



Silphids in urban forests: Diversity and function

JORDAN M. WOLF

JAMES P. GIBBS*

jpgibbs@syr.edu

250 Illick Hall, 1 Forestry Drive, State University of New York College of Environmental Science and Forestry,
Syracuse, NY 13210, USA

Abstract. Many ecologists have examined the process of how urbanization reduces biological diversity but rarely have its ecological consequences been assessed. We studied forest-dwelling burying beetles (Coleoptera: Silphidae)—a guild of insects that requires carrion to complete their life cycles—along an urban-rural gradient of land use in Maryland. Our objective was to determine how forest fragmentation associated with urbanization affects (1) beetle community diversity and structure and (2) the ecological function provided by these insects, that is, decomposition of vertebrate carcasses. Forest fragmentation strongly reduced burying beetle diversity and abundance, and did so far more pervasively than urbanization of the surrounding landscape. The likelihood that beetles interred experimental baits was a direct, positive function of burying beetle diversity. We conclude that loss of burying beetle diversity resulting from forest fragmentation could have important ecological consequences in urban forests.

Keywords: diversity, ecological function, forest fragmentation, Silphidae, urban forests

Introduction

Parks, natural preserves, and even roadside vegetation are the limited habitats available for native fauna within urban ecosystems (Dreistadt *et al.*, 1990). Managing these resources for the benefit of the physical environment (Nowak and Dwyer, 2000) and for native wildlife and biodiversity are common goals (Nilon and Pais, 1997; Marzluff and Ewing, 2001). Moreover, maintaining functional relationships among species is an important aspect of the overall health of these ecosystems (Mooney *et al.*, 1996; Gering and Blair, 1999). Although many ecologists have evaluated how urbanization and habitat fragmentation alter patterns of biodiversity (Andren, 1994; Blair, 1996; Blair and Launer, 1997; Chernousova, 2001; Kozlov, 1996; Mills *et al.*, 1989), rarely have ecologists examined the consequences of impoverishment of any functional guild of organisms for the specific ecological function it provides (Tilman, 2000).

Insects are a group of organisms that perform diverse and vital ecosystem functions (Didham *et al.*, 1996; Fisher, 1998). One such group is the burying beetles (Coleoptera: Silphidae), which are decomposers in forested ecosystems, using vertebrate carcasses for feeding and reproduction (Anderson and Peck, 1985; Scott, 1998). Moreover, burying beetle diversity and success are inversely related to increasing habitat fragmentation (Lomolino and Creighton, 1996; Trumbo and Bloch, 2000; Gibbs and Stanton, 2001). In urban areas there are generally few forested areas (McDonnell and Pickett, 1990) large enough to support

*To whom correspondence should be addressed.

a burying beetle community as diverse as that found in natural forested areas (Gibbs and Stanton, 2001).

Despite the noticeable trend in forests along an urban-rural gradient to decrease in size and quality closer to the urban core, in many cities forest patches can vary greatly in size, structure, composition, and juxtaposition with other land uses (Zipperer *et al.*, 1997). Systems of forest patches in urban areas thus provide an opportunity to elucidate the importance of habitat loss versus “matrix effects” (*sensu* Forman, 1983) on biodiversity. They also permit evaluation of whether the specific ecological function provided by a particular ecological guild is unique or whether it is made redundant by other guilds of organisms not affected by habitat fragmentation.

In this study, we measured burying beetle abundance and diversity in a system of 30 forest patches along an urban-rural gradient in Baltimore, Maryland. We also experimentally placed mouse carcasses in those same patches and recorded their fates. Together our investigations generated information about diversity, abundance, and the ecological role of burying beetles in relation to forest fragmentation and urbanization. Our data were used to evaluate two hypotheses germane to understanding patterns of change in insect diversity in urban forests and the ecological consequences of such changes: (1) forest fragmentation and associated urbanization alter the diversity of burying beetle communities, and (2) changes in burying beetle diversity alter patterns of interment of carcasses of vertebrate animals.

Methods

Study organisms

Burying beetles are a specialized group of insects that rely on an ephemeral resource—carrion—for their reproduction (Anderson and Peck, 1985; Scott, 1998). Populations of these beetles are easily surveyed with low-maintenance, baited traps (Shubeck, 1984; Coyle and Larsen, 1998). Declines in burying beetle populations are caused by reductions in the number and size of vertebrates (Trumbo and Eggert, 1994; Holloway and Schnell, 1997; Merrick, 1998; Smith and Merrick, 2001), and are particularly associated with habitat loss and fragmentation (Lomolino *et al.*, 1995; Lomolino and Creighton, 1996; Trumbo and Bloch, 2000; Gibbs and Stanton, 2001). Burying beetles are subject to interspecific competition for carcasses with several other taxa including vertebrates, fungi, and other insects (Scott, 1998). It is often suggested that burying beetles inter carcasses to avoid competition with one group of organisms in particular, carrion-feeding flies (Suzuki, 2000), competition with which may cause a reduction in burying beetle success in fragmented and urban habitats (Gibbs and Stanton, 2001).

Study sites and their characterization

Thirty forested sites within Baltimore City and Baltimore, Carroll, and Howard Counties, Maryland were selected for this study (Appendix A). The Baltimore area was chosen because it contains a large number of forest remnants of varying size and surrounding land use

within a small geographic area. It is also the site of long-term ecological research on urban environments (Collins *et al.*, 2000). The forests were closed-canopy temperate deciduous forests, ranging in size from 1–250 hectares with surrounding land uses varied from mostly urban to mostly agricultural.

