Ecology of Urban Arthropods: A Review and a Call to Action

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ABSTRACT A review of the entomological literature revealed relatively few general studies on arthropods in urban environments, excluding those in the context of pest control or epidemiology, and all were limited in scope and duration. Most studies documented the presence and abundance of species in a variety of poorly quantified urban categories. There also were a number of studies on the effects of urban pollution and changes in arthropod community composition over time (particularly in urban green areas). From these studies, three groups of arthropods could be identified: (1) "rural" taxa not present (or at lower abundance) in urban settings, (2) "urban" taxa present only (or at higher abundance) in urban settings, and (3) taxa present in both rural and urban settings with no particular affinity for either. The lack of a basic understanding of the mechanisms accounting for distributional and abundance patterns of urban arthropods illustrates the many opportunities for entomological research that exist in urban settings. Some of these opportunities are outlined to encourage further work on the ecology of urban arthropods.

KEY WORDS urban ecology, urban entomology, urbanization

ARTHROPODS HAVE BEEN ASSOCIATED with humans and their activities and constructions since recorded history (Curran 1937, Montgomery 1959, Hogue 1987, Cloudsley-Thompson 1990). Despite this long association, however, relatively little research has been done on how arthropods use urban habitats. An urban environment is a heterogeneous mosaic of residential dwellings, commercial properties, parks, and other land-use types that provides an array of habitat types that can be used by arthropods. Although there have been some studies done on arthropods in certain urban settings, such as landfills (Crawford 1979), residential yards (Owen 1971, Owen and Owen 1975), and recreational parks (Faeth and Kane 1978, Sawoniewicz 1986, Kozlov 1996), few studies have compared arthropods in various urban land-use types, and those few have focused on specific arthropod species or families rather than on broader patterns of diversity (Ehler and Frankie 1979a, b; Vincent and Frankie 1985). Although there is an enormous body of literature on synanthropic arthropod species that transmit diseases to humans or livestock or that harm agricultural crops (see reviews in Olkowski et al. 1976, Ebeling 1978, Frankie and Ehler 1978, and Dreistadt et al. 1990), there has been surprisingly little attention paid to how urban development affects the abundance and diversity of nonpest arthropods and of arthropods in general. This lack of attention to urban environments in entomological research reflects a more widespread pattern of overlooking urban environments in the natural sciences in general (Matson 1990, McDonnell 1997, Walbridge 1997). Urbanization is considered one of the primary causes for declines in arthropod populations, however, making the study of arthropods in urban environments an extremely important and timely avenue for research (Pyle et al. 1981).

Effects of Urbanization on Arthropods

Urbanization is associated with a variety of effects on arthropods, including pollution, drainage and diversion of watercourses, and habitat fragmentation and loss (see discussion in Pyle et al. [1981]). These factors have led to declines and even extinctions of some arthropods (e.g., the loss of coastal sand dunes to urban development around San Francisco, CA, USA, has been implicated in the extinction of three butterfly species [Tilden 1956]). Urbanization also usually involves the introduction of exotic flora for landscaping. Some exotic arthropods have been inadvertently introduced in landscaping materials (Nowakowski 1986, Barthell et al. 1998, Krell and Hangay 1998); these exotic species may then displace native arthropods (Suarez et al. 1998). There may thus be both direct and indirect effects from urbanization on arthropods.

Why Study Arthropods in Urban Environments?

Arthropods are particularly logical choices for studying effects from urbanization for the following five reasons: (1) they are diverse and thus may provide a snapshot of overall biological diversity in an area; (2) their relatively short generation times mean that they may respond quickly to anthropogenic changes to soil and vegetation; (3) they are fairly easy to sample (and many of the general public do not object to sampling arthropods as opposed to vertebrates); (4) they represent a spectrum of trophic levels; and (5) they may...
be important sociological, agronomical, and economical components of human-altered habitats. Any changes in their environment may disrupt the functions that arthropods play in the ecosystem. By the year 2000, an estimated 50% of the world's human population is expected to live in urban settings (Rodick 1995); and with the world's annual human population growth rate at 1.8% (which translates into ~90 million more people each year [Matson 1990]), urban development will accelerate in the foreseeable future. How will arthropods be affected by this trend? Unless work begins now on arthropods in urban environments, we may miss the opportunity to answer this question.

