.82 (6.8)
Meadow	Shannon	--	3.27	3.01	3.07	3.01	2.87	3.05 (0.40)
Marsh	1/Simpson's	--	17.5	12.7	12.7	12.7	9.6	13.04 (7.9)
Hardwood	Shannon	2.79	2.48	3.25	3.12	2.94	2.69	2.88 (0.77)
Forest	1/Simpson's	11.5	5.8	15.9	13.3	10.8	8.3	10.9 (10)

Notes. For the Macon Co. sites (Ellicott Forest, Ellicott Clear-cut, Horse Clear-cut), S1-S4 correspond to the surveys conducted in 1976, 1995, 1996, and 1997 respectively. For the GSMNP sites, S1 and S2 correspond to the early and late summer collections of 1995, S3 and S4 correspond to the early and late summer collections of 1996 and S5 and S6 for early and late summer 1997. The indices were calculated on the entire sample (including juveniles) for all sites. It is important to note that the sampling intensity varied considerably from sample to sample within a site (see Table 2 and the main text for details) and no attempt was made to standardize for differences in sample size.

of sampling for Beech Forest and Meadow Marsh and two hours of sampling for Hardwood Forest. Each litter sample was considered equal to one sampling hour. To illustrate the shape of these curves and the differences between the three sites, I chose data from August 1996 which was the only time that all three sites were sampled during the same month and year. The species accumulation curves and confidence intervals for all sites are given in Figure 8. I did the same for the Macon County sites using data from 1996 (Figure 9). Finally, I made summary accumulation curves by first pooling data from all years within a site, then pooling data from all sites within a region, and finally pooling data for both regions (Figures 11 to 17).

Of the single-survey accumulation curves (Figures 11 and 14), only the curve for Beech Forest appears to be approaching an asymptote, which is not surprising since this is the site with the least species recovered (Table 3). The curve for Meadow Marsh appears to level off the least, and also exhibits the most variability between samples. Ellicott Forest and Ellicott Clear-cut had considerably more samples than Horse Clear-cut, and thus appear more asymptotic. Of the Macon County sites, Ellicott Forest appears to be the closest to an asymptotic curve, yet none of the three sites have truly reached an asymptote. Turning to the multiple-year accumulation curves (Figures 12 and 15), the same patterns hold, except that Hardwood Forest now appears to be more asymptotic, as does Horse Clear-cut. Neither of the regional accumulation curves appear to be leveling off (Figures 13 and 16), which is not surprising due to the heterogeneity of the study sites. And finally, Figure 17 contains the species accumulation curve for the entire study. Again, it appears that an asymptote is not near, which is as expected due to the marked regional differences between the two study areas.

Species accumulation curves only make use of presence/absence data to evaluate the completeness of a survey. A way to incorporate abundance information into this

Figure 11. Fully randomized species accumulation curves with associated confidence intervals for the three GSMNP sites, Hardwood Forest, Beech Forest, and Meadow Marsh. The data for these plots were from the August 1996 surveys. The values were calculated using the program EstimateS. Each sample is equivalent to two hours of sampling for (A) and one hour of sampling for (B) and (C). The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation).

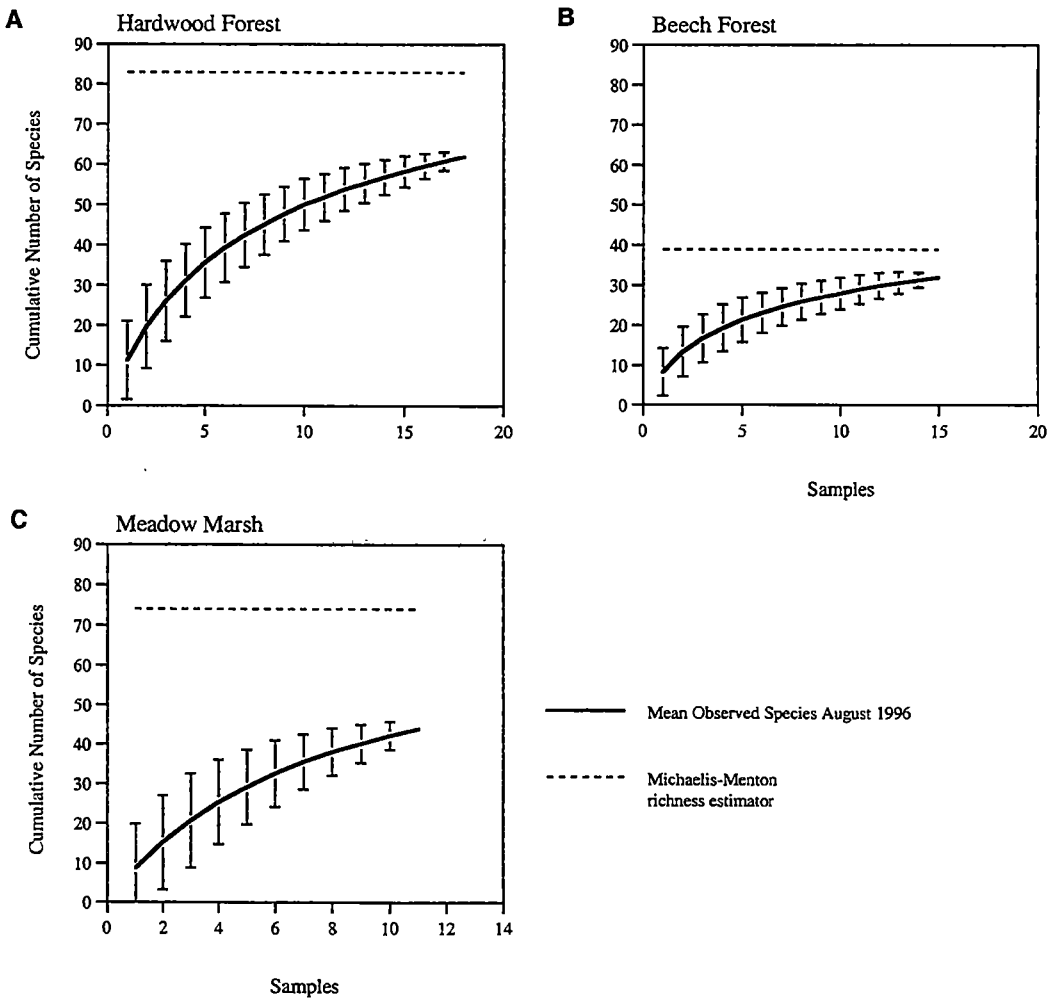


Figure 12. Fully randomized species accumulation curves with associated confidence intervals for all samples across all years for the three GSMNP sites, Hardwood Forest (A), Beech Forest (B), and Meadow Marsh (C). Samples from all three years of collection were used to construct these accumulation curves. The values were calculated using the program EstimateS. Each sample is equivalent to two hours of sampling for (A) and one hour of sampling for (B) and (C). The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation).

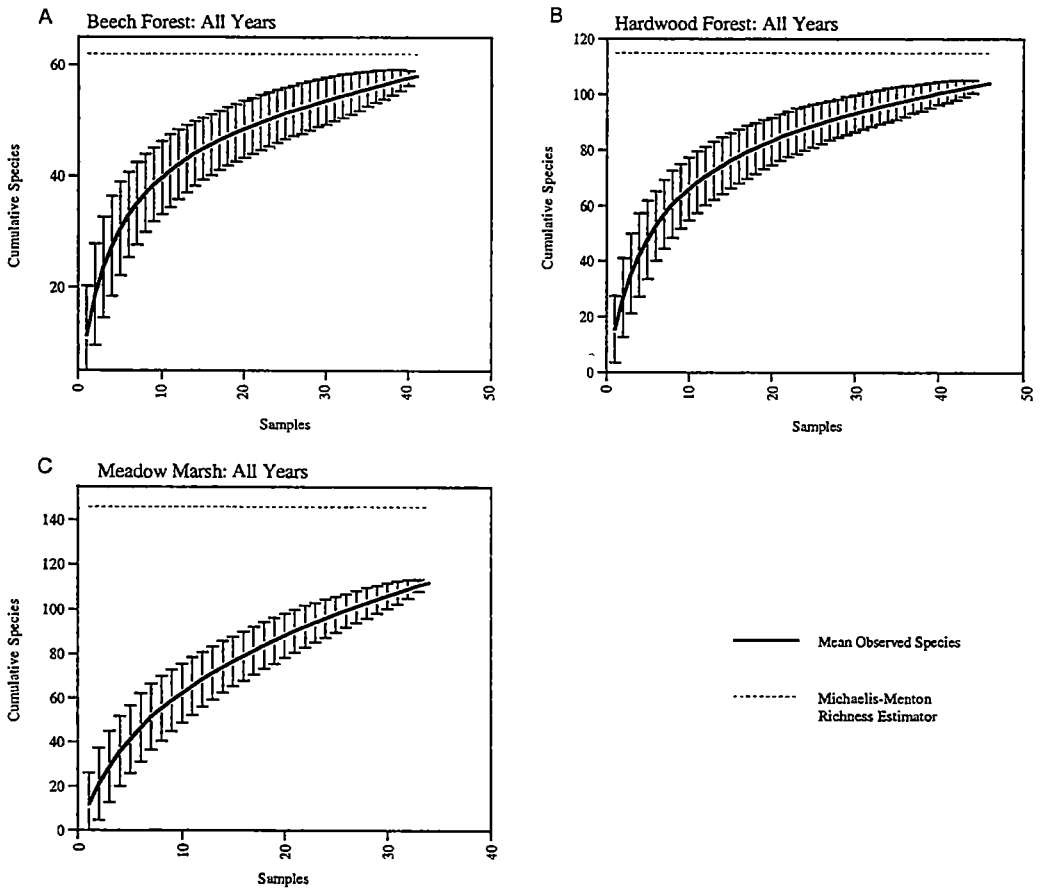


Figure 13. Fully randomized species accumulation curve with associated confidence intervals for all three years of collection data across all three GSMNP sites. The values were calculated using the program EstimateS. Each sample is equivalent to one or two hours of sampling as described in Figure 12. The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation).

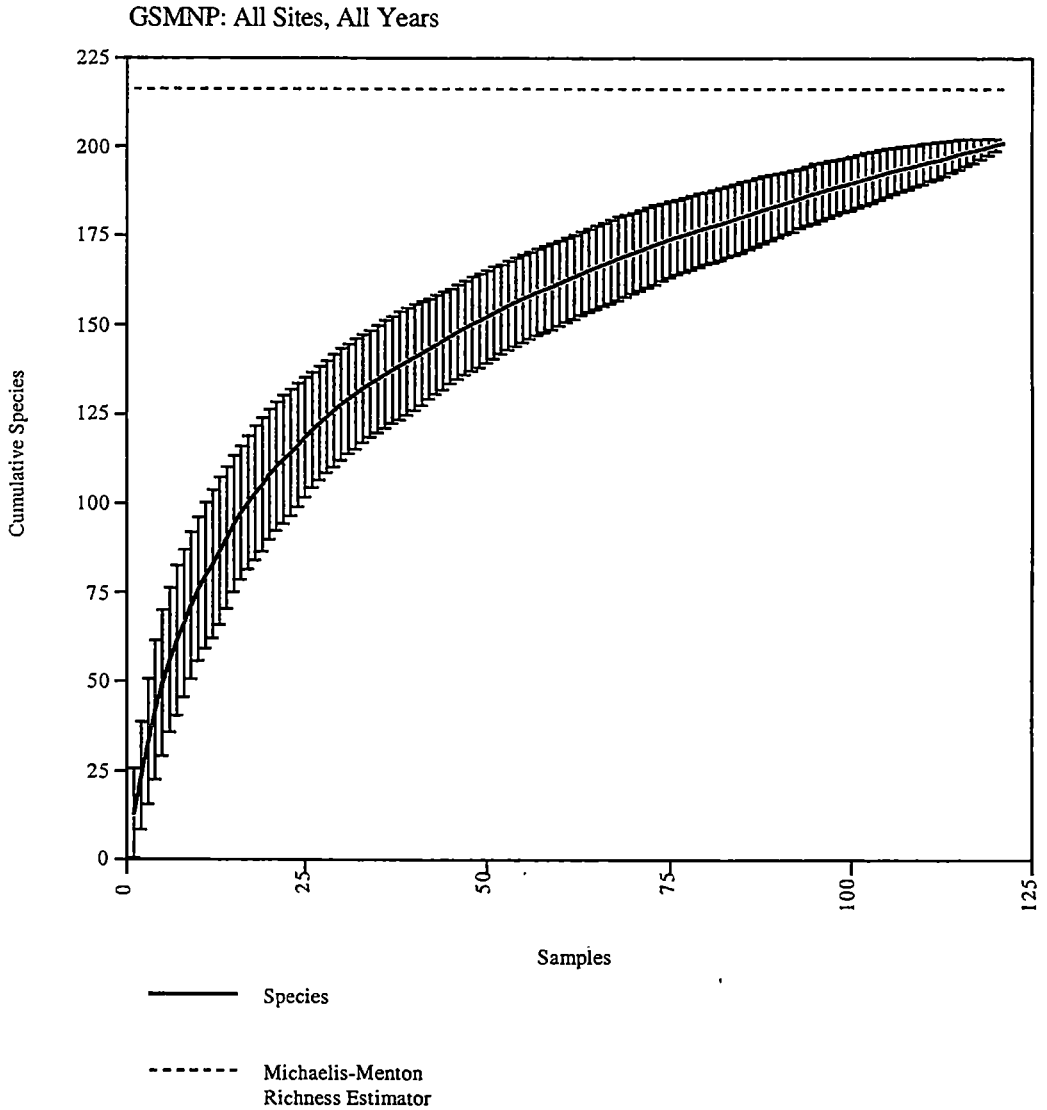


Figure 14. Fully randomized species accumulation curves with associated confidence intervals for the three Macon Co. sites, Ellicott Forest (A), Ellicott Clear-cut (B) and Horse Clear-cut (C). The data for these plots were from the 1996 surveys. The values were calculated using the program EstimateS. For (A) and (B), each sample consisted of either the data collected at a single node along a transect (one sweep sample, one hour hand collection, catch of one pitfall trap), or a set of ten litter samples or the catch from sixteen pitfall traps (over one week), for a total of 17 samples. For (C), each sample consisted of either an hour of hand collection, a set of eight sweep net samples, a set of ten litter samples, or the catch from a set of pitfall traps (over one week), for a total of 11 samples. See text for a detailed description of the sampling protocol carried out for each of these sites. The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation).

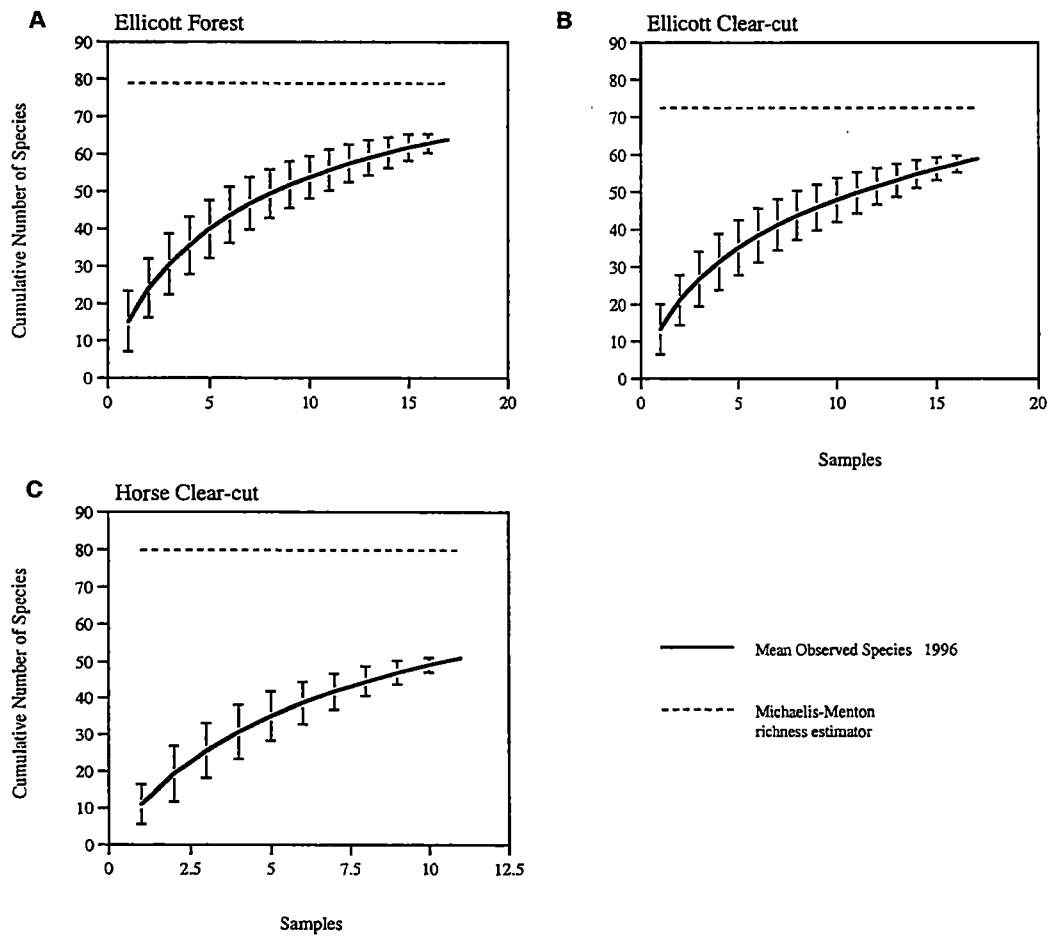


Figure 15. Fully randomized species accumulation curves with associated confidence intervals including all samples for the three Macon Co. sites, Ellicott Forest (A), Ellicott Clear-cut (B) and Horse Clear-cut (C), respectively. The data for these plots were taken from all four collection years for (A) and for the three modern surveys for (B) and (C). The values were calculated using the program EstimateS. For (A) and (B), each sample consisted of either the data collected at a single node along a transect (one sweep sample, one hour hand collection, catch of one pitfall trap), or a set of ten litter samples or the catch from sixteen pitfall traps (over one week), for a total of 17 samples. For (C), each sample consisted of either an hour of hand collection, a set of eight sweep net samples, a set of ten litter samples, or the catch from a set of pitfall traps (over one week), for a total of 11 samples. See text for a detailed description of the sampling protocol carried out for each of these sites. The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation).

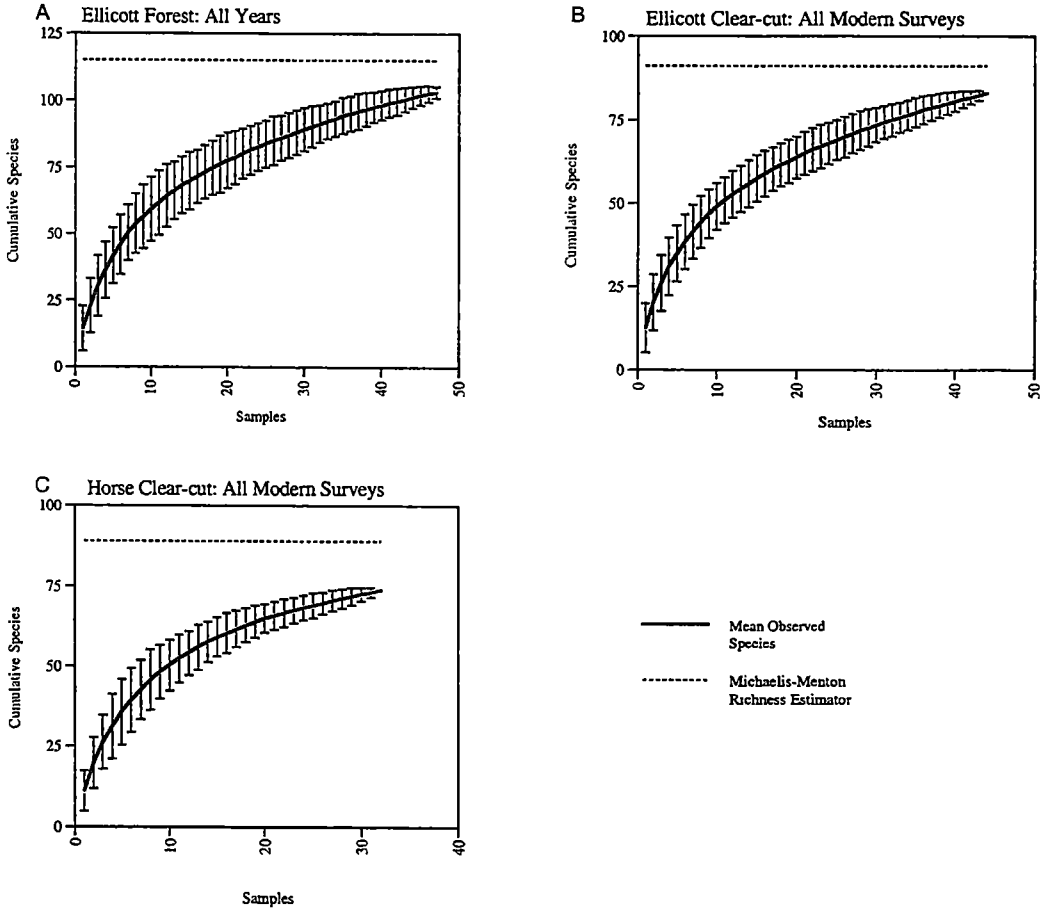


Figure 16. Fully randomized species accumulation curve with associated confidence intervals for all the collections conducted in Macon Co. The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation). Samples are as defined above for each site.

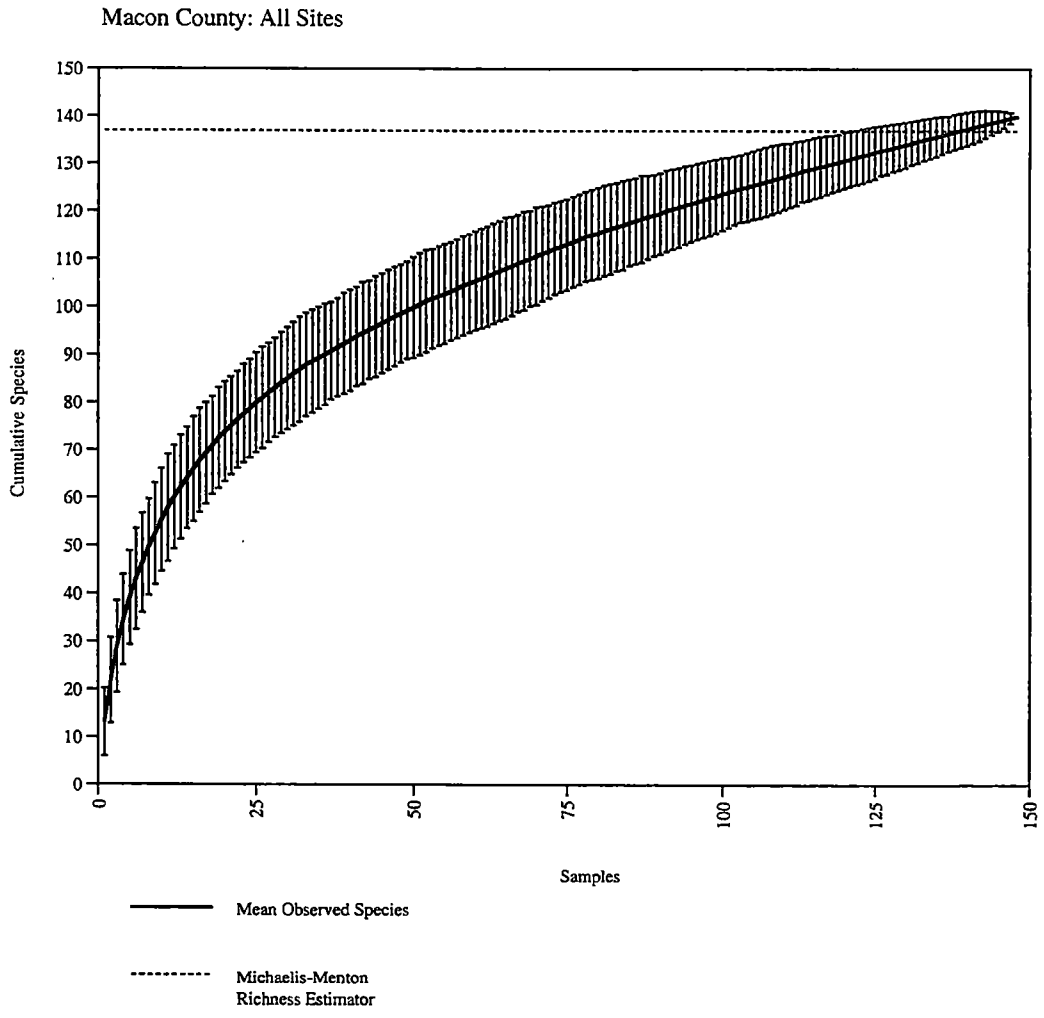
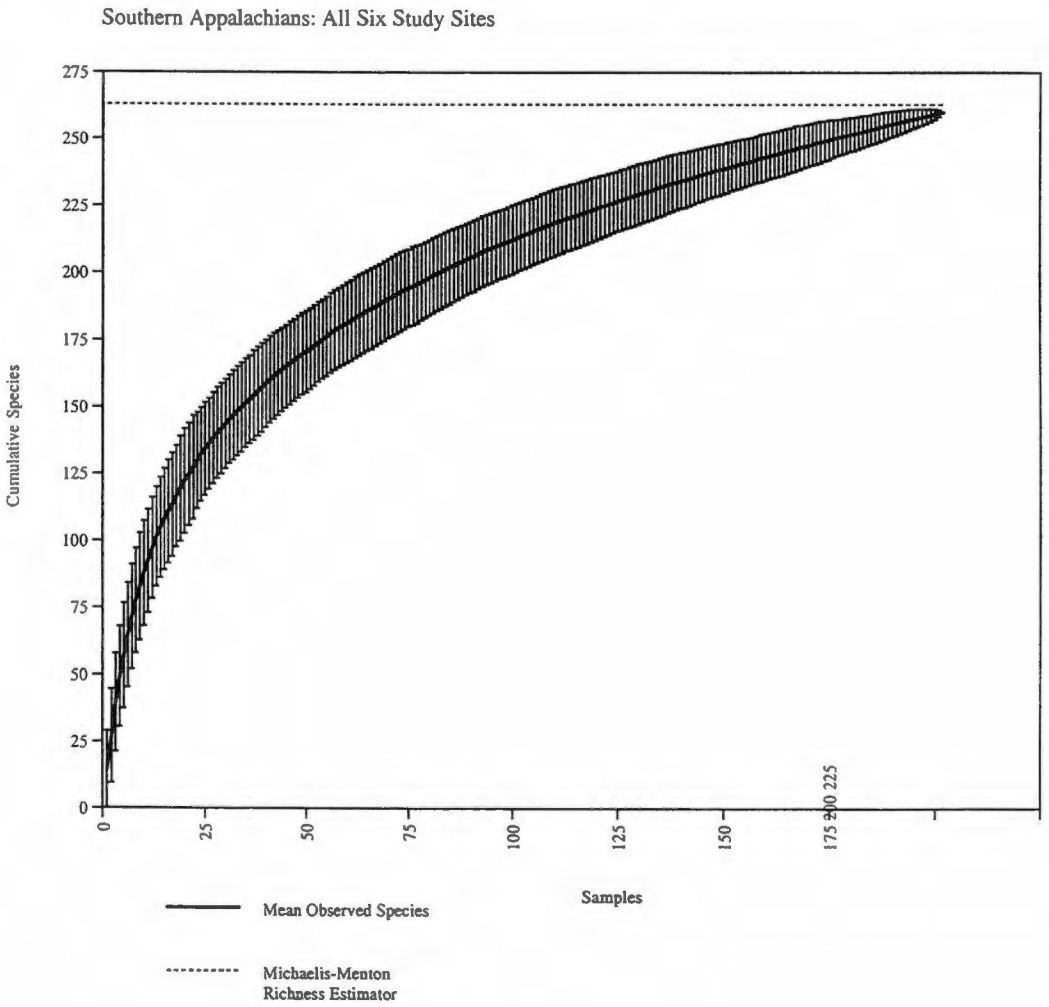


Figure 17. Fully randomized species accumulation curve with associated confidence intervals for all the collections conducted in the Southern Appalachians (all six sites combined; all years combined). The dotted line is the estimated asymptote for each curve (equivalent to an estimate of the 'true' richness of a site) calculated using the Michaelis-Menton richness estimator (see text for equation). Samples are as defined above for each site.



evaluation is to calculate the percentage of species in a sample represented by a single individual, defined here as a 'singleton' (Coddington *et al.* 1996). Although even a truly comprehensive sample may still have some singletons, the percentage of singletons should go down as sampling becomes more complete. Among surveys of equal sampling intensity, Beech Forest had the lowest average percent of singletons at 20%. Hardwood Forest was the second lowest, averaging 25% and Meadow Marsh had the highest at 36% singletons. Of similar sized surveys, Horse Clear-cut had the lowest percentage at 32% with Ellicott Forest and Ellicott Clear-cut having 48% and 45% singletons, respectively. In 1996 and 1997, when Ellicott Forest and Ellicott Clear-cut were more intensively surveyed, the percentages dropped to 32% and 33%, respectively.

Perhaps a more straightforward way to evaluate the completeness of a survey is to compare the initial richness measured by the sample to the 'true' richness of the site. In most cases, the 'true' richness of a site is not known, and therefore an estimate of the 'true' richness must be calculated. There are a number of ways to extrapolate species richness from a data set. I have chosen two extrapolation techniques, which have been recommended for use with hyperdiverse taxa, the Chao1 estimator and the Michaelis-Menton richness estimator (Coddington *et al.* 1996; Chazdon *et al.* 1996; Colwell and Coddington 1994). The Michaelis-Menton richness estimator (MM) estimates the asymptote of a species accumulation curve, and thus provides a quantitative estimate for the true richness of a site. The equation is:

$$S_4^* = S_{obs}(n)\left(\frac{B+n}{n}\right)$$

where S_4^* is the estimate of the asymptote, S_{obs} is the observed number of species, B is the number of samples needed to collect half the total species and n is the number of individuals.

I have plotted the MM mean estimate (this uses the mean accumulation curve after randomization to calculate MM) on top of the species accumulation curves presented in Figures 8 through 17.

For the GSMNP sites, it appears that the measured richness of Beech Forest is closest to the extrapolated richness calculated with the Michaelis-Menton richness estimator. Meadow Marsh had the greatest discrepancy between the initial species data and extrapolated richness, indicating that it is the most undersampled, with Hardwood Forest somewhere in between. Like the species accumulation curves, this indicates that Beech Forest is the most comprehensively sampled site and Meadow Marsh is the least. In Macon County, the more completely sampled Ellicott Forest and Ellicott Clear-cut are closer to their estimated asymptotes than the less sampled Horse Clear-cut.

Because MM uses the accumulation curves to predict richness, it could be quite sensitive to differences in the total number of samples and/or minor differences in what constitutes a sample. For example, we might ask how different is a litter sample from the catch of 16 pitfall traps in a week?. In addition, it also only makes use of presence/absence data. The Chao1 estimator (Chao 1984) is a non-parametric richness estimator, which requires abundance data (number of individuals of each species collected). The formula is:

$$S_1^* = S_{obs} + \left(\frac{a^2}{2b}\right)$$

where S_{obs} is the number of species observed, a is the number of singletons, and b is the number of doubletons (species represented by exactly two individuals).

Using the same data-sets I used to calculate MM for each site, I calculated Chao1. For the GSMNP sites, Chao1 gave richness estimates of 40 species for Beech Forest, 95 species for Hardwood Forest and 54 species for Meadow Marsh. As for Macon County,

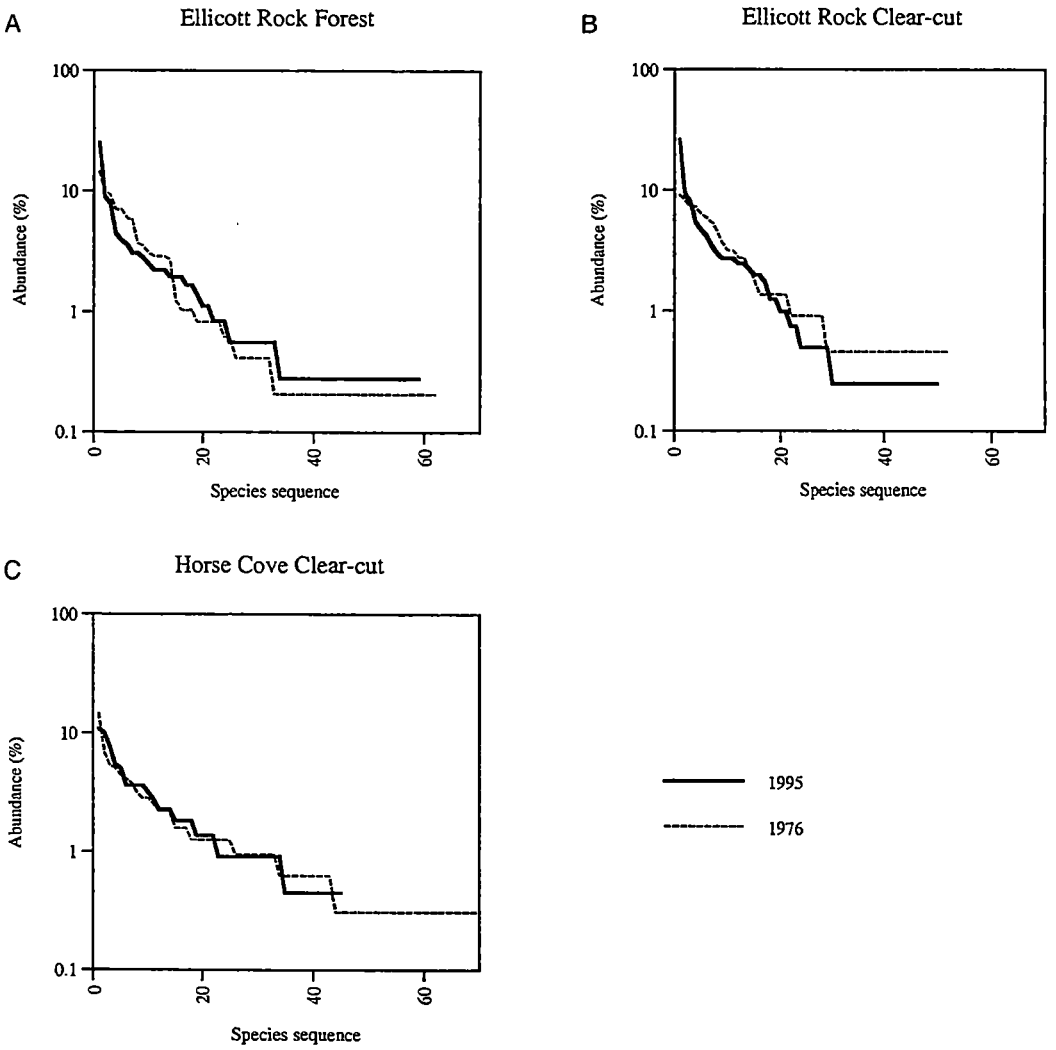
Chao1 gave richness estimates of 75 species for Ellicott Forest, 79 species for Ellicott Clear-cut, and 58 species for Horse Clear-cut. Comparing these to the Michaelis-Menton estimators for the GSMNP sites, Chao1 gave a very similar richness estimate to MM (40 vs. 39) for Beech Forest, a larger estimate for Hardwood Forest (95 vs. 83 species) and a much smaller estimate for Meadow Marsh (54 vs. 74 species). As for Macon County, Chao1 gave a slightly lower richness estimate for Ellicott Forest (75 vs. 79), a slightly higher estimate for Ellicott Clear-cut (79 vs. 73), and a much lower estimate for Horse Clear-cut (58 vs. 80). We seem to have two anomalous sites (Horse Clear-cut and Meadow Marsh) for which different extrapolation techniques vary considerably from each other.

DISCUSSION

Species abundance distributions are appealing diagnostic tools simply because they make use of all the data collected in the study of an assemblage. We can compare abundance distributions created with empirical data to a set of theoretical species abundance models, each of which is based on a different presumption of how ecological resources are partitioned within the community. When plotted as rank abundance, the four most common models range in appearance from a very steep line (the geometric series), through lesser slopes, progressively dropping to a fairly flat curve (broken stick) as represented in Figure 7. The steeper the curve, the more the assemblage surveyed is dominated by a few species and therefore the less equally vital, limiting resources are shared. A curve that is flatter represents a situation where there are more species of intermediate abundance in the assemblage and therefore resources are partitioned more evenly (Magurran 1988).

Of the six sites examined in this study, the two with the flattest curves, and therefore the most equable assemblages were Horse Clear-cut and Meadow Marsh, both in proximity to extensive, heterogeneous wetlands. In a temperate forest, secondary succession produces assemblages which become more dominated by fewer species, resulting in lower evenness through time. Although Horse Clear-cut is slightly older than Ellicott Clear-cut, instead of being surrounded by older-growth forest on all sides it is bordered by a combination of bog, tree plantation, and land cleared for housing. So perhaps its greater equitability is actually a sign that it is less insulated from disturbance, and therefore slower to reach maturity. Another related possibility is that the heterogeneous environment, which surrounds Horse Clear-cut is actually a source for greater and more varied 'pools' of potential spider colonizers. To examine this more closely, I plotted the rank abundance for the Macon County sites, this time overlaying the data from 1976 on the data from 1995 (Figure 18). Looking at the two clear-cut sites, Ellicott Clear-cut has become less equitable (the curve is more steep) through time, while Horse Clear-cut has changed little. Ellicott Forest has changed somewhat, but no clear pattern of change in equity is apparent. Meadow Marsh, as a grassy marsh/meadow, floristically resembles an old field in secondary succession. Old fields (early successional habitats) often consist of plant assemblages, which are not dominated by only one or two species and therefore exhibit a higher compositional and structural heterogeneity than later successional stages (e.g., Buss 1956 cited in Brewer 1988). In contrast, Beech Forest, which represents an old growth stand dominated by beech trees, has the steepest rank abundance distribution indicating that a few species dominate the spider community. Again, the homogeneous spider assemblage seems to reflect the homogeneous character of the prevalent vegetation.

Figure 18. Rank abundance distribution of species collected in 1976 (dashed lines) for Ellicott Forest (A), Ellicott Clear-cut (B), and Horse Clear-cut (C). Solid lines represent the rank abundance distribution of species collected in 1995 for these same sites. The y-axis is the abundance of the species measured as a percent, plotted on a logarithmic scale. The x-axis ranks the species from the most to the least abundant. The least abundant species are always singletons.



Ordering these six sites from the most to the least diverse is not as simple as it seems. Depending on the diversity index used, the exact ordering of the sites changes. Overall, one could reasonably conclude that Hardwood Forest and Ellicott Forest are the most diverse sites and Beech Forest the least. One of the difficulties in comparing the diversity of these sites is that because we are actually only measuring a portion of the entire community and at different points in time, often one site is more diverse one year or season, and less diverse the next. Also, as previously mentioned, there was a certain amount of variability in sampling effort and yield from sample to sample, making any conclusions on the relative diversity of these sites uncertain. Because there is some degree of turnover from month to month and year to year, pooling samples across months and years is somewhat suspect. Still, to get the most complete estimate of diversity for each study site and study region, I pooled the data first across months and years, then across sites within region, and finally across regions to obtain a grand total for the sites in the Southern Appalachians. These totals are presented in Table 4. In Macon County, Ellicott Forest remains the most diverse with 109 species. The richness totals for Ellicott Clear-cut and Horse Clear-cut are actually a bit inflated, as data from 1976 was included (some species no longer live in these sites due to vegetation changes associated with succession). Among both the GSMNP sites and the Macon County sites, Meadow Marsh has the highest richness when yearly and monthly samples are pooled (110 species). Overall, more species were collected in the GSMNP than in Macon County (200 vs. 164) which is as expected due to the greater vegetational differences between the GSMNP sites compared with the Macon County sites. Still, the 200 species collected at these three sites is less than half of the roughly 500 to 550 species of spiders collected by Fred Coyle across the 18 habitat types in the Park (Coyle, written communication, 2000). Combining

the two study regions, a total of 290 spider species were collected, presumably just a small fraction of the total.

Returning to the six individual study sites, a more relevant question to ask of these data is how well each sample did of measuring the 'true' diversity of each site. Ultimately, we want to know how close the sampled richness of a site is to the true richness. This will give us some idea of the proportion of the community we have successfully sampled. In the absence of data on the true richness of a site, we must use extrapolated richness estimates as a surrogate. Yet, a problem arises when different richness estimators yield contradictory results. For example, when comparing the raw richness to the Chao1 estimates for Meadow Marsh, one could conclude that the majority of species had been sampled at that site. Yet, just the opposite seems true when viewing the species accumulation curve and the MM estimate. Which is correct? The third technique I used to gauge inventory completeness is the percentage of singletons in a sample; Meadow Marsh had the highest percentage of singletons. This further supports the conclusion that this site has not been adequately sampled. Still, it is difficult to make any firm conclusions due to the non-independence of these techniques (i.e. MM estimate is derived from the species accumulation curve and Chao1 uses the number of singletons as part of the formula to extrapolate richness). Perhaps only further collecting and/or other extrapolation techniques are necessary to answer this question. What we do know is that Meadow Marsh is vegetationally distinct from the other sites, as it is a montane grassland in an alluvial glade wetland, as opposed to a woodland. On the other hand, the same pattern is observed for Horse Clear-cut. Based on one richness estimate, the site appears to be fairly well sampled; yet based on another richness estimate it is quite under-sampled. In addition, Horse Clear-cut had the lowest percentage of singletons indicating it was well sampled. Certainly, both of these sites is unique in that they surrounded not by

forest, but by a more heterogeneous environment consisting of a mixture of wetland and forest. Perhaps many of the species collected at these sites were merely transients from nearby habitats and not part of the true assemblage. This external influence could certainly effect the accuracy of sampling curves and extrapolation techniques.

One thing that Horse Clear-cut and Meadow Marsh have in common is that they both had the lowest intensity sampling regime for each of their study areas. In addition, they both had the flattest of the rank abundance distributions. Therefore, these results could indicate either that they are merely the most under-sampled of the sites, or that the differences in richness estimates are due to their underlying species distributions of greater equitability. If most species in an assemblage are either equally abundant or equally rare, then the species accumulation curve would be expected to be slightly less asymptotic. Extrapolators, like indices, are based on particular assumptions about the underlying 'true' abundance distribution, which may be incorrect. Therefore richness estimators relying on these curves (such as MM) may be estimating an asymptote that doesn't truly fit the character of the site. It is not possible with these data to confidently choose between these alternatives. Perhaps calculating a number of different extrapolated richness estimates and completing among estimate comparisons within a site might best determine whether the survey was complete; If all estimates agree that the measured richness is very close to the 'true' richness, then you can conclude that you have a complete survey. But if the estimates don't agree or they all agree that the true richness is much higher than the measured richness, then more sampling is necessary.

CONCLUSIONS

Based on the species accumulation curves and high proportion of singletons, it can be concluded that none of the surveys conducted at each of the six sites presented

here was entirely complete. Ideally, one could structure the sampling protocol such that sampling would continue until either an asymptote on a species accumulation curve was reached or until a low enough percentage of singletons were collected. Unfortunately, this is difficult to accomplish with arthropod data due to the significant processing time necessary prior to species identification.