Land use in regions surrounding trapping sites was estimated from the 30-meter resolution National Land Cover Data (NLCD) classified LANDSAT Thematic Mapper image of the Baltimore-Washington, DC metropolitan area taken in 2000 (Homer *et al.*, 2002; USEPA, 2002). Percentage land use and degree of forest fragmentation (average proportion of cells surrounding a forested cell that were also forest) were calculated at several spatial scales (0.1 km², 1 km², 10 km²) for circular areas centered at each site (Hepinstall and Sader, 1997; Chust *et al.*, 2000). Preliminary analysis indicated that the 1.0 km² spatial scale provided the clearest associations between land use and invertebrate carrion-feeding populations; therefore, all results presented pertain to landscape composition as measured at this scale. Extent of deciduous forest was therefore calculated as a percentage of a circular 1.0 km² area centered at a particular sampling site. Other land uses were calculated as percentages of the remaining non-forested land uses (see *Statistical Analysis* for rationale). Only major land use types (>10% averaged across all sites) were included in the analysis. Soil compactness (kg-force per square cm required to penetrate 7.5 cm) was determined using a DICKEY-John soil compaction tester because it potentially also would affect beetle burying ability.

Characterization of carrion-feeding insect communities

Communities of carrion-feeding insects at each site were characterized through the use of baited traps (Coyle and Larsen, 1998; Gibbs and Stanton, 2001) during two, two-week periods (15 June–4 July, 2002 and 28 July–12 August, 2002). Trapping periods were interspersed within the peak of seasonal activity of most beetle species present in the area. Traps were constructed from one-liter plastic containers and plastic cups, and baited with a single chicken leg (Coyle and Larsen, 1998). Bait was placed inside the smaller plastic cup and protected using metal screen mesh secured by a rubber band and duct tape. The mesh prevented insects attracted to the bait from accessing it, thus increasing the longevity of the bait's attractiveness. Insects attracted to the bait would fall into a larger outer cup, which contained 100% propylene glycol killing solution. The entire trap was protected from rain by a plastic plate folded into a hood over the top of the trap. Burying beetles were identified in the lab to species according to Anderson and Peck (1985). Carrion-feeding Dipterans (Families Caliphoridae, Muscidae, and Sarcophagidae) were identified to family according to Borror and White (1970).

Assessment of ecological function provided by burying beetles

Patterns of carrion utilization were contrasted among study sites by placing experimental baits in the field for standardized time periods (Wilson *et al.*, 1984; Trumbo, 1990). During July and early August 2002, four dead adult mice (25–40 g) were placed at each study site, one mouse per site per week. Approximately 1 m of dental floss was tied to the hind

leg of each mouse bait to aid in relocating any bait buried (Trumbo, 1990). Baits were checked after one week. Baits buried were examined for the beetles or larvae associated with it. Missing, unburied baits were assumed to have been taken by vertebrate scavengers. Unburied baits unoccupied by burying beetles were assumed to have been consumed by other terrestrial invertebrates.

Statistical analysis

Carrion-feeding insect communities were characterized based on several metrics: total number of individuals per burying beetle species, total abundance of all burying beetles, number of burying beetle species, burying beetle diversity (rarefied Simpson's D; Magurran, 1988), and total number of carrion-feeding Dipterans. Potential for fly-beetle interactions was contrasted among sites based on the ratio of total flies to total beetles captured at each site. All species and diversity measurements except species richness were non-normally distributed ($\alpha = 0.05$, based on the Shapiro-Wilk test for normality, Zar, 1984; SAS Institute, 2002), and were normalized through log-transformation as $\ln(x + 1)$.

The relationship between the structure of carrion-feeding insect communities and land use was examined using a combination of single and multiple regression analyses (Chust *et al.*, 2000), an approach that permitted identification of those predictor variables (measures of species abundance and diversity) that were most important while avoiding problems of multicollinearity and partial correlation (MacNally, 2002). First, a Pearson correlation (Zar, 1984; SAS Institute, 2002) was calculated for each insect community and land use parameter. Because extent of deciduous forest was a consistent and highly significant predictor of insect community parameters, each land use measurement was subsequently paired with forest extent and regressed against insect community parameters in a multiple regression model (Zar, 1984; SAS Institute, 2002). The single-variable regression indicated the strength of correlation between individual land use and community, whereas the multiple regressions indicated how much variation in the insect community parameters each land use type explained beyond that already explained by forest cover alone.

To examine correlates of bait use, sites where 0 versus ≥ 1 bait were used were contrasted with each metric associated with the carrion-feeding insect community using a two-sample *t*-test adjusted for unequal variance (Zar, 1984; SAS Institute, 2002).

