α and β Diversity of a Tachinid Parasitoid Community Over Space and Time

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ABSTRACT Many species of Tachinidae are important parasitoids of herbivorous insects in natural and managed systems; yet, little is known about tachinid diversity and how this diversity is distributed across space and time. Here, pan trap sampling was used to analyze the richness, microhabitat specificity, and seasonal diversity of a tachinid parasitoid community in an oak–mesquite savanna of Southeastern Arizona. Twenty-four traps were set out monthly during the growing season in three different microhabitats (open grassland, woodland understory, and woodland canopy). In total, 79 tachinid species were sampled with an estimated total diversity of 122 species. Most individual traps sampled few species; yet, variation in species composition (β diversity) among sampling dates and microhabitats was high, accounting for 40–70% of the total diversity. Significant intraspecific aggregation was not observed across traps or microhabitats, but it was observed across dates, suggesting that the activity of tachinid species may be associated with host phenology and seasonal periods of precipitation. The β diversity associated with microhabitat and sampling date was significantly greater than expected. Tachinid species diversity was highest in the canopy traps, whereas the open-exposed traps exhibited high abundances of relatively few species, and understory traps sampled few individuals of few species. Most species tended to be sampled where their hosts would be expected to be found, although males were also frequently sampled in microhabitats associated with mate finding. These patterns of diversity and abundance may aid in understanding parasitoid–host associations and variation in rates of parasitism by tachinid flies.

KEY WORDS Tachinidae, parasitoid diversity, β diversity, habitat specificity, species richness host associations

Understanding patterns of the diversity and abundance of species is a foundational goal of ecology. Although knowledge of how many species reside in a given area is one important aspect of diversity, there has been increasing emphasis on how species are distributed over space and time (DeVries et al. 1999, Summerville et al. 2003, Crist and Veech 2006, Crist et al. 2006). Illuminating the "structure" of diversity is not only necessary for understanding larger patterns of biodiversity and community structure, but also has important implications for applied fields such as conservation, land/water management, forestry, and agriculture. In addition, the distribution of biodiversity at various scales can lead to inferences regarding the ecological and evolutionary processes responsible for generating and maintaining this diversity. Yet, for many groups of organisms we have little empirical knowledge of how diversity varies over space and time. One such group, the subject of this study, is tachinid flies.

The Tachinidae comprise one of the largest, if not the largest, families of Diptera (≈10,000 described species; Irwin et al. 2003), and they are second only to the hymenopteran Parasitica in importance as parasitoids of insects (Stireman et al. 2006). Despite their diversity, ubiquity, and ecological importance, the family remains relatively little studied, particularly with regard to ecology and behavior. Our knowledge of most species is restricted to a taxonomic description. Although some large-scale biogeographical patterns of tachinid diversity have recently been compiled (O'Hara 2006, Stireman et al. 2006), information about how tachinid diversity varies at finer scales, between habitats, or over time is lacking.

Understanding the fine-scale spatial and seasonal distribution of tachinid diversity can provide insight into many aspects of tachinid ecology and behavior. These include the host associations of species (Belshaw 1992), how host associations may be influenced by microhabitat (Ohsaki and Sato 1999, Stireman and Singer 2002), and the effectiveness of tachinid parasitoids as natural enemies in natural habitats, managed habitats, or both (Weseloh 1982,

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Felland 1990). A particularly elegant demonstration of the influence of microhabitat on tachinid parasitism can be seen in Roland and Taylor (1997), a study of parasitoids of the forest tent caterpillar, *Malacosoma disstria* Hübner. Using a landscape-scale sampling protocol, they found that parasitism by each of three tachinid species (and a parasitoid sarcophagid) varied strongly with forest structure and that increased forest fragmentation dramatically reduced parasitism rates of the three dominant parasitoids. With these data, they were able to gain insight into how outbreaks of forest tent caterpillars may be related to forest structure and under what conditions outbreaks might be controlled or limited by parasitoids.

Here, I analyze patterns of diversity over space (microhabitat) and time (season) in a tachinid community in the uplands of southwestern Arizona. The goals of this survey are several. First, I provide an estimate of the α diversity of tachinids in this community. Surveys of tachinid diversity are rare (but see Belshaw 1992), and there appears to be no published literature quantitatively documenting α diversity of Tachinidae for any site in North America. Although just a point estimate, this estimate of species richness can serve as a baseline for understanding the diversity of this important group across North America. Second, I assess the turnover in species (β diversity) over a season and across microhabitats, and examine how β diversity contributes to total community diversity. This partitioning of diversity into temporal and spatial components allows exploration of the contribution of these factors to the total diversity of the community and provides information on microhabitat use. Finally, data on microhabitat use and seasonality are used to explore patterns of host use and mating systems. Although this study is focused on elucidating patterns of diversity and microhabitat use in tachinids, the results may yield insight into the contribution of spatial and temporal turnover to the total diversity of other ecologically important natural enemies as well.