Nonetheless, it appears as though the majority of each assemblage was sampled (approximately 60-75% of all the species) and certainly all of the most abundant species. The resulting data-sets will be useful as long as care is taken to avoid treating these sampled communities as complete surveys, where every species is accounted for. Based on the analyses presented above, the most structurally homogeneous site, Beech Forest, appears to be the most completely surveyed site for an apparently homogeneous spider assemblage. When looking at the individual surveys, Hardwood-Forest certainly seems to be the most species rich site. However, the site richness total across all surveys in the case of Hardwood Forest is actually smaller than Meadow Marsh because of the relatively low turnover between surveys. Interestingly, although Hardwood forest was subject to the most intensive sampling protocol, there was a high degree of variability between surveys in terms of overall abundance of spiders resulting in highly variable richness estimates based on different surveys (see Figure 5). Note that these differences in yield may make this site ideal for an examination of the effects of sample size on analytic tools. Spider data from Meadow Marsh exhibit atypical patterns for extrapolated richness estimates, species accumulation, and mean number of species collected per capita (Figures 5,6,11,12). With the exception of the rank abundance distributions, the three Macon County sites appear to be more uniform, with differences being mostly attributable to differences in sampling intensity between Horse Clear-cut and Ellicott

Clear-cut/Ellicott Forest. When a comparable subset of data is compared between the sites, they seem quite similar (Figure 3).

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PART III: A TEST OF A PATTERN RECOGNITION SYSTEM FOR IDENTIFICATION OF SPIDERS

PREFACE TO PART III

When dealing with any hyperdiverse group of organisms, the time and effort involved after the specimens have been collected in the field and prior to the initialization of any analyses is considerable. In fact the species identification process is arguably the most time consuming portion of any biodiversity study and for all but the most experienced workers, the most fraught with uncertainty. Taxonomic keys are often widely dispersed in the literature and even unavailable for some groups. Even with proper keys, consistency between inexperienced workers cannot be guaranteed due to the lack of comprehensive reference collections and the subjectivity of matching line drawings to specimens. For these reasons, often arthropods are ignored in biodiversity studies, or merely identified to the Order or Family level. One potential way to cope with these difficulties and thereby promote the inclusion of arthropods in community level studies would be to partially automate the identification process. While at the University of Tennessee, I became involved in a project which sought to automate the identification of spider species using neural networks. Unfortunately, the system was not developed fully enough for me to use it for the species identifications necessary for my dissertation work. Nonetheless, it is exactly this technology which would have saved me hundreds of hours of work as well as improved the accuracy/consistency of my identifications. For this reason, I have included the following chapter in the body of my dissertation.

This chapter has been published as: Do, M.T., J.M. Harp and K.C. Norris. 1999. A test of a pattern recognition system for identification of spiders. *Bulletin of Entomological Research* 89, 217-224. This project was originally conceived as part of Do's Masters thesis in Computer Science at the University of Tennessee. I began collaborating with Mr. Do in 1995/96 and was ultimately responsible for the writing and

submission of this manuscript for publication. I was involved in acquiring specimens, taking a portion of the digital images, and advising Do on ways to improve the system and make the interface more user friendly and informative.

ABSTRACT

Growing interest in biodiversity and conservation has increased the demand for accurate and consistent identification of arthropods. Unfortunately, professional taxonomists are already overburdened and underfunded and their numbers are not increasing with significant speed to meet the demand. In an effort to bridge the gap between professional taxonomists and non-specialists by making the results of taxonomic research more accessible, we present a partially automated pattern recognition system utilizing artificial neural networks (ANNs). Various artificial neural networks were trained to identify spider species using only digital images of female genitalia, from which key shape information had been extracted by wavelet transform. Three different sized networks were evaluated based on their ability to discriminate a test set of six species to either the genus or the species level. The species represented three genera of the wolf spiders (Araneae: Lycosidae). The largest network achieved the highest accuracy, identifying specimens to the correct genus 100% of the time and to the correct species an average of 81% of the time. In addition, the networks were most accurate when identifying specimens in a hierarchical system, first to genus and then to species. This test system was surprisingly accurate considering the small size of our training set.

INTRODUCTION

Physicist and Nobel laureate, Richard Feynman, once said that knowing the scientific name of an organism tells you only the name and nothing else (NOVA, 1975). Though literally true, the scientific name is the handle by which all known information regarding the species can be accessed. The scientific name is also the common 'currency'

in biodiversity studies. An incorrect identification can be disastrous (see Miller & Rossman, 1995; Davis, 1995).

Given the need for making accurate identifications, we find that there are two major obstacles. The first is a general lack of funding and personnel for doing taxonomic research to properly classify and describe the vast diversity of organisms. This problem has been comprehensively documented (Systematics Agenda 2000, 1995). The second obstacle to accurate identifications is the difficulty involved in becoming proficient at recognizing arachnids and other arthropods at the species level. Species identification is a daunting task for the non-specialist and the results are often disappointing and inaccurate. The cost of acquiring proficiency is high and, for the non-specialist, the long-term benefit is low.

A partial solution to the problem, which would serve both to alleviate the time demands on taxonomists and to make specimen identification easier and more accurate for the non-specialist, is to partially automate the process. We present a computerized pattern recognition system that, though potentially useful to the systematist, is designed to make the results of taxonomic research available to workers in disciplines that require identification of collected specimens. We have chosen artificial neural networks as our pattern recognition tool. Neural networks are programming algorithms which simulate the structure of the brain and the processing of information therein (see Boddy *et al.* 1990 for an introduction to neural networks). Neural networks have been shown to be remarkably apt at learning. They are also capable of detecting subtle differences between similar objects. Once trained, a network can classify objects (e.g., individuals) that it has never encountered before as long as the group they belong to (e.g., genus or species) was part of the training process. It can also be trained to identify unknown objects as such.

After the training process the network is time efficient, making rapid identifications while using insignificant computer time and resources.

One of the more commonly known applications of neural network technology comes from the field of forensic science. Finger-print analysis technology developed by NIST (National Institute of Standards and Technology) uses a probabilistic neural network to look for similarities in location of whorls and curves in order to determine whether an unknown print is the same as any it has been previously shown. This is a simpler procedure than training a network to identify an organism to the species level, since there is much greater variability between two individuals of the same species than two fingerprints from the same individual. Handwriting analysis provides a more reasonable comparison, as handwriting varies from signature to signature for the same person.

The possibility of using computer-aided identification systems in biodiversity studies has recently been reviewed by Edwards and Morse (1995) and Weeks and Gaston (1997). Concerned primarily with invertebrate identification, Weeks and Gaston (1997) suggest that multi-access keys, or something similar, might be useful for identification to higher taxonomic levels, but that species identification could be better attained using image analysis and/or neural networks. They review the techniques being developed and the opportunities and limitations of each.

Microbiologists, marine biologists and entomologists have been working on ways to use this technology to differentiate species of bacteria (Bungay & Bungay, 1991; Rataj & Schinder, 1991), classify human cell types (Moallemi, 1991), identify phytoplankton species (Simpson *et al.*, 1992; Boddy *et al.*, 1994; Wilkins *et al.*, 1996), and discriminate between closely related species of ichneumonid wasps (Yu *et al.*, 1992; Weeks *et al.*, 1997). Weeks *et al.* (1997) achieved an identification accuracy of 94% by using principal

components analysis to distinguish five species of ichneumonid wasp using information derived from images of wing venation. A disadvantage of this system is its limitation to one sort of information input at a time (i.e. wing morphology). With the exception of the wasp identification, all of these studies made use of neural networks to discriminate visually between groups.

This study is the first attempt that we know of to use neural networks to identify macroscopic organisms. We will demonstrate that this system can classify spider individuals to genus and to species based only on digital images of the ventral view of the female epigyna. In this preliminary study, the training and testing sets are small and the neural networks are required to make identifications based only on single photomicrographs of each test individual. A human making the same identifications would have access to much larger quantities of information. More information could be incorporated into the system, but we hope to demonstrate the utility of this method by showing its performance under such minimal conditions.

METHODS

The data

Two species from each of three different genera of the family Lycosidae were used in the training sessions. The species were: *Arctosa rubicunda* (Keyserling), *Arctosa emertoni* Gertsch, *Pardosa groenlandica* (Thorell), *Pardosa dromaea* (Thorell), *Alopecosa aculeata* (Clerck), and *Alopecosa kochii* (Keyserling) (see Dondale & Redner, 1990). These specimens allowed us to test the network's ability to classify individuals in three ways: to genus, to species, and to species within genus (i.e. the program first classifies to genus and then to species for each specimen).

Image acquisition

Due to variability in the condition of the epigyna and the quality of the resulting images, between 14 and 21 individuals of each species were photographed. The epigyna were photographed in 70% ethanol using an Olympus SZX70 microscope equipped with a Sony CCD video camera. Images from the CCD camera were captured using a Snappy™ and recorded in Tag Image Format (TIF). The preparation of each specimen for imaging involved aligning the plate of the epigynum approximately normal to the viewing axis of the microscope through the use of forceps and cotton padding. All specimens were illuminated using a fibre optic light source.

Image pre-processing

The images were cropped to include only the epigynal boundaries. The two dimensional wavelet transform, described below, requires the input image to be a square with dimension 2^j X 2^j. As a consequence, the image was scaled down to a dimension of 128 X 128 pixels. Beyond this routine processing, no attempt was made to scale the images to account for overall body size. An example of a cropped original image is shown in Figure 1A.

Wavelet transforms

Neural networks vary in the amount of information they are designed to receive. In general, a network will have n inputs, corresponding to n numerical values. If n is too large, one of two problems may arise; the computer resources required may be excessive, or the network may lose the ability to generalize when discriminating images unseen in the training set. We found 256 inputs to be the maximum feasible in this study. Thus the input data had to be tailored to the size of the input layer. In this case the input was an image, so one option was to input the greyscale values of each pixel. To do this, the

Figure 1. An epigynum as viewed on the monitor through the CCD camera (A). (B) An epigynum after wavelet transformation illustrating the loss of high resolution detail with the maintenance of gross shape information.

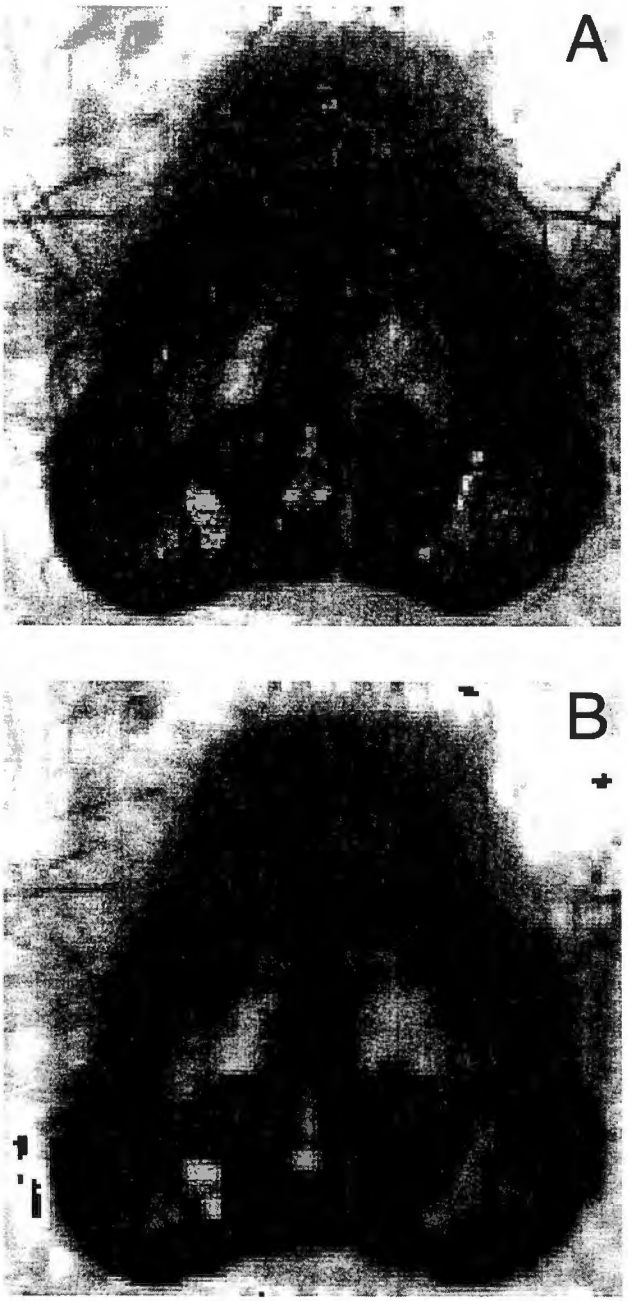
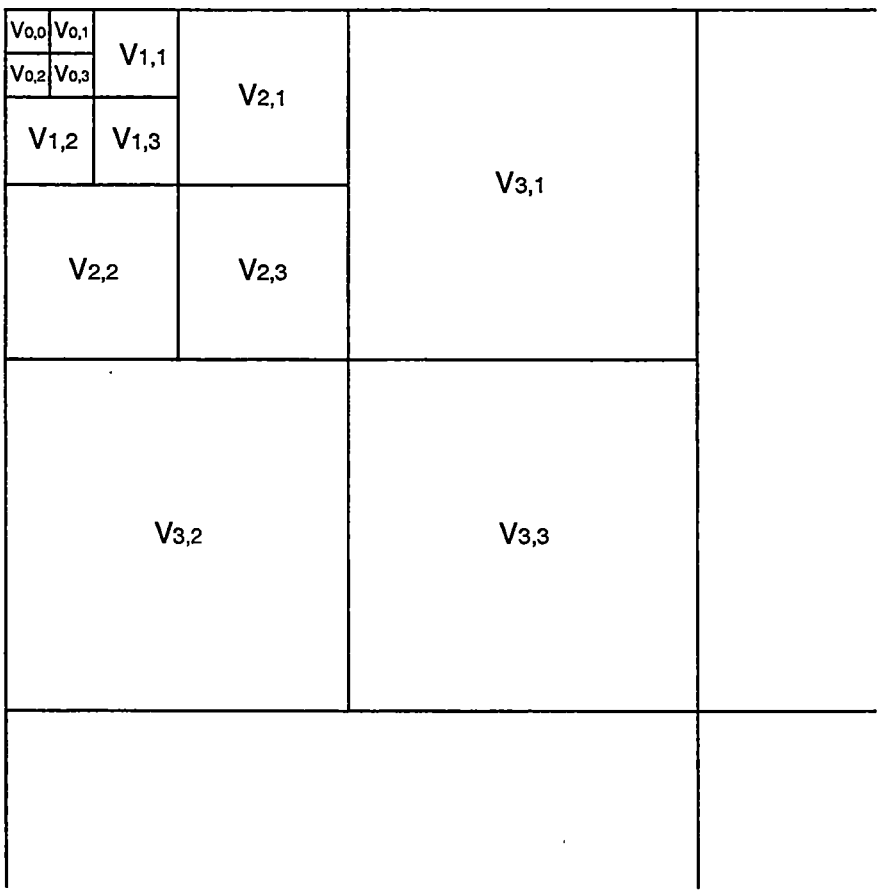


image would have to be reduced to the appropriate number of pixels. For a network with 256 inputs, our maximum, this would mean an image of 16 X 16 pixels. Such an image contains very little information about the shape of the epigynum, which we know is the most useful information when discriminating species. Therefore, what was needed was a way to decrease selectively the information contained in the original high-resolution image down to a maximum of 256 values, such that less useful details such as spines and hairs were eliminated while shape information (to allow species identification) was maintained. This was accomplished using a type of mathematical transform called wavelet transform (Graps, 1995).

Wavelet transforms are similar to the more commonly encountered Fourier transform. They are an iterative procedure in which an image is successively reduced to a coarser version of itself, through the removal of high frequency information contained in wavelet coefficients (sometimes referred to as detail coefficients). These coefficients are parameters that modify the shape of a pre-determined function, called a wavelet. The particular wavelet function chosen for this work was the 'Daubechies 4', based on the success of a previous application of neural nets to static signature analysis (McCormack, 1994). At each iteration, the image is partitioned into one vector space containing the low frequency information (low resolution) and three vector spaces containing the higher frequency information. At this point, each vector space contains many wavelet coefficients. In the next iteration, the low frequency vector space is itself partitioned into one low, and three high frequency vector spaces (see Figure 2). Through this procedure, more and more of the high frequency information is removed, until finally, all that is left are the four vector spaces, each with a single coefficient. The original, high resolution image can be reconstructed by successively re-applying the high frequency data represented by the wavelet coefficients contained in the higher frequency vector spaces to

Figure 2. A wavelet coefficient layout diagram for an image that has undergone wavelet transformation. The set of coefficients corresponding to each iteration is called a vector space. V_0 is the single pixel to which the image is reduced, plus its three coefficients. V_1 is the four values of V_0, plus the set of twelve coefficients that would be applied to the four pixels of V_0 after reconstruction. V_2 is the sixteen values of V_1, plus the corresponding 48 coefficients and so on. The higher resolution information is represented by the wavelet coefficients at the higher level vector spaces (toward the right side of the figure).



the lower frequency information contained in the low frequency vector spaces. Of course, when the image is reduced to only a 4 X 4 matrix of wavelet coefficients, it will be considerably blurred and barely recognizable. Figure 1B shows the image from Figure 1A, after wavelet transform followed by reconstruction using only the coefficients from the later iterations. The transformed image, while containing as many pixels as the original, shows a loss of high resolution detail. The gross shape of the epigynum, however, is still evident. The input into the network actually consists of the remaining wavelet coefficients which could be used to reconstruct the image.

As mentioned above, the set of coefficients corresponding to each iteration is called a vector space. These vector spaces are numbered as follows. V_0 is the single wavelet coefficient to which the image is reduced, plus its three detail coefficients. V_1 is the four values of V_0, plus the set of twelve detail coefficients that would be applied to the four pixels of V_0 after reconstruction. V_2 is the sixteen values of V_1, plus the corresponding 48 detail coefficients, and so on (see Figure 2). Thus for our smallest ANN, the SANN (sixteen inputs), we use the coefficients from V_1, for the medium sized ANN, the MANN (64 inputs), we use V_2, and for our largest ANN, the LANN (256 inputs), we use V_3. The larger networks get input from detail coefficients that correspond to finer resolution, but none of our networks get the finest detail from the original image, which has 4096 wavelet coefficients and would require V_5.

Image classification

Artificial neural network structure

An artificial neural network (ANN) is a computing algorithm based on a simplistic model of the brain or, perhaps more accurately, a ganglion. The massively parallel architecture of the ANN consists of multiple layers of simple computing elements with many interconnections between the layers. The computing elements are functionally

analogous to neurons. They receive signals and in turn transmit a signal which is a function of the inputs. The function by which the inputs are evaluated may be a simple logic gate but more generally involves summation of weighted input signals. A threshold function is then applied to the weighted inputs to determine the output of the neuron. A simplified ANN architecture is presented in Figure 3. This is a fully connected three layer network.

The initial architectures of our ANNs were established according to the number of input neurons and the number of classifications that the program was being designed to distinguish. Each initial ANN consisted of a layer of input neurons and a layer of output neurons, fully interconnected by random initial weights. Each input layer neuron corresponded to a wavelet coefficient, which represented the detail contained in a set of pixels. Each output neuron was assigned to a genus or species that we were attempting to identify. Separate ANNs were developed and tested with 16, 64, and 256 inputs (corresponding to different amounts of detail in the images) and three, six, or two output neurons (corresponding to identification to genus, species, or species within genus). These last ANNs, with only two output neurons, could then be used to evaluate the ability of the pattern recognition system to identify specimens first to genus, then to species within a genus—the hierarchical approach. Other ANNs were developed with six output nodes and trained using the entire set of species in the three genera. These ANNs were used to evaluate the performance of the ANN in identifying species without regard to genus classification—the nonhierarchical approach.

After acquiring and processing the images from all samples, the set of images was divided into a training set and a testing set. The composition of the training set is shown in Table 1. Subsets of the entire testing set were made to test ANNs at different hierarchical levels as described above.

Figure 3. A simplified three layer, fully connected artificial neural network showing the input of a hypothetical image containing four wavelet coefficients (C1 through C4), encapsulating the information of 16 pixels. The number of nodes in the input and output layers are determined by the number of inputs to the network and the number of classification options, respectively.

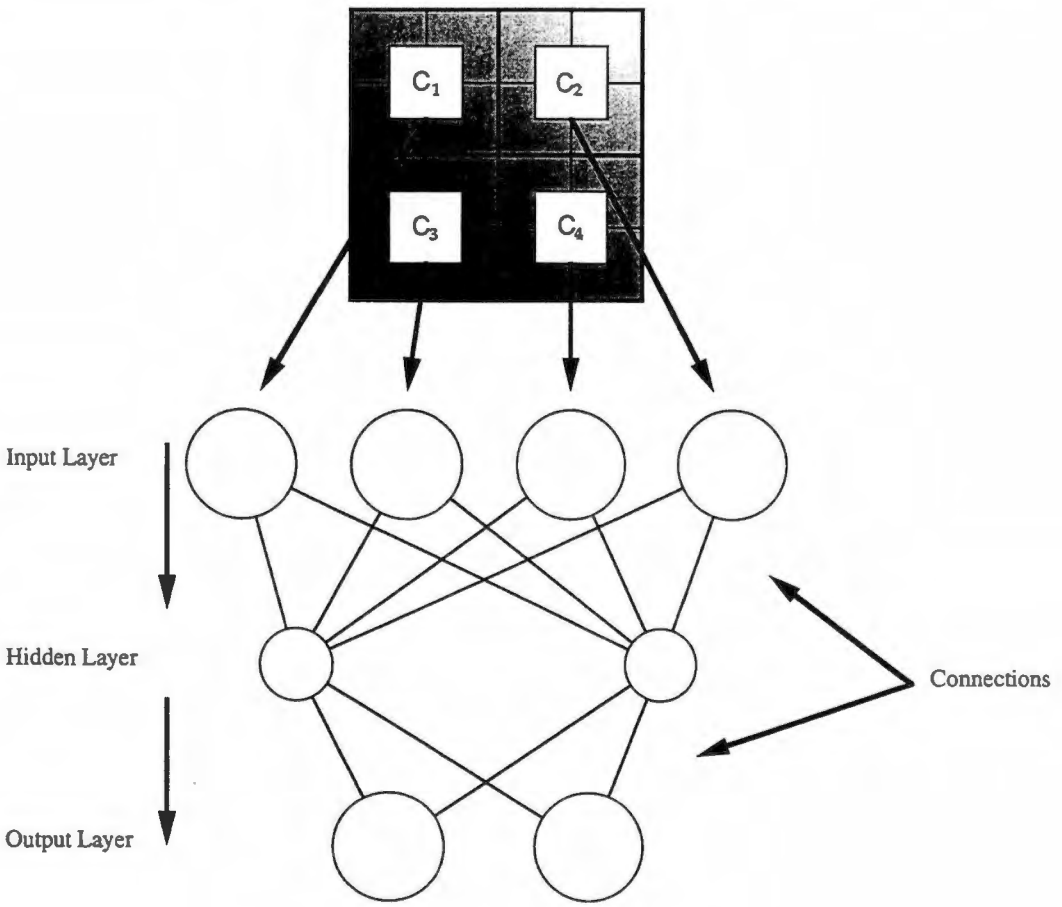


Table 1. Composition of the training sets used to train the artificial neural networks

Training set	Genus	Species	N
	Alopecosa	*A. aculeata*	11
		A. kochii	7
Lycosidae	*Pardosa*	*P. groenlandica*	8
		P. dromaea	10
	Arctosa	*A. rubicunda*	8
		A. emertoni	9

The training cycle

The following is a generalized description of the steps necessary to train and test any ANN, along with details specific to this study. Training involves effort in three phases: 1) assembly of the collection of object classes (in our case, spider species) by a taxonomist, 2) construction of the training data set and processing of the data into a form capable for input into the neural network (digital images in this study), and 3) the actual training of the neural network to recognize the object classes based on the training data set. Training continues until the desired level of accuracy is attained. It is at this point that the network is tested with previously unseen individuals to asses its ability to classify them into appropriate groups based on what it has learned from the training process (i.e., the network's ability to generalize). The idea is to 'teach' the ANN to set the output neuron, assigned to a given genus or species, to its maximum value of '1.0' when it sees a pattern indicative of that genus or species and set all other output neurons to a minimum value of '0.0'. In practice, the ANN will set the output neurons to an intermediate value depending on the certainty of its identification (e.g., an output of 0.9999 indicates certainty while 0.6 indicates less certainty). The training process introduces new neurons in a hidden layer between the input and output layers. These act as feature detectors to look for a specific pattern unique to a given genus or species. The resulting output vector is then evaluated against the target function to compute an error. This error is then used to modify the weights in the connections. An entire training cycle is referred to as an epoch. Training stops when the error becomes sufficiently small (in our case 0.001). The number of epochs required to reach the target error varies considerably (tens to many thousands) depending on the ease/difficulty in discriminating between the output groups and the amount and resolution of data being used. In this work, all ANNs were trained over 300

epochs and adjustable parameters such as learning rate and momentum were held constant.

Several algorithms exist to train an ANN, each of which possesses certain strengths and weaknesses. We used Cascade correlation in conjunction with quick propagation (Fahlman, 1988,1991). Cascade correlation adds hidden layer neurons one at a time throughout training. This allowed for quick learning and the ability to generate a near minimal ANN consisting of only those feature detectors that are needed. Minimizing computational time and resources is essential if this technology is to be widely accessible.

The time required for training should not be overly long. However, since the performance of the ANN is very fast after training, sufficient attention should be paid to the training process as to make the final structure as accurate as possible. At present, training the ANN requires considerable attention from the human operator. As we gain more experience with the behavior of the algorithms when applied to spiders, the process should become standardized.

Testing

For each size of network (SANN, MANN, LANN) and for each level of identification (genus, species alone, and species within genus), inputs were taken from subsets of a testing set consisting of images which the network had not seen before. The composition of the testing set can be read from Tables 2-4. Specimens from unknown species or genera were not presented to the network as part of this study.

RESULTS

Recognition of epigyna at the genus level

Training was performed over the entire Lycosidae training set (17 to 18 individuals per genus). The results of testing runs on the trained ANNs are given in Table

Table 2. Testing results for the artificial neural networks trained using the full Lycosidae training set

Taxon	N	SANN (%)	MANN (%)	LANN (%)
Alopecosa	16	100	100	100
Pardosa	19	74	100	100
Arctosa	16	100	100	100
overall	51	90	100	100

Note. The data represent the percentage of correct responses from the ANN over the total number, N, of unknowns presented to the trained ANN.

Table 3. Non-hierarchical testing results for the artificial neural networks (MANN and LANN only) trained on the Lycosidae training set

Taxon	N	MANN (%)	LANN(%)
Alopecosa aculeata	10	70	80
Alopecosa kochii	7	57	71
Pardosa groenlandica	9	44	44
Pardosa dromaea	9	89	89
Arctosa rubicunda	9	67	56
Arctosa emertoni	9	86	86
overall	52	69	73

Note. The data represent the percentage of correct responses over the total number, N, of unknowns presented to the trained ANN.

Table 4. Hierarchical testing results for the three artificial neural networks using training sets containing only specimens within a single genus

Training set	Taxon	N	SANN (%)	MANN (%)	LANN (%)
Pardosa	*P. groenlandica*	10	40	50	50
	P. dromaea	9	89	100	100
	overall	19	63	74	74
Arctosa	*A. rubicunda*	9	56	56	78
	A. emertoni	7	86	86	86
	overall	16	63	69	81
Alopecosa	*A. aculeata*	8	75	100	100
	A. kochii	8	75	100	75
	overall	16	75	100	88

Note. The data represent the percentage of correct responses over the total number, N, of unknowns presented to the trained ANN.

2. Both the MANN and the LANN were 100% accurate in their identifications to genus, while the SANN had an average accuracy level of 90%. Therefore, it is apparent that the system was more than adequate for distinguishing spiders to genus based solely on shape features of the female epigynum. This was true even given the small size of the training set.

Recognition of epigyna at the species level

The non-hierarchical approach

Only the MANN and LANN networks were used for this experiment. The ANNs were trained over the entire Lycosidae training set. The results of testing runs on this series of ANNs are given in Table 3. The overall accuracy level for identifications to species for the MANN and LANN were 69% and 73%, respectively. The overall results suggest that the LANN performed better than the MANN although some peculiarities exist in the results. The ability of the LANN to identify *Alopecosa* species was considerably better than that of the MANN but the performance of the LANN actually fell below that of the MANN for *A. rubicunda.* We are unable to explain these discrepancies except to point out that the training set was quite small (only 7-11 individuals per species). It should be noted that the probability of correctly identifying, by chance, a specimen taken at random from a set containing six species is only 16.7%.

The hierarchical approach

The SANN, MANN, and LANN were trained over the appropriate subset of the Lycosidae training set. The results of testing runs for all three sets are given in Table 4. The overall accuracy levels for the SANN ranged from 63% to 75%, from 69% to 100% for the MANN and from 74% to 88% for the LANN. Here again, the overall performance of the ANN improved with increasing number of included vector spaces represented in the input vectors. In this case, the performance of the LANN is less than that of the

MANN for *A. kochii* and the greatest improvement with size of ANN was seen in the *Arctosa* ANNs. It is clear that the SANN was inadequate but these results suggest that there may a point at which increasing the size of the ANN will not significantly improve performance.

DISCUSSION

The performance of the trained ANNs in the testing runs demonstrated that the pattern recognition system was capable of identifying lycosids with an accuracy level of 100% to genus and an average of 81% to species. This level of accuracy was surprising given the small size of the training set used in this study (7 to 11 individuals per species) and the limited amount of information on which the identification system was based. We feel that the size of this training set was inadequate to assess fully the abilities of the pattern recognition system; this was designed solely as a proof-of-principle study to evaluate the feasibility of using such pattern recognition systems for species identification in spiders. Increased accuracy could be attained simply by increasing the size of the training set (Simpson *et al.*, 1992). We also limited the information input to shape features of the female epigynum. A fully developed system could incorporate more types of information (e.g. carapace length/width, locality, distinguishing markings, etc.) which would again increase accuracy, particularly when species have very similar genitalia. In addition, the use of higher quality cameras, microscopes, etc. during the training process might enhance precision. However, the accuracy obtained through the use of such accessible equipment as used in this study further demonstrates the potential of this system and the feasibility of its use by the general scientific community. Once trained, the neural network software could run on most personal computers.

Based on the comparative performances of the small (SANN) and large (LANN) networks, it was apparent that the SANN did not incorporate adequate data to distinguish spider species. Although it is clear that future ANNs should be at least the size of the MANN (medium sized with 64 input neurons), it is not clear whether they will necessarily always perform better with larger amounts of input neurons. The data also indicated that a hierarchical ANN was preferable to a non-hierarchical ANN. In other words, higher accuracy was attained when the network first classified the specimen to genus and then to species as opposed to going straight to species (81% vs. 73%, respectively). We would expect this to be true as long as the higher organizational group (in this case, the genus) is well defined with respect to the characters examined (in this case, the epigyna). Boddy *et al.* (1994) found that the hierarchical approach was not as good when identifying phytoplankton because the classification scheme used was not compatible with the characters fed into the network. Some species within one group resembled those in another group enough that they were always initially misclassified and therefore always misidentified. In the identification of spiders using genitalia, we speculate that although it would be beneficial to use the hierarchical approach to the level of genus, it would not be acceptable to have the network classify to the family level since these classifications are often made based on other characteristics. A separate network for each family may be the best option, since identification to family is more easily accomplished by the non-specialist. In future work, we will explore these options by testing the network on more than one family group.

In this study, we chose to use the epigynum as a test case. The essentially two dimensional nature of the ventral view of the structure served to simplify technical aspects of the work. We also used a subset of spiders which can be readily identified based on external genitalia; this will not always be the case, as some species can only be

identified based on internal genitalia or other characteristics. Nonetheless, this system has the potential to read any visual input and artificial neural networks can be designed and trained specifically for any group. The next step in the development process will be the addition of another dimension to make possible an ANN capable of identifying species on the basis of a single view of the adult male spider's genitalia, the palpus. Future development will involve the training of an ANN using multiple views of the same adult male palp or epigyna for those species which require this information for accurate identification. It is proposed that the ANN will avoid the need of reconstructing a three dimensional image of these complex structures simply by learning to recognize a set of two, two dimensional images taken at arbitrary angles. This technology is not limited to arachnology. The methods being developed here will transfer to any other taxa for which visual traits are used to distinguish genera or species (e.g. wasps (wing venation), scale insects (scales), many other insect groups (genitalia)).

We have undertaken this study as a first step toward making routine, accurate species identification of spiders accessible. We suggest that the ANN as a pattern recognition system will be useful in making the results of taxonomic research widely available by encapsulating the subjective impression of shape, and variability in shape, and making that information available to any user who may be viewing a structure for the first time. Because the network is trained on multiple individuals of each species, it has the advantage of incorporating intraspecific variation. Obviously, this system must be tested on a much larger set of species before we will know for sure how well it will perform as a tool in biodiversity studies. If the system continues to perform adequately when processing larger numbers of genera and species and/or different kinds of visual data, we suggest that these systems could become one end product of taxonomic research. Databases could incorporate artificial neural networks to make taxonomic knowledge

available to anyone who could benefit from the ability to make accurate identifications of genera or species. At the very least, these systems could be used in biological monitoring programs where the ANN could be trained with the initial species collected at the site of interest. All subsequent collections would then at least be 'standardized' to the original, regardless of changes in taxonomic nomenclature and/or personnel.

We should emphasize that the methods used in this work can not supplant the role of the taxonomist. Pattern recognition systems are only useful for encapsulating the results of taxonomic investigations and are not capable of independently ordering or explaining organic diversity. The ANN is a system which can simulate learning and make use of that learning. But, one should bear in mind that the software can only learn what it is presented during the training process. Also, the ANN can not replace the revision as an end product of taxonomic investigation. What we have done here is to address the limitation of the revision as a vehicle for making the results of taxonomic investigation accessible to the end user. By freeing taxonomists from the burden of identifying collections of known species sent to them by other workers, they will have more time for the most important aspect of their work— description and revision of species and species groups.

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PART IV: TOOLS FOR BIODIVERSITY STUDIES: RAREFACTION, EXTRAPOLATION AND INDICES

INTRODUCTION

In most biodiversity studies, the goal is not merely to establish the species composition of a specific site at a specific time, but rather to somehow quantify the differences between sites or between surveys from the same site. Sometimes the purpose is to measure the effect of a known disturbance at one or more of the sites, or to decide which of a series of candidate sites would be the best to conserve. The presence or absence of a set of species may be used to indicate either that a habitat is free of anthropogenic disturbance, or that it is in an unnaturally 'disturbed' state. These kinds of comparisons necessitate the use of mathematical tools which yield comparable entities such as an index or sample of similar size. Indices collapse down the information from one site (or between two sites) into a single number which can then be used to distinguish between or compare sites. Differences in sample size or sampling intensity may also require some method of standardization prior to the calculation of an index. Even before sampling begins at the start of a study or monitoring program, it is important to decide what kind of analyses and indices will be used once the sampling is complete, as this may determine how the data should be collected.

With the ultimate goal of measuring the dynamics of spider assemblages at six sites in the Southern Appalachians, I selected a range of commonly used indices to evaluate their usefulness in a study of this sort. Extrapolated richness and various diversity, turnover, and similarity indices may be used to quantify changes in community structure through time. In this chapter, I examine the degree to which the indices and richness estimates are correlated, their sensitivity to differences in sample size (and the use of rarefaction to correct for this), and their ability to detect changes in spider assemblages in response to gross changes in vegetation structure.

METHODS

The Data

Spider species abundance lists from six sites in the Southern Appalachians were used as sample data-sets for the analyses that follow. The sites are located in two study areas, Macon County and the Great Smoky Mountain National Park (henceforth GSMNP). Five of the six sites are forested and of these, two are undergoing secondary succession as they were clear-cut within the last 30 years. Sampling of the spider assemblages was completed in 1976, 1995-1997 in Macon County and 1995-1997 in the GSMNP (see Table 1 for details). A full description of the sites, sampling protocols and results of sampling are given in Part II of this dissertation. The only significant change from the sampling results reported in Table 3 of Part II, concerns the Ellicott sites in Macon County. A subset of the total sample for 1996 and 1997 was selected for this analysis, reflecting equivalent sampling effort to the 1976 and 1995 surveys. Additional sampling effort beyond what was conducted in 1976 and 1995 was eliminated from the analyses because the distribution of effort among sampling methods was not the same in the expanded effort in 1996-7 as in the earlier surveys. As different sampling methods collect different subsets of the spider assemblage, the distribution of effort among the methods must be the same prior to making comparisons between assemblages. See Table 2 for a description of the data in the subsets.

Table 1. Characteristics and sampling history of study sites

Location	Site Name	Habitat Type	Size	Methods (each year)	Dates of Surveys
Nantahala National Forest, Macon Co., NC	Horse Cove	forest (clear-cut 1971)	16ha	*8, 16 pitfall traps 10 (.25-m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Nantahala National Forest, Macon Co., NC	Ellicott Rock Clear-cut	forest (clear-cut 1974)	8ha	8, 16 pitfall traps 10 (.25-m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Nantahala National Forest, Macon Co., NC	Ellicott Rock Forest	forest (mature; pine-hardwood)	8ha	8, 16 pitfall traps 10 (.25-m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Great Smoky Mountains National Park, Sevier Co., TN	Old growth hemlock/ hardwood	forest (mixed hemlock-hardwood)	2ha	6 (1-m2) litter samples 8 hours beating 16 hours hand collection	**Ju95,A95 M96,A96 M97,A97
Great Smoky Mountains National Park, Swain Co., NC	Beech Gap Forest	forest (beech gap)	1.5ha	3 (1-m2) litter samples 4 hours beating 8 hours hand collection	**Jul95 Ju96,A96 Ju97,A97
Great Smoky Mountains National Park, Blount Co., TN	Meadow Branch	marsh/meadow	1ha	3 (1-m2) litter samples 2 hours sweep netting 6 hours hand collection	**Ju95 M96,A96 M97,A97

*if two numbers are given, the first pertains to the 1976 survey only

**a less intensive sampling regime was carried out in 1995 for these sites

Table 2. Collection data used for analysis

A. Macon County

		1976	1995	*1996(l)	1996(t)	1997(l)	1997(t)
Ellicott	#individuals	583(217)	387(215)	416(123)	828(272)	425(245)	708(387)
Forest	#species	60	58	51	64	56	71
	#genera	55	48	51	58	48	58
Ellicott	#individuals	284(131)	463(212)	417(117)	793(236)	340(163)	613(302)
Clear-cut	#species	53	50	46	59	44	61
	#genera	51	49	44	52	42	56
Horse	#individuals	378(184)	219(127)	358(158)	---	456(225)	---
Clear-cut	#species	71	45	51	---	56	---
	#genera	61	40	47	---	48	---

*l and t refer to limited and total collections

B. GSMNP

		*E1995	L1995	E1996	L1996	E1997	L1997
Beech	#individuals	---	252(252)	669(491)	855(464)	662(390)	702(356)
Forest	#species	---	22	35	32	36	36
	#genera	---	21	30	28	30	31
Hardwood	#individuals	113(112)	116(114)	983(707)	813(229)	1835(988)	1566(411)
Forest	#species	30	29	63	62	73	57
	#genera	26	28	46	51	55	47
Meadow	#individuals	163(160)	---	353(257)	264(130)	421(292)	313(214)
Marsh	#species	45	---	46	44	52	47
	#genera	37	---	39	34	41	37

*E and L refer to early and late summer collections.

Notes. In Macon County, the 1996 and 1997 surveys were more intensive than the 1976 and 1995 surveys, including additional hand collection, sweep netting, and pitfall trapping. The total data resulting from these surveys is noted by (t). A subset of this data (l), is directly comparable to the 1976 and 1995 surveys as it is the result of an equal amount of sampling effort. The number of adult specimens collected are in parentheses. Juveniles which could not confidently be assigned to species are included in the individual counts and counts of genera, but not in the species counts. The only exceptions to this were cases where the juveniles were the only representatives of a genus which had not been collected at the site previously. In this case, the juveniles were included in the species count. It was assumed that those specimens represented at least one unique species. For the GSMNP sites, little attempt was made to identify juveniles from the 1995 surveys.

Because evaluation of the indices is based on their ability to quantify changes in community structure through time, some non-mathematical standardization of the surveys was conducted. Thus, to make the Macon County historical survey and my surveys comparable, identifications were made according to the systematic literature at the time of the first survey. For example, if a species had been subsequently split into two species, only the single species was counted for comparison. This only occurred twice, with species in the genera *Wadotes* and *Schizocosa*. All 1976 specimens which were identified to morphospecies, but not given a species name, were eliminated if no individuals were available for comparison or no match could be made with the recent collections. One exception to this was a case where a numerically prominent species from the 1976 survey (Salticidae sp. A) was included in the analysis based on the fact that no unknown adult specimens were collected at all in that family in the 1995-97 surveys. It was, therefore, concluded that that species could not have been present in any of the recent surveys and thus represented a real change in the assemblage. A total of 11 morphospecies (20 individuals) were eliminated from the 1976 survey and five morphospecies (12 individuals) were eliminated from the 1995-1997 surveys.

Indices

I chose two sets of indices. The first set ('diversity indices') includes those which are calculated at an instant in time and then used to compare years or months within years at each site. The second set ('similarity/difference indices') quantifies the difference in species composition between years or between months within years.

Diversity Indices

Although this type of index proved not to be terribly informative when attempting to compare the diversity between the six sites (Part II, this dissertation), I've included them here for two reasons. The first is that instead of attempting to compare between sites

which differed in habitat type and sampling intensity (and/or methods), I will be examining the behavior of these indices within sites, through time. This should reduce some of the variability and make the indices more comparable. The second reason is simply because these indices are extremely common in the literature and used by many workers.

These indices can be divided into two types. The first simply attempts to assess the richness of species at a particular time and place. Probably the most straightforward approach is to extrapolate the richness of a site based on some characteristics of the sample. For this purpose, I used the Chao1 estimator (Chao 1984) because it has recently been used in several biodiversity studies and is reported to be relatively insensitive to differences in sample size (Dobyns 1997, Coddington *et al.* 1996, Chazdon *et al.* 1996). It is non-parametric, though it makes use of relative abundance data. It is calculated using the formula

$$S_1^* = S_{obs} + \left(\frac{a^2}{2b}\right),$$

where S_{obs} is the number of species observed, a is the number of singletons (species represented by exactly one individual), and b is the number of doubletons (species represented by exactly two individuals). Other richness indices make use of both the number of species collected and the total number of individuals collected. As an example of this type, I used Margalef's diversity index (Clifford and Stephenson 1975) which is calculated with the simple formula

$$D_{Mg} = (S-1)/\ln N,$$

where S is the number of species recorded and N is the total number of individuals summed over all S species.

The second type of index includes information on the proportional abundance of species in a sample. I used the Shannon index, the Brillouin index, and Simpson's index. These indices are widely used in the literature and their attributes are discussed at length by Magurran (1988). A complete list of formulae for these indices can be found in Appendix II.

I used the Shannon index because it is ubiquitous in the literature, and one can use parametric statistics to test for significant differences between surveys. I also used the Brillouin diversity index for comparison with the Shannon index because some of the sampling methods used in this study (e.g., pitfall traps) do not necessarily collect a random sample of the community. The Brillouin index is recommended for situations where the randomness of the sample cannot be guaranteed (Magurran 1988). The evenness measures associated with these two indices were calculated as well. I used the Simpson's index because it is considered a dominance measure, as it is weighted towards the abundances of the most common species in the community. The collections made at each site were not exhaustive and therefore the number of 'rare' species was artificially elevated. Simpson's index partially counteracts this effect.