Results

Characterization of carrion-feeding insect community

A total of 3,346 beetles were captured at the 30 study sites during the two, two-week trapping periods: 1,957 in June and 1,389 in August. During June, *Nicrophorus tomentosus* and *Oiceoptoma noveboracense* were the most widespread and abundant species: they were found in all but one trap and represented 76.9% of total captures, with 768 (39.2%) and 736 (37.7%) individuals, respectively. During August, *Nicrophorus orbicollis* was the most common and widespread: it was present at all but one site, and comprised 955 (68.8%) of

Table 1. Seasonal variation in carrion-associated insect community at 30 forested sites near Baltimore, Maryland, in 2002

	Mean per site \pm SE			
	June	August	<i>t</i>	<i>P</i> ¹
<i>N. sayi</i> (individuals)	1.33 \pm 0.97	0.00 \pm 0.00	1.37	0.1803
<i>N. orbicollis</i> (individuals)	4.67 \pm 0.88	31.83 \pm 5.30	-5.39	0.0001
<i>N. tomentosus</i> (individuals)	25.60 \pm 3.66	2.37 \pm 0.49	6.93	0.0001
<i>N. pustulatus</i> (individuals)	1.53 \pm 0.47	0.67 \pm 0.21	2.59	0.0149
<i>Ne. americana</i> (individuals)	4.30 \pm 1.61	11.37 \pm 2.57	-3.26	0.0029
<i>O. noveboracense</i> (individuals)	24.57 \pm 5.38	0.07 \pm 0.05	4.56	0.0001
<i>O. inaequale</i> (individuals)	3.23 \pm 0.67	0.00 \pm 0.00	4.85	0.0001
All Beetles (individuals)	65.23 \pm 9.36	46.30 \pm 7.08	2.36	0.0253
Species richness	4.67 \pm 0.28	2.83 \pm 0.22	8.33	0.0001
Diversity ²	2.48 \pm 0.16	1.67 \pm 0.08	6.08	0.0001
Caliphoridae (individuals)	61.97 \pm 6.28	45.90 \pm 4.35	2.23	0.0337
All flies (individuals)	72.37 \pm 7.90	60.53 \pm 5.99	1.50	0.1444
Flies:Beetles	2.60 \pm 0.61	8.60 \pm 4.36	-1.41	0.1702

¹ *P*-value according to paired-sample *t*-test of June values vs. August values.

² Simpson's D.

all beetles. *Necrophila americana* was the second most common beetle, representing 341 (24.6%) of the beetles trapped. Captures of *Nicrophorus sayi* were infrequent and sporadic: 29 of the 40 total *N. sayi* captured were taken from one trap in June. *Ne. americana* followed a similarly uneven distribution in the June traps: 76 individuals of the 129 captured were found at 3 sites.

Burying beetle communities showed substantial seasonal variation (Table 1), with higher abundance, species diversity, and species richness in June than August. *N. tomentosus*, *Nicrophorus pustulatus*, *O. noveboracense*, and *Oiceoptoma inaequale* were more abundant in June. *N. orbicollis* and *Ne. americana* were more abundant in August than June.

Carrion-feeding Dipterans (Caliphoridae, Muscidae, and Sarcophagidae) were also captured in the traps: 2,171 in June and 1,816 in August. Caliphoridae were found at all sites and comprised 85.6% and 75.2% of all Dipterans in the first and second trapping periods, respectively. There were more Caliphoridae in June than August (Table 1).

Characteristics of study sites

Mean extent of forest at the 1.0 km² scale surrounding study sites was 25.0% and varied from <1.0% to 97.2%. The remaining non-forested land use was predominantly light urban and agricultural: parks/open spaces and low-intensity development comprised 40.9% of the remaining area and cultivated crop and hay/pasture comprised 33.4%. Soil compaction,

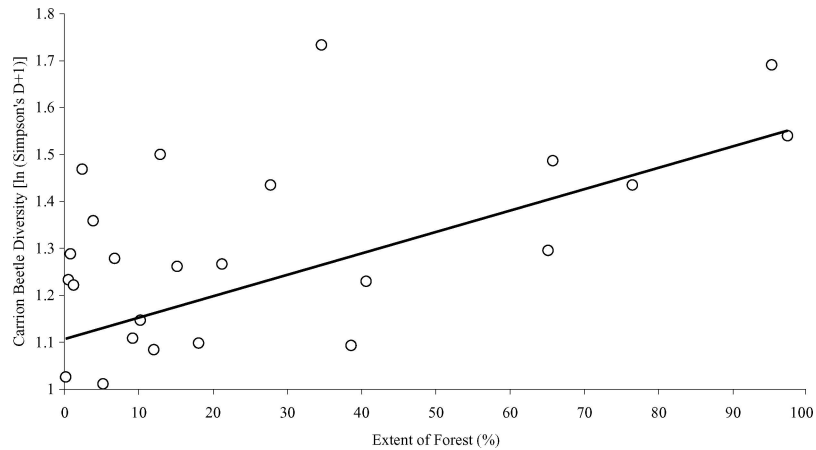


Figure 1. Relationship between diversity of carrion beetle community (Simpson's D) and extent of forest within 1 km² at 30 sites near Baltimore, Maryland, in June 2002 ($R^2 = 0.30$, $P = 0.0017$).

which averaged 6.97 kg force/cm across sites, was not correlated ($P < 0.10$) with the amount of urban land surrounding the sites ($R^2 = 0.0042$, $P = 0.735$) but was modestly correlated with forest extent ($R^2 = 0.10$, $P = 0.089$).

Relationship between characteristics of study sites and carrion-feeding insect communities

Extent of deciduous forest was positively correlated ($P < 0.10$) with abundance of 6 of 7 beetle species (all except *N. americana*) in June and 4 of 5 in August (all except *O. noveboracense*). *N. pustulatus* was negatively correlated with urban land uses, positively correlated with forest extent and rural land uses, and was the only species whose abundance was associated with extent of any land cover other than forest. Total beetles, species richness, and diversity (Simpson's D) were positively correlated with extent of deciduous forest in June and August (figure 1). Flies:beetles was negatively correlated with extent of forest in both June and August. Fly abundance showed no consistent association with any land use.

