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Diversity of Parasitic Hymenoptera (Ichneumonidae: Campopleginae and Ichneumoninae)
in Great Smoky Mountains National Park and Eastern North American Forests
(Under the direction of JOHN PICKERING)

I examined species richness and composition of Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) parasitoids in cut and uncut forests and before and after fire in Great Smoky Mountains National Park, Tennessee (GSMNP). I also compared alpha and beta diversity along a latitudinal gradient in Eastern North America with sites in Ontario, Maryland, Georgia, and Florida. Between 1997- 2000, I ran insect Malaise traps at 6 sites in two habitats in GSMNP. Sites include 2 old-growth mesic coves (Porters Creek and Ramsay Cascades), 2 second-growth mesic coves (Meigs Post Prong and Fish Camp Prong) and 2 xeric ridges (Lynn Hollow East and West) in GSMNP. I identified 307 species (9,716 individuals): 165 campoplegine species (3,273 individuals) and a minimum of 142 ichneumonine species (6,443 individuals) from 6 sites in GSMNP. The results show the importance of habitat differences when examining ichneumonid species richness at landscape scales. I report higher richness for both subfamilies combined in the xeric ridge sites (Lynn Hollow West (114) and Lynn Hollow East (112)) than previously reported peaks at mid-latitudes, in Maryland (103), and lower than Maryland for the two cove sites (Porters Creek, 90 and Ramsay Cascades, 88). These subfamilies appear to have largely recovered 70+ years after clear-cutting, yet Campopleginae may be more susceptible to logging disturbance. Campopleginae had higher species richness in old-growth coves and a 66% overlap in species composition between previously cut and uncut coves. Ichneumoninae had similar richness in both cut and uncut coves and a 75% overlap in species composition. Parasitoid relative abundance declines one year post fire, but community composition appears the same. Campopleginae parasitoids may be more susceptible to fire disturbance, one year post fire. Eastern North American Campopleginae and Ichneumoninae, in most cases, appear to have a consistent pattern of decay in similarity with distance. Altitude may be a confounding factor. In general, common species represent a higher percentage of species richness at distant sites than do rare species. Stratified

sampling methods are superior to sampling at one location or at one time, and undisturbed habitats contain more species of specialized groups like the Campopleginae.

INDEX WORDS: Biodiversity, Species Richness, Ichneumonidae, Campopleginae, Ichneumoninae, Fire, Clear-cut, Habitat, Latitude, Beta Diversity

DIVERSITY OF PARASITIC HYMENOPTERA (ICHNEUMONIDAE:
CAMPOPLEGINAE AND ICHNEUMONINAE) IN GREAT SMOKY MOUNTAINS
NATIONAL PARK AND EASTERN NORTH AMERICAN FORESTS

by

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CHAPTER 1
INTRODUCTION

Written accounts of parasitoids date back as early as the seventeenth century. In the following 300 years the focus of researchers was on basic biology of these organisms. At the turn of the last century, researchers began in earnest to examine parasitoids for their use in controlling pest populations in agricultural systems as a result of the successful control of the cottony cushion scale by the vedalia beetle *Rodolia cardinalis* (Mulsant) in California (Pedigo 1989). As a result, a large portion of our knowledge of parasitoid ecology stems from work on using natural enemies in agricultural systems (Clausen 1940, Godfray 1994, Hawkins 1994).

Askew (1961) shifted the focus of parasitoids from largely a study of pest population dynamics to the study of “bottom up” influences setting the framework for modern parasitoid community ecology. He asked what effects the host had on the parasitoid complex that attacked it, and since this seminal paper, parasitoid ecologists have focused on a resource based approach to understanding parasitoid communities. Price (1970, 1971) brought the study of parasitoid communities to the forefront of ecological thought through analysis of the importance of competition and niche partitioning in the coexistence of parasitoids. He found that density-dependent parasitoid interactions between individuals lead to dispersal and ultimately higher niche breadth. These contributions sparked debate on the ecological and evolutionary forces that influence parasitoid community structure and composition that continues today.

Parasitoids, their hosts and host plants comprise a large portion of the world's biodiversity (Price 1980; Strong et al. 1984). The parasitic Hymenoptera may comprise over a quarter of a million species world wide (Gauld 1985). The Hymenoptera are extremely important in terms of species richness and economic importance. Parasitoids comprise approximately 80% of the Hymenoptera, they develop on or in a wide variety of hosts and can be important in regulating their host populations (Gauld and Bolton 1988). For example, outbreaks of host populations may occur when parasitoids are killed to a

greater extent by pesticide applications (DeBach 1964, Huffaker and Messenger 1976). Cornell and Hawkins (unpublished, in Hawkins 1994) reported that parasitism was the most identifiable source of mortality in 30.8% of 123 holometabolous insect host species examined. Many parasitoids have also been shown to be important in biological control programs. Despite their importance in ecosystems, many species remain undescribed and little is known about how parasitoid species respond under variable patterns of disturbance, (ie., logging or fire) (Fisher 1998). Key factors governing insect response to disturbance are dispersal, host selection behavior, and resource quality and quantity (Schowalter 1985). Parasitoids may also show successional trends following changing host populations (Price 1973) that may be seen by comparing activity between intermediate and climax forest stages.

There is considerable support for the idea that vegetation influences upper trophic levels (Southwood 1975, 1977, 1988; Lawton and Schröder 1977; Brown 1984; Crawley 1989; Hunter and Price 1992, Price 1992, Dutton et al. 2002, Gingras et al. 2002), and that certain kinds of disturbance may be a source of mortality for certain species through changes in temporal and spatial heterogeneity of habitats (Harmon et al. 1983, Runkle 1982, Denslow 1985, Doak 2000). Forest communities can be viewed as open systems where interactions of disturbances, including variation in frequencies and intensities, and the life histories of species determine the pattern of succession in a given patch. In ecological time, maximum species diversity may therefore be expected in systems where disturbances are consistent with historical patterns (Denslow 1985).

While disturbance regimes are important in shaping plant communities, little is known about how disturbance influences parasitoids within temperate forests. In protected coves, even small disturbances, at the level of a single tree fall, have been shown to be adequate to provide regeneration of high light tolerating plant species (Runkle 1982). Larger scale disturbances may affect species colonization by reducing community

heterogeneity and eliminating adequate refugia (Denslow 1985). Disturbance frequency, predictability, area, cycle and severity greatly influence plant community composition, and modification of disturbance patterns from activities such as fire suppression may result in shifts in distributions of both species and communities (Harmon et al. 1983). These shifts in species distributions may ultimately lead to the loss of species diversity (Denslow 1985, Baker 1992). Parasitoid species richness of external feeders, hosts that feed unconcealed on the surfaces of plant material, has been shown to increase in later successional stages with higher diversity associated with increasingly complex host plant architecture (Hawkins 1994). One might therefore expect higher parasitoid diversity in old-growth forests than in logged, second growth forests or in forests where natural disturbances, such as fire, have not been suppressed by human intervention. By examining species richness under different disturbance regimes one can begin to understand the relative importance of disturbance in influencing parasitoid community structure.

It has been shown that plant defenses differ along successional gradients. There is evidence to suggest that earlier successional plants are defended by toxins such as alkaloids, mustard oils and cardenolides, in contrast to later successional plants, that rely on digestibility reducers such as tannins, lignins and high fiber content (Feeny 1976, Rhoades and Cates 1976, Coley et al. 1985, Coley and Aide 1991). In (1991), Price predicted that earlier successional stages would contain more specialist parasitoids (koinobionts) and that later successional stages would contain more generalists parasitoids (idiobionts). Comparisons of generalists and specialist ichneumonids in varying age loblolly pine stands support Price's (1991) prediction (Gaasch 1996) of more specialist parasitoids in earlier successional stages with the proportions of generalists increasing in later successional stages. For 22 ichneumonid subfamilies, there were more numbers of koinobiont individuals in earlier successional stands and significantly more idiobionts in more mature stands (Gaasch 1996). This was not true for the species composition between earlier and

later successional stages. Ichneumonids may therefore be well distributed throughout the landscape, but congregate in specific habitats based on host availability. Additionally, Shapiro and Pickering (2000) report higher ichneumoninae activity in a tropical wet than in a tropical moist forest and suggest that ichneumonines may be restricted by hot, dry conditions. Thus, one might expect shifts from more generalists in old-growth coves and old-growth pine stands to more specialists in second growth coves.

Other studies have indicated that parasitoids may be more susceptible to habitat reduction than their herbivorous hosts. Kruess and Tschamtkke (2000) conducted field experiments with insects feeding on bush vetch, *Vicia sepium* L. examining the effects of area and fragmentation on insect diversity within experimental plots. Some of the most abundant parasitoids present in the study belonged to the Braconidae, the sister group to the Ichneumonidae. Results showed that both parasitoid and host diversity declined with decreasing habitat area. Furthermore, results from regression analysis showed a steeper slope for parasitoids than their herbivorous hosts indicating parasitoids had a lesser ability to colonize, small, isolated patches. Thus, parasitoids may be more susceptible to habitat fragmentation and disturbance than lower trophic levels. Furthermore, how generalist and specialist parasitoids respond to disturbances within a landscape is not well understood.

One step toward understanding parasitoid community structure is to examine how differences in habitat quality and disturbance patterns affect taxonomic composition at large (Tschamtkke et al. 2001) and small spatial scales. For example, how might patterns of parasitoid community organization differ under variable disturbance regimes? To address these issues, I examined parasitoid species richness 1) between mesic old-growth and 2) between mesic mature second-growth mixed deciduous cove forests, and 3) between burned and unburned xeric ridges in Great Smoky Mountains National Park, Tennessee and 4) beta diversity in eastern North American old-growth forests.

We conducted this study in Great Smoky Mountains National Park (GSMNP). The Park comprises over 500,000 acres with enormous biological diversity. It contains the largest stands of rare eastern old-growth forest, totaling over 100,000 acres. Vegetation of the GSMNP has been well documented in Whittaker's (1956) classic study of population and community distributions along environmental gradients. The Ichneumonidae were sampled at eight study sites within GSMNP. Each site includes a 1-hectare plot in 2 old-growth mesic coves: Porter's Creek and Ramsey's Cascade, 2 mature second-growth mesic coves: Fish Camp Prong and Meigs Post Prong, 4 xeric, old-growth treatments: Lynn Hollow. The xeric ridge site at Lynn Hollow contains 2 burn plots and 2 control plots. Porter's Creek and Fish Camp Prong are matched in elevation, aspect, slope and soil type. Ramsey's Cascade and Meigs Post Prong are similarly matched. The second-growth cove stands are 70+ years-old.

The mesic cove hardwood forests in the study are generally characterized by six dominant tree species *Tsuga canadensis*, *Halesia monticola*, *Aesculus octandra*, *Tilia heterophylla*, *Acer saccharum* and *Betula allegheniensis* with *Liriodendron tulipifera* and *Fagus grandifolia* common in some stands (Whittaker 1956, pers. ob.). The forest canopy may reach 30 - 45 meters with a rich layer of mesophytic ferns and herbs covering the forest floor. The xeric ridge sites are described in Whittaker's monograph as Virginia pine forests with *Pinus virginiana* as a dominant species. Other common tree species at the xeric ridge sites include *Pinus rigida*, *Quercus coccinea*, *Pinus strobus*, *Nyssa sylvatica*, *Q. velutina*, *Q. alba*, *Oxydendrum arboreum*, *Acer rubrum* and *Q. marilandica*. The canopy height is generally 15 - 25 meters. The shrub layer is dominated by *Kalmia latifolia* and *Vaccinium vacillans* (Whittaker 1956, pers. ob.).

We focused on Campopleginae and Ichneumoninae parasitoids in the family Ichneumonidae. The Ichneumonidae contains 39 subfamilies (Yu and Horstmann 1997) and an estimated 60,000 species worldwide and are thought to be the most speciose family

in the world, with the possible exception of the Curculionidae (Townes 1969). There are an estimated 8,000 Nearctic species with only 35% described (Yu and Horstmann 1997). They are large parasitoids and very strong fliers. The subfamilies within the Ichneumonidae are highly diverse biologically including both idiobiont and koinobiont lifestyles (Askew and Shaw 1986). Table 1.1 contrasts these two life history strategies. Idiobionts include endo- and ectoparasitoids, that kill or immobilize the host upon oviposition. The host is then consumed at the location and in the developmental stage it is in when attacked. Idiobiont endoparasites generally oviposit in concealed hosts in leaf litter or soil. Contrastingly, koinobionts allow for further host development to occur before the host is destroyed. Koinobiont endoparasitism allows the parasitoid to oviposit inside conspicuous hosts, while using the host's pupation concealment to secure continued development (Gauld 1988). This strategy requires the parasitoid to overcome the immunodefensive encapsulation system of the host leading to a more specialized host range (Salt 1968; Askew and Shaw 1986; Gauld et al. 1992). Idiobionts have a wider host range because they are often ectoparasitoids avoiding internal host defense (Spradberry 1968). Hence, ichneumonid koinobionts are considered specialists and idiobionts generalists (Askew and Shaw 1986; Gauld and Bolton 1988; Pschorn-Walcher and Altenhofer 1989; Sheehan and Hawkins 1991; Kato 1994). The Campopleginae are considered koinobiont parasitoids and the Ichneumoninae are considered idiobiont parasitoids.

In Chapter 2, I compare species richness of Campopleginae and Ichneumoninae parasitoids in two habitat types in GSMNP. To examine how habitat effects may confound larger scale analysis, I then compare species richness in two habitats in GSMNP with results from eastern North American old-growth forests in Ontario, Maryland, Georgia and Florida (Skillen et al. 2000). Furthermore, I address where campoplegine and ichneumonine species richness peaks along a latitudinal gradient in eastern North America.

In Chapter 3, I compare the composition and diversity of Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) in previously cut and never-cut forests. Study sites include two old-growth mesic coves and two mature mesic coves, approximately 70 years post clear-cut in GSMNP. Previous studies suggest that old-growth forests may support a higher diversity of parasitoids than previously logged forests (Miller 1980, Miller and Ehler 1990), yet we know little about whether previously logged forest parasitoid communities have recovered. Furthermore, there is evidence to suggest that higher trophic levels are more sensitive to disturbance (Pimm and Lawton 1978, LaSalle 1993, Kruess and Tschardt 2000; Komonen 2000). Because we know so little about parasitoid composition and recognize the risk of losing never documented species to disturbance, I have selected two parasitoid subfamilies with two life-history strategies to examine whether parasitoids have re-established after logging.

In Chapter 4, I compare species richness of Campopleginae and Ichneumoninae parasitoids before and after fire in burned and unburned plots in GSMNP. Desiccation has been shown to limit parasitoid activity, therefore species hunting for hosts on leaves in the forest canopy may be more prone to desiccation than those hunting on the ground. Thus, I predicted a higher proportion of pupal parasitoids in burned sites when compared to pre-burn years and control sites (Heinrich 1977, Gauld 1987, Shapiro and Pickering 2000). This chapter also addresses how campoplegine and ichneumonine species richness and species composition change after prescribed fire and how fire affects Coleoptera, Orthoptera, Ichneumonoidea, Symphyta, and Formicidae relative abundance.

In Chapter 5, I compare species richness of Campopleginae and Ichneumoninae parasitoids in GSMNP with other sites in eastern North America to address beta diversity, or the turnover of species with distance, within the two subfamilies. Russell (1995) argued that turnover is an “underappreciated and under utilized property of all biological systems.” Further, it is not known whether, beta diversity, or the turnover of species at

different spatial and temporal scales, is the same for all taxa (Caley and Schluter 1997). Currently, there are efforts in GSMNP to conduct a comprehensive inventory of all life within its boundaries (Kaiser 1999). As efforts to document local diversity increase, what can we learn to address issues of regional diversity? In this chapter I will address the following questions: What factors affect the turnover of species as a function of distance (beta diversity)? Is beta diversity the same for generalist versus specialist parasitoids? Does beta diversity differ for rare versus common species? How do temporal and spatial differences in biodiversity affect the efficiencies of inventory studies? In Chapter 6, I summarize the major conclusions of the dissertation research.

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Table 1.1. Summary of general characteristics of koinobiont and idiobionts parasitoid life-history strategies (Askew and Shaw 1986). The two focal groups in the current study, Campopleginae and Ichneumoninae, are given as examples of the two strategies.

Koinobionts (Campopleginae)	Idiobionts (Ichneumoninae)
<ul style="list-style-type: none"> • endoparasitoids • allow host development to continue before the host is destroyed • can attack conspicuous hosts • narrow host range • specialists 	<ul style="list-style-type: none"> • endo- and ectoparasitoids • kill or immobilize the host upon oviposition • generally attack concealed hosts • wider host range • generalists

CHAPTER 2

HABITAT, LATITUDE AND PARASITOID SPECIES RICHNESS OF ICHNEUMONINAE AND CAMPOPLEGINAE (HYMENOPTERA: ICHNEUMONIDAE) IN EASTERN NORTH AMERICA¹

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Abstract

We report the influence of habitat and latitude on species richness of Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) parasitoids. We compared species richness in two habitats, xeric ridges (Lynn Hollow East and West) and mesic coves (Porters Creek and Ramsay Cascades), in Great Smoky Mountains National Park (GSMNP) to other old-growth forests in Ontario, Maryland, Georgia, and Florida in eastern North America (Skillen et al. 2000). We identified a total of 243 species (5,280 individuals): 133 campoplegine species (1,776 individuals) and a minimum of 110 ichneumonine species (3,504 individuals) from all four sites in GSMNP. The highest total richness was in xeric ridge habitats, Lynn Hollow West (114 species) and Lynn Hollow East (112 species), for the two subfamilies combined when compared to the mesic coves, Porters Creek (90 species) and Ramsay Cascades (88 species). Considering subfamilies separately, Ramsay Cascades had the highest Campopleginae richness (58 species) and Lynn Hollow East had the highest Ichneumoninae richness (62 species) of all four sites. Comparing habitat and latitude, both subfamilies had highest richness combined in the two xeric ridge sites (Lynn Hollow West (114) and Lynn Hollow East (112)) than Skillen et al.'s (2000) most speciose site, Maryland (103), and lower than Maryland for the two cove sites (Porters Creek, 90 and Ramsay Cascades, 88). These results show the importance of habitat differences for species richness of ichneumonid subfamilies at larger latitudinal scales. These findings support a wider peak in species richness of Campopleginae that extends from the Southern Appalachians through the Piedmont.

Introduction

Habitat type is an important factor in structuring parasitoid communities. Because parasitoids are tied to their hosts and associated host plants for survival, they generally search for hosts by selecting habitats where suitable hosts are likely to be found (Price 1980, van Alphen and Vet 1986). While specific characteristics of plants such as plant architecture, size or life span (Lawton and Schröder 1977, Askew 1980) play an important role in parasitoid species richness, Hawkins (1994), in his meta-analysis of parasitoid-interactions, found that the effects of plants are largely a result of the habitats in which they grow. He reported that herbivore diversity, patch size, predictability and stability of the habitat, influence species richness over specific plant characteristics. Owen et al. (1981) reported that more common ichneumonid species fly throughout collecting seasons in England and suggested that some ichneumonids are niche specific rather than host specific. This association of habitat type with parasitoid composition and movement between habitats complicates our ability to understand larger continental-scale trends in parasitoid communities. Furthermore, clumped, habitat specific, distributions in speciose groups present difficulties when extrapolating from smaller scale studies to larger scale species richness patterns of regions or continents.

The anomalous diversity gradient of the Ichneumonidae, with peak diversity at mid-latitudes, is well documented (Owen and Owen 1974, Janzen and Pond 1975, Janzen 1981, Gauld 1986, Sime and Brower 1998). This so called 'anomalous' pattern appears despite an increase in tropical host diversity. In a test of latitudinal patterns, Janzen (1981) reported peak ichneumonid diversity to occur between 42-38° N from examination of published distribution maps. While total ichneumonid richness appears to peak in temperate zones, differences in some subfamilies are apparent (Askew and Shaw 1986, Gauld 1987, Gauld 1991, Skillen et al. 2000). For instance, Gauld (1991) and Gaston and Gauld (1993) reported greater diversity of pimpliform subfamilies (Rhyssinae and Pimplinae) in tropical

regions. These differences in subfamily patterns most likely result from the wide range of life-history strategies within the family. Ichneumonids contain an estimated 60,000 species worldwide (Townes 1969) and exhibit a variety of forms of the parasitoid lifestyle including: larval, pupal, endo- and ecto- parasitism. They attack a wide variety of hosts including Lepidoptera, Symphyta, Diptera and Coleoptera (Gauld 1988) and are often locally rare (Owen et al. 1981, LaSalle and Gauld 1993), further confounding efforts to characterize these communities.

In an effort to examine latitudinal patterns using a standard method, Malaise trapping, Skillen et al. (2000) documented the species richness of two ichneumonid (Hymenoptera) subfamilies, Ichneumoninae and Campopleginae, along a latitudinal gradient in eastern North American old-growth forests. We found that while peak diversity occurred at our mid-latitude site in Maryland, which corresponded to Janzen's (1981) band of peak diversity, campoplegine diversity exhibited a higher southern peak than indicated by Janzen.

Given that one expects differences in composition between habitats, how might these results have differed had Skillen et al. (2000) examined multiple habitats along this latitudinal gradient? In this paper, we compare species richness of Campopleginae and Ichneumoninae parasitoids in two habitat types in Great Smoky Mountains National Park (GSMNP). To examine how habitat effects may confound larger scale analysis, we then compare species richness in two habitats in GSMNP with results from eastern North American old-growth forests in Ontario, Maryland, Georgia and Florida (Skillen et al. 2000). Furthermore, we address where campoplegine and ichneumonine species richness peaks along a latitudinal gradient in eastern North America.

Materials and Methods

Study Organisms

Our focal organisms are parasitoid wasps in the family Ichneumonidae (Hymenoptera). There are an estimated 8,000 Nearctic ichneumonid species, of which only 35% have been described. Life-history strategies can generally be categorized into endo- (internal) or ecto- (external) parasitoids and into idiobionts or koinobionts. Idiobionts are generally ectoparasitoids of pupae or pre-pupae. Koinobionts are often endoparasitoids of larvae (Gauld 1988).

Our two focal groups within the Ichneumonidae, the Campopleginae and Ichneumoninae, represent the two principal parasitoid life history strategies. Ichneumoninae attack only Lepidoptera (Gauld 1988). The majority are idiobiont (Askew and Shaw 1986) pupal endoparasitoids. A few are koinobiont endoparasitoids that attack final-instar larvae (Wahl 1993). The Campopleginae are koinobiont endoparasitoids of Lepidoptera or Symphyta larvae (Gauld 1988).

Sites and Sampling

We compared old-growth forests in GSMNP with old-growth forests in Ontario, Maryland, Georgia and Florida (Skillen et al. 2000). Table 2.1 lists site data along the latitudinal gradient. We continuously sampled four sites in GSMNP representing two habitats (mesic coves and xeric ridge), two replicate sites (Ramsay Cascades and Porters Creek, Lynn Hollow East and Lynn Hollow West) and two traps at each site. We collected samples using fine mesh (.33 mm) Townes-style Malaise traps (Townes 1972) oriented with trap heads facing south to maximize the time sunlight shone on the collecting head. We changed traps bi-weekly or monthly in winter months, and preserved trap material in 70% ethanol.

Here we present analyses of samples from two old-growth mesic coves, Ramsay Cascades and Porters Creek between 8 April, 1997 - 18 April, 1998. We have two years of data from two xeric ridge habitats at Lynn Hollow and here analyze samples between 9 April, 1997 and 9 April, 1999. We compare species richness in GSMNP with five old-growth forests from Ontario to Florida, 45°42'N to 29°44'N (Skillen et al. 2000). Sites and collecting periods include: Shaw Woods, Ontario, 6 May - 22 October 1992 and 6 May - 21 October 1993; Patuxent Wildlife Research Center, Maryland, 6 April - 9 November 1992 and 12 April - 25 October 1993; Hitchiti Experimental Forest, Georgia, 23 March - 21 December 1993; Woodyard Hammock at Tall Timbers Research Station, Florida, 30 March - 14 December 1993 and one sample from 4 - 28 March 1994; Hammock State Preserve, Florida, 15 March - 18 December 1993. See Skillen et al. (2000) and Gaasch (1996).

Specimen Identification

All ichneumonine and campoplegine specimens were sorted to species based on Heinrich (1960a, b, 1961a, b, c, 1962a, b and 1977) and Walley (1940, 1947) respectively. Specimens not found in the literature were sorted to morphospecies using reference material at the University of Georgia. Because of sexual dimorphism in the Ichneumoninae, association of males and females was not possible in all genera. Therefore, within those dimorphic genera, we included in our analysis, only the specimens of the sex that contained the most morphospecies. We deposited specimens at the University of Georgia and GSMNP's Museum of Natural History. See Wayman (1994) for details of sorting techniques. All determinations can be accessed by unique specimen barcodes via the Discover Life web site: <<http://www.discoverlife.org>>.

Statistical Estimators

We used the EstimateS <<http://viceroy.eeb.uconn.edu/Estimates>> statistical package version five (Colwell 1997) to estimate species richness. We randomized the data, without replacement, 100 times to calculate the following nine estimators: Abundance-based Coverage (S_{ACE}), Incidence-based Coverage (S_{ICE}), Chao 1 (S_{C1}), Chao 2 (S_{C2}), First-order Jackknife (S_{J1}), Second-order Jackknife (S_{J2}), Bootstrap (S_B), Michaelis-Menten averaged over randomizations (S_{MR}), and Michaelis-Menten computed once for mean species accumulation curve (S_{MM}). Table 2.2 gives a description of the estimators. We used all nine estimators available in the EstimateS software but only present results for the Abundance-based Coverage (S_{ACE}), Incidence-based Coverage (S_{ICE}), and Chao 1 (S_{C1}) estimators. We chose these three estimators based on recommendations for highly diverse groups in Colwell and Coddington (1994) and Colwell (1997). We also compute Fisher's alpha (Fisher et al. 1943, Hayek and Buzas 1996), a frequently used diversity index that is intended to compare diversity independent of the number of individuals sampled. For review of these statistical estimators see Colwell (1997), Colwell and Coddington (1994), and Chazdon et al. (1998).

As all sampling methods have inherent bias, we present the observed data by trap to show between trap variance in sampling plots. We also present results from two years of sampling at the xeric ridge sites at Lynn Hollow to show between year variance at these sites. Because samples in the Skillen et al. (2000) data set were collected weekly, we normalized the collecting period to two weeks to compare like sampling regimes with GSMNP data. Thus, weekly samples were added together prior to entry into EstimateS. To account for sample size differences between plots, we generated Coleman Richness Expectation Curves (Colman 1981, Coleman et al. 1982) with 95% confidence intervals in

EstimateS. These curves provide a method to evaluate sample heterogeneity by plotting the expected richness for randomized subsamples (Colwell and Coddington 1994).

Results

Species Richness

Here we compare observed species richness from xeric ridge and mesic cove habitats in GSMNP, Tennessee with a North American Latitudinal gradient. Mid-latitude sites have the highest species richness for both Ichneumoninae and Campopleginae parasitoids. Table 2.1 presents observed species richness in GSMNP (35°N) and 5 sites in eastern North American old-growth forests: Ontario (45°N), Maryland (39°N), Georgia (33°N), Tall Timbers, Florida (30°N), and San Felasco, Florida (29°N) (Skillen et al. 2000). A comparison of the 9 sites shows that campoplegine species richness appears highest in Tennessee (59 species) and Ichneumoninae richness highest in Maryland (68 species). We found the same results when comparing Fisher's alpha diversity index between all sites (Table 2.3). Skillen et al. (2000) reported peak species richness of campoplegines in Georgia (49 species) showing a broader band of richness than previously reported by Janzen (1981) for that subfamily. The observed data for GSMNP support Skillen et al.'s (2000) finding of high southern Campopleginae richness. Table 2.1 shows that the observed campoplegine species richness at three of the four GSMNP sites was highest when compared to other North American sites, with the exception of Porters Creek. It tied Skillen et al.'s (2000) Georgia species richness with 49 species each. This trend is supported by the Fisher's alpha diversity index (Table 2.3), with all Tennessee sites showing higher values than any of the other North American sites.

Campopleginae species richness was highest in the Southern Appalachians (Tennessee) and Piedmont (Georgia), further south than data from Janzen (1981) would have predicted. To illustrate this trend, we present the Coleman Richness Expectation

curves (Coleman 1981, Coleman et al. 1982) with 95% confidence intervals for Campopleginae collected along the latitudinal gradient. Figure 2.1 shows the wider band of campoplegine species richness in the Southern Appalachians and Piedmont when compared to other sites. Because one year of data showed similar results (not shown), two years of data are presented from Ontario, Maryland, Lynn Hollow East and Lynn Hollow West to further illustrate the differences between sites. For example, species richness is higher with only one year of data from Porters Creek and Ramsay Cascades when compared to the Maryland site with two years of data. Note that the slopes of the curves in all of the Tennessee sites and in Georgia are steep. This indicates that we have not adequately sampled these sites to document total campoplegine species richness at any of these sites, yet we are able to compare between sites and see the wider peak of Campopleginae richness in the Southern Appalachians and Piedmont.

Habitat differences confound the latitudinal trend. While Ichneumoninae species richness is highest in Maryland and GSMNP, richness is higher only for the xeric ridges and not the mesic coves at the GSMNP sites (Lynn Hollow East (62 species); Lynn Hollow West (57 species); versus Porters Creek (42 species); Ramsay Cascades (30 species))(Table 2.1). These results do not show a clear pattern of declining diversity away from the most speciose site in Maryland as data from Janzen's (1981) paper suggested. There seem to be greater differences in species richness between habitats in the Ichneumoninae. For example, had we only data from the mesic coves at Porters Creek and Ramsay Cascades we might have concluded that the GSMNP had a depauperate ichneumonine fauna. Thus, these results indicate the significance of habitat type when documenting species richness for the ichneumoninae.

