EFFECTS OF URBAN HABITAT TYPES AND LANDSCAPE PATTERNS ON
ECOLOGICAL VARIABLES AT THE ABOVEGROUND-BELLOWGROUND INTERFACE

A Thesis in
Ecology
by
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Abstract

Ecologists have not studied urbanized ecosystems extensively even though they are increasing in area globally. For this thesis, three approaches were used to investigate the effects of urban habitat management on ecological variables: 1) an observational study of soil microarthropods in high- and low-maintenance lawns and unmanaged fields; 2) a manipulative study in which soil properties, microclimates, carbon and nitrogen cycles, and invertebrates were measured in plots of lawn, old field, bark mulch and gravel mulch habitat types; 3) a microlandscape study in which the effects of landscape context patterns on arthropods in lawns were tested. In study 1, soil mites were more numerous in high-maintenance lawns while collembolans were more abundant in low-maintenance lawns. In study 2, all measured variables differed significantly among the habitat types. Mulch plots were warmer during daytime hours and had wetter soils as compared to vegetated plots. Gravel plots had the lowest soil organic matter, soil aggregate stability, and earthworm densities. Bark mulch plots had the largest earthworm populations and lowest soil bulk density. Earthworm numbers were intermediate in unmowed and lawn plots, except when they decreased in lawns during drought conditions. Fluxes of carbon dioxide were higher from soils in lawn and bark mulch plots. Decomposition rates of oak leaves in litterbags were greater in mulched plots as compared to vegetated plots. Mowing and mulching promoted higher levels of inorganic soil nitrogen at certain times relative to those in old field plots. In field measurements, nitrous oxide fluxes were highest from gravel-covered soils. Arthropod communities differed significantly among the habitat types although no consistent patterns were seen in relationships between activity-abundance levels and the habitat types. In study 3, arthropod communities differed among patches of lawn surrounded by different levels of landscape heterogeneity, and activity-abundance levels tended to be higher in microlandscapes containing non-lawn habitat patches as compared to those with only lawn. Habitat composition may have influenced the results of this study more than landscape heterogeneity. Data from these studies can be used to guide sustainable landscape management practices that seek to conserve valuable biodiversity and ecosystem services in urbanized ecosystems.
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Finally, but not least, I thank Kim for her love, patience, good humor, delicious food and wonderful friendship. I’m happy that completion of this thesis symbolizes the beginning of a new chapter in both of our lives—a chapter that we will write together. “Celebrate we will ‘cause life is short but sweet for certain.”

This thesis is dedicated to the memory of Uncle Bill Byrne (1952–2006): a lover of life, knowledge and teaching. His good humor, stories and thought-provoking discussions positively influenced everyone he knew.
Chapter 1. Introduction: Humanizing and urbanizing ecology in the 21st Century

“I would humanize ecology, therefore, first by taking the actions and relations of civilized (humans) as fully into account in its definitions, divisions and coordinations as those of any other kind of organism.”
—Forbes (1922)

“Humans dominate Earth’s ecosystems; therefore, humans must be integrated into models for a complete understanding of extant ecological systems.”
—Grimm et al. (2000)

Context of the thesis

In his 1921 presidential address to the Ecological Society of America (ESA), Stephen Forbes called upon ecologists to “humanize” their discipline (Forbes 1922). Eighty-some years later, the 2005-2006 ESA president, Nancy Grimm, has written extensively about the need for integrating humans into ecological science (Grimm et al. 2000, Grimm et al. 2003, Grimm and Redman 2004). While Forbes’ words largely fell on deaf ears, Grimm’s represent an increasingly popular sentiment among contemporary ecologists. Forbes’ suggestion went unheeded throughout most of the twentieth century (with notable exceptions) because ecologists generally excluded consideration of humans from their studies. In contrast, at the turn of the twenty-first century, Grimm has been a leading voice for an increasing number of ecologists who are explicitly incorporating human activities and sociocultural variables into their research. In its fullest expression, this humanizing of ecology has resulted in what is being called the study of coupled sociocultural-ecological systems (Redman et al. 2004).

Several demographic trends of the human population have contributed to the increased interest among ecologists in relationships between sociocultural and ecological systems. The first is the historical and continued exponential growth of the global human population. During Forbes’ lifetime, the Earth was populated by about 1.6 billion people. As I write this thesis, the human population stands at 6.46 billion and is expected to peak at between 9 and 11 billion around the year 2050 (United Nations 2004).

Second, as a result of human population growth, the extent of human-mediated modification of the Earth system reached unprecedented levels during the twentieth century (Sanderson et al. 2002, Steffen et al. 2005). Vitousek et al. (1997) estimated that between one-third and one-half of the Earth’s terrestrial surface has been transformed by humans into agricultural fields, managed forests and inhabited landscapes. Such transformations, combined with other environmental consequences of human activities (e.g., non-native species introductions, climate change), have led some scientists to refer to the current geological period as the “Anthropocene” era due to the
pervasive influence that humans are having on the Earth’s atmosphere, lithosphere, hydrosphere and biosphere (Crutzen 2002, Steffen et al. 2005).

A third demographic trend that has spurred ecologists to integrate human activities and sociocultural variables into their research is the growth in area and human population size of urbanized environments. In 1950, approximately 30% of humans lived in urbanized areas; in 2005, the number increased to 50% and by 2050 the percentage is expected to reach 61 (United Nations 2003). A recent study showed that, in 2000, more than 25% of the continental United States had been urbanized (i.e., urban, suburban and exurban lands), which represents a four- to five-fold increase in urbanized land cover since 1950 (Brown et al. 2005). Despite such trends, most ecologists throughout the twentieth century did not consider areas of dense human inhabitation as worthy of study (McDonnell 1997). (However, intensive studies of urban ecology were initiated in Europe in the 1970’s (e.g., Kubicka et al. 1986).)

These three trends—increases in 1) the size of the human population, 2) the extent and magnitude of human-mediated effects on the environment, and 3) urbanization rates—have synergistically sparked a growth in the number of ecological studies about human-environment relationships especially those in urbanized ecosystems. In the decades preceding and immediately following the turn of the 21st century, the ecological literature blossomed with texts focused on integrating human activities and sociocultural variables with traditional ecological theories and research, as evidenced by the number of texts with “human” and/or “urban” in their titles (e.g., McDonnell and Pickett 1993, Pickett et al. 1997, Vitousek et al. 1997, Redman 1999, Grimm et al. 2000, Sanderson et al. 2002, Alberti et al. 2003, Berkowitz et al. 2003, Turner et al. 2004, Kaye et al. 2006, Shochat et al. 2006). Despite rapid growth of interest in, and research about, urban ecology, very little is known about the effects of urbanization on, for example, changes to biodiversity and biogeochemical cycles at local and global scales. Yet, urban ecology data are increasingly needed to understand and manage complex environmental issues that have relevance to human societies (e.g., pollution, conservation of biodiversity and ecosystem services, global climate change; Palmer et al. 2004).

Because it is unlikely that current rates of human population growth and urbanization will decrease, ecology seems poised to shift from a science that once ignored humans to one dominated by studies about the effects of human activities and sociocultural characteristics on ecological patterns and processes (Palmer et al. 2004, Kingsland 2005, Kaye et al. 2006, Shochat et al. 2006). As suggested by Grimm et al. (2000), the structure and function of most ecosystems cannot
effectively be understood without considering the influences of humans on them. Indeed, the entire Earth system might now best be viewed as one large sociocultural-ecological system (sensu Redman et al. 2004; Vitousek et al. 1997, Crutzen 2002, Steffen et al. 2005).

**Conceptual overview of the thesis**

The paragraphs above summarize the broader context of my thesis. From that global perspective, I have narrowed down my research topic to a more localized scale (i.e., meters) at which to conduct my studies. Specifically, this thesis is about how the creation and management of habitat types (or land covers) in residential urbanized landscapes (i.e., lawns and mulched gardens around buildings) affects ecological variables. For purposes of this thesis, an urban habitat type (or urban land cover type, phrases used interchangeably) is defined as a category of land cover associated with urbanized (i.e., residential, industrial, transportation) land uses that has a distinctive physical structure (i.e., composition and arrangement of material) which distinguishes it from other categories of land cover. The word habitat is used to emphasize that human management of landscapes influences the environmental conditions that affect the abundance and distribution of organisms (see p. 95 for the definition of habitat which differs from that of habitat type). Because the word urban is used in many ways by different people and therefore has many connotations (e.g., it refers to types of land cover and land use as well as areas with high human population density), it is not associated with a clear-cut or widely-agreed upon definition in scientific, political or popular (e.g., newspaper) publications. For this thesis, urban is used in its most general sense to refer to environments containing high densities of permanent human inhabitants. Thus, urban habitat types are those commonly created and managed by humans in areas, e.g., where they live. The habitat types studied in this thesis are commonly found in many urbanized areas of the United States, although variations of them or very different habitat types may be more common in urbanized landscapes around the world. A major interdisciplinary challenge for urban ecologists (further discussion of which is beyond the scope of this thesis) is to examine how the diversity of approaches for designing and managing urban habitat types and urbanized landscapes found around the world are influenced by the diversity of human cultures and their associated philosophies about human-environment relationships.

In the rest of this section, I provide additional context for the thesis by describing two ecological concepts that have guided my research about urban habitat types: habitat structure and landscape context. Then, I briefly discuss what I view as one of the strengths of this thesis: the
blending of basic (i.e., generation of data to create basic knowledge) and applied (i.e., generation of data to address a specific societal problem) scientific approaches. At the end of this section, I present a conceptual framework (Fig. 1-1) that was developed using habitat structure as a central focus and that has helped me organize my thinking and writing.

Habitat structure is defined as the composition and arrangement of physical matter, both abiotic and biotic, at a location (modified from Bell et al. 1990). Although physical matter provides the underlying template for all ecosystems, habitat structure is a relatively underappreciated and underdeveloped concept in ecology (McCoy and Bell 1990). Nonetheless, as a broad concept, it provides a common vantage point from which to examine how and why ecological patterns and processes differ among locations. In my research, I sought to understand how human management of urbanized landscapes—specifically lawn mowing and placement of mulches—affects ecological variables. Because these management activities intentionally alter the composition and arrangement of physical matter at a location, habitat structure provides an appropriate theme for my research interests especially as shown by chapters 3, 4 and 5.

Variation in habitat structure across space gives rise to environmental heterogeneity. Over the past several decades, heterogeneity has become the focus for an increasing number of ecological studies as exemplified by growth in the field of landscape ecology (Lovett et al. 2005, Turner 2005). Many novel insights have been gained from landscape ecology research about the ecological consequences of spatial heterogeneity. One such insight is that ecological variables at a given location can be strongly influenced by the patterns and processes surrounding that location, i.e., the landscape context (see chapter 6 for further discussion and references). Landscape-scale ecological perspectives are especially important for understanding urban ecology because urbanized landscapes often have high levels of fine-scale spatial heterogeneity due to the diversity of ways in which humans manage habitat structure within small areas (e.g., square meters) (Grimm et al. 2000, Band et al. 2005). As such, I wanted to include a landscape ecology component in my thesis. I created a unique experimental design (Fig. 6-1) to examine how ground arthropods in lawns are affected by environmental heterogeneity in the landscape context. For this, I utilized the concept of habitat structure as the focal point for a spatially explicit research project to illustrate how the concept of habitat structure is especially relevant to the field of landscape ecology.

Habitat structure and landscape context provide the theoretical basis for my research. In addition, my work can be viewed in the context of applied environmental issues related to the management of soils, biodiversity and ecosystem services within urbanized environments.
This applied context is woven together with theoretical considerations in each of my chapters. In this regard, I have been influenced by contemporary scientific dialogues emphasizing that scientists should strive to conduct research relevant to important societal issues related to development of sustainable methods for managing ecosystems and landscapes (e.g., Raven 2002, Palmer et al. 2004, DeFries et al. 2005, Millennium Ecosystem Assessment 2005). In other words, scientific research that meshes basic and applied perspectives will have greater potential for generating information needed to reduce and mitigate negative effects of human activities on the environment. In my thesis, integration of basic and applied ecology can clearly be seen in Chapters 3 and 4 regarding the effects of habitat structure on ecosystem services related to carbon and nitrogen cycling. In Chapters 5 and 6, the effects of habitat structure and landscape context on arthropods are discussed in terms of how they can be applied to the design and management of urbanized landscapes that conserve beneficial organisms (e.g., predators that eat pests). I believe that these applied aspects of my research merge nicely with the theoretical context and have made for a richer thesis that exemplifies how scientific endeavors provides foundational information useful for guiding the management decisions of those who want to create sustainable urbanized ecosystems.

In addition to integrating basic and applied scientific approaches, the research included in this thesis encompasses ideas from many sub-disciplines of ecology (e.g., community, ecosystem, landscape, soil and urban ecologies). To show how the diverse, interrelated perspectives emerging from these fields have influenced my thinking, I wanted to adopt a conceptual framework that would help summarize the perspectives and provide a unifying theme for the thesis. Conceptual frameworks (or models) are essential to scientific understanding because they help clarify, organize and illustrate relationships among ideas and can guide the formulation of questions and hypotheses (Heemskerk et al. 2003, Groffman et al. 2004). Interdisciplinary conceptual frameworks have been especially important for guiding the development of urban ecology (e.g., Pickett et al. 1997, Grimm et al. 2000). However, none of the frameworks published to date explicitly utilize the concept of habitat structure or otherwise provided the conceptual basis I sought for supporting the multivariate ecological analysis and comparison of characteristics associated with heterogeneous urban ground covers. Thus, I developed a conceptual framework for this thesis using the concept of habitat structure as a starting point (see the framework and its description in Fig. 1-1). The framework is especially relevant to Chapter 3 in which relationships among habitat structure, above- and belowground abiotic conditions, biological communities, and ecosystem processes related to carbon cycling are discussed. Although the framework is not discussed explicitly in the other chapters (due
Figure 1-1. A conceptual framework illustrating one of the ways in which human activities can affect ecological variables, i.e. through modification of habitat structure (arrow A). Habitat structure—defined as the composition and arrangement of physical matter at a location—is the biogeophysical template underlying all ecosystems and can therefore serve as a common vantage point from which to examine other ecological variables. Habitat structure can be part of (e.g., as vegetation) and/or influence the structure of the biotic community directly (B) (e.g., by affecting the abundances, diversity and interactions of organisms) or indirectly as it mediates the abiotic conditions (e.g., soils, microclimates) and resource availability (e.g., detritus, water) that affect community structure (C, D). Habitat structure may also indirectly mediate abiotic conditions through its effects on the community (D), as when, for example, organisms modify resource availability. Communities, resource pools and abiotic conditions interact to determine rates of ecosystem processes (E), which can therefore be seen as indirectly controlled by habitat structure. In turn, ecosystem processes modify resource pools and communities through time (F) which can then generate temporal variability in habitat structure (B, C). Heterogeneity of habitat structure across space gives rise to landscape patterns (G) which can influence the spatial patterns of abiotic variables, communities and ecosystem processes (H). In addition, spatial variability in the communities, abiotic conditions and ecosystem processes give rise to the ecosystem services across landscapes that have relevance to human societies (I). Whether or not increased knowledge about how habitat structure directly and indirectly affects ecological variables and ecosystem services can influence human activities to manage habitat structure (J) in sustainable ways is an unexplored question.
in large part to the preparation of them as separate manuscripts for publication, see below), it helped me formulate their objectives and storylines in many ways. Thus, the framework is presented here (Fig. 1-1) to illustrate the underlying conceptual basis for each of the chapters.

**Story of the thesis**

I entered graduate school in August 2000 with only one clear objective: I wanted to complete a Ph.D. in ecology. At that time, however, I had no idea what I wanted my thesis topic to be. Thankfully, that changed rather quickly. I became enamored with soil ecology due to my enjoyable experience in the introductory soils course that I took during my first semester. In addition, I became aware of the emerging field of urban ecology. However, as I reviewed the literature, I found that few studies had been conducted about the ecology of soils within urban environments (a situation that remains true as I complete this thesis). Therefore, it seemed that the study of urban soil ecology could provide a meaningful dissertation topic that would be relevant to both science and society.

Any consideration of urban landscapes (at least those in the United States) will inevitably require thinking about lawns. Thus, it wasn’t much of a stretch for lawns to become an additional focus for my thesis. Similar to urban soils, I found that few studies had been conducted on the ecology of lawns. Of those that had, most examined the effects of pesticides on ground arthropods. Yet, I was surprised that none compared the number of arthropods inhabiting lawns to those in unmowed fields. Thus, in the summer of 2001, I conducted a small study about the abundances of soil microarthropods (mites and collembolans) in chemically-treated and untreated lawns and unmowed fields in State College, PA (Chapter 2). Although this work was enjoyable, I realized that sampling arthropods from lawns would not provide for a rigorous thesis. In addition, such work would be challenging because many people are reluctant to allow the pursuit of scientific knowledge to interfere with the upkeep of their lawns. Thus, I began thinking in terms of how I could design a manipulative field experiment that would comprise the bulk of my research.

After two years of intense reading, thinking and discussing my ideas with others, I finally hit upon the relatively simple field experiment that I wanted to conduct. I would “urbanize” an old field by mowing vegetation to create lawns and placing shredded bark and gravel mulches over the soil to create mulched “gardens.” Measurements in experimental lawn and mulch plots could then be compared to unmanipulated plots of the old field vegetation and yield insights about how mowing and mulching alter the ecology of a location. In addition, the lawn, mulch and unmowed habitats
could serve as the habitat structures with which to explore my ideas about the effects of landscape context on ground arthropods. I began creating the urban habitat structure and landscape context plots in April 2003. Initially my research focus was on ground arthropods and I sampled them for two summers (Chapters 5 and 6). However, in 2003 I observed that the soils, plants and microclimates became different among the plots with different types of habitat structure. This sparked my interests in expanding my thesis topic beyond arthropods.

The preliminary data I gathered about soils, arthropods and microclimates in 2003 stimulated my writing of a National Science Foundation Doctoral Dissertation Improvement Grant in the fall of 2003. I received this grant in April 2004. Funds from this award enabled me to hire an undergraduate assistant and pay for additional materials and analyses, both of which facilitated the collection of data that would otherwise not have been possible. As the title of the grant suggests, the quality of my thesis has been greatly improved by the inclusion of Chapters 3 and 4 which contain data collected in 2004 and 2005 about the soil properties, microclimates and carbon and nitrogen dynamics in the habitat structure plots. I was fortunate to receive several other grants (see acknowledgements) that also funded collection of this data.

Over the course of about six years (August 2000 to June 2006), my thoughts about this thesis shifted from only knowing that I wanted to finish it to wishing that I did not have to finish it so soon. In many ways, my field experiment has generated more questions than answers. Nonetheless, I believe that the scientific “stories” conveyed in the following chapters are robust enough to fit within the broader story about how ecologists are increasingly humanizing and urbanizing their discipline (Palmer et al. 2004, Kingsland 2005). Because this story has in many ways just begun, I am excited to be finishing this thesis at a time when it contributes novel insights to a relatively new field of study. I hope that readers will find it as engaging as it has been for me.

**Structure of the thesis**

Each of the data-based chapters in this thesis (chapters 2-6) has been prepared as a separate manuscript for publication in a peer-reviewed journal. Chapter 2 has been published as a short “note” in the Journal of Agricultural and Urban Entomology (Byrne and Bruns 2004); as such, it does not have an abstract or sub-sections. An edited, shorter version of Chapter 3 was submitted in April 2006 to be reviewed for possible publication in Ecological Applications. Chapter 4 will be edited for submission to the journal Ecosystems. Chapters 5 and 6 will be submitted to Oecologia and Ecology Letters, respectively. Given the somewhat unpredictable nature of the peer-review
process and editorial decisions, other journals may have to be chosen if manuscripts are not accepted for publication in these journals. Because each chapter has been written to match the style of a specific journal, each has a slightly different tone and focus for the introduction and discussion sections. It is hoped that these differences do not inconvenience the reader. A concluding chapter is included at the end of the thesis to summarize key results and discussion from the chapters.

References


Chapter 2. The effects of lawn management on soil microarthropods

Lawns are one of the most common habitats in urban landscapes. They support a diversity of arthropods including pests, predators and detritivores, many of which reside in the soil and litter (Falk 1976, Potter and Bramen 1991). Most research in lawns has focused on managing turfgrass pests and soil nutrients to achieve optimum plant growth and health. A smaller number of experimental studies have investigated the effects of lawn chemical applications on non-target, beneficial arthropods (e.g., Cockfield and Potter 1985, Potter et al. 1985, Arnold and Potter 1987, Kunkel et al. 1999). However, little is known about arthropod communities in urban ecosystems (McIntyre 2000).

The objective of the present study was to collect field data on soil microarthropod abundances from pre-existing lawns and unmowed fields within an urbanized environment. A secondary goal was to use this observational data to develop hypotheses for future experimental research. Microarthropods (mites and collembolans) were sampled from three habitat types—high- and low-maintenance lawns and unmanaged fields—to examine their utility for urban arthropod studies. High-maintenance lawns were managed by a commercial lawn care company with fertilizers and pesticides and were mowed regularly to maintain vegetation heights of 5-7 cm; low maintenance lawns received no chemical inputs but were mowed (Cockfield and Potter 1985). Unmanaged fields located near the lawns were used as reference sites for comparison.

Four locations of each of these three habitat types (12 sites total) were located in State College, Pennsylvania, USA (40° 47’ N, 77° 51’ W, elevation 350 m, 975 mm annual precipitation), ensuring that each were of similar environmental conditions (i.e., minimum size of 14 by 7 m, well-drained, no over-hanging trees). Homeowners were consulted to confirm that lawns were managed as either high- or low-maintenance for the previous five years and to obtain permission to sample soils.

Microarthropod sampling was conducted on 26-28 June 2001. At each location, 15 soil cores—5 cm in diameter and 5 cm deep—were collected at 0.5 m intervals along a 7-m transect in the middle of the sampling area, at least 3 m from habitat edges. Soil cores, including decaying grass clippings, were immediately transported to the lab where arthropods were extracted over 4 days into 70% ethanol using modified Tullgren funnels (Crossley and Blair 1991). Five additional cores were collected randomly along each transect and analyzed for soil variables in the authors’ lab (texture, pH, gravimetric moisture, bulk density) or at the Penn State Agricultural Analysis
Laboratory (carbon and nitrogen). Plant species at each location were counted and identified within 0.5 m on either side of the transect. All data were statistically analyzed using analysis of variance (ANOVA) for parametric data and the Kruskall-Wallace test for non-parametric data, a more robust test for non-normal data (Zar 1999), followed by the Tukey and Nemenyii post-hoc tests, respectively, using SPSS for Windows, Release 10.0.1 (1999).

Soil pH, bulk density, moisture, texture and carbon were similar among the three habitat types although soils from lawns tended to contain more carbon than the unmowed fields (Table 2-1). Three classes of loamy soils were distributed evenly among all 12 sites. Total nitrogen contents differed significantly among the treatments ($P < 0.05$; see Table 2-1 for statistics information) with greater levels observed in the high-maintenance lawns, an expected result given the fertilizer input at these sites. Plant diversity also differed significantly among the land use categories (Table 2-1) with more species found in the unmowed fields than the lawns and the least number in the high-maintenance lawns. Kentucky bluegrass (*Poa pratensis*) was the only species present at all locations, and it was the dominant plant in both lawn types. Plant diversity was greater in low-maintenance lawns and unmowed fields due to broad-leaf plants such as *Trifolium repens*, *Plantago* spp. and *Taraxacum officinale*. (Although this difference among the habitat types might influence microarthropods, it is ignored in the discussion below for brevity.) An additional difference observed among the land uses was a greater thickness of thatch—the layer of grass shoots, roots and decomposing organic matter—in high- and low-maintenance lawns as compared to the unmowed sites (L. Byrne, personal observation).

Soil mite abundances were found to be greatest in high-maintenance lawns and least in unmowed reference sites (Table 2-1). Other studies have reported greater numbers of mites in high-maintenance lawns as compared to low-maintenance lawns (Arnold and Potter 1987, Potter et al. 1985, 1990, Kunkel et al. 1999), and Southwood and van Emden (1967) observed more mites in cut than uncut agricultural fields. Taken together, these studies and results from this study suggest that mites, as a group, are not reduced in number by mowing and lawn chemical applications and can actually even increase in abundance. Two hypotheses may be proposed about the mechanisms for increased abundances of mites in lawns. Some species (i.e., detritivores, fungivores) may increase due to the greater availability of decaying organic matter (grass clippings) which they consume directly or graze fungi from, a bottom-up mechanism of population increase (Arnold and Potter 1987, Halaj and Wise 2002). Also, a reduction of macroarthropod predators in high-maintenance lawns, a top-down mechanism, may allow mites to become more abundant, especially in high-
Table 2-1. Mean values of soil properties, number of plant species and soil microarthropods for three management treatments. N = 4 per treatment for each variable. Units are given next to each variable.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean values ± SE for each treatment</th>
<th>Test statistic</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High maintenance</td>
<td>Low maintenance</td>
<td>Unmowed fields</td>
</tr>
<tr>
<td>Soil pH</td>
<td>6.0 ± 0.2</td>
<td>6.2 ± 0.1</td>
<td>6.4 ± 0.2</td>
</tr>
<tr>
<td>Bulk density (g/cm³)</td>
<td>0.99 ± 0.05</td>
<td>1.01 ± 0.07</td>
<td>1.08 ± 0.06</td>
</tr>
<tr>
<td>Soil moisture (%)</td>
<td>22.9 ± 2.3</td>
<td>30.6 ± 2.6</td>
<td>25.1 ± 1.55</td>
</tr>
<tr>
<td>Soil carbon (%)</td>
<td>6.5 ± 1.6</td>
<td>5.5 ± 1.1</td>
<td>3.7 ± 0.1</td>
</tr>
<tr>
<td>Total soil N (%)</td>
<td>0.56 ± 0.14 a</td>
<td>0.46 ± 0.08 ab</td>
<td>0.29 ± 0.009 b</td>
</tr>
<tr>
<td># plant species</td>
<td>2.5 ± 0.5 a</td>
<td>10.25 ± 1.3 ab</td>
<td>26.3 ± 6.3 b</td>
</tr>
<tr>
<td>Acari (mites) c</td>
<td>19.12 ± 5.39</td>
<td>13.90 ± 3.04</td>
<td>10.72 ± 0.5</td>
</tr>
<tr>
<td>Collembolans c</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poduromorpha</td>
<td>0.98 ± 0.54</td>
<td>1.92 ± 0.83</td>
<td>1.77 ± 1.00</td>
</tr>
<tr>
<td>Entomobryomorpha</td>
<td>0.75 ± 0.44 a</td>
<td>15.17 ± 9.36 b</td>
<td>4.32 ± 1.6 ab</td>
</tr>
<tr>
<td>Sminthuridae</td>
<td>1.08 ± 0.54</td>
<td>0.72 ± 0.26</td>
<td>4.45 ± 2.71</td>
</tr>
</tbody>
</table>

a Means followed by different letters in rows differ significantly at $P \leq 0.05$ using the multiple comparison Nemenyi test for non-parametric data (Zar 1996).

b Test statistics are F values from one-way ANOVA for parametric data or H values from the Kruskall-Wallis test for non-parametric data. Data were considered non-parametric if they were found to be non-normally distributed or had unequal variances at $P < 0.05$ using the Kolmogorov-Smirnov test and test of homogeneity of variances in SPSS, respectively. DF = 2, 9 for all analyses.

c Microarthropod data are means ($±$ SE) per soil core.

maintenance lawns, (Cockfield and Potter 1983, Halaj and Wise 2002). These mechanisms are not mutually exclusive and need to be tested in an experimental setting to examine their relative importance for determining mite abundances in lawns.

I was able to sort collembolans into three subdinal groups: poduromorpha, entomobryomorpha and symphypleona (Christiansen and Bellinger 1980). These taxonomic groups are roughly parallel to the three ecomorphological life forms of collembolans: euedaphic, hemiedaphic and epedaphic, respectively (see Fig. 2-1; Christiansen and Bellinger 1980, Hopkin 1997). Although some species’ taxonomic status does not reflect their ecomorphological type (Hopkin 1997), sorting specimens into these sub-order groups provides more ecological information about collembolan communities than grouping them together as “collembolans” as has been done in some previous studies. Total collembolans have been found to be more abundant in high-
Figure 2-1. Three generalized ecomorphological groups of collembolans are depicted, indicating their vertical distributions within the turfgrass-thatch-soil layers of a lawn. The collembolan groups are differentiated by morphological features that reflect adaptations to their preferred habitat within the soil-litter profile. Sizes vary among the groups. A) Epedaphic collembolans (symphypleonans, the globular springtails, include the families Sminthuridae and Neelidae) dwell mostly above the soil among the litter and vegetation and have well-developed eyes, antennae, furculas and pigmentation. B) Hemiedaphic collembolans (entomobryomorphans, including the families Isotomidae and Entomobryidae) have intermediate morphologies of the other two groups (most have furculas and antennae, some have eyes and pigmentation) and inhabit upper soil layers and decomposing surface litter. C) Euedaphic collembolans (poduromorphans, the grub-like springtails, includes the families Onychiuridae and Hypogastruridae) inhabit soil pore spaces as reflected by their reduced or absent eyes, antennae, furculas and pigmentation. Furculas, labeled with an “F,” are the springing organs located on collembolans’ abdomens. (Modified after Coleman & Crossley 1996.)
maintenance lawns with intermediate levels of N fertilizer applications while numbers were sometimes but not always reduced by insecticides (Potter et al. 1985, 1990, Kunkel et al. 1999). No other studies that have compared collembolan abundances in lawns to unmowed fields are known. Thus, data in this study have provided new insights into the effects of lawn management on collembolan communities.

Poduromorpha collembolans mostly inhabit pore spaces within the mineral soil and spend little time aboveground (Hopkin 1997). Poduromorpha springtail abundances were found to be similar between low-maintenance lawns and unmowed sites (Table 1) suggesting that this group is not affected by mowing. In Poland and Russia, respectively, Sterzynska (1982) and Stebeva and Sergeev (1994) also found similar numbers of euedphagic collembolans among lawns and unmanaged habitats. I hypothesize that this euedphagic lifestyle protects poduromorpha collembolans from the disturbance of mowing. Slightly fewer poduromorphans in high-maintenance lawns may indicate a negative effect of chemical applications, but this is not clear due to the lack of significant differences among our data.

Symphypleona collembolans (all specimens collected in our study were from the family Sminthuridae) are generally epedaphic and spend most of their time above the soil in the litter and vegetation (Hopkin 1997). Although not statistically significant due to high variation among the data, fewer numbers of sminthurids were collected from the lawns than the unmowed fields, a trend observed in previous studies (Sterzynska 1982, Stebeva and Sergeev 1994). I hypothesize that sminthurids are negatively affected by mowing due to changes in aboveground environmental conditions (i.e. temperature and moisture) as influenced by shorter vegetation. The effects of chemical applications on sminthurids are less clear, because their numbers were similar in both lawn types.

Entomobryomorpha collembolans can broadly be considered hemedaphic, because most live in upper layers of the soil and within litter layers (Hopkin 1997). These collembolans were nearly four times more abundant in low-maintenance lawns than in reference sites suggesting that their numbers are not reduced by mowing. As is the case for mites, they may increase in low-maintenance lawns because of increased food supplies (grass clippings and associated microbes) or reductions in their predators (Arnold and Potter 1987). Data indicate that although mowing did not reduce entomobryomophan abundances, significantly fewer numbers inhabited high-maintenance lawns. Kunkel et al. (1999) reported a decrease in collembolan population in lawns applied with the insecticide imidacloprid. Although conclusions regarding the effects of specific lawn chemicals on
collombolans are outside the scope of this study, it appears that general management practices associated with high-maintenance lawns negatively affect collombolans (but see Potter et al. 1985).

