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Does Carcass Enrichment Alter Community Structure of Predaceous and Parasitic Arthropods? A Second Test of the Arthropod Saturation Hypothesis at the Anthropology Research Facility in Knoxville, Tennessee*

ABSTRACT: In a second test of an arthropod saturation hypothesis, we analyzed if the on-campus Anthropology Research Facility (ARF) at the University of Tennessee, Knoxville, with its 20+ yr history of carcass enrichment, is comparable to non-enriched sites in community structure of predatory and parasitic arthropods that prey upon the sarcosaprophagous fauna. Over a 12-day period in June 1998, using pitfall traps and sweep nets, 10,065 predaceous, parasitic, and hematophagous (blood-feeding) arthropods were collected from freshly euthanized pigs (*Sus scrofa* L.) placed at ARF and at three surrounding sites various distances away (S2–S4). The community structure of these organisms was comparable in most paired-site tests with respect to species composition, colonization rates, and evenness of pitfall-trap abundances on a per carcass basis. Site differences were found in rarefaction tests of both sweep-net and pitfall-trap taxa and in tests of taxonomic evenness and ranked abundances of sweep-net samples. Despite these differences, no evidence was found that the predatory/parasitic fauna at ARF was impoverished with fewer but larger populations as a result of carcass enrichment. Comparison of the sarcosaprophagous and predatory/parasitic faunas revealed a tighter (and more predictable) linkage between carrion feeders (sarcosaprophages) and their carrion than between carrion feeders and their natural enemies (predators and parasitoids), leading us to conclude that ARF is more representative of surrounding sites with respect to the sarcosaprophage component than to the predatory/parasitic component within the larger carrion-arthropod community.

KEYWORDS: forensic science, forensic entomology, Anthropology Research Facility (ARF), arthropod saturation hypothesis, predatory and parasitic arthropods, carrion-arthropod succession

The on-campus Anthropology Research Facility (ARF) at the University of Tennessee, Knoxville, established by Professor William Bass in 1981 at the present site, is an outdoor laboratory devoted to the scientific study of postmortem human decay. Throughout its 20-year history (not 30 years as we reported in [1]), over 400 sets of human remains have been studied at ARF. Scientific outputs from this site have included insect faunal surveys (2,3) and comparative field experiments with euthanized pigs as model corpses (4,5). Ecological studies have shown that nutrient-enriched ecosystems, like ARF, may become dominated by the most tolerant or competitive species, altering both species richness and evenness of the biological community (6,7). Consequently, one might predict that carcass enrichment at ARF might saturate human (and other animal) remains with arthropods of reduced diversity but high abundance (herein called the arthropod saturation hypothesis)

and that this buildup might modify rates of carcass decomposition, compared to local non-enriched sites.

Using conventional statistics to test between-site differences in decomposition variables and ecostatistical and power tests of arthropod community structure, Shahid et al. (1) found that porcine remains in the ARF decomposed slower (although not significantly so) and that sarcosaprophagous arthropods (e.g., blow flies, flesh flies, skipper flies, carrion beetles, rove beetles) did not occur there in abnormally higher densities nor did they colonize carcasses faster than in surrounding sites. Post-hoc power analyses of three variables (carcass weight, sweep-net taxa, pitfall-trap taxa) showed that a larger number of replicate carcasses, aerial net sweeps, and pitfall traps than those actually used would be required in a future study to detect significant differences between ARF and the other sites, based on the observed differences that were found in these variables. From these results, Shahid et al. (1) concluded that the ARF is representative of surrounding sites, at least with respect to the sarcosaprophagous fauna.

The focus of this first study on the sarcosaprophagous fauna ignored the possibility that carcass enrichment affected the community structure of predatory and parasitic arthropods that prey upon the sarcosaprophagous fauna. Predaceous and parasitic arthropods comprise the second most important group of carrion-associated taxa (8); as such, they have been used as supplemental indicators of succession-based estimates of the postmortem interval (PMI), particularly in cases of advanced decomposition. These predatory taxa have included gamasid mites (9), staphylinid and histerid

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beetles (10), clerid beetles (11), vespidae wasps (12), and ants (13). Through their predatory activities, ants can interrupt the continuity of the successional process (14) and, in conjunction with vespidae wasps, can also retard rates of carcass decomposition (15,16). Omnivorous taxa (e.g., silphid, histerid, staphylinid and clerid beetles), which feed on both carcass tissues and sarcosaprophagous insects, may also slow carcass decay rates (16). Other predators in carrion, such as spiders, harvestmen, and centipedes, although not carrion dependent, exploit the remains nevertheless by consuming sarcosaprophagous insects and sometimes other predaceous arthropods. The effects of parasitoid oviposition on the behavior and development of sarcosaprophagous insects in carrion, although currently understudied, may someday hold forensic significance (8). The discovery of nests or colonies of social insects near human remains (13) underscores the need to better understand the ecological roles of these and other predatory arthropods in both cadaver decomposition and PMI estimation.

Consequently, in this second test of the arthropod saturation hypothesis, we ask if carcass enrichment at the ARF has altered the predatory and parasitic fauna of the carrion-arthropod community, relative to three local non-enriched sites. As before, we sought evidence of altered community structure of arthropod species and individuals in cumulative and time-series tests. A secondary purpose was to determine if the trends in the predatory and parasitic fauna are as strong and repeatable across sites as those found in our earlier analysis of the sarcosaprophagous fauna. Comprehensive details of the experimental design, habitat descriptions and microclimate, ecological variables, statistical analyses, and participating individuals and institutions are presented in Shahid et al. (1) and are only summarized here.