Similarity/Difference Indices

These indices can also be divided into two types. The first quantifies change in species composition alone, with no reference to abundance. The simplest way to quantify local colonizations and extinctions in an area is by use of an index of turnover. Turnover, as defined by MacArthur and Wilson (1967) simply estimates the number of local colonizations and extinctions relative to the number of species in the community. Even though this idea was originally developed for island situations, it also can be applied to the overlapping metapopulations which exist in a particular habitat.

The formula I used to calculate turnover (following Russell *et al.* 1995) is simply

$$T_n = \frac{E_n + I_n}{S_y + S_{y+n}},$$

where E_n is the number of observed local extinctions over interval n, I_n is the number of observed immigrations over the same period, S_y is the number of species in the first year (y) and S_{y+n} is the number of species in the second year. This index ranges from 0 to 1.

Turnover is a quantitative measure of change, but it only makes use of presence/absence (qualitative) data. To make use of abundance data for each species, I calculated two more similarity indices: Bray-Curtis and Morisita-Horn. The Bray-Curtis similarity index (Bray and Curtis 1957) is probably the most widely used of the similarity indices (Magurran 1988) and one of the most simple. It is calculated using the formula

$$C = \frac{2w}{(a+b)},$$

where a is the total number of identified individuals in one sample, b is the total number of identified individuals in the other sample, and w is the sum of the lesser relative abundances for those species present in both samples. This index ranges from 0 to 1.

I also calculated the Morisita-Horn index of community similarity because it is considered to be less sensitive to sample size and species richness (Smith 1986, Wolda 1981). It is expressed as follows

$$C = \frac{2\sum n_{i1} n_{i2}}{(\lambda_1 + \lambda_2) N_1 N_2},$$

where

$$\lambda_j = \frac{\sum_i n_{ij}^2}{N_j^2}$$

C is the index of community similarity, N_j is the number of individuals in sample j, and n_{ij} is the number of individuals of species i in sample j. This index also ranges from 0 to 1.

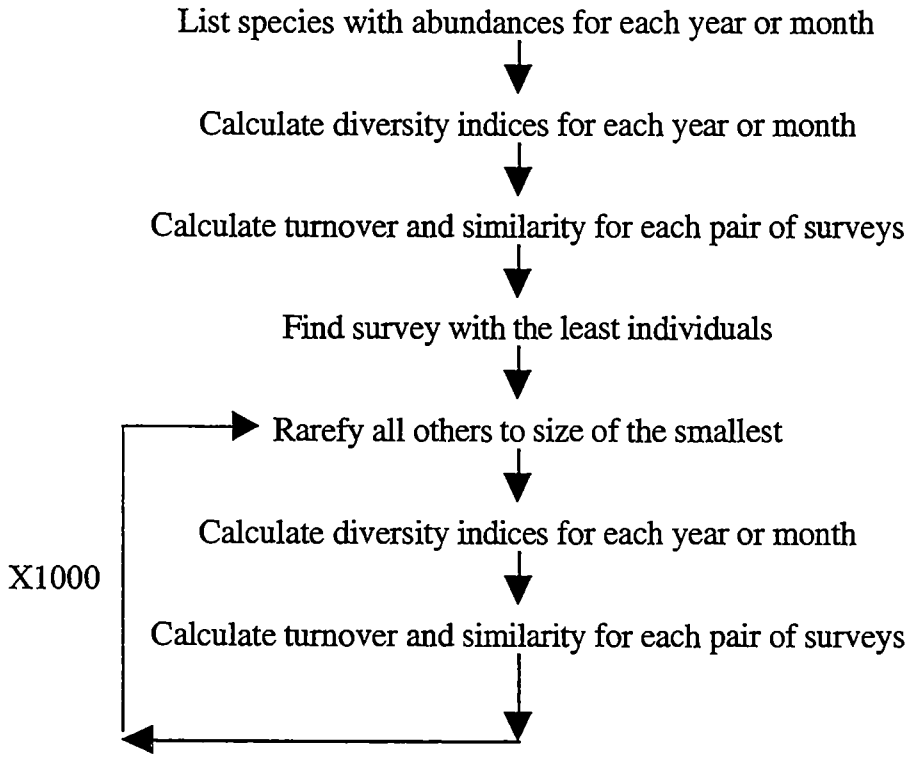
Rarefaction

It is inevitable that differences in sample size will exist between both the historic and present surveys and between the yearly surveys, even if the sampling protocol is followed exactly. Except under certain conditions, it is meaningless to compare the diversity or measure the turnover of different sized collections. Therefore, I scaled all samples to the size of the smallest sample; a procedure called rarefaction. Rarefaction was originally used to calculate $E(S_n)$, the expected number of species in a sample of n individuals selected at random from a collection containing N individuals of S species (Heck *et al.* 1975). From the list of individuals in all but the smallest of the samples, a number equal to the number of individuals in the smallest sample was randomly selected. This generates a new species list and associated abundance distribution. The indices were calculated using this 'rarefied' sample and the procedure was repeated 1000 times to obtain a mean and spread of simulations for the indices. See the flow chart presented in Figure 1 for details of this process. Because different subsets of the data were used for different analyses (i.e. comparison of methods, adults versus juveniles), the year or month which produced the smallest sample did vary. It is important to note that doing more stochastic rarefactions will cause the means of the indices to converge on a particular value. After 50 rarefactions, the confidence interval for the mean for each index was typically less than 1% of the range of the index (for those indices which range from 0 to 1).

RESULTS

Applying the techniques discussed above, an initial analysis of community change through time was carried out using the sample data.

Figure 1. Flow chart illustrating the sequence of calculations for an analysis within each site. The calculation of the diversity indices both before and after rarefaction, allows us to examine the effect of rarefaction (and therefore sample size) on these indices. The rarefaction procedure is repeated 1000 times in order to obtain a mean and a variance for the estimates.



Correlation of indices

The Shannon index, Brillouin index, Simpson's index and Margalef's index were calculated for each year's data at the three sites in Macon County Within each site, all indices showed the same gross trends through time. The correlation of the indices is illustrated by data from Ellicott Clear-cut in Figure 2. In contrast, the Chao1 extrapolated richness estimates did not seem to be correlated with the other indices and no clear trends through time were evident (Figure 3). Bray-Curtis and Morisita-Horn similarity were highly correlated with each other, and though consistently showing the same patterns (Figure 4), Morisita-Horn was almost always higher than Bray-Curtis. As turnover measures change in the assemblages, it was negatively correlated with the similarity indices (Figure 4).

Long-term turnover and similarity

Long-term turnover (19, 20, and 21 years) was much greater than short-term turnover (one and two years) for the Macon County sites (Figure 4). The same pattern can be seen for the Similarity indices, with similarity lower for long-term comparisons (Figure 4).

Figure 4 also illustrates that the differences between the long and short-term measures of turnover and similarity are greater for the old clear-cuts than for the mature forest.

Trends in diversity indices

In Macon County, with the exception of the Chao1 richness estimates, the values of all other indices for 1995, 1996, and 1997 are more similar to each other than to the values calculated for 1976. In addition, for both clear-cut sites (Horse clear-cut and Ellicott clear-cut), there is a definite trend through time for all the indices except Chao1.

Figure 2. Trends in diversity indices through time for Ellicott Clear-cut. Solid circles with error bars represent the mean of the index estimates after 1000 rarefactions. The error bars contain 95% of the estimates after rarefaction. Solid circles without error bars indicate the index as calculated for the smallest survey (no rarefaction necessary).

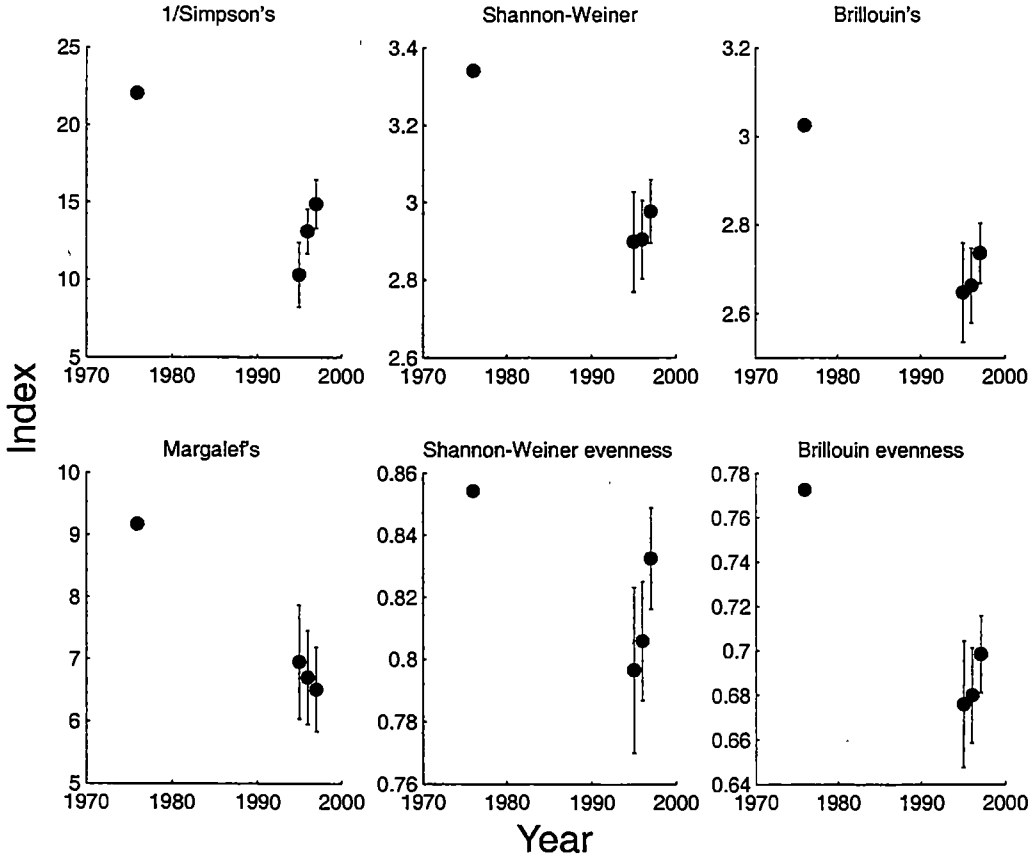


Figure 3. Chao1 richness estimates for sites in Macon County. Solid circle represent the extrapolated richness estimate of Ellicott Forest (A), Horse Clear-cut (B), and Ellicott Clear-cut (C) calculated using the Chao1 richness estimator (Chao 1984). Error bars show 95% confidence intervals based on the expected variance associated with this index (see Appendix 2 for formula).

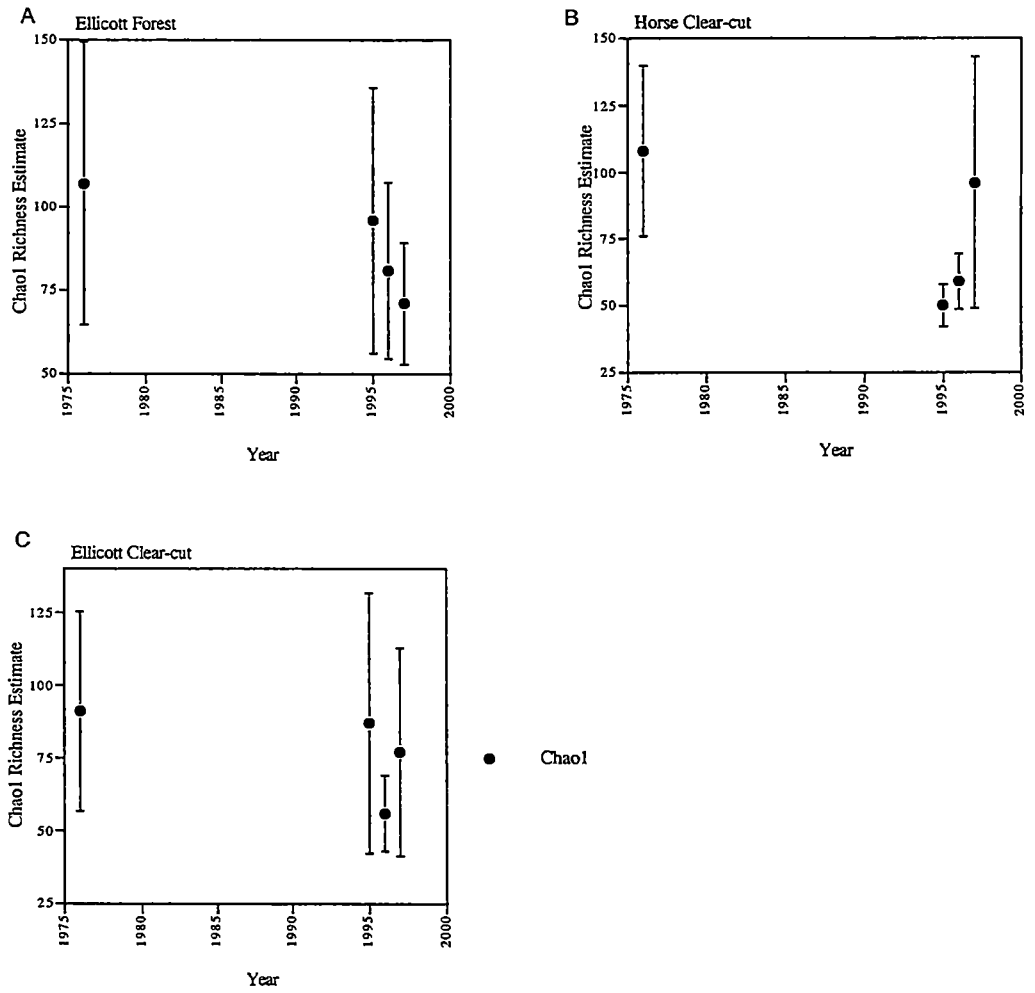
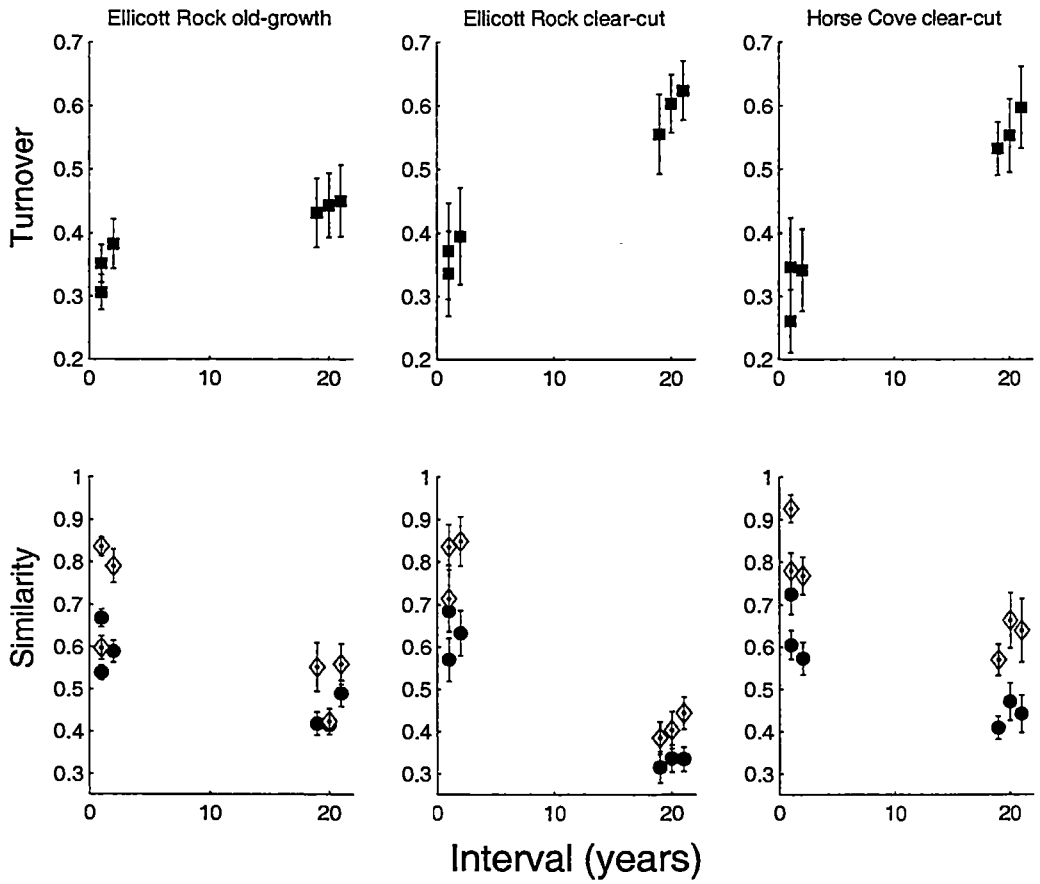


Figure 4. Turnover and similarity index values for sites in Macon County. Squares represent mean turnover estimates after the data had been rarefied and turnover calculated 1000 times. Circles represent mean Bray-Curtis similarity estimates and diamonds represent mean Morisita-Horn similarity estimates, also after 1000 rarefactions. The error bars contain 95% of the rarefied turnover and similarity estimates.



These show a decrease in diversity, richness, and evenness, and an increase in dominance (data from Ellicott clear-cut only are shown in Figure 2). The mature forest (Ellicott Forest) shows less of a trend, and when a trend is apparent, it is in the opposite direction (increase in diversity, richness and evenness and a decrease in dominance). Figure 5 illustrates these trends with the Shannon index (all indices were, to some extent, correlated with each other). I carried out pairwise significance tests on the Shannon-Weiner index following Magurran (1988). The *t*-values and significances are reported in Table 3. For Ellicott clear-cut and Horse clear-cut, all but one of the pairs that included the 1976 data were significantly different ($p<0.01$ after the Bonferroni correction for multiple tests). For Ellicott Forest, none of the three pairwise tests using the 1976 data were significant. For Horse clear-cut, the difference between two of the recent years (1995, 1997) was significant, again in a positive direction. To be sure that the differences between the 1976 samples and the 1995, 1996 and 1997 samples for the clear-cut sites couldn't be attributed to a difference in collectors (a non-random sampling effect), the analysis was repeated using only the pitfall trap and litter sample data. These methods are likely to be the least subject to sampler bias because the techniques used to take and process litter samples and install pitfall traps are more clearly defined and less likely to vary from individual to individual (see 'Sampler Bias' in Part VI). As shown in Table 3, the trends still hold, and now the difference between 1995 and 1997 for Horse clear-cut is no longer significant.

The only other site to show a consistent trend in the diversity indices through time is the beech gap forest (Figure 6). Although only three years of data have been collected, a trend is apparent in all of the diversity indices. This trends indicates a decrease in dominance and an increase in diversity (Shannon's index increases from 2.07 in May 1995 to 2.25 in May 1996 to 2.72 in May 1997; Shannon's index also increases from 2.35

Figure 5. Trends in the Shannon-Weiner diversity index for sites in Macon County. Solid circles with error bars represent the mean of the Shannon-Weiner estimates after 1000 rarefactions. The error bars contain 95% of the index estimates after rarefaction. Solid circles without error bars indicate the index as calculated for the smallest survey (no rarefaction necessary). Data from all collection methods were used in the calculation of Shannon-Weiner diversity for the top three graphs and only data collected using pitfall traps and litter samples were used to calculate Shannon-Weiner diversity for the bottom three graphs.

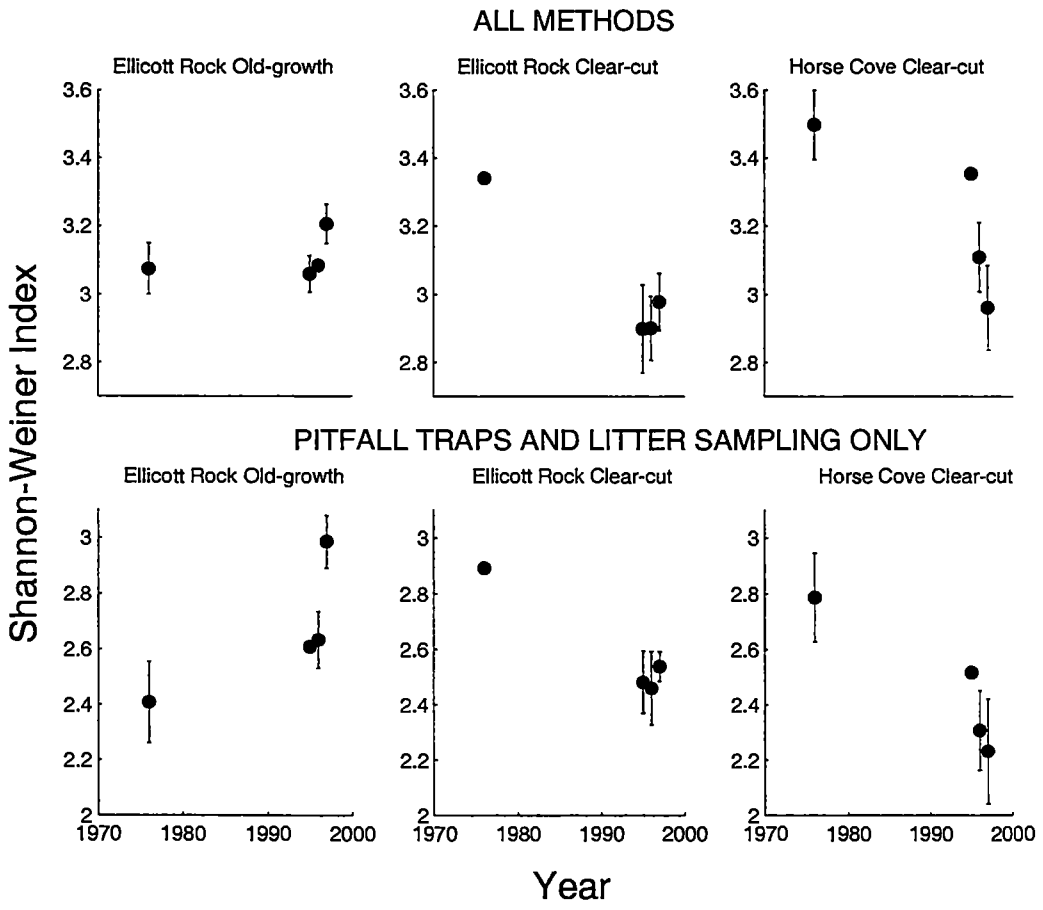


Table 3. Significance of trends in the Shannon-Weiner Index *t*-values for paired tests

Paired years	Ellicott Forest	Ellicott Clear-cut	Horse Clear-cut
76,95	0.3986	4.0875**#↓	2.4278
76,96	0.2932	4.4278**#↓	4.5105**#↓
76,97	1.3631#↑	3.7898**↓	6.0379**#↓
95,96	0.1130	0.2617	2.1794
95,97	1.5466#↑	0.4926	3.6796**↓
96,97	1.5105#↑	0.7777	1.4069

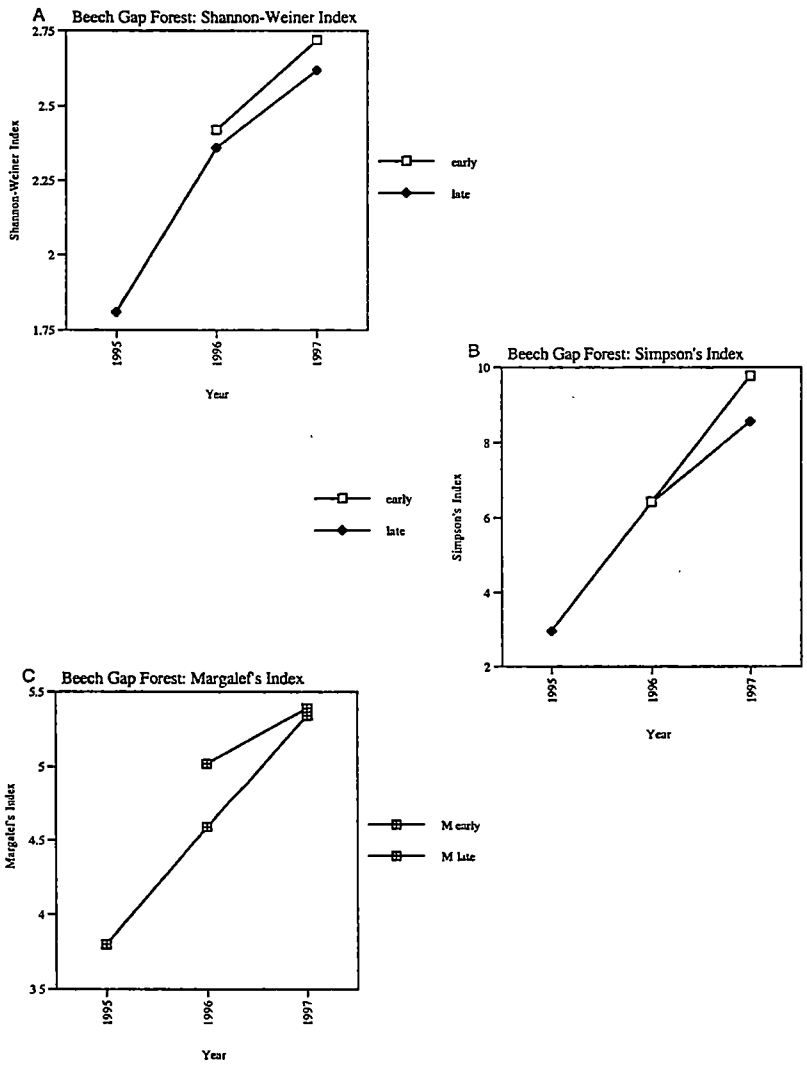
* $p<0.01$

** $p<0.001$

\# $p<0.001$ for analysis using data from pitfall and litter samples only

Notes. Variance and *t*-values were calculated following Magurran (1988). Arrows indicate the direction of the change in the index to illustrate the contrast between the mature forest and the clear-cut sites. Significance is reported with Bonferroni correction for paired tests.

Figure 6. Trends in diversity indices through time for Beech Forest. (A) Open squares represent the Shannon-Weiner Index calculated for early summer 1996 and 1997. Solid diamonds represent the Shannon-Weiner Index calculated for late summer 1995, 1996, and 1997. (B) Open squares represent 1/Simpson's Diversity Index calculated for early summer 1996 and 1997. Solid diamonds represent1/Simpson's Diversity Index calculated for late summer 1995, 1996, and 1997. (C) Same timing as above, only squares represent Margalef's Diversity Index. Lines connecting these values are illustrative and indicate comparable surveys (i.e. early 1996 can be compared with early 1997, but should not be compared with late 1997 as this community was sampled during a different season and is therefore not representative of the same assemblage).



in August 1996 to 2.62 in August 1997). I conducted pairwise significance tests on the Shannon index values and all but one of the pairs were significant ($p<0.05$ after Bonferroni correction), indicating that overall there is a significant change in diversity.

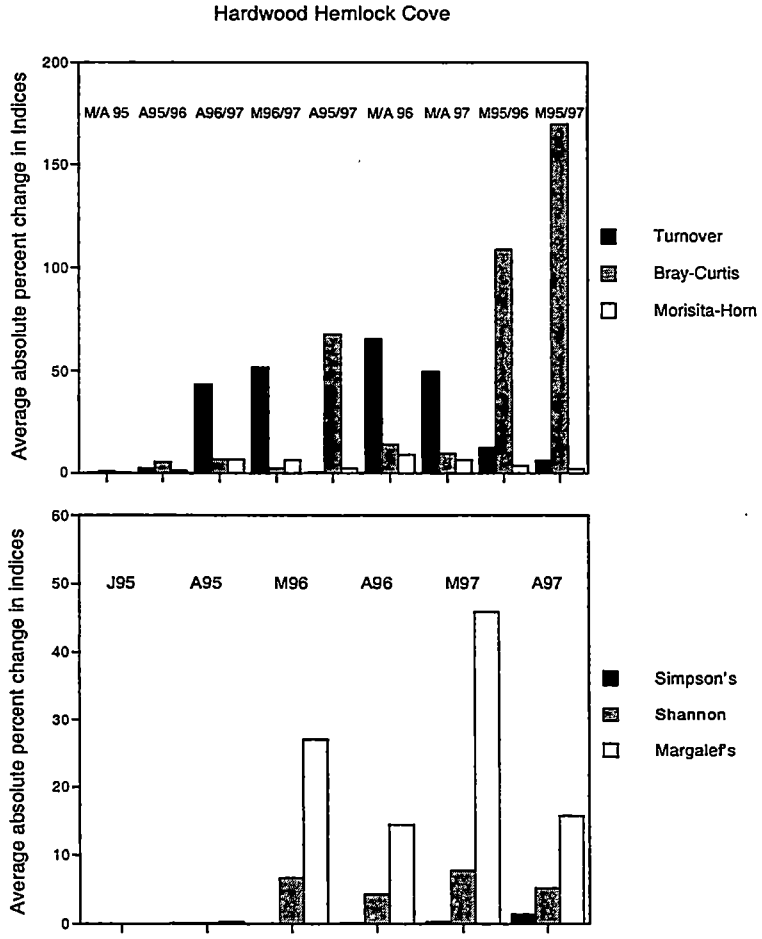
Sensitivity of indices to sample size

All indices (except Chao1) were calculated both before and after rarefaction for each analysis to compare the sensitivity of all the aforementioned indices to sample size. To best illustrate the trends, data are presented from the site for which there were the greatest differences in sampling effort and, therefore, sample size: the old-growth hemlock hardwood cove (Hardwood Forest). One hundred and eleven adult specimens were collected in May 1995, compared with 113 in August 1995, 230 and 701 in May and August 1996, and 412 and 986 in May and August 1997. Only adult specimens were used in the analysis because only adult specimens were identified from the 1995 surveys.

Comparisons were made between the same months in different years and between different months in the same year, both before and after the data had been rarefied down to the size of the 1995 sample for the Hardwood Forest site. Of indices which compare pairs of samples, turnover and Bray-Curtis similarity were the most sensitive to sample size. Morisita-Horn similarity was the least sensitive (Figure 7). Of the diversity indices, Simpson's is the least sensitive to sample size and Margalef's is the most, with Shannon in the middle, as predicted by Magurran (1988).

Chao1 was examined separately because it is an extrapolation technique and so instead of collapsing down the information of a survey into a comparable index (like the others), it actually attempts to estimate the 'true' richness of a site based on a sample. Therefore, rarefaction should not be necessary and so was not used prior to extrapolation. Instead, Chao1 was calculated on raw samples of different sizes using data from the same site (Hardwood Forest). The richness estimates were plotted against sample size,

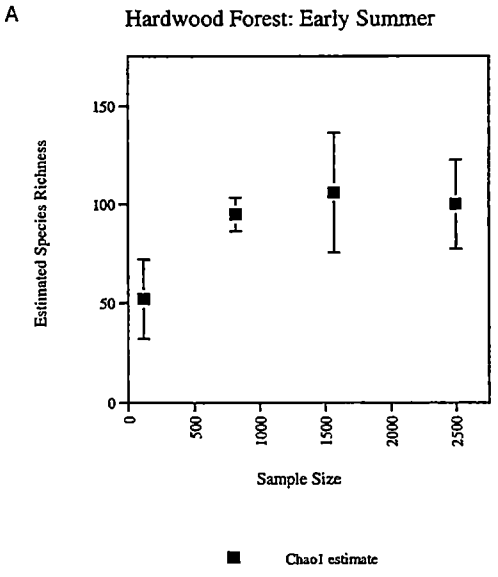
Figure 7. Effect of sample size on index values illustrated using data from Hardwood Forest. Indices were calculated both before and after rarefaction. The May 1995 sample had the fewest adult individuals (111), therefore all other samples were rarefied down to 111 individuals from 113 in the August 1995 sample, 230 and 701 in the 1996 sample and 412 and 986 in the 1997 sample. The mean of the rarefied index estimates (after 1000 repetitions) was subtracted from the index calculated from the raw data and then divided by the raw index to get a measure of the average percent change. All possible pairwise comparisons are shown for Turnover, Bray-Curtis similarity, and Morisita-Horn similarity (A) and the results are ordered based on the similarity of the samples in each pairwise comparison (the comparisons with the most similar sample sizes prior to rarefaction are to the left). The changes in Simpson's index, Shannon-Weiner (H') index and Margalef's index are illustrated in chronological order (B) for all samples collected.



separating out the early and late summer surveys, as the 'true' richness is probably different at these times due to seasonal turnover (Figure 8). The same plots were made for the Ellicott sites (Figure 9). Based on these analyses it appears that very low sample sizes produce quite different richness estimates than larger samples. But, this may not be a suitable analysis because the data-points represent surveys which have taken place either in different years, or with slightly different sampling methods. Therefore, some of the variability of the richness estimates must be attributable to actual differences in the 'true' richness of the habitats at different points in time. To correct for this, using data from Macon County, I took the combined data-set for both Ellicott Forest and Ellicott Clear-cut and randomly selected a set number of individuals from the larger sample and re-calculated Chao1 (Figure 9). This removes the temporal and methodological bias from the data, allowing a direct examination of the index's behavior with respect to sample size. As is clear from Figure 9, the Chao1 richness estimates on the rarefied data were all very similar to each other.

Because of these rather contradictory results, I looked at the data a third way, this time examining the behavior of the index as sub-samples were added sequentially. Like species accumulation curves, the index is plotted against cumulative samples or individuals. If the index is rather insensitive to sample size, we would expect it to level off rather quickly as individuals were added to the sample. Using the Hardwood forest data, I plotted Chao1 vs. cumulative individuals (Figure 10). From this plot, it is evident that the richness estimator did not appear to level off in three out of four surveys. For comparison, I made the same plots for the Shannon index and the Simpson's Index (Figure 11A,B). Both of these plots show that these indices converge once sample sizes reach a certain threshold.

Figure 8. Estimated richness of a sample calculated using the Chao1 richness estimator (squares). Early summer (A) and Late summer (B) surveys were plotted separately, as the 'true' richness is probably different at these times due to seasonal turnover. Three of the four estimates plotted were calculated from the results of separate surveys carried out in 1995, 1996 and 1997. The estimate with the largest sample size was calculated based on the combined total of the three surveys for each season. Error bars show 95% confidence intervals based on the expected variance associated with this index (see Appendix 2 for formula).



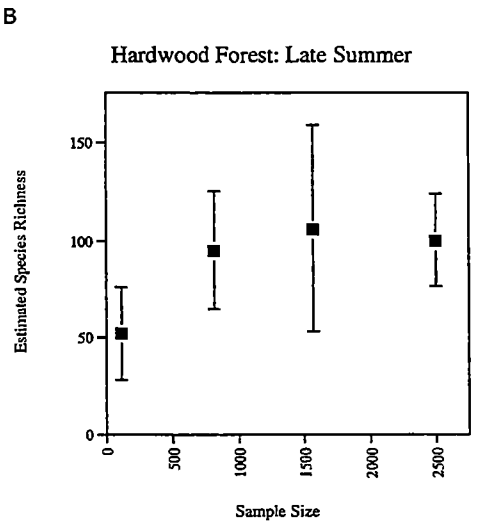


Figure 9. Estimated richness of Ellicott Forest (A) and Ellicott Clear-cut (B) based on different sized samples (squares) as calculated using the Chao1 richness estimator. Error bars show 95% confidence intervals based on the expected variance associated with this index (see Appendix 2 for formula). The data used to calculated these indices was taken from the 1995, 1996 and 1997 surveys only. The seven datapoints represent independently calculated richness estimates based on the three years of limited surveys, the two years of surveys along the transects, and the sum of these two types of surveys. Solid circles represent the richness estimates calculated from data which had been rarefied down to a percentage of the largest sample (i.e., 90%, 80%, 70%, etc.). Error bars show 95% confidence intervals based on the expected variance associated with this index.

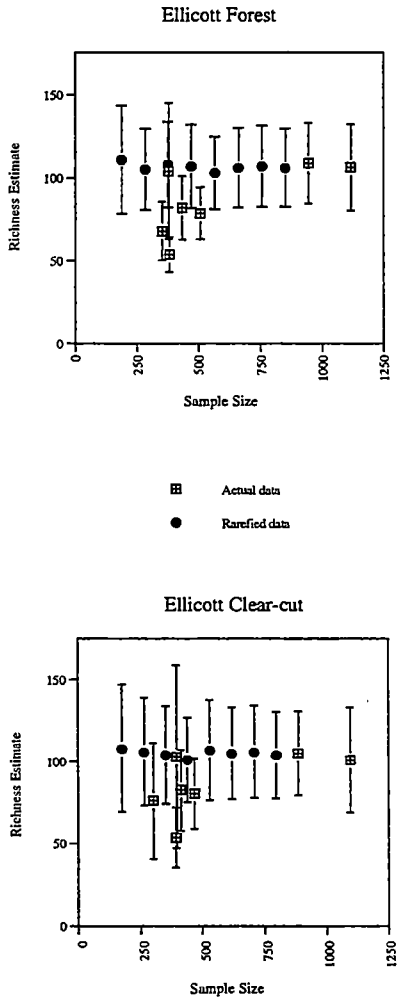


Figure 10. Cumulative number of individuals (average after randomization of the 18 sample units) versus the extrapolated richness estimates calculated using the Chao1 richness estimator for Hardwood Forest. The richness estimate was re-calculated after each sampling unit was added. Each season/year combination was kept separate for this analysis. Squares show the richness estimates based on the early summer 1996 samples. Diamonds show the richness estimates based on the early summer 1997 samples. Circles show the richness estimates based on the late summer 1996 samples and Triangles show the richness estimates based on the late summer 1997 samples.

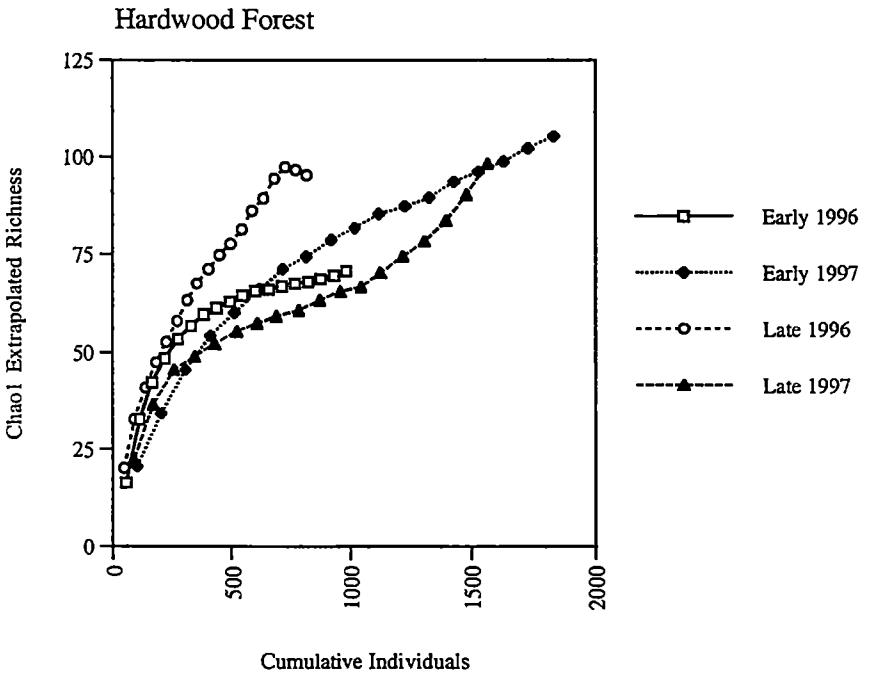
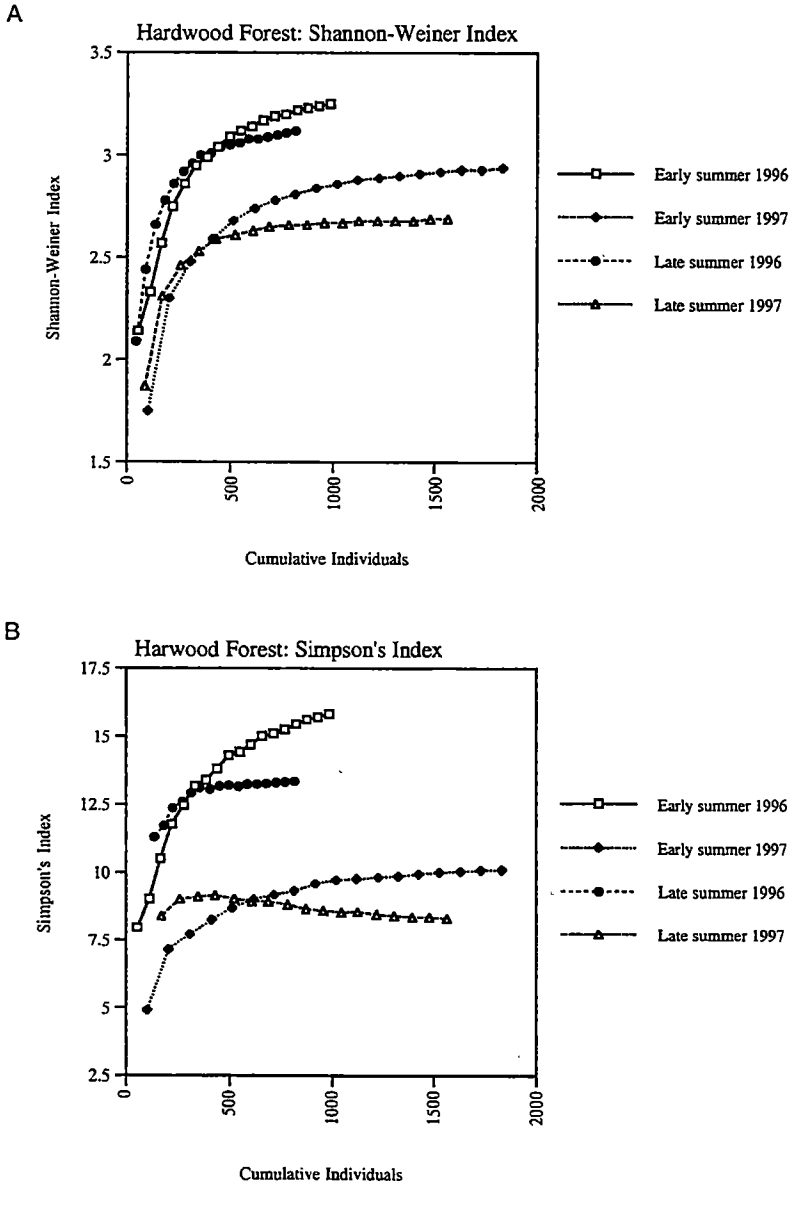


Figure 11. Cumulative number of individuals (average after randomization of the 17 sample units) versus the values of the Shannon-Weiner Index (A) and 1/Simpson's Index (B) for Hardwood Forest. Squares show the index calculated from the early summer 1996 samples. Diamonds show the index calculated from the early summer 1997 samples. Circles show the index calculated from the late summer 1996 samples and triangles show the index calculated from the late summer 1997 samples.



DISCUSSION

Not surprisingly, most of the diversity indices chosen were correlated with each other and showed the same general trends through time. The only exception was the Chao1 richness estimator, which was not similar to any other diversity index. Again, this is probably due to the fact that Chao1 attempts to estimate the 'true' richness of a site, whereas the other indices merely attempt to collapse down the richness and evenness of an assemblage into a single, comparable number. In addition, all but the Chao1 estimator assume that the entire assemblage has been sampled; an assumption that has clearly been violated in this case (see Part II). The two similarity indices also gave similar results and turnover was inversely correlated with them.