In summary, this study found that mowing and chemical applications in lawns affects soil mites and the three sub-order groups of collombolans in different ways. Because no differences were found among most soil variables within the habitat types, I am confident that the microarthropod data are reflective of the impacts of habitat management on their abundances. Although this study was limited temporally and taxonomically (because specimens were not identified to lower levels of taxonomic classification), this report is useful for guiding future studies on microarthropods inhabiting lawns. Specifically, the proposed hypotheses should be tested in field experiments with more refined treatments of mowing and chemical applications and more detailed identification of mites and collombolans. Although the effects of specific fertilizer and pesticide applications on arthropods were not part of this study’s objectives, this should also be a primary focus for future work. Such information would benefit lawn managers who wish to conserve beneficial arthropods within urban habitats. In addition, ecological research on arthropods in lawns will contribute needed data about the impacts of urbanization on biodiversity (McIntyre 2000).

References


SPSS for Windows, Release 10.0.1. 1999. SPSS Inc., Chicago, IL, USA.
Chapter 3. Differences in microclimates, soil properties and carbon dynamics among four urban habitat types

Abstract

Although urbanization rates continue to increase globally, the basic ecology of urbanized ecosystems is poorly understood. In this study, the microclimates, soils and carbon dynamics of three habitat types commonly found in urbanized residential landscapes—lawns, shredded bark mulch and gravel mulch—were examined and compared to those of reference plots of unmowed old field vegetation. The concept of habitat structure (i.e., the composition and arrangement of matter at a location) was used as a framework to facilitate comparisons. Replicated plots of the four habitat types were created in a field experiment and variables within them were measured using standard methods. Nearly all variables differed among the habitat types producing a distinctive ecological profile for each. Mulched plots had significantly warmer daytime surface temperatures and their soils were consistently wetter than those of vegetated plots. Gravel-covered soils had significantly lower levels of soil carbon and aggregate stability due to the absence of organic matter (OM) inputs. In contrast, bark mulch plots received large inputs of OM which probably contributed to high CO\textsubscript{2} fluxes on several dates and significantly higher earthworm densities that lowered the soil bulk density. Mowing facilitated colonization of lawns by many species that were not seen in unmowed plots. These species probably contributed to the high aboveground net primary productivity measured in lawns (>800 g biomass m\textsuperscript{-2} year\textsuperscript{-1}) which was similar to that of unmowed plots when it was measured with greater sampling intensity. Although net productivity of lawns was high, their aboveground living and dead biomass was lower than that of unmowed habitats because of continual removal of living biomass by mowing and rapid decomposition of high quality (i.e., high N content) clippings. In addition, clipping inputs probably contributed to the higher soil CO\textsubscript{2} flux from lawns than measured from unmowed habitats. This study shows that different types of habitat structure create fine-scale heterogeneity of microclimates and biogeochemical cycling in urbanized ecosystems. Future studies are needed to understand how different habitat types give rise to spatial dynamics of ecological patterns and processes across heterogeneous urbanized landscapes. In addition, urban ecology data can be applied to the development of management guidelines that seek to increase the sustainability of urbanized ecosystems.
Introduction

Human-mediated modification of habitats and landscapes are among the most important drivers of local and global changes in biodiversity and biogeochemical cycles (Vitousek et al. 1997). Humans alter native habitats for many reasons including agricultural production, natural resource extraction and inhabitation. Of these, ecologists have studied impacts of the former two more extensively than the latter, so that relatively little is known about the ecology of environments where humans live, i.e., urban, suburban and exurban landscapes. Collectively, these urbanized landscapes cover greater than 25% (or 1.4 million km$^2$) of the continental United States, are inhabited by over 80% of the U.S. population, and represent the fastest growing land use categories (Brown et al. 2005). Similar patterns of urbanization are evident around the world (Cohen 2005). Such demographic and land use trends have spurred increasing numbers of ecologists to study urbanized ecosystems, contributing to rapid growth in the field of urban ecology (Grimm et al. 2000, Kaye et al. 2006, Shochat et al. 2006, Pouyat et al. in press).

The study of urbanized ecosystems is challenging for many reasons including the need for interdisciplinary knowledge and perspectives (e.g., that integrate ecology and sociology) and unique research methods adapted to working in inhabited landscapes (Cook et al. 2005, Felson and Pickett 2005). In addition, urbanized ecosystems are associated with extremely high levels of temporal and spatial heterogeneity in both ecological and sociocultural variables (Grimm et al. 2000, Band et al. 2005). This heterogeneity is generated, in part, by the diversity of urban habitat types created by human activities that remove, create and maintain abiotic and biotic physical structures. Thus, another major challenge for urban ecologists is generation of basic data, currently lacking, about the ecology of distinctively urban habitat types that have not been previously studied.

Urban heterogeneity can be examined at a range of spatial scales, from that of meters in residential yards to kilometers across cities. At various scales, urban habitat types are designed and managed by a diversity of actors, including homeowners, public landscape managers and developers. Thus, the emergent structure and function of urbanized ecosystems—and their associated environmental effects—result from the aggregation of many localized decision-making processes and management activities (Kaye et al. 2006, Pouyat et al., in press). However, landscape managers, especially homeowners, may not consider their activities, e.g., lawn mowing and fertilization, as related to broader environmental concerns such as soil, air and water pollution (e.g., Robbins et al. 2001). Nonetheless, data about the ecological effects of creating and managing urban habitat types—especially at household scales—are needed to understand the internal dynamics of
urbanized ecosystems. In addition, such data can be applied to the development of 1) sustainable landscape design and management practices, 2) environmental education programs and 3) public policies, all of which might target the conservation and restoration of beneficial biodiversity and ecosystem services, and thus promote improved environmental quality, in urbanized ecosystems (Berkowitz et al. 2003, Palmer et al. 2004).

Using residential urbanized landscapes as a model system, I initiated a study to help fill in knowledge gaps about basic ecological characteristics (microclimates, soil physical, chemical and biological variables, carbon dynamics in plants, detritus and soil) associated with three common urban habitat types created in residential landscapes: lawn, shredded bark mulch and limestone gravel mulch. Although the ecology of these habitat types has been previously examined to various degrees (e.g., Falk 1980, Mueller and Day 2005, Scharenbroch et al. 2005), to my knowledge this is the first comprehensive study of them using a field experiment. In addition, the ecological characteristics of unmowed, old field vegetation were examined to assess its suitability as an alternative, low maintenance habitat type for sustainable urban landscape design. To guide comparisons of these diverse habitat types, I adopted the broad but integrating concept of habitat structure—defined as the composition and arrangement of physical matter at a location (modified from Bell et al. 1991)—to provide an organizing framework for this study (Fig. 1-1). I hypothesized that the ecological characteristics of the four habitat types would be directly and indirectly affected by differences among their respective physiochemical properties (i.e., the color, density, and carbon (C) and nitrogen (N) contents of their habitat structure) which are determined by human management inputs. In addition, I predicted that characteristics of the habitat types would be determined by interactions among multiple variables rather than being influenced primarily by single factors. This work differs from other urban ecology studies conducted to date because the urban habitat types were examined 1) with a multivariate ecological perspective (i.e., many variables were studied concurrently) and 2) in a controlled field experiment. As such, it has significance as a contribution to mechanistic urban ecology (Shochat et al. 2006) and for its ability to inform the sustainable management of urbanized ecosystems.

Methods

Study Site

Experimental plots (described below) were established at Penn State University’s Russell E. Larson Agricultural Research Farm (40° 43’N, 77° 55’W, 350 m elevation). This experiment station
is located in Centre County, PA about 10 miles from Penn State’s University Park campus. The climate of central PA is continental with 975 mm mean annual precipitation and mean monthly temperatures ranging from 3°C (January) to 21.6°C (July). Soils at the study site are shallow, well drained lithic Hapludalfs formed from limestone residuum (Braker 1981). Soil texture in the experimental field (measured in each of the experimental plots using the hydrometer method (Gee and Bauder 1986)) was predominantly clay loam with spatial variability in silt (range of 28-34%) and sand (11-38%) content across the field.

The field experiment was created in a 0.84 ha (200 X 42 m) old field that had not been managed (except for once-a-year mowing) for at least the previous 25 years (S. Harkom, farm manager, personal communication). The field was level with gentle sloping on two sides which guided the creation of a randomized complete block design (below). A hedgerow of mature trees and shrubs and a gravel road bordered the field on the western and eastern sides, respectively (Appendix A). Prior to creation of experimental plots, vegetation across the field was dominated by the grasses *Dactylis glomerata* (orchardgrass) and *Poa pratensis* (Kentucky bluegrass). Although soil conditions were not measured in the experimental plots before habitat manipulation, it is assumed that they were relatively homogeneous, which is supported by the observed similarity of variables from each of the reference unmowed plots.

This study was conducted in an experimental field rather than a previously urbanized landscape for several reasons. First, creation of new field plots in a common field provided for greater experimental control in both environmental conditions and time of habitat creation. Second, the study site was located in a rural environment which eliminated potentially confounding factors associated with urbanization that could have affected measurements (e.g., historical disturbance or contamination of soil). Thus, the ability to attribute results to experimental manipulations was increased. Third, carrying out the experiment was made more tractable by locating it at the research farm where access to needed supplies was provided. Although it is recognized that conclusions drawn from this study should be extrapolated to urbanized environments with caution, this study is complementary to those conducted in urbanized settings and contributes needed insights into the basic ecology of urban habitat types.

*Experimental design and habitat creation*

The field experiment was begun in April 2003 when 16 10 X 10m habitat plots were created. The four habitat types included in the study were: lawn, shredded bark mulch, limestone gravel
mulch and unmowed old field vegetation as the control or reference habitat (see Appendix B for photos and descriptions of detritus layers). These are commonly used habitat types for urban landscaping management throughout the U.S. that generate fine-scale heterogeneity within urbanized ecosystems. Each of the habitat types was established in four replicated plots using a randomized block design. (A total of thirty-six plots were arranged across the field but 20 of these were used for the study described in Chapter 6.) All plots were separated from each other, the hedgerow and road by at least 3m wide strips of mowed lawn.

Unmowed vegetation plots did not receive any management inputs (including mowing) throughout the study (2003-05). Lawn plots were created and maintained with regular mowing (~twice per month) with a riding, or occasionally a push, rotary mower to keep vegetation height at 5-7 cm. The lawn plots received no other management inputs and are therefore classified as low-maintenance lawns (Cockfield and Potter 1985). Mulch habitats were created by removing existing vegetation and applying the respective mulches. Vegetation was killed with an application of the herbicide glyphosate (Round-Up, Scotts Co., Marysville, OH) in April 2003. Dead aboveground vegetation was removed by raking with minimal disturbance to the soil. Shredded bark and gravel mulches were purchased from local landscaping companies. Bark mulch was composed of dark brown, finely-shredded, mixed hardwood obtained from timber logged in Pennsylvania. (The exact species composition and location of origin could not be determined.) Gravel mulch was grade 2B light bluish-grey limestone rocks, 2-4mm in diameter. Both mulches were delivered to the field site and spread into the plots using a small front-end loader (making sure that its wheels never entered the plots). Mulches were spread 5-8 cm deep evenly throughout the plots by hand raking. The bark mulch decomposed slowly in 2003 and was not reapplied in 2004. However, fresh bark mulch from the same supplier was applied in April 2005 in the same manner as in 2003. Gravel did not degrade and was not reapplied during the three years of the study. Weeds were removed by hand from the mulched plots by regular weeding throughout the 2003-05 growing seasons; in 2005, glyphosate was used to kill large numbers of dandelions that had invaded certain plots. To prevent confounding effects of the herbicide on soils, minimal amounts were sprayed directly onto individual plants. Locations with weeds were avoided when collecting samples for all variables in the mulch plots.

Although the field plots were created in 2003, all data reported here were collected in 2004-2005. In 2003, I concentrated my work on arthropod communities (Chapter 5) and collected preliminary microclimate, soil and carbon data to guide the research described below.
Microclimates

Daily air temperature and precipitation data were obtained from a weather station located less than one kilometer from the experimental site. However, it was expected that the four habitat types would each have different microclimates at the plot scale. Therefore, ground surface and soil temperatures were recorded in each of the 16 plots every 30 minutes using HOBO four-channel industrial dataloggers (Onset Computer Corp., Pocasset, MA). One soil temperature probe was placed to a depth of 5cm in the center of each plot. One surface temperature probe was laid on top of the mulch (in mulched plots) or soil (in vegetated plots) in the center of each plot. Probes were secured on or in the ground using wire. Dataloggers were installed on April 15, 2004 and removed in September 2005. In this paper, only data for the periods April-September 2004 and April-July 2005 are considered because the focus of the study is on the growing seasons and because many dataloggers were damaged or ceased working after July 2005.

Soil properties

A wide range of soil physical, chemical and biological variables were measured to examine how aboveground habitat structure influences soil characteristics that affect biodiversity and biogeochemical cycles. Except where described otherwise, measurements were made on one homogenized composite soil sample per plot composed of three randomly-collected 2cm Ø by 5cm deep soil sub-samples that were air dried and sieved (2mm).

pH was measured once per year in a 1:1 (wt/wt) water/soil solution with a Thermo Orion meter (Beverly, MA). Bulk density (BD) was measured in September each year from one randomly collected and oven-dried (110°C) soil core (7.5 Ø by 7.6 cm) per plot. Loss on ignition (LOI) soil organic matter (SOM) content was measured on three dates each in 2004 (June, August, September) and 2005 (April, June, September) by burning ~10g oven dry soil at 450°C for 24 hours. Percentage SOM was calculated as (weight of oven dry soil minus weight of burned soil) divided by the weight of oven dry soil. In addition, total soil C was estimated once at the end of the study period on one ground and sieved (1mm) soil sample per plot collected in September 2005. This analysis was conducted by Penn State’s Agricultural Analytical Services using an Elementar Variomax CN analyzer (Hanau, Germany).

Soil aggregate stability was also measured once at the end of the experiment following the wet method described by Kemper and Rosenau (1986). Three randomly collected soil samples (5.5cm Ø, 5cm deep) per plot were air dried and soil around the outside of each core (where
aggregates could have been crushed during removal) was removed. Remaining soil was broken apart, homogenized (giving one composite sample per plot) and sieved to separate the 1-2mm aggregate fraction. Three 4g sub-samples of these aggregates per plot were placed into 0.25 mm sieves and soaked for 5 minutes in distilled water before being subjected to wet disruption by repeatedly dunking them into water (36 dunks per minute) for 5 minutes on a mechanical dunker (Fig. 17-1 in Kemper and Rosenau 1986). During dunking, silt and clay particles dislodged from the aggregates passed through the sieve, were collected in the container of water below, dried and weighed to provide the unstable aggregate weight. Sand is not included in aggregate stability measurements and was separated from the stable aggregate fraction by sonicating the stable aggregates (those remaining after dunking) for 30s in water and passing the silt and clay through a 0.25mm sieve. These fractions were then dried and weighed to provide the weight of stable aggregates. Percentage water stable aggregates (%WSA) for each sub-sample was calculated as the weight of stable aggregates divided by (the sum of the weight of stable and unstable aggregates). The three sub-samples were averaged to give a plot’s mean %WSA.

Soil microbial biomass carbon (SMB-C) and ergosterol content provide reliable estimates of the size of microbial and fungal populations, respectively (Bailey et al. 2002, Ruzicka et al. 2000). These two analyses were completed using one sieved, composite soil sample per plot (composed of 8-10 random sub-samples) collected in June, July and September 2004. (SMB-C samples from September 2004 were lost due to freezer malfunction.) SMB-C was estimated by the chloroform fumigation-extraction (CFE) method (Horwath and Paul 1994). Briefly, composite soil samples from each plot were divided into six 10g sub-samples. Three of these were incubated at room temperature in dessicators with chloroform vapor for five days; the other three were incubated without chloroform. After five days, C was extracted from the soils with a 5:1 0.5 M K$_2$SO$_4$ to soil mixture for one hour with constant shaking and then filtered through #42 Whatman filters. C content of the filtrate was analyzed using a Shimadzu carbon analyzer (TOC-5000A, Columbia, MD). Filtrates were frozen (0°C) between extraction and analysis. SMB-C was calculated as the difference in extracted C between the fumigated and unfumigated samples. Values were corrected for soil moisture content and are reported as $\mu$g SMB-C g dry soil$^{-1}$. Untransformed SMB-C data are reported as the SMB-C flush (Fierer and Schimel 2002) rather than adjusting them with an efficiency correction factor ($k_{ec}$) as suggested by Horwath and Paul (1994) because such factors vary widely among soils (Bailey et al. 2002) and the specific extraction efficiency for the soils were not determined.
Ergosterol content was measured using a modified rapid ultrasonication method (Ruzicka et al. 1995). Soils were processed within 24 hrs after collection and were held at 4°C between sampling and analysis. Two 5g field moist sub-samples per plot were mixed with 10ml methanol:ethanol solution (4:1 v/v) in 50ml centrifuge tubes. Samples were held at 4°C for 2 hours prior to sonication at 150 W for 200s (Fisher Scientific sonic probe FS28). After allowing the sediment to settle for 30s, the tubes were centrifuged at 10,000 rev min⁻¹ for 5 min. One ml of supernatant was filtered with a syringe fitted with a 0.45 μm filter and transferred to a 1ml glass vial. Ergosterol content of the filtrate was analyzed with 20 μl injections through a Waters high performance liquid chromatography (HPLC) system (Milford, MA) composed of a 2690 Alliance separation module, a Waters 2487 dual λ absorbance detector operating at 282 nm and a Nova-Pak 3.9-mm x 150-mm C18 column of 4 μm particle size (Supelco, Bellefonte, PA). The carrier was HPLC grade methanol delivered at a flow rate of 0.5 ml min⁻¹ with a retention time of 6 minutes. The hexane-propanol extraction step of Ruzicka et al. (1995) was eliminated to reduce preparation time. Methodological analyses showed that removing this step did not reduce extraction efficiency (C. Anderson and M.A. Bruns, unpublished data).

Gravimetric soil water content in all the plots was intensively measured throughout 2004 and 2005 with collections once or twice weekly from April through September. Three random soil sub-samples were collected from each plot and immediately transported back to the laboratory where their fresh weight was recorded (soils were not homogenized). Soils were oven dried (110°C) for 24 hours and reweighed. The gravimetric water content of the three sub-samples was averaged to give one mean value per plot per sampling date.

In 2004 and 2005, earthworm densities in the plots were quantified by hand-sorting them from one 25cm⁻³ soil sample per plot in May, July and September of each year. Soil was collected from within a 25cm² quadrat placed randomly within each plot but at least 1m from plot edges. A flat shovel was used to cut and pull the intact soil cube from the ground. Soils were transported in plastic bins immediately to the laboratory where cubes were broken apart and all earthworms were removed by hand. Each sample was hand-sorted twice. Time constraints prevented the sampling of all 16 plots on one day but all plots were sampled within a four day time span to reduce confounding effects of changing weather and soil conditions. Due to the challenges of earthworm identification, especially for juveniles, the effects of the habitat types on earthworm species was not determined.
Carbon dynamics

Production of carbon dioxide (CO$_2$) from soil is an important source of C flux from terrestrial ecosystems but little is known about the rates of CO$_2$ flux from urban habitats (Kaye et al. 2005). CO$_2$ production was measured from the experimental plots on 5 dates between May and August 2005 using enclosed static chambers (Holland et al. 1999). (Measurements were not made in 2004 due to problems with the analyzer.) Chambers were constructed from PVC pipe couplers (i.e., the base, 15.5 cm height X 17 cm inner Ø) and their corresponding PVC lids that fit tightly inside the coupler to provide a sealed chamber. Two holes (1 cm Ø) were drilled in the lids, one to provide a vent (with an associated 10 cm vent tube inside the chamber) and the other for a sampling port that was covered with a rubber septum (2 cm Ø) (following specifications in Holland et al. 1999). Eight chambers were constructed which allowed for sampling of the 16 plots over two days (blocks 1 and 2 on day 1 followed by blocks 3 and 4 on day 2 at each sampling effort). Chamber bases were placed randomly in each plot and pounded 5 cm into the soil 24 hrs before gas sampling. Detritus was removed from within the chambers just before sampling such that the soil surface was exposed. Fifteen ml gas samples were collected zero, 15, 30 and 45 minutes after placing the lid on the base with 30 ml polypropylene syringes fitted with 25 gauge needles and stopcocks (all Cole-Parmer, Vernon Hills, IL). Samples were transferred in the field from the syringes into evacuated 12 ml glass Exetainer vials with butyl rubber septa (Labco, High Wycombe, England). Soil temperatures were measured adjacent to all chambers and two soil samples were collected from inside the chamber for measurement of gravimetric soil water. Air temperatures were measured inside the chambers for comparison to outside air temperature (which never differed by more than 1°C). On all dates, samples were collected between 9 and 11:00 am and analyzed within 24 hrs on a Li-Cor 6262 infrared gas analyzer (IRGA) (Lincoln, NE) using 1 ml injection volumes and helium as a carrier. A range of standards were run at the beginning, middle and end of each analysis period. CO$_2$ flux was calculated as µg CO$_2$-C m$^{-2}$ hr$^{-1}$ following equations given in Holland et al. (1999).

Decomposition rates of surface organic matter in the four habitat types were measured as mass loss from litterbags (Harmon et al. 1999) with two standardized litter types: intact leaves of Dactylis glomerata (orchard grass) and Quercus alba (white oak). Leaves of D. glomerata were collected from an old field adjacent to our experimental field in late April 2004 by cutting them at ground level. Q. alba leaves were collected in October 2003 (immediately after leaf drop to ensure that decomposition did not begin) from underneath two adjacent trees on Penn State’s campus. The oak leaves were brought into the laboratory, air dried and stored in a 4°C cold room through March.
2004. Litterbags (15 X 20cm) were constructed from 2mm mesh plastic screen and closed with wire. Each was filled with 3-4g of oven-dry (55°C) leaf material and the bag plus initial litter weight was recorded. Fourteen oak and 13 grass litterbags were placed—each randomly into one of three groups— into each of the 16 experimental plots on April 16 and May 18 respectively (for a total of 224 oak and 212 grass bags). Bags were fastened to the ground with wire clips. (To facilitate this, bark and gravel mulch was spread thinly under the litterbags.) In addition, four bags of each litter type were used as drop bags that were taken to the field, dropped on the ground and immediately removed to measure any mass lost during transport and placement (determined to be zero or negligible). In 2004, one bag per plot of each litter type was collected 2 and 4 weeks after placement and then every 4 weeks through October (Harmon et al. 1999). Grass litter had fully decomposed by this time and all remaining grass bags were collected. Monthly collection of oak litterbags continued April through October 2005. After collection, all soil and living plant material was carefully removed from litterbags (they were opened when necessary) which were then oven dried (55°C) and weighed. Decomposition rates are reported as percentage mass loss of initial litter mass over time.

Changes in the species composition of lawns as compared to unmowed plots were seen after mowing was initiated in 2003. Although detailed measurements of vegetation dynamics could not be made for this study, the species richness per plot and estimated percent cover of each species was quantified in three random 25cm² quadrats per plot in each of the lawn and unmowed plots in September 2004 and 2005. Due to time constraints, this analysis could not be completed at other times during the season. However, no strong temporal changes were observed in species composition through each year and the most common species were present throughout the year (L. Byrne, personal observation). Plants growing in the mulched plots (< 5% cover) were not identified nor were these habitats included in the standing crop or primary productivity analyses described below for lawn and unmowed habitats.

In addition to plant species composition, aboveground plant biomass (i.e., standing crop) and annual aboveground net primary productivity (ANPP) were measured in lawn and unmowed plots in 2004 and 2005. Aboveground living and dead (i.e., detritus) standing crop was collected from one random 25m² quadrat in each plot 3 times in 2004 (May, July, September) and 7 times in 2005 (monthly from April through October). (All 2004 samples and the May, July and September 2005 samples were collected from the earthworm soil cubes, above.) Living vegetation and detritus was cut at the soil surface and at the quadrat boundaries, respectively, collected, dried at 55°C and
weighed. In lawns, the amount of biomass cut at each mowing in lawns contributes to the annual ANPP (Falk 1980) and was measured just prior to each mowing event by cutting, collecting, drying (55°C) and weighing vegetation taller than 5cm (the same cutting height of the mower) from three 25m$^2$ quadrats in each plot. The standing crop and lawn clipping data were used to estimate annual ANPP for the lawn and unmowed habitats using published calculations (Falk 1980, Scurlock et al. 2002; Appendix C). For calculation of lawn ANPP with Falk’s (1980) equation, his estimate of 0.6 for stubble turnover (the growth and death rate of vegetation below mowing height) was used as representative for a northeastern U.S. low-maintenance lawn (his measurements were taken in MD). Methods 1-6 from Scurlock et al. (2002) were used to estimate both lawn and unmowed ANPP with the following modifications. The yearly sum of mowed clipping biomass was included in all the calculations for lawns. For estimating unmowed vegetation ANPP, it was assumed that living aboveground biomass was zero (or negligible) at the beginning of each growing season; therefore, the first living biomass measurement of each year was considered a contribution to ANPP (necessary for methods 3, 4, and 6 in Scurlock et al. 2002). This is a reasonable assumption given that most, if not all, aboveground unmowed vegetation dies, and new growth is negligible, over the winter in the study area (L. Byrne, personal observation). Method 7 from Scurlock et al. (2002) was not used due to lack of data about decomposition rates of unmowed detritus for our study site.

C and N content of standing crop and litterbag biomass was analyzed on a subset of samples chosen to represent the range of sampling dates. All material was ground in a Wiley mill (1mm mesh) and homogenized prior to analysis of duplicate ~80mg per sample in a Leco 600 CHN analyzer (St Joseph, MI). Living and dead standing crop C and N was analyzed from samples collected in July and September 2004 and April and June 2005. Oak leaves were analyzed from the drop bags and from bags collected on four dates (May 14 and August 9, 2004 and July 22 and September 20, 2005). C and N content of the grass leaves used in the litterbags was analyzed on initial samples and those collected on June 1, 2004. In addition, the C and N content of one composite sample of bark mulch per plot from May and September 2005 was measured for comparison to vegetation. C and N data were used to calculate C-to-N ratios (C:N) of biomass and for conversion of ANPP biomass values to g C m$^{-2}$ year$^{-1}$.

Data analyses

All data were analyzed using general linear models (GLM) with habitat type as the between-subjects factor and, where appropriate, sampling date and/or year as within-subjects factors (i.e., for
repeated measures data such as temperature and decomposition). Block was included as a between-subjects factor in all initial analyses, but was never significant ($P > 0.05$), and thus, is not included in the reported statistical models. To meet the assumptions of the GLM, monthly daytime soil temperature, earthworm and grass decomposition data were square root transformed, and monthly daytime surface temperature and dead OM C:N data were log transformed. Untransformed data are presented. Wet aggregate stability data could not be adequately transformed and were analyzed using the Kruskal-Wallis non-parametric test (Zar 1999). Tukey’s honestly significant differences (HSD) test was used for all post-hoc comparisons. Significant differences were evaluated at $P < 0.05$. All analyses were completed using Statistica 6.1 (StatSoft, Tulsa, OK). Many statistics are presented in the table and figures.

Two key questions were identified to focus the analysis of temperature data: 1) does temperature differ significantly among the habitats, and if so, when (i.e., time of day, season)? 2) Is air temperature a good predictor of surface and soil temperatures and is surface temperature a good predictor of soil temperature? To examine the range of possible temporal scales at which temperature data could be examined to address these questions, several sets of temperature data were used. First, two four-day periods (April 22-25 and July 15-18, 2004) were chosen to exemplify the spring and summer hourly and daily fluctuations in soil and surface temperatures and the day-to-day variation in those patterns (addressing question one above). The mean daily maximum and minimum temperatures for each of the four days for each habitat were analyzed with a repeated measures GLM using day and time of day (day or night which corresponds to maximum and minimum temperatures, respectively) as within-subjects factors. Second, six data sets using two types of temperature data (the daily and daytime means with temperatures averaged for the periods 0:00 to 23:30 or 11:00 to 17:00hrs respectively) each considered at three temporal scales (daily, weekly and monthly means) were analyzed for each habitat separately (i.e., the six types of temperature by temporal scale combinations) with repeated measures GLM, also to address question one. To address question two, each of the six data sets was used to examine all pair-wise relationships (18 total) among surface, soil and air temperatures for each habitat in regression analyses. It was expected that results would differ among these analyses due to averaging different numbers of data points across the three temporal scales. GLM was utilized to evaluate differences among the regressions for each habitat type within each pair-wise combination. To maintain an experiment-wise alpha level of 0.05 for these temperature relationship analyses, a Bonferroni correction was used and significant differences were assessed at $P < 0.003$. For brevity, only results
that best exemplify the important temperature relationships and differences among the habitats (i.e., daytime means) are presented.

**Results**

**Microclimates**

Soil (5cm deep) and surface (on top of the soil in vegetated plots or mulch in mulched plots) temperatures differed among the habitats with degree of differences dependent on hour, day and season. Within each day (0:00-23:30 hrs), temperature fluctuation patterns generally exhibited significantly different maximum daytime (11:00-17:00), but similar minimum nighttime to early morning (4:00-8:00), temperatures among the habitats and 2) significant day-to-day differences among the values of the maximum and minimum temperatures (Fig. 3-1). For the two four-day periods analyzed (which are representative of all the temperature data), the maximum daytime soil and surface temperatures were significantly different among the habitats. Both the soil and surface temperatures of the mulches were up to 10-15°C warmer than the vegetated plots on most days during the periods April 22-25 and July 15-18 (Fig. 3-1). There was variation among days in this general pattern, however, with gravel mulch surface and soil temperatures higher on many, but not all, days than bark mulch which had similar temperatures to lawn and unmowed on some days. In addition, the maximum temperatures reached in the habitats differed between days with some days warmer than others and variability in the range of differences among the habitats in their maximum surface and soil temperatures (5-20°C and 2-10°C, respectively). During the day (11:00-17:00), surfaces were often warmer than the soil but overnight (4:00-8:00) the soil and surface temperatures converged and were more similar. Minimum daily surface temperatures (0:00-23:30) were also similar among the habitats. In addition to these within- and between-day patterns, high hour-to-hour variability in surface temperatures were observed within the habitats, with rapid temperature changes of ± 3-10°C within one or several hours (Appendix D; see July 16 daytime hours in graph C). Maximum and minimum soil and surface temperatures rarely matched the air temperature at the same point in time (Fig. 3-1, also see below and Fig. 3-3). Surface temperatures in all the habitats were generally warmer than the concurrent air temperature during the day but cooler at night. Soil temperatures were more similar to air temperatures but were occasionally warmer or cooler by a few degrees or more during both days and nights.
Figure 3-1. Daily mean (+ SE) maximum and minimum surface and soil temperatures in four urban habitat types and air temperature over four consecutive days. (A) Surface and (B) soil (5 cm depth) temperatures for April 22-25, 2004. (C) Surface and soil (D) temperatures for July 15-18, 2004. Data points are means of four replicated plots per habitat except for bark which had only three replicates for April surface temperatures and July surface and soil temperatures. SE bars are generally small (range of 0 to 4.2) and therefore not visible at all data points. GLM analyses showed significant effects of habitat, time of day (day or night), date and all their interactions \( (P < 0.01) \). Means with different letters differ significantly \( (P < 0.05) \) with Tukey's post hoc tests.
Because temperatures differed among the habitats primarily during the day, additional analyses were focused on mean temperatures of the daytime hours (11:00-17:00) and differences among the habitats across seasons were examined using monthly means (which provided the clearest figure and simplest analysis; observed patterns were similar for data averaged over days and weeks). Mean daytime surface and soil temperatures significantly differed among habitats and months (Fig. 3-2). For all months, gravel soil and surface daytime mean temperatures were significantly higher than lawn and unmowed plots. Gravel and bark surface temperatures never differed from each other and soil temperatures between these habitats only differed significantly in April-July 2004 and May 2005. Unmowed soil and surface temperatures were generally coolest although differences were non-significant on most dates and soil temperatures were similar among unmowed, lawn and bark temperatures in April and May 2004 and April 2005. Variation in the differences among habitat types between seasons resulted in a significant \( P < 0.001 \) and marginally significant \( P = 0.07 \) month x habitat interaction for soil and surface temperatures, respectively, in the GLM analyses (see legend of Fig. 3-2 for statistics).

