Contributed Papers

Indicator Taxa, Rapid Biodiversity Assessment, and Nestedness in an Endangered Ecosystem

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Abstract: *To prioritize areas for conservation, biologists and managers need information on species diversity in threatened habitats. The resources available for such inventories remain severely limited, increasing the need to develop speedier ways to estimate the status of target habitats. We present a study of the use of such techniques in the highly fragmented oak savannas of southern Ontario, including selection of indicator taxa, use of rapid biodiversity assessment based on morphospecies, and analysis of community structure. We found that butterflies and skippers can be used to predict richness among Hymenoptera in the study sites, which is consistent with the hypothesis that these easily surveyed Lepidoptera are good candidates for indicator status. Richness values for hymenoptera morphospecies in these savanna remnants were strongly correlated with species richness scores as estimated by systematists, although nonspecialists tended to "split" species into more than one morphospecies. Finally, both the Hymenoptera and Lepidoptera communities in these oak savannas exhibited a high degree of nestedness, suggesting that local extinctions, mostly undocumented, are important determinants of the richness patterns across these widely separated savanna study sites. We found no evidence of significant spatial autocorrelation, probably because of the wide separation of study sites.*

Taxones Indicadores, Evaluación Rápida de la Biodiversidad y la Importancia del Anidamiento en un Ecosistema en Peligro

Resumen: *Para priorizar áreas para la conservación, los biólogos y manejadores necesitan información sobre la diversidad de especies en hábitats amenazados. La disponibilidad de recursos para llevar a cabo tales inventarios es aún muy limitada, incrementando la necesidad de desarrollar formas rápidas de estimar la situación de los hábitats que son objeto del estudio. Presentamos un estudio sobre el uso de estas técnicas en las sabanas altamente fragmentadas de robles del sur de Ontario, incluyendo la selección de taxones indicadores, el uso de evaluaciones rápidas de la biodiversidad basadas en morfoespecies y un análisis de la estructura comunitaria. Encontramos que las mariposas y saltadores pueden ser usados como predictores de la riqueza entre himenópteros en los sitios de estudio, lo cual es consecuente con la hipótesis de que estos lepidópteros fácilmente muestreables son buenos candidatos para ser considerados indicadores. Los valores de la riqueza de morfoespecies de himenópteros para estos remanentes de sabana estuvieron fuertemente correlacionados con datos de riqueza de especies estimados por sistematistas, a pesar de que los sistematistas tienden a "dividir" especies en más de una morfoespecie. Finalmente, tanto las comunidades de himenópteros como de lepidópteros de estas sabanas de robles exhibieron un nivel alto de anidamiento, sugiriendo que las extinciones locales, mayormente no documentadas, son determinantes importantes de los patrones de riqueza a lo largo de estos sitios de estudio de sabana ampliamente separados. No encontramos evidencia de una autocorrelación espacial significativa, probablemente debido a la amplia separación entre sitios de estudio.*

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Introduction

The enormity of the present extinction crisis and the limited time and budgetary resources available for conservation force biologists to take shortcuts in biodiversity assessment. One such approach is to use selected indicator taxa as proxies for the biodiversity of a habitat in the hope that, by successfully conserving reasonable numbers of the indicator taxon, a large proportion of local biodiversity can also be saved (Landres et al. 1988; Karr 1991; Crisp et al. 1998; Duelli & Obrist 1998; Rodrigues et al. 1998; Tardif & DesGranges 1998). Candidates for indicator status should reflect the diversity of other taxa in the target habitats and should be relatively easy to sample (Kremen et al. 1993; Pearson 1994). Higher taxa are more commonly used than single species as indicators for biodiversity monitoring (Pearson 1994; Howard et al. 1998) because individual species, although occasionally useful, may not be sensitive to habitat changes that affect other species of concern (Noss 1990; Simberloff 1998). Some have proposed certain higher-level taxa for broad consideration (e.g., Coleoptera: Cicindelidae; Pearson & Cassola 1992; Carroll & Pearson 1998). Ultimately, such taxa must be evaluated at the scale of the habitat, despite the attractiveness of relying on broad-scale analyses (e.g., Kerr et al. 1998; Rodrigues et al. 1998; Currie et al. 1999). Large-scale correlations among the diversity patterns of different taxa do not necessarily translate to similar habitat-scale patterns.