Modern ecological thought views communities as dynamic entities. Even communities which are thought to have reached a 'climax state', really exist in a state of dynamic equilibrium. Because of this, we would expect assemblages from one year to the next to be more similar to each other than to the assemblage that existed five, 10 or 20 years ago, even in the absence of dramatic environmental change. With the exception of Chao1, all the indices were able to detect the short vs. long-term changes in the spider assemblages under study through time. Likewise, one and two-year turnover was lower than 19, 20 and 21 year turnover and one and two-year similarity was higher than 19, 20, and 21 year similarity (although the similarity indices did not show such a sharp difference).

In the presence of dramatic environmental change, we would expect these changes in the assemblage to be even greater. Two of the three sites in Macon County had been clear-cut a few years prior to the historic survey of the spider fauna, and thus have been undergoing significant changes in vegetation over the last 20 years. Again, when comparing the magnitude of the difference between the short and long-term

turnover, all the indices were successful in distinguishing the mature forest from the two clear-cuts showing that the clear-cuts have experienced more significant changes in their spider assemblages than the mature forest. More specifically, the diversity indices illustrated definite trends through time in the direction of change (e.g., higher to lower diversity). These trends represent forest succession from the spiders' perspective, as the spider assemblages of the clear-cut site converge with respect to the diversity and evenness on the mature forest site. As mentioned previously, the only other site to show a trend in the diversity indices was the Beech Forest. Although this site has never been logged, it is currently being degraded by the invasion of the beech scale insect, which creates wounds on the trees that facilitate the invasion of a fungus (Coyle, written communication, Houston 1994a,b). As the beech trees die, gaps in the canopy are formed, creating habitat for early successional species. This may explain the increase in diversity and decrease in dominance for this site.

In summary, most of the indices looked at were correlated with each other and were able to detect changes in the spider assemblages as a function of time, succession, and disturbance. Of these, the Shannon index has a definite advantage over the others due to the parametric statistics associated with it. Nevertheless, it is important to remember that this study has violated the main assumption of the Shannon index (that all species are represented) and therefore statistical tests may not be wholly appropriate. Chao1 did not seem to be useful in this context because it was unable to detect these obvious changes, and therefore should not be used as a way to detect change through time in spider assemblages.

Results indicate that turnover was the most sensitive to sample size, and Morisita-Horn the least of the comparative indices. This result is intuitive, in that turnover makes use of only presence-absence data and therefore gives equal weight to common and rare

species. Although both Bray-Curtis and Morisita-Horn make use of abundance data, so that sample size is less important to the outcome, Bray-Curtis is biased toward the overall abundance of the sample. Morisita-Horn is much less sensitive to sample size because it gives particular weight to the most dominant species. Of the diversity indices, Margalef's appears to be the most affected by sample size and Simpson's the least for the same reasons as stated above. Margalef's is calculated using only the number of species collected and the number of individuals collected, while Simpson's is biased toward the more abundant species and is, therefore, more of a dominance measure. Chao1 appears to be insensitive to differences in sample size, but the results are not directly comparable to the other indices.

In conclusion, several of the indices are highly sensitive to the total number of individuals collected. In the data presented here, these differences in sample size were due almost entirely to differences in sampling intensity. Therefore, standardization of the surveys through rarefaction is the only way to meaningfully compare the surveys, particularly if turnover and Bray-Curtis similarity are to be used. If sampling intensity were to remain constant and abundances still fluctuate, is rarefaction necessary? It depends on what sort of change in a community you are trying to detect. For example, the sampling intensity in August of 1996 was identical to that of August 1997 for Hardwood Forest and yet the number of individuals collected almost doubled in 1997. Comparing the richness of these two samples without rarefaction, we find that the larger sample collected 5 fewer species and perhaps we would conclude that the samples are not that different. Yet, looking back to Figure 3 (Part II, this dissertation) which plots the number of species versus the number of individuals collected we can see that the difference between these two samples is much greater (closer to 20 species) if we compare samples of similar size. In the unlikely event that all species in a community were collected at

higher abundances one year than the previous year, but the relative abundances stayed the same, would this be considered significant? If the answer is yes, then perhaps it would not be appropriate to standardize the sample sizes through rarefaction as long as sampling intensity stayed constant. A more likely scenario would be one in which the total abundance increased or decreased, but some species were more affected by whatever environmental factor was causing the change and, therefore, the relative abundances of species would also change. In this situation, rarefaction should still be used, because the differences in relative abundance of the species will still be apparent after rarefaction.

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PART V: COMMUNITY DYNAMICS THROUGH TIME

INTRODUCTION

Due to the hyperdiverse nature of arthropods, the lack of either taxonomic or ecological information on most species, and the rate of habitat alteration and destruction, traditional single species management is often not feasible. For a species to be listed as Endangered, it must not only have a name and be recognized as a unique taxonomic entity, but also some biogeographical and basic life-history information must be documented. Only an estimated 7-10% of all insect species have been described to date (Samways 1993) and of those, only a small percentage have enough known about their biology to allow for the construction of informed recovery plans. Our options seem to be limited to the "quick and dirty" conservation techniques of evaluating ecosystems, designating reserves to protect 'valuable' habitats, and monitoring the success of those reserves (Ehrlich 1992). Most conservation biologists, along with government agencies, have focused on the first two of these objectives (Soulé and Simberloff 1986). However, as more land is set aside for conservation, attention has turned to methods of monitoring the success of the ecosystems within these reserves (Spellerberg 1991). Rapport *et al.* (1985) suggest six symptoms of ecological stress for assessing reserve success: changes in nutrient cycling, changes in primary productivity, changes in species diversity, retrogression (large fluctuations in populations that reproduce rapidly), changes in the size distribution of species, and changes in the amplitude of fluctuations in component populations. Many of these indices are difficult and costly to measure. Rapport *et al.* (1985) state that the earliest indications of ecosystem response to disturbance are abnormal fluctuations in 'sensitive' populations. If we can identify such species, they may be used as indicators to detect stress in the community. But this assumes we know

the 'normal' dynamics of these species, as well as how to measure and quantify significant deviations from this state.

Aquatic arthropods such as amphipods and isopods have been used as indicators of water quality since the 1970s (Rosenberg *et al.* 1986). In terrestrial systems, indicator assemblages have been used primarily to compare richness and diversity between sites. Sometimes the purpose is to measure the effect of a known disturbance at one or more of the sites, or to decide which of a series of candidate sites would be the best to conserve. The presence or absence of a set of species may be used to indicate either that a habitat is free of disturbance, or that it is in a 'disturbed' state. Fewer studies have actually tried to measure the change in an assemblage through time at a series of sites to see how the assemblage naturally fluctuates or how these fluctuations might be affected by a disturbance (Spellerberg 1991). Yet maintenance of diversity on protected land often relies on this type of monitoring program. Implementation of a monitoring protocol before problems arise allows comparison between 'normal' fluctuations and those which may indicate an unwanted change in the assemblage structure.

Using spiders as a representative hyper-diverse taxon, which shows potential as an indicator group (see Part I, this dissertation), I attempt to quantify the 'normal' fluctuations of the assemblage through time. I do this using data from six sites in the Southern Appalachians of the southeastern United States. Using data from these sites, I examine the dynamics of the spider assemblages at three time scales: within-year (seasonal), between adjacent years (yearly), and over periods significantly longer than the life-span of the individuals (long-term/multiple years). Using the whole assemblage, I examine the effects of gross habitat structure and disturbance on the variability of this group. In addition, I explore whether certain subcategories (e.g., guilds) of the spider

fauna are more variable than others. It is possible that some subgroups may either be too variable or too invariant to be useful as biological indicators.

METHODS

The Data

Spider species abundance lists from six sites in the Southern Appalachians were used as sample data-sets for the analyses that follow. The sites are located in two study areas, Macon County and the Great Smoky Mountain National Park (henceforth GSMNP). A full description of the sites, sampling protocols and results of sampling are given in Part II of this dissertation. In summary, these six sites can be classified into three groups: mature forest, young forest, and grassland. The three mature forests differ significantly in vegetation type. One is mostly a pine-hardwood community (roughly 90%) which is bisected by a stream and associated cove forest, another is a rich hemlock-hardwood cove forest, and the third is dominated by beech. The two young forests are classified as such because they are undergoing secondary succession having been clear-cut within the last 30 years. One grassland was included in the study. It is classified as a montane marsh/meadow. The sampling of the spider assemblages was completed in 1976, 1995-1997 in Macon County and 1995-1997 in the GSMNP.

Techniques

To quantify change through time in the spider assemblages, I focussed primarily on indices used to compare surveys: Turnover, Bray-Curtis Similarity, and Morisita-Horn Similarity. These techniques are discussed at length in Part IV (Methods) of this dissertation. Prior to the use of these indices, species lists were standardized with respect to taxonomy in order to make them comparable. Unless stated otherwise, rarefaction was

also used prior to the calculation of the indices to standardize for differences in sample size (see Figure 1, Part IV this dissertation).

Analyses

The analyses conducted fall into two categories. In the first, comparisons are made between seasonal, yearly, and multiple year changes in the assemblage and how these may be affected by such factors as habitat structure and/or disturbance. Turnover and similarity indices were calculated between all pairs of surveys. The early and late summer collections of the GSMNP sites were used to establish the importance of seasonal turnover. Because of the historical surveys completed at the Macon County sites, these sites could be used to make comparisons between long and short-term changes in the spider fauna. However, all six sites yielded estimates of turnover for one and two-year periods.

The second category of analysis examines the differences between certain subgroups of the spider assemblage to ascertain whether some groups are more variable than others. Turnover and similarity indices were also used in these analyses. The assemblages were partitioned in three different ways: 1) spatially (aerial vs. ground), 2) functionally (web builders vs. hunters and/or sit and wait), and 3) in terms of mechanism of juvenile dispersal (ballooning vs. ground dispersal). These particular partitions were chosen for the following reasons.

Spatial Partitioning

Leaf litter and herbaceous vegetation buffer temperature and humidity, thereby offering ground dwelling spiders an ameliorated physical environment compared to that experienced by aerial spiders. I expect that population numbers and species composition of the ground-dwelling spider assemblage would be more consistent from year to year as a consequence of a more constant microenvironment. Previous studies on litter

arthropods support this hypothesis. Bengtsson (1994), for example, in a review found that litter arthropod population numbers and species composition were quite consistent from year to year in forested systems.

Functional Partitioning

Web builders and hunting spiders occur at all strata in the habitat, and each group contains many subcategories. For example, orb web spiders are quite different from sheet web spiders and hunting spiders like wolf spiders are quite different from sit-and-wait webless spiders like thomisids. Unfortunately, using these finer subdivisions was not possible because of the small sample sizes of the data-sets. All web builders must invest energy in the creation and construction of a web in order to trap food. Although many web builders (e.g., orb weavers) rebuild their webs every day, they often leave support strands in place continuously in order to conserve effort. Other species maintain the same web for long periods of time and expend effort only to repair the web when it is damaged (funnel-web spiders). The result of the web, therefore, is to anchor the spider to a particular area. Web builders will move in response to the destruction of their web or low prey availability, but I would expect them to be less likely to move than hunting spiders who have expended no energy on a prey-catching device. Therefore, hunting spiders may be quicker to respond to habitat changes or changes in prey abundance than web builders.

Mechanism of dispersal

Some spiders disperse from the maternal web cursorially ("walk away"), while others disperse by a process called ballooning which involves the letting up of a silk line to catch uplifting air currents that carry off the attached spiderlings. Because ballooning spiders are carried passively by wind currents, they can travel great distances if they are lifted up and out of the canopy of a forest or are in a place otherwise free of entanglements (like a grassland). Another important distinction between these two groups

is that ballooning species are completely dependent on the vagaries of wind currents and so their dispersal can be considered somewhat random. Cursorially dispersing species, in contrast, control their own movement and direction and therefore exhibit purposeful or non-random dispersal. Due to stochastic processes, then, ballooning spiders may be more variable from season to season than ground dispersers.

Classification

Little is known about the natural history of many of the species present in the six sampling areas. Thus, spider species were assigned to 'aerial' or 'ground' assemblages based on which sampling methods collected them. All spiders collected in litter samples, pitfall traps, and ground hand collection were designated as ground-dwellers. Those collected in sweep-net samples or by aerial hand collection were designated as aerial-dwellers. Note that in using this method of partitioning, some species were present in both ground and aerial categories. Spider species were classified based on family assignment as web building versus non-web building (Kaston 1978). Web construction is generally considered to be a family level trait, but exceptions do exist in some families. However, these exceptions are rare (<1%) and so this method of partitioning is still reasonably accurate. The third and final classification is based on the mode of dispersal employed by the spiders. Unfortunately, the data just aren't available at the species level to be able to establish with confidence which method is employed. As a surrogate for this species-specific information, I used data collected by Leslie Bishop (1989) to place species in a category based on familial membership. Bishop surveyed ballooning spiders in a mixed species hardwood stand (oak hickory) using the forest meteorology tower of the Atmospheric Turbulence and Diffusion Laboratory on the US Department of Energy's reservation 10 km southwest of Oak Ridge, TN. Because she was sampling the fauna in a similar habitat in the same gross region of the country, I approximated the

mode of dispersal for the species in my study based on her results at the Family level. Specifically, Bishop found that 98% of the fauna found in her survey of ballooning spiders were placed in five families: Thomisidae, Linyphiidae, Araneidae, Salticidae, and Clubionidae. Therefore in this study, species in those five Families were designated as 'ballooners' and taxa belonging to other families were classified as 'ground dispersers'. I only performed this analysis on the Macon County sites, as these were the most similar in species composition to the Bishop study.

Using the methods described above and in more detail in Part IV of this dissertation, I compared the yearly and long-term turnover and similarity within each site, first for the whole data-set, and then for each of the subcategories described above. I used only the data based on adult specimens where sample sizes permitted it (GSMNP), for reasons discussed in Part VI. Results are for species-level analyses except when stated otherwise.

Interpretive limitations

It is important to understand that the following estimates of arthropod community dynamics are not strictly comparable to those calculated for vertebrate groups. This is because vertebrate studies (particularly those for birds) can, with a small degree of error, identify every species present in a given year at a given site (assuming that the worker conducting the survey has had proper training). Studies which include a hyperdiverse group such as arthropods can only hope to detect a proportion of the species, particularly for large sites with many microhabitats. In this study, it is obvious that sample sizes are too small to approach a comprehensive survey (see Part II, this dissertation) and, therefore, the species collected are only a sample of the total richness of these sites. Turnover, then, is really *apparent* turnover as it would be measured by a rapid survey attempt. It is unlikely that any monitoring program would have the resources necessary to

perform complete surveys, and the data presented in this analysis illustrate what would typically be available to managers. Because we are forced to deal with 'samples' instead of comprehensive surveys, there are also additional sources of error (i.e. sampler bias, taxonomic uncertainty, stochastic effects). I address these in Part VI of this dissertation. However, monitoring the dynamics of even the most common 50 spider species should still give higher resolution information than monitoring a single indicator species or a much smaller group of vertebrate species. This is because a single species or a small number of species only occupy a small fraction of the niche space in any habitat. Although these species may react to changes in this small fraction of the environment, other perturbations impacting other aspects of the environment may go undetected. The more species you can monitor, the more information you can get about the habitat.

Comparisons of the turnover and similarity of spider assemblages over time intervals of different lengths, or of various partitions of the assemblage are, by constraint, qualitative. No statistical tests have been developed to test the significance of differences in turnover or similarity indices. It is also important to note that although rarefaction produces a mean and a variance for these indices, these cannot be used to test significance. This is because they are the result of a simulation and are, therefore, not the same as the mean and variance produced by a set of independently measured data-points. The 'error bars' plotted on the figures in this chapter merely illustrate the spread of the rarefied estimates after 1000 simulations and so include 95% of these estimates after rarefaction.

RESULTS

Long-term turnover and similarity

Long-term turnover was greater than short-term turnover for the Macon County sites (Figure 1). The same pattern can be seen for the similarity indices, with similarity lower for long-term comparisons (Figure 1). Because slight differences in sampling regime (i.e., numbers and duration of pitfall traps) between the 1976 study conducted by Coyle and the 1995-97 studies conducted by Norris (see Part II, this dissertation for details) could produce the above trends, I re-ran these analyses excluding the pitfall trap data. Although the overall measures of turnover increased due to even smaller sample sizes, the same trends were observed with respect to short vs. long-term turnover at the Macon County sites. Long-term turnover ranged from 0.46 to 0.50 for Ellicott Forest and from 0.54 to 0.63 for Horse Clear-cut and Ellicott Clear-cut, with short-term turnover ranging from 0.34 to 0.39 for Ellicott Forest and from 0.23 to 0.39 for Horse Clear-cut and Ellicott Clear-cut.

The differences between the long and short-term measures of turnover and similarity are greater for the old clear-cuts than for the mature forest (Figure 1). This is not surprising, as the clear-cut sites have been undergoing succession over the past 20 years and, therefore, the structure of the vegetation at these sites has changed considerably.

Yearly turnover and similarity

A summary of the yearly turnover and similarity estimates is given in Table 1. The goal of this analysis was to get the most accurate measures of yearly turnover for each of these sites (see interpretive limitations discussed above). Therefore, only the most comparable data-sets were used to produce the values given in Table 1. For example only

Figure 1. Long-term versus short-term turnover and similarity for sites in Macon County. Squares represent mean turnover estimates after the data had been rarefied and turnover calculated 1000 times. Circles represent mean Bray-Curtis similarity estimates and diamonds represent mean Morisita-Horn similarity estimates, also after 1000 rarefactions. The error bars contain 95% of the rarefied turnover and similarity estimates.

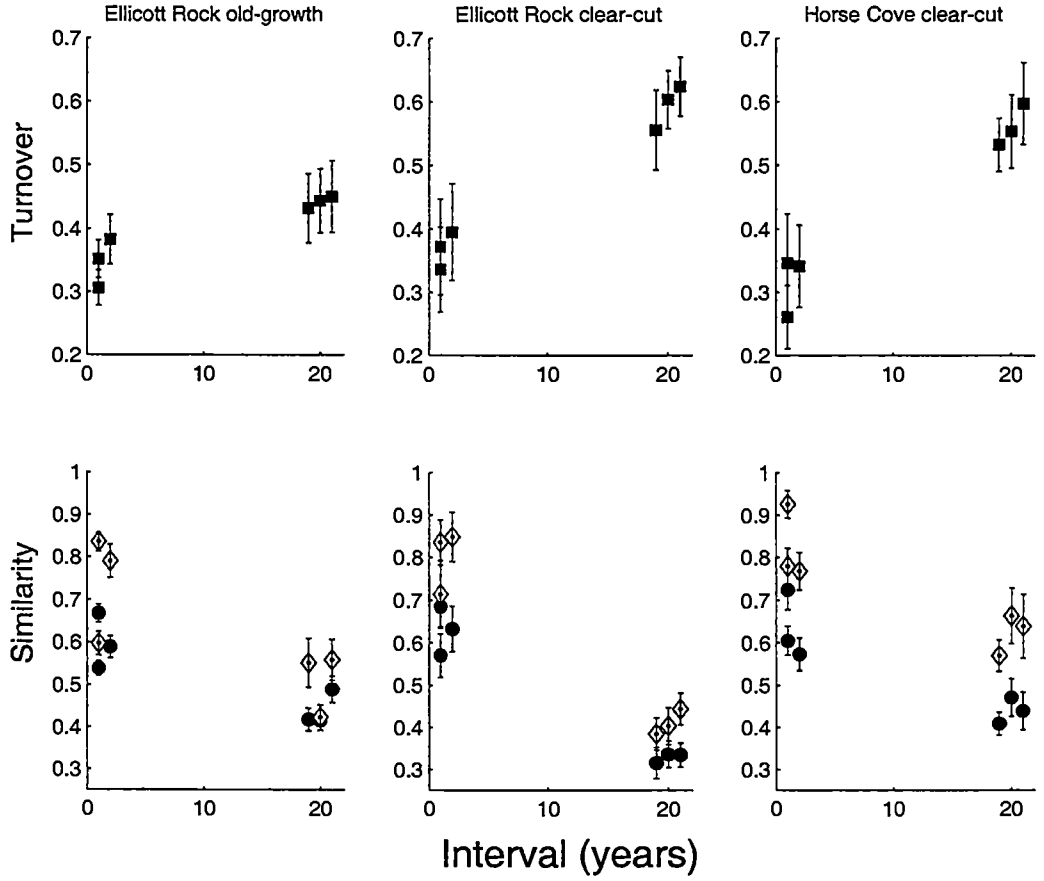


Table 1. One year turnover and similarity estimates

		One year Turnover (mean after rarefaction)	One year BC Similarity (mean after rarefaction)	One year MH Similarity (mean after rarefaction)
Mature Forests	Hardwood Forest	0.228	0.677	0.825
		0.274	0.723	0.908
	Beech Forest	0.296	0.709	0.888
		0.281	0.587	0.692
	Ellicott Forest	0.353	0.549	0.614
		*0.274	*0.731	*0.923
Young Forests	Ellicott Clear-cut	0.315	0.568	0.621
		*0.288	*0.708	*0.851
	Horse Clear-cut	0.267	0.603	0.779
		0.354	0.721	0.925
Grassland/marsh	Meadow Marsh	0.481	0.435	0.513
		0.412	0.494	0.675

*results from a higher intensity sampling regime in 1996 and 1997

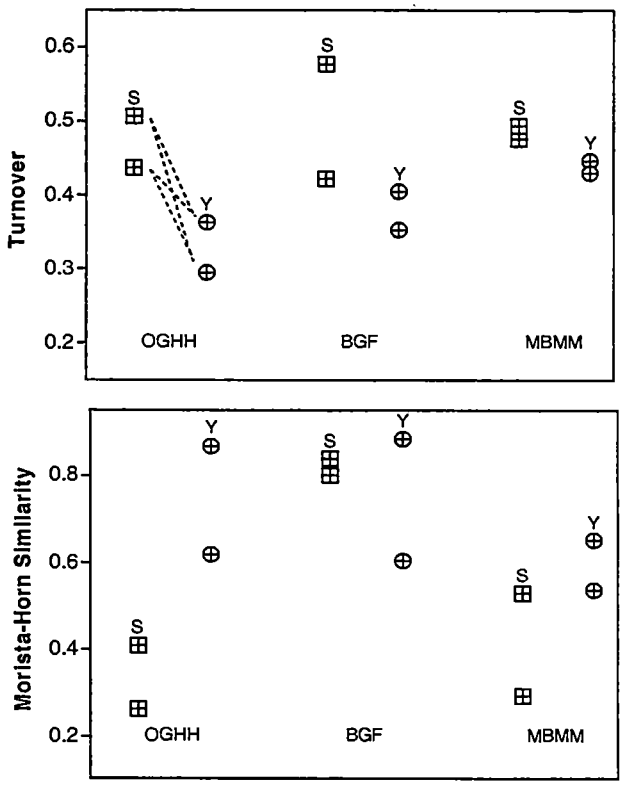
Notes. 'BC' refers to the Bray-Curtis similarity index and 'MH' refers to the Morisita-Horn similarity index. The one year turnover and similarity estimates for Hardwood Forest, Beech Forest, and Meadow Marsh correspond to comparisons between data from early summer 1996 with data from early summer 1997 and data from late summer 1996 with data from late summer 1997. For Ellicott Clear-cut, Ellicott Forest, and Horse Clear-cut, the two estimates of one year turnover and similarity correspond to comparisons of data from 1995 with data from 1996, and data from 1996 with data from 1997.

data from 1996 and 1997 GSMNP data-set were used since sampling intensity varied considerably from 1995 to 1996/7. In Macon County, data from the increased sampling program conducted in 1996 and 1997 were used to estimate turnover for that year, instead of the subset of data used in the analysis of long vs. short-term turnover. All forested sites (Macon County and GSMNP) had mean one-year turnover estimates ranging from 0.23 to 0.35, and mean one-year similarity estimates from 0.73 to 0.55 for Bray-Curtis and 0.93 to 0.61 for Morisita-Horn (see Part IV, this dissertation for a description of these indices). Marsh Meadow had relatively high one-year turnover (0.48, 0.41) and low one-year similarity (0.44, 0.49 for Bray-Curtis and 0.51, 0.68 for Morisita-Horn). Taking the mean across sites, the mature forests had turnover, Bray-Curtis similarity, and Morisita-Horn similarity estimates of 0.284, 0.663, and 0.808 respectively. The young forests had estimates of 0.306 (turnover), 0.650 (BC similarity), and 0.794 (MH similarity) and the grassland had estimates of 0.447 (turnover), 0.465 (BC similarity), and 0.594 (MH similarity).

Seasonal turnover and similarity

For the three sites which had seasonal data (Beech Forest, Meadow Marsh, Hardwood Forest), a total of four comparisons were possible at each site: May vs. August in each of the two years (seasonal comparison) and 1996 vs. 1997 for each of the two months (yearly comparison). All twelve of these comparisons show seasonal turnover is higher than yearly turnover. Nine out of twelve comparisons show that samples taken in the same month of sequential years are more similar as measured by Morisita-Horn than samples taken during different months of the same year (Figure 2). Only data from 1996 and 1997 were used for this analysis because of the huge differences in sample size between the 1995 survey and the 1996/1997 surveys.

Figure 2. Seasonal versus annual turnover and similarity for sites in the GSMNP. Squares represent the two measures of seasonal turnover or similarity calculated for each site. Circles represent the two measures of yearly turnover or similarity for each site. 'OGHH' refers to the Hardwood Forest site, 'BGF' refers to the Beech Forest, and 'MBMM' refers to the Meadow Marsh. Turnover and Similarity were calculated using only adult specimens. The dotted lines illustrate the possible comparisons, e.g. May 96/August 96 vs. May 96/May 97 or August 97/August 98 and May 97/August 97 vs. May96/May 97 or August 97/August 98. All twelve comparisons show seasonal turnover is higher than yearly turnover for these sites. Nine out of twelve comparisons show that samples taken within in the same month, between years are more similar than samples taken during different months of the same year.



Guild Comparisons

In the GSMNP sites unless stated otherwise, only data from 1996 and 1997 were analyzed. In Macon County, only data from 1995, 1996, and 1997 were used to eliminate any possible error associated with sampler bias and to increase the resolution of the analysis by allowing the inclusion of morphospecies (See Part VI for a discussion of sampler bias and use of morphospecies). Also, as the assemblages are broken down into smaller subgroups, small sample sizes become more of a concern. Because the Morisita-Horn similarity index is less sensitive to sample size than Bray-Curtis (see Part IV, this dissertation), all subsequent analyses will use the Morisita-Horn index of similarity.

Aerial vs. Ground

Five sites were included in this analysis. Meadow Marsh was excluded because as a grassland, it was not possible to clearly designate which sampling methods would predominantly collect which sub-group. A summary of the number of individuals comprising each group for each site is given in Tables 2 and 3. For Ellicott Forest and Ellicott Clear-cut, aerial spiders gave somewhat higher estimates of turnover than ground dwelling spiders (Figure 3), although much less of a pattern exists for Morisita-Horn similarity. Horse Clear-cut showed no discernible pattern, except that the Morisita-Horn estimates were very low (and highly variable) for the aerial species (Figure 3). To increase the sample size by including juvenile specimens, the same analysis was performed at the genus level. Now all three Macon County sites show a weak trend indicating that aerial species exhibit higher turnover than ground species (Figure 4). This inclusion of juveniles appeared to have no effect on the relative value of the Morisita-Horn similarity indices.

As indicated in Table 3, the raw abundance of ground and aerial specimens in Beech Forest and Hardwood Forest appeared to fluctuate significantly from year to year.

Table 2. Total abundance of aerial dwelling versus ground dwelling species

	1995		1996		1997	
	Aerial	Ground	Aerial	Ground	Aerial	Ground
Ellicott Clear-cut	175	226	101	254	111	181
Ellicott Forest	185	157	125	231	108	233
Horse Clear-cut	67	142	93	232	120	304

Table 3. Abundance of ground vs. aerial adult spiders for beech and hardwood forest

	E1996		L1996		E1997		L1997	
	Aerial	Ground	Aerial	Ground	Aerial	Ground	Aerial	Ground
Beech Forest	360	131	363	101	198	192	212	144
Hardwood Forest	205	502	100	129	400	588	181	230

Figure 3. Turnover and similarity of ground dwelling versus aerial dwelling species for sites in Macon County. Solid squares represent the ground dwelling spiders collected at these sites and open circles represent the aerial dwelling spiders. The turnover and similarity calculations were conducted at the species level. The mean turnover and Morisita-Horn similarity estimates are plotted after 1000 rarefactions with error bars containing 95% of the rarefied estimates. The interval between the surveys is consistently either one or two years, yet the data-points are staggered for clarity.

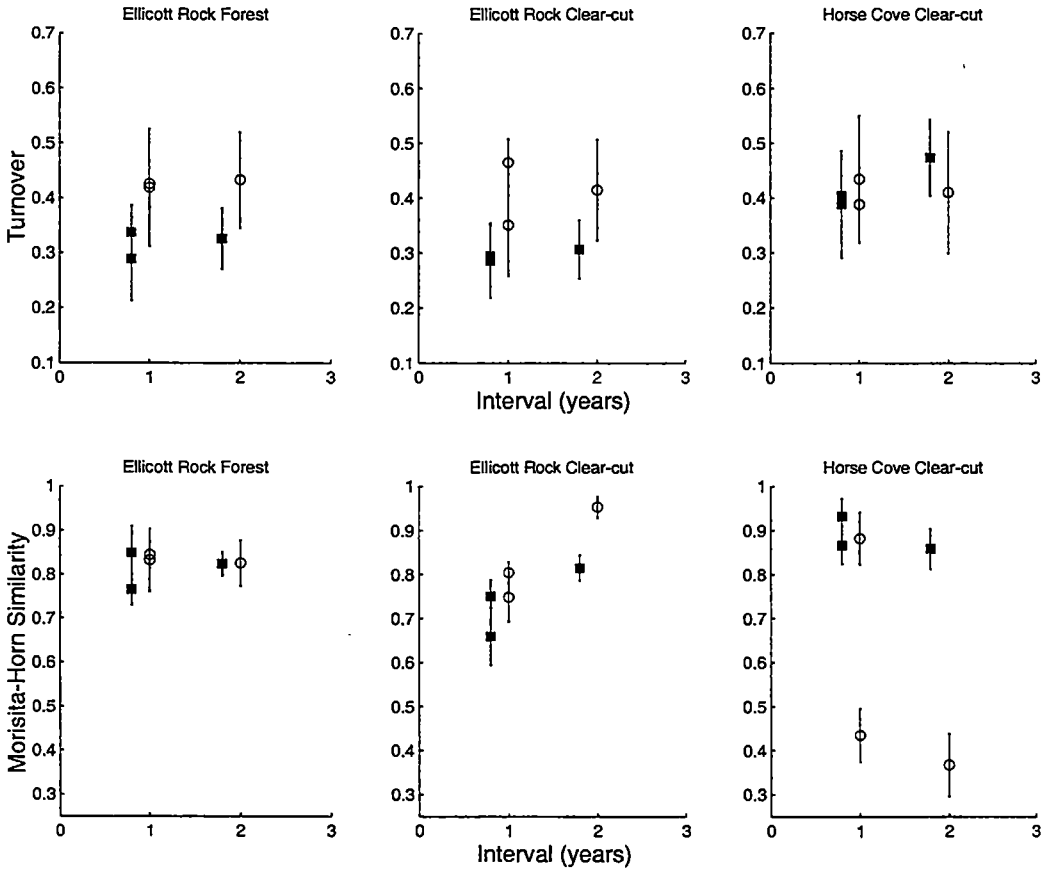
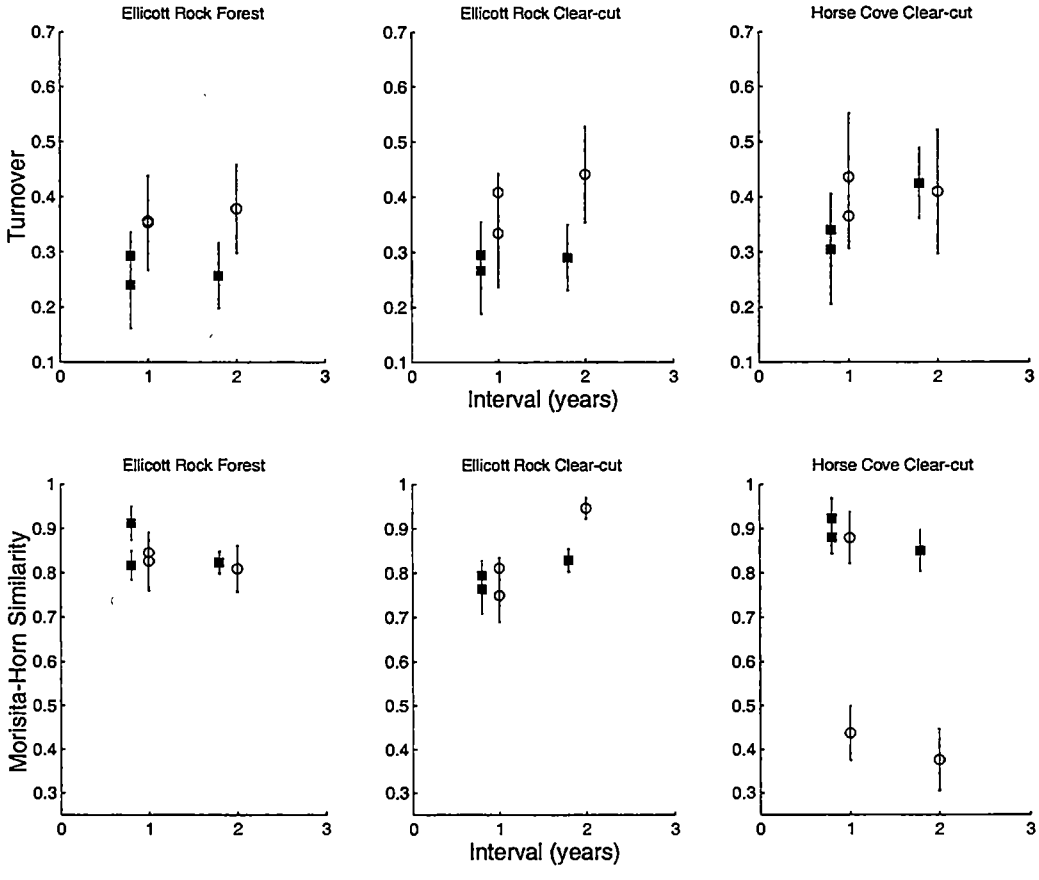


Figure 4. Turnover and similarity of ground dwelling versus aerial dwelling genera for sites in Macon County. Solid squares represent the ground dwelling spiders collected at these sites and open circles represent the aerial dwelling spiders. The turnover and similarity calculations were conducted at the genus level. The mean turnover and Morisita-Horn similarity estimates are plotted after 1000 rarefactions with error bars containing 95% of the rarefied estimates. The interval between the surveys is consistently either one or two years, yet the data-points are staggered for clarity.



Because this fluctuation in abundance may be significant in terms of the relative variability of each group, I performed the same analysis first with and then without rarefaction. The results from Hardwood Forest clearly indicate that the aerial dwelling species are more variable from year to year, both with and without rarefaction (Figure 5 and 6), though the differences appear more extreme in the unrarefied data. Beech Forest shows conflicting results in both turnover and similarity, also in both cases (Figure 5 and 6).

Hunting vs. Web

All six sites were used in this analysis. The abundance, number of species and number of genera for each subcategory are presented in Table 4 for the Macon County sites and Table 5 for the GSMNP sites. Although genus level analyses were completed for each site, the results were qualitatively similar to the species analyses and so only the species-level results are presented here. In Macon County, I chose to calculate turnover and similarity for hunting spiders and web building spiders over all four years of surveys because I wanted to elucidate how these subcategories responded to the secondary succession occurring at the two clear-cut sites. I expected that the web builders would show the greatest variability between the historic and recent surveys at the young forest sites due to the increase in vertical complexity of the habitat.

In order to use rarefaction in this case, we must expect the numbers of hunting spiders or web-building spiders to be the same from year to year. In this situation, we are comparing historic data to modern data. Based on what we know of the effects of clear-cutting, I would not expect the number of web-builders or hunting spiders to remain constant as the forest regenerates, particularly over long time intervals. Therefore, I plotted both the rarefied and raw data in Figure 7 (see Part IV for a complete discussion of rarefaction). In both Ellicott Forest and Ellicott Clear-cut, the data indicate that

Figure 5. Contrasting dynamics of the ground fauna versus the aerial dwelling fauna for Beech Forest (A) and Hardwood Forest (B). Because turnover and similarity are inversely correlated, 1-similarity is plotted in figures (A) and (B) for easier comparison. Grey bars represent the aerial dwelling fauna and white bars represent the ground dwelling fauna. The two measures of turnover, 1-Bray-Curtis and 1-Morisita Horn correspond to the two estimates of yearly turnover possible for these sites (early 1996 with early 1997 and late 1996 with late 1997). The turnover and similarity estimates are mean values after 1000 rarefactions.

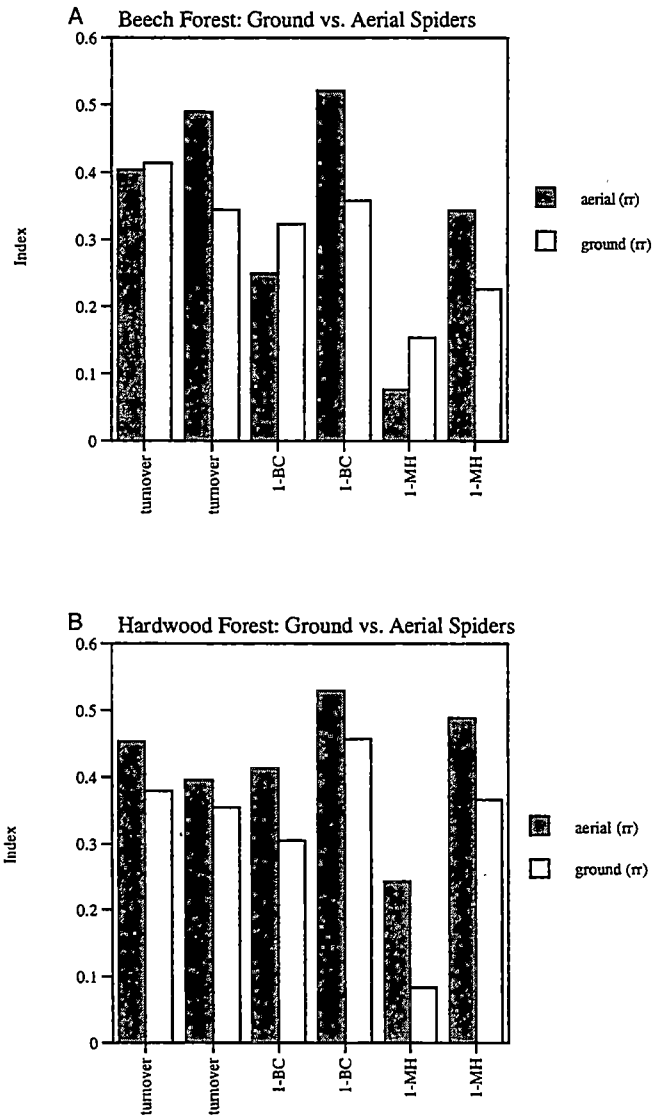


Figure 6. Contrasting dynamics of the ground fauna versus the aerial dwelling fauna for Beech Forest (A) and Hardwood Forest (B) without rarefaction. Because turnover and similarity are inversely correlated, 1-similarity is plotted in figures (A) and (B) for easier comparison. Grey bars represent the aerial dwelling fauna and white bars represent the ground dwelling fauna. The two measures of turnover, 1-Bray-Curtis and 1-Morisita Horn correspond to the two estimates of yearly turnover possible for these sites (early 1996 with early 1997 and late 1996 with late 1997). The turnover and similarity estimates are actual values. No attempt was made to standardize these sub-samples with respect to sample size and therefore rarefaction was not used.

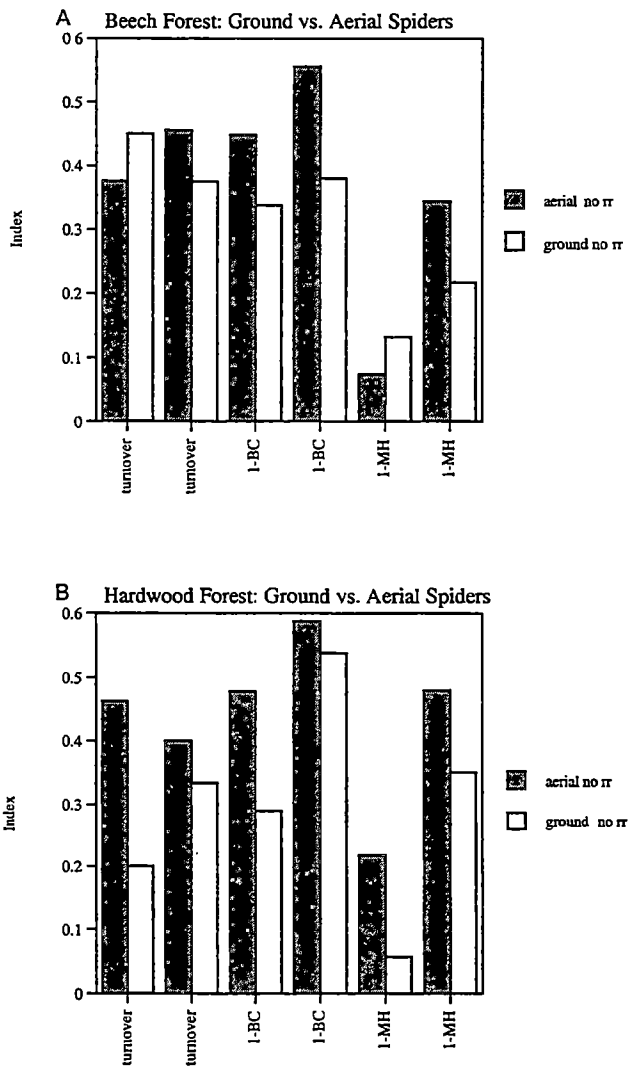


Table 4. Total abundance of hunting versus web building species

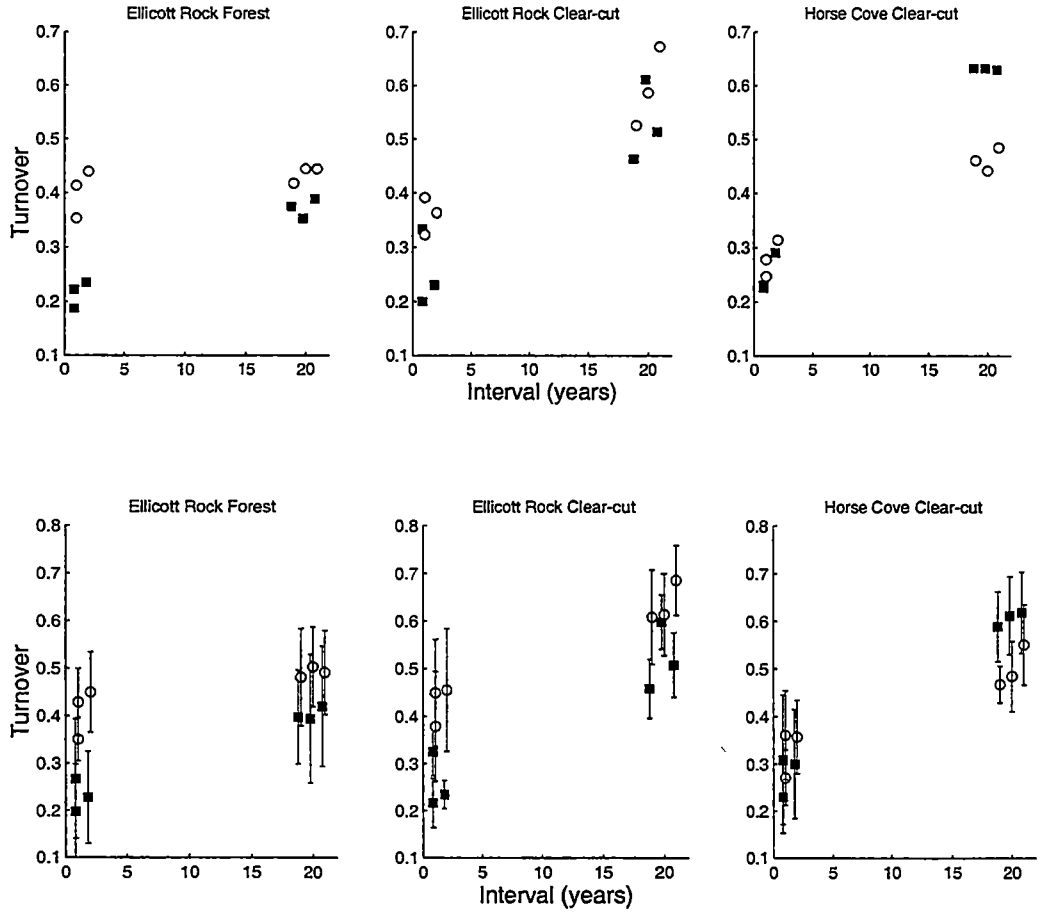
Site		1976		1995		1996		1997	
		hunt	web	hunt	web	hunt	web	hunt	web
Ellicott Forest	#individuals	126	307	88	252	174	134	178	182
	#species	17	38	16	41	18	34	20	34
	#genera	19	36	17	31	17	34	16	32
Ellicott Clear-cut	#individuals	123	86	100	301	165	155	103	195
	#species	26	24	15	34	10	34	11	31
	#genera	26	25	15	33	14	32	12	32
Horse Clear-cut	#individuals	152	148	81	128	123	200	182	245
	#species	36	31	13	32	13	37	18	35
	#genera	31	30	12	28	13	34	18	30

Notes. All specimens (including juveniles) which could be confidently identified to species were used in the species level analyses of the dynamics of hunting versus web-building spiders. The generic level analyses included all specimens, including those juveniles which could only be identified to genus. Therefore in some instances, the number of genera used in an analysis could be greater than the number of species from the same data-set.