**Objectives**

Although there have been previous reviews of arthropods in urban environments (Frankie and Ehler 1978, Dreistadt et al. 1990), they focused mainly on insects rather than terrestrial arthropods as a whole, and both considered insects primarily with respect to pest control and epidemiology in urban environments. There are also several edited volumes that can be considered reviews, although they, too, are dominated by papers dealing with management of pest species (e.g., Frankie and Koehler 1978, 1989; Bornkamm et al. 1982). Another review by Zapparoli (1997) did consider the general ecology of insects in urban environments, but this review was confined to the insects of a portion of Rome, Italy. In this current review I summarize the ecological research done on urban arthropods, other than in respect to pest control and epidemiology, to determine any general patterns of how arthropods respond to urbanization. This focus is appreciably different from those taken in previous assessments of arthropods in urban environments. I will also discuss some of the many opportunities that exist for future work on arthropods in urban environments. My primary objective is to generate impetus for studies on the ecology of urban arthropods.

**Types of Papers Reviewed**

In my literature search I found 79 peer-reviewed journal articles on the ecology of arthropods in urban environments, dating from 1933 to 1999. I excluded papers that considered urban arthropods solely as epidemiological vectors and papers evaluating the efficacy of pest-management methods. This criterion did not exclude papers that included pest species if the primary focus of the paper was not pest control per se (e.g., Hanks and Denno 1993, 1994). All the papers used included at least an abstract in English. Although there probably is a fair amount of literature about urban arthropods written in languages other than English, this literature is unfortunately poorly known. The papers that were reviewed represent studies from >51 cities in 14 countries on six continents. For each paper, I identified the urban land-use type(s) present and the arthropod taxa studied. I summarized the conclusions from each paper and tallied any similarities among papers. I also looked for trends in study topics or methodology over the years.

**Results of Review**

**Scope and Duration of Studies.** For most cases, there was insufficient replication to tally results by site or taxon to determine if any population and community responses to urbanization are repeated across different cities, countries, or continents. Most studies focused on Lepidoptera and Coleoptera, and most arthropod orders were not included (Fig. 1). In addition, many studies did not identify arthropods beyond the order or family level. These shortcomings illustrate the need for more work on arthropods in...
important when considering that different areas of open space may not be equally attractive to arthropods, and these differences would only be detected if aspects of "open space" are quantified. For example, certain grasshoppers (Orthoptera: Acrididae) and mining bees (Hymenoptera: Andrenidae) are more common in parks than in residential yards, even though both areas are often considered collectively as "green areas" (Gilbert 1989). Despite their superficial similarities, such areas may differ in characteristics as grass height and plant species diversity, which may differentially attract or repel certain arthropods. Thus, it is important to describe and quantify urban habitats in detail.

Features that should be measured in an urban study site include the type and amount of vegetation, soil, and built structures present; the height of vegetation and buildings; presence of host plants and oviposition sites; canopy cover; wind speed; humidity; water current speed, pH, turbidity, oxygenation, and salinity; human population density; and other environmental characteristics (see reviews in Rowntree 1984, 1986; Sutherland 1996). Statistical ordination techniques such as correspondence analysis may be useful in relating patterns of arthropod abundance and diversity with quantified urban habitat measurements, such as percent ground cover or vegetation height (ter Braak 1995). There is no standard methodology for studies of arthropods in urban environments, nor should there be given the variety of organisms, locations, and research questions. However, measurement of study site variables will permit a deeper and more precise understanding of the biological patterns and mechanisms present.

Types of Studies on Urban Arthropods

A number of the studies were concerned with documenting species' presence and abundance, sometimes comparing different sites (e.g., Bristowe 1939; Edelsten 1940; Woodroffe 1955; Klausnitzer and Richter 1983; Lazenby 1983, 1988; Kirby 1984; Sustek 1992, 1993). Most of these inventories were conducted in "green areas" such as parks, residential yards, woodlots, and vacant lots and thus are probably not representative of a heterogeneous urban environment as a whole. For the studies that did not focus on composing species lists, two general research themes emerged: (1) effects of urban pollution on arthropods, and (2) changes in arthropod communities over time during vegetational succession.