Rapid biodiversity assessment, based on morphospecies or "recognizable taxonomic units" (RTU), provides a second possible shortcut in assessing habitat status (Oliver & Beattie 1993). This procedure remains controversial because of the difficulty of establishing consistent nomenclature for morphospecies across independent samples and because rapid biodiversity assessments may not always be much faster than more traditional systematic approaches to identification (Brower 1995; Goldstein 1997; Oliver & Beattie 1997). Nonetheless, correct species-level identification of specimens from large collections, although desirable, is often impractical (Oliver & Beattie 1996*a*). The promise of rapid biodiversity assessment is in its potential to predict species richness despite a dearth of systematics expertise. The presence of a strong relationship between morphospecies and actual species richness scores would indicate that the approach represents a reasonable surrogate for the traditional, systematic identification of samples for biodiversity monitoring.

Assessments of community nestedness (Patterson & Atmar 1986; Blake 1991; Atmar & Patterson 1993; Worthen & Rohde 1996; Fleishman & Murphy 1999) provide vital information beyond the simple species counts typically included in indicator monitoring programs and may assist with predictions of biotic responses to environmental change (e.g., McDonald & Brown 1992). A series of biotic communities exhibits a nested pattern when the species complement in patches of low diversity is a predictable subset of the biotas found in richer sites. When communities exhibit strongly nested patterns, it may be possible to predict which species are likely to disappear from small habitat patches in response to human or natural fragmentation of the landscape or other perturbation. Nestedness analyses remain primarily post hoc descriptors of extinction patterns and possibly of colonization dynamics (Boecklen 1997), but they can generate testable predictions regarding diversity in unsampled habitats; for example, based on known levels of disturbance in the area, a particular species complement may be expected given the nested pattern found in the sampled habitats.

Nested subset patterns are expected in fragmented habitats in which past extinctions have been prominent in shaping present-day diversity patterns (Atmar & Patterson 1993; Worthen 1996). Consequently, nested subset patterns are common in systems of land-bridge islands as well as human-modified landscapes (Wright & Reeves 1992) and may provide insight into reserve selection methodology (the SLOSS [single large or several small reserves] debate; Burkey 1989; also Boecklen 1997). Small reserves are unlikely to conserve diversity well across a strongly nested community structure because such areas would maintain redundant assemblages of relatively common species (Worthen 1996). Several small reserves together are unlikely to harbor diversity comparable to that of a single large reserve in such circumstances, clearly demonstrating the preferable conservation strategy. In communities characterized by frequent extinctions, the presence of a strongly nested subset structure may, for example, permit the prediction of species composition following habitat modification (McDonald & Brown 1992; Worthen 1996).

We tested the utility of butterflies and skippers as indicators of hymenopteran diversity in the globally endangered and highly fragmented oak savanna ecosystem. A detailed natural historical account of this ecosystem, including past and present North American distributions, is provided by Kurczewski (1998). Butterflies and skippers have been used as indicators in many habitats (e.g., Kremen 1992; Kremen et al. 1993; Wood & Gillman 1998), are relatively easily sampled and identified, and are sensitive to changes in habitat quality (Murphy & Ehrlich 1989; Packer 1994). The hymenopterans we sampled are far more diverse than butterflies and skippers, are readily collected with passive sampling techniques (e.g., Darling & Packer 1988), but are relatively difficult to identify to species level. Using rapid biodiversity assessment (Oliver & Beattie 1996*b*), we tested the morphospecies approach to estimating actual species richness in samples of Hymenoptera. Finally, using a recently developed nestedness algorithm that distinguishes

between the observed degree of nestedness and that expected to occur randomly (Atmar & Patterson 1993), we examined nestedness among both Hymenoptera and Lepidoptera samples in the oak savanna fragments. Because past extinctions are believed to be important in shaping the present-day diversity patterns of these savanna communities, we predicted they would exhibit a significant nested structure.

Methods

Study Sites

Oak savanna is a critically threatened habitat that has been reduced to between 0.02% and 0.10% of its presettlement range (Nuzzo 1986; Leach & Givnish 1996). In southern Ontario, almost no large tracts of this habitat remain, although significant savanna remnants persist or have been restored along Lake Huron (the Karner Blue Sanctuary and Pinery Provincial Park) and just north of Lake Erie at the Manestar Tract and along the Delhi-Simcoe Railway (Gore and Storrie Limited 1993; Kurczewski 1998; Fig. 1). Other savanna remnants may be found in southern Ontario, but many are arguably of secondary importance for conservation because of their isolation, levels of human disturbance, and small size.