Table 5. Abundance of Hunting versus Web Building Species

Site		E1995		L1995		E1996		L1996		E1997		L1997	
		hunt	web	hunt	web	hunt	web	hunt	web	hunt	web	hunt	web
Beech Forest	#adults	---	---	10	242	12	479	6	458	41	349	20	336
	#species	---	---	2	20	3	25	3	19	5	26	5	26
	#genera	---	---	2	18	3	23	2	16	3	23	4	23
Hardwood Forest	#adults	9	103	13	101	132	584	28	201	837	806	41	373
	#species	4	25	5	23	11	44	9	44	15	48	7	43
	#genera	4	22	5	23	8	38	8	43	12	43	7	40
Meadow Marsh	#adults	92	68	---	---	143	114	59	71	148	144	89	125
	#species	21	23	---	---	23	19	17	18	26	22	23	16
	#genera	18	18	---	---	21	17	17	17	22	19	21	16

Figure 7. Long-term versus short-term turnover for the web building species and hunting species found in the Macon County sites. Circles represent turnover estimates based on the web building spiders, only. Squares represent turnover estimates based on hunting spiders, only. In (A), rarefaction was not used and so the estimates are not simulated. In (B), rarefaction was used and therefore the estimates represent the mean after 1000 rarefactions with the error bars containing 95% of the rarefied estimates.



turnover is higher for web builders than for hunting spiders. Although showing a roughly similar pattern in short-term turnover, Horse Clear-cut shows just the opposite pattern for the long-term comparisons with hunters being more variable at this time scale. Looking more closely at the Ellicott Clear-cut data, the long-term data show less of a pattern than the short-term data (i.e. the turnover estimates for the long-term comparisons show that web builders and hunters are less different than at the short-term time scale). The similarity results (Figure 8) showed roughly the same pattern with Horse Clear-cut and Ellicott Clear-cut indicating that hunting spiders show less variability (are more similar) over the long-term than the web building spiders, while not showing much of a pattern at all in short-term variability. Ellicott Forest again shows a consistent, yet opposite pattern in that long-term variability is higher for the hunting spiders and lower for the web builders. And yet, short-term variability is lower for hunting spiders at this same site. Because some of the inconsistencies in the results of these analyses could be due to the effects of sampler bias (see Part VI), I eliminated the 1976 data and focussed on comparing the short-term variability of these groups. Figure 9 illustrates a strong pattern in Ellicott Forest indicating higher turnover and lower similarity of web builders at this time scale. Ellicott Clear-cut does not appear to show a consistent pattern of any sort in turnover, but a weak opposite pattern in similarity indicating lower variability through time of web builders at this site. Horse Clear-cut shows a very weak pattern indicating the higher variability of web builders.

In GSMNP, Meadow Marsh shows a very consistent trend (both with and without rarefaction) indicating higher variability of web builders (Figure 10). Beech forest, on the other hand does not yield any consistent patterns, although the magnitude of the difference when hunting spiders showed higher variability was greater than when the web builders were more variable (Figure 11). Hardwood Forest showed an interesting pattern

Figure 8. Long-term versus short-term similarity for the web building species and hunting species found in the Macon County sites. Circles represent Morisita-Horn similarity estimates based on the web building spiders, only. Squares represent Morisita-Horn similarity estimates based on hunting spiders, only. Rarefaction was used in this analysis and therefore the estimates represent the mean after 1000 rarefactions with the error bars containing 95% of the rarefied estimates.

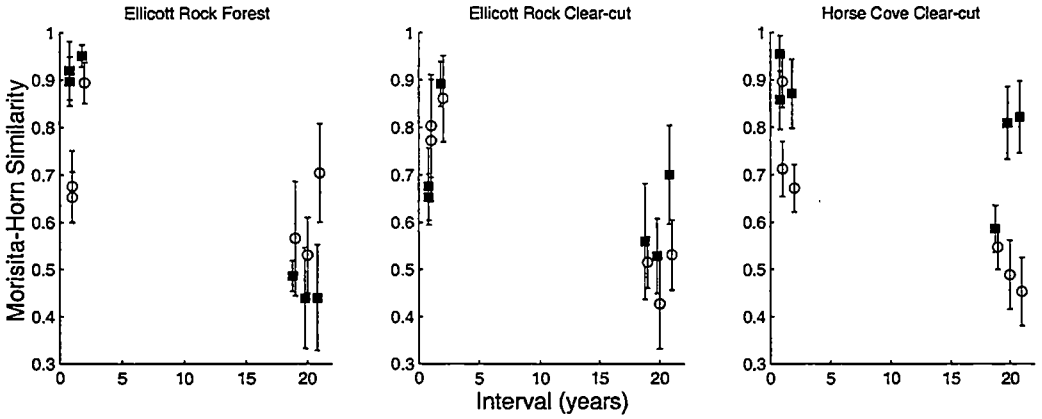


Figure 9. Short-term turnover and similarity for the web building species and hunting species found in the Macon County sites. Solid squares represent the hunting spiders collected at these sites and open circles represent the web building spiders. The turnover and similarity calculations were conducted at the species level. The mean turnover and Morisita-Horn similarity estimates are plotted after 1000 rarefactions with error bars containing 95% of the rarefied estimates. The interval between the surveys is consistently either one or two years, yet the data-points are staggered for clarity.

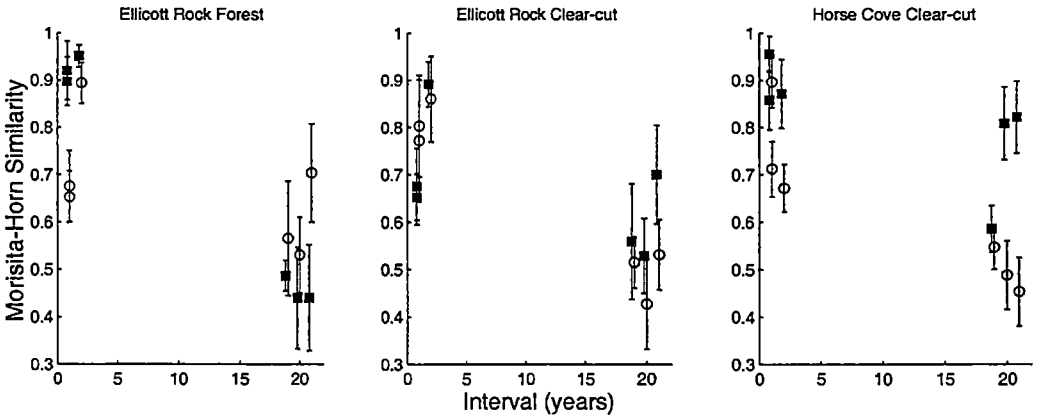
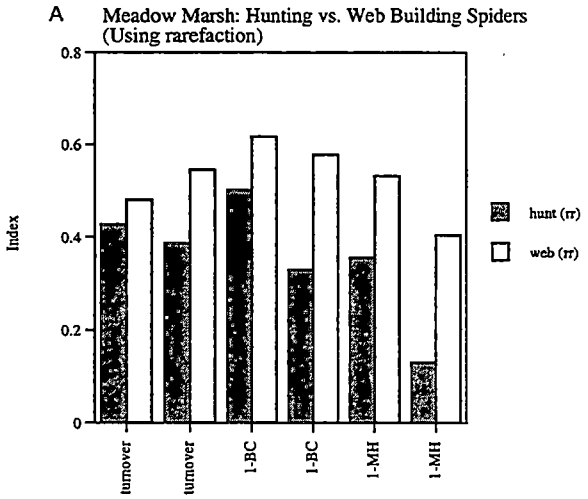


Figure 10. Contrasting dynamics of the web building species versus the hunting species for Meadow Marsh. Because turnover and similarity are inversely correlated, 1-similarity is plotted in figures (A) and (B) for easier comparison. Grey bars represent the hunting species and white bars represent the web building species. The two measures of turnover, 1-Bray-Curtis and 1-Morisita Horn correspond to the two estimates of yearly turnover possible for this site (early 1996 with early 1997 and late 1996 with late 1997). Rarefaction was used in (A) and therefore the index values are means after 1000 rarefactions. In (B), rarefaction was not used and therefore the index values are calculated values based on the raw data.



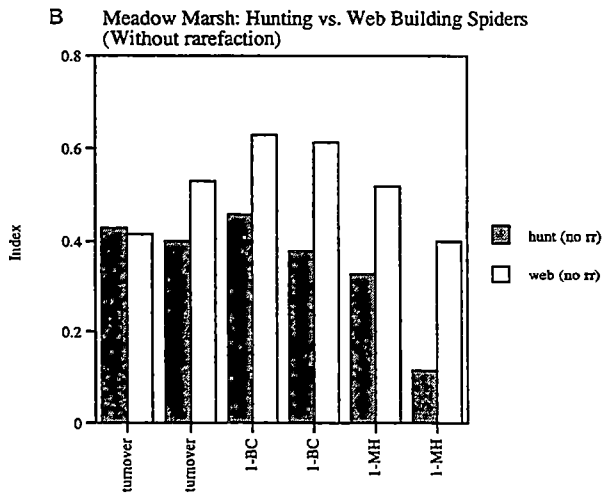
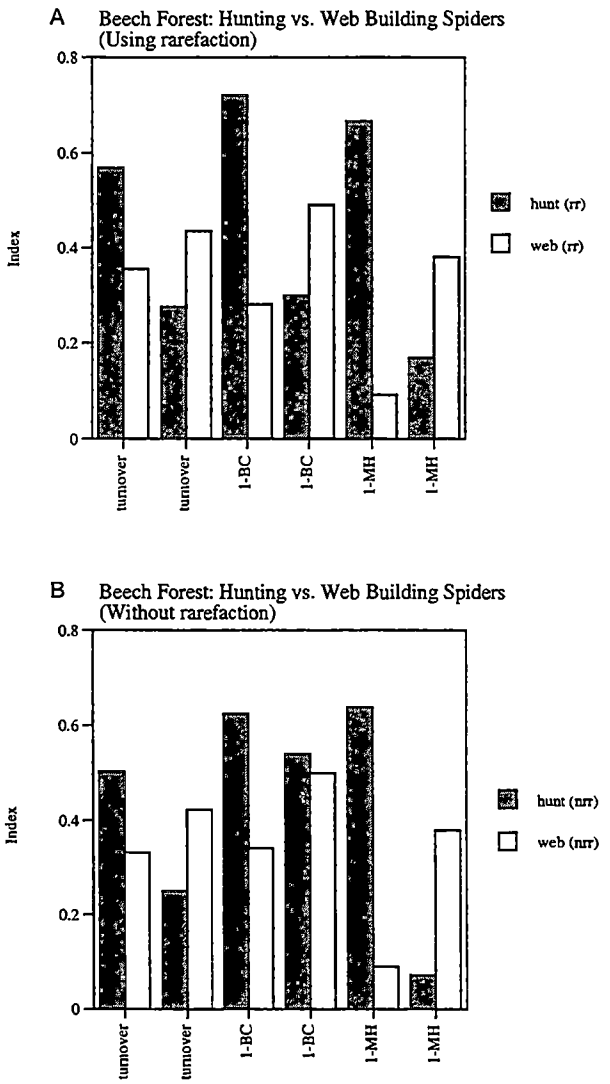


Figure 11. Contrasting dynamics of the web building species versus the hunting species for Beech Forest. Because turnover and similarity are inversely correlated, 1-similarity is plotted for easier comparison. Grey bars represent the hunting species and white bars represent the web building species. The two measures of turnover, 1-Bray-Curtis and 1-Morisita Horn correspond to the two estimates of yearly turnover possible for this site (early 1996 with early 1997 and late 1996 with late 1997). Rarefaction was used in (A) and therefore the index values are means after 1000 rarefactions. In (B), rarefaction was not used and therefore the index values are calculated values based on the raw data.



in that based on the turnover estimates, the hunting spiders were more variable but based on the similarity indices, the web-building spiders were more variable. In other words, the species composition of the hunting spiders changed more than the species composition of the web-builders but the relative abundances of the web builders was more inconsistent from year to year (Figure 12).

Ballooning vs. Cursorial

As mentioned previously, only the Macon County sites were used for this analysis. The abundance of each group for these three sites is given in Table 6. Figure 13 shows the three estimates of turnover (from 1995-1997 data) and Morisita-Horn similarity for each subgroup at each site. Although Ellicott Forest shows a consistent trend indicating that ballooning species are more variable from year to year, results from Ellicott Clear-cut and Horse Clear-cut are less consistent. In an attempt to clarify the results with additional data, I repeated the analysis for Ellicott Forest and Ellicott Clear-cut, comparing data from the larger surveys completed in 1996 and 1997. As is evident from Figure 14, Ellicott Forest still shows the same pattern with ballooning species more variable than cursorial species. But this time, Ellicott Clear-cut shows a clear, but opposite pattern with *cursorial* species being the most variable.

DISCUSSION

Whole Assemblage Dynamics

As expected, these data confirm that the longer the time interval between surveys, the more changes in the species composition and relative abundance of species are likely to have occurred. Of course, it is important to note that for annual organisms such as most spiders, this trend only holds if the shortest time interval is one year or greater. As in other annual organisms, this study confirms that spiders show considerable seasonal

Figure 12. Contrasting dynamics of the web building species versus the hunting species for Hardwood Forest. Because turnover and similarity are inversely correlated, 1-similarity is plotted for easier comparison. Grey bars represent the hunting species and white bars represent the web building species. The two measures of turnover, 1-Bray-Curtis and 1-Morisita Horn correspond to the two estimates of yearly turnover possible for this site (early 1996 with early 1997 and late 1996 with late 1997). Rarefaction was used in (A) and therefore the index values are means after 1000 rarefactions. In (B), rarefaction was not used and therefore the index values are calculated values based on the raw data.

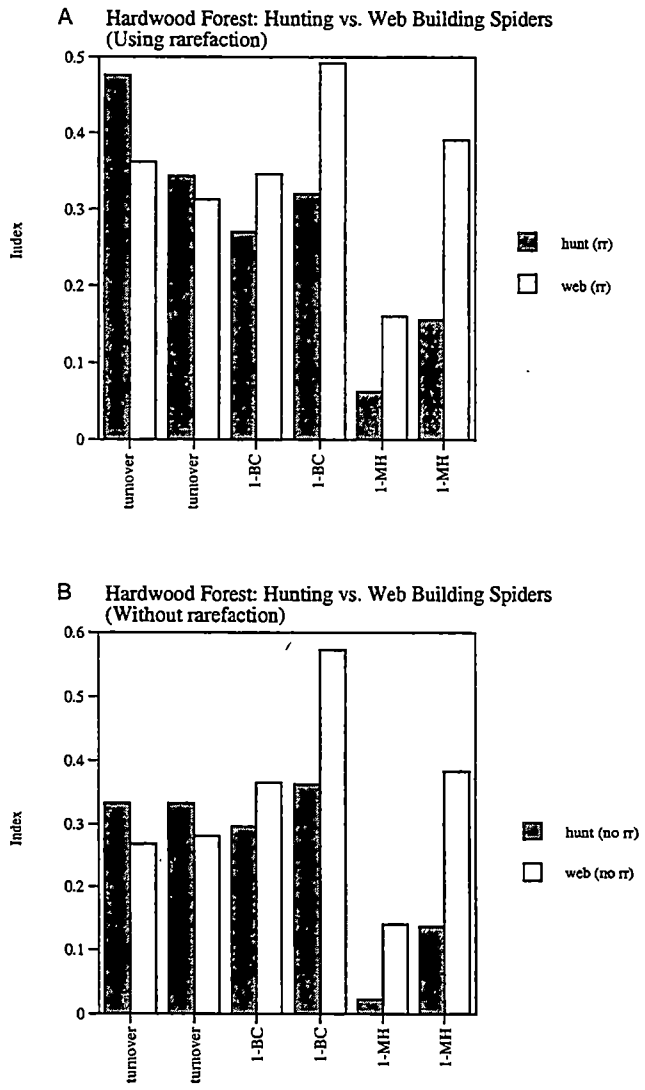
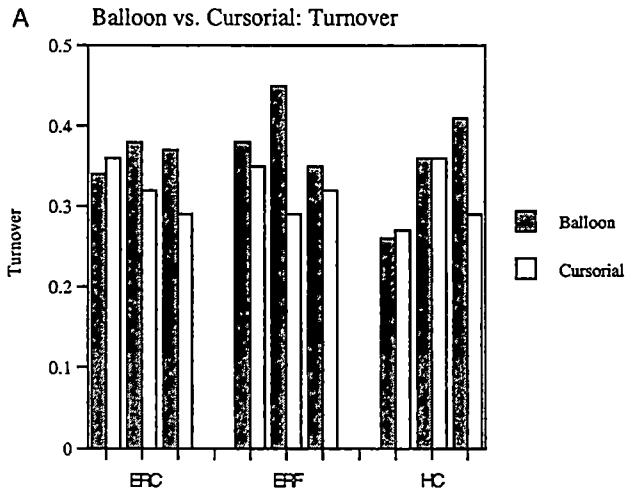


Table 6. Total abundance of ballooning versus cursorial dispersers

	1995		1996		1997	
	Balloon	Cursorial	Balloon	Cursorial	Balloon	Cursorial
Ellicott Clear-cut	255	146	131	189	149	149
Ellicott Forest	245	97	164	145	207	156
Horse Clear-cut	88	121	156	169	202	228

Figure 13. Short-term data comparisons for all three Macon County sites illustrating differences in turnover (A) and 1-similarity (B) between ballooning and cursorially dispersing species. Grey bars represent the dynamics of ballooning species and white bars represent the dynamics of cursorially dispersing species. The three comparisons for each site correspond to two estimates of one-year turnover or similarity and one estimate of two-year turnover or similarity (1995 vs. 1996, 1996 vs. 1997 and 1995 vs. 1997).The index values were calculated using the raw data, without rarefaction.



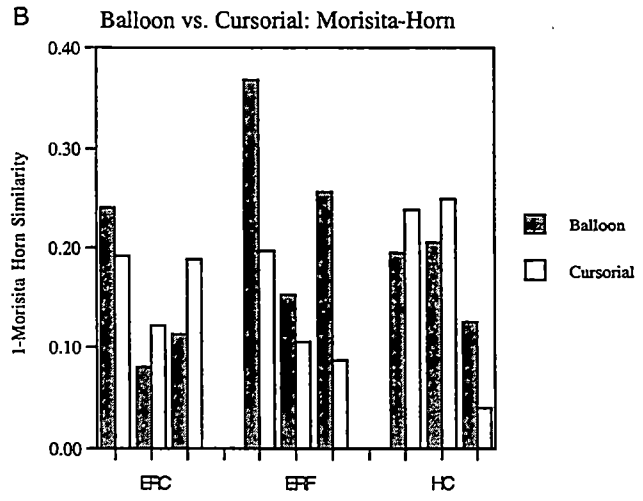
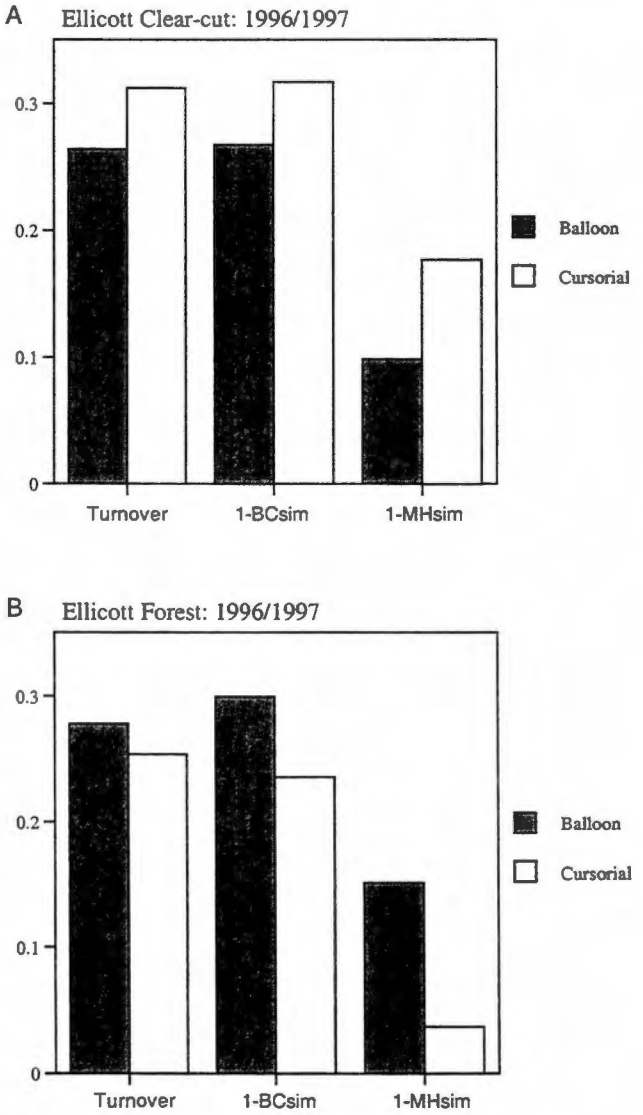


Figure 14. One-year data comparisons for Ellicott Clear-cut (A) and Ellicott Forest (B) illustrating differences in turnover and 1-similarity between ballooning and cursorially dispersing species. Turnover, 1-Bray-Curtis similarity and 1-Morisita-Horn similarity were calculated again using data from the more comprehensive surveys conducted in Ellicott Clear-cut (A) and Ellicott Forest (B). Grey bars represent the dynamics of ballooning species and white bars represent the dynamics of cursorially dispersing species. The index values were calculated using the raw data, without rarefaction.



variation (from early spring to late summer) in species composition and relative abundance of species and that this variation is greater than that experienced on a yearly basis. That fact aside, changes in species assemblages increase in magnitude through time either by chance alone in a habitat which has reached a stable equilibrium (Ellicott Forest) or forced by an ecological process like succession (Horse Clear-cut and Ellicott Clear-cut). In the latter case, we would expect the long time interval to produce much greater changes in species composition and relative abundance, which is again confirmed in this study. One might also expect that even short-term changes in the community may be effected by successional state. This study failed to show clear differences between the mature forest and the old clear-cuts in terms of yearly turnover. One possible explanation is that these 22- and 25-year-old clear-cut forests are approaching a climax state and therefore no significant structural changes are taking place within them. This is unlikely, however, since even 50 year old forest stands show marked differences in forest structure and composition from old growth stands elsewhere in the Southern Appalachians (Clebsch and Busing 1989). Another possibility is that the structural changes still taking place in the forest are insignificant from the viewpoint of the spider community and their use of the habitat. This also seems unlikely due to the very tight relationships that certain genera of spiders have shown to habitat type elsewhere in the GSMNP (Coyle, unpublished data), indicating that relatively minor differences in habitat structure can lead to measurable differences in the spider assemblage. A more reasonable explanation is that the successional changes still taking place at these sites are just not visible in a one or two-year window of time. Perhaps the differences would be detected if samples were taken every four or five years. It is interesting to note that overall, the sites with the highest estimates of yearly turnover and lowest estimates of yearly similarity are the youngest of the two clear-cut sites, and a grassy meadow. In addition, if the sites are

broken down into the groups presented in Table 1 (mature forests, young forests, and grassland) and averages calculated across sites within each grouping, the mature forests have the lowest estimates of yearly turnover (0.284) and highest estimates of yearly similarity (0.663 BC and 0.808 MH). The young forests have an average yearly turnover which is slightly higher (0.306) than the mature forests sites and an average similarity (0.650 BC and 0.794 MH) which is slightly lower. And finally, the grassland site has the highest yearly turnover (0.447) and lowest yearly similarity (0.464 BC and 0.594 MH). So on average, gross habitat structure (or 'disturbance' if you choose to classify it as such) does have an effect on the short and long-term dynamics of spider assemblages. In addition, the turnover of spider assemblages in the mature forests was fairly consistent between sites (range of 0.068 for comparable surveys), considering the significant differences in vegetation type, species richness (of the spider assemblage) and sampling regime. Turnover estimates seemed to hover at around 0.23 to 0.27 for the most intensively samples sites. These turnover values can by no means be considered a reason to exclude spiders as potentially useful biological indicators because they are 'too variable', especially considering that a portion of this turnover is due to under-sampling bias. Table 7 gives some estimates of short-term turnover for a variety of taxonomic groups. Unfortunately, little comparable data are available for most taxa, as many estimates (including some in Table 7) are 1) based on a subset of the entire assemblage, 2) are only calculated based on two surveys, or 3) the methods/formulae used to calculate turnover was unclear. Of the values given in Table 7, the turnover estimates reported for birds on British islands (Russell et al. 1995) are the most comparable to the turnover estimates I present. This is because the entire bird assemblage was used in the analysis, there were multiple replicates of one-year turnover, and the exact same formulae were used. In this system, annual turnover ranged from 0.07 to 0.19.

Table 7. Estimates of community turnover for a variety of taxa

Organism	1 to 2-year turnover	Notes, reference (*taken from Schoener 1983)
Arthropods	0.339	*mangrove arthropods, Simberloff and Wilson 1969
	0.252 to 0.344	*mangrove arthropods, Simberloff 1976b
	0.333	*ants on small islands (<30-m^2), Goldstein 1975
	0.342 to 0.590	*orb spiders on small islands (<<1-ha), Toft and Schoener 1983
Vertebrates	.07 to 0.19	birds on British islands, Russell et al. 1995
	0.005 to 0.019	*birds on Channel Islands, Jones and Diamond 1976
	0.004 to 0.75	*birds on miscellaneous islands, Jones et al. upubl.
	0.012	*lizards on Bahamian islands
Plants	0.014	*plants on islands near Perth, Abbott 1977
	0.08 to 0.11	*plants on islands near Rotnest Is., Abbott and Black 1980
	0.019 to 0.033	*plants on Lake Mockeln islands, Nilsson and Nilsson, 1982
Spiders	0.283	forest spiders in the Southern Appalachians, this dissertation
	0.4465	grassland spiders in the Southern Appalachians, this dissertation

Guild Dynamics

The guild-level analyses presented here did not seem to yield satisfying results in terms of producing consistent generalizations. In part, this may be due to the fact that as each study site has a unique spider fauna associated with it, which is determined by attributes specific to each habitat. Because of this, there is no reason to believe that a particular guild will consistently be more or less variable across sites. Within-site processes may be controlling the dynamic nature of each subgroup. More generally, for this type of analysis, a beech forest may not be comparable to a cove-hardwood forest or to a pine-hardwood forest. Nevertheless, I will attempt to summarize the results.

Aerial vs. Ground

On average, the aerial fauna appears to be more variable than the ground fauna, particularly in species composition as measured by turnover. In Ellicott Forest and in Hardwood Forest the aerial fauna consistently produced higher estimates of turnover. One could interpret this to mean that the litter produced by forests creates a buffering effect such that year to year fluctuations in rainfall or temperature have little effect on the ground fauna relative to the aerial fauna, which is more exposed. Unfortunately, this could also be an artifact of sampling bias since the guild designations are 100% correlated with sampling method (discussed at length in Part VI).

Hunting vs. Web

There seemed to be even less consistency when comparing the dynamics of hunting and web building species. On average, the web building species were more variable than the hunting species, particularly in terms of the relative abundance of species as measured by Morisita-Horn and Bray-Curtis similarity. Interestingly, the site for which the numbers of hunting and web-building spiders were the most similar

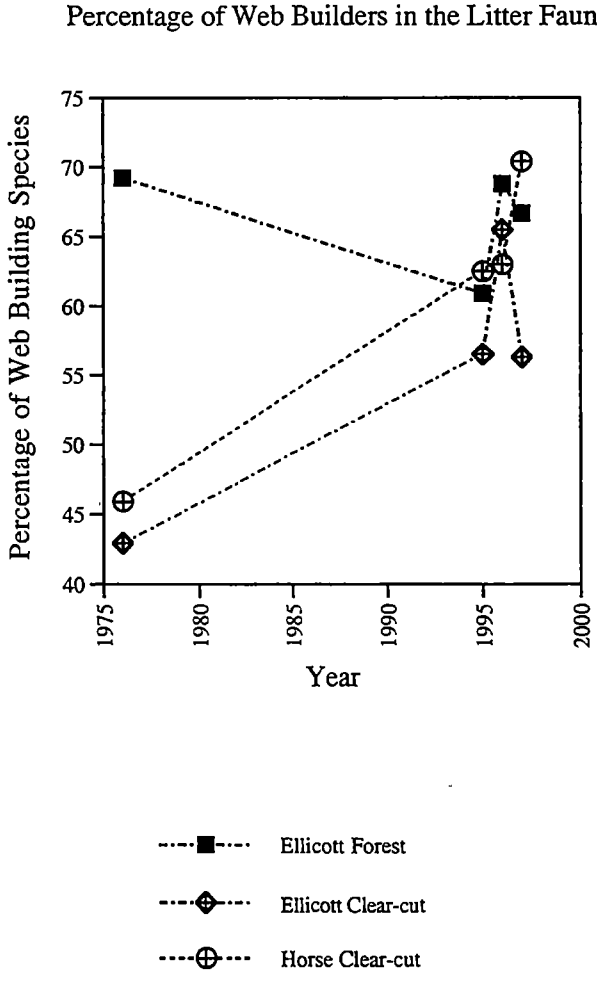
(Meadow Marsh) also exhibited the most consistent trend. Web building species were much more variable than hunting species in this grassland site.

Successional effects. Looking more closely at the clear-cut sites, it appears that hunting spiders are more similar over the long-term (1976 to present) than web building spiders. This implies that web building species are more affected by clear-cutting and subsequent re-growth than are hunting species. Perhaps as the forest grows vertically after clear-cutting, more and different web-builders move in, while the primarily ground-level hunting spiders remain relatively constant. Studies on the effects of clear-cutting have shown that clear-cuts are dominated by visual hunting species and mature forests more by sit-and-wait web-building species (McIver et al. 1992, Coyle 1981), particularly in the ground-level stratum. If this is a predictable guild-level pattern in forested systems undergoing secondary succession, then the two clear-cut sites in my study should show an increase in the dominance of the web-building guild through time. In Figure 15, I plot the percentage of web-building species relative to the total number or species through time for all three Macon County sites. In order to avoid problems with sampling bias, I used only data from litter samples and pitfall traps. The pattern appears to hold; the percentage of web-builders in the ground fauna increases over the long-term for the two clear-cut sites, while staying approximately the same for the mature forest. Based on the turnover and similarity data presented above, it would seem that the majority of this change is due to the influx of new and more species of web-builders rather than a decrease in the number or kinds of hunting species.

Ballooning vs. Cursorial

No generalizations can be made about the ballooning vs. cursorial dispersing species because the two sites with the most complete data-sets showed completely opposite patterns. The cursorially dispersing species in Ellicott Clear-cut were more

Figure 15. Percentage of web building species present in the ground stratum for 1976, 1995, 1996 and 1997 for Ellicott Forest (squares), Ellicott Clear-cut (diamonds) and Horse Clear-cut (circles). Species collected in litter samples and pitfall traps for each year were assembled and each species was classified as being a hunting species or a web-building species. Percentages correspond to the number of web-building species divided by the total number of species collected by litter samples and pitfall traps for that year.



variable than the ballooning species, while in Ellicott Forest the opposite pattern was observed. One possible explanation for this has to do with the structure of the vegetation underneath the canopy. Like most mature/old-growth forests, Ellicott Forest has a fairly open understory with few bushes, weeds and young saplings. Ellicott Clear-cut has a much more dense understory with a large amount of ground vegetation. Ballooning spiders may travel freely both through the understory and up and out of the canopy of the mature forest site. This enables the spiderlings to travel greater distances, producing higher year to year variability. Ballooning spiders in the clear-cut may be more likely to get 'snagged' and be kept within the canopy and closer to the site of dispersal; their year to year variability will be lower. Obviously this is just one possibility and I do not have the data to test this hypothesis. One serious problem with this analysis in general, is the indirect way in which the species were assigned a dispersal mode. Bishop's study was conducted over a relatively brief period of time and certain ballooning groups were obviously underrepresented (Riechert, personal communication). In fact, a later study by Bishop and Riechert (1990) concluded that ballooning accounts for all dispersal of spiders into agroecosystems as no difference was detected in species composition or abundance in balloon plots versus those where both ground and aerial dispersal were possible. Direct observations of the individual species which occur at these sites would provide much more accurate designations and might clarify existing patterns.

In conclusion, based on the analyses presented here, no clear recommendations can be made concerning which spider guilds may be more or less appropriate for use in biological monitoring programs. The inconsistent results may have been due to under-sampling bias, or specific problems with the data as discussed above. Just as likely, the 'inconsistencies' may simply reflect the fact that generalizations outside of a specific

habitat type are not possible for this type of analysis. Multiple data-sets from similar forest types may be the best approach to determine relative variability of spider guilds.

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PART VI: BIOLOGICAL MONITORING AND POTENTIAL SOURCES OF ERROR

INTRODUCTION

Biological monitoring is simply a way of estimating the 'health' or 'stability' of a community by examining how the resident species populations fluctuate through time. Sometimes the species being monitored is actually the target of conservation efforts, but more likely the species or group of species represent an indicator species or group. The indicator is usually chosen based on some prior knowledge of its reaction to specific kinds of disturbance and/or because it is thought to accurately represent some larger subset of the community in which it belongs. As previously discussed, terrestrial arthropod groups show promise for use in conservation planning because they are numerically abundant in a wide variety of microhabitats and functional niches at virtually all temporal and spatial scales. The cost of an arthropod inventory is substantially lower than for most vertebrate groups (unless payment of taxonomic specialists is required for species identifications), and statistically rigorous sample sizes are more easily obtained (Brown 1991; Murphy *et al.* 1990). Arthropods are also responsive to habitat fragmentation and to fluctuating environmental conditions but have been underutilized in terrestrial environments (Kremen *et al.* 1993). There are two primary reasons why terrestrial arthropods have often been ignored in conservation planning. The first involves what is sometimes called the taxonomic impediment. This refers to the problem that many species of arthropods have yet to be described and even the identification of known species can sometimes be a daunting and inaccurate task (see Part III, this dissertation). The second problem is that when dealing with hyperdiverse taxa, surveys are almost never complete. Studies which include arthropod groups can only hope to detect a portion of the species, particularly for large sites with many microhabitats. This means that for studies which attempt to either compare diversity indices across sites or to monitor the

population fluctuations through time at a particular site, surveys are really only a sample of the species populations that occur at a particular place and time. Therefore, before these data are used in any sort of analyses, it is important to take into account the implications of using samples instead of complete surveys and to correct for any biases. A knowledge of what biases and/or sources of error may exist when dealing with arthropod data should influence both the structuring of the sampling protocol and the analyses chosen.

Using the same sample data-set described in detail in Part II of this dissertation, I examine four of the most important potential sources of error encountered when using arthropod data: sampler bias, the inclusion of juveniles, taxonomic uncertainty and stochastic sampling effects. Based on the results of these analyses, I make general recommendations for community studies which choose to include spiders or other hyperdiverse taxa.

The Data

Spider species abundance lists from six sites in the Southern Appalachians were used as sample data-sets for the analyses that follow. The sites are located in two study areas, Macon County and the Great Smoky Mountain National Park (henceforth GSMNP). A full description of the sites, sampling protocols and results of sampling are given in Part II of this dissertation.

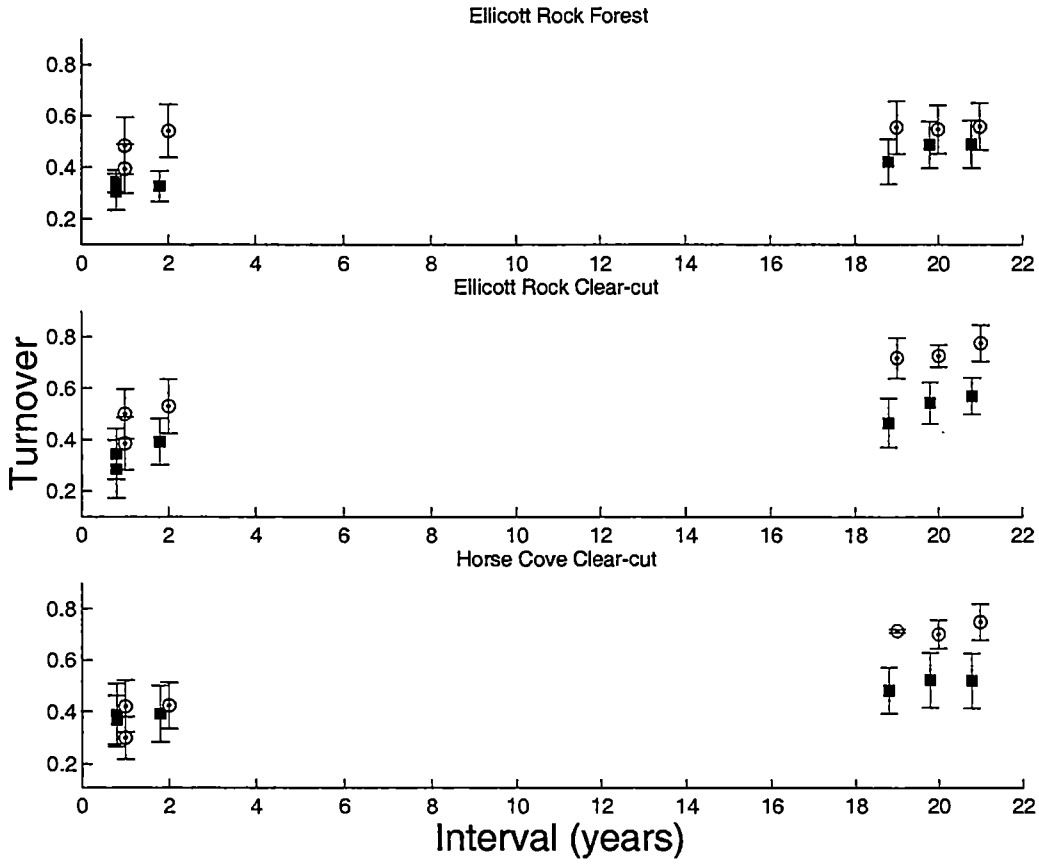
Collector bias

Dealing with samples, or subsets of the total richness for a site, is not necessarily an obstacle unless the sampling is in some way non-random. Recent studies of spider species richness have shown that there can be a significant sampler (collector) effect, usually in the form of differences in yield when the experience level of the collectors is

different (Coddington *et al.* 1996, Dobyns 1997). Differences in experience could mean either that the collector was more familiar with spider collecting in general, or just more familiar with collecting in a particular habitat and/or location. Sampler efficiency is less of a problem because of standardization tools such as rarefaction (see Part IV, this dissertation). But if different collectors show systematic bias in the species they collect, then making comparisons between samples collected by different workers will artificially elevate the degree of change in the community. Some techniques will be more subject than others to this type of bias. Hand collection, where workers collect in a particular area for a designated amount of time, will be subject to collector bias while standardized litter samples and pitfall traps will not.

To explore potential collector biases, I calculated turnover (see Part IV, this dissertation for a discussion of turnover calculations) between all pairs of surveys (1976 through 1997) completed at the Macon County sites, separated by sampling group: 1) high potential for bias and 2) low potential for bias. The estimates of turnover from sweep netting and hand collection (high potential) were consistently higher than those from litter extraction and pitfall traps (Figure 1). One possible cause that is not collector bias is that aerial spiders (spiders living in vegetation above the ground) are more variable from year to year than are ground dwelling species. Another possibility is that there is a higher diversity of species in the upper stratum and therefore the same effort may produce higher apparent turnover due to under-sampling bias. Neither explanation is completely satisfactory because although litter samples and pitfall traps do collect primarily ground dwelling species, the hand collection samples included specimens collected on the ground ('hand collect down') as well. Therefore, the correlation of hand collection and sweep netting samples with aerial dwelling species is not a strong one. Also, adult males of many of the typically aerially dwelling species will be collected in

Figure 1. Mean turnover estimates after 1000 rarefactions as calculated using only those species collected with pitfall traps and litter extraction (solid squares) versus using those species collected in sweep net samples and hand collection samples (open circles). Sample sizes were standardized between the two sets of methods through rarefaction, in order to make the turnover estimates comparable. The error bars include 95% of the turnover estimates calculated from the rarefied data. Squares and circles were staggered slightly for ease of viewing; this does not indicate differences in the years of collection. Turnover estimates at the shorter intervals are based on data collected by the same collector, while turnover estimates at the longer intervals are based on data collected by different collectors.



pitfall traps, as they move along the ground in search of mates. Finally, the differences in turnover are more pronounced when there is no overlap in collectors compared to when one of the two collectors was the same from year to year (Figure 1). This suggests that the differences are indeed due to collector bias.

