Species Richness of the Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) Along a Latitudinal Gradient in Eastern North American Old-Growth Forests

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ABSTRACT   We ran 10 Malaise traps along a latitudinal gradient in five old-growth forests: San Felasco Hammock, FL (30° N, 82° W); Tall Timbers Research Station, FL (31° N, 84° W); Hitchiti Experimental Forest, GA (33° N, 84° W); Patuxent Wildlife Research Center, MD (39° N, 77° W), and Shaw Woods, Ontario (46° N, 77° W). Of 18,791 ichneumonid wasps collected, 1,487 campoplegines and 4,494 ichneumonines were sorted to 241 species (95 species of Campopleginae and 146 of Ichneumoninae). Campoplegine species richness was highest at the Georgia site: San Felasco (20 species), Tall Timbers (32), Hitchiti (49), Patuxent (35), and Shaw Woods (12). Ichneumonine species richness was highest at the Maryland site: San Felasco (47), Tall Timbers (30), Hitchiti (44), Patuxent (68), and Shaw Woods (37). The results confirm reported trends that peak North American ichneumonid species richness lies at midlatitudes. However, they document greater biodiversity in the southern states and a broader peak than previously reported.

KEY WORDS   Ichneumonidae, biodiversity, parasitoids, latitude, old-growth forests

NUMEROUS STUDIES DOCUMENT and attempt to explain why floral and faunal diversity generally increase as one approaches the equator (Dobzhansky 1950, Stevens 1989, Sime and Brower 1998). Certain taxa of parasitic Hymenoptera are notable exceptions to this pattern. Owen and Owen (1974) first proposed that the trend for the Ichneumonidae runs contrary to that for most plant and insect families; they reported more species in samples from temperate Europe than in tropical Africa. Janzen (1981) analyzed published distribution maps of 1,717 North American ichneumonid species and concluded that their peak species richness lies at midlatitudes between 38 and 42° N. On the east coast, for instance, his analysis suggested that species richness from central Virginia to central New York is 1.5 times higher than in central Georgia and 2.5 times higher than in central Florida. He further predicted fewer species of ichneumonids per host species as one approaches the equator, with proportionately fewer species of tropical specialists.

More recently, Gauld (1986, 1987, 1991) and Gaston and Gauld (1993) examined latitudinal trends for a number of subfamilies of the Ichneumonidae. Their results are equivocal. Some subfamilies appear more diverse in the tropics, others, in temperate areas. Gauld (1986) presented evidence suggesting that Australian ichneumonid diversity decreases slightly nearer the equator. In part, this is because of the absence in northern Australia of taxa such as the Ctenopelmatinae, which parasitize sawflies and are relatively rare in the tropics. Gauld (1987) reported higher diversity for the Cryptini, Pimplini, and Ophioninae toward the equator and higher diversity of sawfly parasitoids away from it. In Gauld's (1991) monograph of the lower pimpliform subfamilies of Costa Rica and later analysis by Gaston and Gauld (1993), both local and regional richness of these wasps is generally higher in the tropics than elsewhere. In contrast to the Ichneumonidae, other parasitic families such as the Chalcididae (Hespenheide 1979) and the Encyrtidae (Noyes 1989) appear to be more speciose in the tropics.

It is difficult to weigh the relative importance of factors that govern parasitoid community composition as a function of latitude. It requires comparable diversity estimates between locations. Few studies have employed the same sampling methods across large geographic areas to obtain comparable site or regional diversity estimates. With speciose taxa, estimates of species richness generally increase with sampling effort (Colwell and Coddington 1994). Well-collected areas can, therefore, be expected to yield higher estimates of species richness than poorly collected areas. Janzen's (1981) finding that the peak of North American ichneumonid species richness lies at midlatitudes and a similar finding by Quicke and Kruft (1995) for the Braconidae are based on published records over large geographic areas. We suspected that their results may have been in part an artifact of the proximity of major collections and may not reflect underlying biological processes. The current study was designed to overcome this potential artifact. We examine species diversity of two ichneumonid subfamilies along a lat-

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itudinal gradient in eastern North America using Malaise traps as a standard sampling technique at five sites from Ontario to Florida.