Study sites consisted of four different "complexes," each containing between two and five savanna habitat fragments. These savannas were selected because the Ontario Ministry of Natural Resources identified them as botanically important remnants of this formerly extensive habitat type (Bakowsky & Riley 1992; Gore and
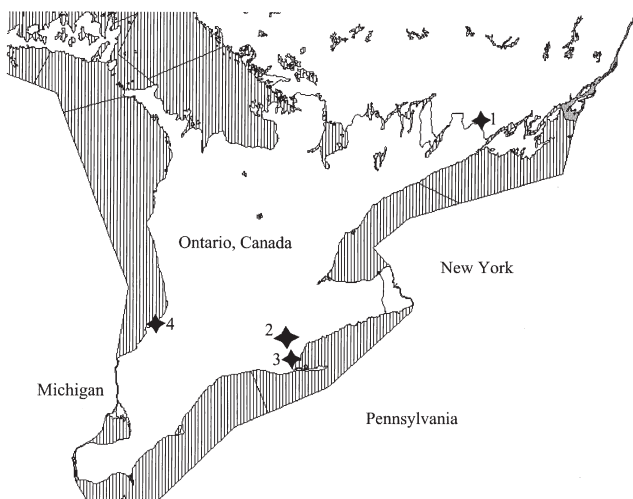

Figure 1. Distribution of field sites in southern Ontario: (1) Trent River prairie (3 locales); (2) Delhi-Simcoe Railway (5 locales); (3) Manestar (3 locales); (4) Karner Blue Sanctuary (2 locales). Approximate scale is 1 cm = 31 km.

Storrie Limited 1993; Fig. 1) and so our sampling regime would include a large proportion of the range occupied by oak savannas in Ontario. Several provincially rare species persist in some of these savanna remnants, including wild lupine (*Lupinus perennis*; Smith 1996), dwarf hackberry (*Celtis tenuifolia*; Oldham 1991), and a rare sphecid wasp (*Tachysphex pechumani*; Kurczewski 1998). Other species, including the Karner blue butterfly (*Lyceides melissa samuelis* Nabokov; Packer 1991), frosted elfin (*Callophrys irus*; Packer 1994), and eastern pine elfin (*Callophrys niphon*), are known or believed to have been extirpated recently from Ontario savannas.

Survey Techniques

We sampled butterflies and skippers using standard transect techniques (Pollard & Yates 1993) during the summers of 1994 to 1996. Transect sampling techniques have been discussed extensively elsewhere (e.g., Pollard & Yates 1993; Beavers & Ramsey 1998) and are thought to provide good estimates of local butterfly and skipper species richness (e.g., Kremen 1992; Natuhara et al. 1998). We conducted five or six sampling transects in each savanna habitat between mid or late May and the end of August or beginning of September. This is comparable to the sampling intensity in other butterfly surveys in similar habitats (e.g., Debinski & Babbit 1997). Transects were designed to cover the complete range of local topographical heterogeneity (Swengel 1998) within individual habitat patches. This serves to incorporate some variability in local microclimates and should increase the number of butterfly and skipper species detectable along the transect route. All target organisms visible in a "moving circle" extending approximately 3 m from the observer were recorded in the transect sample. Most species could be identified without capture, but some were trapped with a standard butterfly net and identified either in the field (then released) or at the lab with a field guide (Opler 1994). The few butterflies and skippers that could not be identified were typically too fast to catch or see clearly or could not be pursued because of intervening scrub; these were scored as "unknown." We also collected data on regional butterfly and skipper species richness to determine whether patterns we observed among lepidopterans might be a function of factors operating on a larger scale (Kerr et al. 1998). Butterfly and skipper diversity varies relatively little across the regions in the study sites, so we did not expect this to strongly influence our landscape-scale findings.