Effects of Urban Pollution on Arthropods

British peppered moth (Lepidoptera: Geometridae, *Biston betularia* L.), whereby increases in airborne sulfur dioxide killed light-colored lichens on tree trunks where the moths rested during the day, making the moths more conspicuous against the dark trunks to predators such as birds. In addition, tree trunks themselves became darkened from build-up of soot deposits. Through natural selection, light-colored moths decreased in frequency, whereas a darker-colored morph became more abundant in woods near industrial centers. Light-colored moths were still more abundant in rural areas exposed to less air pollution (Kettlewell 1955a, 1955b 1956, 1958). More rigorous industrial emissions standards have decreased the amount of airborne SO$_2$, which has permitted re-growth of lichens and a shift in selection to favor light-colored morphs over darker ones once again in many areas of Britain and the United States (Grant et al. 1996, 1998). Although certain authors (e.g., Sargent 1968, Clarke et al. 1994, Coyne 1998, Sargent et al. 1998) have found fault with various aspects of this system, the existence of industrial melanism is indisputable (see reviews in Kettlewell 1973, Majerus 1998, Grant 1999).

The pollution-related decline of tree lichens has caused declines in other arthropods from trophic effects. For example, lichenophages and herbivores (especially *Psocoptera*) decreased in British woods that experienced a pollution-related lichen die-off, although some omnivores (*Isoptera, Dermaptera, and Diptera: Psychodidae*) actually increased in abundance (Leblanc and DeSlover 1970, Gilbert 1971, Wiackowski 1978). Industrial melanism was also once thought to account for the dominance of dark-colored morphs of the two-spot ladybird beetle (*Coleoptera: Coccinellidae, Adalia bipunctata* L.) in urban areas compared with more rural sites (Creed 1971, 1974), although it is now believed that a dark morph in this species actually is an adaptation to capture solar heat efficiently in areas that may be cooled from smoke clouds (see review in Muggleton et al. [1975]). Air pollution (particularly from sulfur compounds) has been implicated in declines in spiders in London, England (Bristowe 1939), mites and springtails in urban forests (Hanks and Denno 1993). In another example, holly leaf miners (*Diptera: Agromyzidae*) were more abundant on urban than rural holly trees near Newark, DE (USA), because the urban trees were exposed to more sunlight (not being shaded by overstory trees, as they would be in a natural forest setting), which hastened leaf senescence and abscission. Although this process did not affect the leafminers per se (which completed their larval development in the fallen leaves), it did lower rates of parasitism from hymenopteran parasitoids, which did not search for hosts among fallen leaves. Lower rates of parasitism among the urban leafminers thus promoted higher leafminer densities in urban areas than in rural forests (Kahn and Cornell 1989). Regular pruning of plants in urban settings may stimulate new plant growth,

Thermal Pollution and Latitudinal Gradients. In a study by Tischler (1973), the effect of urban “thermal pollution” (i.e., cities as “heat islands” from both increased production of heat from concentration of people and machines as well as increased heat reflectance and absorbency from pavement [Kim 1992]) offset a latitudinal gradient in the population density and cycling of various arthropods in Europe, so that populations in cities at more northern latitudes were more similar to those in rural settings at more southern latitudes than rural populations farther north. A similar example of how urbanization can counteract latitude has been noted for bird diversity (Jokimaki and Suonen 1993).