Materials and Methods

Study Site. The study was conducted in an oak–mesquite savanna habitat situated in the northwestern foothills of the Santa Rita Mountains of southeastern Arizona along Empire Gulch, 1.5 km north of Greaterville, AZ (31° 47′51″ N, 110° 45′05″ W; 1,575 m). Drainages and low-lying areas between hills were characterized by grassland (e.g., *Muhlenbegia* spp. and *Bouteloua* spp.) with a diverse forb community and occasional shrubs (e.g., *Prosopis* spp., *Acacia* spp., and *Rhus* spp.). Slopes were largely covered with oak–uniper woodland (*Quercus emoryi* Torr., *Quercus arizonica* Sarg., and *Juniperus deppeana* Steud.).

Sampling Protocol. Twenty-four rectangular white plastic pans (39 by 15 by 5 cm) were arrayed linearly along a shallow, slightly sloped, approximately north-south-oriented draw in triplets. Within each triplet, one pan was placed on the ground in the middle of the open grassy draw ("open" traps), one pan was placed on the ground under the canopy of trees at the edge of the draw ("understory" traps), and one pan was suspended in an oak tree (primarily *Q. emoryi*, but also *Q. arizonica*) with bailing wire ≈2 m from the ground ("canopy" traps). Open and understory pans were placed ≈5 m apart, with canopy pans hanging within 2 m (horizontally) of the understory traps. Understory and canopy pans were placed 3–6 m from the woodland–grassland boundary. Each set of pans (triplets) were separated by 15–20 m.

Pan sampling was conducted in early and mid-September 1998 (6 and 18 September, respectively), and each month in March–September in 1999. In each sampling period, pans were set out for 46–48 h, starting near noon on day 1, and they were collected around noon on day 3. Only open and understory sampling treatments were conducted in 1998. Due to destruction of open traps by cattle in August 1999, all traps were relocated to a similar habitat 2.0 km away for the final September 1999 sampling date.

Each pan was filled to a depth of 3.5 cm with water to which a drop of liquid soap was added. Small holes were drilled in the sides of pans to prevent overflowing in the event of heavy rain. Samples were collected by pouring the liquid through a fine 1-mm mesh and then washing the strained material into glass jars with 70% ethanol. Lepidoptera and Orthoptera were removed before straining of the samples.

Specimen Identification. Tachinid flies were separated from remaining trap contents and placed into labeled, alcohol-filled vials within 1 wk after collection. All tachinid specimens were pinned and chemically dried by overnight immersion in ethyl acetate. Tachinid specimens were identified using the taxonomic literature (e.g., Wood 1987 for genera) and with reference to specimens housed in the Canadian National Collection of Insects. In addition, a number of species were identified by J. E. O'Hara and D. M. Wood (Agriculture and Agri-food Canada). All specimens are currently housed in the Wright State University Insect Collection curated by J.O.S.

Analysis. The pattern of species accumulation over all samples was examined using the software EstimateS (Colwell 2006) using 500 randomizations to generate a species rarefaction curve (using Mau Tao estimates of S_{obs}; Colwell 2006). Rarefaction is a standardization procedure that calculates expected species accumulation curves and allows comparison of species richness among samples of different sizes. Rarefaction curves were also estimated for samples pooled within date (month) and microhabitat (open, understory, and canopy) to visually examine β diversity associated with these variables (see Crist and Veech 2006). Similarly, rarefaction curves using 500 resampled replicates were generated independently for samples within each microhabitat type. EstimateS also was used to estimate the number of shared species and similarity metrics (i.e., Jaccard and Sorenson indices) across microhabitats and dates. Estimates of the total spe-

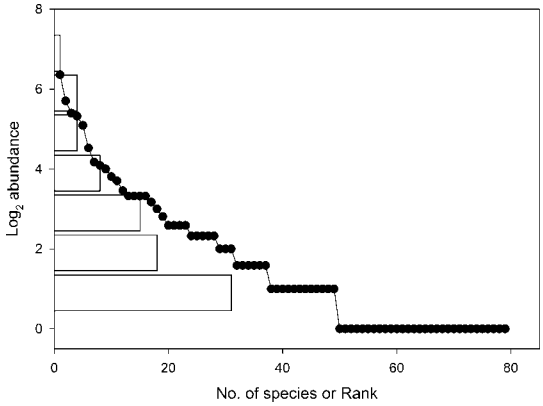

Fig. 1. Log_2 abundance distribution and rank-abundance curve of tachinid species sampled in this study. The x-axis is the number of species for the abundance histogram and rank for the rank-abundance curve.