We sampled "flying" Hymenoptera in 8 of the 13 savanna study sites with malaise traps (Santé traps; Darling & Packer 1988). We examined the aculeate and symphytan hymenopterans in detail. Although the exclusion of parasitoid hymenopterans reduces the species richness of Hymenoptera surveyed, accurate identification of these organisms requires additional resources that

were not available. Malaise traps were also placed in an adjoining ecotonal area for three of the eight habitat fragments. Traps could not be placed in all ecotones or savanna fragments because of problems with human disturbance. We collected samples during approximately the last 2 weeks of August 1994. Technicians sorted the large collections of insects to order, and bees, aculeate wasps, and sawflies (from the Hymenoptera) were then sorted into morphospecies (Oliver & Beattie 1996*a,b*). We excluded ants from the dataset because malaise traps do not sample their diversity effectively (Darling & Packer 1988). We then identified samples to species level if keys were available. Specialists then verified all putative species identifications, providing us with a corrected richness value for Hymenoptera (data in Sugar et al. 1999). We divided morphospecies values by sampling period, which varied slightly between sites, and plotted these against the corrected richness values. We used linear regression to test for a relationship between the morphospecies richness score and actual species richness values and to relate butterfly and skipper species richness to that of the Hymenoptera. To stabilize residual variation, we log-transformed variables for analyses of morphospecies data.

Spatial Autocorrelation

Spatial autocorrelation among study data may lead to violation of the assumptions of independence common to many statistical tests and render them invalid (Koenig 1999). We tested the lepidopteran data for spatial autocorrelation by calculating Moran's I statistic for irregularly distributed collection points (Sokal & Oden 1978*a*, 1978*b*; Sawada 1999). The hymenopteran data were collected from fewer locales than the lepidoptera data ($n = 8$ vs. $n = 13$), and the collection sites tended to be farther apart. Butterflies are expected to be relatively strong dispersers and to respond quickly to environmental variation, so we expected spatial autocorrelation to be stronger for these data. To determine whether correlations remained significant under conservative assumptions, we bootstrapped the hymenopteran data (10,000 repetitions), extracted 8 of the 14 data points (such that the number of degrees of freedom would be half that of the original regression), and recalculated regression statistics for each extraction. We then determined the median and mean probabilities that these regression simulations were significant.

Moran's I is a standard test statistic used to detect spatial autocorrelation (Sokal & Oden 1978*a*) and resembles a correlation coefficient in that it varies from -1 to 1, signifying negative or positive spatial autocorrelation (Sokal & Oden 1978*b*; Sawada 1999). We located the different fragments within each savanna complex on a high-resolution digital map of Ontario (available from the Canada Centre for Remote Sensing) and determined

the Euclidean (x-y) coordinates of each site on the map. Using Rook's Case software package (version 0.9.6; Sawada 1999), we then calculated Moran's I values for the butterfly transect data based on an irregular lattice (that is, spatially noncontinuous data) for adjacent sampling sites. We ran a Monte-Carlo simulation ($n = 10,000$; Sawada 1999) to estimate the probability that the observed Moran's I value falls in the range expected if observations were distributed randomly among sampling locales (Fig. 2). The different savanna complexes we included are separated by distances, ranging from approximately 50 km to more than 450 km, that are large relative to the scale of factors likely to determine local species richness (e.g., levels of human disturbance), so we did not expect to observe significant spatial autocorrelation.

Nestedness

Some techniques for calculating nestedness in a data matrix do not adequately control for the degree of nestedness expected by chance and overestimate the nestedness of some data matrices (Roberts & Willig 1998; Brualdi & Sanderson 1999). The nestedness calculator (Atmar & Patterson 1993) we employed controls for this
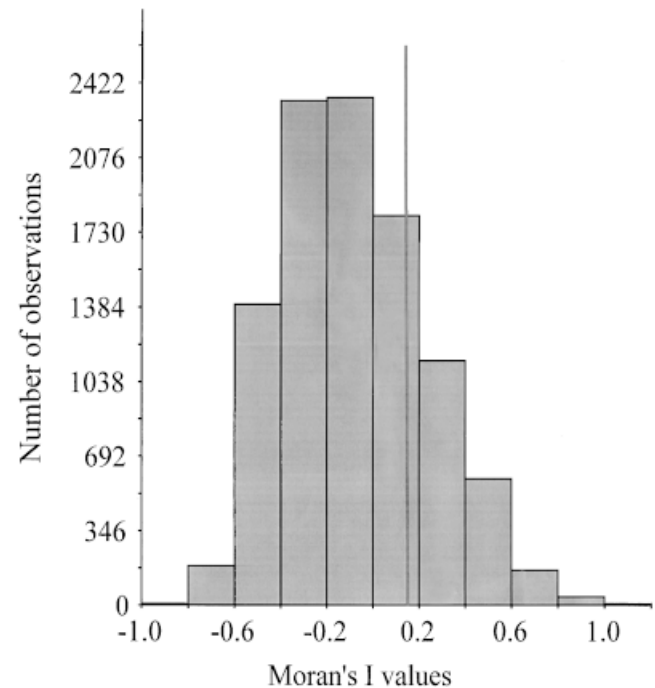
Figure 2. Distribution of Moran's I values after observed butterfly and skipper species richness data is randomly distributed among the 13 field sites 10,000 times. The vertical line represents the observed Moran's I, which is not significantly higher than that expected at random (corresponding to a lack of spatial autocorrelation among the data).