Mean daily (0-23:30hrs) and daytime (11-17:00) temperatures were also used to examine the relationships among air, soil and surface temperatures using data averaged at daily, weekly and monthly scales. Regression analyses for all daily temperature relationships for each habitat were highly significant \( P = 0.00 \) with significantly different relationships among the habitats and significant habitat x temperature interactions for each type of comparison (i.e., air and surface, air and soil, surface and soil; see Fig. 3-3 for statistics). Explanatory power of the regressions differed among the temperature comparisons and the habitats. Daytime air temperature explained more of the variance in soil (Fig. 3-3C, \( R^2 \) values ranging from 0.67 to 0.8) than surface (Fig. 3-3A, \( R^2 \) values ranging from 0.37 to 0.6) daytime temperature for all habitats. Air and surface temperatures had similar explanatory power for soil temperatures in unmowed habitats (\( R^2 = 0.75 \) and 0.77, respectively) but air temperature explained more of the variation in lawn and bark soil temperatures (\( R^2 = 0.75 \) and 0.67, respectively) whereas surface temperatures explained more of the variability in gravel soil temperatures (\( R^2 = 0.8 \)). Linear regressions were the best fit lines for all relationships except for daytime surface and soil slopes for bark and gravel for which exponential equations provided better fits to the data suggesting that mulch soil temperatures were affected differently at different surface temperatures (i.e., soil and surface temperature relationships in mulches are not linear). As compared to regressions using daily mean daytime temperatures, predictive power generally increased, but regression equation parameters changed, when averaging data across
Figure 3-2. Mean (± SE) monthly daytime (11:00-17:00) (A) surface and (B) soil temperatures in four urban habitat types and mean monthly daytime air temperature. N=4 for all months except for the following where N=3: Surface data: April, May and June 2005 for lawn; May, June and July 2005 for unmowed April, May 2004 and July, Aug. and July 2005 for bark; April and May 2005 for gravel; Soil data: April and July 2005 for lawn; May, June and July 2005 for unmowed; Aug. 2004, June and July 2005 for bark; April, May and June 2005 for gravel. N=2 for surface temperatures for gravel in June 2005 and for lawn in July 2005 and for gravel soil temperatures in July 2005. Main effects of habitat and month are significant for both surface and soil temperatures ($P = 0.00$). Month x habitat interactions are marginally significant for surface temperatures ($P = 0.07$) and significant ($P = 0.00$) for soil temperatures. Means with different letters differ significantly ($P < 0.05$) with Tukey’s post-hoc comparisons.
Figure 3-3. Relationships among mean daytime (11:00 to 17:00) or daily (0:00 to 23:30) surface and soil temperatures in four urban habitat (continued on next page)
types and air temperature for the periods April 16-August, 31, 2004 and April 1 to July, 31, 2005. Note different scales on X axes. Regressions between (A) daytime air and surface temperatures, (B) daily surface and air temperatures, (C) daytime air and soil temperatures and (D) daytime surface and soil temperatures. Data points for habitat surface and soil temperatures are means of four replicated plots. Letters next to regression lines represent first letter of habitat type for the respective regression equations. GLM analyses showed significant habitat and habitat x (air or surface) interactions for all analyses. Regression slopes within each graph are all significantly different from each other ($P < 0.01$) except for between gravel and bark in B.

weekly and monthly scales for relationships between surface and air temperatures and soil and surface temperatures (Appendix E). In addition, fewer significant differences among habitat temperatures were detected with analyses using these longer temporal scales than in analyses with daily temperature data (see statistics in Appendix E).

Soil properties

All measured soil variables differed significantly among the habitat types. In general, pairwise comparisons showed that lawn and unmowed soils were similar to each other (except for earthworm abundances in July and September 2005) but differed from at least one of the mulch habitat soils for most variables (Table 3-1, Figs. 3-4, 3-5). Within two years after habitat type creation, mean soil pH was significantly greater under the mulch plots than the vegetated plots and the bark and gravel pH values differed significantly from each other. The mean BD was significantly less (using the least significant differences post-hoc test but not Tukey’s) in bark-covered soils (by $> 0.1$ g cm$^{-3}$) than the other habitat types’ soils which did not differ from each other. LOI SOM was significantly greater under the bark mulch than the other habitats in 2004 but did not differ from the vegetated plots in 2005. In 2005, gravel-covered soils contained significantly less LOI SOM than the other habitats. Similarly, mean total soil C measured at the end of the experiment was significantly less in gravel-covered soils than all other habitat types. Mean total soil C in lawn and bark plots did not differ but were significantly higher than that of soils of unmowed plots. Mean % WSA was also significantly less in gravel soils (> 10% difference) than the other habitat types which had similar values. Mean SMB-C was greater in vegetated plots than the mulched plots although this difference was only significant in comparison to values from gravel-covered soils which did not differ from bark SMB-C. Similarly, mean soil ergosterol content was significantly less (by $~$2 µg g soil$^{-1}$) under gravel than the other habitat types which had similar mean values (4.4-4.8 µg soil$^{-1}$).
Table 3-1. Soil characteristics (means ± SE) of four urban habitats.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Lawn</th>
<th>Unmowed</th>
<th>Bark</th>
<th>Gravel</th>
<th>Statistic(d.f.)</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>6.74 (+ 0.06)a</td>
<td>6.87 (+ 0.04)a</td>
<td>7.21 (+ 0.08)b</td>
<td>7.53 (+ 0.02)c</td>
<td>F3,12 = 49.68</td>
<td>0.00</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)†‡</td>
<td>0.94 (+ 0.05)ab</td>
<td>0.92 (+ 0.02)ab</td>
<td>0.77 (+ 0.007)b</td>
<td>0.97 (+ 0.06)a</td>
<td>F3,12 = 3.89</td>
<td>0.04</td>
</tr>
<tr>
<td>LOI OM (%)§</td>
<td>2004</td>
<td>13.4 (+ 0.47)a</td>
<td>14.1 (+ 0.78)a</td>
<td>17.8 (+ 1.23)b</td>
<td>13.2 (+ 0.34)a</td>
<td>F3,12 = 7.43</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>13.8 (+ 0.86)a</td>
<td>13.3 (+ 0.69)a</td>
<td>14.5 (+ 0.84)a</td>
<td>10 (+ 0.77)b</td>
<td>F3,12 = 6.18</td>
</tr>
<tr>
<td>Total soil C (%)¥</td>
<td></td>
<td>7.8 (+ 0.05)a</td>
<td>6.1 (+ 0.26)b</td>
<td>7.5 (+ 0.26)a</td>
<td>4.0 (+ 0.38)c</td>
<td>F3,12 = 41.58</td>
</tr>
<tr>
<td>Water stable aggregates (%)†</td>
<td></td>
<td>96 (+ 1)a</td>
<td>94 (+ 0.5)a</td>
<td>93 (+ 2)ab</td>
<td>79 (+ 5)b</td>
<td>X²3,12 = 9.8</td>
</tr>
<tr>
<td>Microbial biomass (µg C dry soil⁻¹)*</td>
<td></td>
<td>752 (+ 55)a</td>
<td>727 (+ 19)a</td>
<td>674 (+ 51)ab</td>
<td>534 (+ 33)b</td>
<td>F3,12 = 5.35</td>
</tr>
</tbody>
</table>

Notes: N=4 per habitat per sampling date. Means with different letters differ significantly (P < 0.05, Tukey's post-hoc test).
† Data are means of one sampling date each in 2004 and 2005.
‡ Lawn is marginally different from bark (P = 0.08). Bark mulch was significantly different (P < 0.05) from all habitats with the least significant differences post-hoc test.
§ Data are means of three sampling dates each in 2004 and 2005. The main effect of year and year X habitat interaction were significant in the initial GLM analysis (P < 0.05). Statistics shown are from the analyses among data within each year.
¥ Data are means of one sampling date (September 2005).
* Data are means from one sampling date (September 2005). Data could not be transformed and were analyzed with the Kruskal Wallis non-parametric test.

Across all sampling dates, the mean (+ SE) gravimetric soil water content of the habitat types differed significantly from each other (F3,12 = 36.87, P = 0.00) with bark mulch (0.61 ± 0.11) significantly greater than all other habitats. Soil water content under gravel (0.45 ± 0.1) was significantly greater than that under lawn (0.34 ± 0.05) and unmowed (0.36 ± 0.05) plots which did not differ from each other. These values reflect the temporal trend of mulched plots being wetter than the vegetated plots across all sampling dates (Fig. 3-4). In both years, soil water content in bark soils was significantly greater than in all other habitats on all sampling dates except two (Fig. 3-4). Soil water content in gravel plots tended to be higher than in vegetated plots, although the differences varied by sampling date (Fig. 3-4) and differences were greater in 2005 due to drought conditions that year (which tended to reduce the soil water content in all habitats). Lawn and unmowed soil water contents were similar on all dates and exhibited more temporal variability than the mulched plots which generally appeared to track precipitation events.

Two genera of European earthworms were common in the plots: *Lumbricus* sp. and *Apporectodea* sp. Over ¾ of the earthworms sampled were juveniles which can not be identified to species easily (Szlavecz et al. 2006). Mean earthworm abundances were significantly different among the habitats on all dates with significant year x habitat and year x month interactions.
Figure 3-4. Mean (± SE) gravimetric soil water content in four urban habitat types (lines corresponding to left y axis) and precipitation (bars corresponding to right y axis) in the four days proceeding each sampling date (including sampling date). N=4 per habitat for water content. The main effects of habitat ($F_{3, 11} = 32.9$) and date ($F_{56, 616} = 48.4$) and the habitat X date interaction ($F_{68, 616} = 4.164$) were all significant ($P = 0.00$). Means with different letters differ significantly ($P < 0.05$) with Tukey’s post-hoc comparisons. Only selected significant differences are shown with letters for visual clarity. In 2004, bark was significantly different from all other habitats on all dates except April 28. In 2005, bark was significantly different from lawn and unmowed on all dates except May 24 and bark differed from gravel and gravel differed from lawn and unmowed on most dates. Lawn and unmowed soil water content never differed. 

($P < 0.01$, Fig. 3-5), reflecting different temporal patterns in abundances among the habitats.

Earthworms were significantly greater in bark than gravel mulch plots on all dates although differences among bark and vegetated plots were significant on only several dates, primarily in 2005 (the drought year). Earthworm numbers in gravel soils were lowest of all the habitats in 2004 and were similar to those in lawns in 2005 when both these habitats had fewer earthworms than unmowed and bark mulch plots. Earthworm abundances were lower in July and September 2005 than on all 2004 dates for all habitats except bark mulch which had similar numbers across all dates.
Figure 3-5. Mean (± SE) number of earthworms m\(^{-2}\) to 25 cm depth in four urban habitat types in 2004 and 2005. N=4 per habitat for all dates. Habitat (F\(_{3,12}\) = 72.5), month (F\(_{2,6}\) = 79.0) and year (F\(_{1,12}\) = 820.8) main effects were all significant (P < 0.01). Two-way interactions were significant (P < 0.001) for habitat X year (F\(_{3,12}\) = 147.9) and month x year (F\(_{2,24}\) = 8.7) but not habitat X month (F\(_{6,24}\) = 1.5, P > 0.2). The three-way habitat x month x year interaction was not significant (F\(_{14,24}\) = 10.9, P > 0.3). Means with different letters differ significantly (P < 0.05) with Tukey’s post-hoc comparisons.

Carbon dynamics

Soil CO\(_2\) flux was affected by habitat type and sampling date with a significant habitat x date interaction (Fig. 3-6). Across dates and habitats, CO\(_2\) flux was generally greater in June and July than May and August. In May and early June 2005, lawns had significantly higher mean CO\(_2\) flux rates than the other habitats. At these times, unmowed and bark mulch rates were similar to each other but greater than rates from gravel plots (significantly so for both in May and only for unmowed in early June). In late June, mean CO\(_2\) fluxes in lawn and bark mulch plots were similar and greater than those in unmowed and gravel plots which were similar to each other. In July, CO\(_2\) flux was higher from bark mulch than the other habitats although it was only significantly greater than that from unmowed and gravel plots which had similar rates. CO\(_2\) flux from lawns was significantly greater than that from gravel plots but it did not differ from unmowed and bark mulch flux rates. No significant differences in CO\(_2\) flux were detected among the habitats for August although lawn and bark mulch tended to have higher CO\(_2\) flux rates than gravel-covered soils with intermediate rates in unmowed habitats. Regression analyses indicated that soil water content and temperature were poor predictors of CO\(_2\) flux across all habitats and for each habitat (R\(^2\) < 0.05 for
**Figure 3-6.** Mean (± SE) carbon dioxide flux from soil in plots of four urban habitat types in 2005. N=4 for all habitats on all dates. Habitat (F_{3,12} = 19.1), date (F_{4, 48} = 7.9) and habitat x date interaction (F_{12, 48} = 3.1) were all significant (P < 0.003) in repeated measures GLM using five dates. GLM analysis on means across all dates was also significant (F_{3, 12} = 19.1, P = 0.00). Means with different letters differ significantly (P < 0.05) with Tukey’s post hoc comparisons. * denotes that habitat effect for June 28-29 was significant (P = 0.05) but Tukey’s post hoc comparisons detected no pair-wise differences among the habitats. Letters shown reflect differences detected with the less conservative LSD post-hoc test.

Most analyses; data not shown). However, the relationships between CO₂ flux and soil temperature in bark and gravel habitats was significant (P ≤ 0.01) even though temperature explained little of the variation in CO₂ flux (R^2 = 0.39 and 0.30, respectively).

Percent litter mass remaining from both oak and grass litterbags differed among the habitats on most dates. Grass decomposed quickly with less than 60% mass remaining in all habitats after only two weeks, at which time grass in bark mulch plots had lost significantly more mass (30% remaining) than in the other habitat types (Fig. 3-7A). After three months, almost all grass litter had decomposed in unmowed, gravel and bark mulch plots but significantly more mass (13% ± 0.02 SE) remained in the litter bags in lawns (Fig. 3-7A). After five months, no significant differences were detected in % mass remaining among the habitats as grass litter had completely disappeared from the litter bags. Mean C:N of the initial grass clippings was 15.6 (± SE 4.61); this value did not change among all samples after two weeks in the field.

Oak leaves decomposed more slowly than grass leaves with 75-85% oak mass remaining after five months, at which point there were no significant differences among the habitats (Fig. 3-7B). After six months in the field, significant differences were detected with lower mean (± SE) %
Figure 3-7. Mean (± SE) percent mass remaining of (A) orchard grass (2004) and (B) oak leaves (2004-05) in litterbags from four urban habitat types. N=4 for all habitats on all dates except for N=3 for oak litterbags on 6/24/2005 for gravel, 8/17/05 for unmowed, 10/17/05 for mulch and N=2 for 10/17/05 for lawn. Habitat (grass F$_{3,12}$ = 12.1; oak F$_{3,7}$ = 21.1), date (grass F$_{5,60}$ = 138.5; oak F$_{13,91}$ = 67.03) and habitat x date interactions (grass F$_{15,60}$ = 2.02; oak F$_{39,91}$ = 1.8) are significant (P < 0.03) for both types of litter. Means with different letters differ significantly (P < 0.05) with Tukey's post hoc comparisons. * denotes P = 0.06.
mass remaining from the bark (65 ± 3) and gravel (64 ± 1) litterbags than the lawn (76 ± 4) and unmowed (76 ± 1) habitats. This trend continued through 2005 but with greater variability in decomposition rates within and among the habitats. After 18 months, % mass remaining was less in the bark (28 ± 4) and gravel (32 ± 6) habitats than the lawn (62 ± 8) and unmowed (63 ± 9), although significant differences were only detected between unmowed and mulch habitats due to a low sample size for lawn litterbags at this time (n=2). Mean (+ SE) initial C:N of oak leaves was 47 (+ 1.4). C:N changed significantly as the leaves decomposed (F_{3,36}=198.25, P = 0.00) with a slight increase after two weeks in the field (mean C:N across all habitat types which did not differ, 55.3 ± 1.9). By August of 2004, mean C:N decreased but did not differ among the treatments (37.6 ± 0.8 mean across treatments). C:N continued to decrease through 2005. By September 2005, the mean C:N (+ SE) of leaves collected from the bark (32.4 ± 0.6) and gravel (30.3 ± 2.35) mulch plots (which did not differ from each other) was significantly (P < 0.05) and marginally significantly (P < 0.08) greater, respectively, than that of leaves from the lawn (21.6 ± 1.7) and unmowed (24.2 ± 0.8) habitats (which did not differ). The same pattern was seen for leaves collected in July although C:N were slightly higher (by 5-6 points).

Mean (+ SE) plant species richness was similar between lawn (11.9 ± 0.31) and unmowed (10 ± 0.5) plots although the difference was statistically significant (F_{1,6} = 10.08, P = 0.02). (Species richness and % cover data were averaged across the 2004 and 2005 sampling dates.) *P. pratensis*, the dominant species in both habitat types, had similar mean (+ SE) % cover in them (31 ± 4.2 for lawn, 30 ± 7.3 for unmowed; F_{1,6} = 0.02, P = 0.88). However, the % cover of most other species differed between lawns and unmowed plots (P < 0.05) with many species abundant in one of these habitat types and rare or absent in the other. Along with *P. pratensis*, unmowed plots were dominated by *D. glomerata* (29% cover ± 4.4), a species that covered significantly less area in lawns (7.6 ± 2) (F_{1,6} = 19.3, P = 0.005). Many more species were common in lawns (> 10% mean cover) but not in unmowed habitats (0-1% cover) including *Trifolium repens*, *Taraxacum officinale*, and *Plantago lanceolata*. In contrast, species such as *Cirsium* sp., *Asclepias syrica* and *Rosa multiflora* were found only in unmowed plots but as only one to several individuals per plot. Other species encountered in both habitats but in low abundances included *Lolium multiflorum*, *Daucus carota*, *Oxalis* sp. and *Prunella vulgaris*.

Total (living + dead) and dead (i.e., litter) aboveground standing crop (i.e., plant biomass) were significantly greater (often by a factor of two or more) in unmowed than lawn habitats on all
Differences in living standing crop between the habitats depended on date; no differences were detected for May 2004 and 2005 and July 2004. Lawns had significantly greater living standing crop than unmowed plots for April and October 2005; unmowed was significantly greater than lawn for June-September 2005 (Appendix F). Mean (± SE) biomass of lawn clippings per plot collected at each mowing event ranged from 40 (± 6) to 123 (± 9) g m⁻² with mean (± SE) annual totals of 668 (± 37) and 653 (± 34) g m⁻² for 2004 and 2005, respectively.

Annual ANPP was calculated for lawn and unmowed habitats using a variety of published equations (Falk 1980, Scurlock et al. 2002) with necessary modifications to account for grass clippings and early season growth in the unmowed habitats (Appendix C). In general, these very different calculations yielded similar mean ANPP values for both habitats (Appendix G). After critical assessment of the strengths and weaknesses of each method, it was concluded that modifications to method 6 of Scurlock et al. (2002) provided the most reasonable, and hopefully accurate, estimates of ANPP, and therefore the focus here is on these results. Mean (± SE) ANPP (g biomass m⁻² year⁻¹, Fig. 3-8B shaded bars) was similar among both years in lawns (811 ± 43 in 2004, 874 ± 33 in 2005) and unmowed in 2005 (852 ± 120) but unmowed ANPP in 2004 (433 ± 100) was lower, although not significantly (F₁,₅ = 0.12, P = 0.74). However, this lower value resulted in significant effects of year (F₁,₅ = 15, P = 0.01) and habitat x year interaction (F₁,₅ = 9.8, P = 0.03) in the GLM. Using the C to N ratios of plant biomass (below), ANPP was also calculated as g C m⁻² year⁻¹ which showed the same patterns as those above (Fig. 3-6B open bars).

Mean (± SE) C:N of living and dead plant biomass were significantly higher in unmowed habitats (25 ± 0.6 and 29 ± 2.1, respectively) than lawns (17 ± 0.6 and 18 ± 1.2; Fig. 7C). These values were similar for biomass collected at different dates. Bark mulch C:N (average of May and September samples, which did not differ) was 123 (± 6.9) which is significantly greater than both the C:N of lawn and unmowed dead biomass.

Discussion

Novel concepts and frameworks have been, and remain, needed for urban ecology research because those developed for non-urbanized ecosystems may not always be adaptable to urbanized ones (Grimm et al. 2000, Kaye et al. 2006). Although largely undeveloped and underappreciated in ecology, the fundamental concept of habitat structure provides a multivariate framework (Fig. 1-1) to guide comparisons of heterogeneous urban habitat types (Bell et al. 1991). This is particularly true since most urban landscape management activities are specifically targeted at maintaining
Figure 3-8. (A) Mean (+ SE) oven dry (55°C) weight of dead (open symbols) and total (shaded symbols) standing aboveground plant biomass m⁻² in lawn (diamonds) and unmowed (squares) habitats. For each pair of data, means differ significantly on all dates. Living biomass values are not shown for visual clarity but differed significantly on 7 dates (Sept. 2004, April, June-Oct. 2005). (B) Mean (+ SE) annual aboveground net primary productivity in lawns and unmowed plots in 2004 and 2005. Shaded bars are g dry biomass m⁻² year⁻¹ (left axis) and open bars are g C m⁻² year⁻¹ (right axis). (C) Mean (+ SE) C to N ratios of living and dead biomass in lawn and unmowed plots and bark mulch. N=4 for all data except May lawn living standing crop (N=3). C:N data for lawn and unmowed habitats are means of two sampling dates each in 2004 and 2005. C:N data for bark mulch are from fresh mulch applied to plots in April 2005. Means with different letters are significantly different (P < 0.05) with Tukey's post hoc comparisons.
desired habitat structure, e.g., lawn mowing keeps vegetation short and of even height. Thus, results are discussed using habitat structure as an organizing concept.

Significant differences between at least two of the habitat types, and often more than two, were observed for almost all variables examined in this study. Thus, each of the four habitat types was associated with a distinctive ecological profile (or set of characteristics) as summarized in Table 3-2. This supports the hypothesis that human management of habitat structure influences the ecological characteristics of a location. Below, the direct and indirect effects of the four habitat structures examined (Appendix B) on microclimates, soil properties and carbon dynamics are discussed with a focus on comparing results to those of similar studies about urban habitats.

**Microclimates**

Most studies of temperature patterns in urbanized ecosystems have been conducted at larger spatial scales than that of this study. The influence of urbanization on broad-scale (km) climatic and weather patterns has long been recognized as the urban heat island effect, a phenomenon in which densely urbanized environments have warmer air temperatures as compared to surrounding

| Table 3-2. Comparative summary of above and belowground habitat characteristics and diagram of soil-litter-plant profiles. |
|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| **Aboveground variables**        | **Unmowed vegetation**          | **Lawn**                        | **Bark Mulch**                  | **Gravel Mulch**                |
| Daytime Surface Temperatures     | Cooler                          | Intermediate                    | Intermediate to warmer          | Warmest                         |
| Litter Layer (OM)               |                                 |                                 |                                 |                                 |
| Quantity                        | High                            | Low                             | High                            | None                            |
| C:N                             | Intermediate                    | Lowest                          | Highest                          | N/A                             |
| Litter Decomposition Rate       | Intermediate                    | Fast                            | Slow                            | N/A                             |
| CO₂ Flux                        | Intermediate to Low             | Highest                          | Intermediate to High            | Low                             |
| Net Primary Productivity        | High                            | High                            | Low to none                      | Low to none                      |
| Total standing Crop             | High                            | Low                             | Intermediate                    | None                            |

| **Belowground variables**       | **Unmowed vegetation**          | **Lawn**                        | **Bark Mulch**                  | **Gravel Mulch**                |
| Soil Temperature                | Cooler                          | Intermediate                    | Intermediate                    | Warmest                         |
| Soil water content              | Low, high variability           | Low, high variability           | High, low variability           | Intermedi ate, low variability  |
| Soil Organic Matter             | Intermediate                    | Intermediate                    | Higher                          | Lowest                          |
| Microbial Biomass               | High                            | High                            | High                            | Low                             |
| Root Density                    | Intermediate                    | High                            | None                            | None                            |
| Earthworm Abundance             | Intermediate                    | Intermediate to Low             | Highest                          | Lowest                          |
| Bulk Density                    | Intermediate                    | Intermediate                    | Lower                            | Higher                          |
| Aggregate Stability             | High                            | High                            | High                            | Lower                            |
non-urban locations (Goward 1981). Urban heat islands arise from the aggregation of localized air temperatures within urbanized ecosystems which are in turn influenced by habitat structure (Goward 1981, Mueller and Day 2005). Different habitat structures exhibit various thermal properties (i.e., absorption, storage and re-radiation of solar energy) and therefore create different urban microclimates which contribute differently to the urban heat island effect (see Goward 1981, Geiger et al. 2004 and Mueller and Day 2005 for detailed discussions about thermal properties). For example, Stabler et al. (2005) observed in Phoenix, AZ that local air temperatures within land use types (i.e., residential, agricultural, industrial) were determined by the presence and relative densities of vegetation and abiotic structures (e.g., pavement, buildings). Few studies have examined ground-level microclimate patterns associated with urban habitat structures, especially in temperate biomes of the northeastern U.S. Nonetheless, both above- and belowground microclimate patterns are important considerations in urbanized, as well as non-urbanized, ecosystems because they affect variables such as water and nutrient availability, plant growth and local community structure (e.g., Mueller and Day 2005).

Each of the four habitat types in this study had a different surface and soil temperature profile with many underlying temporal patterns (both obvious and subtle, not all of which can be discussed here; Figs. 3-1, 3-2, 3-3 Appendices D, E). However, the greatest differences in soil and surface temperatures among the four habitat types were observed during the daytime. The intuitive importance of solar radiation as a driver of these patterns is confirmed by: 1) predictable within-day temperature fluctuations in all the habitats that included warmer and significantly different daytime (11-18:00hrs) temperatures among the habitats and cooling and convergence of temperatures overnight (0-6:00) (Fig. 1); 2) less predictable between-day variation in range of temperature fluctuations and daytime maxima which can differ among consecutive days by as much as ~10-15°C (Fig. 3-1); and 3) hour-to-hour variability (up to ±10°C changes) of temperatures within a habitat (Appendix D; Byrne et al. unpublished data). These latter two points reflect the influence of rapid changes in solar energy inputs due to changing weather conditions (e.g., cloud cover) on temporal patterns of microclimate. Such information has implications for field measurements (e.g., CO₂ flux, animal movements,) that are affected by microclimates. In addition, fine-resolution (i.e., day versus night) temperature heterogeneity provides an interesting research topic in itself that may yield important—and perhaps different—insights than examination of data averaged across time.

The temperature data also provide insights about how solar radiation interacts with properties of habitat structure (i.e., those that affect thermal behavior: color, composition, density
and vertical arrangement of matter) to create fine-scale spatial differences in surface and soil temperatures. Mean daytime surface temperatures in mulched plots were generally higher (by up to 15°C) throughout this study than in vegetated plots reflecting the greater capacity of dark-colored bark and mineral gravel mulches to absorb solar radiation (and re-radiate it as “micro-urban heat islands”) as compared to herbaceous detritus (Figs. 1A, C; 2A; Montague and Kjelgren 2004). In addition, dissipation of heat through evapotranspiration by plants probably contributed to the relatively cooler daytime temperatures in vegetated plots. Taller vegetation in unmowed plots shaded the ground and kept it slightly (but not always significantly) cooler on average than lawns (Fig. 3-2A).

Soil temperatures can largely be expected to follow surface temperatures within the constraints of physiochemical factors of the surface matter and soil related to thermal balance and flux (Geiger et al. 2004). Thus, although soil temperatures at 5 cm depths were cooler than surface temperatures during the daytime, they exhibited broadly similar differences among the habitat types in fluctuation patterns. Gravel-covered soils were, for the most part, significantly warmer than all the other habitat types’ soils throughout the study, reflecting the ability of this habitat structure (which is comparable in composition to pavement) to transfer heat energy into the soil (Figs. 3-1B, D; 3-2B; Celestian and Martin 2004, Montague and Kjelgren 2004). Although gravel and bark plots often had similar surface temperatures, bark-covered soils did not, on average, attain the same daytime maximum temperatures as gravel-covered soils. The most probable explanation for this difference is that bark-covered soils had significantly greater water contents (Fig. 3-4) and would therefore have required additional energy inputs to reach the same temperatures as gravel-covered soils (an indirect effect of habitat structure). However, the heat flux from bark into soils can be greater than or similar to that of vegetated habitats, depending on the day (Fig. 3-1D), season (Fig. 3-2B) and water content of the vegetated soils (which was highly variable; Fig. 3-4). Unmowed soil temperatures were expected to be lower than those in lawns due to the shading property of taller vegetation (especially in mid-summer and early fall). This pattern was seen on three of the July 2004 dates examined (Fig. 3-1D) and the average monthly daytime temperatures in June through September 2004 (Fig. 3-2B). It is not fully clear as to why soil temperatures in unmowed, lawn and bark plots did not differ from each other as greatly in 2005 as they did in 2004. Two possible explanations include less rainfall in 2005 (Fig. 3-4) and, less likely, a reduction in reliability of data loggers that year (some logged inaccurate daytime temperatures on some days or failed completely). Despite the temporal variability, it is clear that the ranges of soil and surface temperatures in each of
the habitat types were affected by interactions among sunlight, habitat structure and other properties (e.g., soil water content) that are indirectly mediated by habitat structure. Almost identical temperature patterns (but with warmer absolute temperatures) have been observed in the arid, southwestern U.S. for temporal fluctuations in, and differences among, soil (Green and Oleksyszyn 2002. Celestian and Martin 2004) and surface (Zajicek and Heilman 1991, Montague et al. 2000, Montague and Kjelgren 2004, Mueller and Day 2005) temperatures in bark and gravel mulches, lawns and paved areas.

The extensive temperature data set allowed examination of relationships among surface, soil and air temperatures averaged across three temporal scales (day, week and month) using both daily (0-23:30hrs) and daytime (11-17:00) means (Fig. 3-3, Appendix E; all results not shown). The key objectives of these analyses were to examine the ability of 1) air to predict surface and soil temperatures, 2) surface to predict soil temperatures and 3) the variation in these relationships among data averaged across different time spans. Four key points are discussed about these analyses with a focus on predictive power ($R^2$ values) rather than significance of relationships ($P$ values) because most regressions were highly significant due to 1) the large number of data points or 2) co-varying seasonal patterns of air, surface and soil temperatures.