**Host-Plant Stress from Pollution and Human Activity.** The presence of pollution (particulate or thermal) means that the biota in and around urban areas are subjected to different stresses than would be the case in more isolated areas. For example, because host plants in urban settings are exposed to different ambient conditions than are the same plant species in more rural areas, host plants may differ in their “attractiveness” to herbivorous insects between these two settings. Insect diversity and densities on those plants may consequently differ between urban and rural areas. This appears to be the case for a scale insect (*Homoptera: Coccidae, Pulvinaria regalis Canard*). Soil compaction and the presence of concrete made the ground surface impenetrable to precipitation and nutrients, which affected the health of the scale’s host trees in urban areas and, thus, increased their susceptibility to scale colonization (Speight et al. 1998). A similar kind of relationship was discussed by Schmitz (1996), who speculated that aster plants (*Asteraceae*) that are stressed from lack of water create sap with higher concentrations of free amino acids than do watered plants. Urban asters may receive less water than rural plants because of soil compaction and distance from natural water sources such as rivers or swamps. Thus, concentrated sap from urban plants may be a higher-quality resource to plant-sucking insects such as aphids (*Homoptera: Aphididae*), leading to higher aphid densities on urban than on rural plants (Schmitz 1996; but see Connor 1988, Hanks and Denno 1993, Nuckols and Connor 1995). Additionally, urban plantings that are scattered may be unable to support high densities of predatory arthropods (because of dispersion of prey), enabling urban herbivores (e.g., scale insects, *Homoptera: Diapсидidae*) to attain higher densities than in natural habitats (Hanks and Denno 1993). In another example, holly leafminers (*Diptera: Agromyzidae*) were more abundant on urban than rural holly trees near Newark, DE (USA), because the urban trees were exposed to more sunlight (not being shaded by overstory trees, as they would be in a natural forest setting), which hastened leaf senescence and abscission. Although this process did not affect the leafminers per se (which completed their larval development in the fallen leaves), it did lower rates of parasitism from hymenopteran parasitoids, which did not search for hosts among fallen leaves. Lower rates of parasitism among the urban leafminers thus promoted higher leafminer densities in urban areas than in rural forests (Kahn and Cornell 1989). Regular pruning of plants in urban settings may stimulate new plant growth,
thereby providing consistent tender forage for caterpillars (Owen 1971). These studies illustrate how urban areas may actually support higher numbers of phytophagous insects than would otherwise be expected in such an altered environment, but more research is needed to determine whether this is a general pattern and to rule out the importance of other mechanisms (e.g., urban plants may support higher densities of phytophages than do rural plants simply because there are fewer plants upon which to settle in urban areas).

**Water Pollution.** Just as air and soil characteristics may differ between urban and rural areas, water quality may similarly be affected by pollution and drainage or diversion of watercourses. These habitat changes may thus affect aquatic arthropods. For example, benthic arthropod communities differed among streams that ran through settlements with different human population densities (Jones and Clark 1987). Although upstream human population density was not a good predictor of the total number of arthropods or arthropod density, urban streams were dominated by midges (Diptera: Chironomidae), whereas more rural streams had a more diverse arthropod community. Streams near larger human settlements differed from streams near fewer people in terms of several abiotic variables (such as dissolved oxygen, alkalinity, sediment load, heavy-metal concentration), and midges appear to be more tolerant of the urban conditions (Jones and Clark 1987). Similarly, fewer arthropods were found near human-frequented boardwalks in mangrove swamps around Sydney, Australia, than in more secluded areas farther away from the boardwalks, although the reasons for this pattern are not fully understood (Kelaher et al. 1998). Finally, Claassen (1933) discusses how pollution from such sources as milk treatment factories and salt purification centers in New York perturb stream arthropod communities to the detriment of the entire stream ecosystem.

**Changes in Arthropod Communities Over Time During Vegetational Succession**

Habitat alterations that result from urbanization affect the arthropods present. As urbanization continues over time, there are concomitant changes in arthropod community composition over time. Sites that are cleared and left undeveloped attract different species as they undergo vegetational succession. For example, the arthropod communities in 12 vacant lots were found near human-frequented boardwalks in mangrove swamps around Sydney, Australia, than in more secluded areas farther away from the boardwalks, although the reasons for this pattern are not fully understood (Kelaher et al. 1998). Finally, Claassen (1933) discusses how pollution from such sources as milk treatment factories and salt purification centers in New York perturb stream arthropod communities to the detriment of the entire stream ecosystem.

Although many references state that some taxa "decline in abundance" with seral age, a distinction should be made between numeric and proportionate declines. In a numeric decline, a taxon decreases in absolute number. In a proportionate decline, a taxon decreases in its importance to an overall assessment of diversity. In such a case, a taxon may be increasing in absolute number but be only one of an increasing number of taxa present. In some cases (e.g., Gilbert 1989), a numeric decline is used; in other cases (e.g., Lazenby 1988), a proportionate decline is meant but it is unclear whether a numeric decline is also present. Therefore, it is important to note the distinction.