To further illustrates Ichneumoninae differences in species richness between habitats, we present the Coleman Richness expectation curves as in Figure 2.1. Figure 2.2 shows higher species richness for Ichneumoninae in Maryland than at all other sites.

Again, we show two years of data at Ontario, Maryland, Lynn Hollow East and Lynn Hollow West as with the Campopleginae because one year of data showed similar results (not shown). Furthermore, we can see that additional sampling at Lynn Hollow East (78 species) and West (57 species) does not result in higher richness than in Maryland (89 species). Again, the slope of the curves are steep, indicating that, even after two years of collecting, we have not sampled all species at these sites. Had we only sampled Porters Creek and Ramsay Cascades, we would have concluded that species richness was much lower at this latitude along Skillen et al.'s (2000) gradient.

Estimates of Species Richness

We used species richness estimators that model species accumulation as a function of sampling-effort to further compare species richness between sites. Table 2.4 presents the Abundance-based Coverage (S_{ACE}), Incidence-based Coverage (S_{ICE}) and Chao 1 (S_{C1}) estimator for Campopleginae and Ichneumoninae at the four GSMNP sites. The estimators showed variable results when compared with the observed data from the GSMNP xeric ridge and mesic cove communities (Table 2.1). The observed data most certainly represent an underestimate of total richness at each of the sites. However, because none of the estimators have reached an asymptote had steep slopes (not shown), we are unable to predict total species richness at any given site. We have little confidence in the estimators ability to provide much power in extrapolation beyond the observed data in species rich groups like the Ichneumonidae. Hence, to examine the effects of habitat on documenting larger scale patterns, we have more confidence in the Coleman Richness expectation curves presented in Figures 1 and 2. These curves provide a method to evaluate sample heterogeneity by plotting the expected richness for randomized subsamples (Colwell and Coddington 1994). Thus, while we are unable to predict total species richness at each site with the estimators,

the Coleman Richness Expectation curves provide a method to evaluate species richness helping to account for variable sample sizes between sites.

Between Trap and Between Year Variance

To show between trap and between year variance at the GSMNP sites, Table 2.5 presents Campopleginae and Ichneumoninae observed species richness by trap in 1997 and 1998. Between trap differences are presented in Table 2.1 of Skillen et al. (2000) for the other 5 sites. Table 2.5 shows the distribution by trap of the 5,280 individuals that we collected and sorted to a minimum of 243 species from 198 Malaise trap samples. These totals include 133 campoplegine species (1,776 individuals) and a minimum of 110 ichneumonine species (3,504 individuals) from all four sites in GSMNP. There appears to be high between trap variance at Ramsay Cascades. Trap catches from Trap 2 appear low for both subfamilies and thus collected fewer individuals. This may be a result of poor trap performance, however, even with poor trap performance, total richness was higher for the Campopleginae at Ramsay Cascades than at all other sites.

Between year variance appears low for xeric ridge sites for which we have data (Table 2.5). However, we continue to collect new species with additional trap years. This further highlights the difficulty in understanding this extremely diverse parasitoid community.

Habitat, Latitude and Species Richness

With the diversity of life-history strategies within the parasitoid life-style, the idiobiont/koinobiont (Askew and Shaw 1986) dichotomy has been used to examine parasitoid responses to food plant type, host range, or latitude regardless of taxonomic lineage. Idiobiont larvae consume the host in the stage in which attacked and are thus considered to have a wider host range. In contrast, koinobionts oviposit in earlier host

stages emerging later in host development and are thus considered to have more narrow host ranges. Not surprisingly, patterns of richness have been shown to differ between these variable life-history strategies. Gauld (1986) found that Australian koinobiont richness decreased towards the tropics whereas, idiobiont richness did not. In a similar study of North American richness, Askew and Shaw (1986) reported a sharper decline towards the tropics in koinobiont richness as compared to idiobiont richness.

Campopleginae parasitoids in the current study appear to have similar diversity in all habitats examined, while Ichneumoninae parasitoids show greater differences in species richness between habitats. This seems contrary to predictions about koinobiont specialized and idiobiont generalized biology (Askew and Shaw 1986). We would expect the opposite to be true, with campoplegines (koinobiont) having greater habitat specialization and ichneumonines (idiobionts) having less habitat specialization. However the factors contributing to idiobiont and koinobiont diversity within different habitat types are exceedingly complex.

One key factor that affects parasitoid distribution within a landscape is the location of their hosts. Hawkins (1994) examined the effects of foodplant and habitat on generalist and specialist parasitoids' host range and found the patterns to be 'complicated'. He did find general patterns and concluded that idiobionts are most diverse on hosts that feed on trees whereas koinobionts showed differing patterns on endophytic and exophytic hosts. He found koinobionts to be richer on endophytic hosts on herbs and richer on exophytic hosts on trees. We have no host records to test this finding.

One might expect that the mountainous terrain in GSMNP may create harsh environments for certain parasitoids. For example, Randall (1982) found an inverse relationship between a Lepidopteran caterpillar parasitoid host complex richness and altitude. He found no parasitoids attack *Coleophora alticolella* Zeller (Lepidoptera: Coleophoridae) above 400m. Our xeric ridge sites are located at approximately 664 meters,

whereas our cove sites, Porters Creek and Ramsay Cascades are located at 957 and 1183 meters respectively. Furthermore, the Fisher's alpha value for Ramsay Cascades (13.51) is similar to both Lynn Hollow sites (14.26, 13.56) yet higher than the value for Porters Creek (11.4). Elevation is a confounding variable. Based on Randall (1982) one would expect to have lowest richness at our highest site; yet, in our study, Ramsay Cascades, had the highest Campopleginae richness. It is important to note that we have not examined beta diversity between like habitats. Tarmo and Seppo (1999) found a higher proportion of *Eulophus larvarum* (Eulophidae: Hymenoptera) at higher altitude sites and *Cotesia jucunda* (Braconidae: Hymenoptera) at lower altitude sites in parasitoids reared from *Epirrita autumnata* (Lepidoptera) larvae feeding on mountain birch in Finland. Thus, the turnover of species within these habitat and altitudinal gradients may be high while total species richness may not vary with altitude at the scale we examined. Our data show that the effects of habitat may be more important in structuring local parasitoid richness in GSMNP.

Sample size differences between xeric ridge and mesic cove sites may confound our results on habitat. Table 2.3 shows Fisher's alpha computed for the 9 sites examined. On the issue of ichneumoninae diversity, the Fisher's alpha value for Ramsay Cascades (13.51) is similar to both Lynn Hollow sites (14.26, 13.56). Yet Ramsay Cascades had a higher value than for Porters Creek (11.4). Thus, this index indicates that Ramsay Cascades has similar diversity to the xeric ridge sites that had almost 10 times the number of ichneumonine individuals collected at each site. While the sampling effort was the same for each of the sites, we collected fewer Ichneumoninae at the cove sites. Campopleginae sample sizes were similar at all Tennessee sites (Table 2.4). Thus, we collected fewer individuals and species at Ramsay Cascades. The differences in sample size may account for the differences in diversity we observed. Had we collected the same number of Ichneumoninae individuals in both the coves and ridges, we may have found that the cove

diversity was more similar to the ridge habitat. However, these data indicate that sampling the ridge yields more individuals, and thus more species, in a shorter period of time.

Along the latitudinal gradient, our results generally support a peak of ichneumonid diversity at mid-latitudes with the additional Tennessee sites, while the band of diversity seems to be wider as predicted by Skillen et al. (2000). However, we emphasize the importance of habitat differences in examining larger scale diversity patterns. The highest species richness for the two subfamilies combined was in xeric ridge sites, yet this result is not consistent in our cove forests. The differences in species richness within habitats is subfamily dependent with ichneumonines showing greater differences in species richness and campoplegines showing higher richness in all habitats sampled in GSMNP. These results indicate the importance of sampling multiple habitats when examining large-scale diversity patterns.

Conclusions

The results from the current study show the importance of habitat differences when examining the trends in latitudinal species richness. We report higher ichneumonid richness in xeric ridge habitats (Lynn Hollow West (114) and Lynn Hollow East (112)) when compared to Skillen et al.'s (2000) most speciose site, Maryland (103), and lower than Maryland for the two cove sites (Porters Creek, 90 and Ramsay Cascades, 88). We did find subfamily differences in species richness with campopleginae richness higher in all sites when compared to Skillen et al.'s (2000) latitudinal gradient. Thus, we conclude that the Piedmont and Southern Appalachians appear to be an area of high biodiversity for the Campopleginae. This high campoplegine diversity at all Tennessee sites widens previously reported peaks of diversity along the latitudinal gradients (Janzen 1981, Skillen et al. 2000). Furthermore, the higher total richness at our xeric ridge sites emphasizes the importance of habitat types in structuring local diversity in old-growth forests. In part, these results may

be because of between trap and between site differences in trapping efficiencies. We will investigate this possibility in a future manuscript.

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Table 2.1 Campopleginae (C) and Ichneumoninae (I) species (individuals) collected in old-growth forests in Eastern North America. Data from 1993 in Skillen et al. (2000).

Site	Habitat	Latitude (N)	Elevation	Year	C	I	Total
Shaw Woods Ontario	Beech Forest	45° 42'	160 m	1993	12 (23)	37 (117)	49 (140)
Patuxent Maryland	Broadleaf Forest	39° 03'	60 m	1993	35 (312)	68 (730)	103 (1042)
Ramsay Cascades Tennessee	Cove Forest	35° 43'	1183 m	1997	59 (331)	30 (111)	89 (442)
Porters Creek Tennessee	Cove Forest	35° 40'	957 m	1997	49 (152)	42 (442)	91 (594)
Lynn Hollow East Tennessee	Oak/Pine Forest	35° 38'	640 m	1997	50 (441)	62 (1088)	112 (1529)
Lynn Hollow West Tennessee	Oak/Pine Forest	35° 38'	670 m	1997	57 (407)	57 (895)	114 (1302)
Hitchiti Georgia	Oak/Pine Forest	33° 03'	400 m	1993	49 (572)	44 (693)	93 (1265)
Tall Timbers Florida	Mixed Forest	30° 39'	40 m	1993	32 (213)	30 (682)	62 (895)
San Felasco Florida	Mixed Forest	29° 44'	50 m	1993	20 (84)	47 (663)	67 (747)

Table 2.2 Summary of species richness estimators.

Variable	Estimator	Method	Reference
ACE	Abundance-based Coverage Estimator of species richness	based on those species with 10 or fewer individuals in the sample	Chao, Ma, and Yang (1993), Chazdon et al. (1998)
ICE	Incidence-based Coverage Estimator of species richness	based on species found in 10 or fewer samples	Lee and Chao (1994), Chazdon et al. (1998)
C1	Chao 1 richness estimator	estimates richness in an assemblage based on the number of rare species in a sample	Chao (1984) Chao (1987)
C2	Chao 2 richness estimator	estimates richness in an assemblage based on the distribution of species among samples	Chao (1987)
J1	First-order Jackknife richness estimator	technique for reducing bias in an estimates by $1/n$ where n is the number of samples	Burnham & Overton (1978, 1979), Smith van Belle (1984), Heltshe & Forrester (1983)
J2	Second-order Jackknife richness estimator	technique for reducing bias in an estimates by $1/n^2$ where n is the number of samples	Burnham & Overton(1978, 1979), Smith & van Belle (1984), Palmer (1991)
B	Bootstrap richness estimator	assume that a sample captures the essential aspects of the assemblage and take repeated samples with replacement from a sample and average over all samples	Smith & van Belle (1984)
MR	Michaelis-Menten richness estimator	estimators averaged over randomizations (runs)	Raaijmakers (1987)
MM	Michaelis-Menten richness estimator	estimators computed once for mean species accumulation curve	Raaijmakers (1987)

Table 2.3 Fisher's alpha for Campopleginae and Ichneumoninae species collected in old-growth forests in Eastern North America. Data from Skillen et al. (2000) indicated by *.

Site	Fisher's Alpha	
	Campopleginae	Ichneumoninae
Shaw Woods, Ontario *	10.12	17.48
Patuxent, Maryland *	9.74	18.16
Ramsay, Tennessee	20.65	13.51
Porters, Tennessee	25.07	11.4
Lynn Hollow East, Tennessee	14.51	14.26
Lynn Hollow West, Tennessee	18.04	13.56
Hitchiti, Georgia *	11.86	11.39
Tall Timbers, Florida *	9.36	6.68
San Felasco, Florida *	11.69	12.24

Table 2.4 Abundance-based Coverage (ACE), Incidence-based Coverage (ICE) and Chao 1 (C1) estimates of campopleginae and ichneumoninae species richness and percent singleton's (P_s) collected in Great Smoky Mountains National Park.

Site	Year	ACE	ICE	C1	ACE	ICE	C1	P_s
		Campopleginae			Ichneumoninae			
Mesic Coves:								
Ramsay Cascades	1997	91	93	84	40	37	38	40
Porters Creek	1997	88	98	76	86	71	142	50
Xeric Ridges:								
Lynn Hollow East	1997	68	67	68	77	76	80	30
	1998	94	98	91	92	97	96	42
	1997+98	120	121	116	99	99	100	34
Lynn Hollow West	1997	86	88	81	86	92	74	38
	1998	79	83	72	68	65	77	37
	1997+98	96	96	98	87	92	82	30

Year refers to the beginning of the field season starting in April.

Table 2.5 Campopleginae and Ichneumoninae species (individuals) collected in Great Smoky Mountains National Park.

Site	Year*	Trap 1	Trap 2	Total	Trap 1	Trap 2	Total
Campopleginae				Ichneumoninae			
Mesic Coves:							
Ramsay	1997	56 (240)	21 (91)	59 (331)	27 (85)	13 (26)	30 (111)
Cascades							
Porters	1997	41 (101)	23 (51)	49 (152)	31 (219)	31 (223)	42 (442)
Creek							
Xeric Ridges:							
Lynn Hollow	1997	36 (191)	38 (250)	50 (441)	45 (372)	48 (716)	62 (1088)
East							
	1998	39 (88)	41 (132)	60 (220)	43 (280)	44 (268)	61 (548)
	1997+98	56 (279)	59 (382)	79 (661)	57 (652)	62 (984)	78 (1636)
Lynn Hollow	1997	32 (115)	49 (292)	57 (407)	44 (479)	39 (416)	57 (895)
West							
	1998	42 (108)	34 (117)	54 (225)	38 (214)	36 (206)	48 (420)
	1997+98	52 (223)	61 (409)	74 (632)	58 (693)	50 (622)	68 (1315)

* Year refers to the beginning of the field season starting in April.

Figure. 2.1 Coleman richness expectation curves with 95% confidence intervals of Campopleginae at four sites in Great Smoky Mountains National Park, Tennessee, Lynn Hollow East, Lynn Hollow West in 1997 and 1998, Porters Creek and Ramsay Cascades in 1997, Shaw Woods, Ontario 1992 and 1993, Patuxent, Maryland 1992 and 1993, Hitchiti, Georgia, Tall Timbers, Florida and San Felasco, Florida in 1993 (Skillen et al. 2000). Samples from Skillen et al (2000) are normalized to two week samples for like comparison with the current study. Sampling effort refers to samples that contain at least one campoplegine.

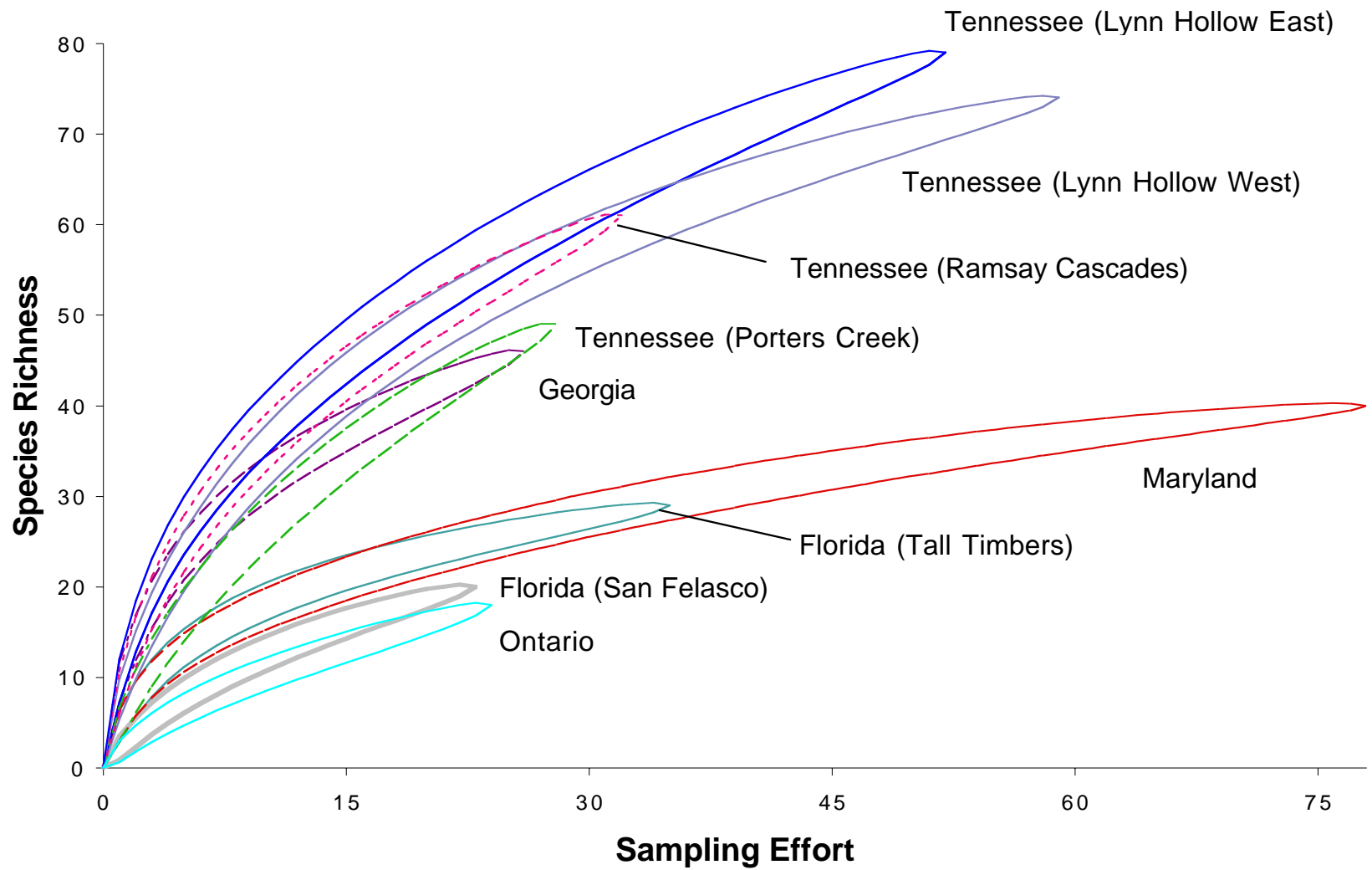
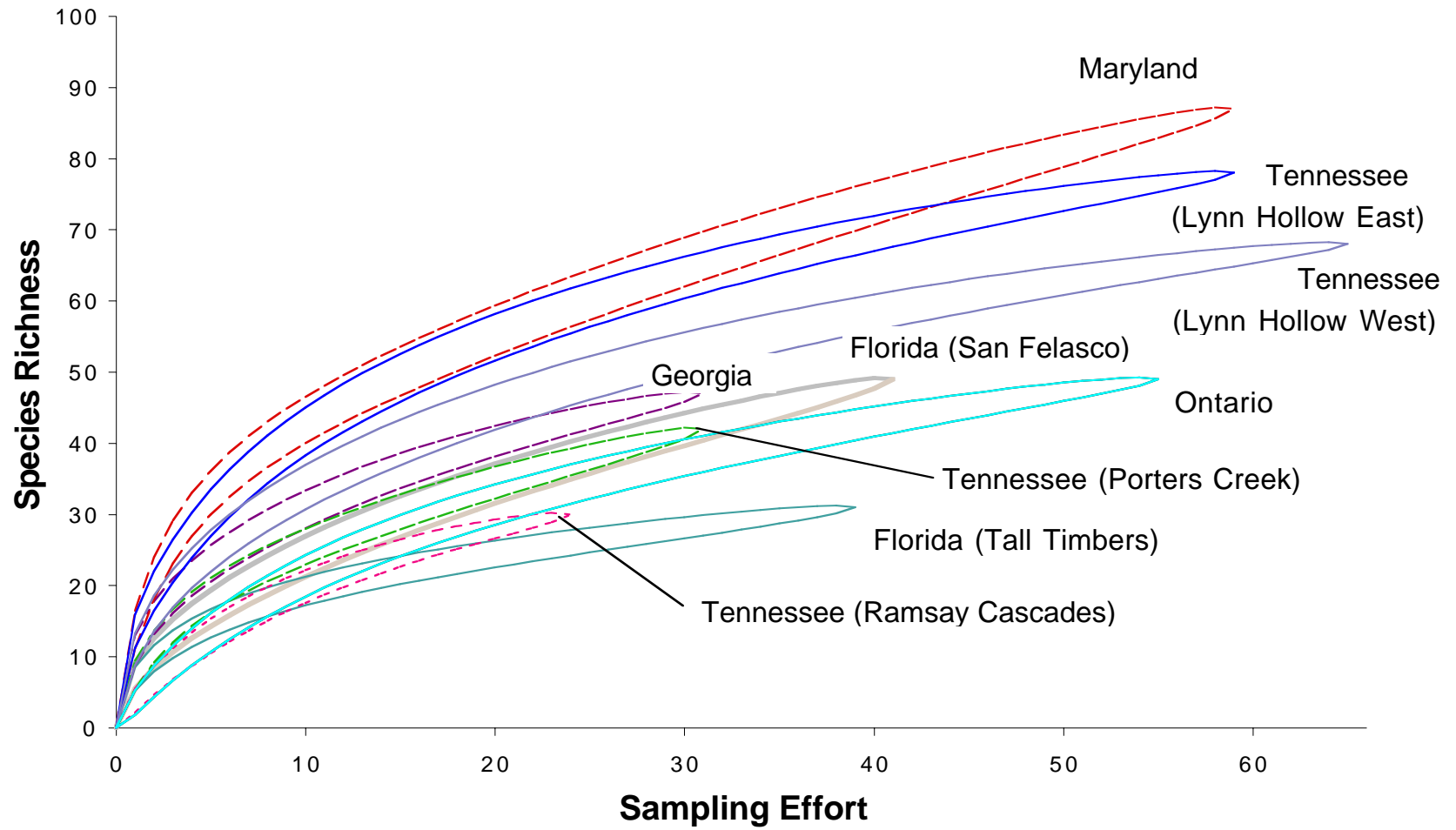


Figure. 2.2 Coleman richness expectation curves with 95% confidence intervals of Ichneumoninae at four sites in Great Smoky Mountains National Park, Tennessee, Lynn Hollow East, Lynn Hollow West in 1997 and 1998, Porters Creek and Ramsay Cascades in 1997, Shaw Woods, Ontario in 1992 and 1993, Patuxent, Maryland in 1992 and 1993, Hitchiti, Georgia, Tall Timbers, Florida and San Felasco, Florida in 1993 (Skillen et al. 2000). Samples from Skillen et al (2000) are normalized to two week samples for like comparison with the current study. Sampling effort refers to samples that contain at least one ichneumonine.



CHAPTER 3

BIODIVERSITY IN CLEARCUT VERSUS NEVER CUT EASTERN DECIDUOUS FORESTS: PARASITOID WASP (HYMENOPTERA: ICHNEUMONIDAE) DIVERSITY IN GREAT SMOKY MOUNTAINS NATIONAL PARK, TENNESSEE 70 YEARS AFTER LOGGING STOPPED¹

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Abstract

We compare the diversity of the parasitoid subfamilies Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) in old-growth and mature coves following logging in Great Smoky Mountains National Park, Tennessee. We captured insects using Malaise traps in old-growth coves between 8 April, 1997 - 18 April, 1998 and second-growth coves between 10 April 1997 - 9 April 1998. The study design included 2 old-growth coves (Ramsay Cascades (35° 43' N, 83° 8' W) and Porters Creek (35° 40' N, 83° 23' W)) and 2 second-growth coves (Meigs Post Prong (35° 36' N, 83° 31' W) and Fish Camp Prong (35° 37' N, 83° 33' W)) with 2 traps in each cove. We identified 163 species: 95 Campopleginae and 69 Ichneumoninae. Total species richness was higher in old-growth coves (130 species: 79 Campopleginae, 51 Ichneumoninae) as compared to second-growth coves (115: 57 Campopleginae, 58 Ichneumoninae). Yet subfamily differences were evident. Campopleginae (larval parasitoids) had higher species richness in old-growth coves and a 66% overlap in species composition between previously cut and uncut coves. Ichneumonine (pupal parasitoids) had similar richness in both previously cut and uncut coves and a 75% overlap in species composition. Thus, Ichneumonine wasps appear to disperse easily and recolonize well after disturbance, yet Campoplegines may not disperse as rapidly and may be more susceptible to habitat destruction. We conclude that these subfamilies appear to have largely recovered 70+ years after clear-cutting. However, there are a few species that may specialize in old-growth forests. *Phaeogenes_sp_GSMNP_2*, *Rhimphoctona_sp_GSMNP_1* and *Dusona_sp_GSMNP_2*, appear to only occur in old-growth forests and may be species of conservation concern. We are hampered by a lack of natural history information and recognize the need for further study of these highly diverse organisms.

Introduction

Over 99% of the original forest in the eastern United States has been cleared for timber, agriculture or urbanization, with adverse effects on plant and animal communities. One consequence of habitat destruction is extinction. Habitat destruction has been cited as the prime cause of species extinction on the planet today (Pimm and Raven 2000). In the eastern United States, we have lost approximately 1% of the terrestrial plants and vertebrates in recent times (Pickering et al. 2002). Freshwater invertebrate losses are considerably higher: 12% of the bivalve mollusks and over 11% of the aquatic snails that occurred in the southeastern United States are presumed extinct (Neves et al. 1997). Even widely-distributed, common species have succumbed: passenger pigeons (*Ectopistes migratorius* L.), carolina parakeets (*Conuropsis carolinensis* L.) and ivory-billed woodpeckers (*Campephilus principalis* L.). However, we know little about extinction in hyper-diverse groups such as the insects (Hilton-Taylor 2000). Furthermore, disturbance is often listed as a primary force controlling diversity patterns (Noss 1996), yet we still know little about the response of forest insect communities to habitat destruction.

Insects are integral components of forest ecosystems. The sheer number of insects gives some indication of their importance. They are the most speciose taxa on the planet (Stork 1988, Price 1997). Even when one considers all described species from viruses, bacteria to chordates, insects represent about 60% of the known biota (Hammond 1992, Samways 1994). They are often the most abundant as well. In a Brazilian tropical forest, the biomass of ants is four times that of all vertebrates combined (Wilson 1990). Insects provide a variety of ecosystem services as herbivores, pollinators, predators, parasitoids, and decomposers. Insect herbivores are estimated to remove about 20% of foliage each year worldwide (Samways 1994). Parasitoids play a significant role in terrestrial ecosystems because of their potential ability to regulate their herbivorous prey (LaSalle and Gauld 1992). The effects of removing one or more species of parasitoids in bio-control systems

can result in explosive pest populations resulting in defoliation, death of host plant, or exclusion of other herbivores (DeBach and Rosen 1991). Furthermore, the parasitoid lifestyle has been cited as contributing to ecosystem stability and longer food chains when compared to predators because of specialized behaviors (Pimm and Lawton 1978, Toft 1986, LaSalle 1993). These examples underscore the importance of the interactions of insects in terrestrial communities and illustrate that losses of species could have detrimental effects. Unfortunately, we know little about how the effects of habitat disruption compromise these myriad plant-insect-parasitoid interactions. Parasitoids are strongly tied to their hosts' food plants because they often cue on host plants to find hosts (Strong et al. 1984, Hawkins 1994). Thus, recovery of lower trophic levels is essential to support parasitoids in recovering forests.

Duffy and Meier (1992) found evidence that the recovery of herbaceous understory communities in mixed mesophytic forests of the Southern Appalachians may require centuries, much longer than the present logging cycles of 40-150 years for Appalachian cove hardwoods. Some species, such as federally listed *Panax trifolium*, have not yet dispersed to disturbed coves (Meier et al. 1995). Thus, certain herbs may be unable to cope with severe habitat disturbance. Others have challenged this finding and have suggested that Duffy and Meier's (1992) results reflect the spatial scale they examined. For example, old-growth coves may have higher species richness at the level of square meter plots, but species richness of entire coves may be virtually identical (Steinbeck 1993, Elliott and Loftis 1993). This argument may be moot, because, as forests become more fragmented, they may not continue to function as before. For instance, changes in species richness and abundance of pollinators may further disrupt plant dynamics within these fragmented systems (Aizen and Feinsinger 1994).

Invertebrates are also vulnerable to habitat destruction (Wells et al. 1983). Habitat change and loss has been cited as the main causes of the decline of moths in Britain, one of the best studied Lepidopteran communities in the world (Young 1997). Lepidoptera are hosts for countless parasitoids within these communities, of which many species remain undescribed (LaSalle and Gauld 1992). The International Union for Conservation of Nature, now called the World Conservation Union, began to categorize species according to risk of extinction in the 1960's in documents called Red Data Books. Current Red data document 300 invertebrates and an additional 255 mollusk species as threatened or endangered in the United States (Hilton-Taylor 2000). When one examines the United States Endangered Species List, butterflies (Lepidoptera) make up less than 1% of global insect species richness yet they comprise 53% (15 of 28) of federally protected insects (Opler 1995). The Lycaenidae, a large family of Lepidoptera representing between 30 and 40% of all butterfly species, represents 50% of the listed butterfly taxa. Habitat destruction is believed to play an important role in threatening these species because populations are often associated with one host plant in temporary or early successional environments (Cushman and Murphy 1993). Thus, herbivorous insects suffer from habitat loss even if their food plants recover.