First, at the scale of days, daytime air temperature was a poorer predictor of daytime surface temperatures (range in $R^2$: 0.37 to 0.6; Fig 3-3A) for all the habitat types as compared to daily mean temperatures (all $R^2 > 0.7$) because daily means masked day-night temperature fluctuations. (This is also reflected by the differences between air and surface temperatures at any given time; Fig. 3-1, Appendix D). Second, at the scale of days, daytime soil temperatures in lawn and bark plots had much stronger relationships with air ($R^2$= 0.75 and 0.67, respectively; Fig. 3-4C) than surface ($R^2$= 0.57 and 0.46; Fig. 3-4D) temperatures, while $R^2$ values for these comparisons with unmowed and gravel data were more similar to each other and higher. This is likely a consequence of the thermal properties of air and soil which absorb heat more slowly than soil surface materials (see above and Geiger et al. 2004). Third, the predictive power of air for surface and surface for soil temperatures generally increased as data were averaged across weeks and months, although the degree of increases varied among the habitat types (see Appendix E for $R^2$ values). However, even at these longer temporal scales, the mean daytime surface temperatures of the bark still explained little of the variation in bark soil temperatures ($R^2<0.4$; Appendix E). Fourth, significant differences among the mean habitat temperatures were less apparent with data averaged across longer time spans (due, in part, to fewer data points in those data sets), as reflected by the fewer significant differences.
among the habitats found in those analyses (Fig. 3-3, Appendix E).

Taken together, the results and discussion about soil and surface temperatures in different urban habitats and their relationships with air temperature suggest two important insights about the measurement, reporting and interpretation of microclimate data. First, air, surface and soil temperatures may not be good predictors of each other in certain habitat types. Thus, in any study where microclimates are important variables, local surface and soil temperatures should be measured concurrently in situ rather than using air temperatures from weather stations to approximate them (as is often done). Second, detailed temporal (preferably hourly or at least once each at midday and late night) measurements of local surface and soil temperatures will be more informative and useful for interpreting other data than temperatures collected or averaged at daily, weekly or monthly scales over which important patterns may disappear. These considerations are likely to be especially important for the study of urban ecosystems because of their extreme fine-scale heterogeneity in habitat structure (Grimm et al. 2000). Given that urban habitat types may show unique temperature profiles, detailed urban microclimate measurements are needed to better understand the effects of fine-scale microclimate patterns on communities, biogeochemical cycles and other variables within urban ecosystems (Shochat et al. 2006, Kaye et al. 2006).

Soil properties

The importance of soils in urban ecosystems has long been recognized, especially as related to horticulture (e.g., Craul 1985). However, few studies have been conducted about the structure, chemistry and ecology of soils impacted by urbanization (e.g., Pouyat et al. 2002, Scharenbroch et al. 2005). This study appears to be the first to report results about the short-term effects of creating urban habitat types on soil variables from a field experiment. Even though soils were not disturbed directly by experimental habitat manipulations, belowground habitat structure was affected by changes in aboveground habitat structure. Results suggest that the 1) density and 2) composition of surface materials and 3) presence or absence of vegetation in each habitat type interact to affect many soil properties. In addition, the fine texture (clay loam) of soils in the experimental field likely influenced the results (especially high SOM content) even though, for brevity, its relationship to all variables is not discussed.

In urbanized landscapes, mulches are used for aesthetic and functional reasons, one of which is to reduce evaporative water losses from soil (Skroch et al. 1992). Not surprisingly, mulch-covered soils were consistently wetter throughout this study than vegetated soils, as was most
apparent during the drought conditions of 2005 (Fig. 3-4). This pattern has two simple but co-varying explanations: 1) greater soil water retention in mulch habitats due to their thicker and denser layers of surface material; 2) greater soil water removal in vegetated plots via evapotranspiration (which interacted with rainfall events to produce higher fluctuations in soil water content in vegetated plots). Bark mulch was more effective at retaining soil moisture than gravel (possibly due to greater heat flux to soil by gravel), an important insight for guiding landscape management decisions. Because plants were continuously removed from mulched plots in our study, these plots did not exactly mimic real-world mulched gardens which might contain horticultural plants that remove soil water. These observations, combined with Scharenbroch et al.’s (2005) report of higher soil water contents in recently mulched landscapes, supports the conclusion that habitat structure characteristics associated with ground cover materials on the soil and vegetation will be important local-scale drivers of soil water content in urbanized landscapes.

The chemical composition of the four habitat structures differed, especially in their quantity and quality (C:N) of carbon inputs to the soil. The limestone gravel mulch was unique due to its high inorganic (CaCO₃) and low (i.e., zero) organic C content. These resulted in, respectively, significantly higher soil pH (as expected) and lower LOI OM (in 2005), total soil C, SMB-C and ergosterol content as compared to the other habitat types’ soils (Table 3-1). Reductions of soil OM and C, and consequently microbial biomass, in gravel-covered soils were not surprising considering this habitat’s higher soil temperatures (Fig. 3-2) and water content (Fig. 3-4), variables which stimulate microbial mineralization of C (Raich and Tufekcioglu 2000). These SOM reductions, in combination with the absence of plant roots and earthworms (see below), probably contributed to the significantly lower % WSA in gravel soils due to the loss of organic materials that promote soil aggregation (Jastrow et al. 1998). As aggregate stability decreased, it is plausible that C within aggregates was exposed to microbial mineralization which contributed to the temporal decline in SOM and C in the gravel soils (Table 3-1; data from 2003 not shown) (Bossuyt et al. 2001). That soil C pools under gravel showed significant changes within 2 years after habitat structure transformations suggests that land uses and management practices that reduce C inputs to the soil but do not disturb them directly (e.g., paving, abiotic mulching) may reduce the capacity of some soils in urbanized ecosystems to store C.

The bark mulch plots received high inputs of low quality (i.e., high C:N) OM which could be expected to promote larger soil OM and C pools as compared to the vegetated plots. However, C-related soil variables remained generally similar among the bark, unmowed and lawn habitat
types throughout this study (although bark soils did have slightly and significantly higher total soil C in 2005 as compared to the unmowed soils; Table 3-1). Several characteristics of the bark’s habitat structure profile (Table 3-2) may have had contrasting effects on soil OM and C. Although warmer, wetter soil conditions should have promoted higher SMB-C and ergosterol content, microbial growth may have been limited by N due to the high C:N (125) of the bark (Bossuyt et al. 2001). This is supported by N measurements in these plots that showed very low and sometimes negative N mineralization rates (i.e., microbial uptake of N) in the bark-covered soils (see Chapter 4). Although SMB-C and ergosterol did not increase under bark mulch, microbial activity, and thus, N turnover could have increased C mineralization rates (i.e., CO₂ production) which prevented buildup of soil C (see below). High abundances of earthworms under bark mulch (Fig. 3-5) could also have been an important factor that affected the C pools under bark mulch although their relative influence is not clear. Previous studies have shown that earthworms can contribute to both the buildup and loss of organic matter in soils because their casts both promote the formation of stable aggregates that protect C from decomposition (Pulleman et al. 2005) and provide hotspots (i.e., fragmented OM in casts) for microbial activity that mineralizes soil C (Burtelow et al. 1998, Borken et al. 2000). Additionally, the large amount of fresh OM inputs to bark mulched plots in April 2005 may have created a “priming effect” that stimulated microbial activity and higher decomposition rates (e.g., Fontaine et al. 2004) as supported by the decrease in LOI-OM observed in 2005 after new mulch was applied. Although the bark itself has a high C:N, dissolved organic molecules with lower C:N could have leached into the soil from new mulch to provide labile C sources that promoted microbial activity (Lajtha et al. 2005). All these possibilities may have operated concurrently to result in no year-to-year net change in soil OM and C in bark-covered soils. Although it is possible that longer-term increases in soil OM and C under bark could occur (as suggested by the slight increase in total C in bark soils by the end of this study), another study found that SOM did not accumulate in soils that had been covered by bark mulch for 15 years (Scharenbroch et al. 2005). In contrast to SOM, soil pH did change under the bark as compared to vegetated soils as it reached a mean value (7.2) similar to that of the bark’s pH (~7.45). This change can probably be attributed to the incorporation of bark-derived OM into the soil via leaching of dissolved compounds or earthworm activity.

No differences were found for soil pH, %WSA and OM-related variables between soils from lawn and unmowed plots. However, total soil C was significantly greater by about a third in lawn soils three years after the start of regular mowing suggesting that this management practice alters
belowground C pools and fluxes (see below). Several studies of lawn C dynamics suggest that turfgrass habitats can rapidly accumulate belowground C (e.g., Qian and Follett 2002, Milesi et al. 2005) although these studies compared turfgrass habitats of different ages and management regimes rather than lawns and other habitat types. In studies similar to this one, soil C pools were greater under lawns than unmanaged grasslands (Dickenson and Polwart 1982, Byrne and Bruns 2004, Kaye et al. 2005). Thus, available data suggest that lawn mowing stimulates belowground C storage as compared to unmowed habitats although the exact mechanisms and long-term dynamics of this are unknown and warrant additional research.

Several studies have shown that earthworms can be more abundant in urban than rural forests (Steinberg et al. 1997, Szlavecz et al. 2006). However, no other studies have reported comparisons of earthworm populations among different urban habitat types. Results from this study provide several insights about the importance of three soil variables affected by habitat structure—OM, moisture and temperature—as interactive drivers of earthworm abundances (Curry 2004).

First, reduced OM availability can limit earthworm numbers, as reflected by their consistently low abundances in gravel plots throughout this study (Fig. 3-5). Second, even if OM is available, reduced soil moisture can cause declines in earthworm population sizes as shown by the correlation between lower soil water content due to drought (Fig. 3-4) and decreases in earthworm numbers in the vegetated habitats in 2005 (Fig. 5). The importance of soil water to earthworms is also shown by their consistently higher numbers, especially through 2005, in the wet soils under bark mulch.

Third, as suggested by Curry (2004), soil temperatures of 25-30°C may be the maximum tolerable range for temperate earthworms. This is supported by the observation that the highest mean monthly soil temperatures seen during this study in lawns (28°C) and gravel (31°C) plots (Fig. 3-2) occurred at the same time as the lowest densities of earthworms in these habitat types (almost zero; Fig. 3-5). On these dates, however, earthworms were significantly more abundant and daytime soil temperatures were on average cooler in unmowed habitats than lawns. As compared to 2004 when earthworms abundances were similar between unmowed and lawn plots, the significant differences between these habitats in 2005 suggest that the higher average soil temperatures in lawns did not affect earthworms until soil water was also reduced. In contrast, high soil water content and warmer temperatures (and possibly OM) may have interacted to increases in earthworm numbers in bark plots. The comparative habitat approach utilized in this study helped reveal that several variables associated with habitat structure—rather than any factor acting alone—can interact to influence the temporal patterns of earthworm abundances within a habitat type. It is unknown from this study
how earthworm activities in deeper soil layers (i.e., below 25cm) may have been affected by the habitat types. It is possible that earthworms moved deeper in the vegetated plots during drier soil conditions and were not detected by the sampling method used.

It is clear that the characteristics of a given habitat structure influence earthworm abundances. In turn, earthworms can influence habitat structure, especially that of the soil. For example, Rossi (2003) showed that earthworm densities were highly correlated to BD but that different species are associated with lower (compacting species) or higher (decompacting species) BD depending on the types of casts they produced. Thus, in this study, the significantly lower BD in bark mulch plots can certainly be attributed to the high density of decompacting earthworms in them (Table 1; Fig. 5). In contrast, a recent study of earthworms in urban and rural forests found that bulk density was positively correlated with earthworm abundance (Szlavecz et al. 2006, K. Szlavecz, personal communication). Given that many factors besides earthworms can affect BD at a location (e.g., soil texture, compaction, C content), it is likely that urban landscapes will be associated with a range of soil BD values that may or may not be correlated with the structure of earthworm communities (Scharenbroch et al. 2005). Thus, as shown by the discussion above, the rigorous study of soils in urban habitat typess can benefit from the multivariate perspective emphasized by the habitat structure (Fig. 1-1) and ecological profile (Table 3-2) frameworks.

*Carbon dynamics*

Few studies have been conducted on the C dynamics in urbanized ecosystems, especially ones comparing different urban habitat types. Three studies reporting field measurements of CO$_2$ flux from lawns found that they were several orders of magnitude greater than fluxes from native desert (Green and Oleksyszyn 2002, Koerner and Klopatek 2002) and shrubgrass steppe habitats (Kaye et al. 2005). In comparing lawns and bark mulched soils of different ages, Scharenbroch et al. (2005) found in laboratory measurements that soils recently covered with bark mulch tended to have higher C mineralization rates although there were no clear differences between bark-covered and lawn soils. In this study, CO$_2$ flux rates in vegetated plots were lower than those reported in other studies probably because of drought conditions throughout 2005 that resulted in low soil water contents which may have limited microbial activity (Raich and Tufekcioglu 2000, Green and Oleksyszyn 2002). Nonetheless, CO$_2$ flux tended to be higher (significantly so on three dates) from lawns than unmowed habitats in this study (Fig. 3-6). Two factors might have produced this pattern, either separately or in concert: 1) higher root density in lawns or 2) large inputs of high quality (i.e.,
low C:N) OM from cut vegetation, both of which would have stimulated microbial activity and greater CO₂ production (Landi et al. 2006, Shi et al. 2006). Support for these hypotheses are provided by studies that have shown higher belowground plant productivity in managed than unmanaged grasslands (Dickenson and Polwart 1982, Seastadt 1985) and observations that lawns had significantly higher soil C content (Table 3-1) and that lawn clippings decomposed quickly (L. Byrne, personal observation; see also Shi et al. 2006) Thus, the management of aboveground habitat structure by mowing altered belowground C dynamics in this study.

In contrast to vegetated plots, mulched plots remained wet throughout 2005 and, with warmer soil temperatures, provided favorable conditions for soil microbes. However, microbial activity was probably limited in gravel and bark plots by low C and N availability, respectively, both of which influence soil CO₂ flux (Raich and Tufekcioglu 2000). Gravel soils had the lowest average CO₂ flux rates (Fig. 3-6) certainly due to the absence of OM inputs and reductions in the soil C pool (Table 3-1). However, CO₂ production and microbial biomass were still detected in the gravel plots suggesting that some soil microbes remained active due to favorable soil conditions and utilization of in situ C pools that likely became available as soil aggregates disintegrated (see above). C was not limiting in bark mulch plots due to the high quantity of OM inputs. However, higher rates of CO₂ production were probably prevented by low N availability (Landi et al. 2006) in bark plots as indicated by 1) the high C:N (123) of bark mulch, 2) similar SMB-C between bark and vegetated plots (Table 1) and 3) low and negative N mineralization rates in the bark-covered soils (see Fig. 4-2, p. 73). Interestingly, CO₂ flux from bark soils exhibited a distinct temporal pattern with higher rates in late June and July (Fig. 3-6). A plausible explanation for this is that microbial activity was stimulated by a flush of dissolved, lower C:N organic matter into the soil as dense fungal populations began to decompose the bark aboveground (L. Byrne, personal observation). Additional longer-term studies are needed to evaluate the unknown relationships between above- and belowground C dynamics of mulch habitat types in urbanized ecosystems.

Studies of leaf litter decomposition in urban forests have shown that urbanization affects many factors that control leaf litter mass loss including microclimates (e.g., Pouyat and Carreiro 2003, Pavao-Zuckerman and Coleman 2005). However, the decomposition dynamics of surface litter in other urban habitat types have not been previously examined. Results from the litterbag experiment (Fig. 3-7) showed that mass loss rates of surface litter differed among various urban habitat structures and, for oak leaves, were greater in mulched habitats and similar to or lower in vegetated habitats than rated measured in urban forests (Pouyat and Carreiro 2003, Pavao-
Differences in decomposition rates among the habitat types were probably driven by the interactive effects of each habitat’s 1) microclimate, 2) surface litter density and 3) biota. Microclimate has been shown to be an important driver of decomposition in other studies with higher temperatures and humidity generally promoting faster decay rates (Aerts 1997, Pouyat and Carreiro 2002). In this study, higher surface temperatures in bark and gravel plots (Figs. 3-1, 3-2) were associated with faster decomposition rates over, but not after, one month for grass leaves and after four months for oak leaves. However, higher temperatures also created drier surface conditions in the mulch plots which may have limited microbial activity in the litterbags. Alternatively therefore, decomposition in mulched plots may have been promoted by higher colonization and consumption of litter by invertebrates (Vossbrink et al. 1979) due to the lower densities of palatable surface OM in mulch relative to vegetated plots (i.e., the litterbags were microhabitat islands). Similarly, decomposition of grass litter in lawns (Fig. 3-7A) may have been slower than in the other habitats because lawns contained a higher density of rapidly decomposing grass litter; as such, invertebrates may have been less likely to remain in litterbags which were surrounded by preferable food sources. However, this suggestion is not supported by observations that numbers of detritivorous arthropod (e.g., collembolans) were often high in the lawns (see Fig. 5-4, p. 108) which could have been expected to contribute to rapid colonization and decomposition of the oak and grass litterbags. Clearly, future experiments are needed to tease apart the direct and indirect effects of urban habitat structures on the decomposition rates of surface litter.

A significant proportion of the carbon cycle in urban ecosystems is associated with lawns, which can comprise upwards of 50% of urbanized landscapes’ surface area (Robbins et al. 2001, Milesi et al. 2005). Most research about lawns has compared the effects of different management regimes on their ecology (e.g., with or without chemical inputs; Cockfield and Potter 1985, Milesi et al. 2005) whereas few have compared the ecological characteristics of lawns to those of other habitat types (e.g., Pouyat et al. 2002, Byrne and Bruns 2004, Kaye et al. 2005). Such comparisons are needed to understand the broader ecological consequences of urbanization and lawn management (e.g., are lawns sources or sinks for C?). In this study, the effect of mowing on vegetation and its associated C dynamics was assessed by comparing lawn with unmowed old field plots.

Immediately after mowing was initiated in the experimental field, the plant communities in lawns began to change as compared to the unmowed plots. A number of common lawn “weeds” became abundant in the mowed plots that were absent or uncommon in the unmowed plots.
including white clover (*Trifolium repens*), dandelion (*Taraxacum officinale*), and plantain (*Plantago* spp). In addition, *D. glomerata*, the dominant grass in unmowed plots, became less abundant in lawns during the course of the study. Three factors probably contributed to these shifts in the plant community: reductions in the 1) surface detritus and 2) canopy cover in lawns which allowed plants that did not grow well in unmowed plots to colonize lawns; 3) increases and declines in species that can and cannot persist, respectively, with repeated mowing disturbances. Future studies are needed to examine the relative contributions of these three factors. Studies of lawns in England (Smith et al. 2006), New Zealand (Roxburgh and Wilson 2000), and the U.S. (California, Maryland and Pennsylvania; Falk 1976, 1980, Byrne and Bruns 2004) reported the presence of many of the same species seen in our lawns. This suggests that a suite of species well adapted to the lawn environment may contribute to the biotic homogenization of urban flora among distant geographic locations (McKinney 2006).

Plant species are known to vary widely in their growth forms and effects on ecosystem processes (Eviner 2005). In this study, mowing facilitated the dense colonization of lawns by highly productive, low- or horizontally-growing plants. This indirect effect of mowing may have caused the ANPP in lawns to be as high as or higher than that of unmowed habitats in which productivity was primarily driven by vertical growth of grasses (Fig. 3-8B). Falk (1976, 1980) was the first to note that lawns are highly productive ecosystems and suggested 1000-1700 g biomass m⁻² year⁻¹ as a probable range for lawn ANPP in temperate biomes, a higher range than that for ANPP in the native grasslands of the central U.S. (150-700; Sala et al. 1988). Recent studies support this conclusion: Kaye et al. (2005) and Gloubiewski (2006) found that high-maintenance lawns in Colorado had higher ANPP than nearby native grasslands. The estimated mean ANPP for low-maintenance lawns (811-874 g biomass m⁻² year⁻¹) in this study is more than double those suggested by a recent modeling study (Milesi et al. 2005) but within the range of values reported for mowed pastures in Pennsylvania (550-1000; Tracy and Sanderson 2004). The 2005 estimate for mean ANPP in unmowed plots (852 g biomass m⁻² year⁻¹) was also within this range and very similar to the ANPP of lawns for both 2004 and 2005. The much lower estimate of ANPP in unmowed plots in 2004 was likely an artifact of low sampling effort (3 dates). Thus, in agreement with Dickerman et al. (1986), these results suggest that accurate estimation of ANPP is influenced by sampling frequency. This is particularly true when using calculations that depend on summing incremental increases of plant biomass between sampling dates (method 6 in Appendix C). Based on the data of the current study (Appendix G), and in agreement with Scurlock et al. (2002), it is suggested that
using these types of calculations provide more accurate estimates of unmowed ANPP than other methods (i.e., maximum standing biomass) and that plant biomass samples should be collected at least once a month to detect mid-season increases in plant growth (Fig. 3-8A). Because estimation of ANPP for lawns is influenced more by the inclusion of grass clippings than calculations used (Appendices C, G), clippings should be collected at all mowing events in future studies as suggested by Falk (1976). In addition, because lawn ANPP is highly influenced by management inputs such as fertilizer and irrigation (Milesi et al. 2005, Golubiewski 2006), it is also critical that future studies document all management inputs associated with studied lawns. This will help ensure that comparisons among lawns in different biomes and under different management regimes are straightforward, reliable and informative.

Although lawns were just as productive as unmowed plots during this study, they contained 1/4 to 1/6 of the dead plant biomass present in unmowed habitats (Fig. 3-8A), a pattern also reported by Dickenson and Polwart (1982). Similarly, Falk (1976) noted that the living biomass was greater than detritus in lawns. However, these authors did not discuss the potential mechanisms underlying these patterns which seem unexpected given that clipped OM enters a lawn’s detritus pool at every mowing. Differences in the amount of dead biomass between mowed and unmowed habitats likely resulted from differences in the structure and composition of the detritus entering each habitat. Detritus in lawns was highly fragmented due to mowing (i.e., it had high-surface area) and had a low C:N (Fig. 8C), both of which promoted fast decomposition and the rapid disappearance of detritus in lawns (Vossbrink et al. 1979, Pouyat and Carreiro 2003, Shi et al. 2006). In contrast, detritus in unmowed habitats was composed of intact stems and leaves (i.e., lower surface area) with higher C:N, certainly due to the presence of structural organic molecules (e.g., lignin). These properties probably slowed decomposition rates of unmowed plant detritus and thus allowed accumulation of a thicker litter layer in the unmowed habitats. Although simplistic, these interpretations highlight the need to explore the different mechanisms of C cycling among lawns and other habitat types so that we may better assess their basic ecology and contributions to regional and global C cycles (e.g., Kaye et al. 2005). For example, rapid mineralization of lawn clippings may have contributed to the higher rates of CO₂ production observed in this habitat (Fig. 3-6) through continuous inputs of OM into the soil that stimulated microbial activity (Shi et al. 2006). It can be hypothesized that lawns have faster rates of C cycling than other ecosystems because the direct (detritus fragmentation) and indirect effects (creation of unique plant communities) of mowing increase ANPP and decomposition rates of lawn clippings. However, this
The hypothesis is preliminary given that so few studies have been completed about C dynamics in lawns, especially using a comparative ecosystem approach (e.g., Kaye et al. 2005). In particular, critical components of the belowground C cycle remain almost fully unexplored in lawns, although several recent studies indicate that high maintenance lawns can rapidly accumulate soil C (Qian and Follett 2002, Milesi et al. 2005). In contrast, results presented here show that aboveground plant biomass can be greater in habitats that are not mowed. Thus, comprehensive, comparative studies among different urban and non-urban habitat types are critically needed to develop deeper understanding about the consequences of creating and managing lawns for C pools and flux rates.

Conclusions

Two of the central objectives of urban ecology are to 1) investigate how sociocultural and ecological variables interact to generate the spatial heterogeneity in urbanized ecosystems and 2) examine how relationships among ecological and sociocultural patterns and processes vary across spatial scales (Grimm et al. 2000, Band et al. 2005, Pouyat et al., in press). Although consideration of the sociocultural variables that drive human activities is outside the scope of this chapter, data clearly show that human activities generate ecological heterogeneity through creation and management of habitat structures that have distinctive ecological profiles (Table 3-2). As such, habitat structure links the sociocultural causes and ecological consequences of human landscape management activities (Fig. 1-1). Regarding issues of scale, Pouyat et al. (in press) suggested that two approaches would facilitate the study of urbanized ecosystems: 1) comparing the ecological characteristics of similar habitat types among different locations (i.e., within-habitat heterogeneity) and 2) examining how the creation of different habitat types within a given area influences the net ecological changes associated with urbanized as compared to other ecosystems (i.e., using input-output budgets; Kaye et al. 2006). To date, few studies have been conducted using either of these approaches. Thus, this study has generated new data about differences among the basic ecology of urban habitat types commonly created in residential landscapes (lawns, bark and gravel mulches). As such, it provides a needed springboard for future *in situ* observational and experimental research about the ecology of urban habitat structures.

As hypothesized, examined variables differed significantly among all the habitat types as a result of multiple direct and indirect effects of habitat structure properties (e.g., color, C and N content, presence or absence of vegetation) which were dictated by human management inputs (i.e., mowing or mulching). In particular, great variability was seen in surface and soil temperatures, soil
moisture and structure, C pools and fluxes and earthworm abundances (Table 3-2). For example, creation of dense layers of surface material that readily absorbed solar radiation created warmer and wetter conditions in mulched plots; however, the influence of mulches on other soil properties depended on their chemical composition (i.e., abiotic or biotic). Mowing created a community of low growing plants and large inputs of fragmented high quality (i.e., low C:N) OM that decomposed quickly. In contrast, unmowed habitats had the most structurally complex habitat structure due to the vertical distribution of OM and accumulation of a thick, low density layer of intact detritus. Although simple, these basic descriptions of each habitat type facilitate examination of how habitat structure—the arrangement and composition of matter at a location—influences a wide variety of ecological patterns and processes (Fig. 1-1). Essentially, the concept of habitat structure forces one to thoroughly describe the fundamental template of physical material at a location rather than categorize it as a generic type of land cover or land use, each of which may contain many kinds of habitat structure. As such—and as shown by this study—I conclude that use of habitat structure as a central concept will benefit urban ecology research by encouraging 1) descriptive examination of novel urban habitat types from the ground-up (literally and figuratively) and 2) explicit consideration of relationships among physiochemical properties of matter and other ecological variables. Better consideration of both of these issues will certainly promote progress in understanding the mechanisms driving distinctive ecological patterns and processes in urbanized habitats and ecosystems (Shochat et al. 2006).

In addition to creating basic knowledge, studies of urban habitat types are also needed to inform the sustainable management of urbanized ecosystems for reducing potentially negative environmental consequences of urbanization (e.g., nutrient runoff, loss of soil C; Palmer et al. 2004). Ecological data on such topics can be used to guide public policies that influence urban landscape management. In addition, the ecology of urban habitats provides a nexus for education programs that utilize our everyday surroundings to teach basic ecological principles and encourage people to think about their private yards as ecosystems (Berkowitz et al. 2003). Results from this study have relevance to all three of these topics. For example, the observed loss of soil carbon from underneath gravel mulch suggests that this may not be an appropriate material to use in and around gardens. Likewise, shredded bark mulch may not be a desirable ground cover in locations where non-native earthworm invasions are a concern (Burtelow et al. 1998). In addition, the micro-heat islands created by these materials can have negative effects on garden plants (Mueller and Day 2005). Public policies (i.e., “weed laws”) that seek to limit areas of unmowed vegetation in
urbanized landscapes might be re-evaluated in light of data showing that unmowed habitats store more aboveground C and have more complex plant and detritus structure. Thus, incorporating small patches of unmowed habitat into large lawns could increase landscape heterogeneity and provide refugia for beneficial organisms that perform important ecosystem services (e.g., arthropod predators that eat pests, birds that provide pleasing wildlife) (Palmer et al. 2004, Byrne and Bruns 2004, Chapter 6). The possibilities for conducting such applied ecological research in urban habitats are endless and will certainly provide ecologists with engaging research topics for decades to come.

In conclusion, this study has yielded many novel insights that can guide future studies about the ecological characteristics of urban habitats. Data from such research are needed to facilitate communication between ecologists, the public, policy makers, urban planners and others about the effects of human activities on ecological patterns and processes, environmental quality and ecosystem services in urbanized areas (Palmer et al. 2004). Urban habitats also provide a novel focus for developing new methods of experimental research within urban ecosystems that simultaneously examine sociocultural and ecological variables (Cook et al. 2004). As the number of ecologists studying urban habitats and ecosystems grows so will the possibility that scientific ecological knowledge will influence human decisions about how to create and manage urban habitat structures that have desirable ecological properties (i.e., arrow H in Fig. 1-1). However, realizing this possibility will depend upon future investigations about the mechanistic relationships among sociocultural and ecological patterns and processes across residential yard, regional and global scales (Shochat et al. 2006, Kaye et al. 2006, Pouyat et al. in press). Hopefully, foundational studies such as this one will stimulate questions and research about the characteristics of urban habitats that contribute to greater understanding of the ecological consequences of heterogeneity in urban ecosystems.

References


Chapter 4. Differences in nitrogen cycling and associated ecosystem services among four types of urban land cover

Abstract

Human activities have dramatically altered the global N cycle such that excessive amounts of nitrate (NO$_3^-$) and nitrous oxide (N$_2$O) are negatively impacting air, soil and water quality and human health. Data are currently lacking about how human-mediated changes in land cover associated with urbanization affect N cycling. However, such data are needed to inform methods of managing urbanized landscapes in which excessive production of NO$_3^-$ and N$_2$O is prevented and ecosystem services that mitigate their negative environmental effects are conserved. In this chapter, results from a study on N cycling within four types of urban land cover—lawn, gravel and bark mulches and unmanaged old fields—are reported. Replicated plots of these land covers were created in a field experiment and pools and fluxes of inorganic N were measured in the plots over two years using standard methods. N cycling differed significantly among all the land cover types. Compared to the unmanaged old fields, lawns had higher mean rates of net nitrogen mineralization (NNM) and larger NO$_3^-$ pools suggesting that mowing stimulated microbial activity and N cycling via rapid decomposition of cut vegetation and, possibly, increases in root biomass and exudates. In contrast, NNM rates in mulch-covered soils tended to be lower than those of unmowed plots suggesting that microbes were limited by N due to the high C-to-N ratio of shredded bark mulch inputs and lack of organic matter inputs in gravel plots. However, NO$_3^-$ pools were larger in mulched plots on certain dates indicating that their NNM (and especially nitrification) rates were more variable than those of unmowed plots. Soils under lawns and unmowed old field vegetation generally had very low rates of N$_2$O production as measured in the laboratory and field whereas laboratory rates were higher for both bark- and gravel-covered soils, which is attributable to their wetter soils. However, field measurements of N$_2$O flux from bark mulch plots did not differ from those of vegetated plots while those from gravel plots tended to be higher, especially in 2004 when rainfall was greater. Higher earthworm densities in bark mulch plots may have altered N dynamics in ways that limited N$_2$O production despite their wet soils. Although differences in N pools and fluxes among the land cover types varied among sampling dates, it is clear that overall patterns of N cycling differed among them with lawn and mulch plots exhibiting greater potential to produce NO$_3^-$ and N$_2$O than unmowed plots. Additional studies are needed to increase understanding of how urbanization and urban land covers impact ecosystem services associated with N cycling.
Introduction

Over the past several centuries, humans have drastically transformed the Earth’s terrestrial surface and biogeochemical cycles (Vitousek et al. 1997a, b, Sanderson et al. 2002). As a result, the ability of many ecosystems to provide life-supporting services (e.g., regulation of nitrogen cycling) has been reduced with potentially irreversible, negative impacts on the sustainability of the biosphere as we know it (MEA 2005). Thus, a major challenge facing humanity is conserving, restoring and managing ecosystem services (and their associated biodiversity) in human-modified landscapes (Dale and Haeuber 2001, Palmer et al. 2004, DeFries et al. 2005, MEA 2005). In turn, a major challenge for ecologists is generating data about ecosystem services (Kremen 2005, Kremen and Ostfeld 2005), especially regarding the effects of human-driven land use changes on the biogeochemical cycles that underpin them (DeFries et al. 2005).