I did the same analysis comparing data obtained through hand collection versus sweep netting for the Meadow Marsh site in the GSMNP region and again found that hand collection gave higher estimates of turnover than sweep netting. The analysis was repeated for the two forest sites in the GSMNP region, this time separating out all methods in order to distinguish the effect of ecology from that of method. No trends were apparent. For each of these analyses, I had to rarefy the data from each method down to the smallest yield (number of individuals collected). For the GSMNP sites, the smallest yield was always from the litter samples, which were highly variable from year to year. All litter samples are pooled, and for the sites in the GSMNP, a small number of large samples were pooled, compared to a large number of small samples at the Macon County sites. The high variability at the GSMNP sites may be due to inadequate sampling of spatially clumped spider distributions. Unlike the Macon County sites, no pitfall traps were used, so these data could not be added to the litter data as another 'unbiased' method. That might explain the lack of clear trends in the turnover analyses.

The above analysis was indirect in that assumptions were made concerning which methods would be more subject to bias than others. To explore the problem of sampler bias more directly, I used raw data from the GSMNP sites which has the collections separated by method and by collector. I used data from the species poor forested site, Beech Forest and the species rich forested site, Hardwood Forest because they both had sampling protocols resulting in a fairly equal distribution of effort across collectors. I also thought that these two sites would provide an interesting contrast of a species-poor site

which has been adequately sampled and a species-rich site which has been rather under-sampled (Part II, this dissertation). Of the eleven collections conducted at these sites (see Table 2, Part II, this dissertation for details), eight were chosen to test for sampler bias because the sampling effort was distributed precisely evenly among the collectors. For all but one of the samples, sampling was broken up between four collectors of which three varied from year to year, but were consistent within years. The question I am asking is whether or not each collector is sampling a random subset of the community. As stated above, differences in sampler efficiency (i.e., the number of individuals collected per hour) is not of much concern as long as the sampling is random. One way to statistically test for systematic bias is to separate out the species abundance distributions for each collector and compare this distribution to the overall species distribution. We can do this by using the heterogeneity G-test (Sokal & Rohlf 1981).

The G-test is a likelihood ratio test for goodness of fit. It is a way of comparing a set of observed relative frequencies (proportions) to a set of expected relative frequencies, similar to the more familiar Chi-square test. The expected relative frequencies can either be determined based on a specific model which is extrinsic to the sample data (e.g., expected phenotype ratios based on the rules of Mendelian genetics) or can be determined based on hypotheses intrinsic to the sample data. In this case, we calculate our expected frequencies based on the pooled sample of all the collectors as a surrogate for the whole community. This analysis makes use of only species obtained by beating and hand collection, which collect a specific subset of the community. As a result, it is more accurate to use the pooled data obtained using only these methods, than to use a larger sample which contains species collected by other means as our surrogate for the whole community. Because we are comparing more than one set of observed frequencies to the expected, we use the heterogeneity G-test to determine if the

subsamples could have been drawn from a single population or community. First, the expected species relative frequencies are calculated and these are scaled down to the size of each subsample by dividing by a number which results in the pooled sample having the same number of individuals as the subsample. The difference between these scaled-down expected relative frequencies and the observed relative frequencies of the first sample is quantified by calculating G (as in Sokal & Rohlf 1981). This process is repeated for each subsample (collector) and the G values are added together to produce G_h, a measure of the heterogeneity of the set of samples. Next, through Monte-Carlo randomization a distribution of G_h values is produced for comparison to our calculated G_h (Manly 1997). The details of this randomization process are as follows. Based on the total number of specimens collected by each collector, a subset of the pooled sample is drawn without replacement creating a simulated random subset of the community. G_h is then calculated comparing this random species distribution to the expected values, and the process is repeated 9999 times. The degree of significance is determined by the placement of the calculated G_h within the simulated distribution of G_h values. If the calculated G_h is the largest of all the G_h values and 9999 simulated G_h s were calculated, then we would reject the null hypothesis that the subsamples are homogeneous with a p value of <0.0001. Put simply, they would be found to be significantly different from random, indicating bias in the samples.

The collectors were not sampling a random subset of the total, irrespective of the total number of individuals they collected (see Table 1). For an illustration of how different the calculated G_h value was from the simulated G_h values, see Figure 2. Because of potential problems with using juvenile specimens in analyses which make use of abundance data (see discussion below), I ran the analysis again, using only the adult specimens. The p-values ranged from 0.001 to 0.006, all highly significant. It should be

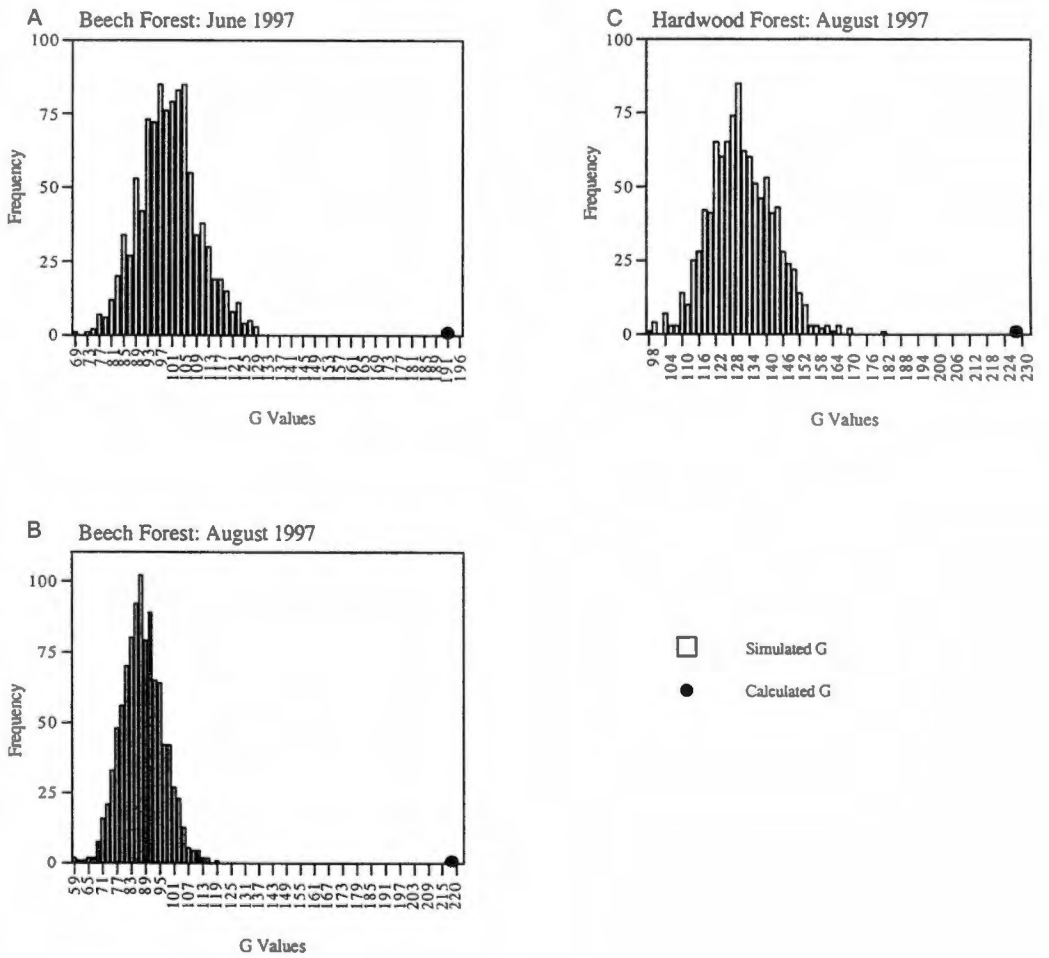
Table 1. Results of heterogeneity *G*-test

Site and Date	G_h	P_t
OGHH 8/96 Total	248.25	0.0001
*OGHH 8/96 Adults only	153.81	0.003
OGHH 5/97 Total	335.38	0.0001
*OGHH 5/97 Adults only	194.81	0.001
OGHH 8/97 Total	226.47	0.0001
*OGHH 8/97 Adults only	141.97	0.006
BGF 7/95 Total	54.64	0.005
*BGF 7/95 Adults only	54.64	0.006
BGF 6/96 Total	176.04	0.0001
*BGF 6/96 Adults only	87.08	0.003
BGF 8/96 Total	145.713	0.0001
*BGF 8/96 Adults only	109.39	0.001
BGF 6/97 Total	191.33	0.0001
*BGF 6/97 Adults only	118.87	0.001
BGF 8/97 Total	217.44	0.0001
*BGF 8/97 Adults only	112.87	0.001

* the simulations were only run 1000, instead of 10,000, so the smallest p-value possible is 0.001.

Note. OGHH is the Hardwood Forest and BGF is the Beech Forest.

Figure 2. Simulated distribution of G_h values, created through Monte-Carlo randomization and calculated G_h value. In this process, a subset of the pooled sample based on the total number of specimens collected by each collector is drawn without replacement creating a simulated random subset of the community. G_h is then calculated comparing this random species distribution to the expected values, and the process is repeated 9999 times. The solid circle represents the G_h value, calculated by summing the G values which compare the distribution of species in each sub-sample (results from a single collector) to the pooled sample.



noted that because I only ran 999 simulations on the adult data, the lowest p value possible for these tests is 0.001. An advantage of the G-test is that because the G values are additive, the significance can be partitioned out among the collectors. We are thus able to determine whether some collectors were consistently more biased than others. If not, then perhaps the bias is of less importance and more of a reflection of the spatial distribution of species in a given habitat. I looked at the number of times within a certain combination of collectors that a particular collector was the most significantly biased. The most biased collectors seemed to fluctuate from survey to survey (Table 2). But there were collectors which were never the most biased in either the total or adult analysis. Interestingly, these 'least biased' collectors were all relative newcomers to spider collecting (Coyle, personal communication).

To look more closely at whether some sampling methods are more susceptible to sampler bias than others, I used the same set of data, only this time separated by sampling method. Since hand collection seems less standardized in terms of technique, and relies more on the expertise of the collector than a more structured method such as vegetation beating, I would predict that samples obtained through hand collection by different collectors would be less similar than those obtained by vegetation beating. To test this, I calculated a similarity index between samples taken at the same site at the same time by different collectors using the same method (either hand collection or beating). I chose the Morisita-Horn index because it is less sensitive to small sample size as discussed in Part IV of this dissertation. I then plotted the frequency distribution of similarity values to see whether the beating samples were more similar to each other on average than the hand collected samples. As Figure 3A shows, more of the beating samples fell into the higher similarity categories than the hand collected samples and conversely, the hand collected samples are more likely to be found at the low end of similarity values. I did the same

Table 2. Most vs. least biased collectors as measured by the *G*-test for each survey

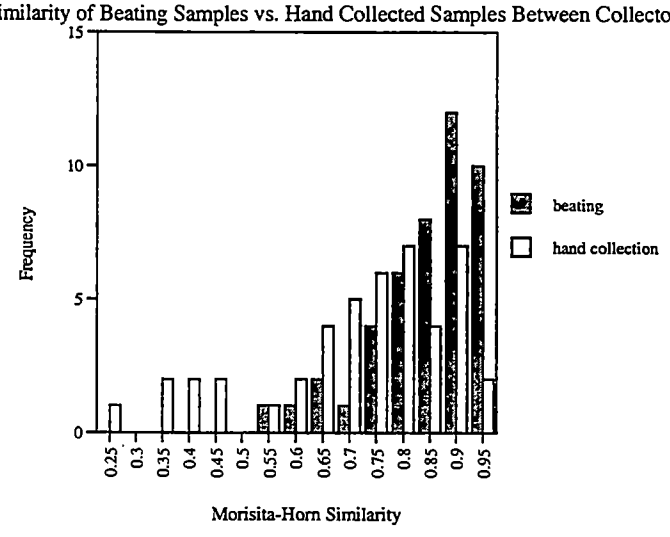
Survey	Collector 1	Collector 2	Collector 3	Collector 4
Beech Forest 6/97	A	B	C*	D^
Beech Forest 8/97	A*	B	C^	D
Hardwood Forest 5/97	A	B^	C	D*
Hardwood Forest 8/97	A	B^	C*	D
Beech Forest 7/95	A*	E^	F	---
Hardwood Forest 8/96	A*	G	H	I^
Beech Forest 6/96	A	G*	H^	I
Beech Forest 8/96	A	G*	H^	I

* collectors who contributed most to the high G-value, indicating that their sample was the least random

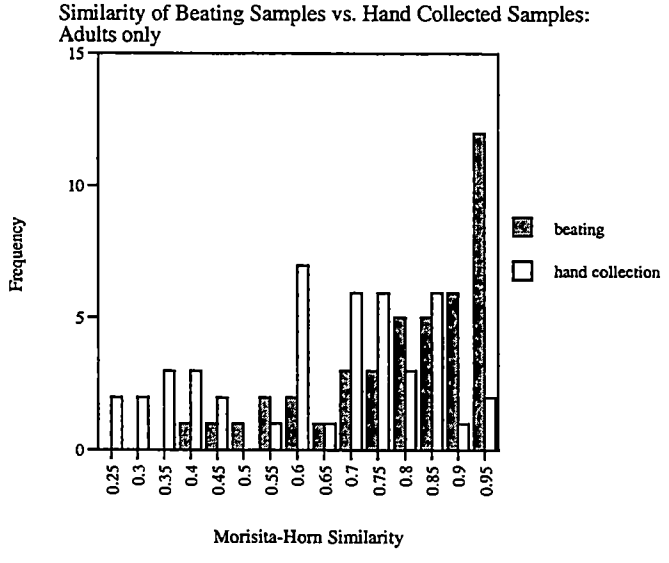
^ collectors who contributed the least to the high G-value

Figure 3. Frequency distribution of Morisita-Horn similarity values calculated between samples taken at the same site (Beech Forest or Hardwood Forest) at the same time by different collectors using the same method. Grey bars represent the similarity between beating samples taken by different collectors and white bars represent the similarity between hand collection samples taken by different collectors. In (A), similarity was calculated using data which included juvenile specimens, while in (B) the analysis was limited to adult specimens.

A



B



analysis using only the adult data and although slightly less extreme, Figure 3B shows the same pattern. As clear from Figure 4A&B, the mean similarity of the beating samples is higher than the mean similarity for the hand collected samples. Although this could be interpreted as further proof that hand collected samples are more likely to be biased than beating samples due to sampler bias, other interpretations are possible. Because the hand collection technique samples a slightly different microhabitat than the beating samples (beating samples are restricted mainly to tree branches and bushes, which is only a subset of the habitat searched during hand collection), one could also interpret these results to merely provide evidence that the fauna associated with bushes and trees is less variable than the fauna associated with the area sampled during aerial and ground hand collection. One way to partially test this idea is to compare the similarity of samples for each method taken by the same collector. If hand collected samples are indeed more variable even within collectors, then perhaps the fauna itself is more variable. One of the sites (Hardwood Forest) did have multiple samples (with the same method) taken by each collector on the same day. Unfortunately, only data for early 1996 were sufficiently subdivided for this analysis. Of the seven similarity estimates for beating samples and five estimates of hand collection similarity, all hand collected samples were more similar to each other than were the beating samples (Figure 5). Therefore, collectors were consistently collecting a more similar fauna from one hour to the next of hand collection than one hour to the next of vegetation beating. This indicates that the fauna collected through vegetation beating may actually be more spatially variable than the fauna collected through hand collection. In summary, the collectors were consistently sampling a biased subset of the spider fauna through hand collection, while the beating samples (though variable from sample to sample) did not exhibit systematic bias of the collectors.

Figure 4. Mean of the Morisita-Horn similarity values calculated between beating samples taken by different collectors (solid square) and between hand collection samples taken by different collectors (open squares). Error bars contain 95% of the expected variance, treating similarity values as data points.

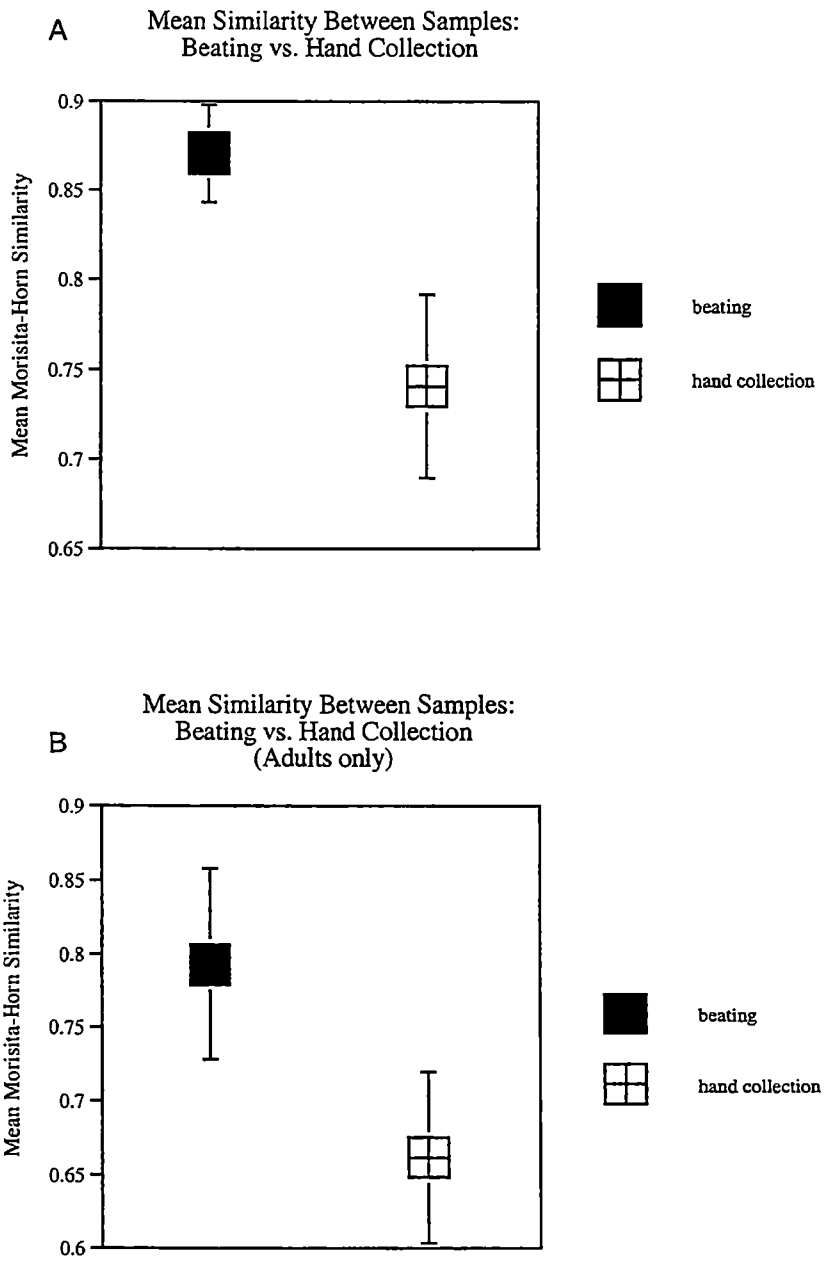
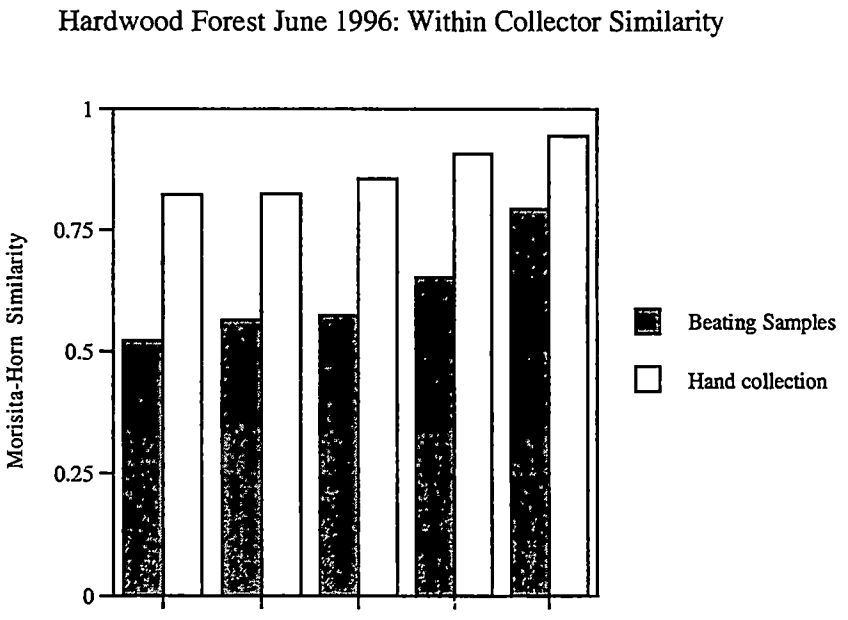


Figure 5. Within collector similarity of beating and hand collection samples. Grey bars represent the Morisita-Horn similarity index for samples collected at the same site, on the same date, by the same collector, using the method of hand collection. White bars represent the Morisita-Horn similarity index for samples collected at the same site, on the same date, by the same collector, using the method of vegetation beating.



Potential Solutions? In terms of a sampling regime set up for monitoring a spider assemblage, the systematic sampling bias illustrated above would be most detrimental in cases where there are few collectors conducting each survey and where there is a high turnover of collectors from survey to survey. A larger number of collectors would counter some of this effect, since all will exhibit a slightly different bias which may average out when the data are pooled. Otherwise, each new collector should be fully trained in collection techniques prior to any turnover of personnel and preferably systematic bias should be tested for in advance with both new and old collectors completing at least one sampling cycle together. Perhaps a more failsafe way to reduce this kind of bias is to use only those sampling methods which are largely sampler independent (e.g., vegetation beating, sweep netting, and pitfall traps). These techniques have a standardized protocol which limits the potential for collector bias.

Inclusion of juveniles

In most of the analyses performed in this dissertation, juveniles were included if they could be confidently identified to species. They significantly boosted sample sizes, as the total number of adults in each sample was relatively small (particularly for the Macon County sites). In addition, some common species were present only as juveniles because of the time of year during which the sampling was conducted. Inclusion of juveniles seemed justified, as long as the criteria remained constant for each survey. Nevertheless, there are potential problems, particularly for analyses which make use of relative abundance information. First, without prior knowledge of the demography of the species involved, it may not be reasonable to assume that the abundance distribution of juveniles is the same as that for adults. Even though most juveniles that can be identified to species are from later instars, it is still possible that significant mortality occurs prior to their molt into adulthood; Thus, are 25 penultimate instars of one species equivalent to 25

adults of another species? Are 35 adults collected in year 1 of a study equivalent to 5 adults and 30 juveniles collected the next year? These questions are important for most terrestrial arthropod groups where juvenile mortality is extremely high.

The relative abundance of species in a community can be drastically changed if juveniles are weighted the same as adults. Just looking at August data from 1997 for the Hardwood Forest site, there were a total of 1567 specimens collected, of which only 412 were adults. I ranked the species based on their abundances for that year using the adult data only, the juvenile data only, and the combined data (see Table 3). Only nine species are present in the top twenty on the adult and juvenile lists and only four species are present in the top ten. In addition, those species which were present on both lists were ranked in different orders relative to each other. This would not necessarily be a problem if the ratio of adults to juveniles remained constant from year to year, thus allowing comparison of the total data, including adults and juveniles. Again, this does not seem to be the case, at least for many species. For example, in the August sample of 1996 from the same site, the species *Hyptiotes cavatus* (Hentz) was represented by 142 individuals, of which 22 were adults. In August 1997, this species was represented by 390 individuals but zero adults. Another common species, *Neriene radiata* (Walckenaer), had a total specimen:adult ratio of 110:33 in May 1996 and 109:21 in August 1996. The next year, these ratios changed to 440:51 in May and 247:75 in August. It should be noted that this site represents a rather extreme case compared with other sites in this study (see Table 2, Part II). These examples are meant merely to illustrate that the fluctuations in juvenile abundance do not seem to be correlated with the fluctuations in adult abundance. In part, these inconsistencies could be explained by the fact that juveniles are more likely to be spatially clumped than adults (Riechert 1974). Thus chance will be more significant (i.e., a sample is more likely to either contain a large number of juveniles or none at all).

Table 3. The effect of juveniles on abundance rankings

	rank by total	rank by adults	rank by juveniles
1	(NR) Hyptiotes cavatus	Neriene radiata	(NR) Hyptiotes cavatus
2	**(1) Neriene radiata**	Araneus nordmanni	(NR)Pitiohyphantes costatus
3	(NR) Pitiohyphantes costatus	Callioplus pantoplus	**(1) Neriene radiata**
4	**(2) Araneus nordmanni**	Agelenopsis utahana	**(2) Araneus nordmanni**
5	**(4) Agelenopsis utahana**	Theridiosoma gemmosum	**(4) Agelenopsis utahana**
6	(NR) Tetragnatha versicolor	Ceraticelus carinatus	(NR) Tetragnatha versicolor
7	**(3) Callioplus pantoplus**	*Pirata montanus*	(NR) Meta menardi
8	(NR) Meta menardi	Robertus frontatus	(NR) Dictyna maxima
9	**(10) Hypochilus pococki**	*Achaeranea rupicola*	(NR) Callobius benneti
10	(NR) Callobius benneti	*Hypochilus pococki*	**(10) Hypochilus pococki**
11	(NR) Dictyna maxima	*Leucage venusta*	(NR) Spintharus flavidus
12	**(5) Theridiosoma gemmosum**	Scotinella redempta	(NR) Cyclosa conica
13	(NR) Spintharus flavidus	Coras montanus	**(13) Coras montanus**
14	**(13) Coras montanus**	Wadotes tennesseensis	**(12) Scotinella redempta**
15	**(12) Scotinella redempta**	*Centromerus denticulatus*	**(17) Cybaeus patritus**
16	**(6) Ceraticelus carinatus**	*Collinsia oxypaederotipus*	**(19) Philodromus rufus**
17	(NR) Pirata montanus	Cybaeus patritus	**(14) Wadotes tennesseensis**
18	**(8) Robertus frontatus**	*Theridion differens*	(NR) Tetragnatha viridis
19	**(17) Cybaeus patritus**	Philodromus rufus	(NR) Araneus miniatus
20	**(14) Wadotes tennesseensis**	*Ghelna canadensis*	(NR) Ariadna bicolor

Notes. Data from the August 1997 sample of Hardwood Forest. The numbers in parentheses represent the ranking of that species based on the adult data only. Species in bold are species which are present on both that list and the list based on the adult specimens. Species names in italics are species unique to the top twenty species list as determined by the adult data.

Inclusion of juveniles in a monitoring program may obscure trends that are present, or conversely suggest trends that are misleading.

I tested for a juvenile bias, first using the Hardwood Forest data-set. I chose Hardwood Forest because sample sizes were large enough to allow reasonably accurate analyses without the juvenile data. In addition, it represents an extreme case in which large numbers of juveniles could be identified to species. The trend examined in this case is the higher seasonal variability of the spider fauna as compared with the yearly variability (see Part V, this dissertation). I plotted the mean estimates of seasonal and yearly turnover and Morisita-Horn using data with and without juveniles (Figure 6). Although the trend still holds (seasonal variability is higher than yearly variability), the magnitude of the difference is reduced when juvenile data are included. I would have expected Morisita-Horn similarity to be the most affected by the inclusion of juveniles because it uses abundance information on the species. This does not seem to be the case. A second trend investigated using this technique is the increasing trend in diversity indices exhibited by the Beech Forest (see Part V, this dissertation). Results were similar to the previous analysis in that the trend toward increasing diversity was still apparent with the inclusion of the juvenile data, but the magnitude of the differences between the indices was greater when only adult data were used (Figure 7). I repeated this analysis, but this time using the Macon County data to test whether juveniles affected the short versus long-term trends in the data (Figure 8). This time, the inclusion of juveniles did not seem to affect the trends significantly. Unfortunately, as mentioned earlier, the number of adult specimens was so small for the Macon County sites that accurate comparisons are difficult.

In summary, the inclusion of juvenile data did not significantly effect the direction of a number of trends detected in these sample data-sets. Nevertheless, the

Figure 6. Index values with and without juveniles for Hardwood Forest. Grey bars represent seasonal and yearly turnover and similarity, calculated using all the individuals collected (including juveniles which could accurately be assigned to species) for the Hardwood Forest. White bars represent the same, except as calculated using the adult specimens only. 'T' stands for turnover and 'MH' stands for Morisita-Horn similarity. Rarefaction was used prior to the calculation of these indices, therefore the index values represent a mean after 1000 rarefactions.

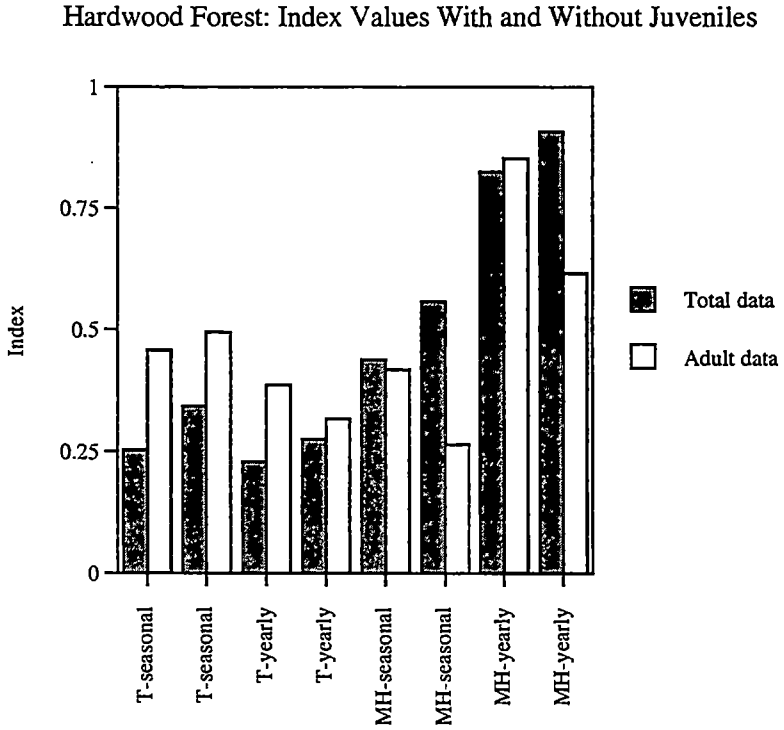


Figure 7. Index trends with and without juveniles for Beech Forest. Grey bars represent the absolute difference in Simpson's index, the Shannon index and Margalef's index through time (1996 vs. 1997) for Beech forest, calculated using all individuals collected. White bars represent the same, only calculated using adult individuals only.

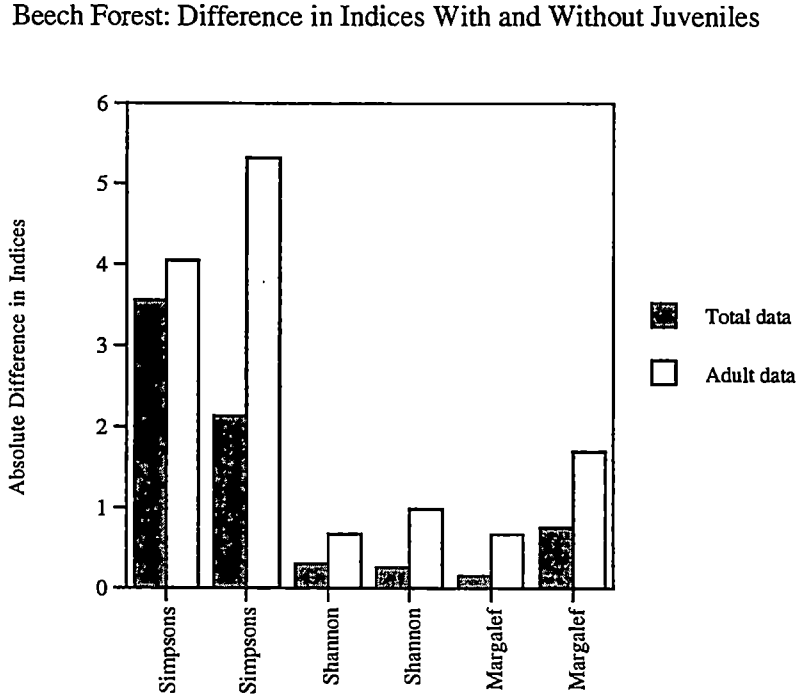
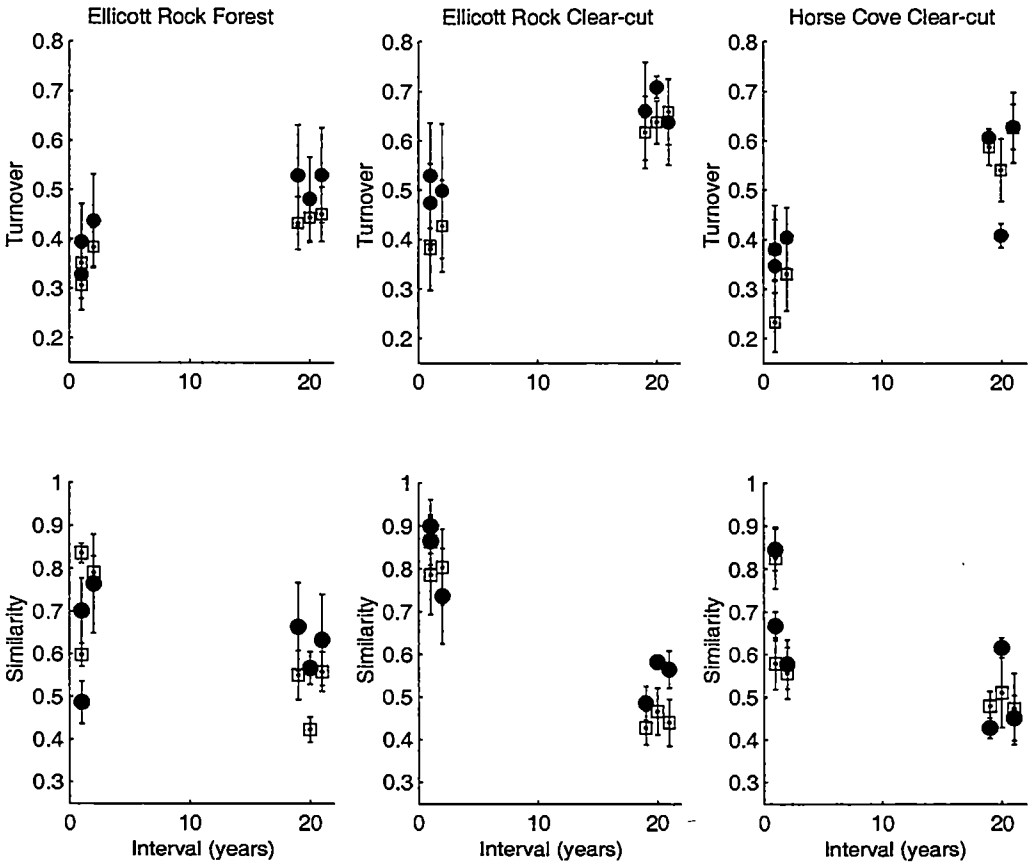


Figure 8. Long-term versus short-term turnover and similarity with and without the inclusion of juvenile specimens for sites in Macon County. Squares represent mean turnover and Morisita-Horn similarity estimates after the data had been rarefied and turnover and Morisita-Horn similarity calculated 1000 times using the complete data-set, including juveniles which could be accurately assigned to species. Circles represent mean turnover and Morisita-Horn similarity estimates after the data had been rarefied, including only adult specimens. The error bars contain 95% of the rarefied turnover and similarity estimates.



magnitude of the trends was obscured and this may become relevant in cases where statistical tests can be used to examine the trends quantitatively. This also suggests that less obvious trends (beyond the few identified here) in these communities may be undetectable if juvenile data are included.

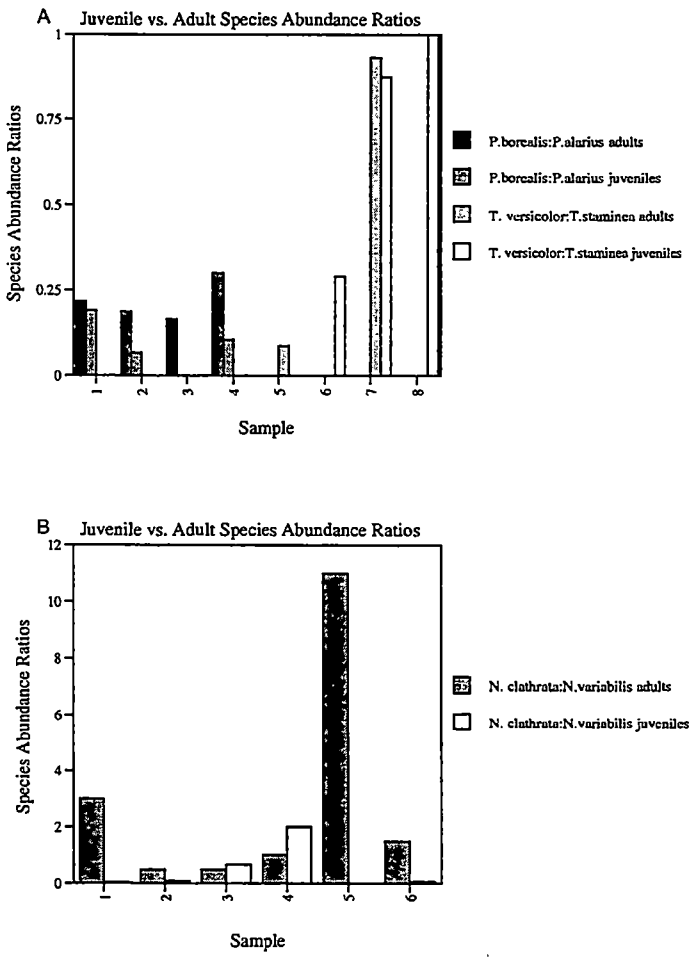
Potential Solutions? Merely throwing away the juvenile data seems extreme, since it is often difficult to avoid collecting juveniles and thus eliminating these specimens from the analyses after they had been collected seems wasteful and inefficient. Not to mention that they do represent a meaningful portion of the community under study. They may not be consuming the same food as adults, but they are an important part of the food chain nonetheless. Finding a way to incorporate the juvenile data would increase the efficiency of the sampling program and should result in a higher resolution analysis. One primary obstacle facing the inclusion of juveniles in community studies is the problem of classifying juveniles to species when there are more than one species in a given genus occurring at the study site. This is particularly frustrating when the proportion of adults of these species is highly skewed, with one very common and the other very rare. Having to throw away every juvenile once the existence of the rare species is discovered seems unnecessary, yet we are obligated to do so in the absence of identifying characteristics aside from the genitalia. Finding a way to estimate the proportion of juveniles based on the proportion of adults would be very useful.

To address this obstacle, I wanted to test the accuracy of estimating the proportion of juveniles from each species based on the relative abundance of the adult specimens in a sample. To do this, I looked for pairs of species in the same genus for which the juveniles could be identified with certainty due to morphological characteristics other than the genitalia. In addition, the species had to be fairly common with both adults and juveniles collected in the same surveys. Using data from both the GSMNP sites and the

Macon County sites, I found three pairs of suitable species, *Phrurotimpus borealis* and *P. alarius*, *Tetragnatha versicolor and T. staminea* and *Neriene clathrata* and *N. variabilis*. I then calculated the adult and the juvenile species abundance ratios for each pair in each sample. For this analysis, a sample is considered a collection of species from a site within a season. Unfortunately, as illustrated in Figure 9A and 9B, there seems to be no consistency from sample to sample in the abundance ratios for juveniles relative to adults. A complete lack of consistency in the ratios means that estimating the proportion of juveniles belonging to one species vs. another in the same genus based on the ratio of adult specimens in the sample would produce inaccurate results. Adult and juvenile numbers may not be correlated as a consequence of sampling error (e.g., juveniles are more likely to be spatially clumped than adults, as mentioned above). In addition, the timing of maturity of these species is influenced by environmental conditions, and the two species may be cueing in on different aspects of the environment. Therefore, the ratio of adults in a sample may not tell you anything about the relative proportion of juveniles, but rather only that one species has reached maturity faster than another. So this obstacle remains in place for now and therefore juveniles whose identity is ambiguous should be left out of any species level analyses making use of abundance data.

After the preceding discussion, one might wonder why bother with juveniles at all, since there seems to be so much uncertainty and effort necessary to incorporate them. In addition to the statements made above concerning the efficiency of sampling, it is also important to understand that sampling is often conducted within a fairly narrow window of time. During this narrow window, some species may be very dominant in the community as evidenced by their numeric abundance and yet may have only a small number of individuals which are sexually mature. So the ecological importance of a species may be grossly underestimated if all juvenile specimens were eliminated from the

Figure 9. Consistency of juvenile to adult species abundance ratios for three pairs of species. Data on three pairs of species in the same genus from both the GSMNP sites and the Macon Co. sites were used to construct these figures. The adult and the juvenile species abundance ratios for each pair in each sample were calculated and plotted. A sample is considered a collection of species from a site within a season. Dark grey columns (A) represent the ratio of adult *Phrurotimpus* borealis to adult *Phrurotimpus alarius* in each sample. Mid grey columns (A) represent these same two species, only the ratio of the juveniles. Light grey columns (A) represent the ratio of adult *Tetragnatha versicolor* to adult *Tetragnatha staminea.* White columns (A) represent the ratio of juvenile *Tetragnatha* versicolor to juvenile *Tetragnatha staminea.* In (B), grey columns represent the ratio of adult *Neriene clathrata* to adult *Neriene variabilis.* White columns (B) represent the ratio of juvenile *Neriene clathrata* to juvenile *Neriene variabilis.*



analyses. From my experience collecting in Macon County, I can say that this is a fairly frequent occurrence and that is why I am loathe to give up this important information. Unfortunately, some data are already lost for those species for which the juveniles cannot be accurately identified, and so under-representation already exists and is a problem. In conclusion, juveniles should only be included in presence/absence analyses and should not be used when relative abundance information is required. A more radical approach would be to either save the effort and resources necessary to identify juveniles and get rid of them entirely, or if possible, analyze these data separately. If sampling were to continue for many years in the same habitat (e.g. as part of a monitoring protocol), it may be possible to learn to recognize the juveniles of most species based on other morphological characters (e.g., spination, coloration). However, confirmation of species designation could only be achieved through rearing the juveniles to adulthood in the lab. This would be relatively labor intensive and perhaps not worth the added effort if time and space are limited.

Taxonomic uncertainty

Two distinct sources of error can be identified under the heading of taxonomic uncertainty. The first involves errors made by non-specialists when identifying specimens to species. Misidentifications can be made due to lack of experience or sometimes just lack of the appropriate up-to-date taxonomic keys. When voucher specimens from the original survey are not available, this could be a potential source of error in constructing species lists. In addition, although the taxonomy of spiders is becoming more stable, there are still many groups for which new synonymies are being announced and for which species groups are identified where once there was only a single species. Until alternative methods are developed to help reduce this error, such as the creation of easily accessible

virtual reference collections on the internet or automated species identification technology (Part III, this dissertation), these problems will continue to exist.