Materials and Methods

Field Sites and Pig Placement

The study was conducted in the summer of 1998 at four sites designated S1 through S4, in and around the Knoxville area of southeastern Tennessee: ARF (S1); S2 (700 m away from ARF), S3 (6 km away), and S4 (40 km away). At each site, three freshly euthanized pigs (*Sus scrofa* L.) were distributed between 1.8 and 2.5 m apart in a linear arrangement. Pig euthanasia was by intracardial injection of sodium pentobarbital (Beuthanasia-D, Schering-Plough Animal Health Corporation). Each carcass was enclosed with a wire-mesh cage to minimize disturbance from vertebrate scavengers. Carcass placement occurred before sunrise to synchronize arthropod visitation times across sites (17). Starting weights (kg) and sexes of pigs were randomized across sites.

Arthropod Sampling and Identification

Ground and aerial arthropods were sampled from pigs using pitfall traps and sweep nets from June 19 to June 30, 1998. Pitfall trap and sweep net methods conformed to protocols described in Catts and Haskell (18). Four pitfall traps were buried around a pig at S1–S3 along the four cardinal directions (Pig “B”); the rocky hillside at S4 permitted only one pitfall trap to be installed near the three carcasses. Pitfall traps were constructed from a 20-cm section of 10 cm diameter PVC pipe, a one-pint wide-mouth canning jar, and a 10-cm maximum diameter plastic funnel with the stem removed. The PVC pipe was buried vertically with its top edge at ground level. Each jar was filled 4-cm deep with 95% ethanol, placed into a PVC pipe, then covered with the funnel. For flying arthropods, three repetitive sweeps of an aerial net were made in rapid succes-

sion over each of the three carcasses at each site. Sweep samples were separated by 5-min intervals to allow arthropod resettlement on the carcass. Daily hand samples were collected by one or more persons on each day but were only used to record the presence of a species on a carcass. Collected materials from both methods were flushed into coded vials containing 75% ethanol.

Using a stereo dissecting microscope, organisms were sorted to stage (immatures, adults) and identified to the lowest possible taxon, usually family or below. Other taxa, such as spiders, centipedes, harvestmen, pseudoscorpions, and mites, were identified to order. Thus, “taxon” is used throughout this report to identify a group of organisms of any rank (class, order, family, genus, species, life-cycle stage) that differed in morphological respects from other such groups. Taxa were identified using the following keys: McAlpine (19), Stehr (20), and Borror et al. (21). All identified specimens were sealed in labeled patent-lip vials containing 75% ethanol. Voucher specimens were deposited in the W. R. Enns Entomology Museum at the University of Missouri.

Statistical Analysis

Because pitfall traps within sites were replicated at only three of the four sites, daily counts were averaged for S1–S3 and rounded to the nearest integer; daily counts from the single pitfall trap at S4 were left unchanged. Site means for sweep-net catches (3 sweeps per site) were similarly calculated. Pairwise differences between S1 and the other three sites were assessed using a combination of graphical methods, conventional statistics, and community-level ecostatistics:

(a) Comparison of arthropod abundances across sites was achieved using matched rank-abundance plots (22) in which one site (S1) was chosen as the reference plot to which the other sites (S2–S4) were compared. When plotted in this way, rank-abundance plots permit a quick visual check of the degree of correspondence between two or more sites (22).

(b) Species and individuals' accumulation curves were plotted separately for pitfall and sweep-net catches, averaged over the replicates at each site, to show the rate of colonization of predatory and parasitic arthropods over time. These curves plot the sums of the number of taxa and their individuals in the previous sample and the number of taxa and their individuals in the present sample that were not observed in any previous sample. For the first sample, the cumulative numbers of taxa and their individuals are defined to equal its numbers of taxa and numbers of individuals. In this analysis, we present two revised plots of individuals' accumulation curves (for sweep-net and pitfall-trap counts) for the sarcosaprophagous fauna, following a more straightforward method that accumulates species abundances regardless of colonization history. The revised plots yielded identical conclusions as the previous plots.

(c) $E(S_n)$, the rarefaction diversity statistic and its variance [$var E(S_n)$] were used to test the null hypothesis that two or more samples have been drawn from the same parent population (23,24). Rarefaction assumes a random spatial dispersion of individuals (25). Between-site analysis relied on complete rarefaction curves bracketed by bands 1.96 and 3 standard deviations wide (i.e., approximately equal to its 95% and 99% confidence limits) for pitfall and sweep-net catches using the sites with the largest total abundance. The null hypothesis was upheld if data points for all remaining sites fell within the 95% or 99% confidence bands of the rarefaction curve and is a test of the homogeneity of the relative abundance distributions of these taxa.

(d) R_s , the nonparametric rank test (26), and its correction for excessive ties (27), was used to test the null hypothesis that species-abundance rankings from site pairs were independent. Rank tests were calculated separately for pitfall and sweep-net samples and for every pairwise combination of sites that included S1. Because each pairwise comparison addresses a common null hypothesis, all correlations were adjusted using the Bonferoni multiple-test procedure (28,29) such that, if a collection of k tests is simultaneously carried out, the Bonferoni adjustment is equal to α/k where α is equal to 0.05. Such adjustment minimized Type 1 errors that might arise due to the high number of pairwise comparisons.