Human-mediated effects on biogeochemical cycles are exemplified by changes to the global nitrogen (N) cycle (Vitousek et al. 1997b, Galloway et al. 2004). Since 1860, human activities have generated a ten-fold increase in the amount of reactive N (Nr) in the environment (i.e., molecular forms of N other than N₂ that are available for use by organisms including nitrate (NO₃⁻) ammonium (NH₄⁺) and nitrous oxide (N₂O)) through cultivation of leguminous crops, industrial fertilizer production and the burning of fossil fuels (Galloway et al. 2004). The potential consequences of increased Nr (particularly NO₃⁻ and N₂O) in the environment include air and water pollution, human health problems and global climate change (see Vitousek et al. 1997b, Driscoll et al. 2003 and Townsend et al. 2003 for specific examples). Thus, conserving ecosystem services that mitigate the negative impacts of excessive NO₃⁻ and N₂O (i.e., through their transformation or reduced production) should be a central objective of ecosystem management (Townsend et al. 2003, DeFries et al. 2005). However, data relevant to this goal are largely lacking especially related to the cycling of NO₃⁻ and N₂O within urbanized ecosystems (Kaye et al. 2004, 2006, Pouyat et al. in press).

Understanding the effects of urbanization on N cycling is increasingly important because the extent of urbanized land uses is increasing around the globe with concomitant growth in the number of humans inhabiting them (UN 2004, Brown et al. 2005, Theobald 2005). Recent studies of urbanized ecosystems have shown that their N budgets (i.e., inputs and outputs of Nr) differ from non-urban ecosystems because of human activities and altered land cover (Baker et al. 2001, Groffman et al. 2004, Wollheim et al. 2005). In addition, N pools and fluxes can differ among forest patches in urbanized versus rural environments (Pouyat and Carreiro 2003, Pavao-Zuckerman and
Coleman 2005) and various urban and native landscapes (Kaye et al. 2004, Hope et al. 2005, Zhu et al. in press). However, very little is known about how or why N cycling differs among urban land uses and what the emergent effects of urbanization are on regional N budgets (Kaye et al. 2004). Information about the biogeochemistry of urban habitats is needed to guide the sustainable management and design of urban landscapes in which ecosystem services that positively regulate the fate of NO\textsubscript{3} and N\textsubscript{2}O are conserved (Palmer et al. 2004, Kaye et al. 2006).

In this chapter, results are reported from measurements of pools and fluxes of Nr made in four types of land cover—lawn, shredded bark mulch, gravel mulch and unmowed vegetation (Appendix B)—commonly found in urbanized ecosystems. I hypothesized that Nr dynamics would differ among the four land cover types due to 1) human management of the quality and quantity of organic matter (OM) inputs and 2) indirect effects of the land covers on soil properties (e.g., moisture, biota) known to affect N cycling. Results support these hypotheses and show that human-mediated land cover changes associated with the creation and management of urban land uses can generate ecosystem “disservices” (i.e., increased production of NO\textsubscript{3} and N\textsubscript{2}O) as compared to unmowed old field vegetation. Thus, data from this study have broad significance for informing the creation of sustainable urbanized landscapes that promote desirable ecosystem services in addition to providing basic insights into how N cycling is regulated in various land covers by different factors.

**Methods**

*Field experiment*

This research was conducted at Penn State University’s Russell E. Larsen Research Farm (40° 43’N, 77° 55’W, 350 m elevation) located in central Pennsylvania, USA, about 10 miles from the University Park campus. Although the study site was within an agricultural rather than urbanized landscape, this location strengthened the experimental design by permitting 1) control of the creation and management of the habitat plots and 2) location of replicate plots within a common field on one soil type. Both of these factors increased the ability to attribute results to experimental manipulations and eliminated potentially confounding effects of the high spatio-temporal heterogeneity in soils and land uses found in urbanized landscapes. As such, this study is complementary to *in situ* urban research and contributes to the development of mechanistic, experimental approaches to urban ecology (Shochat et al. 2006). It is acknowledged that additional studies are needed in actual urbanized landscapes to determine the generality of the results.
Experimental habitat plots were created within a 0.84 ha (200 X 42 m) old field that had not been managed for at least the previous 25 years except for once a year mowing (S. Harkcom, farm manager, personal communication). Soils in the field were clay loam, shallow, well drained lithic Hapludalfs formed from limestone residuum (Braker 1981). Prior to creation of experimental plots, vegetation across the field was dominated by the grasses *Dactylis glomerata* (orchardgrass) and *Poa pratensis* (Kentucky bluegrass). Additional information about the study site and habitat characteristics is provided in Chapter 3 (pp. 20-22) and Appendices A and B.

In April 2003, four land cover (or habitat) types—lawn, shredded bark mulch, gravel mulch and unmowed old field vegetation—were each applied to four 10 x 10 m plots arranged in a randomized complete block design within the field site. All plots were separated by at least 3- m wide strips of mowed vegetation. Unmowed plots were the reference condition and received no management inputs (including mowing) during the study. Vegetation in lawn plots was mowed to 5-7cm height every two to three weeks (clippings were left in place) but received no other management inputs (i.e., low maintenance lawns, Byrne and Bruns 2004). After the initiation of mowing, plant communities in the lawn plots became dominated by *P. pratensis*, *Plantain sp.*, *Taraxacum officinale* (dandelion) and other broad-leaf species while abundances of *D. glomerata* declined (Chapter 3). In mulch plots, vegetation was killed with glyphosate (Round-Up, Scotts Co., Marysville, OH) and then removed by gently raking off aboveground vegetation without disturbing the soil. Mixed hardwood shredded-bark mulch and limestone gravel mulch (2-4mm) were obtained from local landscaping supply companies and applied to their respective plots to approximately 5 cm depths. A fresh layer of bark mulch was applied in April 2005. Plants were regularly removed by hand from the mulched plots throughout the growing seasons and never covered greater than 5-10% of the plots. Locations with plants were avoided when collecting all soil samples from the mulch plots.

A wide range of soil variables that are known to influence N cycling were measured in the plots during the growing seasons of 2004 and 2005 concurrently with measurement of N pools and fluxes. Almost all of them were significantly different among the habitat types (Chapter 3). Those results, summarized in Table 5-1, will be used for interpreting the N data presented below.

**Data collection**

Although the experimental plots were created in 2003, only preliminary N data were collected that year. All data presented below were collected during 2004-2005.
Table 4-1. Soil and detritus characteristics (means ± SE) of four habitat types averaged across measurements collected from May-September in 2004 and 2005.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Lawn</th>
<th>Unmowed</th>
<th>Bark</th>
<th>Gravel</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loss on Ignition Soil OM (%)</td>
<td>13.9 (± 0.6)ab</td>
<td>13.8 (± 0.7)a</td>
<td>16.4 (± 0.9)b</td>
<td>11.4 (± 0.3)a</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Total soil C (%)</td>
<td>7.8 (± 0.05)a</td>
<td>6.1 (± 0.26)b</td>
<td>7.5 (± 0.28)b</td>
<td>4.0 (± 0.38)c</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>0.94 (± 0.05)ab</td>
<td>0.92 (± 0.02)ab</td>
<td>0.77 (± 0.007)b</td>
<td>0.97 (± 0.06)c</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Water stable aggregate stability (%)</td>
<td>96 (± 1)a</td>
<td>94 (± 0.5)a</td>
<td>93 (± 2)a</td>
<td>79 (± 5)b</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Earthworms (# m⁻² to 25 cm depth)</td>
<td>183 (± 13)a</td>
<td>339 (± 24)bc</td>
<td>683 (± 68)c</td>
<td>91 (± 16)a</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Quantity of aboveground OM N inputs (g N m⁻²)</td>
<td>3.5 (± 0.2)a</td>
<td>6.6 (± 0.2)b</td>
<td>28.5 (± 6)c</td>
<td>N/A</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Quality of aboveground OM inputs (C:N)</td>
<td>18.2 (± 1.2)a</td>
<td>28.8 (± 2.1)b</td>
<td>123.0 (± 6.69)c</td>
<td>N/A</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Soil CO₂ flux (µg CO₂-C m⁻² hr⁻¹)</td>
<td>0.23 (± 0.02)a</td>
<td>0.11 (± 0.008)b</td>
<td>0.19 (± 0.03)c</td>
<td>0.05 (± 0.009)b</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Notes. P values were taken from GLM analyses of means across all samples. See Chapter 3 of this thesis for number of sampling dates for each variable and methods of their measurement. Values in each row with different letters differ significantly with Tukey's post hoc multiple comparisons test. OM: Organic matter.

Net rates of N mineralization (NNM, i.e., the production of NH₄⁺-N + NO₃⁻-N), ammonification (i.e., production of NH₄⁺ from organic N) and nitrification (i.e., conversion of NH₄⁺ into NO₃⁻) were estimated by the field-based core incubation method (Robertson et al. 1999) over 7 monthly intervals (dates are given in Fig. 3). At the beginning of each incubation period, two 5 cm inner diameter x 10 cm long PVC cylinders were placed into the soil to 8 cm depth at two random locations within each of the 16 habitat plots. In vegetated plots, cores were placed between dense areas of aboveground plant biomass to minimize the plant uptake of N from cores. After removal for core placement, mulch and dead plant litter were replaced within the cores before loosely capping them. These cores were left in the field to incubate for 28 days and then removed to the laboratory where soils were air dried and sieved (2mm). NO₃⁻ and NH₄⁺ were extracted from one 5g sub-sample per core that was shaken for one hour in 50ml of 2M KCL and filtered through Whatman #42 filters. Extracts were frozen prior to colorimetric analysis of NO₃⁻-N and NH₄⁺-N on a Quikchem FIA+ 800 analyzer (Lachat Instruments, Loveland, CO, USA). Data were transformed to µg N g dry soil⁻¹. Values from incubated cores provided the final concentrations of inorganic N for each incubation period. Initial NO₃⁻-N and NH₄⁺-N concentrations were determined in a core adjacent to each incubated core collected at the beginning of each incubation period. Net N mineralization rates for each incubation period were calculated as the difference between NO₃⁻-N + NH₄⁺-N for each pair of final and initial cores divided by the number of days in the incubation period (Robertson et al. 1999). Net N mineralization was negative (indicating microbial immobilization or loss of inorganic N) if the final was less than the initial concentration of NO₃⁻-N.
+ NH$_4^+$-N. Net ammonification and nitrification were calculated in the same manner but using only values for NO$_3^-$-N and NH$_4^+$-N, respectively. In addition, NO$_3^-$-N and NH$_4^+$-N data from the initial cores of each incubation period were used to examine temporal patterns of inorganic N pools in the habitats. To increase this data set, two additional soil cores per plot were collected in July and September 2004 and analyzed for NO$_3^-$-N and NH$_4^+$-N as described above.

Denitrification is an anaerobic process in which bacteria utilize NO$_3^-$-N as an electron acceptor as they decompose OM. During this process, denitrifying bacteria produce NO, N$_2$O and N$_2$ in proportions determined by soil conditions, especially soil water content (Davidson et al. 2000). N$_2$O can also be produced by nitrifying bacteria as they oxidize NH$_3$ or respire in anaerobic conditions (i.e., nitrifier denitrification; see Bateman and Baggs 2005). Acetylene (C$_2$H$_2$) blocks both the sequential conversion of N$_2$O to N$_2$ by denitrifying bacteria and the production of N$_2$O by nitrifying bacteria. As such, N$_2$O production was measured during laboratory incubations with C$_2$H$_2$ (Groffman et al. 1999) to provide an index of denitrification rates in soils from the habitat plots seven times in 2004-2005 (see Fig. 4 for specific dates). Briefly, two 2 cm inner diameter x 8 cm deep soil cores (using 10 cm long PVC cores) were collected per plot and immediately transported back to the laboratory. Vegetation and mulch were removed from the cores which were then capped on both ends. C$_2$H$_2$ was injected into the cores through a septum on the top cap for 30s to force out ambient air (as checked by placing them underwater) and flush the headspace with C$_2$H$_2$. Caps were then tightened to maintain the C$_2$H$_2$ within the core. At two and six hours after C$_2$H$_2$ injection, one 10 ml gas sample was collected from each core with syringes and injected into an evacuated 10ml glass vial. Before removing a sample, gas within the headspace was mixed by gently pumping the syringe three times. Samples were analyzed for N$_2$O on a Varian 3800 gas chromatograph using an electron capture detector (Varian Inc., Palo Alto, CA, USA). This incubation method differs from that described by Groffman et al. (1999) because cores were flushed with C$_2$H$_2$ rather than adding their recommendation of only 5-10 ml. Additional C$_2$H$_2$ was added in this study to help force it into soil pores and promote anaerobic conditions that would enhance N$_2$O release from the soils. NO$_3^-$-N from denitrification cores was only measured at two sampling times in 2004 (14-16 July, 27 August-3 September) using the extraction and analysis methods described above.

Field-based estimates of soil N$_2$O flux were measured on nine dates (given in Fig. 5) using enclosed static chambers (Holland et al. 1999) that are described in detail in Chapter 3 (p. 26). Briefly, open chambers (15.5 cm height X 17 cm inner diameter) were placed randomly in each plot 24 hrs before sampling. Four (in 2004) or eight (in 2005) plots were sampled per day (by blocks)
and all plots were sampled within one week of each other between 9 and 11:00am. Vegetation and detritus were removed from the chambers just before sampling to expose the mineral soil surface. Fifteen ml gas samples were collected from the chambers at zero, 15, 30 and 45 minutes after closing them with tight-fitting lids. Samples were immediately transferred into evacuated 10ml glass vials and analyzed within 24 hrs for N₂O as described above. Soil temperatures were measured adjacent to the chambers and two soil samples were collected from inside the chamber for measurement of gravimetric soil water content (by oven drying at 110°C for 24 hrs).

Soil gravimetric water content was intensively measured two to three times per week (June-September 2004, May-September 2005) in the plots on three 2 cm diameter x 5 cm deep sub-samples per plot (Chapter 3). These data were converted to percent water filled pore spaces (% WFPS) which is a better predictor of gaseous N fluxes from soil (Linn and Doran 1984, Davidson et al. 2000). For this conversion, soil particle densities were measured as 2.1 g cm⁻³ for lawn, unmowed and bark soils and 2.2 g cm⁻³ for gravel soils using the pycnometer method (Blake and Hartge 1986).

**Statistical analyses**

General linear models (GLM) were used to analyze all data with habitat type as the between-subjects factor and sampling date as a within-subjects factor (i.e., to examine habitat x date interactions). Because sampling effort differed each year, differences between them for each variable were assessed using separate GLM analyses on the means across dates within each year. Block effects were included in all initial analyses but were never significant (P > 0.05) and are excluded from the reported results. The least significant differences (LSD) test was used for all post-hoc comparisons. Differences were considered significant at P < 0.05. All analyses were completed using Statistica 6.1 (StatSoft, Tulsa, OK). Most statistics are given in the figure legends.

To meet the assumptions of the GLM, data for the total N, NO₃⁻-N and NH₄⁺-N pools were log transformed and potential denitrification data were square root transformed. Untransformed data are presented in tables and graphs. Although field N₂O flux data were non-normal, they could not be adequately transformed and residuals were most closely linear for untransformed data. Because GLM performs robustly against violations of its assumptions (Zar 1999), these data were analyzed with GLM for the main habitat and date effects and their interactions and LSD for post-hoc comparisons. To check the reliability of these results, data were also analyzed with the Kruskal-Wallis non-parametric test. Results from the analyses did not differ and GLM results are presented.
**Results**

NNM, ammonification and nitrification rates were very low (<3µg N g soil\(^{-1}\) day\(^{-1}\)) with both positive and negative rates seen in all the habitats. For all three processes, significant differences were detected among the habitats and dates (see statistics in Fig. 4-1) but not between years (all F\(_{1,12} < 1.2, P > 0.2\)). In addition, habitat x date interactions (all F\(_{18,48} > 4.4, P < 0.0001\)) were significant for each. The largest values for all three processes were seen in lawns with the most negative rates seen in mulched plots. Differences among the habitats in 2004 NNM rates were primarily caused by differences in ammonification rates (Fig. 4-1B) which were lower (and negative) in bark mulch soils for June-July and higher in lawns for August-September. In 2005, mean ammonification rates differed among the habitats only for June-July when lawns had higher rates that the other habitats. In contrast, net nitrification rates (Fig. 4-1C) did not differ significantly among the habitats in 2004 but were significantly different for most periods in 2005, thus causing the differences among the NNM rates seen that year. Lawns had higher nitrification rates than the other habitats from June-September 2005 whereas gravel plots had higher rates for April-May, the only period when they were positive for this habitat type. The highest mean nitrification rates in unmowed and bark plots occurred from June-July and July-August, respectively, while at other times rates were low and occasionally negative in these habitats.

Inorganic soil N pools also exhibited high variability among the habitats, dates and years with different patterns seen for NH\(_4^+\)-N and NO\(_3^-\)-N (see statistics in Fig. 4-2). NH\(_4^+\)-N pools were very large in 2004 (mostly > 20 µg g soil\(^{-1}\)). Between June and August 2004, NH\(_4^+\)-N pools increased six-fold in the vegetated plots, by a third in the bark plots and three-fold in the gravel plots to produce the highest levels seen in this study. NH\(_4^+\)-N values decreased in all the habitats between August and September. Bark plots had higher NH\(_4^+\)-N values in June and July than the other habitats but were similar to vegetated plots in August and September when NH\(_4^+\)-N pools in gravel plots were smaller than in the other habitats. In contrast, the much smaller NO\(_3^-\)-N pools were more similar among the habitats in 2004 although gravel plots had significantly more NO\(_3^-\)-N in July-September. Throughout 2005, NH\(_4^+\)-N pools generally remained ≤10 µg g soil\(^{-1}\) in all the plots but increased to ~13µg g soil\(^{-1}\) in lawn plots in July (Fig. 4-2B) and then decreased but remained higher than the other land cover types’ pools through August and September. Similarly, NO\(_3^-\)-N increased in lawn plots in July 2005 to greater levels than the unmowed and bark mulch plots (Fig. 4-2C). However, lawn NO\(_3^-\)-N pools in July were similar to those in the gravel plots which had steadily increased since April and were significantly larger than all the other habitat
Figure 4-1. Mean (± SE) rates of net a) N mineralization, b) ammonification and c) nitrification in four habitat types. Data on the far right are the means of all samples. Means with different letters for each sampling date differ significantly (\( P < 0.05 \)) with LSD post-hoc comparisons. Habitat and habitat x date interactions were significant in GLM models for all three variables (all \( F_{3,8} > 4.4, P < 0.01 \)). Significant differences among dates with each habitat type were detected for Net N mineralization and nitrification rates (both \( F_{6,48} > 6, P < 0.01 \)) but not ammonification rates (\( F_{6,48} = 1.3, P = 0.29 \)). Means did not differ significantly between years for any of the variables (all \( F_{1,3} < 1.3, P > 0.25 \)) but year x habitat interaction terms were significant for all three variables (all \( F_{3,12} > 3.7, P < 0.04 \)).
Figure 4-2. Mean (± SE) pools of a) total inorganic N, b) NH$_4^+$ and c) NO$_3^-$ in four habitat types. Means with different letters within each sampling date differ significantly ($P < 0.05$) with LSD post-hoc comparisons. Habitat, sampling date and habitat x date interactions were significant in GLM models for all three variables (all $F_{3,10} > 4.1$, $P \leq 0.002$). In a separate GLM, means differed significantly between years for total N and NH$_4^+$ (both $F_{1,12} > 300$, $P = 0.00$) but not NO$_3^-$ ($F_{1,12} = 0.44$, $P = 0.7$) and year x habitat interaction terms were significant for all three variables (all $F_{3,12} > 23$, $P \leq 0.001$).
types’ pools in June and August. Similar to the lawn and gravel plots, NO$_3^-$-N pools in the unmowed and bark plots increased between April and May 2005. However, NO$_3^-$-N pools became significantly smaller in these two habitats in June and July. While they remained small in unmowed plots through September, NO$_3^-$-N pools increased seven-fold in bark plots in August. NO$_3^-$-N decreased in all the habitats between August and September 2005. As was seen for the relationships of ammonification and nitrification with NNM, changes in the total inorganic N pools (Fig. 4-2A) for the dates examined were primarily driven by NH$_4^+$-N in 2004 and NO$_3^-$-N in 2005.

Mean laboratory-measured denitrification rates were higher in 2004 than 2005 ($F_{1,12} = 6.34$, $P = 0.03$) when rates tended to be higher in mulch-covered as compared to vegetated soils. However, high variability among the data and low sample sizes in August-September 2004 samples precluded detection of more significant differences (see Fig. 4-3). In May 2005, mean denitrification rates were highest in lawn and lowest in gravel soils with unmowed and bark mulch soils having intermediate rates. For other 2005 dates, rates were closer to zero in vegetated soils while mulched plots tended to have higher rates, which were significantly higher for gravel plots in June and bark plots in August. In regression analyses, %WFPS was not a significant predictor (all $P > 0.05$) of potential denitrification rates across all habitats or within each habitat (all $R^2 < 0.15$, data not shown). For the two dates analyzed, NO$_3^-$-N was not significantly related to potential denitrification rates in lawn, unmowed or gravel plots (all $P > 0.5$, $R^2 < 0.07$). However, the relationship between NO$_3^-$ and potential denitrification rates was significant ($P = 0.02$) in bark plots with an $R^2$ of 0.67.

Significant differences in field N$_2$O flux were detected among the habitats and between years, primarily due to higher flux rates from gravel-covered soils in 2004 (Fig. 4-4). N$_2$O flux from gravel-covered soils was lower in July 2005 than throughout 2004 but was still significantly greater than the other habitats. In August 2005, N$_2$O flux was greater from bark mulch than vegetated plots with values for gravel plots intermediate but not significantly different from the other habitat types. In general, N$_2$O flux rates were small (< 0.1 µg N$_2$O-N m$^{-2}$ h$^{-1}$) in lawn, unmowed and bark plots. Negative flux rates were detected in these habitats but only rarely. In most regression analyses, soil temperature and %WFPS were not significant predictors of (all $P > 0.05$), nor strongly related to, N$_2$O flux rates (all $R^2 \leq 0.25$, data not shown). Significant relationships ($P < 0.03$) were detected between soil temperature and N$_2$O flux for bark plots and between %WFPS and N$_2$O flux for unmowed plots, but these variables explained little of the variation in N$_2$O flux (both $R^2 < 0.25$).
Figure 4-3. Mean (± SE) denitrification rates from soils of four habitat types incubated with acetylene in the laboratory. Means with different letter at each sampling date differ significantly ($P < 0.05$) with LSD post-hoc comparisons. Numbers below data for 27 Aug.-3 Sept. 2004 are sample sizes for each habitat type on that sampling date which was excluded from the statistical analyses. Habitat ($F_{3,12} = 3.8$), date ($F_{5,60} = 8.1$) and the habitat x date interaction ($F_{15,60} = 3.8$) were significant in GLM models for all three variables (all $P < 0.04$). In a separate GLM, data differed between years ($F_{1,12} = 6.3$, $P = 0.03$) but the year x habitat interaction was not significant ($F_{3,12} = 2.7$, $P = 0.09$).

Figure 4-4. Mean (± SE) $N_2O$ flux rates measured in the field in four habitat types. Means with different letters within each sampling date differ significantly ($P < 0.05$) with LSD post-hoc comparisons. Habitat ($F_{3,12} = 19.9$), sampling date ($F_{8,96} = 2.12$) and habitat x date interactions ($F_{8,96} = 1.8$) were significant in GLM models for all three variables (all $P < 0.05$). In a separate GLM, significant differences were detected among the years ($F_{1,12} = 28.06$, $P = 0.001$) and the year x habitat interaction was significant ($F_{3,12} = 21.7$, $P = 0.00$) due to differences between the years in $N_2O$ flux from gravel plots.
Amounts of precipitation were greater in 2004 than 2005 which caused significant differences between the years in %WFPS ($F_{3,12} = 7.07, P = 0.005$) for lawn, unmowed and gravel plots ($P < 0.01$) and marginally significant ($P = 0.07$) differences for bark plots (Fig. 4-5). Percent WFPS was generally >70% in all the habitats in 2004 and did not differ among them. Values were highest at the end of July when %WFPS reached >90% in all the habitats. Gravel plots had %WFPS values that were consistently >80% throughout 2004. In 2005, lawn and unmowed plots had lower %WFPS than the mulched plots (which did not differ from each other) on all sampled dates, except for four date in May and June. While values in mulched plots remained >65%, those in the vegetated plots were mostly ≤ 55%. WFPS reached >80% in bark plots on a few dates in 2005. Percent WFPS values measured within N$_2$O flux chambers were similar to these patterns (data not shown).

Figure 4-5. Mean (± SE) percent water filled pore spaces (%WFPS) (lines, left axis) and precipitation amounts for the fours days preceding each sampling date (bars, right axis). SE bars are only shown on selected dates for visual clarity. Mean %WFPS did not differ among the habitats for any 2004 dates ($F_{3,12} = 0.92, P = 0.45$) but did differ among dates ($F_{35,420} = 3.5$) and the habitat x date interaction ($F_{105,420} = 3.5$) was significant (both $P=0.00$). For 2005 data points, habitat ($F_{3,10} = 12$), date ($F_{20,200} = 618$) and the habitat x date interaction ($F_{60,200} = 3.8$) were all significant in the GLM (all $P < 0.001$). In a separate GLM, the effect of year ($F_{1,12} = 86$) and the year x habitat interaction ($F_{3,12} = 5.5$) were both significant (both $P < 0.02$). %WFPS differed significantly between years ($P < 0.01$) for unmowed, lawn and gravel plots but only marginally for bark plots ($P = 0.07$).
Discussion

In a given type of land cover, Nr pools and fluxes are regulated by a variety of abiotic and biotic factors, especially the quantity and quality of available OM (Firestone and Davidson 1989, Booth et al. 2005). Although these factors remain important in urbanized ecosystems, previous studies have shown that urban N dynamics are primarily determined by human activities. Specifically, the importation of food, fertilization of lawns, burning of fossil fuels and creation of impervious surfaces by humans can generate greater Nr inputs to and outputs from urbanized as compared to non-urban ecosystems (Baker et al. 2001, Groffman et al. 2004, Kaye et al. 2004, Wollheim et al. 2005). In addition, Nr pools and fluxes within remnant patches of desert (Hope et al. 2005, Zhu et al. in press) and forest habitats (e.g., Pouyat and Carreiro 2003, Pavao-Zuckerman and Coleman 2005) in highly urbanized landscapes can be larger than those in less urbanized landscapes. However, few studies have examined how Nr dynamics are affected by the characteristics of uniquely urban land covers such as lawns and mulched gardens. Such research is needed to evaluate their abilities to provide ecosystem services (i.e., reduced production, increased sequestration or transformation of Nr) that mitigate the negative environmental impacts of excessive Nr. This study, designed as a first step toward meeting this need, shows that Nr cycling differs significantly among urban land covers due, in part, to differential management of their OM inputs.

The following sections present a discussion of underlying causes of the observed differences in Nr patterns by comparing results from the lawn, bark mulch and gravel mulch land cover types to those from the plots of reference unmowed land cover. Two conceptual models—one for NH$_4^+$ and NO$_3^-$ dynamics and one for N$_2$O flux—provide the overarching framework for examining Nr cycling. The focus is on broader patterns seen in the land cover types rather than the observed temporal variability (which likely resulted from differences in precipitation between the years and seasonal patterns of plant and microbial activity). Nonetheless, future long-term research on temporal patterns of Nr cycling in urban land cover types is needed because nothing is known about how Nr cycling and its associated ecosystem services change within them through time.

Net pools and fluxes of NH$_4^+$ and NO$_3^-$

Conceptual framework. The model of Schimel and Bennett (2004) emphasizes that the production of NH$_4^+$ (i.e., ammonification) is primarily regulated by the quantity and quality of OM (i.e., its N content) which determines N availability for decomposer microbes. If OM N content exceeds microbial needs, N will be released into the soil solution as NH$_4^+$. In contrast, land cover
types receiving inputs of low quality OM should have lower ammonification rates due to higher microbial assimilation of N from the OM and, if needed, the soil solution (i.e., net immobilization). When net production of NH₄⁺ occurs, it becomes available for 1) uptake by plants or microbes, 2) movement to cation exchange sites on soil colloids, or 3) uptake by microbes N or 3) transformation to NO₃⁻ by nitrifying bacteria (Schimel and Bennett 2004). Thus, factors regulating these possible fates of NH₄⁺ (e.g., plant density, soil mineralogy, soil moisture and biota) will interact with OM availability to determine the size of NH₄⁺ and NO₃ pools within a given land cover type and net N transformation rates. It is not surprising therefore that Nr pools and fluxes differed among the land cover types in this study because their OM inputs, earthworm densities (Table 4-1), plant communities and soil water contents (Fig. 4-5) differed significantly.

**Unmowed vegetation.** Plots of unmowed old field vegetation provided the reference condition against which to compare the effects of mowing and mulching on Nr dynamics. In unmowed plots, pools and net fluxes of NH₄⁺ and NO₃⁻ were very small (i.e., many flux rates near zero, Fig. 4-1) and exhibited low temporal variability with few exceptions (e.g., an increase in NH₄⁺ pools between June and August 2004 which was seen in all the habitat types and may have been caused by the high rainfall amounts during July; Fig. 4-5) (Bengtson et al. 2005). These patterns follow the model above (Schimel and Bennett 2004) because aboveground OM inputs in unmowed plots 1) were small through most of the year, 2) decomposed slowly (allowing accumulation of surface litter) and 3) had low N content relative to microbial needs (Table 4-1; see also Chapter 3). These factors probably led to high rates of uptake of N by plants and microbes and therefore limited net production of inorganic N. This is also supported by the observation that, in 2004, larger NH₄⁺ pools did not promote higher nitrification rates (Fig. 4-1C) or the accumulation of NO₃⁻ (Fig. 4-2C), suggesting that mineralized NH₄⁺ was rapidly assimilated by microbes and, possibly, plants and stored in their biomass (Fig. 4-2, Dell et al. 2005). Other studies of grasslands have reported low rates of net inorganic N production (e.g., Schimel 1986, Owen et al. 2003) and, with data from this study, support the conclusion that N is highly conserved in unmanaged grasslands due, in part, to rapid assimilation of inorganic N by microbes and plants (Corre et al. 2002, Dell et al. 2005). However, small N pools and net flux rates do not reflect the potentially high rates of gross N production (Booth et al. 2005) and importance of internal N dynamics for sustaining plant growth and microbial activity in grasslands (Davidson et al. 1990, Corre et al. 2002, Dell et al. 2005). Nevertheless, net flux rates and inorganic N pool sizes can be used to assess the potential of a habitat type to produce excess NO₃⁻ that can be lost from the system through leaching or
transformation to $N_2O$. In this study and those cited above, it appears that the tighter cycling of $Nr$ in unmowed old field habitats and grasslands will generally limit $NO_3^-$ production, thus providing a desirable ecosystem service in landscapes where they occur.