Arthropods provide a good system for studying successional processes within urban patches because just as patches may undergo vegetative succession within an urban setting, urban development can itself be considered a form of succession. Changes in land-use may be frequent in urban areas because parcels of land are constantly being annexed, zoned, and built upon or razed and built upon again. Urbanization has traditionally been considered a form of environmental disturbance (Rebele 1994). Several of the studies reviewed here were conducted in parcels of land surrounded by urban development but not themselves developed (i.e., "open space" or "green areas"). Island biogeography theory, which explains how diversity is related to the area and isolation of a site (be it an oceanic island or an "island" of open space surrounded by buildings [MacArthur and Wilson 1967]), was the research paradigm for most of these studies (e.g., Faeth and Kane 1978, Kozlov 1996). In some cases, the arthropod community was described as being similar in composition among sites (Ehler and Frankie 1979).
Effects of Habitat Heterogeneity on Arthropod Distributions in Urban Environments

Urbanization creates a heterogeneous mosaic of patches consisting of built-up areas, areas of construction, and remnants of indigenous habitat. Some arthropods may be able to exploit relatively small and isolated habitat remnants, thereby being able to tolerate a greater degree of urban development than can species that are more sensitive to habitat area and loss. The exotic Argentine ant Linepithema (=Iridomyrmex) humile (Mayr), for example, is able to exploit relatively small patches of riparian and coastal scrub habitats near highly developed areas and patches that are dominated by exotic plants. The native ants, in contrast, appear to be more sensitive to habitat area and disturbance, because they are found only in larger patches in more rural areas with indigenous vegetation (Ward 1987, Suarez et al. 1998). A similar pattern has been found in spider communities in urban woodlots in Japan, where smaller forests had fewer species than did larger forests, possibly because of the lack of larger prey items in the smaller forests (Miyashita et al. 1998). In contrast, many carabid beetle species were found at higher densities in smaller forest fragments than in contiguous forests in Finland, probably because the smaller habitat remnants possessed higher vegetational diversity caused by repeated human disturbance and successional changes (Halme and Niemela 1993). Most of the carabids captured in the smaller fragments were habitat and dietary generalists that also occurred in a variety of other habitats, whereas the species from the contiguous forests were specialists (Halme and Niemela 1993).

Some studies noted that arthropods may be distributed patchily within a city, reflecting heterogeneity of urban land-use types (e.g., Czechowski 1982, Kozlov 1996). Some authors attributed high arthropod diversity to the presence of high vegetative and structural diversity (Owen 1971, Clark and Samways 1997), which follows from theories of MacArthur and MacArthur (1961). This relationship may actually reflect the nearby availability of resources such as host-plants, however, rather than vegetative diversity per se. Although grass lawns supported high densities of Colembola (Natuhara et al. 1994), even relatively thin strips of lawn isolated populations of more sessile taxa (Clark and Samways 1997). Absence of leaf litter in urban areas was thought to expose overwintering arthropods to cold weather; presence of leaf litter was associated with higher diversity of most microarthropods (Davis 1978, 1979).

Although some studies noted no changes in diversity or density with proximity to a city (Lussenhop 1973, Burakowski and Nowakowski 1981, Pouyat et al. 1994), other studies noted that different numbers of species were encountered at different distances from the city center. For example, Davis (1978, 1979) documented an ~60% decline in species richness with proximity to the center of London, England. Declines in species richness with increasing urbanization were attributed to several factors, including isolation from colonizing source populations from natural habitats (Davis 1979, Denys and Schmidt 1998), pollution (Pouyat et al. 1994), and loss of foodplants (Ruszczyk 1996). In other studies, however, higher species richness was documented in centrally located sites than in rural ones; this pattern was attributed to the presence of specialist urban "invaders" (Kozlov 1996), species accidentally introduced by humans from rural areas (Nowakowski 1986), or the greater abundance of resources in urban settings (Schmitz 1996). For example, the number of species of phytophagous carabid beetles was 2.5 times higher and overall abundance was 20 times higher in green areas of Warsaw than in a more rural forest in Poland; this pattern was attributed to the more consistent availability of foodplants in the city throughout the year (Czechowski 1982).