(e) PIE , probability of interspecific encounter or species evenness (23), was used to test the null hypothesis that the distribution of species abundances is statistically indistinguishable for all pairwise combinations of sites that included S1. PIE measures the probability that two individuals, drawn randomly from a sample, belong to different species (30), and ranges from a value close to 0 (all species except dominant represented by a single individual) to unity (all species have equal abundance). The null hypothesis was upheld if evenness indices from non-enriched sites (S2, S3, S4) fell within 95% confidence limits of S1.

Results

The Predatory and Parasitic Fauna

In excess of 81,000 invertebrates were collected over the 12-day period representing 26 orders, 118 families, and 223 individual taxa. Based on descriptions in Smith (8), Catts and Haskell (18), Byrd and Castner (31), and Borrer et al. (21), we then separated each known predator or parasitic taxon and totaled their abundances over all sampling dates. This procedure reduced the pitfall and sweep-net counts to 9,726 and 339 individuals, respectively, for a total predator and parasitic fauna of 10,065 individuals. The identity of each taxon is given in the appendix. Prior to analysis, immatures and adults of the same taxon (subfamily, family) were lumped, as we did in Shahid et al. (1), to permit cross-study comparisons. Predatory arthropods comprised the largest natural enemy group (30 taxa), followed by parasitoids (7 taxa) and hematophagous (blood-sucking) insects (3 taxa) (Appendix). Because 10 of the 40 taxa feed as both sarcosaprophages and predators (=omnivores), they are double listed in this appendix and in the appendix of Shahid et al. (1).

Ranked-Abundance Plots

Invertebrate taxa sampled from pitfall traps spanned a nearly 400-fold range in mean abundance per carcass, whereas, sweep-net invertebrates spanned only a 13-fold range (Fig. 1). Across the four sites, pitfall and sweep-net catches show high compositional similarity in predator and parasitic taxa. Two non-enriched sites, S2 and S3, were most taxonomically similar, sharing 61% of the predatory taxa and 98.5% of their individuals in pitfalls and sweep nets, indicating that the more abundant taxa made up the joint taxa. The two most distant sites, S1 and S4, were least taxonomically similar, sharing 39% and 97% of their predatory and parasitic taxa and individuals, respectively. Across all four sites, staphylinid beetles (#s 125, 126) were the most abundant of the predators sampled, followed by mites (#101), histerid beetles (#116), ants (#152), and harvestmen (#103); whereas, various microhymenopterans (#154) were the most commonly sampled parasitoids across the sites (Fig. 1, Appendix).

Matched abundance plots showed that a few uncommon taxa, collected from S1, were sampled in lower numbers or none at all

TABLE 1—Spearman (tie-adjusted) rank correlations (r_s) of sweep-net and pitfall trap abundances of predaceous and sarcosaprophagous faunas for each pairwise combination of sites that included S1.

Method	Site Comparison*		
	S1 vs. S2	S1 vs. S3	S1 vs. S4
Pitfall Trap Catches			
Sarcosaprophagous Fauna [†]	0.9231	0.8889	0.7707
Predaceous Fauna	0.8448	0.7805	0.7182
Sweep-Net Catches			
Sarcosaprophagous Fauna [†]	0.9187	0.9665	0.8963
Predaceous Fauna	0.8956	0.5441	0.1053

* Numbers in bold type are significant at the 0.05 level using Bonferoni adjustment for multiple test procedures. Because faunas share some taxa in common, they are considered dependent within each method.

[†] from Table 4 in Shahid et al. (1).

TABLE 2—Indices of community evenness (or probabilities of interspecific encounter, PIE) for predatory and sarcosaprophagous taxa sampled from pitfall traps and sweep-nets in each of the four sites. Values are means taken over four pitfall traps at one carcass (all sites except S4) or sweep-net catches taken over three carcasses at each site.

Method	Site			
	S1*	S2	S3	S4
Pitfall Trap Catches				
Sarcosaprophagous Fauna	0.455 (0.058–0.852)	0.504	0.319	0.675
Predaceous Fauna	0.660 (0.495–0.825)	0.751	0.803	0.736
Sweep-Net Catches				
Sarcosaprophagous Fauna	0.685 (0.484–0.886)	0.840	0.811	0.754
Predaceous Fauna	0.835 (0.798–0.872)	0.797	0.899	0.691

* S1 = mean and 95% CI.

at the other sites. The most conspicuous example were cylindrical bark beetles (Colydiidae: Coleoptera, #114) in which 3, 0, 0 and 0 individuals were caught at S1, S2, S3, and S4, respectively. Conversely, several predatory and parasitic species, collected in small numbers at S2–S4, went unsampled at S1 (8, 3, and 10 taxa in S2, S3, and S4, respectively; Fig. 1). On balance, the total number of “missing” taxa in paired site comparisons that included S1 was uneven, with 23 missing taxa from the S1 side compared to 28 from the three non-enriched sites.