**Lawns.** Do pools and fluxes of $NH_4^+$ and $NO_3^-$ differ between unmowed old fields and lawns? Few studies have rigorously examined this question. Results presented here show that mowing promoted significantly higher production (Fig. 4-1) and accumulation of inorganic $N$ (Fig. 4-2) in lawns as compared to unmowed plots at certain times. In the context of the conceptual model (Schimel and Barrett 2004), this difference makes sense because lawns received inputs of higher quality OM (i.e., mowed clippings) every 2-3 weeks (chapter 3) that decomposed quickly aboveground (L. Byrne, personal observation). In a recent laboratory study, decomposing lawn clippings stimulated microbial activity and production of inorganic $N$ (Shi et al. 2006). Previous work has also shown that cutting aboveground plant biomass increased production of root biomass (Dickenson and Polwart 1982) and root exudates, both of which can be expected to increase microbial activity and $N$ mineralization (Hamilton and Frank 2001, Landi et al. 2006). In addition, in this study plant density was greater in lawns due to colonization by species that were not present in unmowed plots, including white clover (*Trifolium repens*) which would have facilitated $N$ inputs into lawns through the N-fixing bacteria associated with its roots. All these factors likely contributed to the significantly greater NNM rates and pools of inorganic $N$ in lawns as compared to unmowed plots on certain dates, especially in 2005.

In contrast, inorganic $N$ pools and net nitrification rates did not differ between lawns and unmowed plots in 2004. This can possibly be explained by increased rates of $NH_4^+$ uptake by lawn plants (and possibly heterotrophic microbes associated with roots) that might have been facilitated by high rainfall that year (Fig. 5). Turfgrasses are known to assimilate inorganic $N$ quickly (Bowman et al. 1989) suggesting that the pools and net production rates of inorganic $N$ in lawns are much smaller than their gross production rates, which may be higher than those in unmanaged grasslands especially during wetter conditions. In 2005, lower rainfall may have limited plant uptake of $N$ and allowed mineralized $NH_4^+$ to accumulate in soil microsites where it would have been readily nitrified (Schimel and Bennett 2004). This is supported by 1) the knowledge that nitrifying bacteria can remain active under dry conditions (Davidson et al. 1990), 2) the observation that the highest rates of nitrification were seen in lawns when soils were very dry (June-September 2005, Figs. 4-1C, 4-5), and 3) the five-fold increase in $NO_3^-$ pools in lawns between June and July 2005 (Fig. 4-2C). In contrast, inorganic $N$ did not accumulate at these times in unmowed plots,
supporting the conclusion that mowing alters N dynamics through greater ammonification rates of OM inputs from roots and clippings. Although soil microbial community compositions were not examined in these plots, it is also possible that these were altered by mowing and affected N cycling rates as suggested by a study showing that intensively grazed grasslands have higher activity of nitrifying bacteria that less intensively grazed systems (Patra et al. 2005).

Clearly, additional work is required to more fully understand how and why N cycling differs between lawns and unmowed fields, especially in different weather and climatic conditions. However, results of this study suggest that inputs of high quality OM from clippings and roots in lawns may sometimes result in “leaky” N cycling in which production of inorganic N exceeds uptake by microbes and plants. Accordingly, and as suggested by previous studies (Kopp and Guilliard 2002, Qian et al. 2003), fertilizer inputs to lawns may create pools of excess NO$_3^-$ that are susceptible to loss via run-off, leaching or denitrification. Previous studies indicate that such losses are highly variable and depend on soil texture, season and type of fertilizer used (Petrovic 1990, Geron et al. 1993, Guillard and Kopp 2004). However, given that such losses can sometimes be high (e.g., Kaye et al. 2004), lawns, especially fertilized ones, may contribute to the higher rates of Nr export from urbanized as compared to native ecosystems (e.g., Groffman et al. 2004, Wollheim et al. 2005). At the same time, lawns can apparently retain a great deal of N fertilizer inputs in their soil OM and plant biomass, although little is known about the mechanisms and long-term dynamics surrounding this (Qian et al. 2003, Groffman et al. 2004). The present study suggests that reducing mowing frequency might be a simple management strategy that helps “tighten” N cycling in lawns by reducing mineralization of NH$_4^+$ from high quality OM inputs. In turn, this would reduce the possibility of negative environmental impacts arising from the excessive production of NO$_3^-$ in lawns. Future work is needed to compare the ability of lawns to provide ecosystem services in urbanized landscapes with those of alternative land covers such as unmowed vegetation and mulch.

*Bark mulch.* Unlike lawn and unmowed habitats, plants were removed from bark mulch plots thus eliminating their influence on N dynamics. Instead, N patterns in bark plots were certainly generated by the their large inputs of low quality (C:N of 123) surface OM. In agreement with the model above (Schimel and Bennett 2004), bark-covered soils had very low and mostly negative ammonification rates (Fig. 4-1B). Despite this, NH$_4^+$-N pools in bark plots were more than double the size of those in unmowed plots in June and July 2004, apparently due to lack of plant uptake and limitations on heterotrophic microbial activity due to the low quality OM inputs. In contrast, they were smaller than or similar to them on all dates in 2005. This difference between
years probably resulted from the timing of mulch applications which were made in 2003 and 2005 but not 2004. Thus, it is possible that by June 2004 mulch may have decomposed enough to allow microbes to mineralize more NH$_4^+$. Nonetheless, soil microorganisms in these plots appeared to remain N limited because larger NH$_4^+$-N pools did not lead to higher nitrification rates (Figs. 4-1C, 4-2C) suggesting that NH$_4^+$ was assimilated by heterotrophic microbes.

Higher NNM rates within soil microsites in bark plots may have been promoted by their high density of earthworms (Table 4-1, also see Chapter 3) which have been shown to increase NNM rates (Steinberg et al. 1997, Szlavecz et al. 2006). Alternatively, NH$_4^+$ may have been incorporated into stable OM in earthworm casts (Bossuyt et al. 2005, Pulleman et al. 2005) and therefore became unavailable to nitrifiers. These contrasting effects of earthworm activity may increase the spatial heterogeneity of N dynamics among soil microsites (Schimel and Bennett 2004) and may help explain seemingly contradictory results in the N data of this study, such as the negative mean ammonification rate but increase in NH$_4^+$ pools seen from June to July 2004. It is possible that reduced earthworm activity within incubating soil cores allowed net immobilization to occur within aging earthworm casts inside the cores (Borken et al. 2000). Thus, bark-covered soils containing large earthworm populations may be useful for testing hypotheses about these relationships between earthworms, their casts and spatiotemporal patterns of N cycling.

In contrast to 2004, applications of fresh bark mulch in 2005 may have prevented net production of NH$_4^+$ due to increased N assimilation by microbes both within the mulch and soil, although details surrounding this possibility are unclear. It seems likely that leaching of dissolved organic matter (DOM) from the mulch into the soil may underlie some of the observed patterns (e.g., Lajtha et al. 2005). This is supported by the increase of NH$_4^+$ and NO$_3^-$ pools in June and August 2005, respectively (Fig. 4-2B, C) and the switch of ammonification and nitrification rates from negative to positive from May to August 2005. Rapid and dense fungal growth in the mulch could have caused the release of DOM that generated these patterns (L. Byrne, personal observation). An increase in soil microbial activity due to leached DOM is also supported by observations of increased CO$_2$ production from bark soils in June-August 2005 (Table 4-1, chapter 3). These factors, combined with the larger NH$_4^+$ pools in 2004, suggest that N dynamics in bark mulch habitats are highly variable through time as influenced by the age of mulch and, therefore, its state of decomposition.

Only one other study on N dynamics in mulch-covered urban soils was found in the literature (Scharenbroch et al. 2005). This study found no differences in N variables between soils
covered by pine bark mulch for \( \leq 6 \) years or \( \geq 15 \) years but did show that net N immobilization occurred on several dates in bark-covered soils regardless of how long they had been in that land use. Data from the present study lend support to the conclusion that application of bark mulch can sometimes lead to reduced inorganic N availability due to suppression of ammonification, incorporation of N into stable OM fractions (e.g., by earthworms), and microbial immobilization of mineralized N. The consistently high %WFPS and earthworm densities in bark plots (Fig. 4-5) would have facilitated movement of DOM and inorganic N through the soil and, as a result, increased the probability of N immobilization by microbes in relatively N-poor microsites (Schimel and Bennett 2004). This might be viewed as an “ecosystem disservice” in mulched gardens with horticultural plantings due to reduced N availability for plant uptake. Because plants were removed from mulched plots in this study, it is not clear how N dynamics might have been affected in them by increased competition between microbes and plants for organic and inorganic N (Schimel and Bennett 2004). Additional research is needed to understand the unique ecology of soil-microbe-plant relationships in mulch-covered soils and evaluate whether any potential costs of bark mulch applications are outweighed by their benefits (e.g., water-holding capacity, limited \( \text{NO}_3^- \) production).

**Gravel mulch.** The most extreme forms of urban landscape management are those that result in complete cessation of OM inputs to the soil as when areas are covered with inorganic materials (e.g., asphalt, gravel) to create roads, parking lots or other land uses. Although they are common, the ecological effects of such land covers on N cycling in their underlying soils have never been investigated. Thus, gravel mulch plots were included in this study as a representative way to examine how soil N dynamics are altered when OM inputs stop but soil moisture is retained due to a dense layer of pervious inorganic surface material (Fig. 4-5).

Despite the lack of new OM inputs, microbes remained active within the gravel-covered soils as indicated by the detection of N (Fig. 4-1, 4-2) and C fluxes (e.g., \( \text{CO}_2 \) production, Table 4-1) within them. In both 2004 and 2005, \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) pools in gravel plots were significantly smaller and larger, respectively, than those in all the other habitats on many dates, indicating the greater relative importance of \( \text{NO}_3^- \) within this habitat type. This pattern is exemplified by the significantly larger increase in gravel plots’ \( \text{NO}_3^- \) pools (July-August 2004) immediately following an increase in \( \text{NH}_4^+ \) pools (June-July) that may have been caused by high rainfall (Fig. 4-5). Although mostly negative net nitrification rates were observed in gravel plots (Fig. 4-1C), the large \( \text{NO}_3^- \) pools indicate that \( \text{NO}_3^- \) may have accumulated rapidly in the spring and was slowly removed...
from the soil solution. Alternatively, NO$_3^-$ dynamics may have been altered within incubating cores (e.g., increased denitrification rates). The former conclusion is supported by observations that the highest nitrification rates seen in gravel plots occurred in April-May 2005 (Fig. 4-1C, 4-2C) and that NO$_3^-$ leaching rates were probably small throughout 2005 due to low rainfall (Fig. 4-5). Data about gross production rates, which were not measured in this study, would be particularly useful in elucidating N dynamics in gravel-covered soils. Nonetheless, it is clear from the data presented that removing plants and adding gravel mulch created N dynamics that significantly differed from the other habitat types, especially the reference unmowed habitat.

Two co-varying factors might explain the N patterns seen in gravel plots, both of which follow from the NNM model (Schimel and Bennett 2004). First, without plant uptake of NH$_4^+$, it would have been more readily available to nitrifying bacteria for conversion to NO$_3^-$. Second, it is likely that nitrifying bacteria gained a competitive advantage over heterotrophic bacteria for NH$_4^+$ because nitrification, as an autotrophic process, is not limited by OM availability (Booth et al. 2005). In contrast, without new OM inputs, the activities of heterotrophic bacteria and, in turn, ammonification rates would have become limited by decreases in OM availability, observations supported by N and C data collected from the plots (Fig. 4-1B, Chapter 3). It is important to note that these patterns were observed within the first 3 years after OM inputs stopped. It is unclear what the longer-term patterns might be as remaining soil OM becomes proportionally more recalcitrant (i.e., of low quality) and resistant to decay. Might ammonification and nitrification cease completely? Answers to this question could be provided by examining in situ urban soils that have been covered by inorganic materials for various lengths of time.

$N_2O$ flux

Conceptual model. A second framework for examining Nr dynamics is provided by the hole-in-the-pipe model which describes factors affecting the production of N gases via denitrification (Firestone and Davidson 1989, Davidson et al. 2000). NO$_3^-$ availability is a primary regulator of denitrification rates with smaller pools limiting and larger pools promoting the process (Groffman et al. 1993). In terms of the model, NO$_3^-$ moves into the “denitrification pipeline” where it is transformed by microbes into NO, N$_2$O or N$_2$ (Davidson et al. 2000). As an anaerobic process, denitrification is also regulated by soil moisture (which determines oxygen availability) with greater rates seen in wetter soils. In addition, soil water content (specifically %WFPS) influences the proportions in which each of the three gases is produced. In drier conditions ($\leq 60\%$ WFPS),
Denitrification is not thought to occur widely but NO and N\textsubscript{2}O can be produced via nitrification (Davidson et al. 2001, Bateman and Baggs 2005). In wetter soils, however, net production of NO is reduced because it can be converted to N\textsubscript{2}O by denitrifying bacteria before it diffuses out of the soil water. Thus, at WFPS ~60-80\%, N\textsubscript{2}O is the dominant product of denitrification. At %WFPS >~80, anaerobic conditions increase and N\textsubscript{2}O can be reduced by denitrifiers to N\textsubscript{2} which becomes the dominant and final product of denitrification. In the model, NO and N\textsubscript{2}O exit the denitrification pipeline (before they can be transformed to N\textsubscript{2}) through “holes” whose sizes, and subsequently the proportions of NO, N\textsubscript{2}O and N\textsubscript{2} production, are determined by %WFPS as described above (Davidson et al. 2000). Although the concepts underlying this model are robust and helpful for interpreting denitrification processes, the model is silent about the influence of other factors, especially C availability and soil structure, on the production of N gases from soil (Davidson et al. 2000). Denitrifying bacteria are heterotrophic and thus require C sources for activity. The density of anaerobic microsites within a soil is influenced by its bulk density, texture and biota (e.g., earthworms) in addition to water content (Sexstone et al. 1988). Although the effects of these variables are not explicitly included in the hole-in-the-pipe model, it provides a useful starting point for discussing why potential denitrification and field N\textsubscript{2}O fluxes differ among various types of urban land cover (Davidson et al. 2000).

**Laboratory vs. field N\textsubscript{2}O flux.** In laboratory measurements of soil denitrification rates in this study, enclosed soil cores were flushed with C\textsubscript{2}H\textsubscript{2} to 1) inhibit the reduction of N\textsubscript{2}O to N\textsubscript{2} by denitrifying bacteria, 2) block the production of N\textsubscript{2}O by nitrifying bacteria and 3) create more anaerobic conditions within the cores (Groffman et al. 1999, Bateman and Baggs 2005). That these goals were achieved is confirmed by the significantly higher values for N\textsubscript{2}O flux rates from incubated cores (Fig. 4-3) than field chambers (Fig. 4-4). Thus, the laboratory denitrification data represent high-end estimates of denitrification rates and N\textsubscript{2}O production that could possibly occur in the soils under favorable conditions. However, it is unknown whether rates measured in the laboratory were, or could be, achieved under field conditions in our plots because N\textsubscript{2}O flux rates measured in the field were mostly very small (<0.1 µg N\textsubscript{2}O-N m\textsuperscript{-1} hr\textsuperscript{-1}) even when %WFPS in all the plots was >70 (Fig. 5). Nonetheless, it seems possible given that the largest laboratory rates observed were similar to or smaller than field-based N\textsubscript{2}O flux rates measured in grasslands (e.g., Rudaz et al. 1999, Dobbie and Smith 2001, Skiba and Ball 2002) and lawns (Maggiotto et al. 2000, Horgan et al 2002, Kaye et al. 2004). No other published studies on N\textsubscript{2}O production rates from mulch-covered urban soils were found in the literature.
Alternatively, observed differences between laboratory and field-based N$_2$O production rates could indicate that NO or N$_2$ was the primary end product of denitrification under field conditions. Given that %WFPS was generally high (≥ 70) in all plots in 2004 (Fig. 4-5) and in the mulch plots in 2005 and that our plots had fine soil texture (i.e., clay loam) and high aggregate stability (Table 4-1), it is plausible that many anaerobic microsites existed in the studied soils where N$_2$O was readily transformed to N$_2$ (Sexstone et al. 1988). Due to lack of equipment, NO fluxes were not measured in this study and have not been reported by other studies about urban habitats. Thus, it is unclear whether NO could have been a dominant end-product of denitrification in the present study. Other explanations for the low N$_2$O flux rates observed here as related to each habitat type are discussed in the following sections.

**Unmowed and lawn plots.** Laboratory-measured denitrification and field N$_2$O flux rates did not differ between unmowed and lawn plots on any of the sampled dates suggesting that N$_2$O production was influenced by similar factors in these habitats (e.g., plant uptake of N and water). However, those factors are not readily apparent from the data of this study. Soils in these habitats were wet enough throughout 2004 to promote N$_2$O production via denitrification but dry enough throughout most of 2005 to limit it (Fig. 4-5). Following this, N$_2$O production (both laboratory and field N$_2$O flux) tended to be larger on most dates in 2004 than 2005, although the differences for field N$_2$O fluxes were very small (~0.02-0.04) and perhaps not meaningful. Thus, high temporal and spatial variability of results preclude the conclusion that soil water content strongly regulated N$_2$O production in lawn and unmowed habitats. This is supported, for example, by the observation that the largest mean potential denitrification rates for both habitat types were observed in May 2005 when soil %WFPS was <50 (Figs. 4-3, 4-5). In addition, field N$_2$O production rates for both lawn and unmowed plots were similar among several 2005 and 2004 dates despite differences in soil water content between the years. Very low, zero, and negative N$_2$O production rates were prevalent on many dates in previous studies of grasslands (Clayton et al. 1997, Rudaz et al. 1999) and lawns (Maggiotto et al. 2000, Horgan et al. 2002) even when %WFPS was > 70. Thus, it seems that %WFPS alone cannot accurately predict N$_2$O production in grassland and lawn systems.

In this study, several factors may have interacted with soil water content to limit N$_2$O production in unmowed and lawn plots, especially under field conditions in 2004. First, as noted above, the fine-textured and well-structured soils could have promoted the formation of anaerobic microsites within soil aggregates where N$_2$O was reduced to N$_2$ (Davidson et al. 2000). Second, relatively low soil bulk densities may have promoted greater oxygen diffusion into the soil thereby
limiting the formation of anaerobic microsites in soil aggregates (Sexstone et al. 1988). Alternatively, assimilation of inorganic N by plants and heterotrophic microbes may have reduced pools of NO$_3^-$ to levels at which denitrifiers (whose activities would have been spatially restricted) could not compete for it effectively. Although NO$_3^-$ pools increased in lawns in 2005, dry conditions certainly limited denitrification that year. An additional explanation for the lack of large N$_2$O flux rates in our study is that we missed measurement of them if they occurred, e.g., immediately following the spring thaw or rain events. It is possible that N$_2$O production rates differed between lawns and unmowed plots at such times, a possibility that should be explored in future studies.

These data support a tentative conclusion that lawn mowing alone does not promote greater production of gaseous Nr from soils as compared to unmowed fields (although measurements of NO flux are needed). Nonetheless, two points about the broader context of this conclusion should be emphasized. First, gaseous N produced by the burning of fossil fuels for lawn mower operation was not included in this analysis. If it had been, it is likely that lawns would have been associated with significantly larger production of N gases than unmowed plots. Second, lawns in this study were not irrigated or fertilized. However, previous studies indicate that these management practices can sometimes lead to greater N$_2$O production in lawns (Petrovic 1990, Maggiotto et al. 2000, Kaye et al. 2004). These points have relevance to the management of ecosystem services in urbanized landscapes because they suggest that reducing irrigation, fertilizer and mowing inputs to lawns can increase their abilities to favorably regulate Nr (i.e., minimize its production).

*Bark mulch.* As compared to the vegetated plots, the consistently wetter soils in bark plots should have created more favorable conditions for denitrifying bacteria. Laboratory denitrification rates did tend to be larger in bark-covered soils than vegetated plots on 5 of the 7 sampled dates (Fig. 4). However, as was true for the vegetated plots, %WFPS alone cannot explain patterns of N$_2$O flux from bark-covered soils because their laboratory denitrification rates decreased significantly in June and July 2005 even though their soil water content did not (Fig. 4-5). NO$_3^-$ pools were smaller during those months than in May and August 2005 but were similar to those seen in July 2004 when laboratory denitrification rates were larger. Thus, the addition of new mulch in 2005 could have altered laboratory denitrification rates through changes in NO$_3^-$ dynamics as described above. This is supported by the observation that both laboratory denitrification rates (Fig. 4-3) and NO$_3^-$ pools (Fig. 4-2) increased in August 2005 which suggests that denitrification in bark plots was limited more by NO$_3^-$ availability than %WFPS.
In contrast to laboratory denitrification patterns, field $N_2O$ flux rates in bark plots were similar to or lower than those of vegetated plots on all dates except in August 2005. This somewhat surprising pattern has several potential explanations including those described above regarding reduction of $N_2O$ to $N_2$ in anaerobic microsites. In addition, soil bulk density was significantly lower in bark mulch than vegetated plots which may have facilitated diffusion of oxygen into soil pores and water films and thus prevented the development of anaerobic microsites. The lower bulk density can be attributed to significantly larger earthworm populations in bark plots (Table 4-1). Previous studies have shown that earthworm guts and their casts can be “hotspots” of denitrification and $N_2O$ production (Burtelow et al. 1998, Borken et al. 2000, Horn et al. 2003). Given this, it is even more surprising that $N_2O$ flux rates were not higher from bark plots. The high C:N of bark mulch may have caused more immobilization than production of $NO_3^-$ within earthworms casts and therefore reduced the possibility for denitrification to occur despite wet conditions. In short, this study is the first to show that relationships between bark mulch and $N_2O$ production may be indirect and potentially unexpected. No other studies of $N_2O$ production in bark mulch-covered soils were found for comparison.

*Gravel mulch.* As compared to unmowed plots, larger $NO_3^-$ pools and higher %WFPS within gravel plots on most dates should have promoted higher denitrification rates especially in 2005. This pattern was seen for the majority of the laboratory denitrification (Fig. 4-3) and field $N_2O$ flux (Fig. 4-4) measurements due mostly to higher rates in 2004. Strikingly, $N_2O$ production rates in gravel plots in 2005—especially those measured in the field—were much smaller than those of 2004 and were similar to those of the other habitats except in July. Although %WFPS was lower in gravel plots in 2005 (as they were for all land cover types), values remained above 65% which, following the hole-in-the-pipe model, should have allowed denitrification to occur with a greater ratio of $N_2O$ to $N_2$ than in 2004. In addition, $NO_3^-$ pools were larger in 2005 than 2004 which should have given rise to higher, not lower, $N_2O$ flux rates. Although a surprising trend, this temporal variability might be explained by the decline in OM and C content of gravel plots between 2004 and 2005 (Table 4-1). Thus, denitrification and $N_2O$ production may have become limited in this habitat by a lack of labile OM inputs. Nonetheless, larger $NO_3^-$ pools facilitated $N_2O$ production to occur in soil microsites containing C as evidenced by the significantly larger laboratory denitrification rates seen in gravel plots in June 2005. It is currently unknown what the long-term $N_2O$ production patterns are from soils that are covered by abiotic materials (i.e., gravel mulch). These data suggest that $N_2O$ flux may increase over the first several years following cessation of OM inputs but then
decline concomitantly with soil C. Whether these fluxes significantly contribute to changes in the global N cycle remain unexplored but warrant consideration given the prevalence of urban land uses that utilize abiotic ground covers (e.g., roads, parking lots, gardens).

Conclusions

Over the past century, humans have dramatically increased the amount of Nr cycling through the Earth’s atmosphere, hydrosphere and biosphere with negative consequences for soil, air and water quality, biodiversity and human health (Vitousek et al. 1997b, Townsend et al. 2003, Driscoll et al. 2004, Galloway et al. 2004). Thus, mitigating the effects of excess Nr (especially NO$_3^-$ and N$_2$O) has become the focus of many environmental management efforts (e.g., Driscoll et al. 2004). Conserving ecosystem services that favorably regulate Nr should therefore be a central objective of sustainable environmental management and land use (Palmer et al. 2004, MEA 2005, DeFries et al. 2005). Unfortunately, the basic ecology of ecosystem services remain poorly characterized and data that can guide sustainable landscape planning and management are unavailable for most types of ecosystems and land use (Kremen 2005, Kremen and Ostfeld 2005). This is especially true for urbanized ecosystems for which very little is known about the effects of various urban land uses and covers on the production and fate of Nr (Groffman et al. 2004, Kaye et al. 2004, 2006).

This study has provided new data about how pools and fluxes of Nr differ among common urban land covers. Because unmowed plots were the unmanaged reference condition, data from them provide a baseline against which to evaluate the effects of other land covers on Nr dynamics. As such, results presented above support the following conclusions. 1) Lawn mowing increased NNM rates and inorganic N pools on many dates, probably due to inputs of high quality OM in the forms of grass clippings and root exudates. 2) Applying a layer of shredded bark mulch increased inorganic N pools on several dates but its high C:N may have caused immobilization of inorganic N by soil microbes and/or sequestration of organic N within soil aggregates and earthworm casts. 3) In contrast, applying a layer of gravel mulch increased NO$_3^-$ pools and decreased NH$_4^+$ pools. 4) Both bark- and gravel-covered soils had larger rates of N$_2$O production denitrification rates than unmowed plots on certain dates but only gravel-covered soils promoted larger N$_2$O fluxes in the field. 5) Even though mulched plots were consistently wetter than unmowed plots, this did not always promote N$_2$O production, for unknown reasons. The generality of these conclusions should be examined in future longer-term studies using both field experiments and in situ sampling of
urbanized landscapes. Nonetheless, they can be used to assess the ecosystem services provided by different habitat types common in urbanized landscapes.

Ecosystem services related to the regulation of Nr are those that lessen the negative environmental and human health impacts of NO$_3^-$ and N$_2$O by sequestering, transforming or reducing the production of them. Thus, each of the three urban habitat types created in this study provided less favorable levels of ecosystem services than the unmowed plots because they generated significantly larger pools and fluxes of NO$_3^-$ and/or N$_2$O on certain dates. In addition, the potential for immobilization of N to occur under bark mulch could be seen as an ecosystem disservice because it would lessen the inorganic N available to plants in mulched gardens. Data from this study can be used to inform decisions about preferable types of land covers to use when mitigation of Nr is a primary concern. For example, unmowed habitats provided more favorable regulation of NO$_3^-$ than lawns as reflected in their significantly smaller mean NO$_3^-$ pools and nitrification rates. In contrast, lawns and unmowed habitats were similar in their ability to limit potential N$_2$O production and provided this service significantly better than the mulched plots. Whether these differences would be meaningful within the broader context of urbanized ecosystems and when considering the regulation of Nr dynamics at larger scales is an open question. Nonetheless, this study contributes basic knowledge about how ecological data can be discussed within the context of the ecosystem services with which they are associated (Kremen 2005).

As urbanization rates continue to increase around the world so will the demand for studies about how ecosystem processes and services differ among various urban land uses and covers (UN 2003, Palmer et al. 2004, Brown et al. 2005, Kaye et al. 2006). Although challenging, engaging in such research provides ecologists with opportunities to generate new questions and test old hypotheses about, e.g., factors regulating N cycles by using unique urban habitats. In addition, investigating the effects of human activities and land use change on biogeochemical cycles will better enable ecologists to provide insights needed to inform the sustainable design and management of urbanized landscapes in which ecosystem services are maximized (MEA 2005, Kremen and Ostfeld 2005). As data in this chapter have shown, the relative abilities of different urban land covers to provide ecosystem services may not always be intuitive or follow current ecological models (Kaye et al. 2006). Thus, studies about the ecology of urban habitats are critically needed to ensure that common land use and cover changes associated with urbanization are not unknowingly promoting ecosystem “disservices” that irreversibly reduce the sustainability of urbanized ecosystems and the human communities that inhabit them.
References


Chapter 5. Ground arthropod communities and activity-abundance levels differ among urban habitat types

Abstract

During the process of urbanization, humans destroy and create numerous types of habitat with consequences for patterns of biodiversity. Data about relationships between urban habitat types and biodiversity are needed to guide methods of conserving beneficial organisms in urbanized ecosystems. The objective of this study was to evaluate differences in ground arthropod communities and activity-abundance levels among four common urban habitat types: lawn, shredded-bark mulch, gravel mulch, and unmanaged old field. Plots (10 X 10m) of these four habitat types were created in a field experiment. Arthropods were collected from the plots using pitfall traps on three dates each in 2003 and 2004. Results support the hypothesis that arthropod communities would differ among the four urban habitat types but they do not follow the expectation that arthropods would be most abundant in old fields, least in gravel plots, and intermediate in lawn and bark plots. Instead, the activity-abundance data of most taxonomic groups were characterized by significant interactions between habitat type and sampling period due to temporal variation in numbers of arthropods collected from each habitat type. Consequently, it appears that arthropod communities changed through time in different ways in each of the habitat types as shown by a multivariate redundancy analysis. Air and ground temperatures were not strongly related to the activity-abundance data across all habitat types. However, mean ground temperatures differed among the habitat types and might have caused differences in arthropod activity levels among them. In addition, different resources and environmental conditions in each of the habitat types were temporally variable which may have affected the temporal patterns of arthropod activity levels and abundances (and therefore communities) in each. The high spatiotemporal variability among the arthropod data in the current study precludes its ability to provide stronger conclusions about how the four habitat types might provide suitable resources and environmental conditions to promote the conservation of ground arthropods in urbanized landscapes. Results emphasize the need for more studies about how animal movements across heterogeneous landscapes determine spatiotemporal patterns of community structure and activity-abundance levels. The experimental system used in this study might prove useful for development of future studies about how urbanized landscapes can be designed to maximize the activities and abundances of beneficial arthropods which provide valuable ecosystem services (e.g., pest control).
Introduction

The habitat of a particular organism can be defined as the location(s) from which it acquires resources for survival and reproduction (Southwood 1977, Hall et al. 1997). For most organisms, the spatial extent of suitable habitat is limited by a variety of abiotic (e.g., climate) and biotic (e.g., competition) environmental factors, including resource availability (Morris 1987, 2003, Holt and Keitt 2005). Locations of suitable (or preferred) habitat for individual organisms (especially mobile ones) may also change through time due to variation in environmental conditions (e.g., seasons) and/or their resource needs during different life stages. Describing spatiotemporal patterns of habitat use by organisms has long been a primary focus of ecology (e.g., MacArthur and MacArthur 1961, Luff 1966, Price 1978, Morris 1987). In addition, many applied research topics (e.g., biodiversity conservation, biological pest control) are inherently linked to understanding organisms’ habitat requirements.

At a fundamental level, habitats can be described by the physical material that comprises them, i.e., their habitat structure. Habitat structure—defined as the composition and arrangement of abiotic and biotic matter at a location (modified from Bell et al. 1991)—has been shown to influence the local presence, abundance, and diversity of organisms through its mediation of, among other variables, resource availability (shelter, food), microclimates and inter- and intraspecific interactions (predation, competition) (e.g., MacArthur and MacArthur 1961, Petren and Case 1998, Goldsbrough et al. 2004; see reviews in Bell et al. 1991 and Tews et al. 2004). A challenge for ecologists is to assess where, when, why and for whom habitat structure and its spatiotemporal heterogeneity affects population (Fahrig and Nuttle 2005), community (Leibold et al. 2004, Cottenie 2005) and food web (Polis et al. 2004, Denno et al. 2005) dynamics (McCoy et al. 1990).