Little is known about insect species composition within terrestrial ecosystems, yet parasitoids may comprise up to 20% of those species (Godfray 1994). Thus, it is difficult to understand the effects of habitat disruption on these largely unknown organisms (Didham et al. 1996). For instance, current global Red Data list no recently extinct Hymenoptera (ants, bees and wasps) species, primarily from lack of data on these organisms (Hilton-Taylor 2000). To address the problem, the International Union for Conservation of Nature has established a Species Survival Commission Specialist Group to raise awareness about the importance of Hymenoptera in mainstream conservation efforts. This is an important step because effective parasitoids maintain hosts at low numbers and

thus are themselves rare making them more susceptible to extinction as habitats become more fragmented (LaSalle and Gauld 1992).

In this paper, we compare the composition and diversity of Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) in previously cut and never-cut forests. Study sites include two old-growth mesic coves and two mature mesic coves, approximately 70 years post clear-cut in Great Smoky Mountains National Park, Tennessee. The data are part of a larger study examining the influence of habitat, logging and fire on the diversity and composition of parasitoids and other insects within Great Smoky Mountains National Park (GSMNP). In this larger study, we have collected over 100,000 ichneumonoids and pinned over 40,000 ichneumonids from 24 subfamilies. In these 24 subfamilies, we identified a minimum 319 species: 176 campoplegines; 143 ichneumonines. Previous studies suggest that old-growth forests may support a higher diversity of parasitoids than previously logged forests (Miller 1980, Miller and Ehler 1990), yet we know little about whether previously logged forest parasitoid communities have recovered. Furthermore, some evidence suggests that higher trophic levels are more sensitive to disturbance (Pimm and Lawton 1977, LaSalle 1993, Kruess and Tschardtke 1994, 2000). Because we know so little about parasitoid composition and recognize the risk of losing never-documented species to disturbance, we have selected two parasitoids with two contrasting life-history strategies to examine whether parasitoids have re-established after logging.

Materials and Methods

Study Organisms

The Ichneumonidae contain an estimated 60,000 species worldwide (Townes 1969) and an estimated 8,000 Neartic species of which only 35% have been described. Here we examine Campopleginae and Ichneumoninae, two species rich groups with differing life-history strategies. Campopleginae are a species rich group of internal larval parasitoids that

generally attack Lepidoptera and Symphyta (Wahl 1993). Ichneumonines are largely external pupal parasitoids that attack only Lepidoptera (Wahl 1993, Gauld 1988). Because ichneumonines attack later host stages than campoplegines, they may be considered to be more generalized parasitoids. For instance, an ichneumonine female will kill the host immediately when she lays her eggs. In contrast, larval parasitoids, like the campoplegines, develop within a living host. This makes larval parasitoids more specialized in their choice of prey because they must contend with host defenses during development (Salt 1968).

Sites and Sampling

We compared old-growth with mature coves approximately 70 years after clearcutting in Great Smoky Mountains National Park, Tennessee. Over 80% of GSMNP forest has been previously logged including over 100,000 acres in and around the sites where we sampled. Our study was designed to compare parasitoid communities in two never-cut cove forest stands with two second-growth stands matched with respect to altitude, slope and aspect. We continuously sampled 2 old-growth coves (Ramsay Cascades (35° 43' N, 83° 8' W) and Porters Creek (35° 40' N, 83° 23' W)) and 2 second-growth coves (Meigs Post Prong (35° 36' N, 83° 31' W) and Fish Camp Prong (35° 37' N, 83° 33' W)) with 2 traps in each cove. Table 3.1 shows the study design and site elevation.

We sampled old growth coves between 8 April, 1997 - 18 April, 1998 and second-growth coves between 10 April 1997 - 9 April 1998. We collected samples using fine mesh (.33 mm) Townes-style Malaise traps (Townes 1972) oriented with trap heads facing south to maximize the time sunlight shone on the collecting head. We changed the traps bi-weekly or monthly in winter months and preserved all specimens in 70% ethanol.

Database

Data collected in the current study are located on the Discover Life web site <<http://www.discoverlife.org>>. Trap numbers referred to in Appendix 1 may be found in the UGCA database. Ramsay Cascades trap numbers 151 and 152, Porters Creek traps 153 and 154, Fish Camp Prong traps 155 and 156, Meigs Post prong traps 157 and 158 each refer to traps 1 and 2 respectively in Table 3.1.

Specimen Identification

We sorted all Ichneumoninae to species based on Heinrich (1960a, b, 1961a, b, c 1962a, b and 1977) and morphospecies using reference material in the Insect Diversity Project's reference collection at the University of Georgia when specimens could not be identified. We defined morphospecies based on morphological and chromatic differences in the specimens. See Wayman (1994) for details of sorting techniques. We deposited specimens in the Insect Diversity Project's reference collection, University of Georgia and at the Natural History Museum at Great Smoky Mountains National Park. Because of sexual dimorphism in the Ichneumoninae, association of males and females was not possible in all genera. Therefore, within those dimorphic genera, we included in our analysis, only the specimens of the sex that contained the most morphospecies.

Statistical Analyses

We used Coleman Richness Expectation Curves (Coleman 1981, Coleman et al. 1982) with 95% confidence intervals using the EstimateS statistical package version five (Colwell 1997) to compare species richness between plots. These curves provide a method to evaluate sample heterogeneity by plotting the expected richness for randomized subsamples (Colwell and Coddington 1994). To estimate species richness, we conducted analyses for nine estimates as presented by Skillen et al. (2000) using the EstimateS

<<http://viceroy.eeb.uconn.edu/Estimates>> statistical package version five (Colwell 1997). We randomized the data, without replacement, 100 times to calculate the following nine estimators: Abundance-based Coverage (S_{ACE}), Incidence-based Coverage (S_{ICE}), Chao 1 (S_{C1}), Chao 2 (S_{C2}), First-order Jackknife (S_{J1}), Second-order Jackknife (S_{J2}), Bootstrap (S_B), Michaelis-Menten averaged over randomizations (S_{MR}), and Michaelis-Menten computed once for mean species accumulation curve (S_{MM}). We also compute Fisher's alpha (Fisher et al. 1943), a diversity index that allows comparisons that are independent of the number of individuals sampled. Colwell (1997), Colwell and Coddington (1994), and Chazdon et al. (1998) give a review of these statistical estimators. We calculated the Sorenson index (Southwood 1978, Janson and Vegelius 1981) and present scatter plots to examine the similarities between cut and uncut forests.

Results and Discussion

Total species richness was higher in old-growth cove forests for the Campopleginae and Ichneumoninae combined. Table 3.1 presents the observed data by trap to show the between trap variance in sampling plots. We sorted 925 Campopleginae to 95 species and 1,167 Ichneumoninae to a minimum of 69 species during the first year of collecting in the old-growth and second-growth coves. In old-growth coves, we collected 130 species (79 Campopleginae, 51 Ichneumoninae), and in second growth coves, 115 species (57 Campopleginae, 58 Ichneumoninae). For each subfamily we now describe the following four measures of diversity: 1) species richness, 2) species overlap across sites, 3) species composition and 4) potential old-growth specialists.

Species richness

Table 3.1 presents observed Campopleginae and Ichneumoninae species richness between old and second growth cove forests. There appears to be subfamily differences in species richness between coves. The observed data show that campoplegine species richness was higher for both old-growth coves, when compared to matched second growth coves. We found the same results when we computed Fisher's alpha (Table 3.2). We found contrasting results for the Ichneumoninae. Total observed species richness for ichneumonines was higher in each second-growth cove when compared to its matched old-growth cove: Meigs Post Prong (41 species) had more species than Ramsay Cascades (30 species) and Fish Camp Prong (45 species), had more species than Porters Creek (42 species). Yet, while matched coves contain higher species richness in second-growth forests both second-growth forests were not higher than both old growth forests. The Fisher's alpha index showed variable results. We found higher ichneumonine diversity at the second growth cove Fish Camp Prong when compared to Porters Creek. Yet Ramsay Cascades, the old-growth site, had higher diversity than Meigs Post Prong. Thus, the differences in the observed data may be a result of differing sample sizes.

To further examine whether the results between habitat are replicated for both old-growth and both second growth coves accounting for sample size, we examined the Coleman Richness Expectation Curves for each cove separately. Figure 3.1 shows the Coleman curves for Campopleginae at the four sites. Again, total species richness for Campopleginae at our old-growth sites appears higher than our second growth sites when compared to matched second-growth sites (Table 3.1). Coleman curves for the second growth sites do not differ significantly with the 95% confidence intervals overlapping. Yet, the slopes of all the curves are steep, indicating that we do not have adequate sampling to estimate total campoplegine species richness at any one site. It appears that old-growth sites contain higher species richness than second growth sites for campoplegine parasitoids.

Thus, with species richness as a measure of recovery, campoplegines may not have recovered as readily as ichneumonines.

Total ichneumonine species richness appears higher in each second growth cove when compared to each matched old-growth cove. Figure 3.2 is similar to Figure 3.1 showing Ichneumoninae Coleman curves at the four sites. This figure shows higher species richness in both second growth coves with complete overlap of the 95% confidence intervals. Again, the slopes of all the curves are steep indicating that we do not have adequate sampling to estimate total species richness at any one site.

Species overlap

To further address the question of whether these communities have recovered, we compared the overlap between forests by first excluding singletons (species collected only once). We define recovery as the return of species in number and composition to the second growth coves. We assume that if the campoplegine and ichneumonine communities have recolonized the second-growth sites, the overlap in species should be relatively high. Of the 95 campopleginae species collected, 62 were caught more than once (Appendix 1). Table 3.3 presents the distribution of Campopleginae and Ichneumoninae species collected more than once and their distribution across the four sites. We observed a 66% overlap in campopleginae species between cut and uncut sites. We found that the cut and uncut forests to have similar species richness evidenced by a Sorenson index of 0.6029 (Southwood 1978, Janson and Vegelius 1981). This appears to be a high degree of overlap, yet almost a quarter of the species (24%) were found only in old-growth sites. Thus, campoplegines may have a high proportion of endemic species and may be more susceptible to habitat destruction.

The ichneumonine community may have better recovered. Of the 69 ichneumonine species collected, 53 species were caught more than once (Appendix 1). We observed 75%

of species shared between old and second growth forests for the Ichneumoninae (Table 3.3). We found that the cut and uncut forests to have similar species richness evidenced by a Sorenson index of 0.7339 (Southwood 1978, Janson and Vegelius 1981). This degree of similarity seems to indicate that ichneumonine communities have largely recovered after the logging disturbance. Furthermore only 11% of the species were found only in old-growth stands, indicating that a smaller proportion of species may not have yet colonized the disturbed habitat.

We conducted analyses for nine estimates of species richness as presented by Skillen et al. (2000). The slopes of the estimators were steep (not shown), indicating that we have not adequately sampled to estimate total species richness in any of coves. We know that the observed data underestimate total richness at each of the sites. Yet we have little confidence in the estimators ability to predict species richness in speciose groups like the Ichneumonidae because of the steep slopes of the estimator curves (not shown). Thus, we feel that the observed richness and the Coleman curves are adequate measures to compare species richness between sites.

These data suggest subfamily differences in recovery between old-growth and second growth coves. Specifically, that ichneumonine parasitoid species richness is more similar in the cut and un-cut forests than campoplegines. Our findings for the Ichneumoninae are contrary to predictions by Hawkins (1994) for increased diversity in older successional stands. Hawkins (1994) predicted that generalists would frequent large plants that support a more diverse host resource. He found that pupal parasitoid richness increased along the series from monocots, herbs, shrubs to trees. Our results also differ from Gaasch 's (1996) study of specialist and generalist parasitic wasps along a successional gradient from clear-cut to old-growth in the Georgia Piedmont. She found no significant differences in the proportion of campopleginae and ichneumoninae species among the 8 forest stands examined. In contrast, we found higher richness of pupal

parasitoids (ichneumonines) in our second growth stands and a higher proportion of larval parasitoids (campoplegines) in old-growth stands. These differences may be a result of the habitat types examined. However, these differences highlight the difficulty in understanding such hyper-diverse groups.

There are caveats. Evidence to suggest that richness varies with vertical structure in managed forest stands. Su and Woods (2001) collected a greater proportion of insects closer to the forest floor in clear-cut stands when compared to selectively logged or shelterwood stands. Thus, without vertical sampling in the current study, differences between logged and unlogged sites may result from differences in vertical structure of the forest parasitoid communities. Furthermore, logging history may not be a good predictor of parasitoid community patterns. Upon review of current published disturbance-richness relationships, Mackey and Currie (2000) found that disturbance plays only a subtle role in determining patterns of richness. Their Markov models of six real communities predicted that over disturbance gradients from none to complete disturbance, species richness should vary by approximately 3%. These predictions were for non-motile species, and may not apply to the current study. However, the observed data appear to show differences in recovery for the two subfamilies with species richness as a measure.

Species composition

An examination of the composition between these cut and uncut forests further highlights the differences between the subfamilies (Figure 3.3). There appears to be a greater difference in the species composition for the campoplegines when compared to the ichneumonines (Figure 3.4). Figure 3.3 compares campoplegine abundances between second-growth (x-axis) and old growth (y-axis) mesic cove communities. Each of the 95 points represents a species and is plotted on a log scale, therefore, all abundances are plotted as $(n+1)$ to avoid zero values. The line represents the expected distribution if the species

composition is the same in both old-growth and second growth forests. Therefore, if all species occurred in the second growth forest they would fall on the x-axis, and if all species occurred in the old-growth forest they would fall on the y-axis. There appears to be differences in composition between the four sites evidenced by the scatter about the line predicting similar composition. The lower R^2 value of 0.3502 shows less similarity for the campoplegines between the two habitats when compared to the ichneumonines (Figure 3.4).

We found little difference in ichneumonine species composition between previously cut and uncut forests. Figure 3.4 presents Ichneumoninae species abundance in second-growth (x-axis) and old growth (y-axis) communities similar to Figure 3.3. There is little difference in the four sites evidenced by the species clustered along the line predicting similar composition. It appears that the species composition and abundance is quite similar evidenced by the $R^2=0.6142$. This degree of overlap may be a result of the more generalized life-history strategy most commonly used by this pupal parasitoid or greater dispersal ability. For instance, a more generalized strategy would allow dispersing organisms to survive in refugia after a clear-cut because of females' ability to oviposit on a wider variety of hosts. Thus, while we found higher species richness in second growth coves for ichneumonines, we see a higher degree of overlap in the coves (75%) for the ichneumonines than for the campoplegines (66%). With the exceptions presented below, it appears that ichneumonines are well distributed within all four coves regardless of logging history (Table 3.3).

Old-growth specialists

The campoplegines as a whole may not recover quite as readily as the ichneumonines, yet we see different responses on the species level. For instance, *Bathyplectes infernalis* (Gravenhorst) (n=34, Figure 3.3) was the fifth most common

campoplegine collected in the current study, found only in the old-growth coves. However, further investigation of the distribution of *B. infernalis* shows it to occur in second growth forests in Georgia's Piedmont and planted alfalfa fields (Wayman 1994). Twelve individuals of *Dusona*_sp_GSMNP_2 (n=22, Figure 3.3) were collected only in traps at Ramsay Cascades, one of our old-growth sites. This morphospecies is from one of the largest campoplegine genera with distributions in all geographic regions (Krombein et al. 1979). However, it has not been collected in over 9 years of sampling by the authors and may specialize in old-growth coves. *Rhimphoctona*_sp_GSMNP_1 (n= 18, Figure 3.3), collected only from Ramsay Cascades is from a small Holarctic genus with congeners having been reared from Cerambycidae (Coleoptera) in the bark of *Abies concolor* (Gordon & Glendinning). This species may be specializing in the Park's fir remnants at higher elevations. Ramsay Cascades is one of our highest elevation sites at 1183 m. *R.*_sp_GSMNP_1 individuals may be cruising for hosts on fir trees at Ramsay Cascades and may no longer be present in previously logged sites because their hosts are no longer present. Thus, this subfamily may recover more slowly after a clear-cut because dispersing individuals may not be able to find adequate hosts in adjacent habitats. Furthermore, local extinctions may be more common in this more specialized group of parasitoids as evidenced by the absence of some species in previously logged forests, the lower beta diversity (66%) between cut and uncut forests, and the higher total diversity in old-growth forests for this subfamily.

While it appears that ichneumonines are well distributed within all four coves regardless of logging history, we see different responses on the species level as well. *Coelichneumon azotus* (Cresson) (n=12, Figure 3.4) and *Phaeogenes*_sp_GSMNP_male_2 (n=13, Figure 3.4) were only collected in the old-growth coves in the current analysis. This might lead us to conclude that these two species have not been able to recolonized the previous logged coves at Meigs Post Prong and Fish Camp

Prong. However, further examination of the distributions of these species within the Park and elsewhere does not support this conclusion for both species. Data from Gaasch (1996) show *C. azotus* to occur in second growth forests at the Hitchiti Experimental forest in Georgia's Piedmont. Specimens have also been recorded in Patuxent Maryland by the authors and at Lynn Hollow in the current study indicating a broad geographic range of this species. Records from museum collections also indicate a wide range for this species from Quebec to Alabama (Krombein et al. 1979). However, *P._sp_GSMNP_male_2* is a morphospecies, like *D._sp_GSMNP_2*, has not been collected in over 9 years of sampling by the authors and may specialize in old-growth forests. As part of the larger study, a total of 36 individuals have been collected in the Park over a period of 4 years of sampling, yet none have been collected in the previously logged forest. This includes collections from an unlogged xeric ridge forest approximately 40 miles from the old-growth coves examined in the current analysis. While the rarity of this individual may make collecting less likely, its presence only in old-growth sites may indicate that it has not been able to recolonize second growth sites. So, even though the subfamily as a whole may be more generalized and, show higher species richness in matched second growth coves, some species may be less able to cope with habitat destruction.

Understanding dispersal abilities of these organisms is key to understanding their return to clear-cut forests. Ichneumonids are strong flyers (Townes 1969). Biological control programs that track the introduction of parasitoids (Ichneumonidae: Campopleginae) have documented the annual spread of established parasitoids of about 50 km per year (Quednau 1990). Other studies have found ichneumonid individuals up to 900 m away from initial release sites in the first generation (Griffiths and Lyons 1980). Mating behaviors can further facilitate superior dispersal abilities. Females of *Bathyplectes curculionis* (Thompson) (Ichneumonidae: Campopleginae), a parasitoid of the alfalfa weevil *Hypera postica* (Coleoptera: Curculionidae), remain receptive to mating two days after

emerging from hosts and thus mate after dispersal. This behavior promotes genetic diversity and may be partially responsible for the broad geographic range of *B. curculionis* in North America (Dowell and Horn 1978). Furthermore, it has been hypothesized that host phenology is the most important factor in determining peak flight activity (Gaasch et al. 1998). Yet male and female activity may differ depending on habitat quality. Wayman (1994) showed that sex ratios of Malaise trap catches were male biased in suitable habitats and closer to 1:1 in flight-ways or unsuitable habitats. She suspected that females were caught less frequently because they were searching for hosts on plant material in suitable habitats, while males were flying around searching for females and were caught more often. Thus, physical constraints may not be as limiting as locating suitable hosts when colonizing disturbed habitats.

Why might life-history characteristics make certain groups more sensitive to disturbance than others? In addition to physical constraints, parasitoids are limited in distribution by the hosts on which they prey. The idiobiont/koinobiont (Askew and Shaw 1986) dichotomy has been widely used to examine parasitoid responses to food plant type, host range, or latitudinal gradients irrespective of taxonomic lineage. Idiobiont (pupal) parasitoids have relatively long-life spans and generally hit concealed hosts to avoid predation. Because an idiobiont female kills the host immediately when she deposits her eggs, she can attack a wider range of hosts (Gauld 1988). Thus, in the current study, ichneumonine parasitoid species richness may have been higher in the matched previously logged forest because they can more easily colonize disturbed habitats with a wider variety of available hosts. Most koinobionts (larval parasitoids), such as the campoplegines in the current study, are endoparasitoids and their hosts continue to survive after oviposition. With internal oviposition, the parasitoid must battle the immune system of its host (Salt 1968), and koinobionts generally have more narrow host ranges (Askew and Shaw 1986, Sheehan and Hawkins 1991). Thus, dispersing koinobiont campoplegines may be less able

to find adequate hosts after logging because of their more narrow host range and may suffer more from habitat disruption than idiobiont ichneumonines. This may explain the lower degree of overlap between old-growth and second growth forests (66%) for these organisms.

Furthermore, there is evidence to suggest that parasitoids are more susceptible to extinction or population decline than their herbivorous hosts (Kruess and Tschamntke 1994, 2000). The results presented here show evidence of the local rarity of certain specialized parasitoids in terrestrial systems. For example, we collected 33 campoplegine species only once in 8 trap-years of collecting. Thus, 35% of the campopleginae catch were singletons while the ichneumonines contained only 16 singletons representing 23% of the catch (Table 3.3). The large percentage of singletons collected in all habitats may be an indication of the susceptibility of campoplegines to habitat modification or loss, or they may simply be less susceptible to trapping. If these organisms are more susceptible to habitat destruction, this point will become more salient as humans continue to destroy habitat where these organisms persist, and they may be the species of conservation concern.

Conclusions

These data show a high degree of similarity in species composition between similar habitats regardless of logging history. Yet subfamily differences are evident. Campopleginae parasitoids had higher species richness in old-growth coves (79 species) when compared to second-growth coves (57 species), while Ichneumoninae parasitoids had higher species richness in second growth coves (58 species) when compared to old-growth coves (51 species). Furthermore, Campopleginae had 66% overlap in species composition between previously cut and uncut coves, while Ichneumonines had 75% overlap in species composition between previously cut and uncut coves. Because the effects of disturbance are closely tied to dispersal abilities it is not surprising that strong flying pupal ichneumonine

parasitoids could better recolonize disturbed areas than their more specialized larval campoplegine counterparts.

Based on these data, we conclude that:

- the ichneumonine communities, for the most part, have recovered 70+ years after clear-cutting while, campoplegine communities have to a lesser degree;
- ichneumonine (idiobiont) wasps disperse easily between habitats and recolonize well after disturbance;
- campopleginae (koinobionts) wasps may not disperse as easily between habitats or colonize disturbed habitats as rapidly, and thus may be more susceptible to habitat destruction;
- certain species in both subfamilies e.g., *Phaeogenes_sp_GSMNP_2*, *Rhimphoctona_sp_GSMNP_1* and *Dusona_sp_GSMNP_2*, may be susceptible to forest destruction and may be the species of conservation concern.

This study is correlative and not experimental and may raise the issue of pseudoreplication. However, landscape level studies of community change necessitate these types of comparisons (Hargrove and Pickering 1992). Given the rate of destruction of natural areas, comparisons like those conducted in the current study are necessary to better understand how habitat destruction impacts natural communities (Hughes et al. 2000). We must continue to study the effects of disturbance on higher trophic level organisms such as parasitoids to better understand their importance in terrestrial ecosystems.

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Table 3.1 Campopleginae species (individuals) and Ichneumoninae minimum species (individuals) collected in Great Smoky Mountains National Park in 1997-98.

Site [Elevation]	Trap 1	Trap 2	Total	Trap 1	Trap 2	Total
	Campopleginae			Ichneumoninae		
Old Growth Coves:						
Ramsay Cascades [1183 m]	56 (240)	21 (91)	59 (331)	27 (85)	13 (26)	30 (111)
Porters Creek [957 m]	41 (101)	23 (51)	49 (152)	31 (219)	31 (223)	42 (442)
Total for Old-Growth			79 (483)			51 (553)
Second Growth Coves:						
Meigs Post Prong [1150 m]	34 (130)	20 (45)	41 (175)	28 (126)	34 (224)	41 (350)
Fish Camp Prong [950 m]	35 (156)	26 (111)	42 (267)	36 (140)	30 (124)	45 (264)
Total for Second Growth			57 (442)			58 (614)

Table 3.2. Fisher’s alpha computed for Campopleginae and Ichneumoninae species collected in old and second growth forests in Great Smoky Mountains National Park.

Site	Fisher's Alpha	
	Campopleginae	Ichneumoninae
Ramsay Cascades	20.65	13.51
Porters Creek	25.07	11.4
Meigs Post Prong	16.92	12.05
Fish Camp Prong	15.95	15.59

Table 3.3. The distribution of the number of Campopleginae (S=62) and Ichneumoninae species (S=53) collected more than once in Great Smoky Mountains National Park in 1997-98. Species are scored as having been collected in one, two, three or four sites within the old-growth and second-growth comparison. Shared species show the degree of overlap between sites. Percentage of the total number of species per subfamily are given in parentheses. The distribution of singletons, species containing only one specimen, are also listed for each subfamily.

Site	Campopleginae			Ichneumoninae		
	Old	Shared	Second	Old	Shared	Second
Singletons	23 (24%)	-	10 (10%)	5 (7%)	-	11 (16%)
N > 1						
One Site	7 (11%)	-	3 (4%)	3 (5%)	-	5 (9%)
Two Sites	8 (13%)	12 (19%)	3 (4%)	3 (5%)	10 (19%)	2 (4%)
Three Sites	-	12 (19%)	-	-	16 (30%)	-
Four Sites	-	17 (27%)	-	-	14 (26%)	-
Total	15 (24%)	41 (66%)	6 (9%)	6 (11%)	40 (75%)	7 (13%)

Figure 3.1. Comparison of Coleman richness expectation curves with 95% confidence intervals of Campopleginae at two old-growth coves, Porters Creek and Ramsay Cascades, and two second growth coves, Fish Camp Prong and Meigs Post Prong, in Great Smoky Mountains National Park, Tennessee in 1997-98. Sampling effort refers to samples that contain at least one Campopleginae.

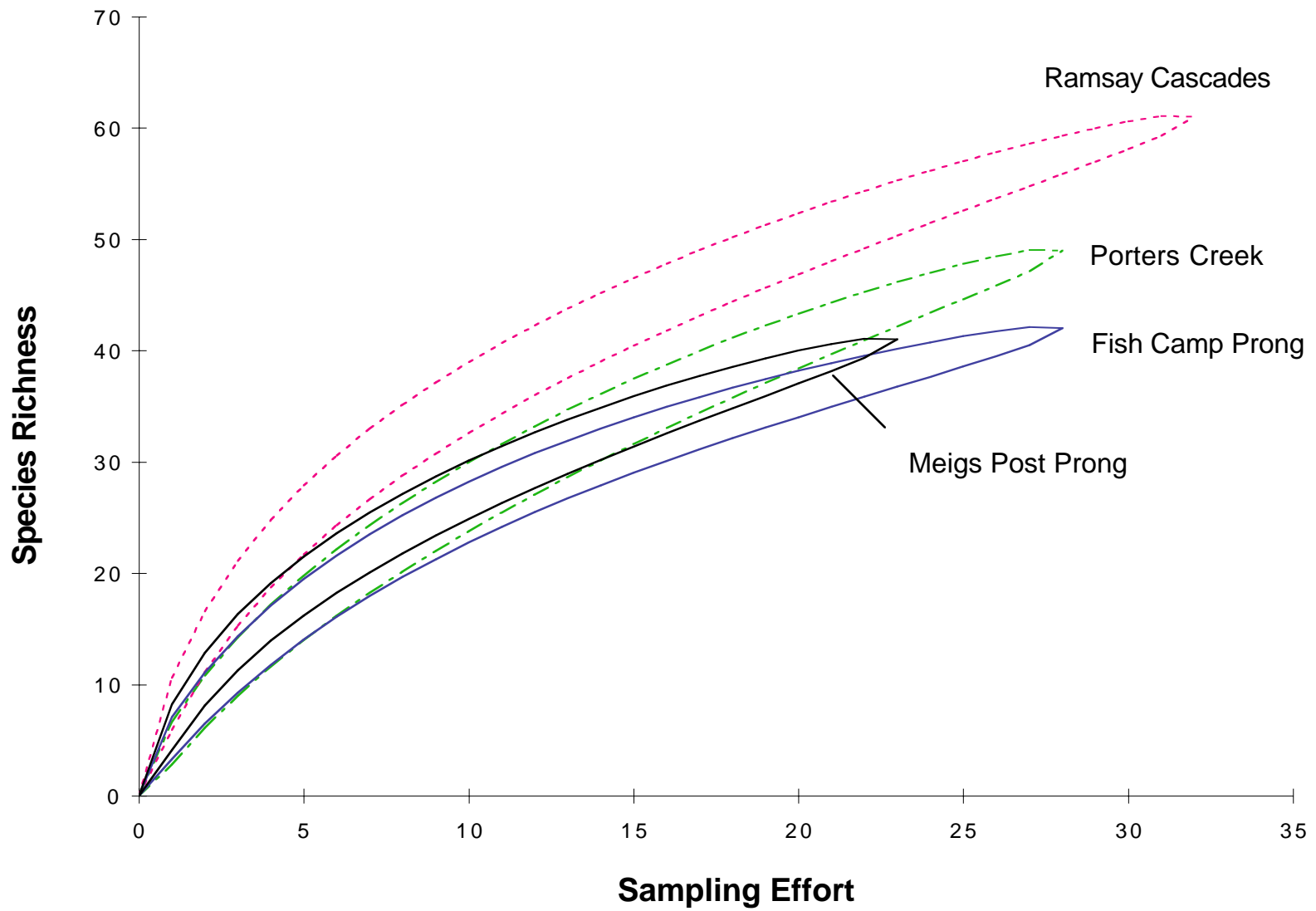


Figure 3.2. Comparison of Coleman richness expectation curves with 95% confidence intervals of Ichneumoninae at two old-growth coves, Porters Creek and Ramsay Cascades, and two second growth coves, Fish Camp Prong and Meigs Post Prong, in Great Smoky Mountains National Park, Tennessee in 1997-98. Sampling effort refers to samples that contain at least one ichneumoninae.