Spearman tests showed that correlations of abundance ranks, although significantly positive between 9 of 12 site pairs that included S1, were stronger for the sarcosaprophagous fauna (mean r_s : 0.8940) than the predatory and parasitic fauna (mean r_s : 0.6481; Table 1). Abundance ranks also revealed a stronger distance effect for predators and sweep-net samples than for sarcosaprophages and pitfall-trap samples (Table 1).

Species Evenness

If the arthropod saturation hypothesis is true, then community evenness indices for S2–S4 should all fall outside and above the confidence interval of S1, reflecting significant differences in species abundance distributions between enriched and non-enriched sites. Between-site differences were revealed only in sweep-net catches, specifically in 3 of 3 cases for the predatory fauna (Table 2).

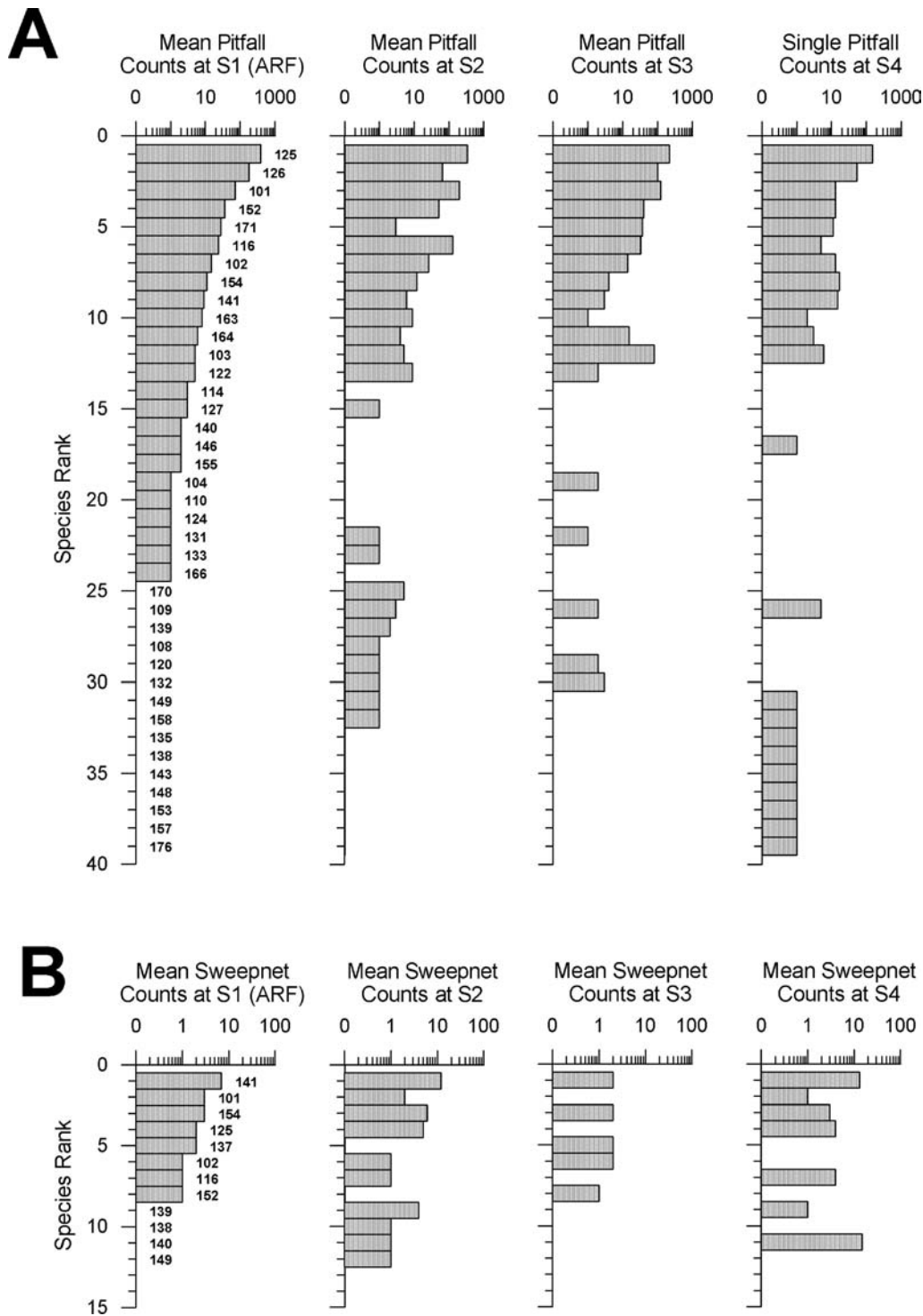


FIG. 1—Matched rank-abundance plots for entire complexes of predatory and parasitic taxa collected from pitfall traps (A) and sweep nets (B), totaled over all twelve sampling dates. The left-most plot (with its abundances arranged in decreasing order) represents the S1 (ARF) site against which all remaining sites (S2, S3, S4) can be compared. Abundances are plotted on a logarithmic scale for readability. Taxon identification numbers are shown in the S1 plot; these numbers and their corresponding identities are listed in the Appendix.

However, contrary to the arthropod saturation hypothesis, neither predators nor sarcosaprophores at S1, based on pitfall and sweep-net catches, were dominated by a few species of high abundance.