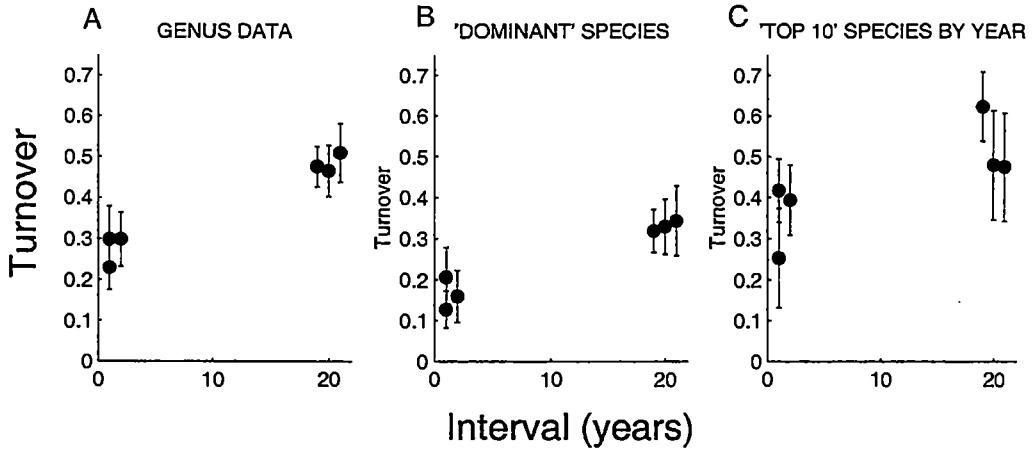
Potential Solutions? One way to avoid this source of error is to conduct genus level analyses. The down side of this is the potential loss of information; it may well be changes at the species level which are most indicative of disturbance. But if the habitat which is being monitored has a low species to genus ratio, then little information is lost and much error is eliminated. In addition, late instar juveniles may then be added to the analysis (since juveniles can usually be confidently identified to genus, but not species), which will elevate sample sizes. To illustrate this, I did a turnover analysis (see Part IV, this dissertation) for all Macon County sites using data only to the genus level. The turnover estimates decrease slightly, but the same patterns are evident (Figure 10A). The species to genus ratio for this site was approximately 1.17:1.

Stochastic sampling effects

Another source of error stems from the abundance distributions of spiders (and most hyperdiverse groups). Over half of the species in the limited collections are represented by one individual per sample. This becomes relevant when monitoring the communities because by chance alone, much of the turnover in species composition could be due to just stochastic effects of sampling. For example, one-year turnover estimates for Ellicott Forest and Ellicott Clear-cut decreased from 0.31 to 0.27 and from 0.34 to 0.29, respectively, when the sampling intensity was doubled in 1996 and 1997.

Potential Solutions? One way to deal with this is to use indices which focus more on the dominant species in the system (such as Simpson's index, or the Morisita-Horn similarity index). Another way is to only monitor the fluctuations in the most abundant groups; simply remove all singletons and doubletons from the samples. To illustrate this, I performed the turnover analysis for the Macon County sites using only those species

Figure 10. Long-term versus short-term turnover of genera (A), dominant species (B), and the ten most abundant species (C) in Horse Clear-cut. Solid circles show the mean of the turnover estimates after 1000 rarefactions. Error bars include 95% of all turnover estimates based on the rarefied data. 'Interval' refers to the time interval between the surveys. See text for details of the analyses.



represented by a minimum of four individuals across the entire duration of the study. I chose four because such a species could potentially be present as a singleton for each year of the study. This reduced the total number of species by 10% to 30%, depending on the site. As expected, this reduced the turnover estimates considerably (Figure 10B). Is important information being lost? The cut-off must be determined arbitrarily, and if the monitoring continues for multiple years, determination of this cut-off becomes more difficult. This could be partially resolved by determining the cut-off based on a percentage of the total (1% to 5% representation is typical for ecological or behavioral studies). Still, this is a somewhat arbitrary way to eliminate species and may result in important species being excluded as sampling continues for multiple years.

Another option would be to only monitor the turnover of the most abundant species and ask how does the species composition of the top 10 species vary from year to year? This is a slightly different technique, because although the number of species to be examined is set arbitrarily, it remains constant from year to year. The results of a turnover analysis using only the ten most abundant species ranked separately for each year is shown in Figure 10C. Oddly, the turnover of the most abundant species is actually higher than for the entire assemblage. This may just be an artifact of small sample size, since even species in the top 10 were only represented by less than 5 individuals in some years.

DISCUSSION

The preceding analyses illustrate that significant sources of error exist when analyzing time-series data on species presence and/or relative abundance, particularly when dealing with speciose groups that are incompletely sampled. Although not nullifying the results of previous chapters in this dissertation, this section does point out problems with the data which may have obscured some ecological trends, while perhaps

exaggerating others. Sampler bias exists and may affect the measured magnitude of ecological changes in the spider assemblages through time. The inclusion of juveniles, particularly in relative abundance measures has the potential to interfere with trends in the data, particularly when only juveniles of some species can be identified with confidence. Based on analyses presented here, inclusion of juveniles may not completely obscure strong ecological trends but rather merely reduce the strength of trends that still exist. Unfortunately, more subtle trends may be overlooked as a result. Taxonomic uncertainty and stochastic sampling effects will always be important when making use of arthropod data, but careful planning can alleviate many of the problems they present. In summary, although many of the sources of error identified have definite effects on the values of the indices, the general trends through time still persist. This is not to say that these sources of error are insignificant, but rather that gross trends (e.g. those associated with succession) are robust to the types of change these data illustrate. Short-term shifts in pattern may be more influenced by data biases. However, it is these phenomena that may be most useful to managers as they may indicate disturbance before significant damage has been imposed on a system. Therefore, any advance effort to avoid these sources of bias will result in a higher resolution and more efficient analysis.

Conclusions and Recommendations

Development of a monitoring protocol for a particular habitat should begin first with adequate background information about the assemblage being used, including knowledge of the underlying abundance distribution of the group and the species:genus ratio. This information is necessary to develop a reasonable and efficient sampling regime, and will help managers to decide whether or not species level identifications are necessary. In addition, repeating the initial survey of the assemblage at least one time within the same sampling season will give a base-line measure of turnover and similarity

(Spellerberg 1994). This will give a clearer picture of how much 'change' you can expect based on stochastic effects of sampling. Although the exact design of such a protocol will be specific to the habitat being monitored as well as the assemblage being used, some general recommendations can be made based on the results of the analyses presented above:

1) Standardized, quantitative sampling techniques (with measures taken to ensure statistically adequate sample sizes) are a must, but for monitoring purposes, additional precautions are necessary. Emphasize methods which are least subject to sampler bias such as pitfall traps, litter samples, or vegetation beating/sweeping. Either prevent frequent turnover of collectors between surveys or be sure that collectors are sufficiently trained prior to the changeover.

2) Set your minimum sample size at a level sufficient to either analyze juveniles separately or remove them completely from the analysis. If this is not possible, then use juveniles only when applying techniques which make use of presence/absence data. Avoid juveniles when calculating relative abundance estimates.

3) Consider using genus level analyses if the species:genus ratio is small to avoid problems with taxonomic uncertainty.

4) Maintain voucher specimens for all species from previous collections, including unidentified specimens, to ensure consistency in identifications.

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PART VII: SUMMARY AND CONCLUSIONS

INTRODUCTION

As mentioned in the introduction, this dissertation sought to address two kinds of research questions; the first methodological and the second ecological. The methodological analyses primarily concern the use of spiders (as a representative hyperdiverse group) as indicators in biological monitoring programs. The ecological analyses attempt to address more specifically what is influencing the character and the dynamics of the spider assemblages occupying these particular sites in the Southern Appalachians. The primary focus and organizing structure of this research has been methodological, while the ecological aspect has been dispersed throughout. Here I attempt to first bring together and summarize the primary ecological findings, followed by a discussion of some of the most prominent methodological and practical applications of this work.

ECOLOGICAL SUMMARY AND CONCLUSIONS

Site characteristics

Results presented in Part II indicate that the richness of spider assemblages is related to the richness/structure of the vegetation at these sites. Beech Forest, the most vegetationally (and structurally) homogenous site had the most homogenous and species-poor spider fauna. Hardwood Forest and Ellicott Forest, both vegetationally complex sites, had the most species-rich spider assemblages. Further analysis of the spider fauna at these sites illustrates that Meadow Marsh and Horse Cove are unusual, particularly with respect to their highly equable spider species distributions, their divergent extrapolated richness estimates, their species accumulations curves and in the case of Meadow Marsh, their high yearly turnover rates. For Horse Clear-cut, some of these peculiarities could be

explained merely as the effects of undersampling bias, as this was the least intensively sampled site. Still, when comparable subsets of the data from the other Macon County sites are compared with Horse Clear-cut, it still stands out. One aspect of these two sites which sets them apart from the other four, is that they are distinctly habitat islands within a heterogeneous surrounding environment. Horse Clear-cut is a regenerating natural forest neighbored in part by a tree plantation, an extensive alluvial wetland, and human development projects. On a slightly larger scale, it lies on a flat, low-point in elevation. Meadow Marsh is bordered in part by a more extensive alluvial wetland and in part by forest. It is also a flat, low-lying area in the midst of an elevationally complex landscape. There are two potential mechanisms by which the common geographical placement of these sites may have influenced the equitability of their spider assemblages. The first is merely their close proximity to a vegetationally distinct habitat or habitats which could lead to 'overflow' or migration of spider species from one habitat into the next. The second is that the low elevation and flat aspect of Horse Cove and the low vegetation and flat aspect of Meadow Marsh result in a greater inflow of ballooning spiders due to wind currents and airflow patterns (i.e. wind carries spiders from high to low elevation or from over the canopy of forest down to the 'dip' of the flat wetland). These two possibilities are not, of course, mutually exclusive. Both could result in (relatively) highly equable species distributions and/or higher turnover rates from year to year through increased colonization of new species form neighboring habitats. More research is necessary to elucidate which, if either, of these explanations is correct.

Secondary succession

As two of the six sites in this research are in the process of regeneration following clear-cutting in the 1970's, the topic of how secondary succession affects the spider assemblages at these sites has been a major theme. Secondary succession of a forest

system from the spider's perspective was clearly exhibited by the data presented here. Long-term trends in diversity indices documented the convergence of the two clear-cut sites on the mature forest in terms of diversity and evenness through time. Long-term turnover and similarity were substantially greater for the clear-cut sites than for the mature forest site, further demonstrating the changes in the spider assemblage during forest regeneration. And finally, as other studies have demonstrated the changes in spider guild-structure resulting from clear-cutting, I have demonstrated that for these stands the patterns do, in fact, reverse themselves as the forest regenerates (Part V). Even within the litter community, a predictable shift from the dominance of visually hunting species to the dominance of sit-and-wait web building species as the forest matures is apparent from the data.

A second form of secondary succession occurring at a smaller scale is demonstrated from the spiders' perspective at the Beech Forest site. As mentioned previously, this forest is currently being degraded by the beech scale insect which has killed a number of adult trees in this stand creating gaps in the canopy. As these gaps undergo regeneration (secondary succession on a microscale), habitat is available for understory spider species. The data show trends in diversity indices through time, indicating an increase in diversity and decrease in dominance. As this forest was the most completely sampled site (see Part II, this dissertation), these trends are not likely to be the result of undersampling bias.

Finally, data from all six sites show that one-year assemblage dynamics are lowest for the mature forests, intermediate for the young forests and highest for the grassland site. This trend (though not a strong one) may be due to the interaction of habitat structure and spider dispersal. Closed canopy, mature forests may prevent the outflow of ballooning spiders by tempering wind-inflow from above and creating a

barrier to dispersal and/or colonization. Younger forests, with a less enclosed canopy may provide uplifting wind currents that facilitate both dispersal from and colonization into these habitats. The grassland site, with no canopy, may serve as a sink and source for dispersing species through time due to its exposure to wind and air currents. It is thus expected to exhibit higher rates of turnover and does. As mentioned above, these wind-structured dispersal patterns may partially explain the unique species distributions of Horse Clear-cut and Meadow Marsh. In addition, the increase in diversity at Beech Forest through time could also be partially attributable to the colonization of early-succession species through the newly formed gaps in the canopy. Again, more research is necessary to elucidate the influence of vegetation structure on colonization and dispersal of spider species.

METHODOLOGICAL SUMMARY AND CONCLUSIONS

Because the majority of this work has focussed on the methodological aspects of biological monitoring, I will not explicitly repeat my results in a summary format. Instead, I will present two practically aimed sections. The first will be a set of generalized guidelines and recommendations for anyone attempting to implement a biological monitoring protocol as a management tool. These recommendations are based on the outcome of the analyses presented in this dissertation. The second pertains more specifically to answering questions about species preservation in the Southern Appalachians from the species/area and nature reserve perspective.

Recommended guidelines

Below is a list of some general guidelines and recommendations for the use of hyperdiverse taxa in community ecology studies based on the results of the analyses presented in this dissertation. These guidelines are primarily for those sampling in

temperate forest or grassland regions. Please recognize that these guidelines are for evaluation of change through time and are NOT meant for full taxonomic inventories.

Sampling

1. **Use pitfall traps, litter extraction, and vegetation beating/sweeping.** These methods give high yields in terms of diversity of species and percentage of adults collected for the time and effort required. They are also less subject to collector bias and will therefore provide a less bias cross-section of the spider community.
2. **Conduct sampling along replicated (minimum of 4) permanent transects or other spatially explicit sampling designs.** This will help reduce the 'noise' associated with habitat heterogeneity within a site by keeping the sampling areas constant from survey to survey. This will also provide spatial replicates which can be used to measure habitat heterogeneity.
3. **Complete two samples of the transects in quick succession.** Instead of one large sample, complete two smaller samples of the transects within as short a time frame as possible. This will yield an estimate of variability due to (under)sampling bias.
4. **Sample within a season or sample year-round.** Seasonal effects can interfere with yearly change estimates. Be as consistent as possible with sampling dates. Conducting at least one year-round sample will give data on when the assemblage is the most 'stable' in terms of species composition. Target this time of stability for sampling to avoid seasonal effects.
5. **Maintain an adequate voucher collection.** Ideally, this should be digital with automated identifications to avoid error when there are changes in personnel.

Indices

The choice of indices will undoubtedly depend on the purpose of the monitoring program (i.e., what aspect of the community dynamics you wish to measure). In addition, only a small subset of available indices were evaluated in this study and so these guidelines are by no means based on an exhaustive review of indices. The following list should be read as "if you are primarily interested in detecting:

1) **Richness changes.** Use
    a) Turnover
    b) Rarefaction
    c) Juveniles
2) **Diversity changes.** Use
    a) Morisita-Horn Similarity
    b) Shannon-Weiner or Simpson's, but look for consistent trends through time
    c) Rank-abundance distributions, look for changes in shape
    d)

    No juveniles

Habitat heterogeneity and nature reserves

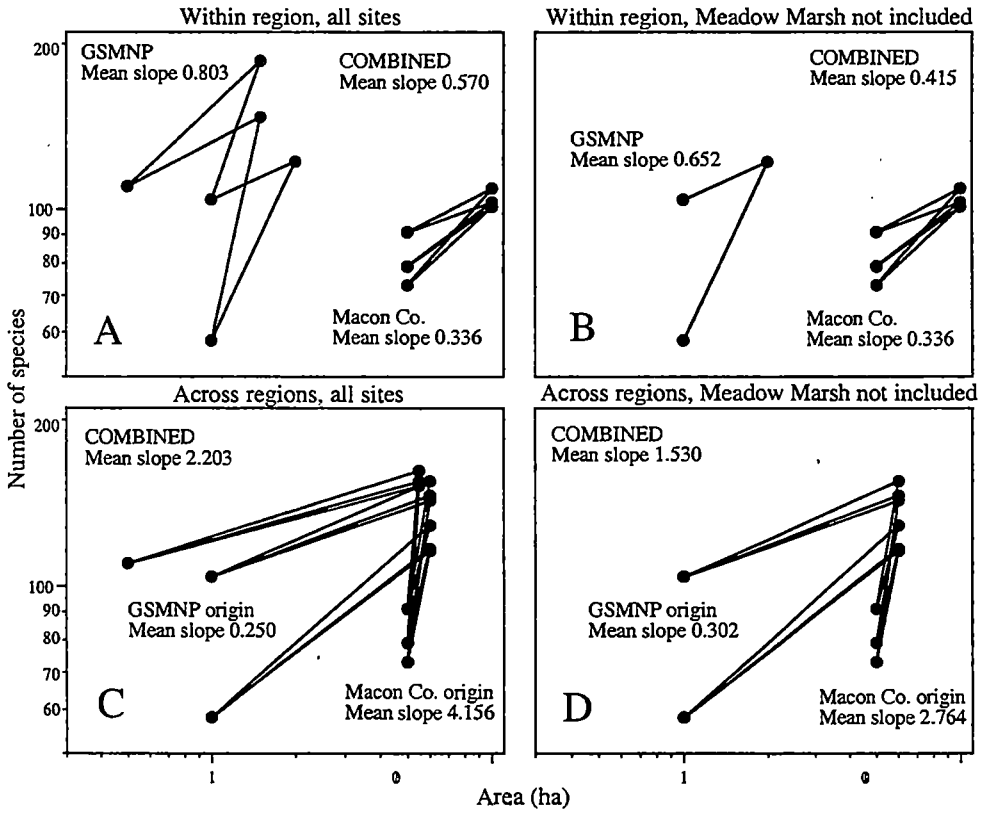
As the philosophy of conservation efforts has begun to switch from the idea of management for the success of specific target species to the management for the preservation of biodiversity, we now think in terms of protecting whole of communities or ecosystems. Assuming that our choice of protected areas is and will continue to be limited, we must elucidate which combination of habitats will preserve the greatest amount of biodiversity. For this discussion, I define biodiversity to mean the number of unique species (although I clearly recognize that there are many other definitions/interpretations of this term!). Using data from this work in the Southern Appalachian Mountains, I try to answer two questions: 1) how well do these sites capture the biodiversity of this region and 2) what combination of sites yields the highest percentage of unique species?.

A total of 290 species in 154 genera were collected as part of this study. One hundred and sixty four species were collected in Macon County and 200 species in the GSMNP. Although no clear estimates exist for the total number of spider species

expected to exist in the Southern Appalachians, according to recent spider surveys in the GSMNP, there are approximately 500 to 550 spider species living in the Park. Therefore, my three sites which constitute three out of the 18 (17%) habitat types defined by the Nature Conservancy as existing in the Park, yielded approximately 36 to 40% of the species. Unfortunately, there are no comparable estimates for the Nantahala National Forest. Still, none of the regional species accumulation curves presented in Part II appear to be substantially leveling off, therefore indicating that many more species exist in this region.

The next question to ask is how much of the total richness of the area is capture by each site or pairs of sites within a study region and by each site and pairs of sites between study regions. (Note that for the following summaries, the 1976 data from Macon County were eliminated and richness re-calculated for only the modern surveys to make them more comparable to the GSMNP sites.) For example, over the three years of the study, Meadow Marsh yielded the highest percentage of unique species over the entire study area (110 out of 244 or 45% of the species). In Macon County, surveys at Ellicott Forest captured 90% of the species of this study region and 37% of the total. The two-site combination that captures the highest percentage of species across sites is Ellicott forest and Meadow Marsh with 66%. The best three-site combination of Ellicott Forest, Hardwood Forest and Meadow Marsh captured 90% of the species and the best four site combination (Ellicott Forest, Hardwood Forest, Meadow Marsh and Beech Forest) captures 95% of the species. To look more explicitly at the relative heterogeneity in proportion to area of the study regions, I plotted species-area curves for each region separately and then both regions combined for all nested pair-wise combinations (e.g., the richness and area of Ellicott Forest followed by the richness and area of Ellicott Forest and Horse Clear-cut combined) (Figure 1). The mean slope of each set of data-points

Figure 1. Species-area exponents obtained when moving from a single site to a combination of two sites. Figures A and B are for cases when the added site is from the same region (Great Smoky Mountains National Park—GSMNP—or Macon Co.), and figures C and D are for cases when the added site is from the other region. Figures B and D differ from figures A and C in that one of the GSMNP sites—Meadow Marsh—is not included. My justification for this is that Meadow Marsh is a very different habitat from the other sites (which are all variations on forest), and so differences in species composition between it and the other sites would be inflated.



gives an estimate of z , the species-area exponent. The higher the value of z, the greater the heterogeneity in species composition. As Figure 1 illustrates, the slope for the GSMNP sites is much higher (0.803) compared with the slope for the Macon County sites (0.336). In essence, this means that the collection of sites in the Park are more different from each other than the three sites in Macon County are from each other. This is intuitive, as the sites in the Park are further apart and represent distinct vegetation types. Still, even the slope for Macon County is quite high compared with the typical z values of 0.15 for within-province comparisons given by Rosenzweig (1995). Insects have been shown to exhibit elevated z values (compared with vertebrate groups) as well (Rosenzweig 1995 using data from Kennedy and Southwood 1984) , so perhaps this is characteristic of small-bodied organisms which operate at a smaller spatial scale. The pair-wise comparisons *across* regions yield a z value of 2.203, indicating a high degree of heterogeneity between study regions. Interestingly, the slopes for comparisons between sites where the origin was in the Park and the additional site was outside the park were actually lower than the slopes for comparisons where both sites were in the Park. This indicates that the addition of a Macon County site to a GSMNP site adds fewer species to the total than the addition of a second site from the Park. One reason for the extreme levels of heterogeneity in the GSMNP is due to the peculiarity of the Meadow Marsh site. As mentioned previously, over the course of the three years of study, Meadow Marsh (which is the smallest of the sites) had the highest richness and yet for any one year, it's richness was less than that of the Hardwood Forest. This indicates that the high yearly turnover at this site is creating an artificially large richness count when surveys across years are combined. Therefore, I repeated the species-area plots excluding the data from Meadow Marsh (Figure 1). The same patterns hold, but the z values are much closer to what would be expected for comparisons of this sort.

In summary, two main conclusions can be drawn: 1) based on the spider data from the All Taxonomic Inventory of the GSMNP and on the regional species accumulation curves presented in Part II, this study did not come close to sampling the spider diversity present in the Southern Appalachian Mountains; 2) Based on the data collected as part of this study, the largest number of spider species for the amount of protected area could be preserved by protecting Ellicott Forest along with the three sites in the GSMNP. Ninety-five percent of the species collected were present in 38 to 53% of the area (range depending on whether area is measured by habitat patch size or sampling area within the patch).

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Rosenzweig, M.L. 1995. *Species Diversity in Space and Time.* Cambridge University Press. Cambridge, UK.

APPENDICES

APPENDIX I: QUANTIFYING CHANGE THROUGH TIME IN SPIDER ASSEMBLAGES: SAMPLING METHODS, INDICES, AND SOURCES OF ERROR

PREFACE TO APPENDIX I

The following is the text as it was published as Norris, K.C. 1999. Quantifying change through time in spider assemblages: sampling methods, indices, and sources of error. *Journal of Insect Conservation* 3, 309-325 . Because this paper is really an overview of the analyses contained in my dissertation which are presented in more detail in the preceding chapters, I thought it would be appropriate to include an intact version as an appendix. Portions of this text, in modified form, are found scattered throughout the preceding chapters.

SUMMARY

Using a sample data-set from six sites in the Southern Appalachian mountains in the United States, I evaluate the usefulness of diversity indices and similarity/difference indices for monitoring the changes in spider (Order Araneae) assemblages through time. The Shannon index, Brillouin index, Simpson's index, and Margalef's index were correlated with each other and were able to detect successional changes in two old clear-cuts as well as disturbance to a Beech gap forest possibly due to Beech Bark Disease. Turnover, Bray-Curtis similarity, and Morisita-Horn similarity also detected successional differences between the forest types and indicated the short-term and long-term changes in a mature forest stand. Seasonal changes (early to late summer) in spider communities were consistently higher than yearly changes. I identify and discuss the implications of various sources of error that will adversely affect the accuracy and efficiency of a monitoring protocol: sensitivity of indices to sample size, sampler bias, inclusion of juveniles, taxonomic uncertainty and stochastic sampling effects. Although gross trends are still apparent in the sample data regardless of these errors, more subtle changes may be obscured. It is these subtle trends which may be more useful to managers attempting to identify disturbance before irreversible damage occurs.

Keywords: biological monitoring; community dynamics; diversity indices; turnover; spiders

INTRODUCTION

Due to the hyperdiverse nature of arthropods, the lack of either taxonomic or ecological information on most species, and the rate of habitat alteration and destruction, traditional single species management is often not feasible. In order for a species to be

listed as Endangered, it must not only have a name and be recognized as a unique taxonomic entity, but also some biogeographical and basic life-history information must be documented. Only an estimated 7-10% of all insect species have been described to date (Samways 1993) and of those, only a small percentage have enough known about their biology to allow for the construction of informed recovery plans. Our options seem to be limited to the "quick and dirty" conservation techniques of evaluating ecosystems, designating reserves to protect 'valuable' habitats, and monitoring the success of those reserves (Ehrlich 1992). Most conservation biologists, along with government agencies, have focused on the first two of these objectives (Soulé and Simberloff 1986). But as more land is set aside for conservation, attention has turned to methods of monitoring the success of the ecosystems within these reserves (Spellerberg 1991). Rapport *et al.* (1985) suggest six symptoms of stress for assessing reserve success: changes in nutrient cycling, changes in primary productivity, changes in species diversity, retrogression (large fluctuations in populations that reproduce rapidly), changes in the size distribution of species, and changes in the amplitude of fluctuations in component populations. Many of these indices are difficult and costly to measure. Rapport *et al.* (1985) state that the earliest indications of ecosystem response to disturbance are abnormal fluctuations in 'sensitive' populations. If we can identify such species, they may be used as indicators to detect stress in the community. But this assumes we know the 'normal' dynamics of these species, as well as how to measure and quantify significant deviations from this state.

Aquatic arthropods such as amphipods and isopods have been used as indicators of water quality since the 1970s (Rosenberg *et al.* 1986). In terrestrial systems, indicator assemblages have been used primarily to compare richness and diversity between sites. Sometimes the purpose is to measure the effect of a known disturbance at one or more of the sites, or to decide which of a series of candidate sites would be the best to conserve.

The presence or absence of a set of species may be used to indicate either that a habitat is free of disturbance, or that it is in a 'disturbed' state. Fewer studies have actually tried to measure the change in an assemblage through time at a series of sites to see how the assemblage naturally fluctuates or how these fluctuations might be affected by a disturbance (Spellerberg 1991). Yet maintenance of diversity on protected land often relies on this type of monitoring program. Implementation of a monitoring protocol before problems arise allows comparison between 'normal' fluctuations and those which may indicate an unwanted change in the assemblage structure.

The methodology used in a monitoring regime will depend on the assemblage being measured. For preference, the natural community dynamics of the group chosen should be known to a certain degree, to better set guidelines for sampling intensity and the frequency of sampling. It would be best to have some prior indication of what potential problems and sources of error there may be in the monitoring process. That way, time and resources will not be wasted collecting unusable data, or data which may not answer the questions being asked.

In this paper, I explore these issues by using a sample dataset. These data are in the form of spider species (Order Araneae) abundance lists for six sites in the Southern Appalachians. I explore the use of rarefaction, turnover and similarity and diversity indices as tools to quantify changes in community structure through time. The intensity of sampling varied both within and between sites, thus allowing me to evaluate the effects of sample size and the use of rarefaction on the indices chosen. Although five of the six sites are forested, they vary in age and dominant vegetation, so I also examine the effect of these variables. Most importantly, I identify and discuss potential sources of error, and make recommendations for those who might choose to use spiders (or other terrestrial arthropods) as their focal group.

THE DATA

Data collection

Data was collected from six sites in the Southern Appalachians of the United States. I chose three of the six sites ('Macon County') because the spider fauna had been sampled in the summer of 1976 by Fred Coyle (Coyle 1981). These three sites include a mature forest (ERF), and two old clear-cuts (ERC and HC). Coyle's sampling protocol was duplicated in 1995, 1996 and 1997, thus allowing a comparison of long- and short-term changes in these assemblages. The sampling protocol consisted of five hours of hand collection (time split equally between the ground fauna (down) and the aerial fauna (up)), eight sweep net samples (of 50 sweeps each), 10 (0.25m^2) litter samples and 16 pitfall traps at each site. Pitfall traps were placed in the same locations each year, following Coyle's original site map. Care was taken to sample during approximately the same weeks of the year as the 1976 survey (beginning in late June and ending in late July).

In Coyle's original study (1981), he states that he completed 4.5 hours of hand collection, but did not mention whether the additional half hour was spent collecting from the ground or aerial fauna. Because of this and my smaller yield per hour in my first year of sampling, I decided to round the sampling time up to five hours for the rest of the study. Also, Coyle used eight pitfall traps, checked every three weeks for 15 weeks. Due to lack of time and resources, I used 16 pitfall traps checked weekly for only five weeks. This did not seem to affect the catch significantly, as the number of adult individuals collected from pitfall traps in 1976 was not consistently greatest among the years for any of the sites. For example, in the mature forest site, 123 individuals and 48 adults were collected in 1976 while 115, 108, and 75 with 37,69, and 58 adults, respectively, were collected in the recent surveys. In 1996 and 1997, I installed 12 more pitfall traps, and

completed an additional 7 hours of hand collection and took 4 more sweep net samples at each of the two sites located in Ellicott Rock Forest. I was unable to take additional litter samples due to a lack of space for processing the samples in Tellugren funnels. Unless stated otherwise, these additional data were not used for comparison with the 1976 surveys, as the sampling methods were no longer directly comparable.

The remaining three sites (in the Great Smoky Mountains National Park, or GSMNP) were sampled by Fred Coyle twice yearly (early and late summer) from 1995 to 1997 (unpublished data), thus allowing a comparison of seasonal and annual changes. Sampling methods for these sites included equal proportions of hand collection, vegetation beating, and litter sampling. These sites include a mature hemlock/hardwood forest (OGHH), a mature beech gap forest (BGF), and a marsh/meadow (MBMM). See Table 1 for site descriptions, sampling techniques, and sampling dates. It is important to note that these collections cannot be assumed to sample the entire spider assemblage at these sites, as no collecting was done at night or in the forest canopy. Nevertheless, since collection techniques remained constant within sites and between sampling periods, the resulting species distributions should reflect the same biases and therefore be comparable.

Species identifications

For the three Macon County sites, all individuals were identified to species where possible. Juveniles were only identified to species and included in the species analyses if the identifications could be made with certainty. If not, these juveniles were only included in the genus level analyses. For the three GSMNP sites, few juveniles were identified in the 1995 samples, but where possible, were included in the 1996 and 1997 samples. As the abundance distribution of juveniles may not be equivalent to the abundance distribution of adults, only the adult specimens from 1996 and 1997 were used when making comparisons with the 1995 data.

Table 1: Summary of Study Sites

Location	Site Name	Habitat Type	Size	Methods (each year)	Dates of Surveys
Nantahala National Forest, Macon Co., NC	Horse Cove (HC)	forest (clear-cut 25yrs BP)	16ha	*8, 16 pitfall traps 10 (.25m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Nantahala National Forest, Macon Co., NC	Ellicott Rock Clear-cut (ERC)	forest (clear-cut 22yrs BP)	8ha	8, 16 pitfall traps 10 (.25m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Nantahala National Forest, Macon Co., NC	Ellicott Rock Forest (ERF)	forest (mature; pine-hardwood)	8ha	8, 16 pitfall traps 10 (.25m^2) litter samples 8 sets of 50 sweeps 4.5, 5 hours hand collection	summer 1976 summer 1995 summer 1996 summer 1997
Great Smoky Mountains National Park, Sevier Co., TN	Old growth hemlock/ hardwood (OGHH)	forest (mixed hemlock-hardwood)	2ha	6 (1m2) litter samples 8 hours beating 16 hours hand collection	**Ju95,A95 M96,A96 M97,A97
Great Smoky Mountains National Park, Swain Co., NC	Beech Gap Forest (BGF)	forest (beech gap)	1.5ha	3 (1m2) litter samples 4 hours beating 8 hours hand collection	**Jul95 Ju96,A96 Ju97,A97
Great Smoky Mountains National Park, Blount Co., TN	Meadow Branch (MBMM)	marsh/meadow	1ha	3 (1m2) litter samples 2 hours sweep netting 6 hours hand collection	**Ju95 M96,A96 M97,A97

*if two numbers are given, the first pertains to the 1976 survey only

**a less intensive sampling regime was carried out in 1995 for these sites

Table 1. The three sites located in Macon County were sampled in 1976 by Fred Coyle (Coyle 1981). All subsequent surveys at these sites were conducted by Norris. Coyle used 8 pitfall traps containing an ethylene glycol-detergent mixture, which were re-set at three week intervals for 15 weeks. I used 16 pitfall traps containing 70% ethanol which were checked weekly for 5 weeks. Litter samples were processed in large Tellugren funnels. Hand collection was divided equally between the ground stratum and the aerial stratum. Care was taken to avoid sampling within 10 meters of the edge of any site. The three remaining sites were sampled as part of a comprehensive taxonomic inventory of the spider fauna contained within the Great Smoky Mountain National Park (GSMNP) under the direction of Fred Coyle.

Taxonomic discrepancies.

In order to make the Macon County historical survey and my surveys comparable, identifications were made according to the systematic literature at the time of the historical survey. For example, if a species had been subsequently split into two species, only the single species was counted for comparison. This only occurred twice, with species in the genera *Wadotes* and *Schizocosa*. All 1976 specimens which were identified to morphospecies, but not given a species name, were eliminated if no individuals were available for comparison or no match could be made with the recent collections. One exception to this was a case where a numerically prominent species from the 1976 survey (Salticidae sp. A) was included in the analysis based on the fact that no unknown adult specimens were collected at all in that family in the 1995-97 surveys. It was therefore concluded that that species could not have been present in any of the recent surveys and thus represented a real change in the assemblage. A total of 11 morphospecies (20 individuals) were eliminated from the 1976 survey and five morphospecies (12 individuals) were eliminated from the 1995-1997 surveys.

Table 2A,B summarizes the numbers of individuals and species collected at each site at each selected interval. Due to space limitations, an appendix listing all species collected at each site during each year could not be provided. These data are available from the author upon request.

TOOLS FOR MONITORING

Before sampling actually begins at the start of a monitoring program, it is important to decide what kind of analyses and indices will be used once the sampling is complete, as this may determine how the data should be collected. I selected a range of

Table 2: Collection Results

A. Macon County

		1976	1995	*1996(l)	1996(t)	1997(l)	1997(t)
ERF	#individuals	583(217)	387(215)	416(123)	828(272)	425(245)	708(387)
	#species	60	58	51	64	56	71
	#genera	55	48	51	58	48	58
ERC	#individuals	284(131)	463(212)	417(117)	793(236)	340(163)	613(302)
	#species	53	50	46	59	44	61
	#genera	51	49	44	52	42	56
HC	#individuals	378(184)	219(127)	358(158)	---	456(225)	---
	#species	71	45	51	---	56	---
	#genera	61	40	47	---	48	---

*l and t refer to limited and total collections

B. GSMNP

		*E1995	L1995	E1996	L1996	E1997	L1997
BGF	#individuals	---	332(252)	588(491)	856(457)	664(380)	701(353)
	#species	---	32	33	32	36	36
	#genera	---	21	30	28	30	31
OGHH	#individuals	112(111)	115(113)	984(701)	814(230)	1842(986)	1567(412)
	#species	30	29	62	62	72	57
	#genera	26	28	46	51	55	47
MBMM	#individuals	163(163)	---	359(263)	263(129)	422(295)	313(214)
	#species	45	---	47	43	52	46
	#genera	37	---	39	34	41	37

*E and L refer to early and late summer collections

Table 2(A and B). This table presents the number of individuals, species (including morphospecies), and genera collected at each site during each sampling period. In Macon County, the 1996 and 1997 surveys were more intensive than the 1976 and 1995 surveys, including additional hand collection, sweep netting, and pitfall trapping. The total data resulting from these surveys is noted by (t). A subset of this data (l), is directly comparable to the 1976 and 1995 surveys as it is the result of an equal amount of sampling effort. The number of adult specimens collected are in parentheses. Juveniles which could not confidently be assigned to species are included in the individual counts and counts of genera, but not in the species counts. The only exceptions to this were cases where the juveniles were the only representatives of a novel genus. In this case, the juveniles were included in the species count. It was assumed that those specimens represented at least one unique species. For the GSMNP sites, no attempt was made to identify juveniles from the 1995 surveys.

commonly used indices in order to evaluate their usefulness as detectors of community change.

Indices

I used two sets of indices. The first set ('diversity indices') includes those which are calculated at an instant in time and then used to compare years or months within years at each site. The second set ('similarity/difference indices') quantify the difference in species composition between years or between months within years.

Diversity Indices. These indices can be divided into two types. The first simply attempt to assess the richness of species at a particular time and place. Commonly, these indices make use of both the number of species collected and the total number of individuals collected. I used Margalef's diversity index (Clifford and Stephenson 1975). The second type of index includes information on the proportional abundance of species in a sample. I used the Shannon index, the Brillouin index, and Simpson's index. These indices are widely used in the literature and their attributes are discussed at length by Magurran (1988).

I used the Shannon index because it is ubiquitous in the literature, and one can use parametric statistics to test for significant differences between surveys. I also used the Brillouin diversity index for comparison with the Shannon index because some of the sampling methods used in this study (e.g., pitfall traps) do not necessarily collect a random sample of the community. The Brillouin index is recommended for situations where the randomness of the sample cannot be guaranteed (Magurran 1988). The evenness measures associated with these two indices were calculated as well. I used the Simpson's index because it is considered a dominance measure, as it is weighted towards the abundances of the commonest species in the community. The collections made at

each site were not exhaustive and therefore the number of 'rare' species was artificially elevated. Simpson's index partially counteracts this effect.

Similarity/Difference Indices.

These indices can also be divided into two types. The first quantifies change in species composition alone, with no reference to abundance. Some studies have shown that terrestrial arthropod groups exist as a collection of subpopulations which undergo frequent extinctions and recolonizations (also referred to as a metapopulation), especially in fragmented landscapes (Hanski *et al.* 1995, Lande 1979, Slatkin 1977). Murphy *et al.* (1990) predict that species with high reproductive rates, small body size, short life-spans and high habitat specificity likely exist as metapopulations, although Hanski and Simberloff (1997) contend that not enough evidence exists for these sorts of generalizations. Nevertheless spiders fit the Murphy *et al.* criteria, and as these assemblages exist in a successional habitat, it is possible that they exist as a system of overlapping metapopulations (Harrison 1994b). The existence of sympatric metapopulations predicts that there will be temporal turnover of species in a given area (Russell 1999). The simplest way to quantify local colonizations and extinctions in an area is use an index of turnover. Turnover, as defined by MacArthur and Wilson (1967), simply estimates the number of local colonizations and extinctions relative to the number of species in the community. Even though this idea was originally developed for island situations, it also can be applied to the overlapping metapopulations which exist in a particular habitat.

The formula I used to calculate turnover is simply:

$$T_n = \frac{E_n + I_n}{S_y + S_{y+n}}$$

where E_n equals the number of observed extinctions over interval n, I_n equals the number of observed immigrations over the same period, S_y equals the number of species in the first year (y) and S_{y+n} is the number of species in the second year (following Russell *et al.* 1995). This index ranges from 0 to 1.

Turnover is a quantitative measure of change, but it only makes use of presence/absence (qualitative) data. To make use of abundance data for each species, I calculated two more similarity indices: Bray-Curtis and Morisita-Horn. The Bray-Curtis similarity index is probably the most widely used of the similarity indices (Magurran 1988) and one of the most simple. It is calculated using this formula:

$$C = \frac{2w}{(a+b)}$$

where a equals the total number of identified individuals in one sample, b equals the total number of identified individuals in the other sample, and w equals the sum of the lesser abundances for those species present in both samples. This index ranges from 0 to 1.

I also calculated the Morisita-Horn index of community similarity because it is considered to be less sensitive to sample size and species richness (Smith 1986, Wolda 1981). It is expressed as follows:

$$C = \frac{2\sum n_{i1}n_{i2}}{(\lambda_1 + \lambda_2)N_1N_2}$$

where

$$\lambda_j = \frac{\sum_i n_{ij}^2}{N_j^2}$$

C is the index of community similarity, N_j is the number of individuals in sample j, and n_{ij} is the number of individuals of species i in sample j. This index also ranges from 0 to 1.

INTERPRETIVE LIMITATIONS

Before discussion of ecological results it is important to understand that the following estimates of arthropod community dynamics are not strictly comparable to those calculated for vertebrate groups. This is because vertebrate studies (particularly those for birds) can, with a small degree of error, identify every species present in a given year at a given site (assuming that the worker conducting the survey has had years of proper training). Studies which include a hyperdiverse group such as arthropods can only hope to detect a proportion of the species, particularly for large sites with many microhabitats. In this study, it is obvious that sample sizes are too small to approach a comprehensive survey and, therefore, the species collected are only a sample of the total richness of these sites. Turnover, then, is really *apparent* turnover as it would be measured by a rapid survey attempt.

Care also needs to be taken when interpreting the significance of differences between arthropod diversity indices, since most of these assume that all species have been sampled. It is unlikely that any monitoring program would have the resources necessary to perform complete surveys, and the data presented in this paper illustrate what would typically be available to managers. Because we are forced to deal with 'samples' instead of comprehensive surveys, there are also additional sources of error (i.e. sampler bias, taxonomic uncertainty, stochastic effects). I address these in a later section. However, monitoring the dynamics of even the most common 50 spider species should still give higher resolution information than monitoring a single indicator species or a much smaller group of vertebrate species.

Rarefaction

It is inevitable that differences in sample size will exist between both the historic and present surveys and between the yearly surveys, even if the sampling protocol is

followed exactly. Except under certain conditions, it is meaningless to compare the diversity or measure the turnover of different sized collections. I therefore scaled all samples to the size of the smallest sample, a procedure called rarefaction. Rarefaction is a method used to calculate $E(S_n)$, the expected number of species in a sample of n individuals selected at random from a collection containing N individuals of S species (Heck *et al.* 1975). From the list of individuals in all but the smallest of the samples, a number equal to the number of individuals in the smallest sample was randomly selected. This generates a new species list and associated abundance distribution. The indices were calculated using this rarefied sample and the procedure was repeated 1000 times to obtain a mean and variance for the indices. See the flow chart presented in Figure 1 for details of this process. Because different subsets of the data were used for different analyses (i.e. comparison of methods, adults versus juveniles), the year or month which produced the smallest sample did vary. It is important to note that doing more stochastic rarefactions will cause the means of the indices to converge on a particular value. After 50 rarefactions, the confidence interval for the mean for each index was typically less than 1% of the range of the index (usually 0 to 1).

RESULTS

Applying the techniques discussed above, an initial analysis of community change through time was carried out using the sample data.

Correlation of indices

The Shannon index, Brillouin index, Simpson's index and Margalef's index were calculated for each year's data at the three sites in Macon County Within each site, all indices showed the same gross trends through time. The correlation of the indices is illustrated by data from ERC in Figure 2. Bray-Curtis and Morisita-Horn similarity were

Figure 1. The flow chart represents the sequence of calculations for an analysis within each site. The calculation of the diversity indices both before and after rarefaction, allows us to examine the effect of rarefaction (and therefore sample size) on these indices. The rarefaction procedure is repeated 1000 times in order to obtain a mean and a variance for the estimates.