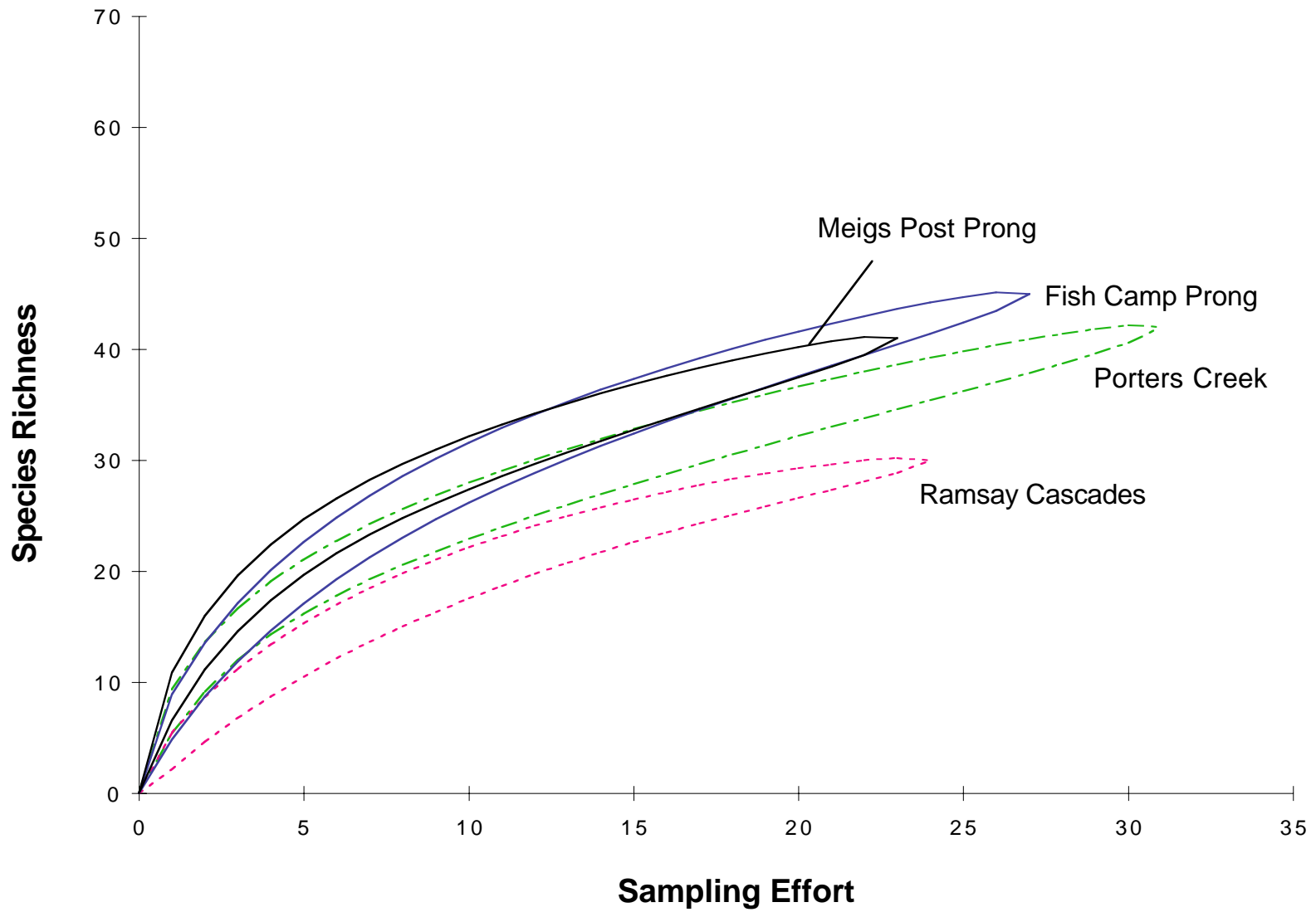


Figure 3.3. Campopleginae species abundance ($N+1$), in old-growth and second growth mesic cove forests in Great Smoky Mountains National Park in 1997-98. The line indicates the expected distribution if the species composition is the same in both habitats.

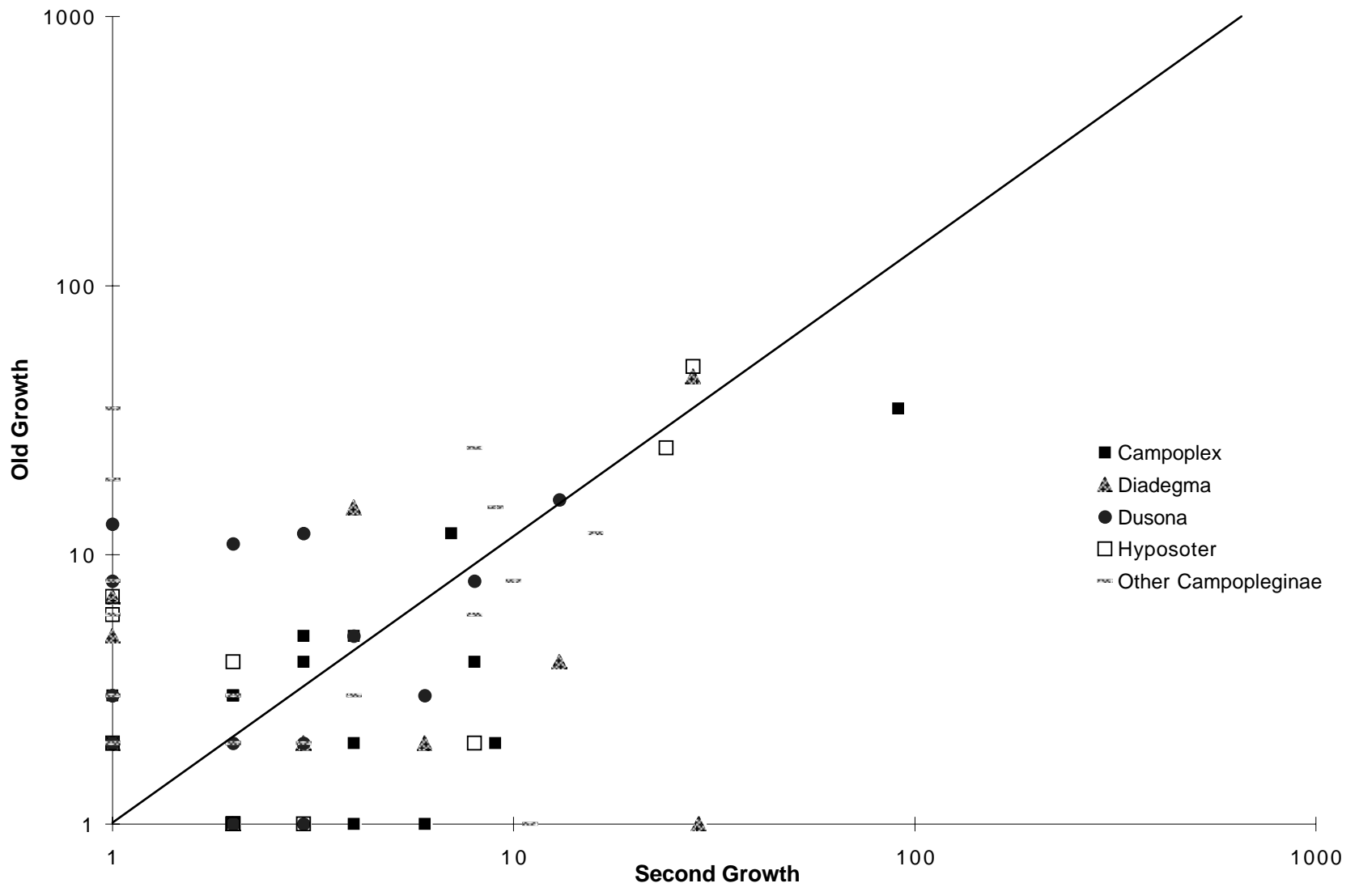
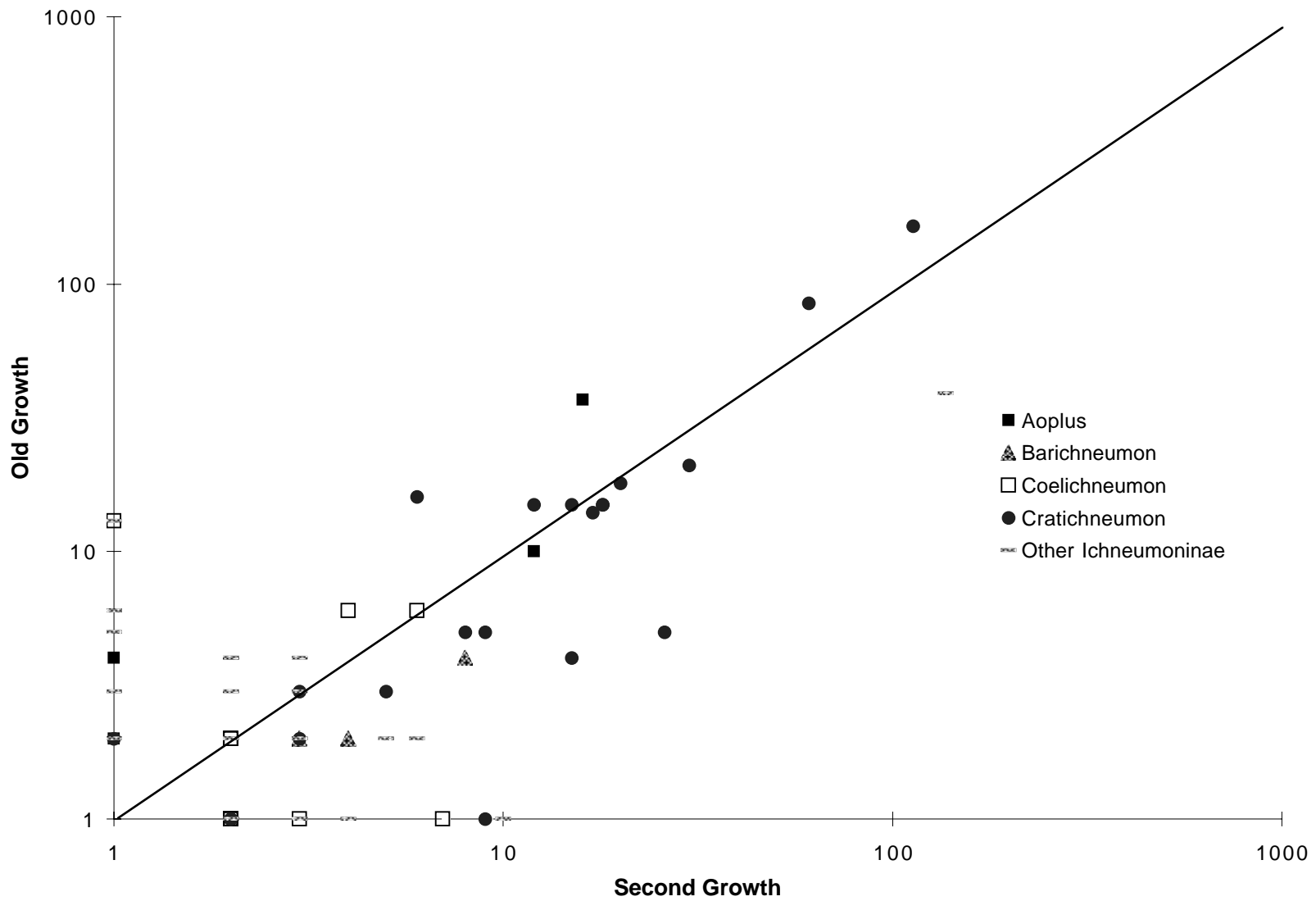


Figure 3.4. Ichneumoninae species abundance ($N+1$), in old-growth and second growth mesic cove forests in Great Smoky Mountains National Park in 1997-98. The line indicates the expected distribution if the species composition is the same in both habitats.



CHAPTER 4

EFFECTS OF FIRE ON INSECT COMMUNITIES IN GREAT SMOKY MOUNTAINS NATIONAL PARK, TENNESSEE, WITH A FOCUS ON ICHNEUMONINAE AND CAMPOPLEGINAE PARASITIDS (HYMENOPTERA: ICHNEUMONIDAE)¹

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Abstract

We compare insect communities before and after fire in burned and unburned plots in Great Smoky Mountains National Park, Tennessee. The prescribed fire conducted at our study site was the first after 70 years of fire suppression. We were interested in whether insect relative abundance, species richness and community composition would change with the return of fire. We sampled one burn and one control plot in the Lynn Hollow Burn Unit (N 38' 20" W 34' 59"; elevation 640-670 m). We sampled with Malaise traps both burn and control plots prior to a prescribed burn between 9 April, 1997 - 9 April, 1999 and one year of sampling after a prescribed burn between 26 June, 1999 - 4 July, 2000. We counted Coleoptera, Orthoptera, Ichneumonoidea, Symphyta and Formicidae from selected samples between 18 June - 6 November, 1998 for pre-burn counts, and between 26 June, 1999 - 5 November, 2001 for post-burn counts. We counted 13,613 Coleoptera, 912 Orthoptera, 3,167 Symphyta, 41,047 Ichneumonoidea, 9,505 Alate Formicidae, and 2,292 Apterous Formicidae from selected samples in the burn and control plots between 1998-2001. Orthoptera relative abundance increased after fire while Formicidae, Coleoptera, Symphyta, and Ichneumonoidea relative abundance decreases immediately after a fire. We compare species richness and composition of the parasitoid subfamilies Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) before and after fire. We identified 6,092 Campopleginae and Ichneumoninae individuals to 230 species. Coleman richness expectation curves show that Campopleginae species richness declines after a burn when control plots are compared to burn plots after the burn. Coleman curves for Ichneumoninae show that species richness was higher in the burn plots than in the control plots, yet this trend is the same each year prior to the burn. Thus, it appears that Campopleginae parasitoids are more susceptible than Ichneumoninae parasitoids to the fire disturbance, in the first year following the fire. Species composition is almost identical ($R^2=0.9244$) for

Ichneumoninae parasitoids in the post fire comparisons. There was a high degree of similarity in species composition ($R^2=0.8702$) between burn and control plots after the fire for the Campopleginae as well. Thus, the relative abundance of parasitoids declines in the year following a fire but their community composition stays the same. These results appear to indicate the resiliency of the Ichneumoninae, Orthoptera and Symphyta communities after prescribed fire. However, prescribed fire may alter insect communities in subsequent years. We need to examine how insect communities respond in subsequent years and whether prescribed fire has long-term effects on these communities.

Introduction

Between 1916 and 1968, the United States National Park Service (NPS) had a strict policy to suppress all fires despite potential benefits to plant and animal communities. The Leopold Report (Leopold et al. 1963) emphasized the importance of restoring ecological processes and subsequently changed the NPS fire management policy. In 1968, the NPS restored fire as a natural component of terrestrial ecosystems. We were interested in whether insect relative abundance, species richness and community composition would change with the return of fire to Great Smoky Mountains National Park (GSMNP).

Historically, fire has been an important factor in structuring floral and faunal communities within the Central Hardwoods region (Braun 1950, Anderson et al. 1999). Fire regimes prior to human settlement are difficult to discover in all areas (Whelan 1995), but it has been argued that promoting an ‘unnatural’ fire regime may make conditions difficult for organisms that evolved under different fire conditions (Howe 1994, Whelan 1995). Thus, which historical fire regime to reconstruct for conserving biodiversity is difficult to discern. When biodiversity conservation is the primary goal of management strategies, greater understanding of fire over evolutionary time scales is an important consideration of conserving the biota (Howe 1994, Whelan 1995). However, human settlements play a role in shaping historical and current fire regimes. For example, Native Americans have used fire to modify this landscape for thousands of years (MacCleery 1992), yet fire suppression following European settlement, timber harvest and plant succession have dramatically changed the composition of this landscape over time (Ware et al. 1993, Bonnicksen et al. 1999, Harrod et al. 2000).

The frequency of fire in a given habitat can strongly influence post successional plant community structure (Hobbs and Gimingham 1987). For example, in the late 19th century, the fire regime in western GSMNP had a mean burn rotation of 12.7 years (Harmon 1982). The majority of fires were set by humans prior to the establishment of

GSMNP in 1934 (Bratton and Meier 1998). Since then, with effective fire suppression beginning in the 1940's, the mean fire rotation (the average time it takes to burn a specified area) has increased to over 500 years (Harmon 1982). With this reduction in fire frequency, there have been significant changes in forest structure including less regeneration of shade-intolerant *Pinus* spp. and reduction in cover and richness of herbaceous species (Harrod et al. 2000). As these floral communities change in response to modified fire regimes, certain species decline from habitat loss. For instance, the Red Cockaded Woodpecker, *Picoides borealis*, is an endangered species that has suffered from habitat fragmentation and loss of old-growth pine forest, its primary habitat. *P. borealis* is currently managed with prescribed fire, yet little is known about how non-pest insect species respond to prescribed fire within this region. Furthermore, concerns have been expressed about potential negative effects of fire on localized or rare insects with fire as a tool for ecosystem management (Opler 1981, Wright and Samways 1999).

As with most living organisms, the effects of fire on invertebrates depend primarily on the severity of the fire. Distinctions have been made between high intensity wild fire and low intensity prescribed fire (Campbell and Tanton 1981), however, under both circumstances, the effects are both immediate and long term (Lyon et al. 1978). For instance, invertebrate abundance generally decreases after a fire because adults and immatures may be killed by the flames, high soil temperatures, or loss of food resources. Insects may continue to decline for weeks following a fire from exposure or starvation (Warren et al. 1987). Alate insects have been reported to be most vulnerable because they are attracted to the fire's heat or smoke. While longer term effects from fire are more variable, grasshoppers (Orthoptera) and ground beetles (Coleoptera: Carabidae) have been reported to be more abundant post fire (Reed 1997, Galley and Flowers 1998). Wood boring beetles can increase soon after a fire because habitat becomes more suitable for those that survive the flames (DeBano et al. 1998, Swengel 2001).

The indirect effects of post fire plant quality may be an important part of structuring insect communities. Burning can remove older, lower quality forage and deposit those plant parts on the forest floor in the form of ash. For instance, low intensity prescribed fires have been shown to improve soil fertility (Lear and Waldrop 1985). The combination of a nutrient pulse in the soil and higher post fire light as a result of a more open canopy can increase plant quality for herbivore forage (DeBano et al. 1998). Whelan and Main (1979) found herbivory to be an important factor in seedling mortality in post fire Australian euclaypt woodlands. Most herbivory occurred one year after the fire. Force (1981) found insect richness and abundance in chaparrals peaks in the first year following a fire when compared to the second and third years. Force attributed this response to invader species that took advantage of lush vegetation in the first year following a fire. Higher foliar concentrations of phosphorus and calcium have been reported in chestnut oak trees post fire when compared to unburned trees (Boerner et al. 1988). Thus, these indirect effects on plant quality may be important in structuring post fire insect communities. For instance, given an increase in herbivore abundance or quality, one might expect an increase in parasitoid flight activity one year post fire as well.

To gain a broader understanding of insect response to fire, we examine how prescribed fire affects Coleoptera, Orthoptera, Ichneumonoidea, Symphyta, and Formicidae relative abundance and compare species richness of Campopleginae and Ichneumoninae parasitoids before and after fire in burned and unburned plots in GSMNP, Tennessee. Desiccation has been shown to limit parasitoid activity, therefore species hunting for hosts on leaves in the forest canopy may be more prone to desiccation than those hunting on the ground. Thus, larval parasitoids may be more susceptible to desiccation in an open environment as they search for hosts feeding on foliage than pupal parasitoids that search for pupae in more concealed environments. Therefore, we might expect a higher proportion

of pupal parasitoids in burned sites when compared to pre-burn years and control sites (Heinrich 1977, Gauld 1987, Shapiro and Pickering 2000).

Materials and Methods

Study Organisms

We examine 5 insect groups identified to order, suborder or family including: alate and apterous Formicidae (apterous and alate), Orthoptera (including only the grasshoppers), Coleoptera and Symphyta.

The Hymenoptera, and particularly parasitic wasps, comprise a large portion of global insect species richness (Quicke 1997). The Ichneumonidae contain an estimated 60,000 species worldwide (Townes 1969). Here we examine Campopleginae and Ichneumoninae, two diverse groups exhibiting different life-history strategies. Campopleginae are internal larval parasitoids that generally attack Lepidoptera and Symphyta (Wahl 1993). Ichneumonines are largely external pupal parasitoids that only attack Lepidoptera (Wahl 1993, Gauld 1988). Because ichneumonines oviposit on later host stages than campoplegines, they may be considered to be more generalized parasitoids. For instance, an ichneumonine female will kill the host immediately when she lays her eggs. In contrast, larval parasitoids, like the campoplegines, develop within a living host. This makes larval parasitoids more specialized in their choice of prey because they must contend with host defenses during development (Salt 1968).

Sites and Sampling

We compared insect communities at burn and control plots in xeric ridge old-growth forest before and after a burn at Lynn Hollow, Great Smoky Mountains National Park, Tennessee. We continuously sampled burn and control plots with two traps in each plot. Table 4.1 shows the study design.

The Lynn Hollow Burn Unit is part of the Cades Cove Ranger District located off of the Foothills Parkway at an elevation between 640-670 m (N 38' 20" W 34' 59"). The site is approximately 24 ha with the slope ranging from 0-40%, and the majority of the unit residing on a 8-10% slope. The site contains southern, eastern and western aspects. Total fuel load was estimated at less than 8 cm dead and live surface material or about 3.5 tons fuel/acre. The dead fuel load was estimated at 1 cm or about 2.9 tons fuel/acre (based on fuel model 9, Anderson 1982). The majority of the unit is comprised of hardwood leaf litter with small areas of *Pinus virginiana* Miller and *Rhododendron maximum* L. Five hundred twenty-nine overstory trees were tagged in the burn and control plots resulting in an approximate 1 : 0.6 ratio of hardwood to pine composition. *Quercus montana* and *Quercus velutina* Lam. were the dominant hardwood species and *Pinus echinata* Miller and *P. virginiana* Miller were the dominant pine species.

We sampled both burn and control plots prior to a prescribed burn between 9 April, 1997 - 9 April, 1999 and one year of sampling after a prescribed burn between 26 June, 1999 - 4 July, 2000. Traps in the burn plots were centralized and away from burn edges. Wet counts for Coleoptera, Orthoptera, Ichneumonoidea, Symphyta and Formicidae are based on selected samples between 18 June - 6 November, 1998 for pre-burn counts, and between 26 June, 1999 - 5 November, 2001 for post-burn counts.

We collected samples using fine mesh (.33 mm) Townes-style Malaise traps (Townes 1972) oriented with trap heads facing south. Traps were changed bi-weekly or monthly in winter months. All trap material was preserved in 70% ethanol.

Database

We make data collected here available on the Discover Life web site <<http://www.discoverlife.org>>. Lynn Hollow burn plot traps 1 and 2 in Table 4.1 refer to traps 159 and 160 in the UGCA database at <<http://www.discoverlife.org>>. Control plot

traps 1 and 2 refer to traps 165 and 166 in the UGCA database at <http://www.discoverlife.org>.

Specimen Identification

Preserved specimens of insects sorted to order, suborder, superfamily or family are based on keys in Borror et al. (1981).

We sorted all Ichneumoninae to species based on Heinrich (1960a, b, 1961a, b, c, 1962a, b and 1977) and morphospecies using reference material in the Insect Diversity Project's reference collection at the University of Georgia when specimens could not be identified. Details of sorting techniques are contained in Wayman (1994). We deposited specimens in the Discover Life reference collection, University of Georgia and at the Natural History Museum at Great Smoky Mountains National Park. Because of sexual dimorphism in the Ichneumoninae, we were not always able to associate males and females in all genera. Therefore, within those dimorphic genera, we included in our analysis only the specimens of the sex that contained the most morphospecies.

Burn treatment

The primary objective for a prescribed burn at Lynn Hollow was to use fire to enhance the habitat for *P. borealis* colonization. The burn opened both the overstory and the understory creating plant community structure favorable for the Red Cockaded Woodpecker and, as an added benefit, reduced fuel build up that threatened the nearby Top-O-World community.

National Park Service (NPS) personnel ignited the burn site at Lynn Hollow on 9 June 1999. The fire continued to burn through 11 June 1999. On 9 June the moisture content of fuels in the burn plot ranged from 12.3 - 200%, with Hairy Blue Berry, *Vaccinium hirsutum* the wettest and fine fuel material the driest. Flame height ranged from

2-3 feet during the burn with fire intensity calculated at approximately 1700 Btu/ft/sec. Fuel model 9 was used (Anderson, 1982). The thick duff layer was reduced from the fire. Small understory plants were largely killed during burn. Lower branches of trees dropped leaves after the burn, but few canopy trees died as a result of the fire.

Statistical Analyses

We used Coleman Richness Expectation Curves (Coleman 1981, Coleman et al. 1982) with 95% confidence intervals using the EstimateS <http://viceroy.eeb.uconn.edu/Estimates> statistical package version five (Colwell 1997) set at 100 randomizations to compare parasitoid species richness between plots. These curves provide a method to evaluate sample heterogeneity by plotting the expected richness for randomized subsamples (Colwell and Coddington 1994). Sample sizes differ on figures because EstimateS only included samples that contained at least one Campopleginae or one Ichneumoninae specimen. We present scatter plots to examine the similarities in species composition between burn and control plots.

Results and Discussion

Insect Relative Abundance

We counted 13,613 Coleoptera, 912 Orthoptera, 3,167 Symphyta, 41,047 Ichneumonoidea, 9,505 Alate Formicidae, and 2,292 Apterous Formicidae from selected samples in the burn and control plots between 1997 - 2001. Figures 4.1 - 4.6 show relative abundance by trap of Orthoptera, Coleoptera, alate Formicidae, apterous Formicidae, Symphyta and Ichneumonoidea in burn and control plots before and after fire respectively. We make a distinction between relative abundance and total abundance because Malaise traps collect only adult stages of holometabolus insects. Thus, we are only able to compare the relative abundance in trap catches between plots. Orthoptera relative abundance (Figure

4.1) increases in burn plots in years following the fire as seen in previous studies (Reed 1997, Galley and Flowers 1998). Increased plant quality from nutrient pulses in the soil may account for increased Orthopteran relative abundance after the fire. Coleoptera (Figure 4.2), alate Formicidae (Figure 4.3) and apterous Formicidae (Figure 4.4), abundance, for the most part, goes down in years following the fire. However, there appears to be some differences in trapping efficiencies or between plot differences, with high between trap variance.

Figures 4.5 and 4.6 show Symphyta and Ichneumonoidea relative abundances respectively. Immediately following the fire, relative abundance is lower in the burn plots for both the Symphyta and the Ichneumonoidea. This is not surprising for the Symphyta, which are phytophagous organisms and usually show peak flight activity in early spring as new vegetation emerges. Thus, the decline may not only result from the fire. Flight activity of the parasitoids superfamily Ichneumonoidea declines after the prescribed fire as shown in Figure 4.6. The decrease in parasitoid activity in the burn plots may be because they are killed as they are attracted to the fire's heat or smoke (DeBano et al. 1998). DeBano et al. (1998) suggested that the indirect effects of post fire plant quality may benefit herbivores. We see, in the spring following the fire, that Symphyta relative abundance increased in both burn and control plots. Thus, we cannot attribute these changes to a post fire nutrient pulse, because the increase appears in both burn and control plots. There is a similar increase in one of the burn traps for Ichneumonoidea abundance two years following the fire. However, because the increase in relative abundance occurred in only one of the burn traps, we cannot attribute this peak to the fire. This peak in parasitoid flight activity may be on a time delay in response to increased herbivore relative abundance in the previous year.

Species Richness

We compare our focal groups, two subfamilies, before and after fire. We sorted 6,092 parasitoids to 230 species: 129 Campopleginae; 101 Ichneumoninae. Table 4.1 presents the observed Campopleginae and Ichneumoninae species richness between burn and control plots before and after fire and shows the between trap variance in sampling plots. We observed subfamily differences in the burn plots after the fire. Campoplegine richness declined in the burn plots after the burn when compared to the control. Ichneumoninae species richness in control and burn plots are similar after the fire. Yet ichneumonine relative abundance in the control plots is much higher when compared to the burn. We did not find a higher proportion of pupal parasitoids (Ichneumoninae) in burned sites when compared to control sites (Table 4.1). This is in contrast to previous observations by Heinrich (1977), Gauld (1987) and Shaprio and Pickering (2000) where desiccation inhibited larval parasitoid flight activity. Thus, desiccation may not be a limiting factor in the larval (Campopleginae) parasitoids we observed, or the ground fire was not large enough to bring about significant changes in species richness.

To further examine whether the differences we observed between the plots are significant, Figure 4.7 presents the Coleman Richness Expectation curves (Coleman 1981, Coleman et al. 1982) with 95% confidence intervals for Campopleginae collected in burn and control plots before and after the burn. Campopleginae species richness declined after a burn as the observed data show (Table 4.1). Control plots have higher species richness compared to the burn plots after the burn. This is in contrast to years prior to the burn, when burn plots were higher or the same as control plots. Thus, it appears that Campopleginae parasitoids are more susceptible to the fire disturbance, in the first year following the fire.

Species richness appears to stay the same for Ichneumoninae after a burn (Table 4.1). Figure 4.8 shows the Ichneumoninae Coleman curves for the burn and control plots

as in Figure 4.7. In the year post-burn, species richness is higher in the burn plots than in the control plots, yet this trend is the same each year prior to the burn. Thus, it appears that Ichneumoninae parasitoids are little affected by the burn.