Accumulation Curves

Comparison of accumulation curves for predatory taxa and individuals at S2–S4, against the approximate 95% confidence intervals

for S1, showed that the three sites, on a majority of days, accumulated new taxa and individuals at comparable rates (Figs. 2–3). For sweep-net samples, S3 accumulated taxa and individuals at a faster rate than S1 and the other sites on days 6–9 and days 6, 7 and 9, respectively (Fig. 2A, 3A). For pitfall samples, S2 and S3 accumulated taxa and individuals faster than S1 and S4 on day 1 and days 2–7, 11, respectively (Fig. 2B, 3C). Taken together, accumulation curves for predators captured at non-enriched sites fell inside S1's

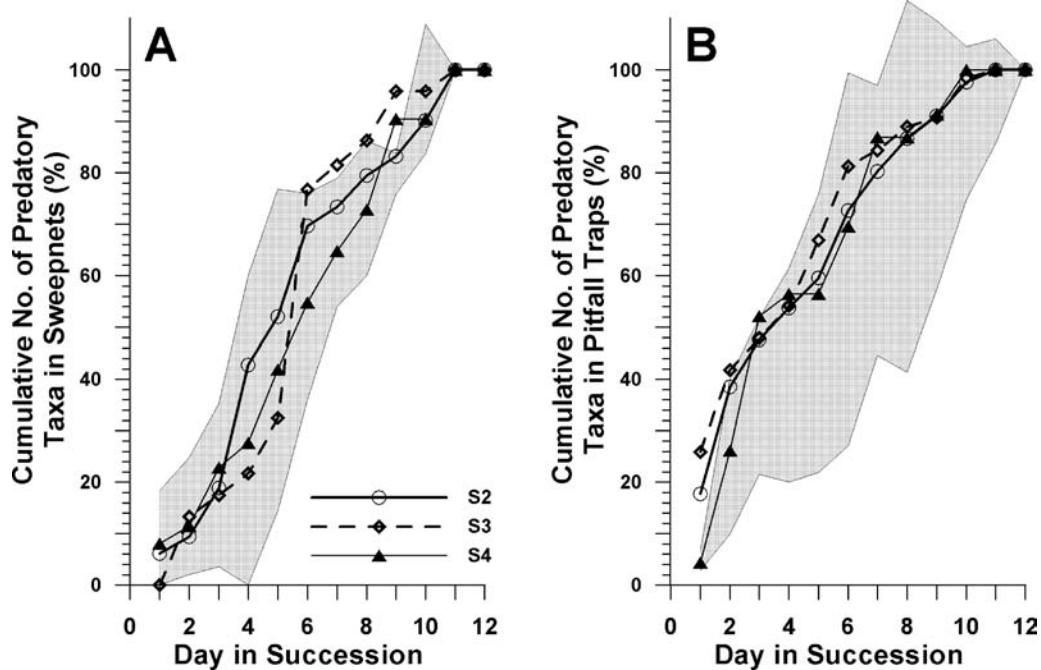


FIG. 2—Cumulative number of predatory taxa for sweep-net (A) and pitfall trap (B) samples. The curve for S1 (shaded region) is the mean bracketed by a band 1.96 standard deviations wide, which constitutes approximate 95% confidence intervals. Curves for sweep-net catches are based on means, over three carcasses, for each site; the curves for pitfall catches are based on means, over a maximum of four pitfall traps, for each site. For both methods, raw means were normalized (to percentages) to permit between-site comparisons.

95% confidence bands in 64 of 72 site-days for taxa (89%) and in 44 of 72 site-days for individuals (61%), for a total of 108 (75%) site-days (Figs. 2–3). These percentages are comparable to those found for the sarcosaprophagous taxa (83%), individuals (69%) and their overall total (76%), based on the same methods (Fig. 3B, D; Fig. 4 in [1]).

At S1, 75% of the sweep-net predatory taxa were captured by day 9, whereas, 75% of their sampled individuals were caught by day 10. In pitfall traps, 75% of the sampled predatory taxa at S1 were captured by day 8 and 75% of the individuals were caught by day 10. After normalizing raw means into percentages, rates of colonization for predators and parasites were found to be slower than those reported by Shahid et al. [1] for sarcosaprovores (Figs. 3A–D).

Rarefaction Analysis

Complete rarefaction curves for the cumulative sample of 41 and 877 predatory individuals at S4 (sweep-net) and S2 (pitfall trap), respectively, were drawn by standardizing (rarefying) the samples at intervals of 5 and 36 individuals, respectively. Both curves were bounded by intervals 1.96 and 3 standard deviations wide, which constitute approximate 95% and 99% confidence limits. For the observed numbers of sweep-net individuals in S1–S3 and pitfall-trap individuals in S1, S3, S4, the observed number of taxa for these sites are also plotted.

If the number of sweep-net individuals in S1–S3 and the number of pitfall-trap individuals in S1, S3 and S4 are drawn at random from their totals in S4 and S2, respectively, and if the null hypothesis is true, then the number of sweep net and pitfall taxa in these sites should all fall within the 95% or 99% confidence intervals. For sweep-net samples, only S2 fell outside both confidence intervals (Fig. 4A), whereas, for pitfall-trap samples, S3 and S4 fell outside

both confidence intervals (Fig. 4B). Thus, sweep-net counts from S2 and pitfall-trap counts from S4 each yielded an overabundance of taxa while pitfall trap counts from S3 yielded a slight underabundance of taxa, relative to the other sites. In contrast to these results, Shahid et al. (1) found that the sarcosaprophagous fauna had comparable taxonomic richness across all four sites, within a 99% confidence interval, for both sweep-net and pitfall-trap samples.