Materials and Methods

Study Organisms. The Ichneumonidae, consisting of 35 subfamilies (Wahl 1993) and an estimated 60,000 species, is thought to be the most speciose family in the world, with the possible exception of the Curculionidae (Townes 1969) or the Staphylinidae. We examined two subfamilies that represent the two major life history strategies within the Ichneumonidae, idiobiont and koinobiont parasitism (Askew and Shaw 1986). The Campopleginae are an abundant group of koinobiont endoparasitoids; hosts are mostly Lepidoptera and Symphyta (Wahl 1993). The Ichneumoninae attack Lepidoptera exclusively (Gauld 1988). Most are idiobiont endoparasitoids that attack pupal stages, whereas others are koinobiont endoparasitoids that attack final-instar larvae (Wahl 1993). The Ichneumoninae are the most speciose group of idiobiont endoparasitoids within the Ichneumonidae.

Sites and Sampling. We collected samples in 1993 with fine mesh (0.33 mm) Townes-style Malaise traps (Townes 1972) purchased from Sante Traps (Lexington, KY). We sampled Ontario and Maryland in 1992 as well. We ran two traps at each site and used 70% ethanol as a preservative. The traps were aligned on a north–south axis, with the collecting head toward the southern end. Collaborators serviced each trap weekly throughout the period of flight activity, except late or early in the season when they collected some samples biweekly or monthly.

We sampled in five old-growth forests from 45° 42″ N to 29° 44″ N. We collected samples at Shaw Woods, Renfrew County, Ontario (45° 42″ N, 77° 4″ W) from 6 May to 22 October 1992 and 6 May to 21 October 1993. This site's trees are dominated by *Fagus grandifolia* Ehrhart and *Acer saccharum* Marshall (Dugaul 1980, Lockard 1995). We collected samples at Patuxent Wildlife Research Center, Prince Georges County, MD (39° 03″ N, 76° 47″ W) from 6 April to 9 November 1992 and 12 April to 25 October 1993. Hotchkiss and Stewart (1947) described this site, which is dominated by *F. grandifolia.* We collected samples at Hitchiti Experimental Forest, Jones County, in Georgia's Piedmont (33° 03″ N, 83° 43″ W) from 23 March to 21 December 1993. Lockard, (1995, *Appendix 2*) lists this site's tree species, dominated by *Acer rubra* L., *Querqus alba* L., and *Lirodendron tulipifera* L. We collected samples in the Woodyard Hammock at Tall Timbers Research Station, Leon County, in Florida's coastal plain (30° 39″ N, 84° 15″ W) from 30 March to 14 December 1993. Because we missed the first part of this flight season, we also include a sample from 4 to 28 March 1994. Hirsch (1981) described this site; dominant tree species include *F. grandifolia* and *Magnolia grandiflora* L. We collected samples at San Felasco Hammock State Preserve, Alachua County, FL (29° 44″ N, 82° 27″ W) from 15 March to 18 December 1993.

Dunn (1982) provides details of this climax mesic hammock in the Coastal Plain.

Specimen Handling and Tabulation. All ichneumonids were sorted to subfamily and all ichneumonines and campoplegines were sorted to morphospecies with the assistance of D. B. Wahl. We identified the Ichneumoninae and the Campopleginae genera *Dusona* and *Casinaria* to species whenever possible. Identifications were based on Heinrich (1960a, 1960b, 1961a, 1961b, 1961c, 1962a, 1962b, 1977), Walley (1940 and 1947), and the resources of the American Entomological Institute (AEI) in Gainesville, FL. Sexual dimorphism in the Ichneumoninae made it impractical to associate males and females in some genera. Thus, within these sexually dimorphic genera where both males and females were present at a site, we counted only the number of species in the most speciose sex. We deposited specimens at the University of Georgia and the AEI. See Wayman (1994) for details of sorting techniques.

Statistical Estimators. Malaise traps are generally recognized as efficient collecting devices of ichneumonoids (Matthews and Matthews 1970, Owen et al. 1981, Darling and Packer 1988, and Noyes 1989). Combining both sites in Florida, for example, we collected 53 ichneumonines in one season, nearly three-fourths of the known species in Florida. Nevertheless, it is unlikely that we collected all the species at any site, and hence, we must consider possible site differences in the proportion of fauna collected. For example, we may have sampled a lower proportion of the species from sites with high diversity. Thus, in comparing species richness among sites, we might underestimate rich taxa and sites relative to depauperate ones. To examine such potential bias across sites, we used statistical estimates of species richness and data from additional years.