Species Composition

Figure 4.9 compares Campopleginae abundances between burn (x-axis) and control (y-axis) plots in the year following a prescribed burn. Each of the 77 points represents a species and is plotted on a log scale. The line represents the expected distribution in the burn and control plots after the prescribed burn based on the proportion of individuals collected in control and burn plots. Therefore, if all species occurred in the burn plots they would fall on the x-axis, and if all species occurred in the control plots they would fall on the y-axis. There appears to be a high degree of similarity between the burn and control sites evidenced by the cluster about the line predicting similar composition ($R^2=0.8702$).

Figure 4.10 compares Ichneumoninae abundances between burn (x-axis) and control (y-axis) plots in the year following a prescribed burn as in Figure 4.9. Again, there is a high degree of similarity between the burn and control plots after the fire treatment with the species clustered about the line predicting similar composition ($R^2=0.9244$). Thus, Ichneumoninae species composition appears similar to the community that did not experience the burn.

Overall relative abundance declined after the prescribed burn, yet the species composition remained, for the most part, unchanged. Thus, the predictions of successional differences are not supported here. A brief caveat is due in this regard. The scale and intensity of the burn must be taken into consideration when drawing conclusions about community organization. The prescribed burn was approximately 24 hectares with a flame height that ranged from 2-3 feet and fire intensity calculated at approximately 1700

Btu/ft/sec. Lamotte (1975) found that strong flying insects were the quickest to recover after a fire. Thus, given the dispersal abilities of ichneumonid parasitoids, they could most likely recolonize the burn site from the surrounding landscape rather quickly. Had a larger portion of the forest been burned then the effects on the community may have been greater.

Conclusions

We document changes in insect relative abundance and community composition following prescribed fire. Specifically,

- Orthoptera relative abundance increases after a fire;
- Formicidae, Coleoptera, Symphyta, and Ichneumonoidea relative abundance decreases immediately after a fire;
- Larval Campopleginae parasitoids appear more susceptible to fire disturbance than their pupal Ichneumoninae counterparts;
- Ichneumoninae parasitoids seem little affected by the fire and appear to recolonize well after disturbance;
- Relative abundance of parasitoids declines in the year following a fire but their community composition stays the same.

While these results appear to indicate the resiliency of the insect communities after the prescribed fire, it is unclear what the effects of subsequent prescribed fires might be. The evidence suggests that changes in fire regime could alter insect species richness and composition. Swengel and Swengel (1997) found that butterflies feeding on herbs responded better to a single wildfire than to rotational burning. Thus, prescribed fire may alter insect communities in subsequent years. We need to examine how insect communities respond in subsequent years and whether prescribed fire has long-term effects on these communities. Furthermore, studies are needed to better understand how changes in fire policy impact insect communities.

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Table 4.1. Campopleginae and Ichneumoninae species (and individuals) collected in Great Smoky Mountains National Park, Lynn Hollow.

Site	Year	Trap 1	Trap 2	Total	Trap 1	Trap 2	Total
Campopleginae				Ichneumoninae			
Preburn	1997-98	36 (191)	38 (250)	50 (441)	45 (372)	48 (716)	62 (1088)
Preburn	1998-99	39 (88)	41 (132)	60 (220)	43 (280)	44 (268)	61 (548)
	1997-99	56 (279)	59 (382)	79 (661)	57 (652)	62 (984)	78 (1636)
Postburn	1999-00	41 (175)	31 (165)	52 (340)	41 (343)	23 (81)	47 (424)
Control	1997-98	32 (115)	49 (292)	57 (407)	44 (479)	39 (416)	57 (895)
Control	1998-99	42 (108)	34 (117)	54 (225)	38 (214)	36 (206)	48 (420)
	1997-99	52 (223)	61 (409)	74 (632)	58 (693)	50 (622)	68 (1315)
Control	1999-00	48 (172)	42 (206)	63 (378)	35 (396)	34 (310)	45 (706)

Figure 4.1. Relative abundance of Orthoptera by trap in burn and control plots before and after fire. Selected samples are presented between July 1998 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots.

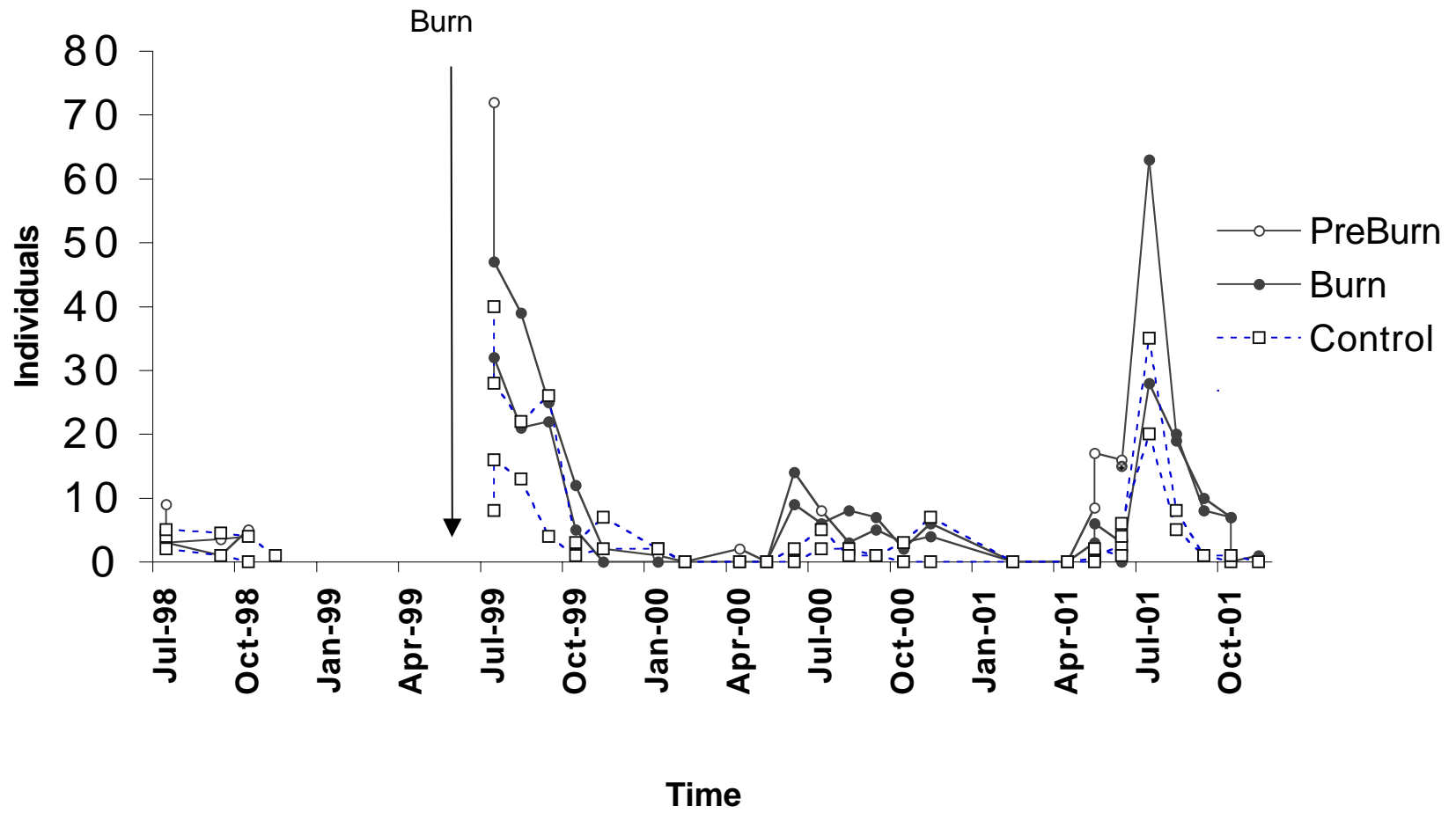


Figure 4.2. Relative abundance of Coleoptera by trap in burn and control plots before and after fire. Selected samples are presented between July 1998 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots.

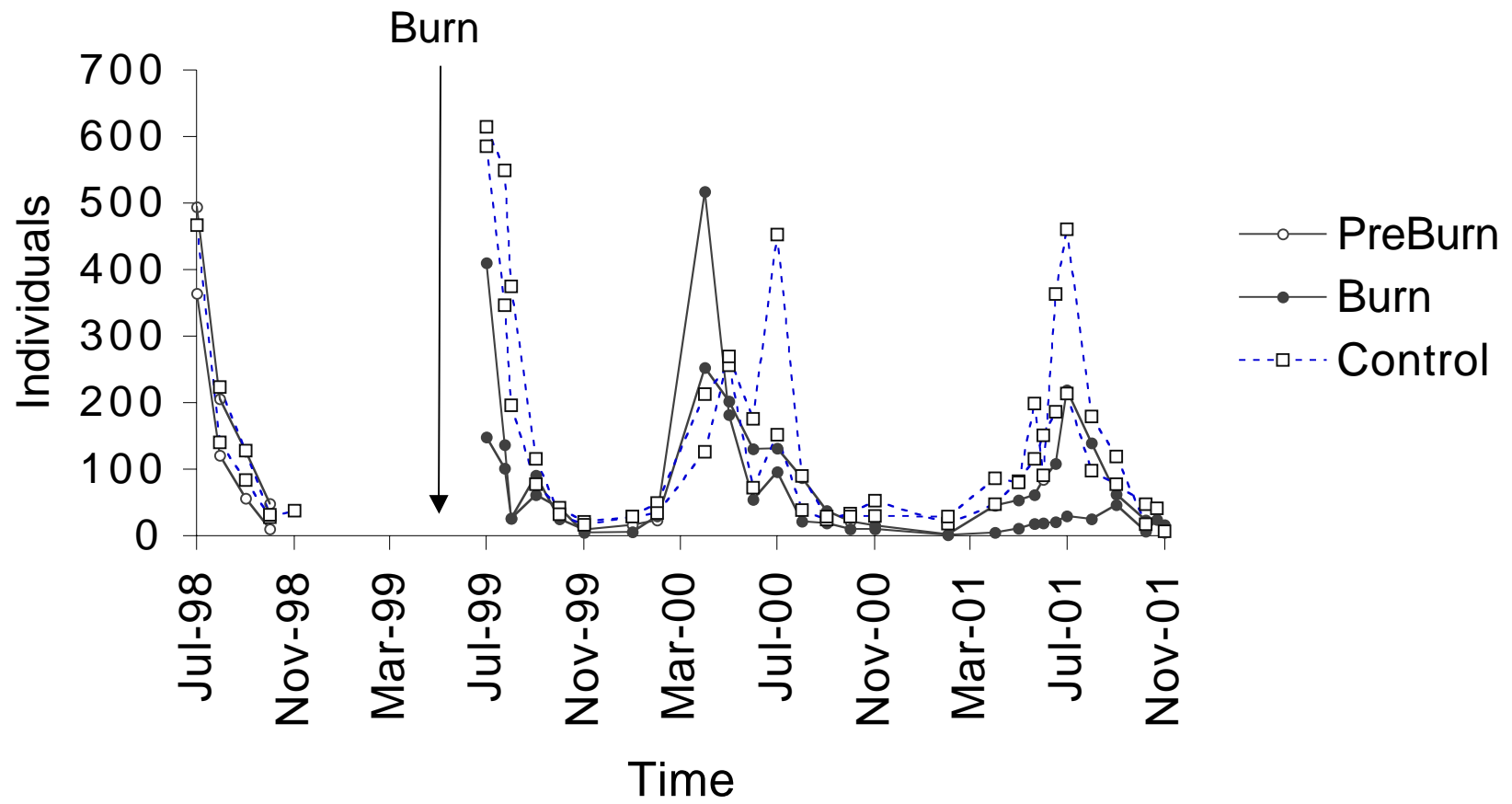


Figure 4.3. Relative abundance of alate Formicidae by trap in burn and control plots before and after fire. Selected samples are presented between July 1998 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots.

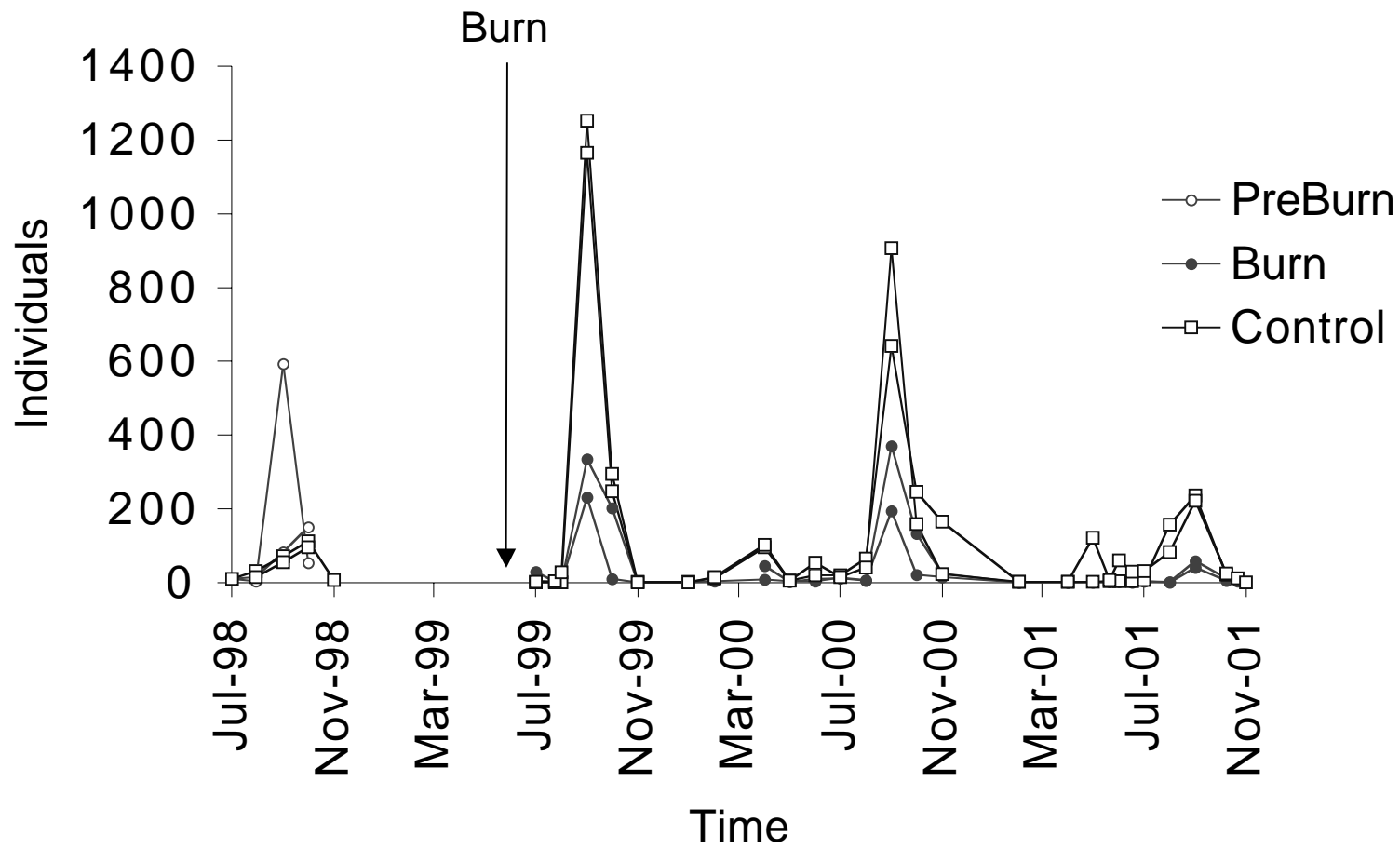


Figure 4.4. Relative abundance of apterous Formicidae by trap in burn and control plots before and after fire. Selected samples are presented between July 1998 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots.

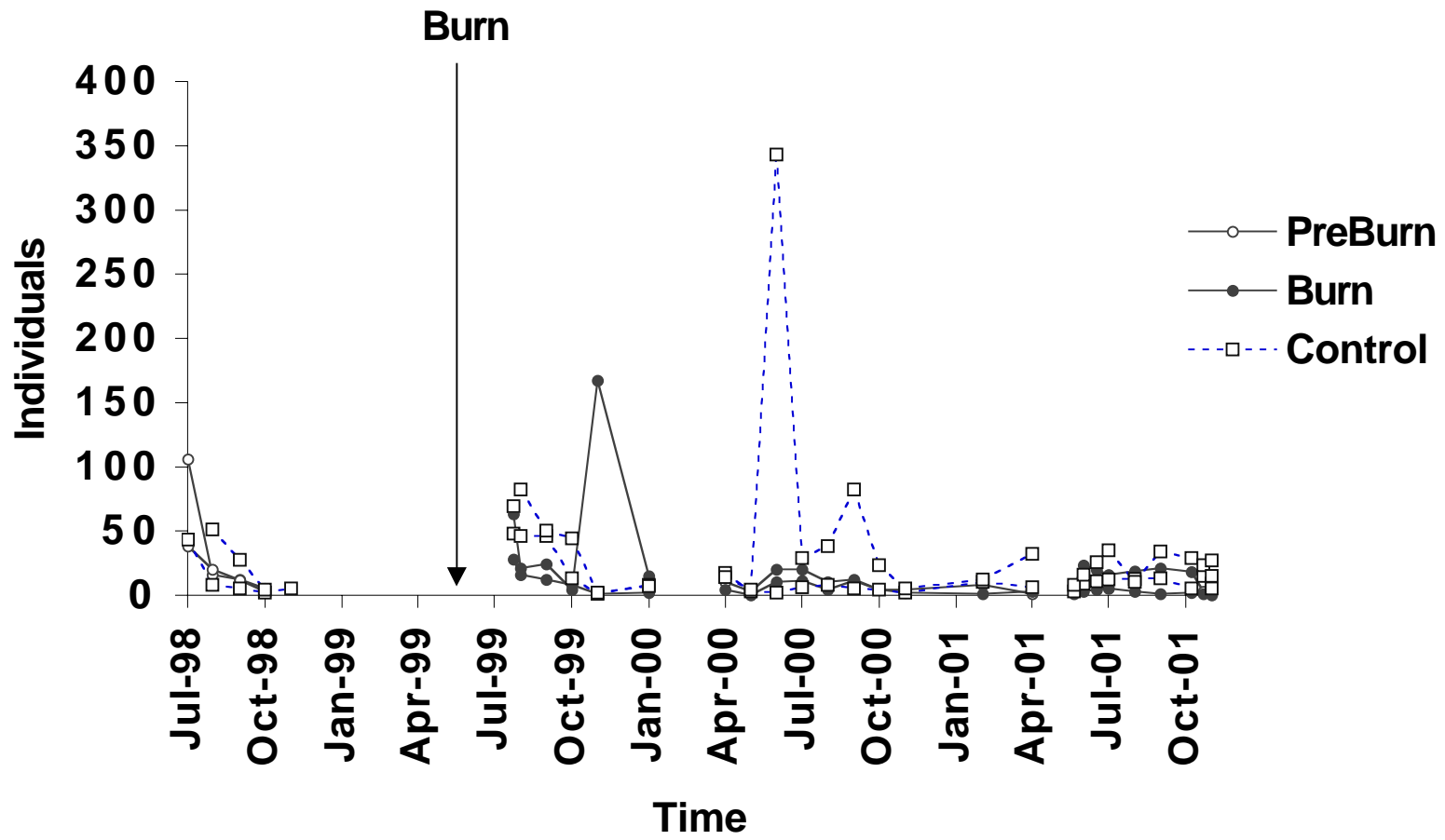


Figure 4.5. Relative abundance of Symphyta by trap in burn and control plots before and after fire. Selected samples are presented between April 1997 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots. Symphyta relative abundance by trap

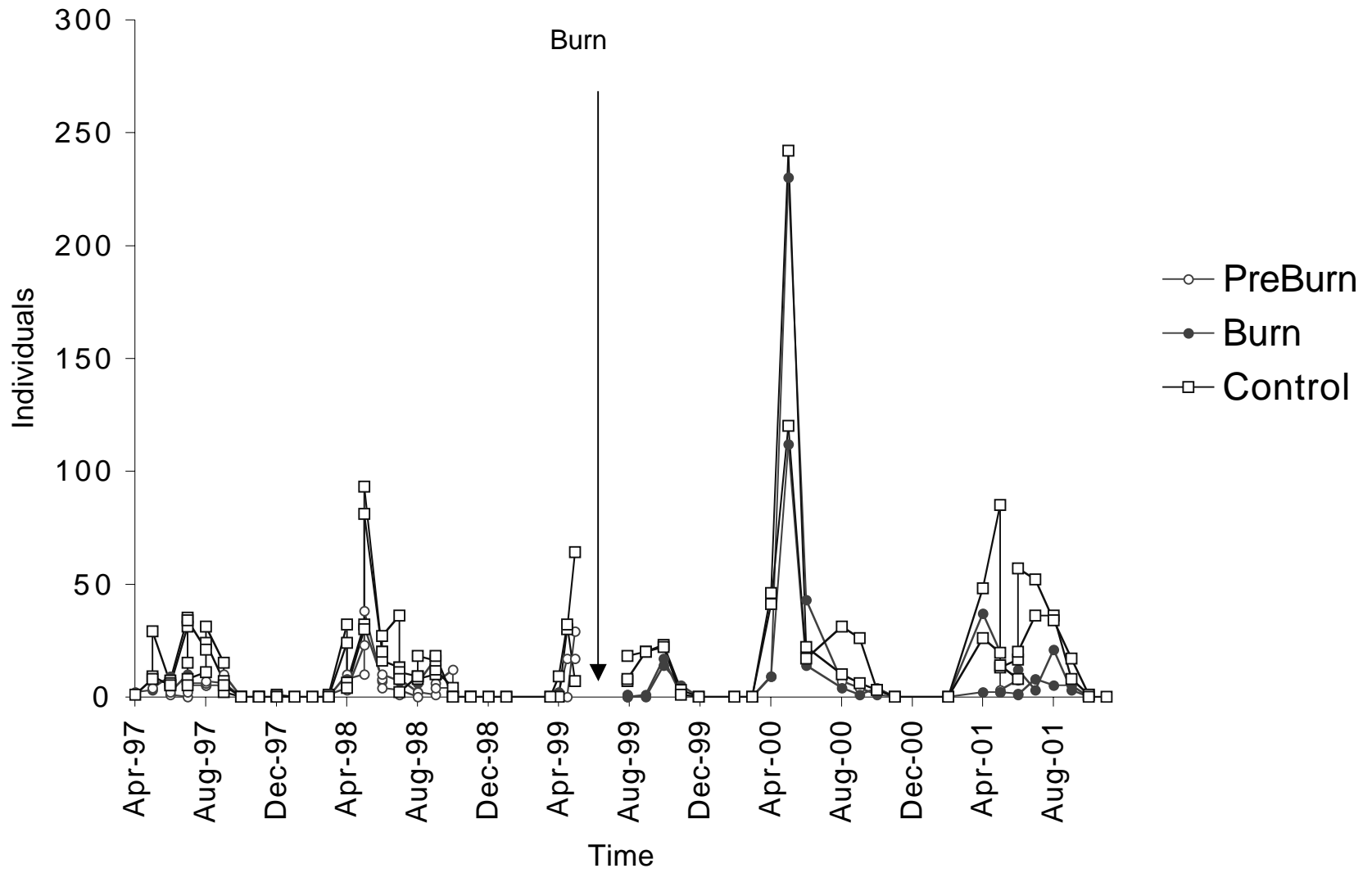


Figure 4.6. Relative abundance of Ichneumonoidea by trap in burn and control plots before and after fire. Selected samples are presented between April 1997 and November 2001. Open circles represent two traps in burn plots prior to the burn on 9, June 1999. Closed circles represent two traps in burn plots after the burn. Open squares represent two traps in control plots.

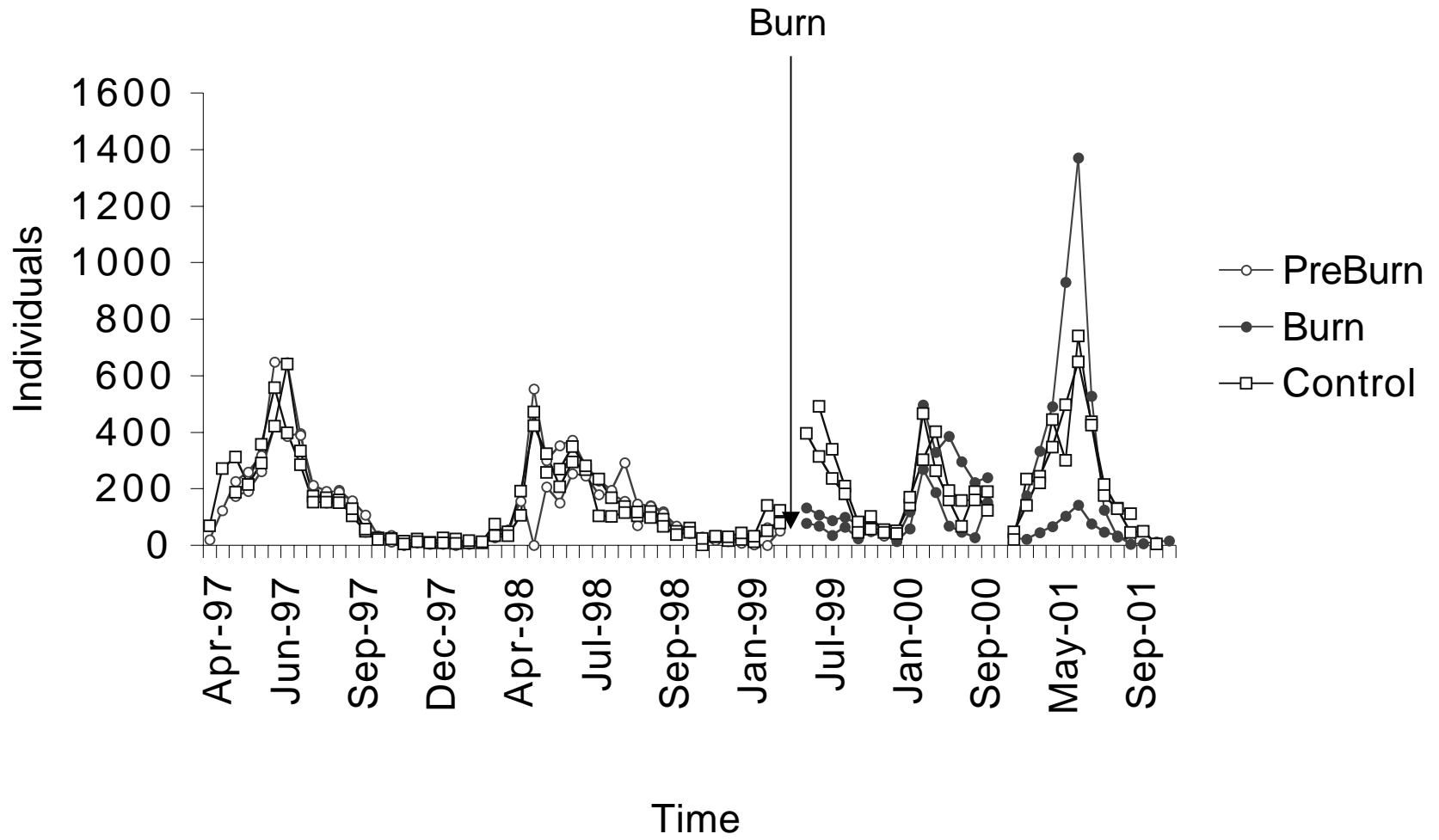


Figure 4.7. Comparison of Coleman richness expectation curves with 95% confidence intervals of Campopleginae before and after a prescribed burn at burn and control plots in Lynn Hollow, Great Smoky Mountains National Park, Tennessee, in 1997-98, 1998-99 and 1999-00. Sampling effort refers to samples that contain at least one campoplegine.