Relationship between carrion-feeding insect communities and patterns of bait use

Of 120 experimental baits deployed, 24 (20.0%) were used by burying beetles and 91 (75.8%) were scavenged by vertebrates. Only five baits were neither scavenged nor buried. In the first trapping period, the abundances of three beetle species (*N. orbicollis*, *N. tomentosus*, and *O. inaequale*) were higher at sites where bait was used versus where it was not (Table 2). Species diversity, total beetle abundance, and species richness, were also higher and flies:beetles was lower at sites where baits were used (Table 2, figure 2). During the

Table 2. Differences in composition of carrion-feeding insect communities between sites where experimental baits were buried versus not buried near Baltimore, Maryland in 2002

Parameter	Bait not buried	Bait buried	<i>t</i>	<i>P</i> ¹
	(<i>n</i> = 18) Mean per site ± SE	(<i>n</i> = 12) Mean per site ± SE		
June				
<i>N. sayi</i> (individuals)	0.33 ± 0.28	2.83 ± 2.39	-1.04	0.320
<i>N. orbicollis</i> (individuals)	2.44 ± 0.58	8.00 ± 1.61	-3.24	0.006
<i>N. tomentosus</i> (individuals)	18.67 ± 3.99	36.00 ± 5.91	-2.43	0.024
<i>N. pustulatus</i> (individuals)	0.72 ± 0.33	2.75 ± 0.99	-1.94	0.074
<i>Ne. americana</i> (individuals)	3.33 ± 1.31	5.75 ± 3.56	-0.64	0.535
<i>O. noveboracense</i> (individuals)	15.78 ± 4.26	37.75 ± 11.05	-1.86	0.084
<i>O. inaequale</i> (individuals)	1.44 ± 0.39	5.92 ± 1.22	-3.49	0.004
All Beetles (individuals)	42.72 ± 8.15	99.00 ± 15.82	-3.16	0.006
Species richness	4.00 ± 0.33	5.67 ± 0.33	-3.54	0.002
Diversity ²	2.19 ± 0.17	2.92 ± 0.28	-2.26	0.036
Caliphoridae (individuals)	63.83 ± 9.43	59.17 ± 7.26	0.39	0.698
All flies (individuals)	78.44 ± 12.03	63.25 ± 7.98	1.05	0.302
Flies:Beetles	3.79 ± 0.92	0.81 ± 0.13	2.60	0.015
Parameter	Bait not buried	Bait buried	<i>t</i>	<i>P</i> ¹
	(<i>n</i> = 17) Mean per site ± SE	(<i>n</i> = 12) Mean per site ± SE		
August				
<i>N. sayi</i> (individuals)	0.00 ± 0.00	0.00 ± 0.00	-	-
<i>N. orbicollis</i> (individuals)	17.35 ± 4.07	55.00 ± 8.22	-4.10	0.001
<i>N. tomentosus</i> (individuals)	1.12 ± 0.37	4.33 ± 0.84	-3.51	0.003
<i>N. pustulatus</i> (individuals)	0.29 ± 0.17	1.25 ± 0.41	-2.16	0.048
<i>Ne. americana</i> (individuals)	6.06 ± 2.56	19.83 ± 4.35	-2.73	0.014
<i>O. noveboracense</i> (individuals)	0.06 ± 0.06	0.08 ± 0.08	-0.24	0.812
<i>O. inaequale</i> (individuals)	0.00 ± 0.00	0.00 ± 0.00	-	-
All Beetles (individuals)	24.88 ± 6.76	80.50 ± 7.40	-5.55	0.0001
Species richness	2.47 ± 0.26	3.58 ± 0.23	-3.22	0.003
Diversity ²	1.58 ± 0.11	1.79 ± 0.11	-1.38	0.179
Caliphoridae (individuals)	51.06 ± 6.45	41.50 ± 4.96	1.17	0.251
All flies (individuals)	65.29 ± 9.04	57.92 ± 6.76	0.65	0.519
Flies:Beetles	14.13 ± 7.35	0.75 ± 0.09	1.52	0.140

¹Results of a two sample *t*-test. Significant *p*-values (*P* ≤ 0.05) in **bold**.

second trapping period, *N. orbicollis*, *N. tomentosus*, *N. pustulatus*, *Ne. americana*, total abundance, and species richness were higher at sites where bait was buried (Table 2). Soil compaction (kg force/cm) was lower at sites where bait was used (4.10 ± 1.13), than where it was not (8.89 ± 0.93) ($t = 3.27$, $P = 0.0032$).

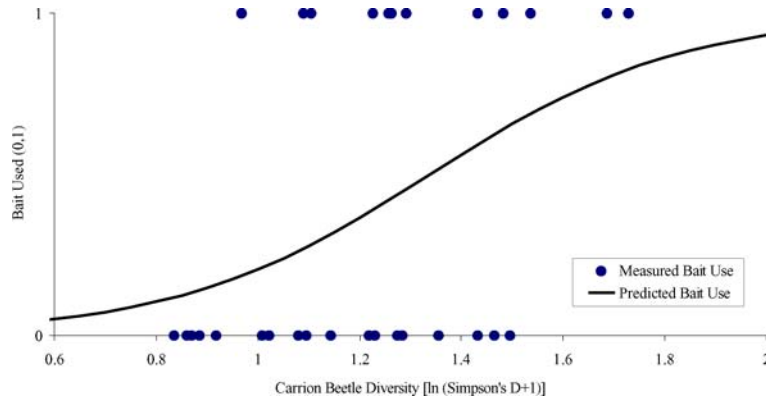


Figure 2. Relationship between diversity of burying beetle community (Simpson's D) and bait use (0,1) within 1 km^2 at 30 sites near Baltimore, Maryland in June, 2002. Curve fit based on logistic regression model ($R^2 = 0.22$, $P = 0.037$).