To estimate species richness, we used the EstimateS statistical package version 5 (Colwell 1997) and used 100 randomizations for 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}). To our knowledge, no one has rated estimator performance using Malaise trap samples. Thus, we used all nine estimators available in the EstimateS software but only present results for the maximum, minimum, and median estimator. For references and review of these statistical estimators, see Colwell (1997), Colwell and Coddington (1994), and Chazdon et al. (1998).

As with all collecting methods, there are inherent biases in using one method over another. For instance, two Malaise traps in the same 1-ha plot may collect significantly different material, making between site comparisons difficult. The observed data are presented by trap and by total to show the between trap differences. To address the difference in sample size between sites, we generated Coleman richness expectation curves (Coleman 1981, Coleman et al. 1982)

Table 1. Campopleginae and Ichneumoninae species (and individuals) collected

Site (latitude)	Year	Campopleginae			Ichneumoninae		
		Trap 1	Trap 2	Total	Trap 1	Trap 2	Total
Shaw Woods, Ontario	1992	7 (11)	5 (9)	9 (20)	24 (46)	21 (50)	29 (96)
(45° 42″ N)	1993	6 (9)	8 (14)	12 (23)	24 (64)	22 (53)	37 (117)
	1992+1993	10 (20)	11 (23)	16 (43)	38 (110)	34 (103)	50 (213)
Patuxent, Maryland	1992	21 (73)	14 (83)	23 (156)	44 (506)	45 (294)	59 (800)
(39° 03″ N)	1993	31 (168)	20 (144)	35 (312)	45 (422)	60 (308)	68 (730)
	1992+1993	37 (241)	23 (227)	40 (468)	64 (928)	73 (602)	89 (1530)
Hitchiti, Georgia							
(33° 03″ N)	1993	35 (252)	41 (320)	49 (572)	30 (320)	38 (373)	44 (693)
Tall Timbers, Florida							
(30° 39″ N)	1993[a]	24 (76)	25 (137)	32 (213)	21 (282)	24 (400)	30 (682)
San Felasco, Florida							
(29° 44″ N)	1993	15 (47)	16 (33)	20 (84)[b]	25 (243)	37 (407)	47 (663)[b]

[a] To standardize trapping duration, data from Tall Timbers include 3 wk in 1994.
[b] Includes 4 *Cratichneumon*, 2 *Campoplex*, 1 *Casinaria*, 1 *Hyposoter*, 1 *Limonthe*, and 8 *Barichneumon* specimens for which trap numbers are unknown.

with 95% confidence interval in EstimateS. These curves (Figs. 1–3) plot the expected richness for randomized subsamples of the entire data set providing a method to evaluate the degree of sample heterogeneity (Colwell and Coddington 1994).

Results and Discussion

Observed Species Richness. We sorted a total of 18,791 Ichneumonidae from the five study sites, including 4,494 ichneumonines in 37 genera and 1,487 campoplegines in 18 genera. Across the five sites, we tabulated a minimum of 146 ichneumonine and 95 campoplegine species. We caught more species at the midlatitude sites (Table 1). The Georgia site had the highest observed campoplegine species richness (49 species), and the Maryland site had the highest observed ichneumonine species richness (68 species). The Maryland site had the highest observed species richness for the two subfamilies combined (103 species), with the Georgia site second (93 species).

Estimates of Species Richness. To estimate species richness at the sites, we modeled species accumulation as a function of trapping effort (Table 2). Some of these species accumulation curves did not reach an asymptote (not shown), indicating that more sampling

is needed to estimate accurately total species richness. The species accumulation curves did not lie below the Coleman (or rarefaction) curves, indicating low sample heterogeneity. For campopleginе species richness, the observed data (Table 1; Georgia highest, Maryland second, Tall Timbers [Florida] third, San Felasco [Florida] fourth, and Ontario lowest) generally correspond with the median rank orders of the estimates (Table 2). The inversion of San Felasco (Florida) and Ontario is the exception, possibly because of the high percent (53%) of singletons at Ontario, a consequence of few individuals being caught. Regarding the Ichneumoninae, the rank order of the median estimator and the observed data are the same. Maryland is ranked first, San Felasco (Florida) second, Georgia third, Ontario fourth, and Tall Timers (Florida) last. Thus, the observed data and the estimators generally support the conclusion that species richness in these two subfamilies is greater at midlatitudes. However, our results suggest relatively higher ichneumonid richness at southern sites, particularly in Georgia, than reported by Janzen (1981).