Discussion

In this study of the enemy fauna of carrion-dependent sarcosaprovores, several measures of community structure, derived from sweep-net and pitfall-trap samples, showed that ARF and three local non-enriched sites were comparable with respect to the cumulative number of taxa (Fig. 2A, C) and, to a lesser extent, cumulative number of individuals (Fig. 3A, C) on a per carcass basis. Notable exceptions were found among nonparametric correlations of ranked abundance (Table 1), taxonomic evenness (Table 2), and rarefaction-adjusted taxonomic richness (Fig. 4A–B).

In contrast with ecological theory (6,7), no evidence was found that the predatory fauna at ARF was impoverished with fewer but larger populations as a result of nutrient (carcass) enrichment. Indeed, rank-abundance plots showed that taxonomic richness at ARF (25 taxa) and the non-enriched sites (range: 19–26 taxa) were comparable (Figs. 1A–B). After rarefying site abundances to a common size, one site difference emerged for sweep-net (S2, Fig. 4A) and two for pitfall-trap (S3 and S4, Fig. 4B) samples, leading us to conclude (at a 99% confidence level) that the predatory fauna has dissimilar abundance distributions across the four sites. Although rarefaction loses information about species identity (25), its use is restricted to studies whose samples contain taxonomically similar organisms (30), as this study revealed (range of shared individuals in paired-site tests: 94–98%).

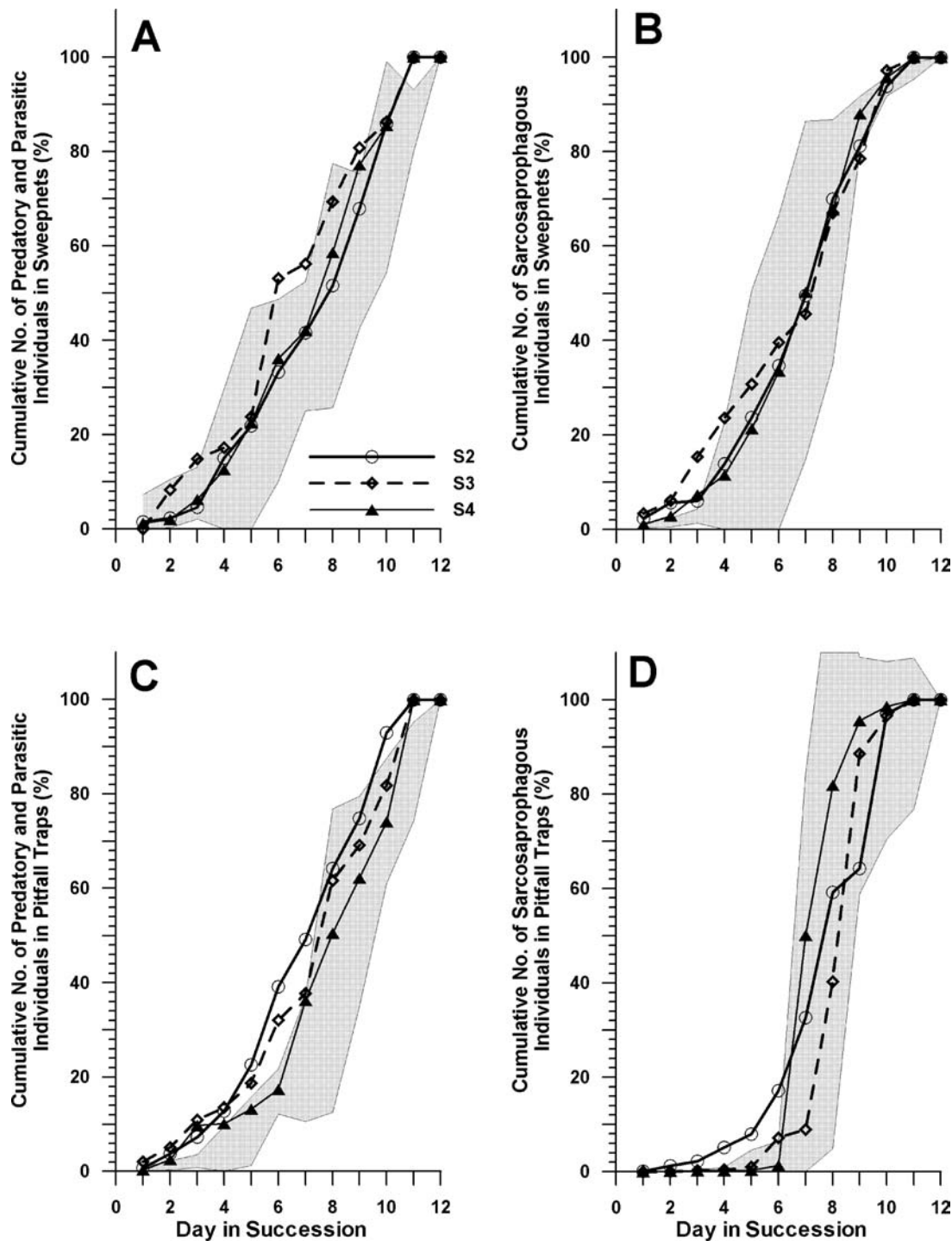


FIG. 3—Cumulative number of predatory (A, C) and sarcosaprophagous (B, D) individuals for sweep-net (A–B) and pitfall trap (C–D) samples. The curve for S1 (shaded region) is the mean bracketed by a band 1.96 standard deviations wide, which constitutes approximate 95% confidence intervals. For both methods, raw means were normalized (to percentages) to permit between-site comparisons. Curves for sarcosaprophagous individuals are revised from Shahid et al. (1), based on a more straightforward counting method (see Materials and Methods: Statistical Analysis).