Discussion

The amount of forest available for discovering and burying carcasses is often the limiting factor for breeding success in many species of burying beetles (Lomolino and Creighton, 1996). With few exceptions, forest size was the primary factor in this study that explained variation in the carrion-feeding community. This indicates that burying beetle diversity along an urban-rural gradient declines as a function of forest loss and fragmentation, and not as a result of increasing amounts of impervious surfaces and buildings surrounding forest fragments. Declines in burying beetle diversity and abundance also evidently compromised the ecological service that these beetles provide, insofar as diversity and abundance of the beetle community were closely associated with patterns of discovery and burial of carcasses.

Notably, sites where bait was used had higher beetle abundance and diversity. Other studies have demonstrated that larger forests support higher species diversity of burying and dung beetles (Klein, 1989; Gibbs and Stanton, 2001) and rates of carcass utilization (Trumbo and Bloch, 2000) than smaller, fragmented forests. Smaller resource bases (Didham *et al.*, 1996; Kozlov, 1996) and disrupted interactions among species (Fisher, 1998; Trumbo and Bloch, 2002) are the mechanisms likely responsible for reductions in beetle diversity and the diminution of their ecological role in fragmented landscapes.

Low diversity, abundance, and success rate using carrion indicate that one or more breeding requirements of burying beetles are not being met in forest fragments. In contiguous forests, low population size of suitably sized mammals may act as a limiting factor on the beetle population (Smith and Merrick, 2001). However, in fragmented landscapes, burying beetle populations may not necessarily be limited by the amount of small mammal and bird carcasses available to them. Despite lower diversity in urban areas, along an urban-rural gradient birds (Mills *et al.*, 1989; Blair, 1996; Gering and Blair, 1999) and small mammals (Chernousova, 2001; Gillies and Clout, 2003) often have highest densities in areas

between rural areas and the high-density urban core, an intermediate zone where many small forest patches are found. In these areas where carcasses may be abundant, the limiting factor may be the amount and quality of soil upon which small vertebrates can be buried.

Vertebrate scavengers evidently took the majority of baits in this study. Vertebrate scavengers may outcompete burying beetles in forest fragments as the result of several interacting factors, for several reasons. Increased habitat edge is associated with increased prevalence of mammalian (Robinson and Wilcove, 1994) and avian (Nilon and Pais, 1997) scavengers. Smaller temperate forests or open canopy forests will receive more solar radiation beneath the canopy, and thereby have higher temperatures than larger forests (Saunders *et al.*, 1991). At higher temperatures, carcasses will decompose more rapidly, thereby speeding up the volatilization of chemical cues, and reducing the amount of time beetles have to discover and bury a carcass before large scavengers can locate it. Once buried by beetles, a carcass may be difficult to control because, unless depth of burial is great, carcass may still be detected by competing beetles (Shubeck and Blank, 1982; Suzuki, 1999) or scavengers. Monitoring of scavenger activity around experimental baits would enhance our understanding of this process, especially in urban areas where scavenging pressure in small forests may be the product of a different suite of species than in agricultural areas.

Flies are one taxon that is often suspected of competing with beetles for carcasses (Scott, 1998; Gibbs and Stanton, 2001). In this study, we found no association between fly abundance and forest size or any of the other land uses, nor was fly abundance higher at sites where bait was not utilized. Lomolino and Creighton (1996) found that although shallowly buried carcasses in forests had more fly larvae than deeply buried carcasses in grassland, the brood success of *Nicrophorus americanus* in forests was higher. Phoretic mite parasitism of fly eggs (Wilson, 1983; Scott, 1998), and parental care for the young, which involves removal of fly eggs and larvae from a carcass (Scott, 1998; Suzuki, 2000), are two possible reasons why fly larvae are not successful competing for carcasses. For these reasons, we suggest that the increased ratio of flies:beetles in forest fragments is a result of declining beetle populations and not a cause.

Seasonal differences in beetle assemblages may be attributable to temperature-dependence and seasonal niche partitioning, traits that have evolved in burying beetles to reduce interspecific competition (Scott, 1998). Larger beetles will typically outcompete (interspecifically or intraspecifically) smaller individuals for carcasses (Wilson *et al.*, 1984; Otronen, 1988; Trumbo, 1990; Safryn and Scott, 2000). To avoid interspecific competition, smaller species of burying beetle have adapted to be more active at times of the season with lower temperatures when larger species are slower to find carcasses (Wilson *et al.*, 1984; Trumbo, 1990; Trumbo and Bloch, 2002). Seasonal changes in beetle populations in this study were consistent with this interaction of temperature dependence with body size. Smaller-bodied species, *N. tomentosus* and *O. noveboracense*, were more abundant earlier in the summer (June), when temperatures were lower. Larger-bodied species, *N. orbicollis* and *Ne. americana*, were more abundant in traps later in the summer (August) when temperatures were higher. *N. sayi* and *O. inaequale*, while present, are active in the early spring (Anderson and Peck, 1985) before trapping was begun in this study, and thus their populations were likely not adequately sampled. The rarity of *N. pustulatus* in captures

may be attributable to it responding to preferential resources other than chicken legs, such as snake eggs (Blouin-Demers and Weatherhead, 2000).