The strength of this conclusion assumes that we can trust the estimators. Some evidence suggests otherwise. Because some estimators did not reach an asymptote, suggesting that two trap-years may be insuf-

Table 2. Median (S_{Med}), maximum (S_{Max}) and minimum (S_{Min}) estimates of campoplegine and ichneumonine species richness and percent singleton's (P_S) collected

Site	Year	Campopleginae			Ichneumoninae			
		S_{Med}	S_{Max}	S_{Min}	S_{Med}	S_{Max}	S_{Min}	P_S, %
Shaw Woods, Ontario	1992	16	24_{MR}	11_B	41	54_{MR}	34_B	45
	1993	40	58_{ICE}	16_B	57	135_{MR}	46_B	53
	1992+1993	43	$77_{C1,2}$	20_B	71	467_{MR}	59_B	47
Patuxent, Maryland	1992	36	40_{J2}	28_B	89	97_{J2}	67_{MM}	36
	1993	45	52_{J2}	40_{MR}	106	114_{J2}	79_{MM}	37
	1992+1993	47	53_{J2}	43_{MM}	131	148_{J2}	94_{MM}	34
Hitchiti, Georgia	1993	67	77_{J2}	57_B	60	87_{C2}	48_{MM}	37
Tall Timbers, Florida	1993	42	52_{J2}	36_{MM}	45	66_{C2}	31_{MM}	34
San Felasco, Florida	1993	27	30_{J2}	23_B	86	119_{C2}	51_{MM}	45

Estimates are shown as some value (S_x), where S is the estimate of species richness and x is the method used to calculate species richness by the incidence-based coverage (S_{ICE}), Chao 1 (S_{C1}), Chao 2 (S_{C2}), 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}).
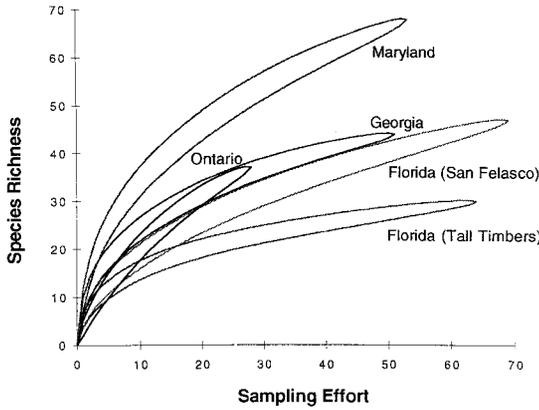
Fig. 1. Coleman richness expectation curves with 95% confidence intervals of Ichneumoninae at Shaw Woods, Ontario; Patuxent, Maryland; Hitchiti, Georgia; Tall Timbers, Florida; and San Felasco, Florida, in 1993. Sampling effort is the number of samples that contain at least one ichneumonine.

ficient to estimate accurately total species richness, we present Coleman curves as an additional means of comparing diversity across sites (Figs. 1–3). For the Ichneumoninae, Fig. 1 shows that the Maryland site has higher species richness than the three southern sites. This figure's Coleman curve for Ontario shows a small sample size and steep slope, indicating that Ontario may have higher ichneumonine richness than the current study's observed value and estimators suggest. For the Campopleginae, the Coleman curves in Fig. 2 strongly suggest that species richness is highest in Georgia. The data in Fig. 3 strengthen this finding. It shows that two trap-years of effort in Georgia (1993) yielded both a steeper Coleman curve and higher absolute species richness than four trap-years of effort, at the second richest site, Maryland (1992 and 1993).
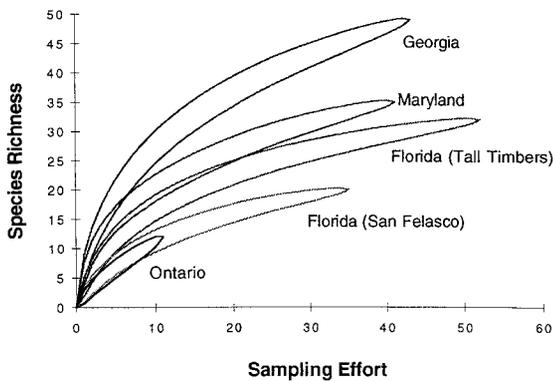