Three Community-Level Responses to Urbanization

Based on species-specific variation in arthropods' responses to urbanization, arthropods can be considered to belong to one of three distinct communities: (1) rural taxa not present (or at significantly lower abundance) in urban settings, (2) taxa present only (or at higher abundance) in urban settings (i.e., synanthropic species), and (3) taxa present in both rural and urban settings with no particular affinity for either (see also Shorrocks 1969, Czechowski and Mikolajczyk 1981, Blair and Launer 1997, Guarisco 1999). Relatively few studies compared arthropod abundance between urban and rural settings. Those that did found that many taxa are found in both urban and rural settings, but certain taxa are consistently more abundant or conspicuous in one or the other setting (Table 1). For example, herbivores often were more abundant in cities than in rural sites, particularly those species that were specialists on horticultural plantings or ruderal plants (Schmitz 1996, Denys and Schmidt 1998), whereas parasitoids usually exhibited the reverse pattern (Sawoniewicz 1986, Denys and Schmidt...
For the urban-dwellers, urban settings provided resources that were scarce in rural areas (Tischler 1973). For example, rubbish and sewage provided food resources to many arthropods. In many cases, these resources offset negative effects of urbanization, such as pollution (Czechowski 1982). Members of this group were often considered preadapted to urban life because of morphological characteristics such as high vagility (especially ability to fly, which enabled them to disperse from natural sources to colonize urban areas) and small body size (which allowed them to take advantage of the small-scale resources characteristic of urban areas, such as individual plants in residential yards) (Tischler 1973, Ruszczyk 1986). Some urban species actually showed physical adaptations to urban life, such as ability to digest new larval host-plants (Owen 1971, Ruszczyk 1986), but more research is needed to determine whether specific genetic adaptations have occurred in urban populations of arthropods (Tischler 1973, Hanks and Denno 1994). Urban species also tended to have large geographic ranges, indicating adaptability to many regions and habitats (Shapiro and Shapiro 1973, Czechowska and Bielawski 1981). It is currently unknown how most arthropod taxa respond to urbanization (positively, negatively, or neutral), which is a topic that merits further investigation.

### Table 1. Examples of the three community-level responses (rural, urban, or either) to urbanization

<table>
<thead>
<tr>
<th>Citation(s)</th>
<th>Taxon</th>
<th>Community type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sawoniewicz 1986, Denys and Schmidt 1998</td>
<td>Parasitoid Hymenoptera</td>
<td>Rural</td>
</tr>
<tr>
<td>Kozlov 1996</td>
<td>Micropteryx cebitella, Lepidoptera: Micropterigidae</td>
<td>Rural</td>
</tr>
<tr>
<td>Bateson and Driggs 1972</td>
<td>Blatta orientalis L., Blattaria: Blattidae</td>
<td>Rural</td>
</tr>
<tr>
<td>Crawford 1979</td>
<td>Enoplognatha thoracica (Hahn), Arachnida: Theridiidae</td>
<td>Urban</td>
</tr>
<tr>
<td>Ward 1987, Suarez et al. 1998</td>
<td>Lepidoptera humile (Mayr), Hymenoptera: Formicidae</td>
<td>Urban</td>
</tr>
<tr>
<td>King and Green 1995</td>
<td>Tetramorium caespitum L., Hymenoptera: Formicidae</td>
<td>Urban</td>
</tr>
<tr>
<td>Kozlov 1996</td>
<td>Caloptilia syringella, F. and Coleophora sibiricella Fky., Lepidoptera: Gracillariidae</td>
<td>Urban</td>
</tr>
<tr>
<td>Ruszczyk 1992</td>
<td>Lepidoptera: Pieridiae, Pieridae</td>
<td>Rural</td>
</tr>
<tr>
<td>Kozlov 1996</td>
<td>Parornix scoticella St., Lepidoptera: Gracillariidae</td>
<td>Urban</td>
</tr>
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</table>

### Indicators of Urbanization

Presence and abundance of the members of these three communities can serve as "indicators" of different degrees of urbanization (Czechowski 1982). These indicators can be used to detect subtle proximity effects of urbanization, even in sites that are not considered urban per se (such as sites on the fringe of developed areas). Indicator taxa should preferably be locally abundant and relatively easy to identify taxonomically (Clark and Samways 1997); thus, local research is necessary to identify potential candidates that would be appropriate for a given region. However, some arthropod taxa were consistently categorized as belonging to one of the three communities, even in different regions of the world. For example, carabid beetles (Coleoptera: Carabidae) were considered to be indicators of urbanization in South Africa (Clark and Samways 1997), Poland (Czechowski 1982), Germany (Klausnitzer and Richter 1983), Slovakia (Sustek 1987, 1992), and Great Britain (Lazenby 1983). Carabids have often been described as "habitat indicators" (Luff et al. 1992, Rykken et al. 1997). Therefore, future studies on arthropods in urban environments may wish to examine closely how carabids respond to land-use changes. Other taxa (e.g., Orthoptera: Gryllidae; Coleoptera: Cetoniidae; Diptera: Syrphidae and larvae from various other families; and parasitic Hymenoptera) may also prove to be useful indicators of various effects of urbanization (see discussion in Clark and Samways [1997]). The taxa denoted "urban" or "rural" in Table 1 may also serve as indicators (presence of "urban," absence of "rural").