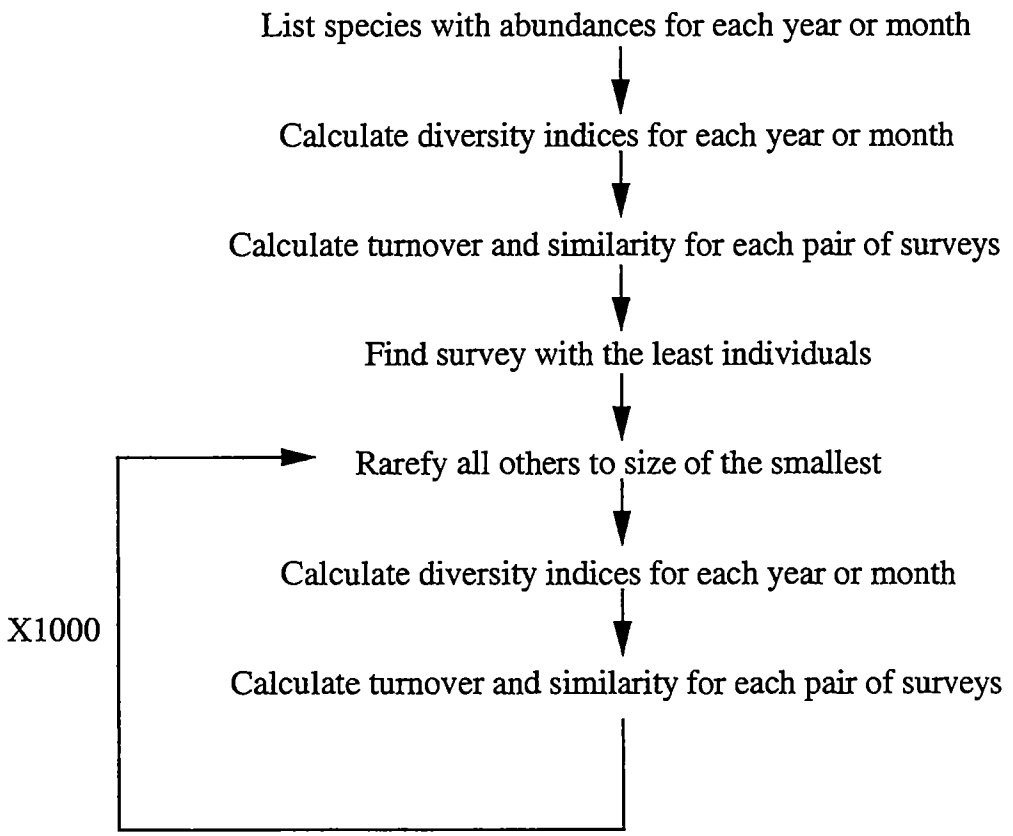
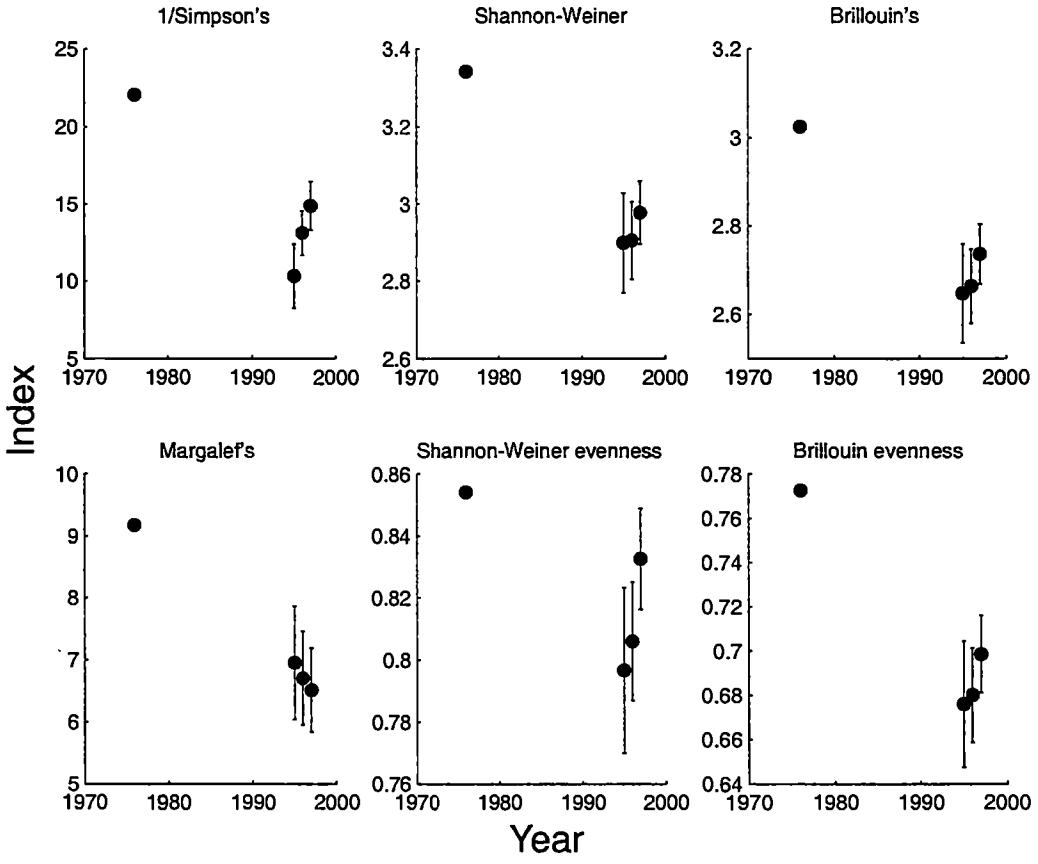


Figure 2. Solid circles with error bars represent the mean of the index estimates after 50 rarefactions. The error bars contain 95% of the estimates after rarefaction. Solid circles without error bars indicate the index as calculated for the smallest survey (no rarefaction necessary).



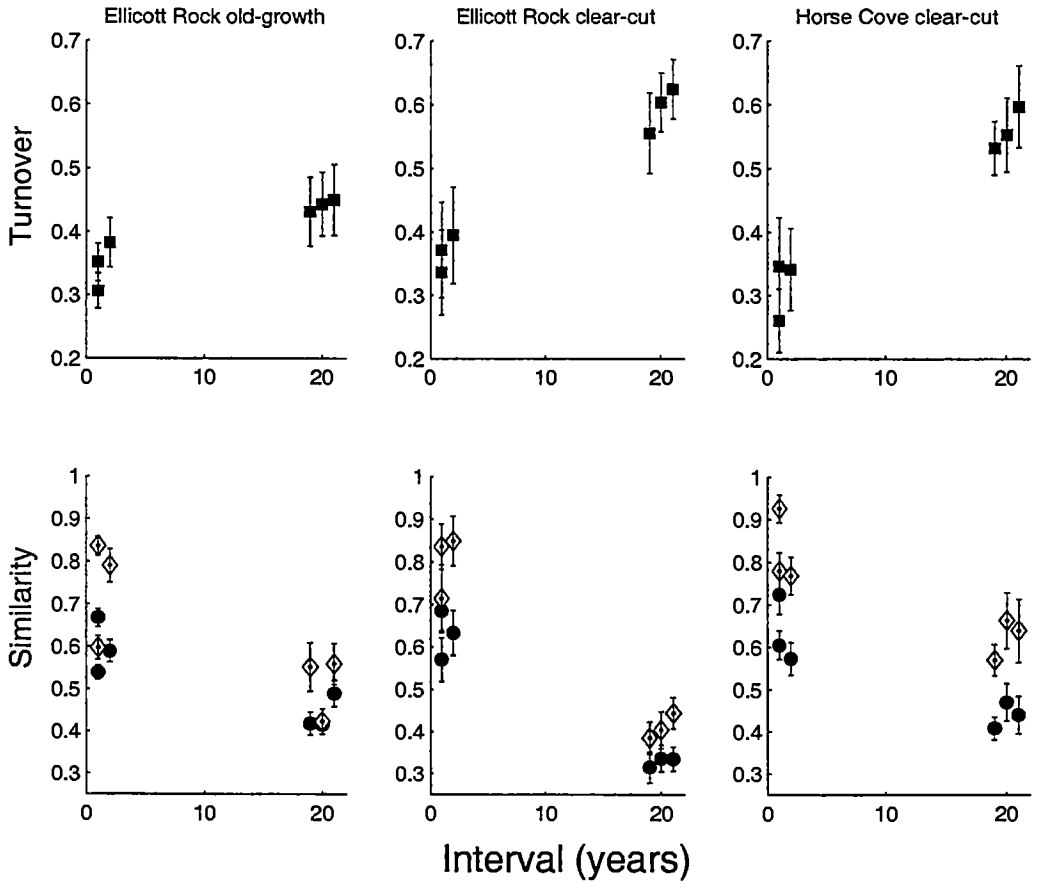
highly correlated with each other, and though consistently showing the same patterns (Figure 3), Morisita-Horn was almost always higher than Bray-Curtis. As turnover measures change in the assemblages, it was negatively correlated with the similarity indices (Figure 3).

Yearly turnover and similarity

All forested sites (Macon County and GSMNP) had mean one-year turnover estimates ranging from 0.22 to 0.39, and mean one-year similarity estimates from 0.74 to 0.54 for Bray-Curtis and 0.93 to 0.54 for Morisita-Horn. The MBMM site had relatively high one-year turnover (0.40, 0.38) and low one-year similarity (0.51, 0.58 for Bray-Curtis and 0.62, 0.72 for Morisita-Horn).

There are no clear differences between the mature forest and the old clear-cuts in terms of yearly turnover. One possible explanation is that these 22- and 25-year-old clear-cut forests are approaching a climax state and therefore no significant structural changes are taking place within them. This is unlikely, however, since even 50 year old forest stands show marked differences from old growth stands elsewhere in the Southern Appalachians (Clebsch and Busing 1989). A more reasonable explanation is that the successional changes still taking place at these sites are just not visible in a one or two-year window of time. Perhaps the differences would be detected if samples were taken every four or five years. It is interesting to note that overall, the sites with the highest estimates of yearly turnover and lowest estimates of yearly similarity are the youngest of the two clear-cut sites, and a grassy meadow. No clear conclusions can be drawn, however, because the slightly older clear-cut, Horse Cove, had consistently low measures of yearly turnover and high similarity compared with the mature forest types.

Figure 3. Squares represent mean turnover estimates after the data had been rarefied and turnover calculated 1000 times. Circles represent mean Bray-Curtis similarity estimates and diamonds represent mean Morisita-Horn similarity estimates, also after 1000 rarefactions. The error bars contain 95% of the rarefied turnover and similarity estimates.



Long-term turnover and similarity

As expected, long-term turnover was much greater than short-term turnover for the Macon County sites (Figure 3). The same pattern can be seen for the Similarity indices, with similarity lower for long-term comparisons (Figure 3).

Because differences in sampling regime (resulting in a different subset of the community being sampled) between the 1976 study conducted by Coyle and the 1995-96 studies conducted by Norris could produce the above trends, I re-ran the previous analyses excluding the data from the pitfall traps. As mentioned previously, the only significant difference in sampling methodology between the historical and recent surveys was the number and duration of the pitfall traps. Although the overall measures of turnover increased due to even smaller sample sizes, the same trends were observed with respect to short vs. long-term turnover at the Macon County sites. Long-term turnover ranged from 0.46 to 0.50 for ERF and from 0.54 to 0.63 for HC and ERC, with short-term turnover ranging from 0.34 to 0.39 for ERF and from 0.23 to 0.39 for HC and ERC.

Figure 3 also illustrates that the differences between the long and short-term measures of turnover and similarity are greater for the old clear-cuts than for the mature forest. This is not surprising, as the clear-cut sites have been undergoing succession over the past 20 years and, therefore, the structure of the vegetation at these sites has changed considerably.

Seasonal turnover and similarity

For the three sites which had seasonal data (BGF, MBMM, OGHH), a total of four comparisons were possible at each site: May vs. August in each of the two years (seasonal comparison) and 1996 vs. 1997 for each of the two months (yearly comparison). All twelve of these comparisons show seasonal turnover is higher than yearly turnover. Nine out of twelve comparisons show that samples taken in the same

month of sequential years are more similar as measured by Morisita-Horn than samples taken during different months of the same year. Only data from 1996 and 1997 were used for this analysis because of the huge differences in sample size between the 1995 survey and the 1996/1997 surveys.

Trends in diversity indices

In Macon County, the values of the indices for 1995, 1996, and 1997 are more similar to each other than to the values calculated for 1976. This likely indicates long-term changes in these assemblages with regards to richness and diversity.

In Macon County, for both clear-cut sites (HC and ERC), there is a definite trend through time for all the indices. These show a decrease in diversity, richness, and evenness, and an increase in dominance (data from ERC only are shown in Figure 2). The mature forest (ERF) shows less of a trend, and when a trend is apparent, it is in the opposite direction (increase in diversity, richness and evenness and a decrease in dominance). Figure 4 illustrates these trends with the Shannon index (all indices were, to some extent, correlated with each other). I carried out pairwise significance tests on the Shannon-Weiner index following Magurran (1988). The *t*-values and significances are reported in Table 3. For ERC and HC, all but one of the pairs that included the 1976 data were significantly different at the $p<0.01$ level (even after the Bonferroni correction for multiple tests). For ERF, none of the three pairwise tests using the 1976 data were significant with or without Bonferroni correction. For HC, the difference between two of the recent years (1995,1997) was significant, again in a positive direction. To be sure that the differences between the 1976 samples and the 1995,1996 and 1997 samples for the clear-cut sites couldn't be attributed to a difference in collectors (a non-random sampling effect), the analysis was repeated using only the pitfall trap and litter sample data. These methods are likely to be the least subject to sampler bias because the techniques used to

Figure 4. Solid circles with error bars represent the mean of the Shannon-Weiner estimates after 1000 rarefactions. The error bars contain 95% of the index estimates after rarefaction. Solid circles without error bars indicate the index as calculated for the smallest survey (no rarefaction necessary). Data from all collection methods were used in the calculation of Shannon-Weiner diversity for the top three graphs and only data collected using pitfall traps and litter samples were used to calculate Shannon-Weiner diversity for the bottom three graphs.

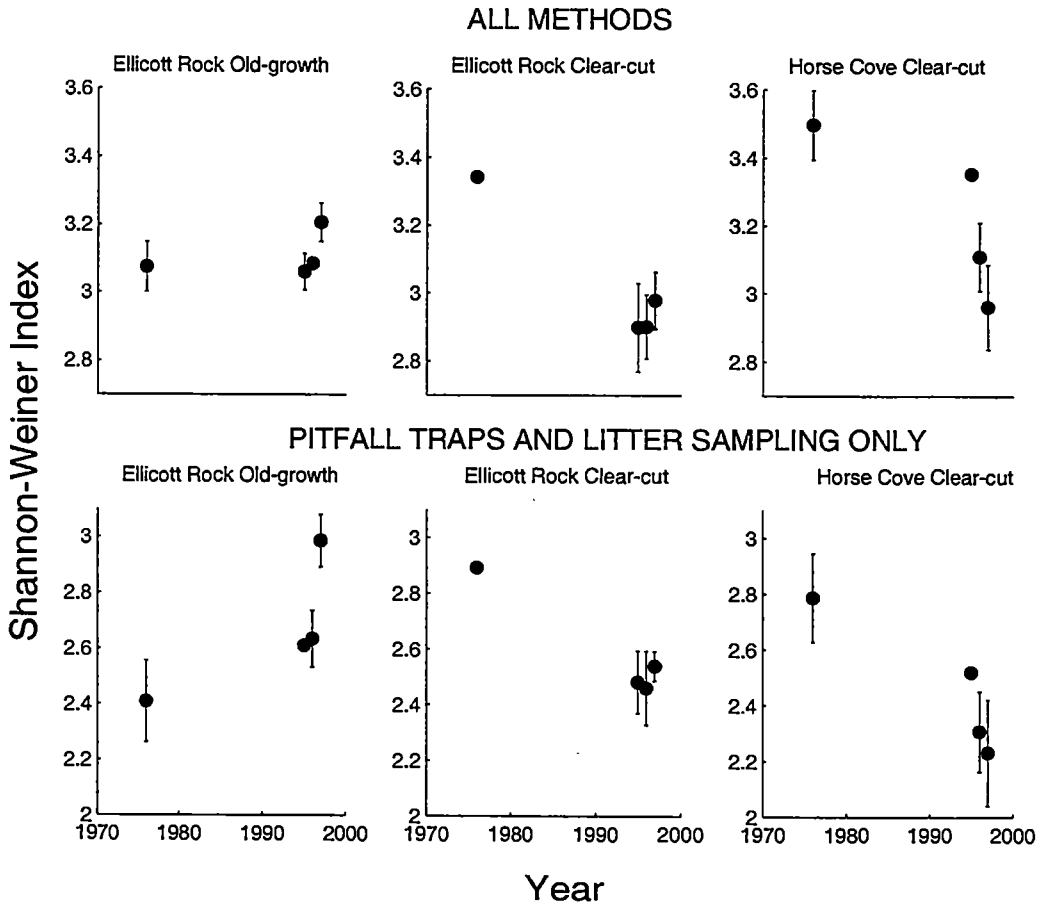


Table 3: Shannon-Weiner *t*-values for Paired Tests

Paired years	Ellicott Forest	Ellicott Clear-cut	Horse Clear-cut
76,95	0.3986	4.0875**#↓	2.4278
76,96	0.2932	4.4278**#↓	4.5105**#↓
76,97	1.3631#↑	3.7898**↓	6.0379**#↓
95,96	0.1130	0.2617	2.1794
95,97	1.5466#↑	0.4926	3.6796**↓
96,97	1.5105#↑	0.7777	1.4069

Table 3. Variance and *t*-values were calculated following Magurran (1988). Arrows indicate the direction of the change in the index to illustrate the contrast between the mature forest (ERF) and the clear-cut sites. Level of significance is designated by * $p<0.01$, **$p<0.001$ (Bonferroni correction for paired tests), and # $p<0.001$ for analysis using data from pitfall and litter samples only.

take and process litter samples and install pitfall traps are more clearly defined and less likely to vary from individual to individual (see 'Sampler Bias' below). As shown in Table 3, the trends still hold, and now the difference between 1995 and 1997 for HC is no longer significant. These trends illustrate forest succession from the spiders' perspective, as the spider assemblages of the clear-cut site converge with respect to the diversity and evenness on the mature forest site.

The only other site to show a consistent trend in the diversity indices through time is the beech gap forest. Although only three years of data have been collected, a trend is apparent in all of the diversity indices indicating a decrease in dominance, and an increase in diversity (Shannon's index increases from 2.072 in May 1995 to 2.2465 in May 1996 to 2.7167 in May 1997; Shannon's index also increases from 2.3527 in August 1996 to 2.619 in August 1997). I conducted pairwise significance tests on the Shannon index values and all but one of the pairs were significant at the $p<0.05$ level (after Bonferroni correction), indicating that overall there is a significant change in diversity. Although this site has never been logged, it is currently being degraded by the invasion of the beech scale insect, which creates wounds on the trees that facilitate the invasion of a fungus (Coyle, personal communication, Houston 1994a,b). As the beech trees die, gaps in the canopy are formed, creating habitat for early successional species. This may explain the increase in diversity and decrease in dominance for this site.

POTENTIAL SOURCES OF ERROR

Sensitivity of indices to sample size

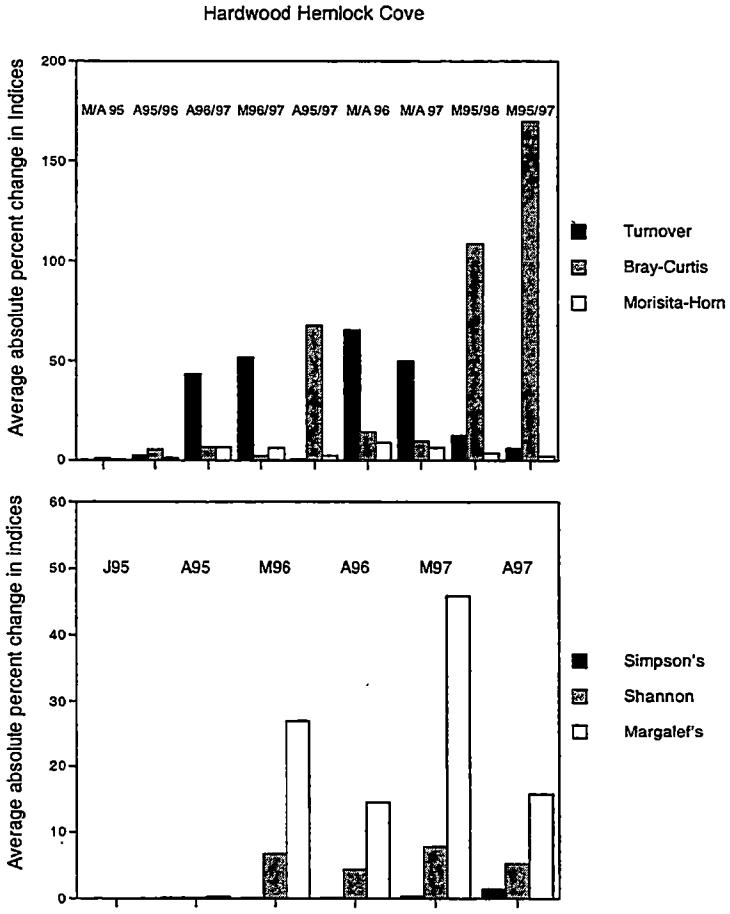
All indices were calculated both before and after rarefaction for each analysis to compare the sensitivity of all the aforementioned indices to sample size. To best illustrate the trends, data is presented from the site for which there were the greatest differences in

sampling effort and, therefore, sample size: the old-growth hemlock hardwood cove (OGHH). One hundred and eleven adult specimens were collected in May 1995, compared with 113 in August 1995, 230 and 701 in May and August 1996, and 412 and 986 in May and August 1997. Only adult specimens were used in the analysis because only adult specimens were identified from the 1995 surveys.

Comparisons were made between the same months in different years and between different months in the same year, both before and after the data had been rarefied down to the size of the 1995 sample for the OGHH site. Of indices which compare pairs of samples, turnover and Bray-Curtis similarity were the most sensitive to sample size. Morisita-Horn similarity was the least sensitive (Figure 5). This result is intuitive, in that turnover makes use of only presence-absence data and therefore gives equal weight to common and rare species. Although both Bray-Curtis and Morisita-Horn make use of abundance data, so that sample size is less important to the outcome, Bray-Curtis is biased toward the overall abundance of the sample. Morisita-Horn is much less sensitive to sample size because it gives particular weight to the most dominant species. Of the diversity indices, Simpson's is the least sensitive to sample size and Margalef's is the most, with Shannon in the middle, as predicted by Magurran (1988).

Several of the indices are therefore highly sensitive to the total number of individuals collected. In the data presented here, these differences in sample size were due almost entirely to differences in sampling intensity. Therefore, standardization of the surveys through rarefaction is the only way to meaningfully compare the surveys, particularly if turnover and Bray-Curtis similarity are to be used. But, if sampling intensity were to remain constant and abundances still fluctuate, is rarefaction still necessary? It depends on what sort of change in a community you are trying to detect. In the unlikely event that all species in a community were collected at higher abundances

Figure 5. Indices were calculated both before and after rarefaction. The May 1995 sample had the fewest adult individuals (111), therefore all other samples were rarefied down to 111 individuals from 113 in the August 1995 sample, 230 and 701 in the 1996 sample and 412 and 986 in the 1997 sample. The mean of the rarefied index estimates (after 1000 repetitions) was subtracted from the index calculated from the raw data and then divided by the raw index to get a measure of the average percent change. All possible pairwise comparisons are shown for Turnover, Bray-Curtis similarity, and Morisita-Horn similarity (A) and the results are ordered based on the similarity of the samples in each pairwise comparison (the comparisons with the most similar sample sizes prior to rarefaction are to the left). The changes in Simpson's index, Shannon-Weiner (H') index and Margalef's index are illustrated in chronological order (B) for all samples collected.



one year than the previous year, but the relative abundances stayed the same, would this be considered significant? If the answer is yes, then perhaps it would not be appropriate to standardize the sample sizes through rarefaction as long as sampling intensity stayed constant. A more likely scenario would be one in which the total abundance increased or decreased, but some species were more affected by whatever environmental factor was causing the change and therefore the relative abundances of species would also change. In this situation, rarefaction should still be used, because the differences in relative abundance of the species will still be apparent after rarefaction.

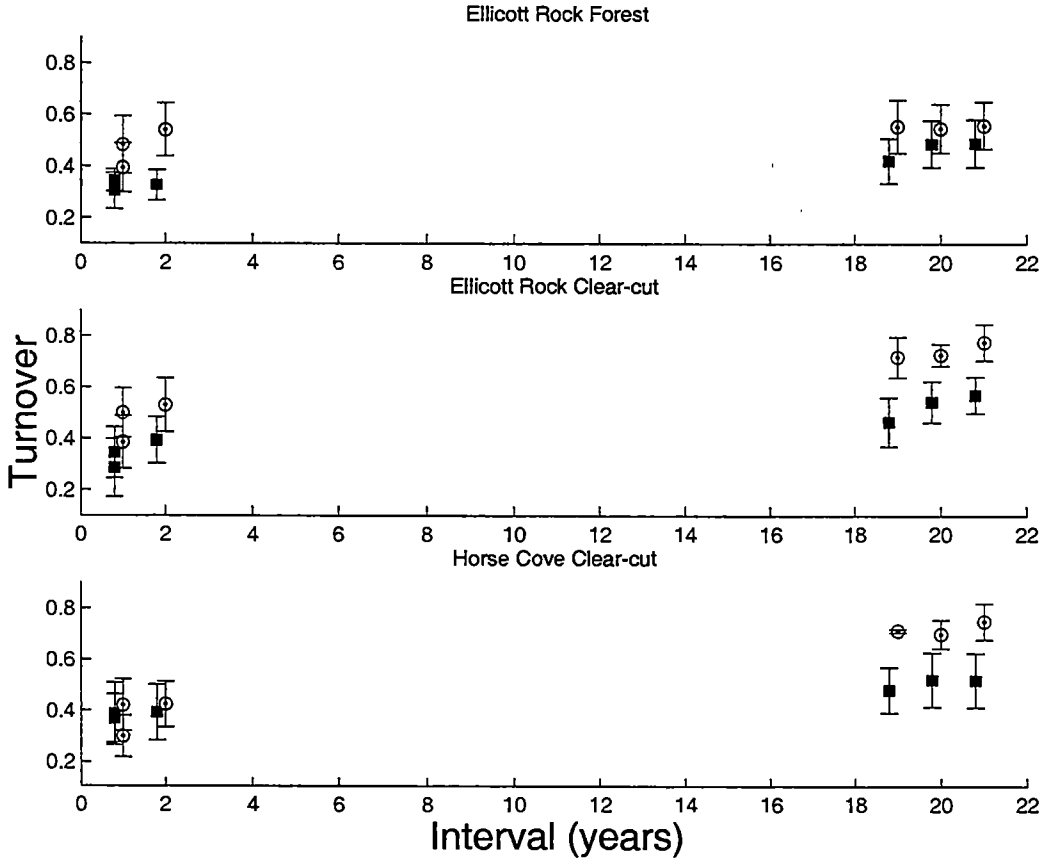
Sampler bias

Dealing with samples, or subsets of the total richness for a site, is not necessarily an obstacle unless the sampling is in some way non-random. Recent studies of spider species richness have shown that there can be a significant sampler effect, usually in the form of differences in yield when the experience level of the collectors is different (Coddington *et al.* 1996, Dobyns 1997). Differences in experience could mean either that the collector was more familiar with spider collecting in general, or just more familiar with collecting in a particular habitat and/or location. Sampler efficiency is less of a problem because of standardization tools such as rarefaction. But if different collectors show systematic bias in the species they collect, then making comparisons between samples collected by different workers will artificially elevate the degree of change in the community. Some techniques will be more subject than others to this type of bias. Hand collection, where workers collect in a particular area for a designated amount of time, will be more subject to sampler bias than standardized litter samples or pitfall traps. To explore these biases, the turnover analysis was run again using the Macon County data, this time separating out the different methods into two groups—those likely to show a lot of bias and those likely to show less. The estimates of turnover from sweetening and hand

collection were consistently higher than those from litter extraction and pitfall traps (Figure 6). One possible cause that is not sampler bias is that aerial spiders (spiders living in vegetation above the ground) are more variable from year to year than are ground dwelling species. Another possibility is that there is a higher diversity of species in the upper stratum and therefore the same effort may produce higher apparent turnover due to undersampling bias. Still, the differences are more pronounced when there is no overlap in collectors compared to when one of the two collectors was the same from year to year. This suggests that the differences are indeed due to sampler bias.

The same analysis was performed comparing data obtained through hand collection versus sweep netting for the MBMM site in the GSMNP region and again found that hand collection gave higher estimates of turnover than sweep netting. The analysis was repeated for the two forest sites in the GSMNP region, this time separating out all methods in order to distinguish the effect of ecology from that of method. No trends were apparent. For each of these analyses, I had to rarefy the data from each method down to the smallest yield (number of individuals collected). For the GSMNP sites, the smallest yield was always from the litter samples, which were highly variable from year to year. All litter samples are pooled, and for the sites in the GSMNP, a small number of large samples were pooled, compared to a large number of small samples at the Macon County sites. The high variability at the GSMNP sites may be due to inadequate sampling of spatially clumped spider distributions. Unlike the Macon County sites, no pitfall traps were used, so these data could not be added to the litter data as another 'unbiased' method. That might explain the lack of clear trends in the turnover analyses.

Figure 6. Solid squares indicate the mean turnover estimates after 1000 rarefactions as calculated from those species collected with pitfall traps and litter extraction. Open circles indicate the mean turnover estimates as calculated from species collected from sweep net samples and hand collection. Sample sizes were standardized between the two sets of methods through rarefaction, in order to make the turnover estimates comparable. The error bars include 95% of the turnover estimates calculated from the rarefied data. Squares and circles were staggered slightly for ease of viewing; this does not indicate differences in the years of collection. Turnover estimates at the shorter intervals are based on data collected by the same collector, while turnover estimates at the longer intervals are based on data collected by different collectors.



Inclusion of Juveniles

In most of the analyses performed in this study, juveniles were included if they could be confidently identified to species. They significantly boosted sample sizes, as the total number of adults in each sample was relatively small (particularly for the Macon County sites). In addition, some common species were present only as juveniles because of the time of year during which the sampling was conducted. Inclusion of juveniles seemed justified, as long as the criteria remained constant for each survey. Nevertheless, there are potential problems. First, without prior knowledge of the demography of the species involved, it may not be reasonable to assume that the abundance distribution of juveniles is the same as that for adults. Even though most juveniles that can be identified to species are from later instars, it is still possible that significant mortality occurs prior to their molt into adulthood; are 25 penultimate instars of one species equivalent to 25 adults of another species? Or rather are 35 adults collected in year 1 of a study equivalent to 5 adults and 30 juveniles collected the next year? These questions are important for most terrestrial arthropod groups where juvenile mortality is extremely high.

The relative abundance of species in a community can be drastically changed if juveniles are weighted the same as adults. Just looking at August data from 1997 for the OGHH site, there were a total of 1567 specimens collected, out of which 412 were adults. I ranked the species based on their abundances for that year using the adult data only, the juvenile data only, and the combined data (see *Table 4). Only nine species are present in the top twenty on the adult and juvenile lists and only four species are present in the top ten. In addition, those species which were present on both lists were ranked in different orders relative to each other. This would not necessarily be a problem if the ratio of adults to juveniles remained constant from year to year, thus allowing comparison of the total data, including adults and juveniles. Again, this does not seem to be the case, at least

for many species. For example, in the August sample of 1996 from the same site, the species *Hyptiotes cavatus* (Hentz) was represented by 142 individuals, of which 22 were adults. In August 1997, this species was represented by 390 individuals but zero adults. Another common species, *Neriene radiata* (Walckenaer) had a total specimen to adult ratio of 110:33 in May 1996 and 109:21 in August 1996. The next year, these ratios changed to 440:51 in May and 247:75 in August. It should be noted that this site represents a rather extreme case compared with other sites in this study (Table 2). These examples are meant merely to illustrate that the fluctuations in juvenile abundance do not seem to be correlated with the fluctuations in adult abundance. Therefore, inclusion of juveniles in a monitoring program may obscure trends that are present, or conversely suggest trends that are misleading. It would be advisable to either save the effort and resources necessary to identify juveniles and get rid of them entirely, or if possible, analyze these data separately.

Taxonomic uncertainty

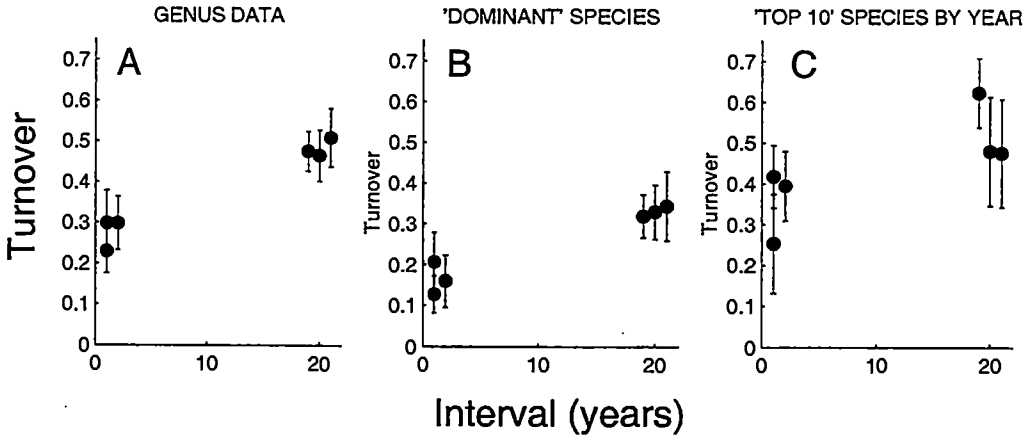
Two distinct sources of error can be identified under the heading of taxonomic uncertainty. The first involves errors made by non-specialists when identifying specimens to species. Misidentifications can be made due to lack of experience or sometimes just lack of the appropriate up-to-date key for a given genus. When voucher specimens from the original survey are not available, this could be a potential source of error in constructing species lists. In addition, although the taxonomy of spiders is becoming more stable, there are still many groups for which new synonymies are being announced and for which species groups are identified where once there was only a single species. One way to avoid this source of error is to conduct genus level analyses. The down side of this is the potential loss of information; perhaps it is changes at the species level which are most indicative of disturbance. But if the habitat which is being monitored has a low

species to genus ratio, then little information is lost and much error is eliminated. In addition, late instar juveniles may then be added to the analysis (since juveniles can usually be confidently identified to genus, but not species), which will elevate sample sizes. To illustrate this, I did the turnover analysis for all Macon County sites using data only to the genus level. The turnover estimates decrease slightly, but the same patterns are evident (Figure 7a). The species to genus ratio for this site was approximately 1.17:1.

Stochastic sampling effects

Another source of error stems from the abundance distributions of spiders (and most hyperdiverse groups). Over half of the species in the limited collections are represented by one individual per sample. This becomes relevant when monitoring the communities because by chance alone, much of the turnover in species composition could be due to just stochastic effects of sampling. For example, one-year turnover estimates for ERF and ERC decreased from 0.31 to 0.27 and from 0.34 to 0.29, respectively, when the sampling intensity was doubled in 1996 and 1997. One way to deal with this is to use indices which focus more on the dominant species in the system (such as Simpson's index, or the Morisita-horn similarity index). Another way is to only monitor the fluctuations in the most abundant groups; simply remove all singletons and doubletons from the samples. To illustrate this, I performed the turnover analysis for the Macon County sites using only those species represented by a minimum of 4 individuals across the entire duration of the study. I chose 4 because such a species could potentially be present as a singleton for each year of the study. This reduced the total number of species by 10% to 30%, depending on the site. As expected, this reduces the turnover estimates considerably (Figure 7b). Is important information being lost? The cut-off must be determined arbitrarily, and if the monitoring continues for multiple years, determination of this cut-off becomes more difficult.

Figure 7. Data presented in A, B, and C are from the Horse Cove clear-cut surveys. Solid circles show the mean of the turnover estimates after 1000 rarefactions. Error bars include 95% of all turnover estimates based on the rarefied data. 'Interval' refers to the time interval between the surveys. See text for details of the analyses.



Another option would be to only monitor the turnover of the most abundant species and ask how does the species composition of the top 10 species vary from year to year? This is a slightly different technique, because although the number of species to be examined is set arbitrarily, it remains constant from year to year. The results of a turnover analysis using only the ten most abundant species ranked separately for each year is shown in Figure 7c. Oddly, the turnover of the most abundant species is actually higher than for the entire assemblage. This may just be an artifact of small sample size, since even species in the top 10 were only represented by <5 individuals in some years.

DISCUSSION

The results presented in this paper are only suggestive of the amount of seasonal and yearly change in spider assemblages because of the sources of error discussed above. More rigorous, large-scale sampling would be necessary to get 'true' measures of local extinction and colonization. Nevertheless, most of the ecological trends discussed do hold true. For example, many indices were found to be quite sensitive to sample size, yet the trends involving seasonal change versus yearly change and yearly change versus long-term change still hold for almost every site when the unrarefied raw data were used in the analysis. The only exception was the site with the greatest disparity between samples (OGHH). At this site, the indices shown to be most sensitive to sample size, turnover and Bray-Curtis similarity, did not show consistent trends when comparing yearly and seasonal changes using the raw data, yet the Morisita-Horn index did. Also, the differences observed in the trends of diversity indices between the mature forest and the two clear-cut sites in Macon County persist with or without rarefaction, as do the trends in diversity indices for the beech gap forest. Sampler bias, although potentially elevating the observed magnitude of change in these assemblages, did not seem to affect the trends.

The inclusion of juveniles seems to be the most likely to have a significant effect on the trends due to the pronounced changes in the relative abundance of species they produce. Unfortunately, I could not repeat all of the analyses without the juveniles because for the Macon County sites, the sample size would have become inadequate. Of the GSMNP sites, the inclusion of juveniles obscured the seasonal vs. yearly change trends for the OGHH site only. Trends in the diversity indices for the Beech gap forest were unaffected by the inclusion of juveniles. Also, the marsh-meadow still had the highest turnover and lowest similarity between years with or without juveniles. In summary, although many of the sources of error identified have a definite effect on the values of the indices, the general trends through time still persist. This is not to say that these sources of error are insignificant, but rather that gross trends such as those due to succession may still be apparent despite flaws in the data, while more subtle trends may be obscured. It is these subtle trends which may be more useful to managers attempting to identify disturbance before it causes too much damage.

Conclusions and Recommendations

Development of a monitoring protocol for a particular habitat should begin first with adequate background information about the assemblage being used, including knowledge of the underlying abundance distribution of the group and the species:genus ratio. This information is necessary to develop a reasonable and efficient sampling regime, and will help managers to decide whether or not species level identifications are necessary. In addition, repeating the initial survey of the assemblage at least one time within the same sampling season will give a base-line measure of turnover and similarity (Spellerberg 1994). This will give a clearer picture of how much 'change' you can expect based on stochastic effects of sampling. Although the exact design of such a protocol will be specific to the habitat being monitored as well as the assemblage being used, some

general recommendations can be made based on the results of the analyses presented above:

1) Both qualitative and quantitative measures of change in species compositions should be taken to ensure maximum resolution for detecting disturbance. Calculation of species turnover in combination with some measure of similarity such as Bray-Curtis or Morisita-Horn would be a good starting point. Diversity indices may not be as informative. For example, a site could have diversity indices which change very slightly over time, but whose species composition has changed considerably. If diversity indices are to be used, directional trends (as seen in the clear-cuts and fungus-degraded forest) will probably be more informative than pairwise significance tests, since even 'undisturbed' sites can have significant differences in diversity between years.
2) Standardized, quantitative sampling techniques are a must, but for monitoring purposes, additional precautions are necessary. Emphasize methods which are least subject to sampler bias such as pitfall traps, litter samples, or vegetation beating/sweeping.
3) Always sample during the same month each year , or if sampling throughout the year, only compare sampling done in the same months.
4) Consider using genus level analyses if the species:genus ratio is small to avoid problems with taxonomic uncertainty.
5) Maintain voucher specimens for all species from previous collections, including unidentified specimens, to ensure consistency in identifications.
6) Set your minimum sample size at a level sufficient to either analyze juveniles separately or remove them completely from the analysis.

7) Use rarefaction to standardize samples, especially when using turnover, Bray-Curtis similarity, or richness estimates to evaluate change in an assemblage.

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APPENDIX II: MATHEMATICAL FORMULAE

DIVERSITY INDICES

Shannon-Weiner Index

$$H' = -\sum_{i=1}^{S} \frac{n_i}{n} \ln \frac{n_i}{n}$$

Brillouin's Index

$$H = \frac{1}{N} \ln \frac{N!}{\prod_{i=1}^{S} N_i!}$$

Margalef's Index

$$D = \frac{S-1}{\ln N}$$

Simpson's Index

$$D = \frac{\sum_{i=1}^{S} n_i\left(n_i - 1\right)}{n\left(n = 1\right)}$$

DIFFERENCE/SIMILARITY INDICES

Turnover

$$T_n = \frac{E_n + I_n}{S_t + S_{t+n}}$$

Bray-Curtis Similarity

$$C = \frac{2w}{a+b}$$

Morisita-Horn Similarity

$$C = \frac{2\sum_i n_{i1} n_{i2}}{(\lambda_1 + \lambda_2) N_1 N_2}, \qquad \lambda_j = \frac{\sum_i n_{ij}^2}{N_j^2}$$

EXTRAPOLATION

—estimating total species richness (S_{tot}) from a single collection of species (Chao 1984)

Chao Estimator

$$S_{\text{tot}} = S_{\text{obs}} + \frac{a^2}{2b}$$

where

$$\sigma^2_{S_{\text{tot}}} = b\left[\left(\frac{\frac{a}{b}}{4}\right)^2 + \left(\frac{a}{b}\right)^3 + \left(\frac{\frac{a}{b}}{2}\right)^2\right]$$

VITA

Kimberly Carol Norris was born in Rochester, New York in the summer of 1970. She is the youngest of five children and spent all of her childhood years in the same house in the suburb of Fairport. She attended Fairport High School where she played violin in the orchestra and spent the afternoons editing the yearbook. There she developed an interest in biology, although her primary interest at that time was writing. Summers were spent at her parents' cottage on Canandaigua lake, which contributed to her growing respect and love of nature. Kimberly graduated from high school in the spring of 1988 and began college at Colgate University in Hamilton, New York in the fall. There she studied the liberal arts and although having developed a keen interest in the Russian language (which led to a semester abroad in Moscow in the fall of 1990), finally settled on a major in biology. She developed an interest in behavioral ecology and spent two semesters doing small research projects on the feeding behavior of birds and the behavioral physiology of dragonflies. In the spring of 1992 she graduated *magna cum laude* with honors in Biology.

Not knowing whether to attend veterinary school or graduate school after graduation, Kimberly worked for a year at a veterinary hospital as a receptionist and technician's assistant. Although enjoyable, her time at Pittsford Animal Hospital convinced her that she needed a more creative outlet than medicine. and so she began applying to graduate programs. Wanting to leave upstate New York to experience a new part of the country, she headed down to the University of Tennessee to pursue her graduate work under Dr. Susan Riechert. Although having never thought twice about spiders before beginning graduate school, Kimberly developed a keen interest in spiders through her work with Dr. Riechert. Her experience in graduate classes and seminars

convinced her that the world of ecology and conservation biology had been too long dominated by the study of vertebrates, and so she shifted her research focus from behavior to ecology. At the University of Tennessee, Kimberly met her future husband, Gareth Russell, who was also a graduate student in the department at the time. They were married on February 26, 2000. She received her Doctor of Philosophy degree in Ecology and Evolutionary Biology in May 2000.