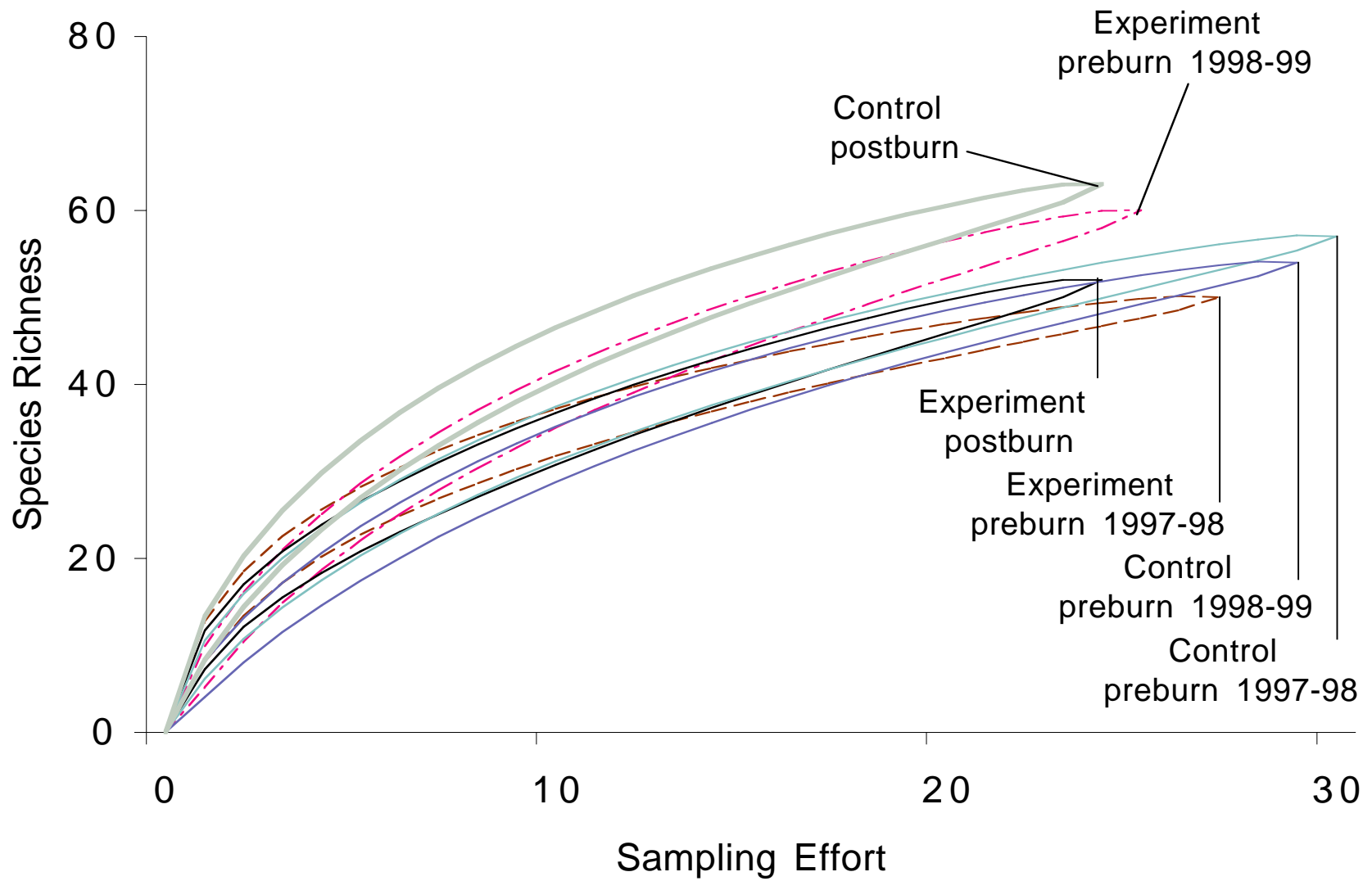


Figure 4.8. Comparison of Coleman richness expectation curves with 95% confidence intervals of Ichneumoninae before and after a prescribed burn at burn and control plots in Lynn Hollow, Great Smoky Mountains National Park, Tennessee, in 1997-98, 1998-99 and 1999-00. Sampling effort refers to samples that contain at least one ichneumonine.

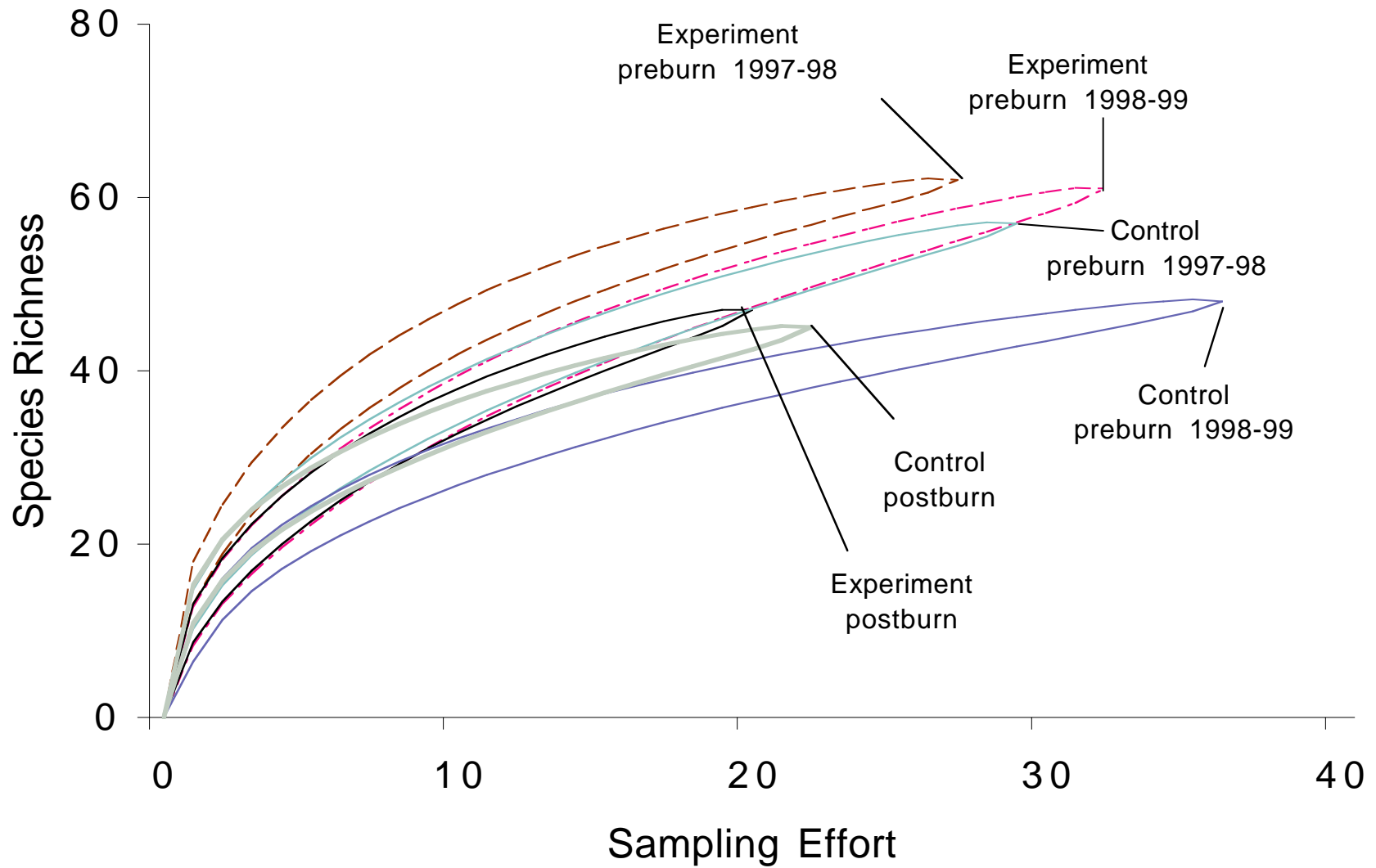


Figure 4.9. Campopleginae relative species abundance ($N+1$), in burn and control plots in a xeric ridge forest in Great Smoky Mountains National Park in 1997-98. The line indicates the expected distribution if the species composition is the same in both habitats.

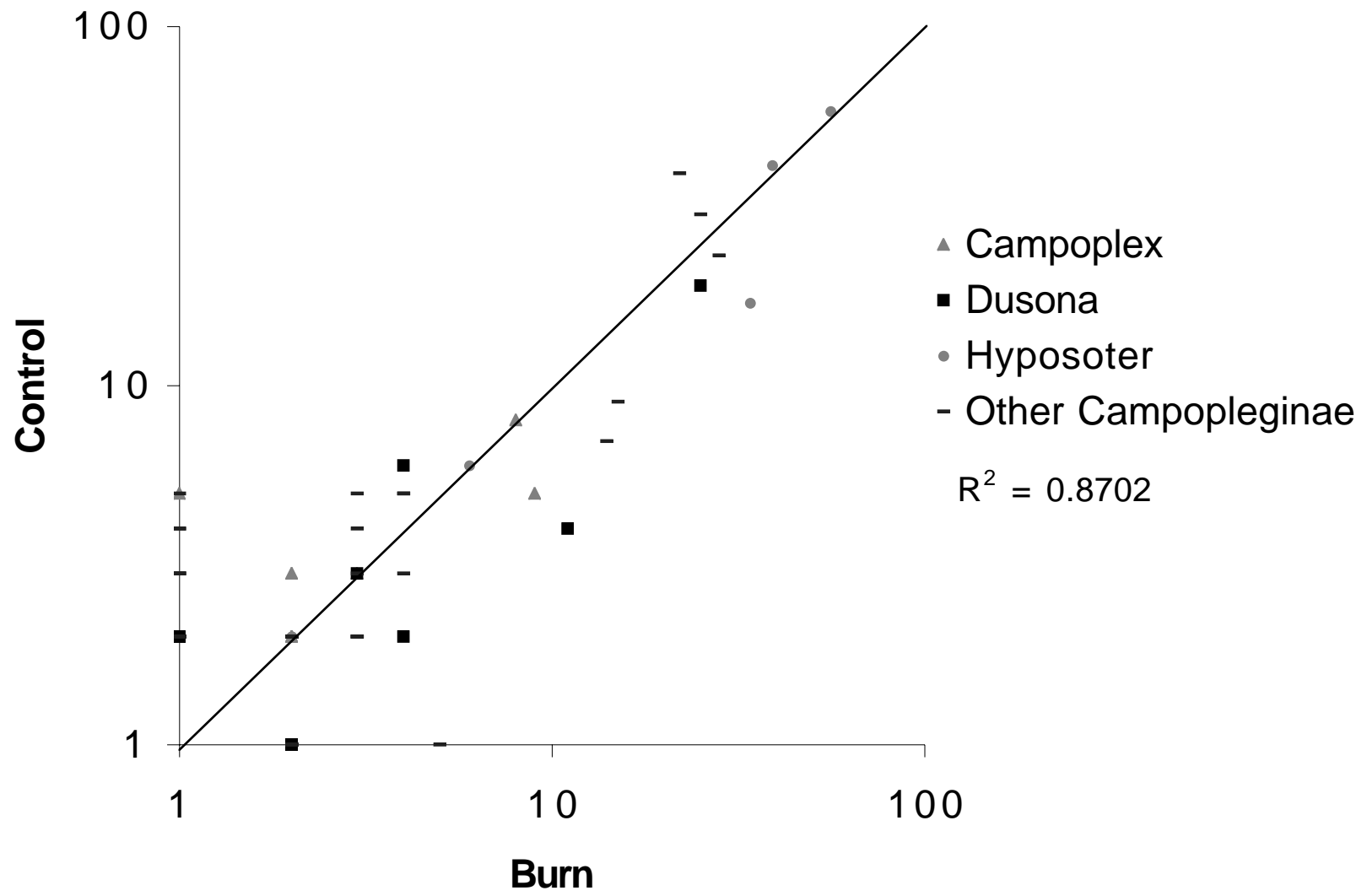
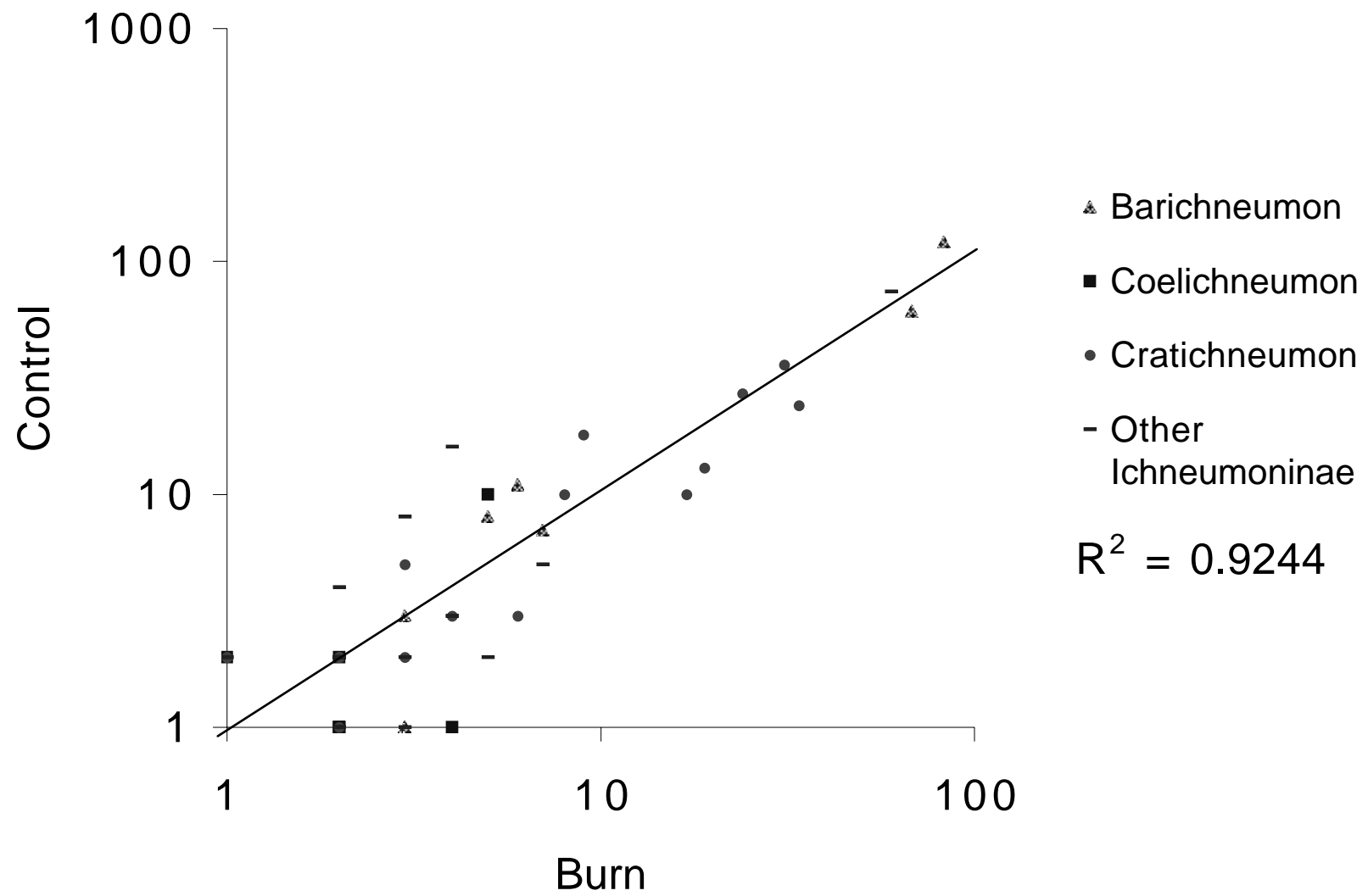


Figure 4.10. Ichneumoninae relative species abundance ($N+1$), in burn and control plots in a xeric ridge forest in Great Smoky Mountains National Park in 1997-98. The line indicates the expected distribution if the species composition is the same in both habitats.



CHAPTER 5

TURNOVER OF PARASITIC WASP SPECIES IN EASTERN NORTH AMERICA AND IMPLICATIONS FOR BIODIVERSITY INVENTORY DESIGN¹

¹ Skillen, E.L. and J. Pickering. 2002. To be submitted to *Ecological Entomology*

Abstract

This study compares parasitoid communities across sites in Eastern North America. The objectives were to examine 1) the turnover of species as a function of distance (beta diversity), 2) whether beta diversity differs for generalist versus specialist parasitoids, 3) or for rare versus common species, and 4) how temporal and spatial differences in biodiversity affect the efficiencies of inventory studies. We analyzed over 90 trap years of data including 614 species (25,109 individuals) of parasitoids from 7 localities in Eastern North America between 1991 and 2000. We focus on 2 subfamilies with different life-history strategies and report on 165 Campopleginae species (3,273 individuals) and 142 Ichneumoninae species (6,443 individuals) in the current study. We consider data from Wayman (1994), Gaasch (1996) and Skillen et al. (2000) including 189 Campopleginae species (6,432 individuals), and 239 Ichneumoninae species (8,961 individuals). We constructed a randomization test using Monte Carlo methods to account for differences in sampling effort. We randomized sampling efforts 1,000 times and present 95% confidence intervals over the 1,000 randomizations to compare the relative effects of distance, habitat and rarity on species richness over large and small spatial scales. While beta diversity is expected to increase with distance, we found two exceptions to this pattern. We report a greater percentage of Maryland Campopleginae species in Georgia than in Tennessee and a greater percentage of Florida Campopleginae species in Maryland than in Tennessee. The drops in community similarity from Tennessee to Maryland and Georgia to Tennessee could not be explained by differences in habitat. In general, the common species represent a higher percentage of distant fauna than rare species as expected. The results here have implications for better inventory design. We analyzed samples of a largely unknown fauna to quantify the benefits of structured sampling methods in space and time. Structured sampling methods are generally superior to sampling at one location or at one time. At regional scales a 9 to 20 percent more species were captured when samples were taken

randomly from multiple sites compared to sampling at the most species rich sites.

Undisturbed habitats contain more species of specialized groups like the Campopleginae.

Introduction

How many insect species exist today? Our inability to come up with a number within several orders of magnitude illustrates the difficulty in answering questions of biodiversity. Terry Erwin's (1982) paper predicting that there are as many as 30 million insect species began the debate on estimating global insect species richness. Many say his estimates are too high. Hammond (1992) estimated 8 million insect species globally and argued that Erwin's estimates could not be substantiated without knowing which organisms were tourists and which were residents. He added that central to estimating insect species richness is understanding how richness increases from fine to coarse scales. Thus, local surveys tell us little about global biodiversity if we do not understand the turnover of species in space and time. Given the magnitude of the task, efforts to document diversity have led to the proliferation of methods to estimate numbers of species (Burnham and Overton, 1978, 1979, Chao 1984, Lamas et al. 1991, Colwell 1997, Colwell and Coddington 1994, Chazdon et al. 1998). However, in highly diverse, mobile groups of organisms the curves remain steep (Skillen et al. 2000). Furthermore, we don't know how beta diversity, or the turnover of species at different spatial and temporal scales, affects these estimates.

Russell (1995) argued that turnover is an "underappreciated and under utilized property of all biological systems." For example, our ability to estimate insect herbivore species numbers on large spatial scales is confounded by our lack of knowledge on host specificity. Furthermore, there has been a resurgence in the ecological literature about the role regional processes play in local patterns of species richness (Ricklefs 1987, Cornell and Lawton 1992, Cornell 1993, Caley and Schluter 1997, Huston 1999, Hubbell 2001). Novonty et al. (2002) contend that previous estimates of global species richness are too high because researchers overestimated the degree of endemnicity of the insect herbivores. They found that closely related plants have a higher degree of overlap of insect herbivores than previously thought and suspect that global insect species richness may be only 4.6

million. Similarly, Odegaard et al. (2000) found only 7% to 10% host specificity of phytophagous beetles occurred in a tropical dry forest in Panama. These studies highlight the importance of processes acting at larger spatial and temporal scales, such as evolutionary relationships of plants and herbivores, in governing species diversity patterns (Caley and Schluter 1997).

There are many factors that govern parasitoid community structure including direct effects of host plants (Askew and Shaw 1974, Vinson 1976), plant apparency (Southwood 1977, 1988, Price 1991), host habitat (Shaw and Askew 1979), host immobility or refuges (Hochberg and Hawkins 1992, Hawkins 1994) and host taxonomy (Askew and Shaw 1974, Sime and Brower 1998). Parasitoids are strongly tied to their hosts' food plants (Strong et al. 1984, Hawkins 1994), thus changes in plant communities can affect parasitoid community composition. Furthermore, insect parasitoids are often locally rare (Owen et al. 1981, LaSalle and Gauld 1993). The turnover of rare species over regional scales has been shown to be different than locally abundant species. Current theory suggests that distance decay in similarity is steeper for rare species than for common, locally abundant species (Hubbell 2001). For example, Nekola and White (1999) found no change in similarity with distance for rare species in white spruce stands (data from LeRoi 1967). In other words, because rare species are locally distributed, they are highly dissimilar even at small spatial scales. Hence there was no decay in similarity with distance. Yet, it is not known whether rare and common parasitoid species have similar distance decay patterns.

There are difficulties in documenting species-rich communities, especially in organisms with many rare species. Few studies are able to apply standard sampling techniques across regional scales. Because we have regional data we can compare between sites and examine diversity at large and small spatial scales. We are also able to estimate how well local studies predict regional richness. Currently, there are efforts in Great Smoky Mountains National Park (GSMNP) to conduct a comprehensive inventory of all life within

its boundaries (Kaiser 1999, Sharkey 2001). The questions raised here are crucial to design a comprehensive inventory that can help address the issues of beta diversity in GSMNP and further understanding of regional insect diversity patterns. Here we address the following questions:

- What factors affect the turnover of species as a function of distance (beta diversity)?
- Is beta diversity the same for generalist versus specialist parasitoids?
- Does beta diversity differ for rare versus common species?
- How do temporal and spatial differences in biodiversity affect the efficiencies of inventory studies?

Methods

Study Organisms

Our focal organisms are parasitoid wasps in the family Ichneumonidae (Hymenoptera) with an estimated 8,000 Nearctic ichneumonid species. Only an estimated 35% Nearctic Ichneumonidae have been described. The two principal life-history strategies can generally be categorized as endo- (internal) or ecto- (external) parasitoids or into idiobionts or koinobionts. Idiobionts are generally ectoparasitoids of pupae or pre-pupae. Koinobionts are often endoparasitoids of larvae (Gauld 1988).

Here we examine two subfamilies, Campopleginae and Ichneumoninae. Ichneumoninae attack only Lepidoptera (Gauld 1988). The majority are idiobiont (Askew and Shaw 1986) pupal endoparasitoids. A few are koinobiont endoparasitoids that attack final-instar larvae (Wahl 1993). The Campopleginae are koinobiont endoparasitoids of Lepidoptera or Symphyta larvae (Gauld 1988).

Sites and Sampling

We compared Campopleginae and Ichneumoninae communities in GSMNP Tennessee, with communities in Ontario, Maryland, Georgia and Florida (Wayman 1994 Gaasch 1996, Skillen et al. 2000). Table 5.1 lists site data. We continuously sampled six sites in GSMNP with a study design including two habitat types, mesic coves and xeric ridges. Field sites in Georgia included a recently clear-cut site and an alfalfa, *Medicago sativa* L., field. Cove sites in Tennessee included old and second growth (> 70 years) mesic cove forest and old-growth xeric ridge before and after a burn. We sampled using fine mesh (.33 mm) Townes-style Malaise traps (Townes 1972). We faced the trap heads south to maximize the time that light would shine on the collecting head. We changed the traps bi-weekly or monthly in winter months and preserved specimens in 70% ethanol.

Here we analyze samples from GSMNP between 8 April, 1997 - 4 July, 2000. We include here samples collected after a prescribed burn at Lynn Hollow West on 9 June, 1999. We compare beta diversity in GSMNP with sites from 45°42'N to 29°44'N (Wayman 1994, Gaasch 1996, Skillen et al. 2000). Sites and collecting periods include: Shaw Woods, Ontario, 6 May - 22 October 1992 and 6 May - 21 October 1993; Patuxent Wildlife Research Center, Maryland, 6 April - 9 November 1992 and 12 April - 25 October 1993. The Shaw Woods and Patuxent sites are primarily beech hardwood forests (*Fagus grandifolia*). Specimens from Sam's Farm, University of Georgia were collected between 9 September 1991 - 9 July 1993. This site contained an alfalfa *Medicago sativa* L field and second growth mixed pine (*Pinus taeda*) hardwood forest. The authors and Gaasch (1996) sampled the Hitchiti Experimental Forest, Georgia, between 23 March - 21 December 1993. This site contained variable age stands ranging from old-growth mixed pine hardwood forests to 3-year-old loblolly (*Pinus taeda*) plantation. Samples in Florida were collected at Woodyard Hammock, Tall Timbers Research Station, Florida, 30 March - 14 December - 28 March 1994, at San Felasco Hammock State Preserve, Florida, 15 March - 18 December

1993, and at American Entomological Institute (AEI), Florida, 14 March 1992 - 20 November 1992. All Florida sites were beech-magnolia (*Magnolia grandiflora*) hammocks. San Felasco and Tall timbers were both old-growth sites; the AEI had been previously logged. See Skillen et al. (2000), Wayman (1994) and Gaasch (1996) for references on habitats and flora at these sites.

To examine how best to maximize sampling effort in designing sampling methods, we created a structured sampling regime by dividing sampling effort among sites at multiple spatial and temporal scales. We used the same Monte Carlo randomization test to account for differences in sampling effort. We then compared the structured method to sampling at any one place or time. For comparisons of structured sampling we set simulations to 1,000 randomizations.

Specimen Identification

All ichneumonine and campoplegine specimens were sorted to species based on Heinrich (1960a, b, 1961a, b, c, 1962a, b and 1977) and Walley (1940, 1947) respectively. Specimens not found in the literature were sorted to morphospecies using reference material at the University of Georgia. Because of sexual dimorphism in the Ichneumoninae, association of males and females was not possible in all genera. Therefore, within those dimorphic genera, we included in our analysis only the specimens of the sex that contained the most morphospecies. We deposited specimens at the University of Georgia and GSMNP's Museum of Natural History. See Wayman (1994) for details of sorting techniques. All determinations can be accessed by unique specimen barcodes via the Discover Life web site: <<http://www.discoverlife.org>>.

Statistical Analyses

Because species richness generally increases with sampling effort, we constructed a randomization test using Monte Carlo methods to account for differences in sampling effort. We used individuals as sampling units. In each analysis, we chose the maximum sample size to allow comparisons at each of the sites. Samples of North American species richness were drawn from a pool of Campopleginae and Ichneumoninae collected by the authors, Wayman (1994), and Gaasch (1996), in Eastern North America between 1991 and 2000. We randomized sampling efforts 1,000 times and present 95% confidence intervals over the 1,000 randomizations in the tables and figures to compare the relative effects of distance, habitat and rarity on species richness over large and small spatial scales. Because sample size was so small, we only included the Ontario specimens in the pool of North American specimens and not as a separate sampling site.

Results and Discussion

We analyzed over 90 trap years of data including 614 species (25,109 individuals) of parasitoids from 7 localities in Eastern North America between 1991 and 2000. We focus on 2 subfamilies with different life-history strategies and report on 165 Campopleginae species (3,273 individuals) and 142 Ichneumoninae species (6,443 individuals) in the current study. We consider data from Wayman (1994), Gaasch (1996) and Skillen et al. (2000) including 189 Campopleginae species (6,432 individuals), and 239 Ichneumoninae species (8,961 individuals). However, we have yet to saturate statistical estimates of species richness (Skillen et al. 2000) and are unable to predict total richness at any one sampling site (Lockard 1995). Hubbell (2001) argues that these models cannot predict total richness at a given site because “they will always underestimate the number of rare species in the community.” It is well understood that the richness of local assemblages are strongly influenced by regional richness (Ricklefs and Schluter 1993, Gaston 2000).

However, our estimates of Campopleginae and Ichneumoninae richness in Eastern North America are confounded by our limited understanding of turnover at larger spatial scales for these groups. Here we examine the relative importance of distance, habitat and rarity in the turnover of parasitoid species with different life-history strategies and the best methods for documenting their diversity in GSMNP.

Distance

The negative relationship between distance and similarity, or distance decay as it is referred to in the geographical literature (Tobler 1970), is well documented in ecological contexts (Whittaker 1975, Cody 1985, Nekola and White 1999). Our analysis of species turnover in Eastern North America shows that beta diversity increases with distance as expected, in most cases. However, we found subfamily differences in expected patterns. Because inventory work is generally done on local scales, we were interested in how well sampling a local site provided predictions for other sites in the region. We expected the percent of species in common to decline with distance from the sampling site. Table 5.2 shows the percent species richness of 4 target community sites predicted by the same 4 sites sampled in Monte Carlo simulations. We randomly sampled 500 specimens from 4 sites: Maryland, Tennessee, Georgia and Florida 1,000 times and present the percent in common between the target community and the sites sampled as 95% confidence intervals from the simulations. The total individuals sampled from each site are presented in Table 5.1 for comparison of sample sizes. In two cases, for the campoplegines (indicated by * in Table 5.2), there is a reversal in the percent in common that would have been expected by monotonic distance decay in similarity. It appears that in our sample, Georgia has more species in common with Maryland than it does with Tennessee, and Maryland has more species in common with Florida than it does with Tennessee. This trend is statistically

significant with no overlap of the 95% confidence intervals. This may be a result of differences in sampling years between sites. The ichneumonines show a straight-forward decline in percent species in common away from each site sample for each target community as predicted by distance decay.

Habitat

It is unknown how habitat heterogeneity influences the relationships between local and regional diversity (Caley and Schluter 1997). We suspected that the reversals we found in distance decay for campoplegines may have resulted from differences in habitat sampled along the latitudinal gradient. However, by dividing Georgia and Tennessee into two habitat types: forest and field (Georgia) and cove and ridge (Tennessee) we found no significant differences between the habitats in percent overlap for either Maryland or Florida. Table 5.3 shows the percent of species in common at 6 target communities and 4 habitat types (sites sampled) in Georgia and Tennessee. We randomly sampled 500 specimens from Georgia forest and field habitats and Tennessee cove and ridge habitats 1,000 times to determine the percent of species in common with sites along the gradient. We present the percent of species in common of target communities at sampling sites as 95% confidence intervals from the 1,000 simulations (Table 5.3). In the case of the Maryland Campopleginae reversal in distance decay, the results do not show clear habitat differences. There were no statistical differences ($p < 0.05$) in percent overlap of Maryland richness between the cove and ridge sample sites or between the field and forest sample sites. In the case of the Florida campopleginae reversal in distance decay, there were no statistical differences ($p < 0.05$) in predicting Florida richness between the cove and the ridge sample sites or between the field and forest sample sites. Thus, the drop in community similarity from Tennessee to Maryland cannot be explained by differences in habitat between the cove and the ridge sites alone.

This analysis also shows some broad patterns of distribution between habitats for the two subfamilies. By randomly sampling Georgia forest and field habitats, we found statistical differences ($p < 0.05$) between the two habitats in overlap of percent species richness between Tennessee cove and ridge habitats and Georgia forest and field habitats (Table 5.3). We found no habitat differences in predicting richness at other sites when we sampled Tennessee cove and ridge habitats separately. Thus, pupal parasitoids, like the ichneumoninae may be more divided on gradients of succession from field to forest within terrestrial communities, rather than forest type such as coves and ridges.