In addition to seasonal variation, temperature and beetle size can also help explain reduced burying beetle success at bait use in small forests. In fragments, higher temperatures will favor larger beetle species in outcompeting smaller beetles. However, forest fragments are too small for large species reliant on large carrion to find sufficiently large carcasses, as is the case with the American Burying Beetle, *N. americanus* (Lomolino *et al.*, 1995; Lomolino and Creighton, 1996). Even if large species use smaller carrion, smaller and fewer broods would be raised (Trumbo and Eggert, 1994; Xu and Suzuki, 2001). In fragmented forests, temperatures may be too high for smaller beetle species to compete with larger ones for carrion, larger beetles may be restricted by search area and smaller carcasses, and neither able to stave off competition from vertebrate scavengers. Smaller species of burying beetles can also provide clues to larger species that carrion is available (Trumbo and Bloch, 2002). The loss of species interactions thus potentially reduces the diversity of the entire burying beetle community (Fisher, 1998).

Extent of urban and rural land uses was predictive of few measures of the carrion-feeding community. Despite a low capture rate overall, *N. pustulatus* (found in larger forests) was also found more often in rural than in urban forests. The biology of this species is not as well understood as that of other burying beetles (Anderson and Peck, 1985). *N. pustulatus* is suspected to feed on different resources such as reptiles or their eggs (Blouin-Demers and Weatherhead, 2000), but poorly understood breeding requirements (Trumbo, 1990) warrant further study of this species before any conclusions are made about its association with land uses surrounding forests.

Extent of forest was apparently the largest influence on abundance, diversity, and success of burying beetles in this study. Burying beetle populations within urban forests do not appear to be any more impoverished than those in rural forests of similar size. The true influence of the urban landscape on these beetles is apparently not how it may be acting as a "matrix of less favorable conditions" (Ingham and Samways, 1996) than agriculture, but rather how urban development divides and reduces forest cover into small, isolated patches. Among insects, intolerance for small forests places burying beetles into a similar category of sensitivity to habitat loss as that of many forest-dependent birds (Tilghman, 1987; Gibbs and Faaborg, 1990; Andr n, 1994). Plans for management of urban habitat that target the preservation of birds (Marzluff and Ewing, 2001) address several restoration concepts (i.e. preservation of natural habitat, limited usefulness of habitat fragments, preservation of forest interior) may also be beneficial to burying beetles. The preservation of these beetles in a fragmented, urbanizing landscape would clearly be enhanced by an allocation of larger, more highly connected forest reserves (Saunders *et al.*, 1991; Marzluff and Ewing, 2001).

To conclude, burying beetles are a distinct group of organisms that performs a well-defined ecological function in temperate forests. Their declining diversity and success at burying experimental baits associated with forest fragmentation is a clear indication that their contribution to biodiversity and ecological functionality is reduced in urban areas. Burying beetles can therefore aid in efforts to manage urban forests by serving as useful indicators of the success of efforts to conserve highly mobile species that provide important ecological functions in these areas.

Appendix A

Universal Transverse Mercator (UTM) coordinates (Zone 18N, NAD-1983 Datum) and description of study sites for burying beetle trapping and baiting sites during 2002 in Baltimore, Maryland

Site code	<i>N</i>	<i>E</i>	Site description
Bon1	4370205	0346944	Bonita Avenue
CIm1	4352170	0351964	NW of Colonial Rd. and Lexington Rd., Colonial Park
Col1	4350999	0352196	W of Coldridge Apartments, Coldridge Court
Cyl1	4357143	0357797	Cylburn Arboretum
DcH1	4352715	0353433	Dickey Hill Forest
Doy1	4361898	0346630	Doyle Forest at McDonogh Road
Dru1	4354596	0357596	Druid Hill Park, north side
ECR1	4379749	0340216	3824 Carrollton Rd.
Ess1	4357053	0350799	Forest behind 4000 Essex Rd.
Gar1	4367189	0348106	Maryland National Veterans Cemetery
Hd1	4354175	0353040	HD 1 and 2: Hillside Park, South of California Blvd.
Hd2	4354267	0352782	Permanent plots of Baltimore LTER.
JCR1	4352064	0348970	SE of Johnny Cake Road and Rolling Road
Lea2	4351721	0354068	Leakin Park. Permanent plot of Baltimore LTER.
Lmp1	4370427	0343999	Dead end of Lamport Road
McD1	4361594	0347364	South side of McDonogh Road
MtP1	4359026	0363890	Mt. Pleasant Forest between Loch Raven Blvd. and Hillen Rd.
Nun1	4349246	0352038	Nunnery Lane and Edmondson Ave.
Oak1	4353833	0354605	Oakfield Ave. and Bonner Rd.
Oru1	4371560	0354776	Oregon Ridge Park. Permanent plot of Baltimore LTER.
Oru2	4371975	0354755	Oregon Ridge Park. Permanent plot of Baltimore LTER.
OTR1	4365371	0346008	Old Tollgate Road
Pat1	4351393	0345870	Patapsco State Park, Hollifield Area
Pim1	4356504	0356867	West of Greenspring Ave., north side of Northern Parkway
Pim2	4357646	0356449	Woodland Ave and Virginia Ave.
PmP1	4355003	0352456	Powder Mill Park
REL1	4360043	0358294	Robert E. Lee Park
Sha1	4375469	0341510	Between Mt. Gilead Rd. and Woodens Lane
TmK1	4371601	0347173	Timberknoll Rd. and Worthington Ave.
WvP1	4350636	0349398	Westview Park, Chesworth Rd.