In this study, only a third of the predatory and parasitic taxa were identified to the genus or species level. Typically, predaceous arthropods other than silphids, staphylinids and clerids, which we did identify to species, are unevenly or infrequently reported at the species level in succession-based carrion-arthropod studies (e.g., 2,32–41). Indeed, carrion researchers know that many predators inhabit their study sites before carcass placement (in the soil or nearby vegetation) or accidentally wander there after-

ward as opportunists, such as pseudoscorpions, centipedes, various flies, wasps, true bugs, and crickets. Because these predators are often sampled in very low numbers, as we confirmed in this study (Fig. 1), they are often dismissed as accidentals, incidentals or tourists. For reasons of completeness and future study, we chose to include in our analysis all collected predaceous and parasitic taxa, regardless of their abundance or taxonomic rank.

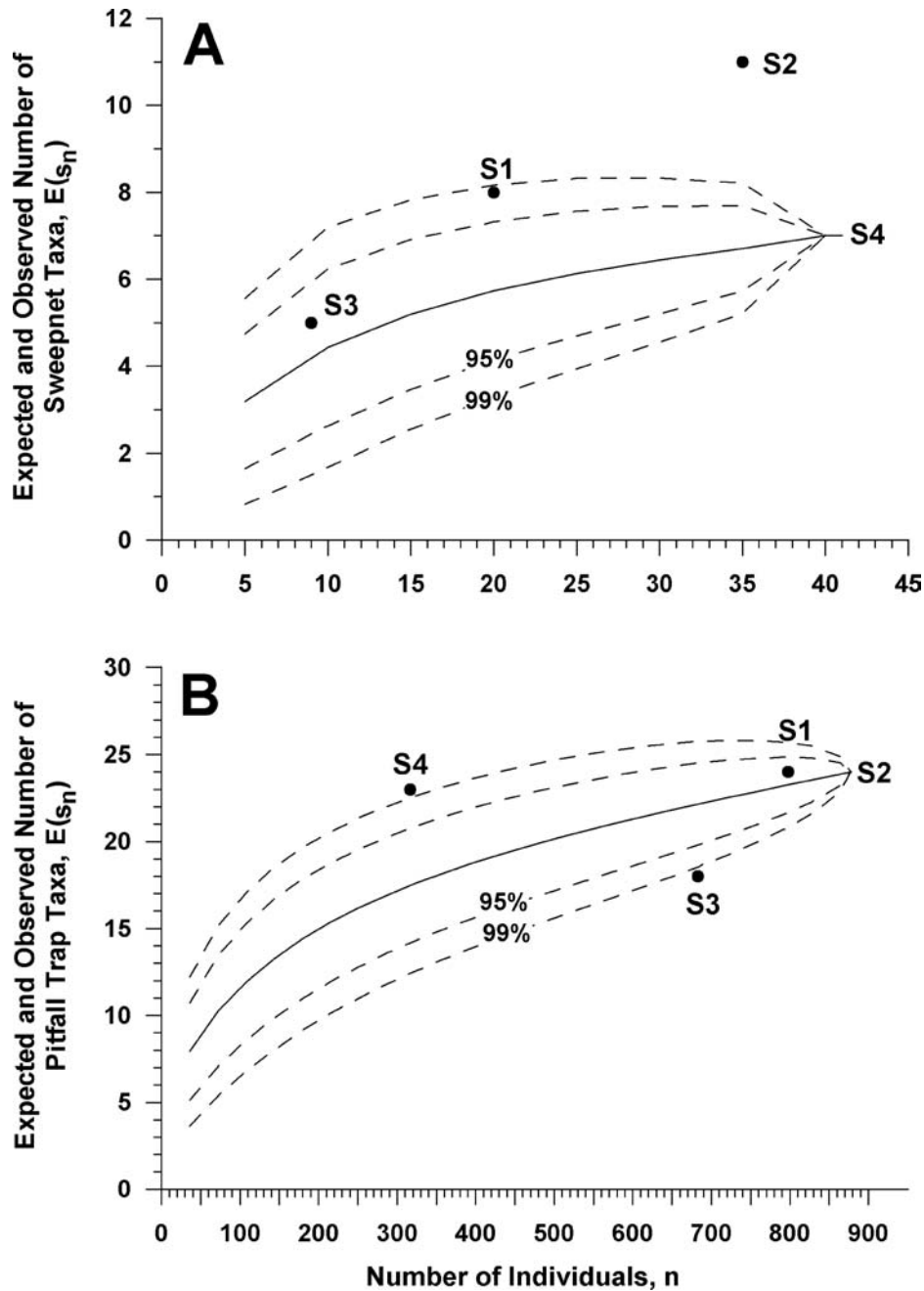


FIG. 4—Complete rarefaction curves (solid lines) and 95% and 99% confidence arcs (dashed lines) for predatory and parasitic taxa in (A) sweep-net and (B) pitfall-trap samples, based on mean abundances per site. Symbols refer to the four sites described in the text, where S1 = ARF.