Spatiotemporal heterogeneity of habitat structure can be generated by many processes including disturbance, succession and ecosystem engineering (sensu Jones et al. 1994). However, in an increasing proportion of landscapes around the globe, humans exert dominant control over patterns of habitat structure (Vitousek et al. 1997). Human-mediated landscape transformations impact about 80% of the Earth’s terrestrial surface (Sanderson et al. 2002) and, in turn, alter the quantity and quality of suitable habitat available to many organisms (Sala et al. 2000, Dirzo and Raven 2003). Urbanization is one of the predominant human-mediated processes now driving global changes in land cover and biodiversity patterns (Vitousek et al. 1997, McKinney 2002, Theobald 2005). Thus, another challenge for ecologists is to investigate how relationships between

Central to the study of urban biodiversity is examination of how organisms interact with, and are affected by, distinctive types of habitat structure that are created and managed by humans (e.g., lawns, roads). For example, mayflies were observed laying eggs on roads because they mistook the polarized light reflected from them as an indication of water (Kriska et al. 1998). Other studies have shown that various urban land covers are associated with different arthropod and bird communities due, in part, to differences in resource availability and microclimates among them (e.g., Nuhn and Wright 1979, McIntyre et al. 2001, Shochat et al. 2004, Donnelly and Marzluff 2006). In general however, very little is known about mechanisms underlying relationships among urban habitat structures and biodiversity patterns (Faeth et al. 2005, Shochat et al. 2006). Information about these relationships is needed to inform methods for conserving and managing biodiversity in urbanized ecosystems (Miller and Hobbs 2002, McKinney 2002).

I hypothesized that arthropod communities would differ among the four urban habitat types primarily due to differences in their microclimates and resource availability (e.g., detritus, prey; see chapter 3). Specifically, I expected that activity-abundance levels of most arthropod taxa would be greater in unmowed habitats (which had the most available resources, i.e., tall vegetation, thick detritus layer, and lowest variation in ground surface temperature; see Chapter 3), intermediate in
lawns and bark mulch plots and least in gravel mulch plots (which contained no organic matter and had the highest variation in ground surface temperature).

Methods

Experimental plots. For this study, arthropods were sampled from the same urban habitat structure plots described in detail in Chapter 3 (pp. 20-22). Briefly, four habitat types (lawn, shredded bark mulch, limestone gravel mulch, unmanaged old field vegetation; see photos in Appendix B) were each applied to four 10 x 10m plots in a previously unmanaged old field (Appendix A) at Penn State University’s Russell E. Larson Research Farm in April 2003 in a randomized complete block design. Lawn plots were managed by mowing with a push or riding rotary mower approximately twice monthly during the growing season to maintain vegetation height at 5-7cm. To create mulched plots, vegetation was killed with an herbicide and removed by raking. Shredded hardwood bark mulch and limestone gravel (2-4mm diameter) were then applied to their respective plots to 5cm depth. Plants were removed from the mulched plots by hand throughout the growing season. Unmanaged old field reference plots were not disturbed throughout the study. All experimental plots were separated from each other by 3-m wide strips of mowed vegetation.

Pitfall traps. Ground arthropods were sampled from each of the 16 habitat structure plots with 5 pitfall traps. Traps were 11cm diameter by 6 cm deep plastic food storage containers (with matching lids) obtained from a local grocery store. Within each plot, trap locations were arranged as one trap in the center (5m from all plot edges) and one in each corner, 2m from the nearest edges. In this study, the spatial intensity of sampling effort was increased (i.e., trap density per plot) relative to other studies as an attempt to minimize potential sampling biases caused by differences in the complexity of the four types of habitat structure. Permanent holes at trap locations were created by placing PVC pipe couplers (~11 cm inner diameter) into the ground in early May 2003 (after placement of the mulches). Soil was filled in around the exterior sides of the couplers to be level with their tops. Couplers were placed in the ground to depths at which tops of the pitfall traps, when placed inside the couplers, were slightly below the surface of mineral soil. Bark and gravel mulch layers immediately surrounding the couplers were thinned such that the soil remained covered but bark or gravel would not fall into the traps during sampling times. Closed traps were placed in the couplers during non-sampling periods.
Pitfall traps were used in this study because they provide a simple, inexpensive and efficient method for collecting ground-dwelling arthropods (Woodcock 2005). Although the ability of pitfall traps to provide reliable data about sampled populations and communities has been questioned (e.g., Luff 1975, Adis 1979, Halsell and Wratten 1988, Topping and Sunderland 1992), most investigators have concluded that the method’s benefits outweigh its costs and that biases associated with pitfall trapping are no more severe than those associated with other sampling methods (Mommertz et al. 1996, Melbourne et al. 1997, Koivula et al. 2003, Phillips and Cobb 2005, Woodcock 2005). However, pitfall trap data must be interpreted with care because the number of trapped arthropods is influenced by both the local abundances and activity levels of arthropods. Thus, pitfall trap data are best viewed as indices of arthropod abundance and activity (i.e., activity-abundance levels) rather than abundance alone and, therefore, should be interpreted in light of environmental factors (e.g., habitat structural complexity, microclimates) that may affect arthropod activity levels (i.e., movement rates; Woodcock 2005). With this in mind however, pitfall trap data are ecologically meaningful and provide useful indices about relative differences in arthropod abundances and communities among habitat types (Mommertz et al. 1996, Melbourne et al. 1997, Woodcock 2005). In this study, all arthropod data are reported as indices of activity-abundance levels and will be discussed in light of differences among the habitat types (i.e., structure, ground temperature) that may have influenced both arthropod abundances and activity levels.

**Arthropod sampling and sorting.** Ground arthropods were sampled three times each in 2003 (June 9-10, July 29-30, October 6-7) and 2004 (May 4-6, June 23-25, August 10-12). On the first day of each sampling period, empty pitfall traps were placed in the field between 9:00 and 10:00. Sampling durations were 24 hours in 2003 and 48 hours in 2004. The sampling period was extended in 2004 to increase the probability that more individuals of certain taxa would be collected on all dates (i.e., taxa for which few individuals were collected on some 2003 dates). However, numbers of arthropods collected in 2004 were halved to make them comparable with 2003 data. Temporal sampling intensity was kept relatively short in this study (as compared to others) as a trade-off for increased sampling intensity across space (i.e., 5 traps per plot) and to therefore avoid over-sampling (i.e., depleting) arthropods and influencing their movements between habitat types (e.g., immigration into plots).

After placement in the PVC couplers, pitfall traps were filled with ~3cm of distilled water. No preservatives were added in the field because of the short sampling duration. At the end of each sampling period, traps were collected, closed and returned to the laboratory where sufficient alcohol
was added to each trap to provide a 70% alcohol mixture. Arthropods were identified and quantified at the ordinal level following keys in Borror et al. (1989) except for collembolans which were sorted into three subordinal eco-morphological groups (entomobryomorpha, poduromorpha and symphypleona; see Fig. 2-1 for descriptions and drawings), and hymenopterans which were separated into ants (Family Formicidae) and wasps (many families). Eleven arthropod taxonomic groups were enumerated: entomobryomorpha collembola, sminthurid collembola (family Sminthuridae of the symphypleona group), Aranae (spiders), Coleoptera (beetles), ants, wasps, Hemiptera, Diptera (flies), Orthoptera (grasshoppers and crickets), Diplopoda (millipedes) and Isopoda (isopods). Individuals from other taxa (including Poduromorpha collembola) were not included in analyses because they were trapped in very low numbers. Most specimens were stored in vials with 70% alcohol; larger specimens (e.g., grasshoppers) were pinned.

**Air and surface temperatures.** Seasonal and microhabitat temperature patterns are known to influence arthropod abundances, activity levels and distribution (e.g., Kingsolver 1989, Gilbert and Raworth 1996, Goldsbrough et al. 2004). To examine seasonal temperature patterns, air temperature data were taken from a weather station located less than one kilometer from the experimental field. Microhabitat temperatures were assessed as ground surface temperatures recorded at half-hour intervals within each of the habitat structure plots using one temperature probe per plot connected to a HOBO datalogger (Onset Computer Corp., Pocasset, MA). Temperature probes were laid on top of the mulch (in mulched plots) or soil (in vegetated plots) in the center of each plot.

**Analyses.** General linear models (GLM) were used to test the hypothesis that ground and air temperatures were significantly related to activity-abundance levels for each arthropod group and total arthropods. In these analyses, mean activity-abundance levels for each habitat type (averaged from the four replicate plots) from each sampling period were paired with the mean surface temperature (averaged from the four replicate plots) from the respective habitat type or the mean air temperature, both averaged from temperatures within a sampling period (Table 5.1). Activity-abundance data from all six sampling dates were used in analyses with air temperature whereas analyses with surface temperature were conducted using only 2004 data because ground temperatures were not collected in 2003. Differences in mean ground temperatures among the habitat types for each sampling period were also assessed using GLM. All GLM analyses in this study were conducted using Statistica 6.1 (StatSoft, Tulsa, OK) and evaluated for significant differences at $P \leq 0.05$. 
Arthropod activity-abundance data were analyzed using both univariate and multivariate methods. Two multivariate ordination methods were used to examine relationships between arthropod activity-abundance levels and habitat types: principal components analysis (PCA) and redundancy analysis (RDA). (These methods were chosen because relationships among arthropod data were determined to be linear in a preliminary detrended correspondence analysis (Lepš and Šmilauer 2003).) PCA is an indirect ordination method that extracts axes (gradients) of hypothetical environmental variation from multivariate (here, activity-abundance) data sets and then graphically displays relationships among those axes, taxonomic groups and individual samples in ordination diagrams (or biplots) (Lepš and Šmilauer 2003). Relationships are interpreted in terms of environmental variables (e.g., habitat type, microclimate) that might explain variation among the data along the axes. The relative proportion (percentage) of variation among the data explained by each axis is provided by the PCA (similar to regression analyses). Thus, PCA is a descriptive statistical method useful for summarizing important relationships among samples and organisms and discussing their potential environmental drivers. In this study, PCA was used to assess whether hypothetical axes of variation extracted from activity-abundance data corresponded to environmental variables that differed among the four types of habitat structure.

RDA is a direct ordination method in which axes of variation among samples and taxonomic data are based on (i.e., constrained to) environmental variables measured in the study system (Lepš and Šmilauer 2003). Similar to PCA, results from RDA can be displayed graphically in biplots that show relationships among the samples, taxonomic groups and axes. The explanatory power associated with each axis is provided and each is interpreted in terms of the variables used in the analysis. To assess which, if any, environmental variables associated with the axes are significantly related to the ordination results, Monte Carlo randomization tests are performed in the RDA to generate probability values that the results differ from those that could be generated by chance alone. In this study, RDA was used to assess whether habitat types or sampling dates were significantly related to activity-abundance data. Air and ground temperatures were not included in the RDA for the following reasons: 1) regression analyses indicated that temperatures were not significantly related to activity-abundance data for most taxa (see Results); and 2) preliminary analyses suggested that interpretation of RDA axes was made more complex by inclusion of temperature data and that axes were related more strongly to habitat type and sampling date than temperature.
PCA and RDA procedures used in this study are summarized briefly here. Detailed description of the methods (including relevance of the procedures listed below) are given by ter Braak and Šmilauer (2002) and Lepš and Šmilauer (2003). These analyses were completed using CANOCO version 4.5 (ter Braak and Šmilauer 2002). For both PCA and RDA, arthropod activity-abundance data were square-root transformed, centered and standardized so that the PCA was based upon the correlation matrix. Analyses were conducted with a focus on inter-species correlations. Arthropod scores used in the biplots were divided by their standard deviations (i.e., post-transformed). Year and Experimental Block were used as co-variables to control for variation associated with them because they were not environmental variables of interest for the ordination analyses. In the RDA, habitat type and sampling date were included as explanatory environmental variables with which to constrain the extraction of axes. For the Monte Carlo permutation tests in RDA, 9999 iterations were utilized to generate \( P \) values for each habitat type and sampling date deemed significant at \( P < 0.05 \). Also for the RDA, one data point per habitat type per sampling date (each representing the mean score of four replicated plots) was passively projected onto the biplot to simplify its presentation and interpretation. For the PCA biplot, one centroid per habitat type was projected onto the biplot to represent the average score for samples from the respective habitat type. General methods for interpreting results from biplots are given below (Table 5-2) and in chapter 10 of Lepš and Šmilauer (2003).

Univariate GLM was used to test hypotheses that activity-abundance levels (i.e., number of arthropods collected per trap over 24 hours) for each taxonomic group and total arthropods differed among the habitat types, sampling dates and years and to test for any significant interactions among these factors. Habitat type was the between-subjects factor and sampling date and year served as within-subjects factors (i.e., repeated measures analysis). Block was included as a between-subjects factor in all initial analyses but was never significant (\( P > 0.05 \)) and is not included in the reported statistical results. To meet the assumptions of the GLM, activity-abundance data were log transformed for all arthropod data sets. Untransformed data are presented. Least significant differences tests were used to examine post-hoc, pair-wise differences among the habitat types within each sampling date.

**Results**

*Temperature.* Air and surface temperatures were not significant predictors of mean activity-abundance levels for most arthropod groups (\( P \geq 0.07 \) and \( R^2 < 0.25 \) for all analyses; data not
shown). Air temperature (values for each sampling period shown in Table 5-1) was significantly related to mean activity-abundance levels for Entomobryomorpha collembola, Aranae ($P = 0.05$ and 16\% of the variation explained by temperature for both) and total arthropods ($R^2 < 0.23$, $P = 0.02$; Fig. 5-1A). Surface temperature was significantly related to mean activity-abundance levels for Orthoptera ($P = 0.05$), explaining 32\% of the variation.

In general, relationships between mean air and surface temperature and mean activity-abundance data for most taxonomic groups are exemplified by patterns seen for the total arthropod data (Fig. 5-1). In particular, activity-abundance values were low in all the habitat types on the two dates when air temperatures were lowest during this study (Fig. 5-1A). Activity-abundance levels were more variable when air temperatures were higher with both high and low levels of activity-abundance observed. In contrast, across the range of surface temperatures observed during the sampling periods (Table 5-1), activity-abundance values for total arthropods (Fig. 5-1B) and taxonomic groups (data not shown) were highly variable (i.e., both high and low).

Mean surface temperatures differed significantly among all four habitat types for the June and August 2004 sampling periods (statistics given in Table 5-1) with temperatures increasing in the habitats in the order unmowed, lawn, bark and gravel. This pattern was also seen for the May sampling period but mean surface temperatures in lawns did not differ from those in unmowed or bark plots. Differences in mean surface temperatures among the habitat types were caused by differential warming of the habitat types by solar radiation types during the daytime hours (11:00-18:00) (Appendix H; see additional temperature results and discussion in Chapter 3).

![Figure 5-1](image_url)

**Figure 5-1.** Relationships between mean (A) air and (B) ground temperatures with arthropod activity-abundance levels during arthropod sampling periods. Results of GLM analyses are shown with each graph.
Table 5-1. Mean air and ground temperatures for each arthropod sampling period used in analyses to examine relationships between temperature and activity-abundance levels.

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>June 9-10</td>
<td>July 29-30</td>
</tr>
<tr>
<td>Mean air temperature (°C)</td>
<td>17.2</td>
<td>19.2</td>
</tr>
<tr>
<td>Mean ground temperatures (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lawn</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Unmowed</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Bark</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Gravel</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>

Notes. Air temperatures were collected at a weather station < 1km from the field site. Ground temperatures were collected in 2004 only with one temperature probe per plot located on the surface of the soil (in lawn and unmowed plots) or mulch layer (in the bark and gravel plots). Ground temperatures are means (+ SE) of four plots per habitat type except when N=3 as denoted by †. Mean ground temperatures in a column with different letters differ significantly (P < 0.05) with least significant differences post-hoc analyses.

Ordination analyses. After controlling for the variation of Year and Experimental Block, the PCA analysis extracted two hypothetical axes that together explained 50.5% of the variation in the entire arthropod activity-abundance data set. Examination of the PCA biplot (Fig. 5-2) shows that samples from lawn and unmowed plots fall toward the right of the diagram whereas those from bark and gravel plots, which lack vegetation, are located predominantly on the left of the diagram. Axis 1 (explaining 32.8% of the variation) could therefore be interpreted as reflecting variables influenced by the presence or absence of vegetation. Along axis 2 (which explained 17.7% of the variation), gravel and lawn samples are mostly located toward the top of the biplot and bark and unmowed samples fall toward the bottom. Lawn and gravel plots had much less surface organic detritus than did unmowed and bark plots (Appendix B; also see Chapter 3), and thus, axis 2 appears to indicate that differences in detritus layers among the habitat types were important drivers of variation in arthropod activity-abundance levels among the habitat types.

The PCA biplot (Fig. 5-2) also shows that samples can be clearly grouped into four clusters corresponding to the four habitat types. However, some samples are closer to those from different habitat types than to others from the same habitat type (e.g., where the bark and unmowed clusters overlap below and to the left of the origin); this suggests that other environmental factors (e.g., sampling date; see results of RDA) interacted with vegetation and detritus to influence patterns of arthropod activity-abundance within each habitat type. Nonetheless, on average, each of the four habitat types had distinct arthropod communities as indicated by the locations of the centroid points.
Table 5-2. Guidelines for interpreting relationships among sample points and taxon arrows in PCA and RDA biplots. Adapted from Lepš and Šmilauer (2003).

1. Location of a sample (denoted by the symbols) in the biplot indicates its relationship to the environmental variables associated with the axes. Interpretation of the environmental variables underlying each axis is done using a priori knowledge of the study system.

2. In general, distance between sample points indicates their relative similarity. Samples that are closer together are more similar than points more distant from each other (but see Lepš and Šmilauer (2003) for additional discussion).

3. To determine relationships among samples and taxa, extend each taxon’s arrow through the biplot. Project a perpendicular line from each sample to the arrow. The order in which these lines intersect with the arrow—starting from the arrow’s front—indicate the relative ranking of their respective samples in numbers of individuals for the taxon predicted to be found in that sample. Samples whose lines intersect at the very front of the arrow will have the largest numbers. Samples whose lines intersect the arrow near the origin have average numbers for that taxon. Samples with lines that intersect on the opposite side of the origin from the direction of the arrow will have lower than average numbers of that taxon. In biplots, the average number represents the mean of all samples.

4. Centroids represent the mean ordination score for samples from the same habitat type (PCA biplot only, Fig. 5-2).

Figure 5-2. Ordination diagram (biplot) generated from principle components analysis (PCA) of activity-abundance levels of 11 arthropod taxonomic groups from samples collected in four habitat types with year (2003 and 2004) and experimental blocks as co-variables. See text for interpretation of axes.
which represent the mean of the ordination scores for each habitat type. The directions of the arrows in the PCA biplot suggest that activity-abundance levels for most taxonomic groups were generally greater in lawn and unmowed samples than in mulched plots (Lepš and Šmilauer 2003).

RDA analysis revealed that community-wide arthropod activity-abundance levels differed significantly among all habitat types and sampling dates (all \( P < 0.0001 \) in Monte Carlo tests). After removing the effects of Year and Experimental Block, Axes 1 and 2 of the RDA explained 55% and 18% of the variation in the arthropod data, respectively. As illustrated in the biplot (Fig. 5-3), these axes seem to have been influenced most by interactions among sampling period, numbers of arthropods collected during each sampling period and habitat type. Along Axis 1, the seven samples (i.e., unmowed samples from June 2003, all habitats’ samples from July 2003, lawn and unmowed samples from June 2004) in which total number of arthropods collected during this study were greatest (see Fig. 5-4A) all fell farthest to the left of the origin on the biplot. Samples from October 2003 (when numbers of sampled arthropods were very low) fall on the far right side. The strong influence of arthropod numbers in each sample is also indicated by all the taxon arrows pointing to

![Figure 5-3](image-url)  
*Figure 5-3.* Ordination diagram (biplot) generated from redundancy analysis (RDA) of activity-abundance levels of 11 arthropod taxonomic groups using habitat type and sampling data as environmental variables and year (2003 and 2004) and experimental block as co-variables. See text for interpretation of axes.
the left which suggests that Axis 1 can be interpreted as a seasonal gradient that affects arthropod communities. Interpretation of Axis 2 is less clear but may reflect interactions of sampling date with community composition in each habitat type especially as caused by variation in numbers of Orthoptera and Diplopoda, the taxa for which arrows are angled more vertically.

Although possible interpretations of axes extracted by the RDA are not readily apparent, the RDA biplot (Fig. 5-3) shows that the mean values of ordination scores for each of the six sampling periods form six well-defined clusters. However, overlap among the clusters suggests that habitat and date interacted to determine arthropod activity-abundance (e.g., some gravel samples from June 2003 and May 2004 are closer to each other than they are to samples of other habitat types from those dates). Such interactions may have influenced the organization of samples along the axes more than habitat type or sampling period alone. As indicated by the direction of the arrows however, activity-abundance levels for most taxonomic groups tended to be greatest during the July 2003 and June 2004 sampling periods.

**Activity-abundance levels.** The effect of habitat type on arthropod activity-abundance levels was significant for nine of 11 arthropod taxa (all but one \( P < 0.02 \)) while the effect of sampling date was significant for all 11 taxa and total arthropods (all but one \( P < 0.001 \); Table 5-3, Appendix I). Numbers of arthropods trapped tended to be lower in 2004 than 2003 (except for Diplopoda; Fig. 5-3, Appendix J), a difference that yielded a significant (\( P < 0.02 \)) year effect for total arthropods and five taxonomic groups (Table 5-3, Appendix I). Within each year, mean activity-abundance levels were highest for most taxa during the July 2003 and June 2004 sampling periods as exemplified by patterns in the total arthropod data (Fig. 5-4A) (and as reflected by the RDA biplot; Fig. 5-3). However, this general pattern was not consistent across habitat types as indicated by the significant habitat x date interactions for nine of 11 taxonomic groups (Table 5.2, Appendix I). In addition, the habitat x year interaction was significant (\( P < 0.02 \)) for sminthurid collembola, Aranae and Orthoptera (all \( P < 0.05 \); Table 5.2, Appendix I). These significant interactions were caused by differences in relative rank (i.e., higher or lower) of the habitat types among the sampling dates and years for the activity-abundance levels of each taxon. Post-hoc multiple comparison tests detected significant differences in activity-abundance levels among the habitat types within at least two sampling periods for all taxonomic groups (Fig. 5-4, Appendix J).

For brevity, temporal patterns in differences of activity-abundance levels among the habitats are discussed for five taxonomic groups (Entomobryomorpha and sminthurid collembola, Aranae, Coleoptera and ants). These groups were chosen because they have been the foci of most studies
Table 5-3  Results of univariate GLM analyses for mean activity-abundance levels of arthropods in four habitat types.

<table>
<thead>
<tr>
<th>Model term</th>
<th>Total arthropods</th>
<th>Entomobryomorpha Collembola</th>
<th>Sminthurid Collembola</th>
<th>Araneae</th>
<th>Coleoptera</th>
<th>Ants</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_{3,12}$</td>
<td>1.8</td>
<td>4.86</td>
<td>5.00</td>
<td>7.15</td>
<td>41.31</td>
<td>2.42</td>
</tr>
<tr>
<td>$P$</td>
<td>0.2</td>
<td>0.02</td>
<td>0.02</td>
<td>0.005</td>
<td>&lt; 0.001</td>
<td>0.11</td>
</tr>
<tr>
<td><strong>Sampling Date</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_{2,24}$</td>
<td>88.88</td>
<td>80.42</td>
<td>15.19</td>
<td>128.7</td>
<td>61.12</td>
<td>223.27</td>
</tr>
<tr>
<td>$P$</td>
<td>0.00</td>
<td>0.00</td>
<td>&lt; 0.001</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Year</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_{1,12}$</td>
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<td>13.31</td>
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<tr>
<td>$P$</td>
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<td>0.38</td>
<td>0.006</td>
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<tr>
<td><strong>Habitat x Date</strong></td>
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<td></td>
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</tr>
<tr>
<td>$F_{6,24}$</td>
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<td>9.74</td>
<td>4.5</td>
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<tr>
<td>$P$</td>
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<td>0.02</td>
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</tr>
<tr>
<td><strong>Habitat x Year</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_{3,12}$</td>
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<td>9.08</td>
<td>4.75</td>
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</tr>
<tr>
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<td>0.002</td>
<td>0.02</td>
<td>0.18</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Notes. Date x Year and Habitat x Date x Year interactions are not shown because sampling dates differed between years and therefore these are not valid interaction terms. Degrees of freedom for each model term are given as subscripts beside the "F" in the model term column. Significant $P$ values (< 0.05) are shown in boldface type.

about the effects of urban and non-urban habitat structure on ground arthropods and because their patterns are broadly representative of those seen for other taxa (Appendix J).

Activity-abundance levels of entomobryomorpha collembolans (Fig. 5-4B) did not differ among the habitats during the first two sampling periods in 2003 but tended to be greater in bark in October 2003 and May 2004, a pattern that was statistically significant in May when, on average, ~20 times more individuals were collected in bark than the other habitats. In June 2004, mean activity-abundance levels of these collembolans in bark plots were half that of the May 2004 level. In contrast, levels were 3, 14 and 4 times higher in June 2004 than May 2004 for lawn, unmowed and gravel plots, respectively. Mean levels were lower in all habitat plots in August 2004 (< 8 individuals trap$^{-1}$ 24hr$^{-1}$) except in one unmowed plot that averaged ~130 individuals trap$^{-1}$ 24hr$^{-1}$.

Sminthurid collembola mean activity-abundance levels tended to be higher in the unmowed habitat in June 2003 and were significantly higher in lawn and gravel habitats than all the others in July and October 2003, respectively (Fig. 5-4C). In October, levels were significantly higher in bark mulch plots that lawn and unmowed plots. In 2004, activity-abundance levels of sminthurids did not differ among the habitats in May but were significantly greater in lawn and gravel plots than unmowed and bark in both June and August (although the difference was much greater in June).

Mean activity-abundance levels of Araneae (spiders) were ~1.5-3 and ~2-4 times greater in bark plots than the other habitats in June and October 2003, respectively, whereas all the habitat
Figure 5-4. Mean (± SE) activity-abundance levels for (A) total arthropods, (B) entomobryomorpha collembola, (C) sminthurid collembola, (D) Aranae, (E) Coleoptera and (F) ants in four habitat types over six sampling period. Means with different letters for a given sampling period differ significantly (P <0.05) with least significant differences post-hoc comparisons. Results of GLM analyses are presented in Table 5-3. Although the effect of habitat type was not significant for total arthropods and ants, the habitat x date interaction term was significant for these taxa which permitted for post-hoc comparisons to be made among the habitat types for each sampling period. * denotes that the difference between lawn and bark in ant activity-abundance levels for July 29-30 approaches significance (P = 0.06). * denotes that the difference between lawn and bark in ant activity-abundance levels for June 23-25 approaches significance (P = 0.08). Inset graphs show data directly below them on an axis with a different scale for visual clarity.
Types had similar levels in July 2003. In June 2003, levels were significantly greater in unmowed plots than lawn and gravel plots which did not differ from each other. In contrast, no spiders were trapped in unmowed plots in October 2003 while significantly more were collected in lawn and bark plots with gravel plots having intermediate levels. Spider activity-abundance levels were consistently lower in 2004 than 2003 for all habitats except lawn in June when the level was more similar to 2003 levels and ~4 times more spiders were caught than in the other habitats.

For Coleoptera (beetles), mean activity-abundance levels in bark and lawn plots did not differ within each of the three 2003 sampling periods but they were greater than those in unmowed and gravel plots which were similar to each other and did not increase between June and July as they did in lawn and bark plots. Similar to the pattern for spiders, few beetles (means of <1 individual trap\(^{-1}\) 24hr\(^{-1}\)) were trapped in all the habitats across all 2004 dates except in June when significantly more were trapped in the lawn (~2 individuals trap\(^{-1}\) 24hr\(^{-1}\)).

Mean activity-abundance levels for ants were similar among the habitat types in June 2003 when there was high variability across all the habitat plots (range of 1.5-36 individuals trap\(^{-1}\) 24hr\(^{-1}\)) although bark plots tended to have lower levels (2.4-13.8 individuals trap\(^{-1}\) 24hr\(^{-1}\)) than the other habitats. In July 2003, levels in bark plots were significantly lower than those in unmowed and gravel plots and marginally (\(P = 0.06\)) lower than those of lawns. In October 2003, mean activity-abundance levels for ants tended to be greater in lawns than the other habitats (in which levels were similar) although this difference was not significant because few ants were collected in one of the lawn plots (mean of 1 individual trap\(^{-1}\) 24hr\(^{-1}\)). For all 2004 sampling periods, mean ant activity-abundance levels in vegetated plots were similar to each other but significantly greater than those in mulched plots which did not differ from each other.

**Discussion**

The effects of urbanization on biodiversity in general (McKinney 2002), and arthropods specifically (McIntyre 2000), have not been studied extensively. Most research on urban arthropods has focused on forest remnants (e.g., Niemalä et al. 2002) and management of pest species, e.g., in lawns (Fermanian et al. 2003). Additionally, a small number of studies have investigated the effects of lawn chemical applications on non-target, beneficial arthropods (e.g., Kunkel et al. 1999, Byrne and Bruns 2004). However, few comparisons have been made of arthropod communities inhabiting the wide spectrum of heterogeneous urban land covers (e.g., Nuhn and Wright 1979, McIntyre et al. 2001, Shochat et al. 2004). As far as is known, this is the first study in which arthropod
communities and activity-abundance levels were examined concurrently in experimental plots of lawn, bark mulch, gravel mulch and old field habitat types. Thus, it provides new insights into how spatial heterogeneity of habitat structures influences spatiotemporal patterns of arthropod communities and activity-abundance levels in urbanized landscapes.

Results support the hypothesis that arthropod communities would differ among the four urban habitat types (Fig. 5-2), but they do not follow the expectation that arthropods would be most abundant in old fields, least in gravel plots, and intermediate in lawn and bark plots. Instead, the activity-abundance data of most taxonomic groups were characterized by significant interactions between habitat type and sampling period (Table 5-3, Appendix I) due to temporal variation in numbers of arthropods collected from each habitat type (Fig. 5-4, Appendix J). Consequently, it appears that arthropod communities changed through time in different ways in each of the habitat types as supported by the RDA biplot (Fig. 5-3). These patterns were probably generated by three factors (air and surface temperature and resource availability) that interacted to differentially affect arthropod activity levels and abundances (and therefore communities) in each of the habitat types during each sampling period. Below, the potential influence of these factors on arthropod activity levels and abundances is summarized and followed by a discussion of possible relationships between characteristics of the habitat types and spatiotemporal patterns of the activity-abundance levels for the arthropod communities and five focal taxa.

Factors influencing arthropod activity-abundance levels

Air temperature. Because arthropods are ectothermic, their growth, reproduction and activity levels are sensitive to thermal conditions (e.g., Hutson 1978, Gilbert and Raworth 1996, McIntyre et al. 2001, Goldsborough et al. 2004). Thus, within and between year variations in their activity-abundance levels can be expected to be broadly related to macroclimate patterns (Kingsolver 1989). In this study, lower activity-abundance levels were observed during the sampling periods with the coolest air temperatures (May 2004 and October 2003) and the highest activity-abundance levels were seen during two warmer summertime sampling periods (July 2003 and June 2004; Table 5-1) in agreement with the general expectation that, across seasons, air temperature and arthropod activity-abundance levels should be positively related. However, across all sampling periods, air temperature was a relatively poor (all $R^2 \leq 0.16$), and mostly non-significant, predictor of arthropod activity-abundance levels because both high and low levels were seen across the four sampling periods that had similar, warm air temperatures (Figs. 5-1A, 5-4, Table 5-1; L. Byrne, unpublished
data. Fluctuations in activity-abundance levels that were unrelated to seasonal macroclimate patterns have been observed in previous studies of ground arthropods in lawns (Arnold and Potter 1987, Bramen and Pendley 1993, Rochefort et al. 2006), agricultural fields (e.g., Lys et al. 1994, Thomas et al. 2001) and forests (e.g., Badejo and Van Straalen 1993, Hasegawa 2002) suggesting that air temperature does not consistently influence, or reliably predict, fine-scale arthropod activity-abundance levels, especially among heterogeneous habitat types. However, it is unclear from this study whether air temperature exerted a greater influence on relative activity-levels or abundances across the sampling periods (e.g., did cooler temperatures limit activity levels or reduce abundances?). Additional research is needed to assess how macroclimate and air temperature patterns might have different relationships with arthropod communities, activity levels and abundances among heterogeneous urban habitat types.