problem by running a Monte Carlo simulation to estimate the distribution of nestedness scores expected in a randomly distributed data matrix of the same dimensions as the actual data matrix. The actual nestedness score for the study data matrix is then compared against the distribution of randomly generated matrices to determine the probability of observing such a score by chance. This approach appears to provide an estimate of nestedness that is relatively robust compared with alternative models, although rapid development of methods of measuring nestedness continues (e.g., Brualdi & Sanderson 1999).

Our nested subsets analyses were based on presence-absence matrices for Hymenoptera (based on malaise trap samples) and butterflies and skippers (based on 3 years of transect sampling) for all savanna fragments from which we made collections. We used Atmar and Patterson's (1993) method to establish the extent to which our data were nested. Nestedness values can range from 0, for species found in patches with low diversity which are always subsets of the total number of species found in richer sites, corresponding to perfect nestedness or minimum disorder, to 100, for species found in any patch which are completely random samples of the total number of species found in all patches, corresponding to maximum disorder. Using this method, we calculated the degree of nestedness of the two matrices and determined the probability of observing these deviations from the respective null values using the Monte Carlo process included in the Atmar and Patterson (1993) calculator (Sokal & Rohlf 1995; number of runs = 1000).

Results

Field Survey Results

We made 1837 butterfly and skipper observations of 44 species during transect sampling (1994–1996) in the oak savanna study sites. Twenty-three observations (1.25% of the total) failed to result in a species identification and were excluded from further analyses. This small proportion is unlikely to have influenced overall species counts in the different habitat patches significantly enough to change any of our major findings. We "jack-knifed" the butterfly-skipper data to estimate our sampling efficiency and develop a "collector's curve" for the database as a whole and for individual savanna habitats. This method provides an assessment of whether the sampling routine was sufficient to have detected most species in the habitat (Fig. 3; see Colwell & Coddington 1994). Jack-knife plots indicate that we missed few butterfly or skipper species. Only two species were observed once: the dreamy duskywing (*Erynnis icelus*) and tawny-edged skipper (*Polites themistocles*). The

mean number of observations of each species was 41 ± 12, median 15). The discrepancy between the mean and median is attributable to the extreme abundance of a few species, particularly the introduced species European skipper (*Thymelicus lineola*) and cabbage white (*Pieris rapae*).