Rare vs. Common Species

Rare species, in local communities, are predicted to be more rare than expected from random sampling of the metacommunity (Hubbell 2001). Further, it is expected that species with larger geographic ranges are usually more abundant locally than species with more restricted ranges (Hanski 1982, Hubbell 2001). Perhaps the reversals in distance decay seen in Table 5.2 result from a differences in the distributions of common and rare species sampled in the metacommunity. In general, the common species represent a higher percentage of distant fauna than rare species as expected, in most cases. Table 5.4 shows the percent in common of rare ($n=1+2$) and common ($n >2$) species between Maryland, Tennessee, Georgia and Florida. In all but one pair wise comparison in Table 5.4, the percent of common species shared exceeds the percent of rare species shared. We found no evidence to suggest that differences in common and rare species distributions could account for the Maryland and Florida reversals seen in Table 5.2. There was a greater percent overlap in common species than rare species in all cases for the Campopleginae. It is interesting to note that at the extent of species ranges, the differences in overlap between common and rare species are similar. For example, we found that 52% of the rare and 50% of the common ichneumonine species sampled from Maryland occurred in Florida. Thus, it

appears that at some point of range, common species may become more locally rare as in the case of some bird populations (Maurer and Villard 1994, Mehlman 1997). However, it appears that common species are well distributed along the Eastern North American latitudinal gradient.

Altitude and Life-history strategies

The reasons for the reversals in distance decay for the Campopleginae are unclear. Brown (1984) hypothesized that generalists are both widely distributed and locally abundant, while specialists are both restricted in distribution and locally rare. The life-history strategies (Askew and Shaw 1986) of the two groups examined may present different biological obstacles to long-distance dispersal. Larval campopleginae parasitoids may be less able to disperse to new habitats because of limited host ranges (Askew and Shaw 1986) than their pupal ichneumonine counterparts. This limitation on Campopleginae dispersal may be exaggerated by the montane habitat. Elevation changes along the transect may be contributing to the differences we found in distance and habitat. The cove sites are at the highest elevation of all the sites in the study ranging from 950 -1183 meters (Table 5.1). The high altitude regions in the Southern Appalachian Mountains may restrict species ranges more than expected by distance. Thus, the high elevation species are not able to colonize lower elevation sites to either the north or south. For example, Tarmo and Seppo (1999) reared parasitoids from *Epirrita autumnata* (Lepidoptera) larvae feeding on mountain birch in Finland. They found a higher proportion of *Eulophus larvarum* (Eulophidae: Hymenoptera) at higher altitude sites and *Cotesia jucunda* (Braconidae: Hymenoptera) at lower altitude sites. Thus, altitude may be an important factor in considering turnover of Campopleginae in Eastern North America.

Structured Sampling

We have shown the difficulties in documenting the turnover of species over large geographic ranges for species rich groups like the Ichneumonidae. With recent attempts at All Taxa Biological Inventories (ATBI) (Kaiser 1999, Sharkey 2001), what have we learned from our analysis to assist in answering questions of local biodiversity? In particular how can we quantify the benefits of structured sampling within sites and between sites to estimate the benefits of conserving effort for maximizing the number of species discovered? We understand that sampling efforts are costly, and thus quantitative estimates of different sampling regimes will help achieve goals of documenting biodiversity more quickly.

Structured sampling appears to benefit significantly at large spatial scales. Table 5.5 shows the 95% confidence intervals of percent species at target sites collected from effort sites generated from Monte Carlo simulations. In general, structured sampling across sites was beneficial at large spatial scales in capturing a greater percentage of regional fauna. The percent species captured in Eastern North America were significantly higher ($p < 0.05$) for the structured sampling than sampling in either Georgia or Tennessee alone for both subfamilies (Table 5.5). We illustrate these trends for the Campopleginae as an example, Figure 5.1 shows the percent of North American Campopleginae species collected by Tennessee and Georgia alone compared with structured sampling across 4 sites: Maryland, Tennessee, Georgia and Florida with 95% confidence intervals. This figure shows a 9 to 20 percent increase in species captured when samples are taken randomly from multiple sites.

On smaller spatial scales, such as within Great Smoky Mountains National Park, differences in space and time decline with structured sampling regimes. As an example, Figure 5.2 shows the percent of GSMNP Campopleginae species collected in cove and ridge habitats alone compared with structured sampling across cove and ridge habitats with 95% confidence intervals. As with larger spatial scales, the structured sampling method

appears to collect a higher percentage of GSMNP Campopleginae species than sampling in either habitat alone, yet the structured sampling method does not differ significantly from the ridge habitat sampling 1,000 specimens. Structured sampling for the Ichneumoninae was better than sampling either the cove or ridge habitats alone (Table 5.5). This indicates that there may be some differences in subfamily distributions across habitats in the Park. Underlying biological differences between pupal and larval parasitoids may account for the differences seen here.

To further illustrate the advantage of structured sampling across habitats, we compared two similar ridge communities. We found no differences in the subfamilies in sampling two similar ridge communities (Table 5.5). Figure 5.3 shows the percent of Campopleginae species collected from two ridge communities alone compared with structured sampling across the two ridges with 95% confidence intervals. There is almost complete overlap of the curves for the East and West ridges alone and structured sampling between the two ridges. There were no statistical differences ($p > 0.05$) between the east and west ridges alone or the structured sampling regime for either subfamily (Table 5.5). Thus, habitat differences on the scale of GSMNP appear to be important. Multiple habitat sampling is recommended to maximize species collected.

Given that habitat differences appear evident between ridge and cove communities within GSMNP, we wanted to examine the differences habitat quality plays in characterizing cove communities. Subfamily differences in old-growth and second growth coves were observed. Table 5.5 shows that samples from old-growth coves alone were not statistically different ($p < 0.05$) from structured sampling across the 4 coves for the Campopleginae. There were no statistical differences for the Ichneumoninae ($p < 0.05$). Thus, for certain groups like the Campopleginae, sampling in less disturbed areas may be important in capturing a higher percentage of the GSMNP fauna.

We also examined temporal effects on maximizing sampling effort. Between year variance in the ridge community highlights the importance of sampling in multiple years. Table 5.5 shows the 95% confidence intervals of percent of Campopleginae and Ichneumoninae species collected from the two ridge communities in 1997-98 and 1998-99 alone compared with structured sampling across the two years. The 1998-99 field season appeared to have higher species richness than 1997-98, as it proved better than structured sampling for the Campopleginae and was not statistically different from structured sampling for the Ichneumoninae. Thus, because we do not have the foresight to predict good years, structured sampling across years is important to account for yearly fluctuation in species richness.

Conclusions

While beta diversity is expected to increase with distance, we found two reversals to this pattern. We report a greater percentage of Maryland Campopleginae species in Georgia than in Tennessee and a greater percentage of Florida Campopleginae species in Maryland than in Tennessee (Table 5.2). These reversals in community overlap with distance could not be explained by differences in habitat. There were no statistical differences ($p < 0.05$) in percent overlap of Maryland campoplegine richness between cove and ridge sample sites or between field and forest sample sites. There were no statistical differences in predicting Florida campoplegine richness between the cove and the ridge sample sites or between the field and forest sample sites (Table 5.3). However, broad habitat patterns did emerge. By randomly sampling Georgia forest and field habitats, we found statistical differences ($p < 0.05$) between the two habitats in percent overlap in species richness between Tennessee cove and ridge habitats and Georgia forest and field habitats (Table 5.3). We found no habitat differences in predicting richness at other sites when we sampled Tennessee cove and ridge habitats separately. Thus, pupal parasitoids like the

ichneumoninae may be more divided on gradients of succession from field to forest within terrestrial communities, rather than forest type such as coves and ridges. The common species represent a higher percentage of distant fauna than rare species, as expected. We found no evidence to suggest that differences in common and rare species distributions could account for the Maryland and Florida reversals seen in Table 5.2 (Table 5.4). We found that 52% of the rare and 50% of the common ichneumonine species sampled from Maryland occurred in Florida. Thus, it appears that at range extents, common species may become more locally rare. We suspect that altitude may pose a barrier to dispersal for some specialized parasitoids and confound the expected distance decay pattern.

In our analysis of inventory efficiencies, we found that structured sampling methods are superior to sampling at one location or at one time. At regional scales, we found a 9 to 20 percent increase in species captured when samples were taken randomly from multiple sites when compared to sampling at the most species rich sites. We also found that undisturbed habitats contain more species of specialized groups like the Campopleginae.

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Table 5.1. Sampling sites with the number of lots (L), individuals (N), and species collected (S) in Eastern North America. Data from Ontario, Maryland, Georgia and Florida previously published in Wayman (1994), Gaasch (1996), Skillen et al. (2000).

Site	° N	Elevation (meters)	Campopleginae			Ichneumoninae		
			L	N	S	L	N	S
Ontario	45	160	24	48	17	55	214	51
Maryland	39	60	83	532	44	113	1592	91
Tennessee	35		339	3273	165	385	6443	142
Cove		950 - 1183	155	1163	101	166	1494	79
Ridge		640 - 670	184	2110	128	219	4949	108
Georgia	33		530	5350	154	543	5425	152
Field		200 - 400	124	1651	92	139	1605	84
Forest		200 - 400	406	3699	120	404	3820	119
Florida	29 - 30	40 - 50	106	502	50	150	1730	61

Table 5.2. Turnover of species in Eastern North America. The 95% confidence intervals are generated from 1,000 Monte Carlo simulations of 500 specimens selected from each sample site. The confidence intervals represent the percentage of species in the target community collected from the site sampled during the simulations. Confidence intervals that do not overlap are significantly different ($p < 0.05$). Reversals in expected decay in similarity with distance are indicated by *. For example, Maryland has significantly ($p < 0.05$) more Campopleginae species in common with Georgia than with Tennessee.

		Target Community			
Site Sampled		MD	TN	GA	FL
Campopleginae	MD	93-100	14-15	18-20	34-38 *
	TN	34-47 *	47-58	18-24	22-32 *
	GA	50-63 *	15-20	38-49	44-58
	FL	43-43	11-11	21-22	98-100
Ichneumoninae	MD	61-75	21-26	26-32	39-46
	TN	30-38	38-50	22-29	33-45
	GA	38-47	26-33	43-53	53-65
	FL	21-31	14-20	21-27	60-78

Table 5.3. Habitat effects on turnover of species richness in Eastern North America. The 95% confidence intervals are generated from 1,000 Monte Carlo simulations of 500 specimens selected from each sample site. The confidence intervals represent the percentage of species in the target community collected from the site sampled during the simulations. Confidence intervals that do not overlap (*) are significantly different ($p < 0.05$) from each other with respect to the target community.

	Target Community					
	MD	TN Cove	TN Ridge	GA Field	GA Forest	FL
Sites Sampled						
Campopleginae						
TN Cove	31-38	67-81	51-62	22-28	19-25	24-30
TN Ridge	31-43	60-73	51-64	22-29	20-26	24-32
GA Field	36-52	16-23	14-21	56-72*	30-39*	32-46
GA Forest	47-59	19-25	17-23	38-48*	42-54*	44-58
Ichneumoninae						
TN Cove	23-31	50-65	38-50	20-29	22-29	31-40
TN Ridge	26-34	50-65	42-55	22-31	24-31	31-42
GA Field	32-40	22-29*	21-27*	58-74*	33-40*	45-57
GA Forest	34-43	30-40*	28-36*	38-49*	48-60*	48-59

Table 5.4. Rare versus common species. Percentage of rare and common species collected at target sites from effort sites Maryland (MD), Tennessee (TN), Georgia (GA) and Florida (FL). For example, 9% of rare and 21% of common TN species were collected in MD.

Rare species include 1 or 2 individuals and common species include 3 or more individuals.

Sites Sampled	Target Community							
	Rare (1+2)				Common (> 2)			
	MD	TN	GA	FL	MD	TN	GA	FL
Campopleginae								
MD	-	9	7	18	-	21	33	64
TN	50	-	23	14	70	-	42	68
GA	67	22	-	50	80	38	-	91
FL	33	9	6	-	55	14	36	-
Ichneumoninae								
MD	-	12	18	52	-	41	51	50
TN	30	-	17	52	62	-	58	59
GA	42	27	-	63	79	52	-	82
FL	23	4	9	-	44	35	45	-

Table 5.5. Inventory efficiency of one site versus structured sampling of multiple sites. Percentage of Campopleginae (C) and Ichneumoninae (I) species in target community collected from sites sampled presented as 95% confidence intervals (95% CI). Confidence intervals were generated from 1,000 Monte Carlo simulations where specimens were selected from sites sampled. Target and sites sampled include North America (NA), Tennessee (TN), Georgia (GA), Maryland (MD), and Florida (FL). Effort (N) refers to the number of specimens sampled in each simulation. In the structured sampling, the effort is divided evenly among each site sampled. Confidence intervals indicated by * are significantly different ($p < 0.05$) from the structured sampling of each target community.

Sites Sampled	Target Community	Effort (N)	% of Target sampled	
			Campopleginae	Ichneumoninae
			95% CI	95% CI
TN	NA	2,000	(45-50)*	(35-41)*
GA	NA	2,000	(34-40)*	(40-45)*
TN+GA+MD+FL	NA	500 x 4	(53-60)	(48-55)
TN Cove	TN	1,000	(55 - 60)*	(45 - 52)*
TN Ridge	TN	1,000	(53 - 63)	(42 - 52)*
TN Cove + Ridge	TN	500 x 2	(63 - 73)	(53 - 64)
TN East Ridge	TN Ridges	500	(52 - 62)	(44 - 57)
TN West Ridge	TN Ridges	500	(51 - 62)	(38 - 50)
TN East + West Ridge	TN Ridges	250 x 2	(51 - 64)	(42 - 55)

Table 5.5. (continued)

Sites Sampled	Target Community	Effort (N)	% of Target sampled	
			Campopleginae	Ichneumoninae
			95% CI	95% CI
TN Old Growth	TN Coves	500	(72 - 80)	(60 - 72)
TN Second Growth	TN Coves	500	(57 - 61)*	(60 - 73)
TN Old + Second Growth	TN Coves	250 x 2	(68 - 81)	(62 - 77)
TN Ridges 1997-98	TN Ridges	420	(35 - 44)*	(37 - 47)
TN Ridges 1998-99	TN Ridges	420	(56 - 57)	(44 - 54)
TN Ridges 1997-98 + 1998-99	TN Ridges	210 x 2	(46 - 57)	(41 - 53)

Figure 5.1. Monte Carlo simulations predicting North American Campopleginae species richness with 95% confidence intervals comparing structured sampling across four sites, Maryland (MD), Tennessee (TN), Georgia (GA) and Florida (FL) with sampling in Georgia or Tennessee alone. Simulations were randomized 1,000 times in an effort to predict the total number of North American Campopleginae species ($S=299$) collected in the current study and from Wayman (1994), Gaasch (1996) and Skillen et al. (2000).

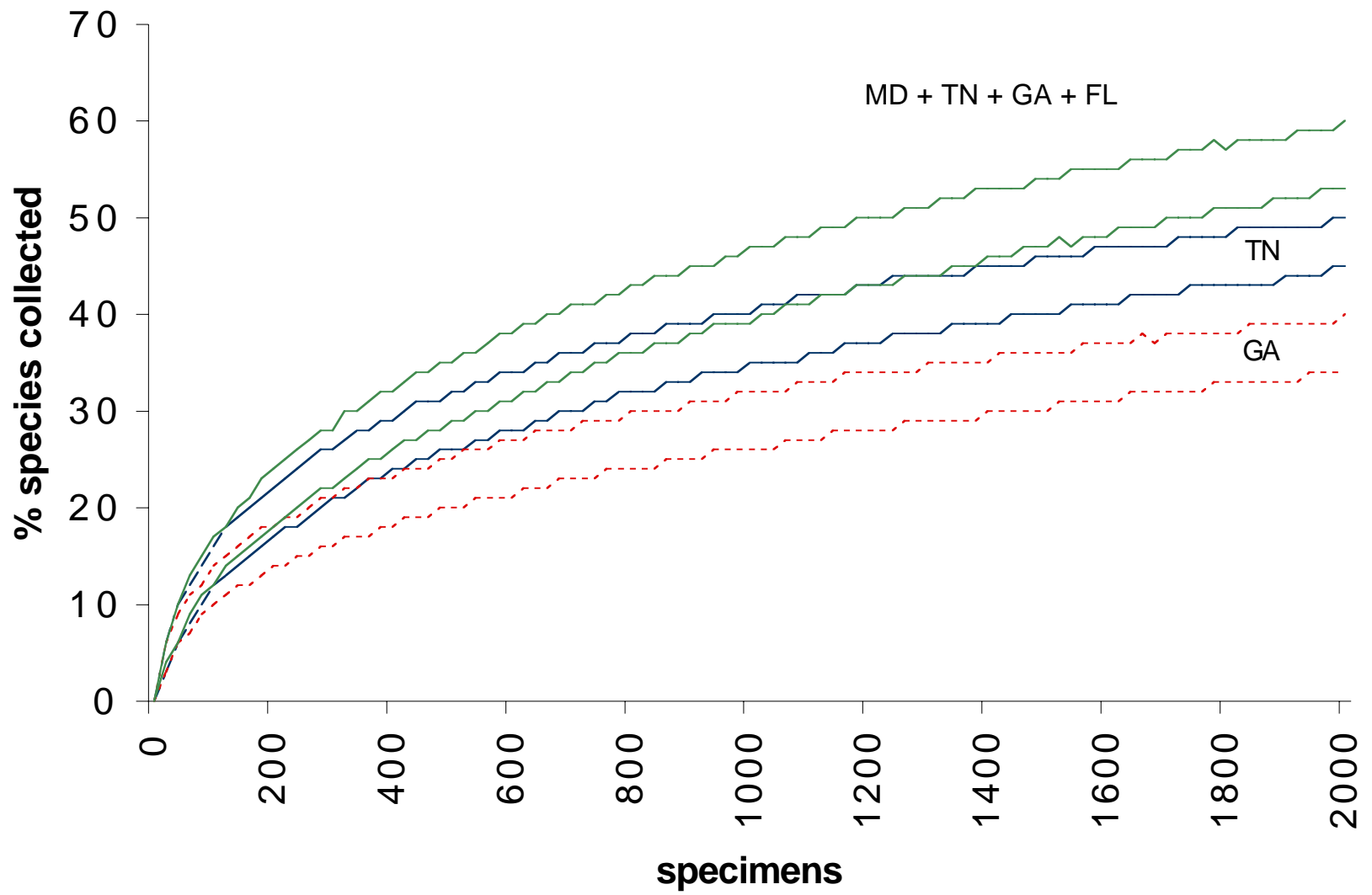


Figure 5.2. Monte Carlo simulations predicting Great Smoky Mountains National Park Campopleginae species richness with 95% confidence intervals comparing structured sampling across ridge (Lynn Hollow East, Lynn Hollow West in 1997-98 and 1998-99) and cove (Porters Creek, Ramsay Cascades, Fish Camp Prong and Meigs Post Prong in 1997-98) habitats in Great Smoky Mountains National Park, Tennessee, with sampling in cove or ridge sites alone. Simulations were randomized 1,000 times in an effort to predict the number of Great Smoky Mountains National Park Campopleginae species ($S=165$) collected in the current study.

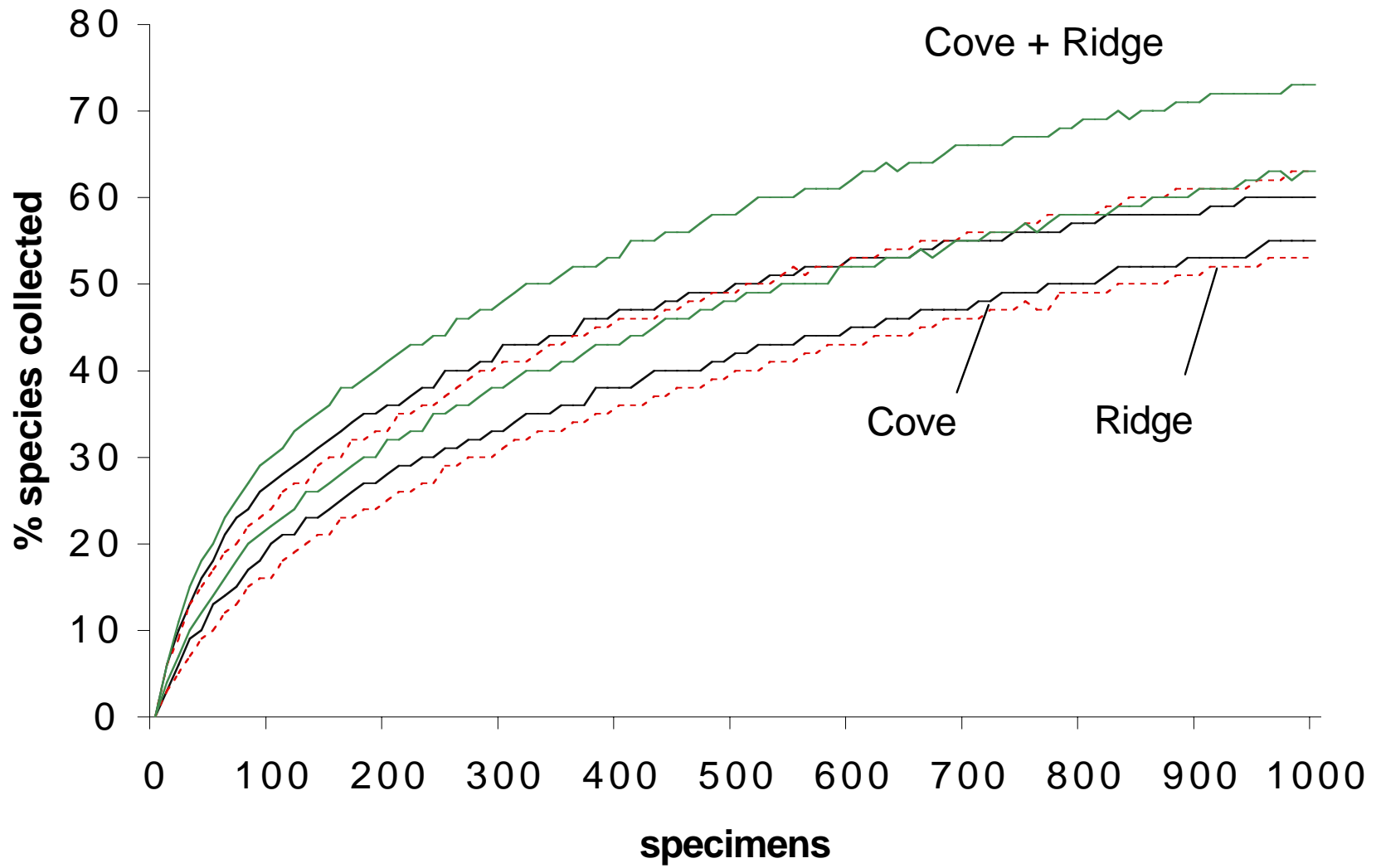
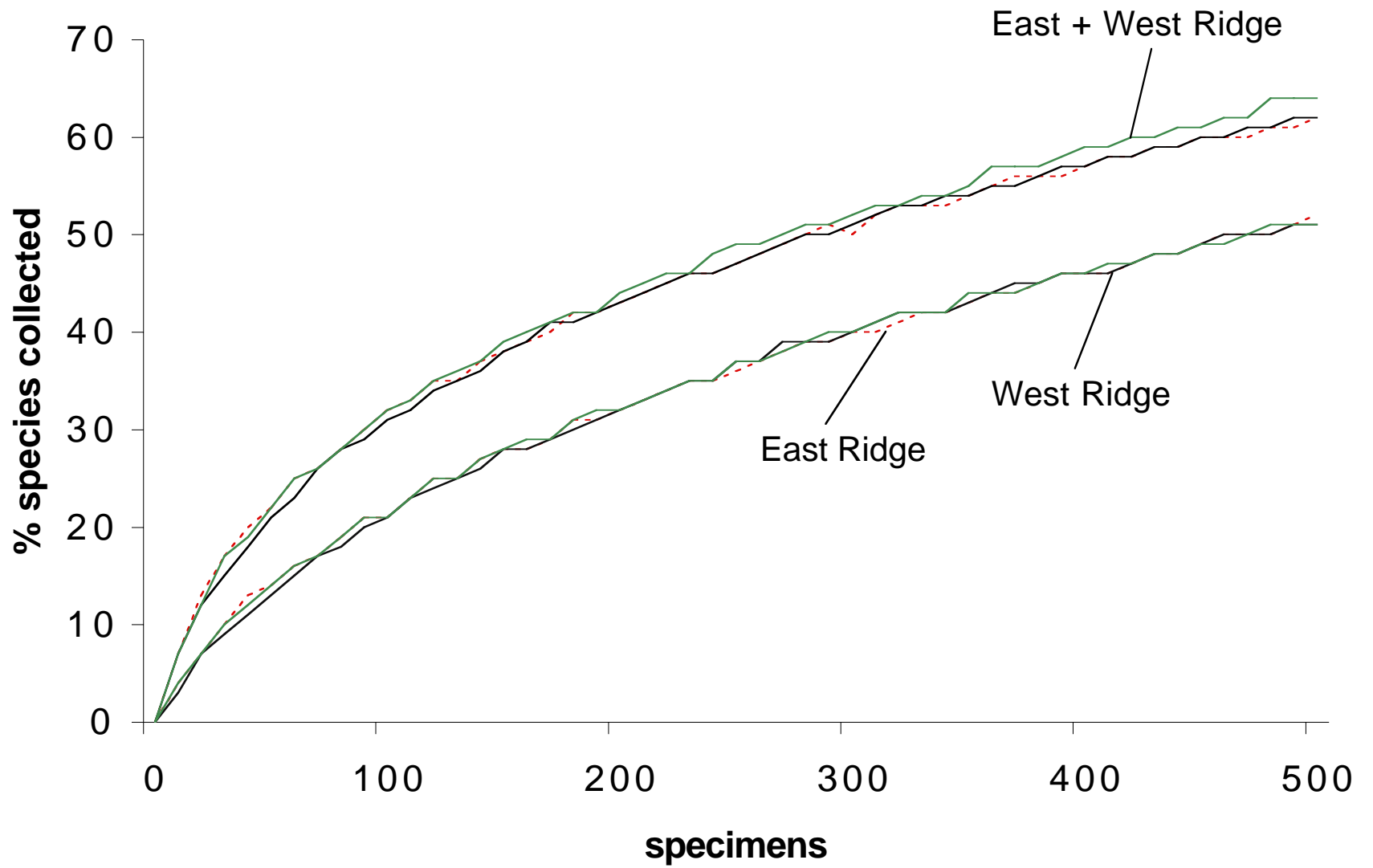


Figure 5.3. Monte Carlo simulations predicting Great Smoky Mountains National Park ridge habitat Campopleginae species richness with 95% confidence intervals comparing structured sampling across two xeric ridges (Lynn Hollow East, Lynn Hollow West in 1997-98 and 1998-99) with sampling in either ridge alone. Simulations were randomized 1,000 times in an effort to predict the number of Great Smoky Mountains National Park ridge habitat Campopleginae species ($S=128$) collected in the current study.



CHAPTER 6
CONCLUSIONS

Ichneumonid parasitoids are one of the most speciose groups of organisms on the planet with many species yet to be described (Wahl 1993, Gauld 1988). Parasitoids are integral components of terrestrial ecosystems, yet we know little about their distribution in terrestrial systems. In starting this research, I was interested in understanding the impact human habitat alterations have had on the richness, composition and distribution of these organisms within Great Smoky Mountains National Park, Tennessee (GSMNP). Further, I was interested in how habitat influences estimates of species richness at small and large spatial scales. To examine richness at larger spatial scales I compared GSMNP parasitoid diversity with previous works including a latitudinal gradient in Eastern North America (Skillen et al. 2000) and extensive collecting in Georgia's Piedmont (Wayman 1994, Gaasch 1996).

In the midst of an All Taxa Biological Inventory (ATBI) (Kaiser 1999, Sharkey 2001), this project has provided an opportunity to examine methodologies for maximizing insect species documented for a single geographic location. In 1997 scientists, educators and administrators began the task of identifying and understanding the distribution and life-histories of all organisms in GSMNP. This task has been compared to a moonshot or the human genome project. The benefits to society are myriad. The life on this planet feeds us, provides clean water and recycles nutrients. Yet we cannot manage our natural resources if we don't have knowledge about the species that provide these essential functions. This undertaking will present many challenges. As part of this project, I have been able to compare trapping between habitats and over time and hopefully provide some strategies for reducing costs and maximizing benefits to our goal.

Because of the large size of the Ichneumonidae I chose two subfamilies, Campopleginae and Ichneumoninae, that represent the two predominant parasitoid life-history strategies within the family. With the diversity of life-history strategies within the parasitoid lifestyle, the idiobiont/koinobiont (Askew and Shaw 1986) dichotomy has

been used to examine parasitoid responses to food plant type, host range, or latitude regardless of taxonomic lineage. Idiobiont larvae consume the host in the stage in which attacked and are thus considered to have a wider host range. In contrast, koinobionts oviposit in earlier host stages emerging later in host development and are thus considered to have more narrow host ranges. Ichneumoninae are predominantly pupal parasitoids and attack only Lepidoptera (Gauld 1988). Campopleginae are koinobiont endoparasitoids of Lepidoptera or Symphyta larvae (Gauld 1988). Patterns of richness have been shown to differ between these variable life-history strategies (Askew and Shaw 1986, Gauld 1986). Throughout the analysis, I found differences in Campopleginae and Ichneumoninae species richness and turnover at both small and large spatial scales. How human habitat destruction impacts these two subfamilies may be a function of these underlying biological differences. For instance, Campopleginae may be more dispersal limited because of greater host specificity and consequently have less of an ability to colonize new habitats than their Ichneumoninae counterparts.