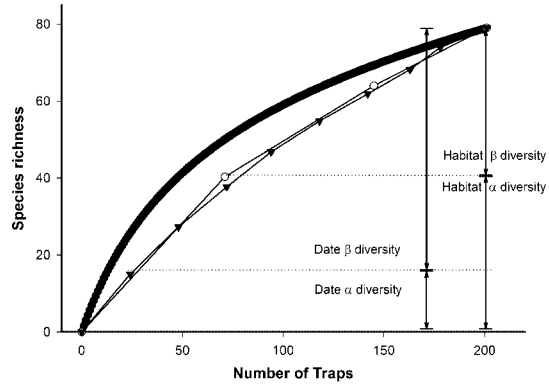

Fig. 2. Species rarefaction curves (Mau Tao) for traps (black circles), dates (black triangles) and microhabitats (open circles) based on 500 replicate randomizations. Dotted lines indicate α and β diversity components for higher strata (microhabitat, date).

cies richness (R) within each microhabitat type and for the tachinid community as a whole were calculated using the classic Chao-2 estimator in EstimateS (Colwell 2006). The data sets were randomized 1,000 times for estimation of log-linear 95% confidence intervals (Chao 1987). Shannon-Weiner (H') and Simpson (D) diversity indices were calculated for each microhabitat (pooled across eight traps), and for each of the sampling dates (1999 only). Due to non-normality, nonparametric Kruskal-Wallis tests were used to assess statistical differences in species richness and abundance relative to microhabitat using SPSS 4.0 (SPSS Inc. 2004). PCORD (McCune and Mefford 1999) was used to perform a Mantel test to examine whether community similarity was associated with sampling date (1,000 randomizations). Because many zeros are present in the data matrix, multivariate ordination (e.g., NMS) of the community proved to be inconclusive and randomization tests could not be performed.

To statistically assess whether β diversity between microhabitats and dates was greater than could be expected if individuals were distributed randomly, diversity was partitioned into within-trap α diversity, between trap β diversity, and either between microhabitat or between sampling date β diversity by using the program PARTITION (Crist et al. 2003). This program partitions diversity components of each strata of a data set (e.g., α, $\beta_1, \beta_2, \beta_3 \ldots$) under the assumption that γ (total species diversity) $= \alpha_1 + \sum_{i=1}^{m} \beta_1$, where i is one of m sampling levels (Crist et al. 2003, Crist and Veech 2006). Significance of diversity components were assessed in PARTITION by randomizing at the individual and trap level 1,000 times to construct diversity distributions and determining whether the probability of the observed diversity was less than or equal to 0.05. Randomizations at the individual level were used to determine whether significant intraspecific aggregation was observed at different sampling strata (e.g., trap, microhabitat). Randomizations at the trap level were used to assess whether community composition differed among traps, microhabitats, or sampling dates (Crist et al. 2003). Because microhabitat and sampling date were completely crossed (not nested), analyses of the β diversity associated with these strata were conducted in separate analyses. Thus, for each of the analyses focusing on microhabitat or sampling date, estimates of β diversity across the lower level of traps also includes a component of β diversity associated with the alternate higher order stratum (i.e., microhabitat or sampling date). Tests for significant departures of β diversity from random expectations were repeated for three measures of diversity: R, H', and D (see above).

Results

In total, 79 tachinid species were collected from 201 pan trap samples (Appendix 1). These species belonged to 45 genera (of the 303 recorded from North America; O'Hara and Wood 2004), 22 tribes (of 46), and all four subfamilies of the Tachinidae. The tribe Blondeliini (Exoristinae) dominated in terms of diversity with 22 species, with the Eryciini (Exoristinae) following in diversity with 10 species. Well represented genera included *Myiopharus* (seven species), *Eucelatoria* (ca. six species), *Paradidyma* (five species), *Lespesia* (four species), and *Ptilodexia* (four species) (Appendix 1). Most species were represented by only one or a few individuals, resulting in a "fat tailed" abundance distribution (Fig. 1).

The species accumulation curve combining all samples showed no sign of reaching an asymptote, although the rate of species accumulation began to decline after ≈50 trap samples (Fig. 2). Estimated total α diversity (species richness) for the site using the Chao-2 estimator (Colwell 2006) was 122.7 (mean of 1,000 resampling runs) with a 95% C.I. ranging from 97 to 189 species (Fig. 3). The Chao-2 estimates (and associated 95% CI) were not asymptotic with increasing sample size, suggesting that the estimates of total

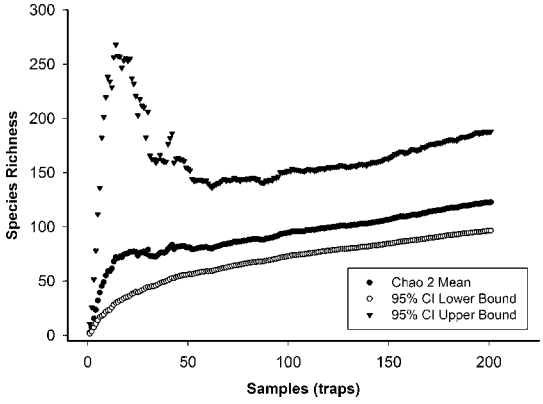

Fig. 3. Classic Chao-2 estimates of total d, randomizations).