Malaise traps captured 1431 Hymenoptera specimens from 196 species, as corroborated by specialists for each subtaxon. A large proportion of these species (60 of 196 species, or 31%) were observed once, indicating that we probably did not sample all species present in the savannas and ecotones during the sampling period. Jack-knife graphical analysis supports this finding. We did not standardize morphospecies across habitats (i.e., give them consistent names between habitats), so we cannot state the total number of morphospecies observed across the different study sites. Within individual habitats, however, there was close correspondence between the number of Hymenoptera morphospecies and actual species richness (Fig. 4; adjusted $R^2 = 0.77$, $p < 0.0001$, $n = 14$, log-transformed data). Bootstrap analysis of these data demonstrates that the significance of this relationship was robust even when the regression was based on about half the sample size. We also found close correspondence between Hymenoptera and butterfly-skipper species richness within the savanna habitats after adjusting for sampling period (adjusted $R^2 = 0.80$, $p < 0.0001$, $n = 8$; Fig. 5).
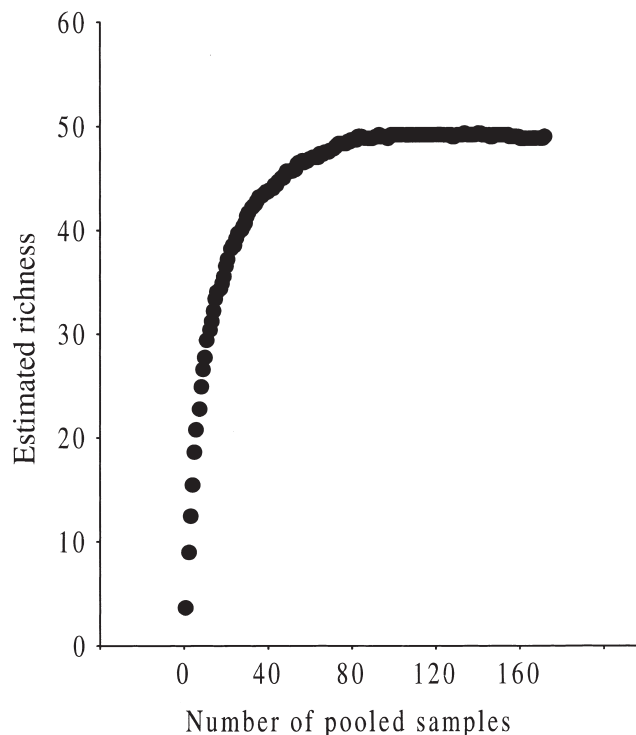

Figure 3. Jack-knife estimation of butterfly and skipper species richness in oak savanna remnants in southern Ontario. This curve suggests that few species were missed during butterfly surveys.
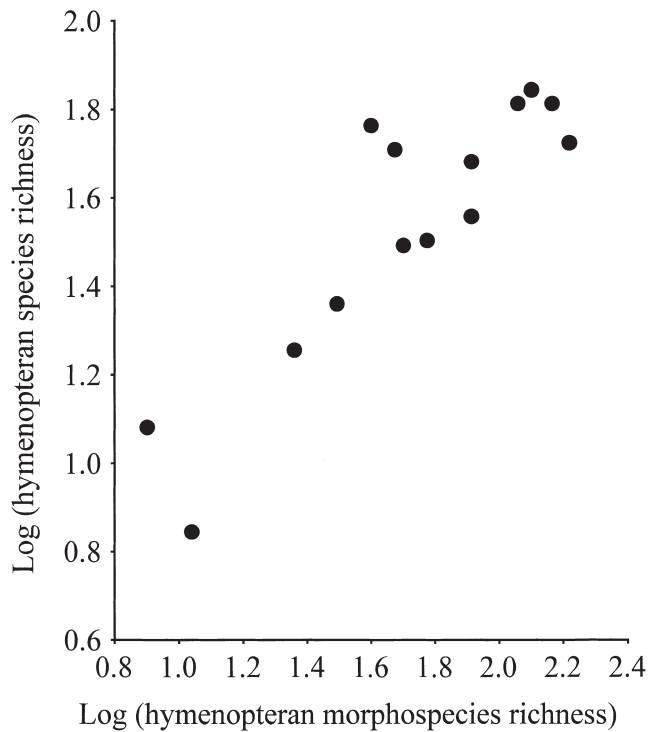
Figure 4. Hymenoptera morphospecies richness versus species richness as verified by systematists (n = 14). Includes data from malaise traps in both savanna interiors and nearby ecotonal habitats.
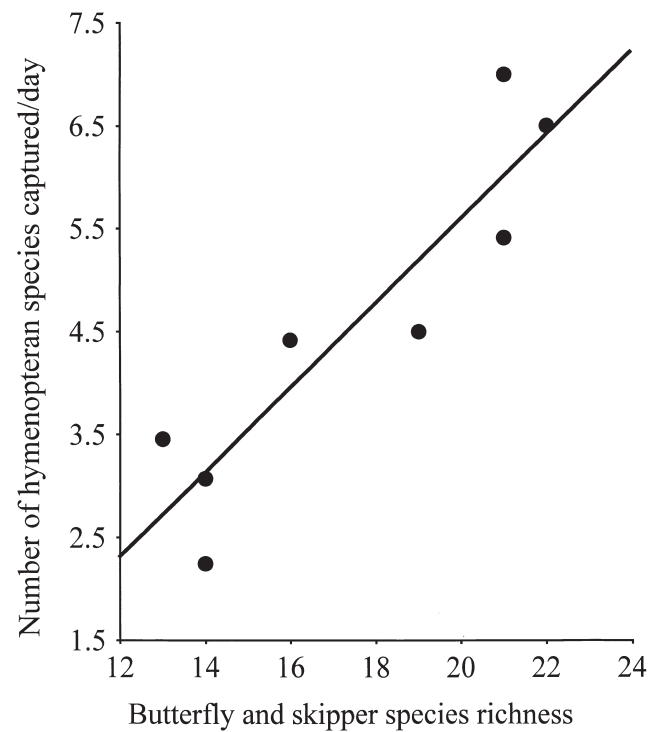