Acknowledgments

We are grateful to many several for their assistance with this study. Charles Nilon and Wayne Zipperer helped to initiate the project. Katalin Szlavecz of The Johns Hopkins University was supportive of the project and provided indirect assistance through NSF grant DEB 97-14835. Limin Yang helped secure landscape imagery, Clint Parker assisted with insect identification, and Steve Stehman, Dylan Parry and two anonymous reviewers provided useful comments on the manuscript.

References

- Anderson, R.S. and Peck, S.B. (1985) *The Insects and Arachnids of Canada: Part 13*. Canadian Government Publishing Centre, Ottawa, Ontario.
- Andr n, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* **71**, 355–366.
- Blair, R.B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications* **6**, 506–519.
- Blair, R.B. and Launer, A.E. (1997) Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological Conservation* **80**, 113–125.
- Blouin-Demers, G. and Weatherfield, P.J. (2000) A novel association between a beetle and a snake: Parasitism of *Elaphne Obsoleta* by *Nicrophorus Pustulatus*. *Ecoscience* **7**, 395–397.
- Borror, D.J. and White, R.E. (1970) *A Field Guide to Insects: America North of Mexico*. Houghton Mifflin Company, Boston.
- Chernousova, N.F. (2001) Specific Features of the Dynamics of Murine Rodent Communities under the Effects of Urbanization: 1. Dynamics of Species Composition and Abundance. *Russian Journal of Ecology* **32**, 122–125.
- Chust, G., Lek, S., Deharveng, L., Ventura, D., Dcrot, D. and Pretus, J.L. (2000) The effects of the landscape pattern on arthropod assemblages: An analysis of scale-dependence using satellite data. *Belgian Journal of Entomology* **2**, 99–110.
- Collins, J.P., Kinzig, A., Grimm, N.B., Fagan, W.F., Hope, D., Wu, J. and Borer, E.T. (2000) A New Urban Ecology. *American Scientist* **88**, 416–425.
- Coyle, D.R. and Larsen, K.J. (1998) Burying beetles (Coleoptera: Silphidae) of northeastern Iowa: A comparison of baits for sampling. *Journal of the Iowa Academy of Science* **105**, 161–164.
- Didham, R.K., Ghazoul, J., Stork, N.E. and Davis, A.J. (1996) Insects in fragmented forests: A functional approach. *TREE* **11**, 255–260.
- Dreistadt, S.H., Dahlsten, D.L. and Frankie, G.W. (1990) Urban forests and insect ecology. *BioScience* **40**, 192–198.
- Fisher, B.L. (1998) Insect behavior and ecology in conservation: Preserving functional species interactions. *Annals of the Entomological Society of America* **91**, 155–158.
- Forman, R.T.T. (1983) An ecology of the landscape. *BioScience* **33**, 535.
- Gering, J.C. and Blair, R.B. (1999) Predation on artificial bird nests along an urban gradient: Predatory risk or relaxation in urban environments? *Ecography* **22**, 532–541.
- Gibbs, J.P. and Faaborg, J. (1990) Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conservation Biology* **4**, 193–196.
- Gibbs, J.P. and Stanton, E.J. (2001) Habitat fragmentation and arthropod community change: Burying beetles, phoretic mites and flies. *Ecological Applications* **11**, 79–85.
- Gillies, C. and Clout, M. (2003) The prey of domestic cats (*Felis Catus*) in two suburbs of Auckland City, New Zealand. *Journal of the Zoological Society of London* **259**, 309–315.
- Hepinstall, J.A. and Sader, S.A. (1997) Using Bayesian statistics, thematic mapper satellite imagery, and breeding bird survey data to model bird species probability of occurrence in Maine. *Photogrammetric Engineering & Remote Sensing* **63**, 1231–1237.
- Holloway, A.K. and Schnell, G.D. (1997) Relationship between numbers of the endangered American burying beetle *Nicrophorus Americanus* olivier (Coleoptera: Silphidae) and available food resources. *Biological Conservation* **81**, 145–152.
- Homer, C.G., Huang, C., Yang, L., and Wylie, B. (2002) Development of a Circa 2000 Landcover Database for the United States. Washington D.C.: *Proceedings of the American Society of Photogrammetry and Remote Sensing Annual Conference, April, 2002*.
- Ingham, D.S. and Samways, M.J. (1996) Application of fragmentation and variegation models to epigeaic invertebrates in South Africa. *Conservation Biology* **10**, 1353–1358.
- Klein, B.C. (1989) Effects of forest fragmentation on dung and burying beetle communities in central Amazonia. *Ecology* **70**, 1715–1725.
- Kozlov, M.V. (1996) Patterns of forest insect distribution within a large city: Microlepidoptera in St. Peterburg, Russia. *Journal of Biogeography* **23**, 95–103.