By extension, many of the predatory and parasitic taxa collected in this study do not depend on carcasses for food, mating or shelter, and are one or more trophic levels removed from their sarcosaprophagous prey or hosts in the carrion-arthropod food web. This feature may buffer (or even exclude) the enemy fauna from the effects of carcass enrichment. Indeed, the magnitude of population fluctuations caused by changes in carcass availability is expected to decrease up the food chain, as other nutrient enrichment studies have shown (42). Thus, between-site repeatability in community structure is expected to be weaker for predators and parasitoids than their prey or hosts. Three findings from this study confirm this prediction. First, the sarcosaprophagous fauna was found to have more taxa in common across the four sites (32%), albeit marginally, than

their natural enemies (30%). Second, nonparametric (Spearman) rank tests showed that correlations, while significantly positive in 9 of 12 pairwise tests that included S1, were stronger for sarcosaprophages (mean r_s : 0.8940) than their natural enemies (mean r_s : 0.6481; Table 1). Third, rarefaction-adjusted species richness was more comparable for sarcosaprophages (1) than for their natural enemies, for both sweep-net and pitfall-trap samples (Figs. 4A–B). Consequently, we are better able to predict the community structure of the sarcosaprophagous fauna on a regional scale than we are for their natural enemies, suggesting a tighter linkage exists between carrion feeders and their carrion than between carrion feeders and their natural enemies. Taken together, we conclude that this outdoor laboratory is more representative of surrounding sites with respect

to the sarcosaprophagous fauna than it is for the predatory and parasitic fauna that preys upon this forensically important group.

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APPENDIX—Code numbers and identities of predaceous and parasitic taxa collected from ARF and three surrounding sites, sorted by identification number (see Fig. 1).

ID No.	Class	Order	Family	Subfamily, Genus or Species	Life Stage*
101	Arachnida	Acarina	?	?	A
102	Arachnida	Araneae	?	?	A
103	Arachnida	Opiliones	?	?	A
104	Arachnida	Pseudoscorpiones	?	?	A
108	Chilopoda	Lithobiomorpha	?	?	A
109	Insecta	Coleoptera	Carabidae	?	I, A
110 [†]	Insecta	Coleoptera	Cleridae	<i>Necrobia ruficollis</i>	A
114	Insecta	Coleoptera	Colydiidae	?	A
116 [†]	Insecta	Coleoptera	Histeridae	?	I, A
120 [†]	Insecta	Coleoptera	Silphidae	<i>Nicrophorus orbicollis</i>	A
122 [†]	Insecta	Coleoptera	Silphidae	<i>Silpha americana</i>	A
124 [†]	Insecta	Coleoptera	Silphidae	<i>Silpha surinamensis</i>	A
125	Insecta	Coleoptera	Staphylinidae	?	I, A
126 [†]	Insecta	Coleoptera	Staphylinidae	<i>Creophilus maxillosus</i>	A
127 [†]	Insecta	Coleoptera	Staphylinidae	<i>Ontholestes cingulatus</i>	A
131 [†]	Insecta	Coleoptera	Staphylinidae	<i>Staphylinus cinnamopterus</i>	A
132 [†]	Insecta	Coleoptera	Staphylinidae	<i>Staphylinus maculosus</i>	A
133 [†]	Insecta	Coleoptera	Staphylinidae	<i>Staphylinus violaceus</i>	A
135	Insecta	Diptera	Asilidae	?	A
137	Insecta	Diptera	Culicidae	?	A
138	Insecta	Diptera	Dolichopodidae	?	A
139	Insecta	Diptera	Empidae	?	A
140	Insecta	Diptera	Muscidae	<i>Stomoxys calcitrans</i>	A
141	Insecta	Diptera	Phoridae	?	I, A
143	Insecta	Diptera	Rhagionidae	?	A
146	Insecta	Hemiptera	Anthocoridae	?	A
148	Insecta	Hymenoptera	Bethylidae	?	A
149	Insecta	Hymenoptera	Braconidae	?	A
152	Insecta	Hymenoptera	Formicidae	?	I, A
153	Insecta	Hymenoptera	Ichneumonidae	?	A
154	Insecta	Hymenoptera	microhymenoptera	?	A
155	Insecta	Hymenoptera	Mutillidae	?	A
157	Insecta	Hymenoptera	Scelionidae	<i>Baeus</i> sp.	A
158	Insecta	Hymenoptera	Sphecidae	?	A
163	Insecta	Orthoptera	Gryllacrididae	?	I, A
164	Insecta	Orthoptera	Gryllidae	?	I, A
166	Insecta	Siphonaptera	Pulicidae	Spilopsyllinae	A
170	Insecta	Coleoptera	Lampyridae	?	I
171	Insecta	Coleoptera	Silphidae	?	I
176	Insecta	Hemiptera	Reduviidae	?	I

* A, adult; I, immature stage.

[†] listed in this study and in Shahid et al. (1) because of their dual role as both sarcosaprophore and predator.