Figure 5. Hymenoptera species richness versus butterfly-skipper species richness among savanna fragments from which Hymenoptera data could be collected. Hymenoptera data are adjusted for sampling period, which varied somewhat between traps.

Spatial Autocorrelation

We found no evidence for spatial autocorrelation among the Lepidoptera data. Monte-Carlo simulation demonstrated that the calculated spatial autocorrelation statistic, Moran's I, was not significantly different from values expected if the observations were placed randomly among sampling locations (Moran's I = 0.143, p = 0.217, n = 10,000). Consequently, we did not modify our statistical analysis of lepidopteran data by reducing degrees of freedom or employing geostatistics (Carroll & Pearson 1998, 2001).

We found that the relationship between Hymenoptera morphospecies and species richness remained strong and generally highly significant (median p = 0.014, mean p = 0.050, df = 6) when the data were bootstrapped and included in regressions (10,000 repetitions). Although we cannot rule out the possibility of a small effect from spatial autocorrelation in these data, if present, it is unlikely to materially influence our findings.

Nestedness

The butterfly and skipper and Hymenoptera communities in these oak savannas were highly nested. The matrix nestedness value of 39.1 for the Lepidoptera was sig-

nificantly lower than the mean score for the randomized matrix of 60.3 ($p \ll 0.0001$, Monte Carlo runs total = 1000), signifying that these data were significantly nested. Similarly, the Hymenoptera matrix was much more nested than expected by chance (29.1 vs. 52.6; $p \ll 0.0001$, Monte Carlo runs total = 1000). That is, the faunas of low-diversity habitat patches tended to be predictable subsets of the faunas with higher diversity for both the Lepidoptera and Hymenoptera. (Presence-absence data matrices used for our analyses are available on request from J.T.K.)

Discussion

We found strong evidence that butterflies and skippers are indicators of the diversity of Hymenoptera at the landscape scale. Other authors have suggested that Hymenoptera themselves should be an indicator of the status of other taxa (LaSalle & Gould 1993; Duelli & Obrist 1998). With the large samples we collected from flight-intercept traps, the amount of time required to sort, identify, mount, and label specimens for later verification by systematists is prohibitive even for short-dura-

tion monitoring of Hymenoptera. A systematist might be able to sort and identify a significant proportion of the Hymenoptera from such samples, but systematists are themselves "rare species" (Wilson 1992; Janzen 1993; Lawton et al. 1998; New 1998). There are few amateur hymenopterists, and there are far too few systematists to run a large number of intensive Hymenoptera monitoring programs (Lawton et al. 1998). There are, however, relatively large numbers of amateur and professional lepidopterists able, even eager, to sample butterflies and skippers along standardized transects that yield consistent results between observers (Pollard & Yates 1993).

Hymenoptera morphospecies richness scores were strongly correlated with actual species richness estimates. The relationship between morphospecies and species richness was approximately linear, although it had a slope greater than one (Fig. 4). This is because of a tendency to "split" some species into two morphospecies, perhaps because of sexual dimorphism, size variation between individuals, or damage to specimens (e.g., variable wing wear). This suggests that morphospecies richness measurements should be calibrated to actual species richness scores: without adjusting for the tendency to "split" taxa in this study, we would have systematically overestimated the numbers of morphospecies captured in the samples. This did not affect our results. This "calibration curve" is unlikely to be consistent between different taxa (Oliver & Beattie 1993) or, possibly, parataxonomists, but it may be consistent among habitats for the same taxon. This requires further investigation. For long-term monitoring programs, the amount of work required to sort and identify morphospecies consistently (i.e., give an RTU the same morphospecies reference) among samples is great enough that traditional species identifications may not be much more difficult (Brower 1995). The severity of this problem will vary among taxa, but is less likely to be a problem for day-flying Lepidoptera.