Fig. 2. Coleman richness expectation curves with 95% confidence intervals of Campopleginae at Shaw Woods, Ontario; Patuxent, Maryland; Hitchiti, Georgia; Tall Timbers, Florida; and San Felasco, Florida, in 1993. Sampling effort is the number of samples that contain at least one campoplegine.
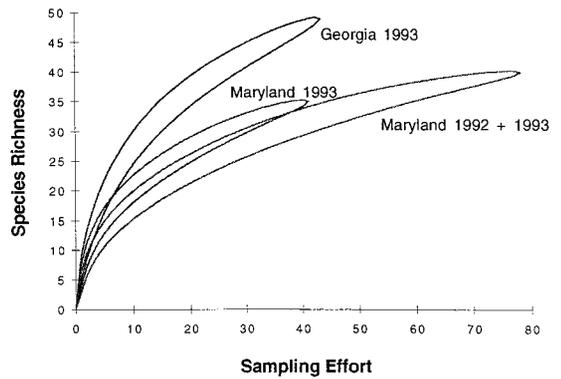

Fig. 3. Coleman richness expectation curves with 95% confidence intervals of Campopleginae at Hitchiti, Georgia, in 1993 and Patuxent, Maryland, in 1992 and 1993. Sampling effort is the number of samples that contain at least one campoplegine.

Furthermore, Gaasch (1996) found 117 ($N = 3395$) campoplegine and 100 ($N = 3106$) ichneumonine species in 1993 and 1994 from a variety of habitats adjacent to our old-growth site in Georgia. These results show that the diversity in the neighboring landscape of our Georgia site exceeds maximum estimates for the Campopleginae ($S_{J2} = 77$) and Ichneumoninae ($S_{C2} = 87$) (Table 2). Thus, unless the additional species found by Gaasch never enter old-growth, it is likely that all the statistical methods that we used underestimate true species richness. Despite such limitations, until further work tests their validity or proves otherwise, we feel that the estimators as a group strengthen our conclusions.

Peak Ichneumonid Diversity. Table 3 shows the comparison of our results to those in Janzen's (1981) report on eight ichneumonid subfamilies. Our analysis for the two subfamilies generally supports his finding of peak parasitoid richness at midlatitudes. However, Janzen reported a 41% drop in species richness from his maximum, between latitudes 38 and 42° N, which includes our Maryland site, to the latitudes 32.5 and 34.9° N, which includes our Georgia site. He noted that the sharpest decline in species richness occurred at ≈37.4° N, with virtually no change of land mass in this

Table 3. Latitudinal trends in ichneumonid species richness

Location	Latitude	Current study		Janzen (1981)	
		S_{OBS}	P_{OBS}	S_{JAN}	P_{JAN}
Ontario	45° 42″ N	49	0.48	992	0.95
Maryland	39° 03″ N	103	1	1039	1
Georgia	33° 03″ N	93	0.90	612	0.59
Florida	30° 39″ N	62	0.60	340	0.33
Florida	29° 44″ N	67	0.65	197	0.19

S_{OBS} is the number of species collected in the current study in 1993. P_{OBS} expresses site species richness as a proportion of that at Maryland, the site with the highest observed species richness, and is $S_{OBS}/103$. Correspondingly, S_{JAN} is the total number of species reported by Janzen (1981) for each latitudinal band that contains one of the current study sites, and P_{JAN} is $S_{JAN}/1039$.

latitudinal band. In contrast, our data show only an 11% decline between Maryland and Georgia. Our results show a wider peak than reported by Janzen, extending south to include the Georgia Piedmont. We presume that insufficient collecting in southern states, particularly in the northern regions of Georgia, contributed to Janzen underestimating species richness in southern latitudes relative to better collected northern ones. Heinrich (1977) stated that ". . . no attempt has been made to explore the [Ichneumoninae] fauna of these areas [Georgia, Alabama, Tennessee, and Arkansas] exhaustively."