### General Patterns of How Arthropods Respond to Urbanization

Arthropods respond both directly and indirectly to urbanization. Arthropods respond directly to habitat loss and pollution (through direct mortality). Arthropods respond indirectly to urbanization in responding to alterations in habitat structure and in the presence and abundance of resources (e.g., host plants). Both direct and indirect effects act on individuals (especially individuals belonging to certain sensitive taxa), which results in changes in local population density and community structure. Arthropod communities in urban environments tend to be more diverse (owing to the presence of exotic taxa) than are communities in nonurbanized areas, but not all portions of a city are equally diverse because of differences in distances from sources of arthropod colonists, land-use types, ages of development, and seral stages. Some taxa benefit from urbanization, whereas others are negatively affected or remain unaffected.

### Future Directions of Research on Arthropods in Urban Environments

Given these general patterns of how arthropods respond to urbanization, it is now possible to formu-
late some testable hypotheses that merit investigation. Some of these hypotheses include the following.

- Arthropod diversity should decrease as the level of pollution (terrestrial, aquatic, or atmospheric) increases.
- Habitat (e.g., a particular host-plant) that is scarce and widely dispersed should experience higher rates of occupation (herbivory, oviposition) than should habitat that is abundant and widespread.
- Areas that have only recently been urbanized should possess relatively more “early successional” taxa (e.g., Lepidoptera: Hesperiidae, Lycaenidae; Hymenoptera: Formicidae, Bombidae; Isoptera) than should an older area. Predators (e.g., Araneae: Linyphiidae; Coleoptera: Carabidae, Staphylinidae) should be particularly well-represented in recently developed sites.
- Diversity should increase with the age of an urbanized area.
- Urban sites that are nearer to undeveloped areas of indigenous habitat should be more accessible to colonizing arthropods than would be sites that are more centrally located in an urban area; therefore, areas on the fringe of development should possess relatively higher diversity than more insular areas. Much of the diversity in fringe areas will be represented by highly vagile taxa (the colonists), whereas insular sites will have a more even representation of mobilities and body sizes.
- The diversity of exotic species will increase with the age of an urbanized area.

Urbanization is no fad, and entomology and ecology should take advantage of the research opportunities made available by the “natural experiment” (Diamond 1986) of urban development. Currently, there is a paucity of work on synanthropic arthropods in South America, Africa, Asia, and Australia, even though these areas are experiencing some of the fastest rates of human population growth and urban development. Addressing the following questions in these and other urban areas would be particularly useful.

- How do most arthropods respond to urbanization (positively, negatively, or neutral)?
- How large do urban green areas need to be to preserve rural levels of arthropod diversity?
- Do exotic arthropod species replace and fill the niches of native species? Are certain niches more resilient or vulnerable to urban change than others? How are these relationships mediated by land-use type? How does the presence of exotic vegetation mediate these relationships?
- Are native arthropods able to maintain their population levels without supplementation from rural source populations? Are population dynamics different for species near the urban fringe than those near the urban center? How does the proximity of remnants of undeveloped open space affect these relationships?
- How do socioeconomic variables interact with physical (habitat) variables to influence arthropod diversity and abundance?

Some of these questions are being addressed by a new long-term research project monitoring arthropod diversity and turnover in various types of urban land use in Phoenix, AZ, USA (http://caplter.asu.edu/research/projects).

Conclusions

The difficulties that will surely be encountered in the identification and study of many synanthropic arthropods do not diminish the importance of understanding arthropods in urban environments. Given that arthropods are being affected by urbanization at an unprecedented rate, the important roles they play in ecosystem structure, function, and dynamics and in comprising the majority of the Earth’s biodiversity are also being altered at an unprecedented rate. Without further research on how arthropods use urban environments, however, we cannot predict how these functions may change with future patterns of urban development. Without such knowledge, we will be unable to plan urban development to facilitate arthropod conservation, a subject whose importance is increasingly being recognized as humans continue to modify the Earth’s ecosystems (Samways 1992).

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