Monitoring programs are more likely to fail if poor indicator taxa are selected (Simberloff 1998). We found that transect surveys of butterfly and skipper communities in oak savanna habitats provide a good representation of aculeate and symphytan Hymenoptera diversity as measured by means of malaise traps. Furthermore, rapid biodiversity assessments of Hymenoptera in this habitat corresponded reasonably well with measurements of actual species numbers collected in the malaise traps, although the tendency for technicians to be "splitters" or, by extension, "lumpers" can be controlled by calibration against actual estimates of species richness as determined by systematists. This baseline calibration can then be used to adjust the results from future collections in the same geographical range of the habitat. The extent to which these calibration curves need to be estimated for different taxa, parataxonomists, and habitat types remains to be determined.

The high degree of nestedness observed for the Lepidoptera and Hymenoptera data matrices was consistent with the hypothesis that selective extinctions have been important in shaping diversity patterns among these remnant oak savannas. Although Lomolino (1996) has pointed out that such strongly nested patterns can be generated across "islands" with high colonization rates, this is unlikely to be the case for the oak savannas in this study. The distances that separate the different savanna complexes we studied are great enough that migration rates between them are almost certainly undetectably low. Our failure to detect spatial autocorrelation in the lepidopteran diversity patterns supports this explanation. Several of the species observed in this study are widely distributed habitat generalists (e.g., cabbage white), but the removal of these species from the database is unlikely to qualitatively affect our findings, given that less frequently observed species were found exclusively in only a few habitat patches.

It would be worthwhile to investigate whether nestedness patterns can arise as a function of incomplete sampling. It is possible that the most common species are observed more easily in small or low-quality habitat patches, while rare species are missed. This could create the false appearance of nested subset structure in these communities. The collector's curve for Lepidoptera suggests, however, that most species were observed, and nestedness and species diversity patterns between Hymenoptera and Lepidoptera were similar. Incomplete sampling is unlikely to have caused the observed nestedness pattern in our study.

One implication of our nested subsets analysis is that many species were likely extirpated with differential frequency among the savanna fragments before we began the study. The latter stages of this extinction process have been observed directly for the butterflies because several species disappeared from some of the study sites just prior to the initiation of our study (e.g., the Karner blue, the frosted elfin, and the Persius dusky wing [*Erynnis persius*]; Packer 1991; Packer 1994). Another species, *Tachysphex pecumanni*, a rare aculeate hymenopteran, was extirpated from one of its remaining habitats in Ontario during this study because rail ties were dumped on its nest colony. Many of the remaining butterflies and skippers we have identified from savannas are broadly distributed and reasonably abundant. We did not observe any Lepidoptera during this study which are thought to be at significant risk of extinction. Preliminary findings from an investigation of carabid diversity in these habitats shows similar results (H. Douglas, personal communication). These documented Hymenoptera and Lepidoptera declines support the hypothesis that selective extinction has created the nested subset structure exhibited among both Hymenoptera and Lepidoptera in the last Ontario oak savanna remnants. The Hymenoptera from these habitats have rarely been collected and even

less commonly identified, and regional species losses are likely to have remained unnoticed in this and many other poorly known taxa.

Despite our relatively extensive Hymenoptera collections, the parasitoids, among other subgroups, were not identified. This leaves a large gap in our estimates of overall Hymenoptera diversity in Ontario oak savannas, and our results may be applicable only for the subset of hymenopterans we could capture during our malaise trapping period. This is a common difficulty in studies of diverse taxa that are difficult to identify. One conclusion that might be drawn from this dilemma is that specific habitat conservation actions are premature given the large number of hymenopterans, not to mention other insect taxa, that we have not assessed. This conclusion, incorrect in our opinion, exemplifies the "Nero dilemma" (Soulé 1986). That is, incomplete evidence, particularly when consistent across several analyses of phylogenetically distinct taxa as in this study, may be the only basis on which conservation decisions can be made. Scientifically rigorous analyses are possible even with fewer data than would be ideal. Furthermore, real-world conservation activities will rarely succeed if every datum must be collected and analyzed before action is taken.

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