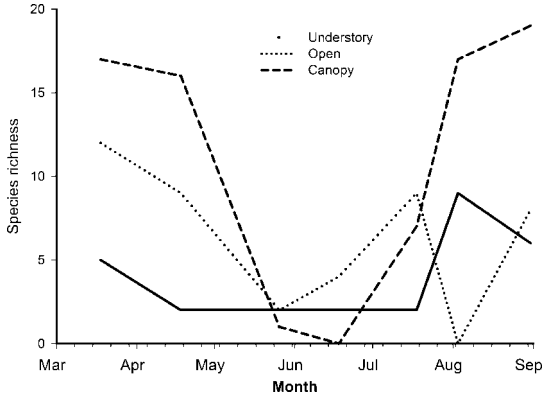

Fig. 5. Total species richness over all traps for each microhabitat over the 1999 sampling season.

community diversity would likely be higher with greater sampling.

Independent rarefaction curves for each microhabitat exhibited distinct rates of species accumulation with Canopy traps displaying the greatest slope, and understory traps displaying the lowest rate of species accumulation (Fig. 4). Classic Chao-2 estimates of total species richness relative to habitat were (mean, 95% CI based upon 500 replicates): canopy: 112, 77–204; open: 73, 48–155; and understory: 58, 37–123. Summing these estimates resulted in a greater total Chao-2 estimate of diversity than in the total data set, reflecting overlap in microhabitat association of species.

Over the year of sampling, there were two apparent peaks in diversity (and abundance) that corresponded with the major growing seasons in southern Arizona (Fig. 5), one peak in the spring following the winter rains and a second peak in the late summer following the "monsoon" summer rains. The August decline in species richness to zero for "open" traps was due to the destruction of most of these traps by cattle. Species

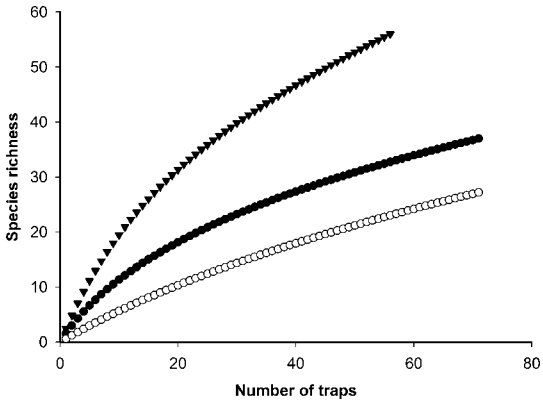

Fig. 4. Species rarefaction curves (Mau Tao) for each microhabitat sampled: canopy (black triangles), open (black circles), and understory (open circles) based on 500 replicate randomizations.

richness was greatest for traps suspended in trees (mean per trap ± SE: 2.56 ± 0.37) and lower for understory traps (1.48 ± 0.14) and open traps (1.53 ± 0.22; Kruskall–Wallis [K-W] test: $\chi^2 = 23.97$, df = 2, $P < 0.001$; also see Fig. 4). Average abundance of tachinids was also greatest in the canopy traps (mean ± SE: 4.8 ± 1.1) and lowest in the understory samples (0.84 ± 0.17), but open traps exhibited relatively high density of tachinids as well (3.31 ± 0.93; K-W test: $\chi^2 = 20.96$, df = 2, $P < 0.001$).

The β diversity or turnover among sampling dates (months) and among microhabitat types (Open, Understory, and Canopy) was quite high (Table 1; Fig. 6). Tests of β diversity against a null distribution, where individuals were randomly distributed among samples, indicated less intraspecific aggregation within traps and microhabitats than expected, but significantly greater aggregation than expected within sampling dates (Table 1). However, in both analyses of community composition where samples were randomized within higher strata (date and microhabitat), species turnover was significantly greater than expected and α diversity was significantly lower than expected (1,000 resampling replicates; Table 1; Fig. 6). Jaccard similarity indices between dates ranged from 0.03 to 0.22 (mean = 0.1) and shared species ranged from 4 to 75% (median = 27.5%). A slight, but significant relationship between date and community similarity was also present, such that consecutive sample dates were more similar to one another than expected by chance (Mantel test, $r = 0.417$, $Z = 0.27$, $P = 0.013$; 1,000 randomizations).

Microhabitat significantly affected tachinid species composition (Table 2; both Jaccard and Sorensen indices are considerably <1), although not to the same extent as sampling date. Strict microhabitat associations were likely due in part to incomplete sampling; however, several species with moderate abundances were recorded in only a single microhabitat. For example, seven of the 45 species found in only a single microhabitat were represented by three or more individuals, and only nine of 37 species represented by more than three individuals were found in all three microhabitats.