From previous work by Janzen (1981) and Skillen et al. (2000), showing ichneumonid richness to peak at mid-latitudes, I expected GSMNP to contain high species richness for both subfamilies examined. The results from Chapter 2 show the importance of habitat differences when examining the trends in latitudinal species richness. I found the highest species richness for the two subfamilies combined in xeric ridge sites within GSMNP. The differences in species richness within habitats appear subfamily dependent with ichneumonines showing greater differences in species richness and campoplegines showing higher richness in all habitats sampled in GSMNP. These results indicate the importance of sampling multiple habitats when examining large-scale diversity patterns.

Furthermore, along the latitudinal gradient, the results from Chapter 2 generally support a peak of ichneumonid diversity at mid-latitudes with the additional Tennessee sites, while the band of diversity seems to be wider as predicted by Skillen et al. (2000). I found

higher ichneumonid richness in xeric ridge habitats (Lynn Hollow West (114) and Lynn Hollow East (112)) when compared to Skillen et al.'s (2000) most speciose site, Maryland (103), and lower than Maryland for the two cove sites (Porters Creek, 90 and Ramsay Cascades, 88). I found subfamily differences in species richness with campopleginae richness higher in all sites when compared to Skillen et al.'s (2000) latitudinal gradient. Thus, the Piedmont and Southern Appalachians appear to be an area of high biodiversity for the Campopleginae. This high campoplegine diversity at all Tennessee sites widens previously reported peaks of diversity along the latitudinal gradients (Janzen 1981, Skillen et al. 2000). Furthermore, the higher total richness at the xeric ridge sites emphasizes the importance of habitat types on structuring local diversity in old-growth forests.

I expected to find greater differences in species composition between habitats that had been clear-cut and those that had not. However, the data from Chapter 3 show a high degree of similarity in species composition between similar habitats regardless of logging history. Again, subfamily differences were evident. Campopleginae parasitoids had higher species richness in old-growth coves (79 species) when compared to second-growth coves (57 species), while Ichneumoninae parasitoids had higher species richness in second growth coves (58 species) when compared to old-growth coves (51 species). Furthermore, Campopleginae had 66% overlap in species composition between previously cut and uncut coves while, Ichneumonines had a 75% overlap in species composition between previously cut and uncut coves. Because the effects of disturbance are closely tied to dispersal abilities it is not surprising that strong flying pupal ichneumonine parasitoids could better recolonize disturbed areas than their more specialized larval campoplegine counterparts.

Based on these data it appears that the ichneumonine communities, for the most part, have recovered 70+ years after clear-cutting over 100,000 acres while, campoplegine communities have to a lesser degree. As expected under the idiobiont/koinobiont dichotomy (Askew and Shaw 1986), ichneumonine (idiobiont) wasps disperse easily

between habitats and recolonize well after disturbance while campopleginae (koinobionts) wasps may not disperse as easily between habitats or colonize disturbed habitats as rapidly. Thus, Campopleginae parasitoids may be more susceptible to habitat destruction. However, certain species in both subfamilies e.g., *Phaeogenes*_sp_GSMNP_2, *Rhimphoctona*_sp_GSMNP_1 and *Dusona*_sp_GSMNP_2, may be susceptible to forest destruction and may be the species of conservation concern.

In addition to habitat destruction from logging practices, the practice of fire suppression has greatly altered forest communities in GSMNP (Harrod et al. 2000). Historically, fire has been an important factor in structuring floral and faunal communities within the Central Hardwoods region (Braun 1950, Anderson et al. 1999). Fire regimes prior to human settlement are difficult to discover in all areas (Whelan 1995), but it has been argued that promoting an ‘unnatural’ fire regime may make conditions difficult for organisms that evolved under different fire conditions (Howe 1994 Whelan 1995). Thus, which historical fire regime to reconstruct for conserving biodiversity is difficult to discern. When biodiversity conservation is the primary goal of management strategies, greater understanding of fire over evolutionary time scales is an important consideration of conserving the biota (Howe 1994, Whelan 1995). However, human settlements play a role in shaping historical and current fire regimes. For example, Native Americans have used fire to modify this landscape for thousands of years (MacCleery 1992), yet fire suppression following European settlement, timber harvest and plant succession have dramatically changed the composition of this landscape over time (Ware et al. 1993, Bonnicksen et al. 1999, Harrod et al. 2000).

The data from Chapter 4 show a high degree of similarity in parasitoid species richness and composition between xeric ridge plots before and after a fire. However, there appears to be some subfamily differences. Based on the data from burned and unburned plots it appears that larval Campopleginae parasitoids may be more susceptible to fire

disturbance than their pupal Ichneumoninae counterparts. For example, Ichneumoninae parasitoids seem little affected by the fire and appear to recolonize well after disturbance. I found that the relative abundance of parasitoids declined in the year following a fire but the community composition was virtually unchanged.

I also examined other insect orders in their response to the fire. In the short term, grasshoppers (Orthoptera) and ground beetles (Coleoptera: Carabidae) have been reported to be more abundant post fire (Reed 1997, Galley and Flowers 1998). I found similar results for the Orthoptera with increases in relative abundance after a fire. The relative abundances of the Formicidae, Coleoptera, Symphyta, and Ichneumonoidea decreased immediately after a fire.

While these results appear to indicate the resiliency of the insect community after the prescribed fire, it is unclear what the effects of subsequent prescribed fires might be. There is evidence to suggest that changes in fire regime could alter insect species richness and composition. Swengel and Swengel (1997) found that butterflies feeding on herbs responded better to a single wildfire than to rotational burning. Thus, the return of prescribed fire to Lynn Hollow after almost 70 years may alter the insect community in subsequent years and continued monitoring of insect populations is warranted.

In the final analysis on beta diversity, the data from Chapter 5 show a consistent pattern of similarity distance decay (Whittaker 1975, Cody 1985, Nekola and White 1999), in most cases. Again, I found subfamily differences. Campopleginae parasitoids had lower species richness than expected by distance decay in comparisons of percent overlap from Maryland and Florida. It appears that Georgia has more species in common with Maryland than Tennessee, and Maryland has more species in common with Florida than Tennessee. I suspected that these reversals may be a result of differences in habitat. However, I found few significant differences in percent species in common between habitats in the regional analysis. Caley and Schluter (1997) claim that we do not know how habitat

heterogeneity influences the relationships between local and regional diversity. The analysis here makes the matter no more clear. However, altitude may pose a barrier to dispersal for some specialized parasitoids and confound the expected distance decay pattern. Because the cove sites in GSMNP are at the highest elevation of all the sites in the study ranging from 950 -1183 meters, the differences may be elevational and not a result of different habitats. Thus, it appears that habitat heterogeneity may be an important factor in species turnover at large spatial scales, but this result may be confounded by elevational differences.

In pair wise comparisons of common and rare parasitoid species, the percent of common species shared exceeded the percent of rare species shared in all cases but one. There appears to be a higher percent of rare species in common in Florida and Maryland than in Florida and Tennessee. It remains unclear why rare parasitoids are better able to disperse to Maryland from Florida and not to Tennessee. Again, the high altitude regions in the Southern Appalachian Mountains may restrict species ranges more than expected by distance. Thus, the high elevation species are not able to colonize lower elevation sites to either the north or south. For example, Tarmo and Seppo (1999) reared parasitoids from *Epirrita autumnata* (Lepidoptera) larvae feeding on mountain birch in Finland. They found a higher proportion of *Eulophus larvarum* (Eulophidae: Hymenoptera) at higher altitude sites and *Cotesia jucunda* (Braconidae: Hymenoptera) at lower altitude sites. Thus, altitude may be an important factor in considering turnover of Campopleginae in Eastern North America.

I have shown the difficulties in documenting species richness over large geographic ranges for hyper-diverse groups like the Ichneumonidae. The estimates of species richness examined remain steep (Coleman et al. 1982, Colwell 1997, Colwell and Coddington 1994) indicating that I am not able to accurately predict total species richness at any site examined. With recent attempts to inventory all organisms in a particular place such as GSMNP, what have I learned from this analysis to assist in answering local and regional questions of

biodiversity? Because sampling efforts are costly, quantitative estimates of different sampling regimes will help achieve goals of documenting biodiversity more quickly. I found that structured sampling methods are superior to sampling at one location or at one time. Between year variance in species richness may be quite high so sampling in multiple years is more important than sampling in multiple plots in the same year. I further recommend sampling in undisturbed habitats, as they may yield more species.

Landscape level studies of community change necessitate these types of comparisons (Hargrove and Pickering 1992). However, given the rate of destruction of natural areas, comparisons like those conducted in the current study are necessary to better understand how habitat destruction impacts natural communities (Hughes et al. 2000). Sharkey (2001) emphasized the importance of understanding our biodiversity as the best way to protect it. He further stated that less than 6% of the invertebrate species have been recorded from an estimated 100,000 total in GSMNP. Thus, research on distribution and turn over of invertebrate species are important contributions in helping conserve our wild lands. As humans continue to alter and destroy habitat, we need to understand how changes in land use affect species richness and composition at both large and small spatial scales. Therefore, we must continue to study the effects of disturbance on higher trophic level organisms such as parasitoids to better understand their importance in terrestrial ecosystems.

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APPENDIX 1

Campopleginae and Ichneumoninae individuals collected in 4 cove forests, in Great Smoky Mountains National Park, Tennessee between 1997-98.

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
Campopleginae												
<i>Bathyplectes infernalis</i> (Gravenhorst)	6	16	22	6	6	12	0	0	0	0	0	0
<i>Campoletis</i> sp GSMNP 4	1	0	1	0	0	0	0	0	0	0	0	0
<i>Campoletis</i> sp GSMNP 5	1	0	1	0	1	1	1	0	1	0	0	0
<i>Campoletis</i> sp GSMNP 6	2	0	2	0	0	0	1	0	1	2	0	2
<i>Campoletis</i> sp Hitchiti Male 1	4	1	5	1	1	2	0	0	0	0	0	0
<i>Campoletis</i> sp Sams Farm 1	3	1	4	1	0	1	0	0	0	0	0	0
<i>Campoplex</i> sp GSMNP 1	1	0	1	1	0	1	0	0	0	0	0	0
<i>Campoplex</i> sp GSMNP 2	1	0	1	0	2	2	1	0	1	1	0	1
<i>Campoplex</i> sp GSMNP 3	0	0	0	1	0	1	5	1	6	2	0	2
<i>Campoplex</i> sp GSMNP 4	3	0	3	1	0	1	1	0	1	2	0	2
<i>Campoplex</i> sp GSMNP 5	2	0	2	1	0	1	5	1	6	1	0	1
<i>Campoplex</i> sp GSMNP 7	0	0	0	0	0	0	0	1	1	0	0	0

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Campoplex</i> sp GSMNP 8	1	0	1	0	0	0	0	3	3	0	0	0
<i>Campoplex</i> sp GSMNP 9	2	0	2	0	0	0	0	0	0	0	1	1
<i>Campoplex</i> sp GSMNP 10	0	0	0	1	0	1	0	0	0	0	0	0
<i>Campoplex</i> sp GSMNP 12	0	0	0	0	0	0	1	0	1	0	0	0
<i>Campoplex</i> sp GSMNP 13	0	0	0	0	0	0	2	0	2	1	0	1
<i>Campoplex</i> sp GSMNP 15	0	0	0	0	0	0	1	0	1	0	0	0
<i>Campoplex</i> sp GSMNP 17	0	0	0	1	0	1	0	0	0	0	0	0
<i>Campoplex</i> sp Hitchiti 1	0	0	0	0	0	0	2	1	3	1	1	2
<i>Campoplex</i> sp Hitchiti Female 4	8	0	8	2	1	3	1	0	1	5	0	5
<i>Campoplex</i> sp Hitchiti Female 5	2	0	2	0	0	0	0	0	0	1	0	1
<i>Campoplex</i> sp Sams Farm Female 5	1	0	1	22	11	33	44	31	75	11	4	15
<i>Campoplex</i> sp Sams Farm Female 12	0	0	0	1	1	2	1	0	1	0	0	0
<i>Campoplex</i> sp Sams Farm Male 8	0	0	0	2	2	4	0	1	1	0	1	1
<i>Casinaria infesta</i> (Cresson)	2	0	2	2	1	3	1	2	3	3	1	4
<i>Casinaria</i> sp Patuxent 1	0	1	1	0	1	1	0	0	0	0	0	0
<i>Charmops</i> sp GSMNP 1	1	0	1	1	0	1	0	1	1	0	0	0

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Diadegma</i> sp GSMNP 1	29	13	42	3	0	3	3	0	3	16	8	24
<i>Diadegma</i> sp GSMNP 3	5	1	6	0	0	0	0	0	0	0	0	0
<i>Diadegma</i> sp GSMNP 4	0	0	0	1	0	1	0	0	0	0	0	0
<i>Diadegma</i> sp GSMNP 5	1	0	1	0	0	0	1	1	2	0	3	3
<i>Diadegma</i> sp GSMNP 6	1	0	1	0	0	0	0	0	0	0	2	2
<i>Diadegma</i> sp GSMNP 7	0	0	0	0	0	0	4	1	5	22	1	23
<i>Diadegma</i> sp Hitchiti Female 3	0	0	0	0	0	0	0	0	0	1	0	1
<i>Diadegma</i> sp Sams Farm Female 1	1	1	2	1	0	1	2	1	3	9	0	9
<i>Diadegma</i> sp Sams Farm Female 5	5	2	7	7	0	7	0	0	0	0	3	3
<i>Diadegma</i> sp Sams Farm Female 6	0	2	2	0	2	2	0	0	0	0	0	0
<i>Diadegma</i> sp Sams Farm Female 7	10	1	0	0	0	0	0	0	0	0	0	0
<i>Diadegma</i> sp Sams Farm Male 5	0	0	0	0	0	0	1	0	1	0	0	0
<i>Dusona americana</i> (Ashmead)	0	0	0	0	1	1	0	0	0	0	0	0
<i>Dusona brachiator</i> (Say)	0	0	0	1	1	2	1	2	3	1	1	2
<i>Dusona downesi</i> (Viereck)	0	0	0	1	0	1	0	0	0	0	0	0
<i>Dusona egregia</i> (Viereck)	3	1	4	6	5	11	2	8	10	2	0	2

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Dusona luctuosa</i> (Provancher)	1	0	1	0	0	0	0	0	0	0	0	0
<i>Dusona planata</i> (Viereck)	0	0	0	1	0	1	1	0	1	1	0	1
<i>Dusona semirufa</i> (Provancher)	3	2	5	2	0	2	4	2	6	1	0	1
<i>Dusona villosa</i> (Norton)	6	1	7	0	0	0	0	0	0	0	0	0
<i>Dusona vitticollis</i> (Norton)	4	0	4	0	0	0	3	0	3	0	0	0
<i>Dusona</i> sp GSMNP 2	11	1	12	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 3	7	3	10	0	0	0	0	0	0	0	1	1
<i>Dusona</i> sp GSMNP 4	0	0	0	1	0	1	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 5	1	0	1	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 7	0	0	0	0	1	1	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 10	0	0	0	0	0	0	0	1	1	0	0	0
<i>Dusona</i> sp GSMNP 11	1	0	1	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 12	2	0	2	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 16	10	1	11	0	0	0	0	1	1	1	0	1
<i>Dusona</i> sp GSMNP 17	1	0	1	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp GSMNP 18	0	0	0	0	0	0	1	0	1	0	0	0

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Dusona</i> sp GSMNP 19	0	0	0	0	0	0	0	0	0	0	1	1
<i>Dusona</i> sp GSMNP 20	0	0	0	1	0	1	1	0	1	0	0	0
<i>Dusona</i> sp GSMNP 21	0	0	0	0	0	0	0	0	0	1	1	2
<i>Dusona</i> sp GSMNP 24	2	0	2	0	0	0	0	0	0	0	0	0
<i>Dusona</i> sp Patuxent 4	0	0	0	0	1	1	0	0	0	0	0	0
<i>Echthronomas</i> sp GSMNP Female 1	2	0	2	5	0	5	0	4	4	5	0	5
<i>Echthronomas</i> sp GSMNP Male 1	0	0	0	1	0	1	0	0	0	1	0	1
<i>Hyposoter</i> sp GSMNP 1	13	3	16	4	4	8	9	8	17	4	2	6
<i>Hyposoter</i> sp GSMNP 2	0	0	0	0	0	0	0	1	1	0	0	0
<i>Hyposoter</i> sp GSMNP 3	25	22	47	1	1	2	11	2	13	8	6	14
<i>Hyposoter</i> sp GSMNP 4	4	0	4	1	1	2	0	0	0	0	0	0
<i>Hyposoter</i> sp GSMNP 5	1	0	1	0	0	0	0	0	0	0	0	0
<i>Hyposoter</i> sp Hitchiti 3	1	0	1	1	1	2	0	0	0	1	0	1
<i>Hyposoter</i> sp Hitchiti 4	0	0	0	0	0	0	1	1	2	0	0	0
<i>Hyposoter</i> sp Hitchiti Male 10	0	0	0	0	0	0	0	0	0	1	0	1
<i>Hyposoter</i> sp Patuxent 1	9	0	9	4	3	7	33	28	61	1	0	1

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Hyposoter</i> sp Patuxent Female 1	0	1	1	0	0	0	5	2	7	0	0	0
<i>Hyposoter</i> sp Sams Farm 10	2	1	3	2	0	2	0	0	0	0	0	0
<i>Nemeritis</i> sp GSMNP 1	0	0	0	0	0	0	0	0	0	10	0	10
<i>Nemeritis</i> sp GSMNP 2	10	11	21	3	0	3	1	2	3	3	1	4
<i>Olesicampe</i> sp GSMNP 1	2	0	2	0	0	0	0	0	0	0	0	0
<i>Olesicampe</i> sp GSMNP 3	1	0	1	0	0	0	0	0	0	0	0	0
<i>Olesicampe</i> sp Sams Farm 3	0	0	0	1	0	1	0	0	0	1	0	1
<i>Phobocampe</i> sp GSMNP 1	1	0	1	0	0	0	0	0	0	0	0	0
<i>Phobocampe</i> sp GSMNP 3	1	0	1	0	0	0	0	0	0	0	0	0
<i>Phobocampe</i> sp GSMNP 5	1	0	1	0	0	0	1	0	1	1	0	1
<i>Phobocampe</i> sp Hitchiti 1	0	0	0	1	0	1	0	0	0	0	0	0
<i>Phobocampe</i> sp Hitchiti 9	1	0	1	0	0	0	0	0	0	0	1	1
<i>Phobocampe</i> sp Sams Farm 3	5	0	5	4	2	6	1	4	5	7	3	10
<i>Rhimphoctona</i> sp GSMNP 1	18	0	18	0	0	0	0	0	0	0	0	0
<i>Scirtetes</i> sp GSMNP 2	0	0	0	0	1	1	0	0	0	0	0	0
<i>Sinophorus</i> sp GSMNP 1	6	6	12	2	0	2	3	0	3	2	3	5

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Sinophorus</i> sp GSMNP 2	0	0	0	1	0	1	0	0	0	0	0	0
<i>Venturia</i> sp Hitchiti Female 7	1	0	1	0	0	0	0	0	0	0	0	0
<i>Xanthocampoplex</i> sp GSMNP 1	0	0	0	1	0	1	0	0	0	0	0	0
Ichneumoninae												
<i>Aoplus</i> sp GSMNP Female 1	2	0	2	1	0	1	0	0	0	0	0	0
<i>Aoplus</i> sp GSMNP Female 4	0	0	0	1	0	1	0	0	0	0	0	0
<i>Aoplus</i> sp GSMNP Male 1	24	1	25	0	0	0	0	0	0	1	1	2
<i>Aoplus</i> sp GSMNP Male 2	1	0	1	0	0	0	0	0	0	0	0	0
<i>Aoplus</i> sp Sams Farm Female 3	4	0	4	3	2	5	1	1	2	6	3	9
<i>Aoplus</i> sp Sams Farm Male 1	1	0	1	0	0	0	0	0	0	1	0	1
<i>Aoplus</i> sp Sams Farm Male 3	1	0	1	1	0	1	0	0	0	0	0	0
<i>Aoplus velox</i> (Cresson)	22	10	32	2	2	4	4	6	10	1	4	5
<i>Barichneumon carolinensis</i> Heinrich	0	0	0	0	1	1	1	0	1	0	2	2
<i>Barichneumon flaviscuta</i> Heinrich	1	0	1	0	0	0	1	0	1	1	0	1
<i>Barichneumon libens</i> (Cresson)	0	0	0	1	2	3	0	1	1	2	4	6
<i>Barichneumon</i> sp GSMNP Male 1	0	0	0	0	0	0	1	0	1	0	0	0

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Coelichneumon azotus</i> (Cresson)	0	0	0	3	9	12	0	0	0	0	0	0
<i>Coelichneumon eximius</i> (Stevens)	2	0	2	1	2	3	1	1	2	0	1	1
<i>Coelichneumon jejunus</i> (Cresson)	0	0	0	0	0	0	1	0	1	0	0	0
<i>Coelichneumon magniscopa</i> (Heinrich)	0	0	0	0	0	0	0	0	0	0	1	1
<i>Coelichneumon navus</i> (Say)	0	0	0	1	0	1	0	0	0	0	1	1
<i>Coelichneumon pervagus</i> (Cresson)	0	0	0	0	0	0	0	0	0	1	0	1
<i>Coelichneumon</i> sp GSMNP Male 13	0	0	0	1	0	1	0	1	1	0	0	0
<i>Coelichneumon</i> sp GSMNP Male 15	4	0	4	0	1	1	3	2	5	0	0	0
<i>Coelichneumon</i> sp GSMNP Male 23	0	0	0	0	0	0	0	2	2	0	0	0
<i>Coelichneumon</i> sp Sams Farm Male 3	0	0	0	0	0	0	5	1	6	0	0	0
<i>Cratichneumon anisotae</i> Heinrich	1	0	1	0	0	0	0	0	0	0	0	0
<i>Cratichneumon annulatipes</i> (Provancher)	3	0	3	5	6	11	3	6	9	4	4	8
<i>Cratichneumon boreoalpinus</i> Heinrich	0	0	0	0	1	1	1	1	2	0	0	0
<i>Cratichneumon carolinae</i> Heinrich	0	0	0	0	0	0	5	1	6	1	1	2
<i>Cratichneumon flavipectus</i> (Provancher)	1	1	2	2	10	12	4	1	5	1	5	6
<i>Cratichneumon georgius</i> Heinrich	2	0	2	0	0	0	1	0	1	3	0	3

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Cratichneumon insulae</i> Heinrich	0	1	1	11	3	14	0	1	1	0	4	4
<i>Cratichneumon paraparatus</i> Heinrich	1	0	1	2	1	3	3	2	5	1	2	3
<i>Cratichneumon paratus</i> (Say)	0	0	0	7	6	13	5	4	9	4	3	7
<i>Cratichneumon proximus</i> (Cresson)	0	0	0	4	0	4	2	2	4	0	3	3
<i>Cratichneumon scitulus</i> (Cresson)	0	0	0	2	1	3	3	1	4	2	8	10
<i>Cratichneumon subfilatus</i> Heinrich	2	2	4	5	5	10	4	1	5	3	6	9
<i>Cratichneumon sublatus</i> (Cresson)	0	0	0	3	1	4	4	4	8	6	11	17
<i>Cratichneumon tyloidifer</i> Heinrich	0	0	0	2	0	2	0	0	0	1	1	2
<i>Cratichneumon variegatus</i> (Provancher)	1	0	1	12	1	13	6	0	6	5	6	11
<i>Cratichneumon vinnulus</i> (Cresson)	0	0	0	13	7	20	2	0	2	19	8	27
<i>Cratichneumon</i> sp GSMNP Female 1	4	2	6	43	63	106	60	36	96	22	11	33
<i>Cratichneumon</i> sp GSMNP Female 2	0	0	0	1	3	4	1	0	1	0	3	3
<i>Cratichneumon</i> sp GSMNP Female 3	0	0	0	0	0	0	1	0	1	0	0	0
<i>Cratichneumon</i> sp GSMNP Female 4	0	0	0	0	0	0	2	0	2	0	0	0
<i>Cratichneumon</i> sp GSMNP Female 5	0	0	0	0	0	0	1	0	1	0	0	0
<i>Cratichneumon</i> sp GSMNP Female 7	0	0	0	1	0	1	0	0	0	0	0	0

APPENDIX 1 (continued)

	Old-Growth						Second-Growth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Cratichneumon</i> sp GSMNP Female 8	0	0	0	1	0	1	0	0	0	0	0	0
<i>Cratichneumon</i> sp GSMNP Female 9	0	0	0	1	0	1	0	0	0	0	0	0
<i>Cratichneumon</i> sp GSMNP Male 2	3	0	3	23	58	81	22	23	45	13	2	15
<i>Cratichneumon</i> sp GSMNP Male 3	0	0	0	0	0	0	0	0	0	0	1	1
<i>Cratichneumon</i> sp GSMNP Male 4	0	1	1	12	4	16	3	5	8	2	9	11
<i>Cratichneumon</i> sp GSMNP Male 5	0	0	0	0	0	0	0	0	0	1	0	1
<i>Cratichneumon</i> sp Patuxent Male 1	4	3	7	85	72	157	27	28	55	25	32	57
<i>Homotherus townesi</i> Heinrich	7	1	8	11	19	30	14	20	34	14	88	102
<i>Ichneumon annulatorius</i> Fabricius	0	0	0	1	0	1	0	0	0	1	3	4
<i>Ichneumon</i> sp GSMNP Female 1	0	0	0	0	1	1	0	0	0	0	1	1
<i>Ichneumon</i> sp GSMNP Female 2	0	0	0	0	0	0	0	0	0	0	1	1
<i>Ichneumon</i> sp GSMNP Female 3	0	0	0	0	1	1	0	0	0	0	0	0
<i>Ichneumon</i> sp GSMNP Female 4	0	0	0	0	0	0	0	0	0	0	1	1
<i>Ichneumon</i> sp GSMNP Female 6	0	0	0	0	0	0	0	1	1	0	0	0
<i>Ichneumon</i> sp GSMNP Female 9	1	0	1	0	0	0	0	0	0	0	0	0
<i>Ichneumon</i> sp GSMNP Male 2	0	0	0	1	0	1	0	0	0	0	0	0

APPENDIX 1 (continued)

	Old-Growth						SecondGrowth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Ichneumon</i> sp GSMNP Male 3	0	0	0	1	0	1	3	0	3	0	0	0
<i>Ichneumon</i> sp GSMNP Male 5	0	0	0	0	0	0	2	0	2	0	0	0
<i>Ichneumon</i> sp Patuxent Female 3	0	0	0	0	0	0	1	0	1	0	0	0
<i>Ichneumon</i> sp Shaw Woods Male 1	0	0	0	0	0	0	0	0	0	0	1	1
<i>Linytus exhortator</i> (Fabricius)	3	1	4	0	0	0	0	0	0	0	0	0
<i>Neolinycus</i> sp GSMNP 1	1	1	2	0	0	0	0	0	0	0	0	0
<i>Patrocloides</i> sp GSMNP Male 1	0	0	0	0	1	1	1	0	1	0	1	1
<i>Phaeogenes</i> sp GSMNP Female 1	0	0	0	0	0	0	4	1	5	0	0	0
<i>Phaeogenes</i> sp GSMNP Female 2	0	1	1	0	1	1	0	0	0	0	0	0
<i>Phaeogenes</i> sp GSMNP Female 5	4	0	4	0	0	0	1	0	1	1	0	1
<i>Phaeogenes</i> sp GSMNP Male 1	1	0	1	0	0	0	1	0	1	0	0	0
<i>Phaeogenes</i> sp GSMNP Male 2	10	1	11	0	1	1	0	0	0	0	0	0
<i>Phaeogenes</i> sp GSMNP Male 4	0	0	0	0	0	0	0	0	0	5	4	9
<i>Phaeogenes</i> sp GSMNP Male 5	0	0	0	0	0	0	0	1	1	1	0	1
<i>Phaeogenes</i> sp Hitchiti Male 1	0	0	0	0	0	0	3	0	3	0	0	0
<i>Platylabus clarus</i> (Cresson)	2	0	2	0	1	1	1	0	1	0	0	0

APPENDIX 1 (continued)

	Old-Growth						SecondGrowth					
	Ramsay Cascades			Porters Creek			Fish Camp Prong			Meigs Post Prong		
	Trap 151	Trap 152	Total	Trap 153	Trap 154	Total	Trap 155	Trap 156	Total	Trap 157	Trap 158	Total
<i>Platylabus hyperetis</i> Heinrich	1	1	2	0	0	0	2	0	2	0	0	0
<i>Platylabus</i> sp GSMNP Male 1	0	0	0	0	1	1	0	0	0	0	0	0
<i>Protichneumon grandis</i> (Brulle)	0	0	0	0	0	0	0	0	0	1	1	2
<i>Rubicundiella mucronata</i> (Provancher)	0	1	1	1	1	2	0	1	1	1	0	1
<i>Setanta compta</i> (Say)	0	0	0	1	0	1	0	1	1	1	0	1
<i>Stenichneumon culpator</i> (Cresson)	0	0	0	1	0	1	1	0	1	0	0	0
<i>Stenobarichneumon</i> sp GSMNP 1	1	0	1	0	1	1	0	0	0	0	1	1
<i>Stenobarichneumon</i> sp Hitchiti 1	0	0	0	0	0	0	1	0	1	0	0	0
<i>Terebraella</i> sp GSMNP 1	2	0	2	0	1	1	0	1	1	0	0	0
<i>Vulgichneumon brevicinctor</i> (Say)	0	0	0	1	0	1	1	3	4	0	1	1
<i>Vulgichneumon</i> sp GSMNP 1	2	2	4	1	0	1	0	0	0	0	0	0
<i>Vulgichneumon terminalis</i> (Cresson)	1	0	1	0	0	0	1	1	2	0	0	0