The difference between Janzen's (1981) findings and the current study may be biological, stemming from differences in the subfamilies used in the two studies or because our eastern old-growth forest sites do not adequately represent the species richness in Janzen's corresponding latitudinal bands. Alternatively, the differences may result from methodological problems. The latitudinal bands of highest ichneumonid diversity reported by Janzen include the Smithsonian Institution and a disproportionate number of other major North American museums. We collected less than half the number of species in Ontario than in Maryland; Janzen (1981), for the equivalent latitudinal bands, reported only a 5% drop in species richness (Table 3). One explanation for the difference in these findings is that collecting around the Canadian National Museum, which is located in Ontario, has uncovered a higher proportion of a relatively depauperate fauna than has occurred elsewhere.

We caution that geographic analyses based on collections and published reports that do not rely on standard methods or equal sampling effort will underestimate biodiversity in under-collected areas. Funk and Morin (2000) document the disparity in collecting effort for plants by surveying the size and activity of southeastern herbaria. For example, in terms of plant collections per square mile, they report that Georgia herbaria contain only 5.66 specimens, under half the average for the United States (minus Alaska) of 13.21 specimens, and considerably under the 33.15 specimens held within the North Carolina herbaria. Similarly, depauperate ichneumonid collections from southern states may explain why Janzen reported an almost twofold drop in species richness between the latitudinal bands corresponding to our Maryland and Georgia sites.

Why Peak in Midlatitudes? We report a peak of ichneumonid species richness at midlatitudes, with lower diversity in Florida and Canada. Why this occurs remains unclear. The processes that determine the relationship between parasitoid species richness and latitude are poorly understood (Hawkins et al. 1992). It has been suggested that resource fragmentation (Janzen and Pond 1975, Janzen 1981, Askew and Shaw 1986, Hawkins 1990), plant-host-parasitoid interactions (Hawkins and Lawton 1987, Gauld et al. 1992, Sime and Brower 1998), competition (Hawkins 1990), predation (Rathcke and Price 1976), and environmental factors (Townes 1972, Hawkins 1990, Gauld 1991, Hawkins et al. 1992) influence parasitoid diversity.

Alternatively, this peak at midlatitudes may also result from the mid-domain effect, a geometric theory used to explain species diversity gradients (Colwell and Lees 2000). This model predicts maximum species diversity at the midpoint of large bounded geographic areas relative to boundary constraints and range centers. In the current study, under the mid-domain effect one would expect species ranges to overlap more in Maryland and Georgia and less in Florida and Ontario where species ranges are constrained by oceans to the south and Arctic climate to the north.

The lower species richness found at our Floridian sites may be explained by climate. 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. Lockard (1995) reports that parasitoid activity at each site peaked before summer temperatures average above 27°C; although such peaks may have been driven by host availability (Gaasch et al. 1998). Heinrich (1977, p. 3) suggests that "the Ichneumoninae have proliferated in speciation only in moderate and cool climates."

Similarly, the lower diversity observed in Ontario may be explained by climate. Canada's harsh winters and short flight season may be adequate enough to explain the low diversity measured at Shaw Woods. Furthermore, Ontario may still be recovering from the last glaciation and still be in the process of accumulating species.

Our data are generally consistent with Janzen's (1981) finding that maximum ichneumonid species richness occurs at midlatitudes in North America. However, we conclude that peak diversity covers a wider area than Janzen reported. Rather than a relatively narrow peak centered around 38–42° N, our data suggest that high ichneumonid species richness occurs in a broad swath from at least Maryland to Georgia's Piedmont, dropping in the south near the Coastal Plain and in the north near Canada. We feel that the almost twofold drop in species richness from 37.5 to 32.5° N (Janzen 1981) is possibly the result of under-collecting in the southeast relative to extensive collecting in proximity to large, northern museums. Alternatively, it may be because Janzen considered eight different subfamilies than the two considered in the current work. Nevertheless, we caution against using museum data to examine geographic trends in biodiversity without correcting for differences in collecting effort.

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