Table 1. Estimates of diversity components assessing intraspecific aggregation (randomization of individuals) and community composition (randomization of samples). Two separate analyses are shown in each case: date, with traps nested within sampling dates; and habitat, with traps nested within microhabitat

	Diversity component	R	*R%*[a]	D	*D%*[a]	H'	*H'%*[a]
Intraspecific aggregation							
Date							
Traps[b]	***α***	**4.9 ↓**	*6.2*	**0.68 ↓**	*71.8*	**1.11 ↓**	*31.7*
	β	**16.4 ↓**	*20.8*	**0.146 ↑**	*15.4*	**1.13 ↓**	*32.2*
Date	***α***	**21.3 ↓**		**0.825 ↓**		**2.24 ↓**	
	β	**57.7 ↑**	*73.0*	**0.121 ↑**	*12.8*	**1.26 ↑**	*36.0*
Habitat							
Traps	***α***	**4.9 ↓**	*6.2*	**0.68 ↓**	*71.8*	**1.11 ↓**	*31.7*
	β	**40 ↓**	*50.6*	**0.21 ↑**	*22.8*	1.77	*50.7*
Habitat	***α***	**44.9 ↓**		**0.895 ↓**		**2.87 ↓**	
	β	**34.1 ↑**	*43.2*	**0.051 ↑**	*5.4*	**0.62 ↑**	*17.6*
Community composition[b]							
Date	***α***	**21.3 ↓**	*27*	**0.825 ↓**	*87.2*	**2.24 ↓**	*64*
	β	**57.7 ↑**	*73*	**0.121 ↑**	*12.8*	**1.26 ↑**	*36*
Habitat	***α***	**44.9 ↓**	*56.8*	**0.895 ↓**	*94.6*	**2.87 ↓**	*82.4*
	β	**34.1 ↑**	*43.2*	**0.051 ↑**	*5.4*	**0.62 ↑**	*17.6*

Estimates of diversity components and percentage of diversity explained do not differ between the intraspecific aggregation and community composition analysis, but tests of significance are performed differently and separately (see text).

[a] The percentage of total diversity explained by each partition of diversity is also indicated (%).

[b] Bold values indicate significant departures from random expectation ($P < 0.01$); arrows indicate whether values are significantly lower or higher than expected.

To explore the association between tachinids and the microhabitat of their hosts, I calculated the binomial probabilities of observing the number of tachinid individuals in the predicted microhabitat of their hosts (as inferred from host associations compiled by Arnaud [1978]) for tachinids of which five or more individuals (per sex) were trapped. For females, nine of nine species exhibited significant associations with the predicted microhabitat of their hosts ($P < 0.05$), and for males, 10 of 14 species exhibited significantly nonrandom associations. Using a Bonferroni corrected α of 0.0022 to correct for multiple tests (23 tests), eight of nine associations were significant for females and seven for males. For example, *Peleteria valida* Curran generally attacks cutworm-type Noctuidae that would be expected to be abundant in open herb-dominated microhabitats. The majority of *P. valida* specimens (92.5%; $N_{tot} = 81$) were trapped in open traps. Conversely, *Carcelia lagoae* (Townsend), which primarily attacks tree feeding Megalopygidae, was primarily found in canopy traps (83%; $N_{tot} = 56$). Finally, *Eribella polita* (Coquillett) which attacks Chrysomelidae, was found primarily in the Understory traps (89%; $N_{tot} = 9$). This association was not predicted a priori, but leads to the hypothesis that Chrysomelidae feeding on understory herbs or shrubs may be likely hosts for *E. polita* in this region.

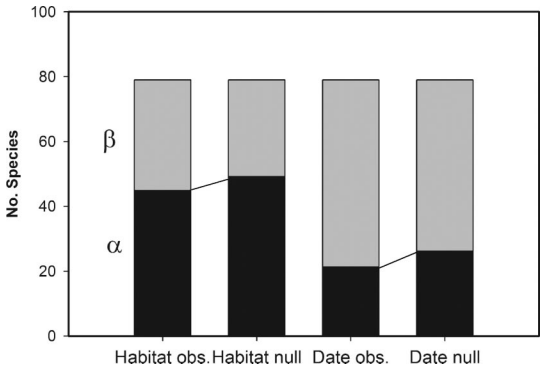

Fig. 6. A comparison of α (black) and β (gray) diversity components for microhabitats and dates to the null distribution of diversity based on 1,000 randomizations of samples among microhabitat or sampling date in PARTITION.