- Lomolino, M.V., Creighton, J.C., Schnell, G.D. and Certain, D.L. (1995) Ecology and conservation of the endangered American Burying Beetle (*Nicrophorus Americanus*). *Conservation Biology* **9**, 605–614.
- Lomolino, M.V. and Creighton, J.C. (1996) Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus Americanus*. *Biological Conservation* **77**, 235–241.
- MacNally, R. (2002) Multiple Regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. *Biodiversity and Conservation* **11**, 1397–1401.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Princeton, Princeton University Press, New Jersey.
- Marzluff, J.M. and Ewing, K. (2001) Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* **9**, 280–292.
- McDonnell, M.J. and Pickett, S.T.A. (1990) Ecosystem structure and function along urban-rural gradients: An unexploited opportunity for ecology. *Ecology* **71**, 1232–1237.
- Merrick, M.J. (1998) Correlating rodent diversity and density with burying beetle population size and reproductive behavior. *Proceedings—The Nebraska Academy of Sciences and affiliated societies* **108**, 72.
- Mills, G.S., Dunning, Jr. J.B. and Bates, J.M. (1989) Effects of urbanization on breeding bird community structure in southwestern desert habitats. *The Condor* **91**, 416–428.
- Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E. and Schulze, E.-D. 1996. What we have learned about the ecosystem functioning of biodiversity. In *Functional Roles of Biodiversity: A Global Perspective*. John Wiley & Sons, Chichester, England.
- Nilon, C.H. and Pais, R.C. (1997) Terrestrial vertebrates in urban ecosystems: Developing hypotheses for the Gwynns Falls Watershed in Baltimore, Maryland. *Urban Ecosystems* **1**, 247–257.
- Nowak, D.J. and Dwyer, J.F. (2000) Understanding the benefits and costs of urban forest ecosystems. In *Handbook of Urban and Community Forestry in the Northeast*. Kluwer Academic/Plenum Publishers, New York.
- Otonen, M. (1988) The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Annals of Zoology Fennici* **25**, 191–201.
- Robinson S.K. and Wilcove, D.S. (1994) Forest fragmentation in the temperate zone and its effects on migratory songbirds. *Bird Conservation International* **4**, 233–249.
- Safryn, S.A. and Scott, M.P. (2000). Sizing up the competition: Do burying beetles weigh or measure their opponents? *Journal of Insect Behavior* **13**, 291–297.
- SAS Institute, Inc. (2002) *SAS (Statistical Analysis System) for Windows, Version 9.00*. Cary (NC).
- Saunders, D.A., Hobbs, R.J. and Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* **5**, 18–32.
- Scott, M.P. (1998) The ecology and behavior of burying beetles. *Annual Review of Entomology* **43**, 595–618.
- Shubeck, P.P. (1984) An inexpensive burying beetle trap (Coleoptera: Silphidae). *Entomological News* **95**, 63–64.
- Shubeck, P.P. and Blank, D.L. (1982) Burying beetle attraction to buried fetal pig carrion (Coleoptera: Silphidae). *The Coleopterist's Bulletin* **36**, 240–245.
- Smith, R.J. and Merrick, M.J. (2001) Resource availability and population dynamics of *Nicrophorus Investigator*, an obligate carrion breeder. *Ecological Entomology* **26**, 173–180.
- Suzuki, S. (1999) Does carrion-burial by *Nicrophorus Vespilloides* (Silphidae: Coleoptera) prevent discovery by other burying beetles? *Entomological Science* **2**, 205–208.
- Suzuki, S. (2000). Carrion burial by *Nicrophorus Vespilloides* (Coleoptera: Silphidae) prevents fly infestation. *Entomological Science* **3**, 269–272.
- Tilghman, N. (1987) Characteristics of urban woodlands affecting breeding bird diversity and abundance. *Land-scape and Urban Planning* **14**, 481–495.
- Tilman, D. (2000) Causes, consequences and ethics of biodiversity. *Nature* **405**, 208–211.
- Trumbo, S.T. (1990) Reproductive success, phenology, and biogeography of burying beetles (Silphidae, *Nicrophorus*). *The American Midland Naturalist* **124**, 1–11.
- Trumbo, S.T. and Eggert, A.K. (1994) Beyond monogamy: Territory quality influences sexual advertisement in male burying beetles. *Animal Behavior* **48**, 1043–1047.
- Trumbo, S.T. and Bloch, P.L. (2000) Habitat fragmentation and burying beetle abundance and success. *Journal of Insect Conservation* **4**, 245–252.
- Trumbo, S.T. and Bloch, P.L. (2002) Competition between *Nicrophorus Orbicollis* and *N. Defodiens*: Resource locating efficiency and temporal partitioning. *Northeastern Naturalist* **9**, 13–26.

- United States Environmental Protection Agency (USEPA). (2002) NLCD Classification Scheme Definitions. Available from: <http://www.epa.gov/mrlc/definitions.html> via the INTERNET. Accessed 2003 April 9.
- Wilson, D.S. (1983) The effect of population structure on the evolution of mutualism: A field test involving burying beetles and their phoretic mites. *American Naturalist* **121**, 851–870.
- Wilson, D.S., Knollenberg, W.G. and Fudge, J. (1984) Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecological Entomology* **9**, 205–216.
- Xu, H. and Suzuki, N. (2001). Effects of carcass size and parental feeding on reproductive success of the burying beetle *Nicrophorus Quadripunctatus* (Coleoptera: Silphidae). *Entomological Science* **4**, 217–222.
- Zar, J.H. (1984) *Biostatistical Analysis*, 2nd ed. Englewood Cliffs, NJ: Prentice Hall.
- Zipperer, W.C., Sisinni, S.M., Pouyat, R.V. and Foresman, T.W. (1997) Urban tree cover: An ecological perspective. *Urban Ecosystems* **1**, 229–246.