Discussion

Diversity. This study is among the few surveys to estimate the diversity of a community of Tachinidae (see Belshaw 1992 and Ceretti et al. 2004). The large number of both observed (79) and estimated (122) species collected in a relatively small area (≈1–2 ha) indicates that this region of the United States supports a relatively rich tachinid fauna (as has been reported by O'Hara 1995, 2000). The presence of several undescribed species, and species in which the identity was doubtful (and may also be undescribed), in a generally well-collected region attests to the large and poorly understood diversity of this family. It is likely that additional sampling methods (e.g., Malaise traps, sweep netting, sugaring) and greater sampling intensity would yield many more species. Limited sampling and rearing of caterpillars from the same site in the same years yielded 10

Table 2. Community similarity across microhabitat types

Microhabitat comparison	Shared species	Jaccard similarity	Sorensen similarity
Open-cover	12	0.226	0.369
Open-canopy	21	0.292	0.452
Cover-canopy	17	0.254	0.405

tachinid species, only 50% of which were represented in the trapping survey reported here (J.O.S. and M. S. Singer, unpublished data). In addition, Tschorsnig (2002) showed that, in at least some habitats, many tachinid species observed visiting flowers are not collected in adjacently located pan traps. In England, Belshaw (1992) trapped 84 species of tachinids in eight Malaise traps that were more or less continuously operated for one season. Although, this richness is slightly higher than that reported in the current study, the number of individuals sampled by Belshaw with Malaise traps was > 5 times greater than in this study (3,055 versus 559, respectively). In a similar single-season study in northern Italy (with Malaise traps suspended in the canopy), Ceretti et al. (2004) recorded 41 species of tachinids from a sample of 964 individuals.

Despite the potential biases associated with the pan-trap sampling methods used here, the Chao-2 estimate of total diversity is probably an underestimate of the diversity of the tachinid community in the area. Rarefaction methods have been shown to perform poorly with diverse communities of arthropods (Brown 2004, Longino et al. 2002) and plants (Chiarucci et al. 2003) that contain many rare species. The Chao-2 metric has, in particular, been shown to consistently underestimate diversity except at very high levels of sampling coverage (Chiarucci et al. 2003).

The heavily skewed abundance distribution with few common species and many rare species (Fig. 1) is fairly typical for samples of diverse insect communities (DeVries et al. 1999, Ulrich and Ollnick 2004, Brown 2004), resembling a geometric series more closely than a log-normal or broken stick distribution (Hughes 1986). Skewed abundance distributions suggest that many species in the community have not been sampled and that many relatively rare species are present. Given the limited sampling effort, ecological interpretation of the observed distribution may be premature (McGill 2003).

The β diversity among microhabitats and among sampling dates was quite high (explaining 73 and 43% of the total diversity, respectively, in each analysis), but these estimates must be interpreted with caution. The analytical method used does not allow both factors to be included in a single model; consequently, it is not possible to accurately estimate the diversity attributed to each factor. The between-trap estimates of β-diversity are inflated because a portion of the diversity attributed to turnover among traps may be due to turnover among microhabitats and dates in the respective analyses. Regardless of the exact partitioning of diversity between microhabitat and sampling date, it is clear that within-trap (α) and among-trap (β) diversity components account for relatively little diversity (6.2 and 20.8% respectively in the date analysis; Table 1). Thus, each trap sampled a very small proportion of the total community. The analyses in PARTITION indicate that within-trap and among-trap components of diversity are lower than would be expected if individuals were randomly distributed among traps. This indicates that if the sampling was restricted to a single microhabitat or confined to a single sampling date, a large proportion of the community would have been missed.

Microhabitat. Analyses of β-diversity among microhabitats revealed significant evidence of both intraspecific aggregation and variation in community composition (Table 1; Fig. 6). Canopy traps exhibited the highest rate of species accumulation whereas understory traps exhibited the lowest. This result contrasts with the low capture rate of tachinid species in canopy-suspended Malaise traps by Ceretti et al. (2004) (although their traps were placed considerably higher [15 m] than in this study). Jaccard and Sorensen similarity indices (Table 2) also indicate high turnover among microhabitats. Interestingly, the open and canopy traps exhibited greater similarity and overlap in species composition (Jaccard: 0.296) than the two ground level microhabitats (open and understory, Jaccard: 0.226) or the two traps located within the tree canopy areas (canopy and understory, Jaccard: 0.254). This may be due in part to the generally low diversity of species observed in the understory traps.

The large β-diversity across both microhabitats and months (date) likely reflects differences in host use among the tachinid species. Although Tachinidae are renowned for polyphagy (Belshaw 1994), many, if not most species have fairly limited host ranges (Stireman and Singer 2003a, Smith et al. 2007). Individuals of more than half of the species recorded were sampled totally or in part where their hosts would be predicted based on host associations reported in Arnaud (1978) and field observations of caterpillar microhabitat use (Stireman and Singer 2003b; J.O.S. and M. S. Singer, unpublished data; Appendix 1). Examination of species collected in appreciable numbers (>10) found most to be significantly associated with the microhabitat of their host (see Results). Malaise trap surveys of Tachinidae in England by Belshaw (1992) also revealed patterns of association between tachinid habitat use and habitat use of their hosts. The lack of clear association between host and tachinid for some species in the current study (≈30%) may be due in part to limited samples sizes, limited information on host use in this geographic area, and the limited observations/information of which habitats these hosts are likely to use. Still, microhabitat affiliations of adult tachinids may provide a valuable clue for determining host associations for those species for which no hosts are currently known (e.g., *E. polita*).

In addition to host microhabitat, another factor that may influence microhabitat associations is site-specific mating areas. Many tachinids are known to congregate in specific sites to wait for females such as hilltops, tree trunks, sun gaps, and habitat edges (Wood 1987, Alcock and Smith 1995). A significant difference in microhabitat use between males and females was observed ($\chi^2 = 41.1$, df = 2, $P < 0.001$), with males being overrepresented in the canopy traps (and understory traps) and underrepresented in the open traps. This may reflect attraction of males of many species to prominent branches or tree trunks. In general, both

understory and canopy traps were located near the woodland–grassland transition and may have sampled tachinids that frequent edge habitats to locate mates. The finding that males were also often trapped in microhabitats where their hosts could be expected to be found suggests that, in at least some species, males may orient toward microhabitats of potential hosts to locate suitable mates. However, the coarse resolution of microhabitat sampling in the current study limits the ability to distinguish between male attraction to host habitat versus male attraction to highly visible perching sites.

Microhabitat specificity of tachinids can have dramatic effects on host parasitism rates and tachinid–host population dynamics. As mentioned previously, Roland and Taylor (1997) showed that habitat preferences of tachinids attacking tent caterpillars resulted in significant variation in parasitism of caterpillars relative to forest structure. In another example of spatial heterogeneity in parasitism, the distribution of tachinid parasitism across an outbreaking population of *Orgyia vetusta* (Harrison) led to suppression of the spatial spread of the outbreak (Brodman et al. 1997, Maron and Harrison 1997, but see Maron et al. 2001). The usefulness of tachinids as biological control agents in agricultural systems also may be affected by habitat structure and habitat specificity. This is exemplified by higher densities of tachinids around vegetated field margins than in cotton fields, even though potential hosts [*Pseudoplusia includens* (Walker)] were found at higher densities in open fields (Olson and Wackers 2007).

Seasonality. The β-diversity among sampling dates was significantly greater than could be expected if species were randomly distributed among traps (intraspecific aggregation) or traps were randomly distributed among dates (community composition; Table 1). This pattern indicates tight clustering of individuals of particular species within dates and a high turnover of species composition over time. This pattern is also indicated by low Jaccard similarity indices ($\approx$0.1) among sampling dates. High β-diversity over time might be expected if relatively specialized tachinid species exhibit seasonal turnover as they track the phenology of their hosts.

The bimodality of precipitation in southeastern Arizona results in two major periods of growth and reproduction for plants and animals and two rather distinct ecological communities. The insect fauna seems to be primarily temperate in the spring growing season, but much more tropical in the warm summer monsoon season, at least as evidenced by the Lepidoptera fauna (e.g., Bailowitz and Brock 1991; J.O.S., personal observation). These seasonal faunal affinities also may be present in the tachinid community, which would aid in explaining the high temporal β-diversity, low Jaccard similarity, and the significant relationship between community similarity and time indicated by the Mantel test. The occurrence of many *Peleteria* in spring (a taxon with many North American species) and the dominance of summer samples by Blondeliini (which are hyperdiverse in the Neotropics; e.g., Wood 1985, Stireman 2007) is suggestive. However, the relative composition and origins of Nearctic versus Neotropical tachinid faunas are generally too poorly understood to address this issue rigorously.

In conclusion, the current sampling study characterizes the richness, microhabitat specificity, and seasonal diversity/abundance of a diverse assemblage of tachinid parasitoids in the oak–mesquite savanna environment of southeastern Arizona. The observed (79 species) and estimated of richness (122 species) indicates the presence of a rich tachinid fauna; yet, this likely represents only a small proportion of the total community. Additional studies of community diversity like the one conducted here will be necessary if the diversity of this important parasitoid group across habitats and regions is to be understood. Most species of tachinids tended to be sampled where their hosts would be expected, although males also may have been more common in mating-associated perching or display areas. Microhabitat specificity may aid in determining host associations for species in which specific hosts are not known and in understanding how agricultural and other ecosystems may be managed to facilitate tachinid parasitism.

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Appendix 1. Tachinid species sampled in this study (in alphabetical order), with abundances of males and females over all samples

Tachinid species	Females	Males	Total	Habitat
Ametadoria harrisinae (Coq.)	1	33	34	Canopy
Anisia sp.	1		1	Canopy
Aplomya theclarum (Scudder)	4	1	5	Open
Austrophorocera coccyx/sulcata	1		1	Understory
Blondelia sp.		1	1	Canopy
Campylochaeta plathypenae (Sabrosky)	1		1	Canopy
Carcelia lagoae (Tnsd.)	19	33	52	Canopy
Carcelia flavirostris (nr.) (Van der Wulp)		1	1	Canopy
Carcelia reclinata (A. & W.)		2	2	Open/Canopy
Ceracia dentata Rondani	25	15	40	Canopy
Ceromya americana complex (Tnsd.)	1		1	Canopy
Chaetogaedia desertorum (Tnsd.)		1	1	Understory
Chetogena parvipalis (Wulp)	3	2	5	Open
Chetogena tachinomoides (Tnsd.)	3	1	4	Open/Canopy
Cholomyia inaequipes Bigot	6		6	Canopy
Chrysoexorista sp.		1	1	Canopy
Cylindromyia nana Tnsd.	21	21	42	Open
Distichona sp.		1	1	Open
Eribella polita (Coq.)	2	7	9	Understory
Eucelatoria dimmocki (Aldrich)	3	3	6	Open
Eucelatoria leucophaeata (Reinhard)	2	8	10	Canopy
Eucelatoria new species 1	1	2	3	Canopy
Eucelatoria rubentis group (Coq.)	1		1	Open
Eucelatoria "texana" sp. 1 (Reinhard)	3	2	5	Canopy
Eucelatoria "texana" sp. 2 (Reinhard)	7	1	8	Canopy/Understory
Euhalidaya genalis (Coq.)	1	1	2	Open
Eunemorilla paralis (Reinhard)	1		1	Canopy
Frontiniella parancilla Tnsd.	1		1	Open
Gymnosoma filiola Loew		1	1	Open
Heliodorus cochisensis Reinhard		2	2	Canopy
Hyphantrophaga blanda (Osten Sacken)		1	1	Canopy
Lespesia aletiae (Riley)	1		1	Canopy
Lespesia archippivora (Riley)		1	1	Open
Lespesia prob. *cuculliae* (Webber)	2		2	Open/Canopy
Lespesia prob. *datanarum* (Twnsd.)	3		3	Open
Lixophaga diatraeae (Twnsd.)	7	10	17	Canopy
Lixophaga new species	1		1	Canopy
Lixophaga plumbea Aldrich	2	3	5	Canopy
Masiphya confusa Aldrich	3	2	5	Open
Microchaetina cinerea Wulp	1		1	Understory
Microchaetina petiolata(Twnsd.)	1	1	2	Open/Canopy
Microphthalma disjuncta Weidemann	3	4	7	Open
Myiopharus ancilla (Walker)	2	16	18	Canopy
Myiopharus doryphorae(Riley)	2	4	6	Canopy
Myiopharus infernalis (Twnsd.)		2	2	Canopy/Understory
Myiopharus sedulus prob. (Reinhard)		2	2	Canopy
Myiopharus sp. 3	2	12	14	Canopy
Myiopharus sp. 4		2	2	Understory
Myiopharus sp. 6		1	1	Canopy
Nigrilypha gnoma O'Hara		3	3	Understory
Orasturmia vallicola Reinhard	1		1	Canopy
Paradidyma melania (Twnsd.)		1	1	Canopy
Paradidyma affinis Reinhard		1	1	Understory
Paradidyma nr. *brasiliensis*		1	1	Open
Paradidyma setigera (Coq.)	9	4	13	Open/Canopy
Paradidyma singularis (Twnsd.)	7	4	11	Canopy
Patelloa facialis (Coq.)	4	6	10	Canopy
Patelloa meracanthae (Greene)	1		1	Canopy
Peleteria valida Curran	55	27	82	Open
Peleteria malleola (Bigot)	1	1	2	Canopy
Peleteria neotexenis Brooks		1	1	Understory
Phasia aldrichii (Twnsd.)	2	2	4	Open
Phasia n. sp. nr. *aldrichii*	2	1	3	Open
Phytomyptera longicornis (Coq.)		1	1	Canopy
Pseudochaeta brooksi (S. & A.)		3	3	Canopy
Ptilodexia californica Wilder	1		1	Open
Ptilodexia conjuncta (Wulp)	3	7	10	Open
Ptilodexia major (Bigot)	4	2	5	Canopy
Ptilodexia agilis/obscura	4		4	Open
Siphona (*Aphantorhapha*) n. sp. 1	2	8	10	Canopy
Siphona (*Aphantorhapha*) n. sp. 2	6	17	23	Canopy
Uramya indita (Walker)		2	2	Understory/Canopy
Uramya pristis (Walker)		3	3	Canopy
Vanderwulpia atrophopodoides (Twnsd.)		2	2	Canopy
Vibrissina hylotomae (Coq.)	7	9	16	Open
Vibrissina texensis (Aldrich)		2	2	Open/Canopy
Wagneria vernata West		1	1	Understory
Winthemia intermedia Reinhard	1		1	Canopy
Zelia wildermuthii Walton	1		1	Open
Total	246	310	559	

For each species the dominant (majority of individuals) habitat(s) or exclusive habitat in which it was collected is listed.