Surface temperature. In general, ground arthropod activity-abundance levels might be expected to be more closely related to surface rather than air temperature. However, across habitat types and 2004 sampling periods, arthropod activity-abundance levels were not significantly or strongly (all $R^2 < 0.15$) related to surface temperatures (except for Orthoptera; Fig. 5-1B; L. Byrne, unpublished data). These results should not be interpreted to mean that surface temperatures do not influence arthropods. Rather, they suggest that surface temperatures alone do not determine activity-abundance levels across habitat types, especially when they co-vary with other habitat structural properties (e.g., resources). However, in this study, warmer mean surface temperatures may have increased arthropod activity levels in the mulch habitat types (Table 5-1) as compared to those in the vegetated plots. In turn, activity levels may have exerted a stronger influence on the overall activity-abundance levels in mulches than abundance (i.e., higher movement rates increased the probability that arthropods would fall into pitfall traps). Alternatively, thermal conditions in the mulches may have provided more or less favorable conditions for growth and reproduction for certain taxa and therefore affected their local abundances in the mulch plots. Crist and Ahern (1999) concluded that surface temperature may have driven spatiotemporal variation of ground beetle activity-abundance levels in mowed and unmowed vegetation. However, detailed measurements of surface temperature were not made in their study, and they did not discuss the influence of activity levels apart from abundance on the data. No other reports about relationships among surface temperatures and arthropod activity-abundance levels have been found in the literature that help provide insights into the results of this study. Future work is needed to tease apart the relative effect
of surface temperature on activity versus abundance levels in heterogeneous habitats. Such research will help interpretation of activity-abundance data collected in urbanized landscapes.

**Resource availability.** The habitat types in this study varied widely in their levels of resource availability which should have had a large influence on arthropod communities and activity-abundance levels. As revealed by the PCA analysis (Fig. 5-2), differences in communities among the habitat types were related to the presence and abundance of vegetation and detritus, both of which provide key resources (food, shelter) for many arthropods which, in turn, are resources for predatory arthropods. In addition, mulched plots had consistently higher soil water content (Fig. 3-4) which may have provided a resource needed by some arthropods. More challenging to discern is how fluctuations in resource availability within the habitat types may have contributed to temporal variation in arthropod activity levels and abundances among them, as exemplified by the following observations. In lawns, new detritus became available at mowing events but decomposed quickly making the availability of this resource highly variable. Also in lawns, the abundance of floral resources (e.g., pollen, nectar, seeds) changed through time as different plant species (e.g., dandelions, clover) bloomed which may have promoted higher activity-abundance levels in this habitat for certain taxa (e.g., beetles, ants) at different times (L. Byrne, personal observation; Harmon et al. 2000). In bark plots, temporal variability of fungal growth on the mulch (caused by, e.g., precipitation events and time since application) may have influenced the activity-abundance levels of arthropods (e.g., collembolans) that consumed this resource (L. Byrne, personal observation). In unmowed plots, detritus was abundant and provided a continuously available resource which might be expected to prevent wide fluctuations in arthropod activity-abundance levels. In contrast, vegetative and detrital resources were almost non-existent in gravel plots during all sampling periods suggesting that fluctuations in food resources was probably not a driver of variability of arthropod communities and activity-abundance levels in this habitat type.

Following these observations, two mechanisms related to resource availability may have influenced temporal variability in arthropod activity-abundance levels in this study: 1) increases in resources within a habitat type that led to higher arthropod abundances (and perhaps activity) or 2) decreased resource availability that caused higher activity levels due to increased movement rates as arthropods more actively searched for the limited resources. Although it is not clear in this study how spatiotemporal changes in arthropod communities and activity-abundances may have tracked fluctuations in resource availability in the habitats, previous research has shown that both vegetation and detritus are primary drivers of arthropod community and population dynamics (e.g., Andow
1991, Langellotto and Denno 2004). Additional discussion about the effects of resource availability on differences in activity-abundance levels among the habitats is provided in the next section.

Spatiotemporal variability in activity-abundance levels

For brevity, the focus of this section is limited to some of the more prominent differences in activity-abundance levels among the habitat types for the five focal taxonomic groups (Fig. 5-4). However, as described above, similarity of activity-abundance levels among the habitat types for a given sampling period does not necessarily indicate that arthropod abundances were similar among them for that period. Activity levels could have had varying degrees of influence on collection of arthropods in pitfall traps among the habitats because of differences in their surface temperatures and density and arrangement of matter. Although animal movement rates in the habitat types were not quantified in this study, field observations suggest that activity levels especially influenced the activity-abundance data for gravel and unmowed habitat types because arthropod movement rates within them were comparatively higher and lower, respectively. As such, activity-abundance levels probably represent over- and underestimates of the actual arthropod abundances in gravel and unmowed plots, respectively. Nonetheless, for discussion purposes here, significant differences in activity-abundance levels among the habitat types is assumed to reflect relative differences in their arthropod abundances and community structure.

Entomobryomorpha collembola. Mean activity-abundance levels of entomobryomorpha collembola were higher in bark plots than those of the other habitat types in October 2003 and May 2004 (Fig. 5-4B). Key factors that may have contributed to this pattern were dense fungal growth (L. Byrne, personal observation) and wetter soil conditions (Fig. 3-4) in the bark plots that may have provided more suitable habitat conditions for survival and reproduction and thus promoted increased reproduction or immigration rates in bark plots at these times. At other times of the year, daytime ground (and sometimes soil) temperatures in bark (and gravel) plots (Appendix H; see also Chapter 3) often exceeded the temperatures that have been reported as most ideal (~15-20°C) for maximum collembolan survival and reproduction (Snider and Butcher 1973, Hutson 1978). Thus, it seems likely that mulched plots were not suitable for collembolan reproduction throughout the year.

Although there was high variability in activity-abundance levels for entomobryomorpha collembola within each habitat type, the highest levels seen during this study were in unmowed plots during July 2003 and August 2004. This suggests that, despite high spatial variability, unmowed habitats might be the most suitable habitat type overall because of its cooler daytime
temperatures during the summer months (Appendix H) and its complex detritus structure which, especially as compared to lawns, provides more abundant food resources and greater possibilities for avoiding predators. This is in contrast with the conclusion made by Byrne and Bruns (2004) that entomobryomorphans might increase in abundance in lawns because of abundant mowed clippings; however, they collected collembola from soil cores rather than pitfall traps and may have collected different species than the ones driving patterns in this study.

*Sminthurid collembola.* In contrast to the entomobryomorpha collembola, more sminthurid collembola were trapped in lawns than the other habitat types during each year of this study (Fig. 5-4C). This pattern also contrasts with the conclusion made by Byrne and Bruns (2004) that lawns should be less favorable habitat than unmowed fields for sminthurids. However, Rochefort et al. (2006) also found that sminthurid collembolans could become abundant in lawns (although they made no comparisons to other habitat types). Reasons why sminthurids might become abundant in lawns as compared to other (especially unmowed) habitat types are unknown. They may have preferred the higher quality (i.e., low C:N) detritus or thermal conditions in lawns more than the other habitats. Alternatively, activity levels of sminthurids could have been very high in lawns giving rise to a much higher probability of being trapped relative to the other habitat types. This seems unlikely however because detritus and thermal conditions in lawns were not as temporally variable as the number of sminthurids trapped (e.g., mean ground temperatures were similar between June and August 2004 but sminthurid numbers decreased).

Also unclear in this study is the reason why sminthurid activity-abundance levels increased in gravel plots to significantly higher levels than the other habitat types in October 2003. As described above for the relationship between entomobryomorpha collembola and bark mulch, sminthurids may have found the combination of daytime thermal conditions and soil moisture levels more favorable in the gravel plots during the autumn. However, given that gravel plots contained no organic matter on which collembolans could feed directly or from which they could graze fungi, it seems unlikely that gravel mulch would have provided more favorable habitat in October 2003 than at other times. Certainly it is possible that other, unknown factors led to higher activity levels or abundances of sminthurids in both gravel and lawn plots. Research to examine other possibilities is clearly needed.

*Aranae.* In an urbanized desert landscape, Shochat et al. (2004) found that spiders were more abundant in lawns than desert remnants and industrial land uses. They concluded that habitat structure was a strong driver of spatiotemporal patterns in spider communities. Habitat structure
also appeared to influence spatiotemporal patterns of arthropod activity-abundance levels in this study although no clear relationships were seen (Fig. 5-4D). Patterns of spider activity-abundance levels were not similar to those of their potential prey groups (e.g., collembola, hemiptera) suggesting that spider activity-abundance levels varied independently of prey availability. However, pitfall trap data may not reflect *in situ* prey availability such that relationships between spiders and prey in the four habitat types cannot be reliably discerned from this study. It is possible that, as for collembola, interactions between resource availability and thermal conditions influenced the spatiotemporal variability of spider activity-abundance levels in unknown ways. For example, it has been observed that spiders will seek out microhabitat conditions that are most favorable for their growth and reproduction (Goldsbrough et al. 2004). Nothing is currently known about the diversity of microhabitat conditions potentially created (but not measured in this study) by mulches and lawns and how spiders might use them.

Alternatively, it is possible that mechanisms unrelated to habitat structure (e.g., biotic interactions, juvenile dispersal) influenced the distribution and movements of spiders across the experimental field and caused the perplexing habitat x date interactions seen in the data (especially between the June and July 2003 sampling periods). This would be especially likely if highly mobile ground-dwelling spiders moved readily across boundaries between habitat types which were located in close proximity to each other. However, given that strong relationships between spiders and habitat structure have been seen in many other studies (see reviews in Uetz 1990, Sunderland and Samu 2000, Langellotto and Denno 2004), it seems unlikely that spider activity and abundance patterns would not be affected at some level by the heterogeneous types of habitat structure included in this study.

**Coleoptera.** As for spiders, many studies have shown that beetle populations are influenced by habitat structure (e.g., Dennis et al. 1994, Lys et al. 1994, Brose 2003, Grandchamp et al. 2005). However, very few have compared beetles’ interactions with different types of urban ground cover (McIntyre et al. 2001). In this study, more beetles were collected from lawn and bark plots than gravel and unmowed plots during all sampling periods in 2003 and from lawns than the other habitat types in June 2004 (Fig. 5-4E). In a previous study of grasslands, beetles increased in number in mowed and grazed fields as compared to unmanaged ones (Grandchamp et al. 2005) and they have previously been collected in large numbers in urban lawns (e.g., Cockfield and Potter 1984, Bramen and Pendley 1993, Kunkel et al. 1999). Thus, lawn mowing appears to create conditions that increase the overall activity and/or abundance of beetles. In this study, numerous
species of plants colonized lawns that were not found in unmowed plots (e.g., dandelions, clover, plantain; see Chapter 3). Flowers of these plants may have provided extra resources (e.g., seeds, pollen and nectar) for omnivorous beetles thus leading to their increased reproductive capacity and abundances in lawns as compared to the other habitat types (e.g., Lys et al. 1994, Harmon et al. 2000).

Given that plant resources were not present in bark plots, it is unknown why beetle activity-abundance levels would have been similar between bark and lawn plots. However, fungi on the bark or the bark mulch itself could have served as a food resource for some species, or perhaps the warmer daytime conditions were more favorable for beetle growth and reproduction (e.g., Gilbert and Raworth 1996, Ernsting and Isaaks 2000). Alternatively, the architectural complexity of bark mulch may have provided preferable enemy-free space (as it could have for all arthropod groups) (Brose 2003). Strikingly however, beetle activity-abundance levels in bark plots in 2004 did not reach the levels seen in 2003 even though those in lawns were higher in June 2004. Such unexplainable temporal variation reflects the need for additional studies of longer duration to thoroughly assess how relationships between ground arthropods and urban habitat structures vary though time.

Ants. In an early study of urbanized landscapes, Nuhn and Wright (1979) observed that ant activity levels and distribution of ant nests were related to spatial patterns of habitat structure, especially that of vegetation. In this study, more ants were collected from the vegetated plots than the mulched plots in 2004 (Fig. 5-4F) suggesting that lawn and unmowed plots provided more favorable resource availability and environmental conditions. Whereas lawns may have provided more floral resources (e.g., seeds, pollen), unmowed plots may have been more suitable locations for nests because of their cooler ground and soil temperatures. This is supported by the observations of Nuhn and Wright (1979) that more ant nests were located in forests and under shrubs than in sunny lawns.

In 2003, differences in ant activity-abundance levels between vegetated and mulched plots were not as distinct. This might be attributable to a delayed response by ants to the disturbance of their habitat from experimental plot creation. Thus, ant nests covered by mulches in late April 2003 could have remained occupied through July 2003 but abandoned (or relocated) by May or June 2004. The response of ants to bark mulch additions appears to have been more rapid than that to gravel because ant activity-abundance levels were much lower in bark plots than all the other habitat types in July 2003. However, as noted by Nuhn and Wright (1979) (and as can be easily
observed in any urbanized landscape), some ant species readily build nests and forage in locations without vegetation cover (e.g., paved sidewalks). It was not determined in this study whether differences in ant activity-abundance levels among the habitat types was influenced by the location of ant nests or their aboveground foraging activities. However, it seems likely that alteration of habitat structure affected both the spatial patterns of ant nests and aboveground foraging activities (e.g., see Braschler and Baur 2003).

**Spatiotemporal variability in arthropod communities**

It is clear from this study (Fig. 5-2) and others (see studies cited previously and review by Langellotto and Denno 2004) that habitat structure strongly influences local abundances of ground dwelling arthropods and, thus, community structure at any given time. Fewer studies have examined how the effects of spatial variation in habitat structure on spatiotemporal fluctuations of arthropod activity-abundance levels might generate spatiotemporal variation in community structure and dynamics (e.g., food web patterns) across heterogeneous landscapes (but see Gardner et al. 1995, McIntyre et al. 2001, Thomas et al. 2001, Perner and Malt 2003).

In this study, arthropod activity-abundance levels changed through time in significantly different ways among various types of habitat structure (i.e., habitat x date interactions; Table 5-3, Appendix I), thereby causing significantly different temporal patterns of community structure in each (Fig. 5-3). Although examination of trophic interactions was outside the scope of this study, spatiotemporal changes in community structure among the habitat structure plots could have generated (or been caused by) spatiotemporal variation in food web dynamics among the habitat types (Polis et al. 2004). For example, spatial shifts in activity-abundance levels of predatory beetles (Fig. 5-4) and spiders (Fig. 5-4D) could have impacted spatiotemporal patterns of collembola (or other prey) populations due to predation or behavioral responses by collembola to increased predator abundances within a habitat type (e.g., Grear and Schmitz 2005). Alternatively, fluctuating abundances of collembola among the habitat types could have led to concurrent spatial shifts in predator abundances and/or activity (e.g., spatiotemporal shifts in bottom-up trophic cascades; e.g., Chen and Wise 1999).

Central to understanding such spatial and temporal shifts in community and trophic dynamics is investigation of temporal patterns of organisms’ movements across heterogeneous landscapes, especially as they relate to fluctuating resources availabilities and environmental conditions in different habitat types (Johnson et al. 1992, Wiens et al. 1993, Leibold et al. 2004).
Results of this study suggest that ground arthropods and urban habitat types might provide an appropriate experimental model system (sensu Wiens et al. 1993) with which to address broader ecological questions about the interactive effects of environmental heterogeneity and animal movements on spatiotemporal variability in the structure of communities and their trophic dynamics (e.g., Polis et al. 2004, Leibold et al. 2004, Knight et al. 2005, Cottenie 2005, Denno et al. 2005).

Conclusions

During the process of urbanization, humans profoundly alter patterns of habitat structure and, in turn, biodiversity (McKinney 2002). Currently, very little is known about the ability of common urban habitat types (e.g., lawns and gardens) to provide suitable habitat space for most organisms, especially arthropods (McIntyre 2000). In this study, ground arthropods were sampled from experimental plots of lawn, shredded bark mulch, gravel mulch and old field vegetation to examine how arthropod activity-abundance levels and communities differ among distinctive types of urban habitat structure.

Results show that communities and activity-abundance levels for each arthropod group differed significantly among the habitat types and sampling periods. However, no clear relationships between habitat type and activity-abundance levels were observed across arthropod groups or within each group, thus precluding stronger conclusions about the suitability of each habitat type for ground arthropods. Instead, temporal patterns of activity-abundance levels for each group differed significantly among the habitat types, yielding statistically significant interactions between habitat type and sampling period for most groups. It is concluded that spatiotemporal variation in arthropod communities and activity-abundance levels among the four habitat types was influenced, in part, by temporal variability in resource availability (e.g., seeds, fungi, prey) and arthropod preferences for certain environmental conditions (e.g., warmer surface temperature) among the habitat types. Although future work is needed to explore underlying mechanisms, this study has clearly shown that spatial variation in habitat structure can give rise to significant spatiotemporal variation in arthropod communities and activity-abundance levels. Thus, the experimental landscape examined in this study might be useful for developing future projects that address questions currently emerging within the field of ecology about how temporal variability in organism movements among different habitat types affect community and food web dynamics (e.g., Polis et al. 2004, Leibold et al. 2004).
In addition to their relevance for exploring basic ecological theories, experimental landscapes composed of urban habitat types are valuable for examining applied questions related to the conservation of beneficial arthropods in urbanized landscapes. In particular, research is needed about the suitability of common types of urban habitat structure to promote the survival, reproduction, and favorable activity levels of beneficial arthropods such as predators that consume lawn pests (Cockfield and Potter 1984, Bramen and Pendley 1993, Fermanian et al. 2003). In addition, manipulating habitat structure patterns across landscapes can influence the spatial dynamics of arthropod activity-abundance levels as shown in this study and others (see Langellotto and Denno 2004, Denno et al. 2005). Therefore, data about both the composition and spatial patterns of habitat structure are needed to guide the design and management of urbanized landscapes in which the activity-abundance levels of beneficial arthropods are maximized throughout the year. Hopefully, this study has provided insights about how the next research steps might be taken in order to increase our knowledge about the spatiotemporal dynamics of arthropod communities in urbanized landscapes.

References


Chapter 6. Effects of landscape context habitat heterogeneity on ground arthropod communities and activity-abundance levels

Abstract

Despite increasing appreciation among ecologists that regional landscape patterns can strongly influence local ecological patterns and processes, knowledge about the effects of broad-scale environmental heterogeneity (i.e., landscape context) on local ecological dynamics remains limited. In this study, an experimental microlandscape system was designed to test the hypothesis that arthropod communities and activity-abundance levels would differ among six microlandscapes that differed in the number (0, 1, 3, or 9) and composition (unmowed vegetation or unmowed vegetation and mulch habitats) of the habitat patches surrounding a central area of mowed lawn. Urban habitats were used to fulfill the applied objective of generating information about how urbanized landscapes can be designed to increase the potential control of lawn pests by predatory arthropods. Each of the six microlandscapes was replicated four times in 10 x 10m plots in an old field. Ground arthropods were sampled with two pitfall traps from the central lawn patch of each microlandscape. Multivariate ordination analyses showed that arthropod communities differed significantly between the microlandscapes composed only of lawn and those containing non-lawn habitat patches. Few significant differences were detected in arthropod activity-abundance levels among the microlandscape patterns. However, they tended to be higher in microlandscapes containing non-lawn habitat patches for several taxa especially spiders, collembola, ants and orthopterans. The primary conclusions drawn from this study are that 1) landscape context influenced the structure of arthropod communities and tended to increase their activity-abundance levels in central patches of lawn and 2) the specific habitat types found in the landscape context exerted a stronger influence on the arthropod communities than the overall patchiness or heterogeneity. It is suggested that the effects of landscape context were driven largely by differences in patterns and rates of arthropod movements within each microlandscape. Data showed that one small (3m x 3m) patch of unmowed habitat increased the activity-abundance levels of arthropods in adjacent lawns but that further increases in landscape heterogeneity did not lead to additional increases. Additional studies are needed to investigate the underlying mechanisms of the patterns seen in this study and how the habitat composition of urbanized landscapes affects the spatial patterns of arthropod abundances and their trophic interactions. Future studies on the ecological effects of landscape context can benefit from the use of urban habitats and landscapes because they are highly heterogeneous in resources and environmental conditions.
Introduction

All organisms inhabit environments that are heterogeneous for many variables across space and time. Although generally avoided historically, the explicit study of environmental heterogeneity has become a prominent theme in ecology over the past two decades (Kolasa and Pickett 1991, Hansson et al. 1995, Lovett et al. 2005). This is exemplified by rapid growth in the field of landscape ecology which focuses on the ecological causes and consequences of environmental heterogeneity (Turner 2005a, b). An important insight gained from landscape-scale studies is that spatial heterogeneity of, e.g., resources, land cover, and disturbance over broad scales influences ecological patterns and processes at local scales. Thus, understanding the ecological dynamics of a particular location is incomplete without considering how they are affected by patterns and processes within the surrounding environment, i.e., within the landscape context (Ricklefs 1987, Mazerolle and Villard 1999, Lawton 2000).

Landscape context patterns can influence the abundance and diversity of organisms at a location by altering dispersal patterns (Ricketts 2001, Haynes and Cronin 2003), trophic interactions (Donovan et al. 1997, Elliott et al. 2002, Harman et al. 2003, Purtauf et al. 2005a), and the spatial extent and distribution of resources and suitable habitat (Andrén 1994, Norton et al. 2000, Brotons et al. 2003, Bergman et al. 2004). Most studies of landscape context have been conducted in agricultural ecosystems where it has been shown that the abundance and diversity of arthropods in cropped fields were positively related to the area of non-crop habitat (e.g., grassland, forest) in the surrounding landscape with potential consequences for pest control (Lys et al. 1994, Menalled et al. 1999, Thies and Tscharntke 1999, Tscharntke et al. 2002, Elliott et al. 2002, Purtauf et al. 2005b) and pollination (Steffan-Dewenter et al. 2002). Similarly, increased landscape complexity has been found to affect the arthropod communities and food web dynamics in urban habitats (Tooker and Hanks 2000, Bramen et al. 2002, Frank and Shrewsbury 2004, Rebek et al. 2005). In these studies, differences in the communities among patches of focal habitat types (i.e., crop fields, lawns) were attributed to differences in landscape context patterns that mediated the abundance of organisms moving from the surrounding landscape into the focal habitat patches.

While the above studies clearly indicate that landscape context can affect local communities within a habitat patch, landscape context does not exert a uniform influence across ecosystems, taxa or spatial scales (e.g., Steffan-Dewenter et al. 2002, Jeanneret et al. 2003). In their literature review, Mazerolle and Villard (1999) found that landscape context was an important factor influencing animal communities in 59% of studies but that vertebrates were affected to a greater degree by
landscape context patterns than invertebrates. More recent research supports (Collinge et al. 2003, Stoner and Joern 2004) and contradicts (Lindenmayer et al. 1999, Norton et al. 2000, Tscharntke et al. 2002) this conclusion. However, too few studies have been conducted to date to justify strong general predictions about the effects of landscape context relative to those of local (i.e., within-patch) variables. Generalizations may prove to be elusive if, as many authors have suggested, organism and local community responses to landscape context are highly species-specific and dependent upon the scale and location of study (Andrén 1994, Söderström et al. 2000, Steffan-Dewenter et al. 2002, Burel et al. 2003, Dauber et al. 2003, Jeanneret et al. 2003). Additional studies, especially ones with manipulative field experiments, are needed to help clarify relationships between landscape context patterns and the structure of local communities.

The objective of the current study was to use an experimental microlandscape system (EMS; sensu Wiens et al. 1993) to test the hypothesis that abundances and communities of ground arthropods would differ among patches of a focal habitat type (lawn) that differ in their landscape context patterns. Lawns and ground arthropods were chosen as foci for this study to fulfill a secondary, applied objective of generating information about how landscape patterns might be managed to increase the number of beneficial arthropods (e.g., predators and detritivores that consume pests and detritus, respectively) in lawns (e.g., Bramen et al. 2002). Thus, experimental microlandscapes were created using habitat types (mulches, unmowed vegetation) that are commonly found in urbanized landscapes and that might provide different degrees of suitable habitat for ground arthropods.

Because very little is known about how arthropod communities differ among urban habitat types (McIntyre 2000), it is not clear how landscape context patterns composed of non-lawn urban habitat types might influence ground arthropods in adjacent lawns. However, it was assumed for this study that the non-lawn habitat types would, in general, provide favorable resources or environmental conditions for ground arthropods and increase their total numbers within each microlandscape. As such, it was expected that arthropod numbers in a central patch of lawn would be positively related to the proportion of non-lawn habitats in its landscape context (see Fig. 6-1).

**Methods**

**Study site**

This study was conducted in the same experimental field at the Penn State University Russell E. Larson Agricultural Research Station as described in detail in Chapter 3 (pp. 20-21;
Appendix A). Briefly, the experimental microlandscape plots (see below) were created in a level to gently sloping, well drained old field that had not been managed (apart from once a year mowing) for the past 25 years (S. Harkom, farm manager, personal communication). Prior to creation of experimental plots, the plant community was dominated by the grasses *Dactylis glomerata* (orchardgrass) and *Poa pratensis* (Kentucky bluegrass).

**Experimental design**

Six microlandscape patterns (Fig. 6-1) were designed for this study. Each differed in the number (0, 1, 3, or 9) and composition (all unmowed or combinations of unmowed and mulch habitats) of the non-lawn habitat patches (each 3m x 3m or 4m x 4m) in the landscape context around a central area of lawn (4m x 4m). The six designs encompassed two series of microlandscapes: one in which the landscape context around the central lawn increased in habitat patchiness (designs L, 1P, 3P and 9P in Fig. 1) and one in which levels of habitat patchiness and heterogeneity in the landscape context increased (designs L, 1P, 3H, 9H in Fig. 1). The two series were designed to determine if the effects of increasing habitat patchiness (i.e., number of distinct habitat patches) on arthropod communities in the central lawn differed from the effects of increasing habitat heterogeneity (i.e., number of habitat types).

Each of the six microlandscape patterns was applied to four replicated 10m x 10m plots in the experimental field arranged in a randomized complete block design. (The lawn plots were the same ones used for analyses described in Chapters 3, 4 and 5. The other microlandscape plots used in this study were interspersed with the 10m x 10m habitat structure plots described in Chapter 3.) Three-meter strips of mowed vegetation separated all microlandscape plots.

Plots were created in late April 2003. Areas of lawn in each plot were mowed regularly with a push rotary mower to maintain vegetation heights of 5-7cm. Patches of unmowed vegetation were not managed throughout the study period. Bark and gravel mulch patches were created by killing vegetation with an herbicide application (glyphosate) and removing dead aboveground vegetation by gentle raking. Double-shredded, hardwood bark mulch and limestone gravel (2-4cm diameter rocks) mulch were purchased from a local supplier and applied to their respective patches to 5cm depth. Weeds were removed by hand from the mulch patches throughout the growing season. Mulches were not reapplied in 2004. These four habitat types are shown and described further in Appendix B.
To complete the design of microlandscape 9H, a fifth habitat type was needed for two patches. In these patches, vegetation was mowed in May 2003 and a thick layer of mowed vegetation clippings—obtained by raking up clippings from the mowed aisles between plots—was applied. These clippings decomposed quickly (within a month) and appeared to fertilize the vegetation in these patches which were noticeably greener than the adjacent unmowed patches (L. Byrne, personal observation). Once-a-year-mowing of these patches changed the growth dynamics of the vegetation and, with added grass clippings, created a habitat that differed in quality from the other unmowed patches. These patches received no other management inputs in 2003 but were mowed once again in late April 2004 when they received another dense application of mowed vegetation clippings.

**Arthropod sampling and sorting**

Ground-dwelling arthropods were sampled from the central lawn patch of each microlandscape using two pitfall traps located approximately two meters from each other and one
meter from the nearest non-lawn patch. (One of the pitfall trap locations in the lawn plots (L in Fig. 1) was the same as that used for collecting arthropods in the study of Chapter 5.) The design and installation of pitfall traps and general sampling protocols were the same as described in detail in Chapter 5 (pp. 97-98). Arthropods were sampled over three 24-hour periods in 2003 (June 15-16, August 20-21, October 13-14) and four 48-hour periods in 2004 (May 4-6, June 23-25, August 10-12, September 21-23). The sampling duration was extended in 2004 to increase the number of individuals collected for some taxonomic groups. However, 2004 data were halved to standardize them with 2003 data. All arthropod data are reported as indices of arthropod activity-abundance levels because both local abundances and activity levels of arthropods influence the probability of capturing individuals in traps (see p. 98 for further discussion).

Collected arthropods were identified and quantified at the ordinal level following keys in Borror et al. (1989) except for collembolans which were sorted into three subordinal eco-morphological groups (entomobryomorpha, poduromorpha and symphypleona; see Fig. 2-1 for descriptions and drawings), and hymenopterans which were separated into ants (Family Formicidae) and wasps (many families). Eleven arthropod taxonomic groups were enumerated: entomobryomorpha collembola, sminthurid collembola (family Sminthuridae of the symphypleona group), Aranae (spiders), Coleoptera (beetles), ants, wasps, Hemiptera, Diptera (flies), Orthoptera (grasshoppers and crickets), Diplopoda (millipedes) and Isopoda (isopods). Individuals from other taxa (including Poduromorpha collembola) were not included in analyses because they were trapped in very low numbers. Most specimens were stored in vials with 70% alcohol; larger specimens (e.g., grasshoppers) were pinned.

Analyses

Multivariate analyses. Differences in arthropod communities among the six microlandscape patterns were assessed using two multivariate ordination methods, principal components analysis (PCA) and redundancy analysis (RDA), which are described in more detail on pp. 100-101. Briefly, PCA was used to extract hypothetical axes (gradients) of variation in the arthropod data set and graphically display relationships among the axes, taxonomic groups, and samples in ordination (biplot) diagrams (Lepš and Šmilauer 2003). RDA extracts axes of variability from the data that are constrained by known environmental variables and assesses their significance using Monte Carlo permutation tests (Lepš and Šmilauer 2003). In this study, RDA was used to determine if arthropod communities differed among the lawns of the six microlandscape patterns. Because community
differences among the microlandscapes were the primary interest in this study rather than temporal variability, activity-abundance data were averaged across all seven sampling dates for the PCA and RDA analyses (i.e., four mean data points for each microlandscape design) which were completed using CANOCO version 4.5 (ter Braak and Šmilauer 2002). Variation due to experimental block was removed by including it as a covariable in both analyses. General methods for interpreting biplots are given in Table 5-4 (p. 104) and in Lepš and Šmilauer (2003).

**Univariate analyses.** General linear models (GLM) were used to assess differences in mean activity-abundance levels (i.e., number of individuals pitfall trap$^{-1}$ 24 hrs$^{-1}$) among the microlandscape patterns for each arthropod taxonomic group and total number of arthropods. In these analyses, microlandscape pattern and sampling date were used as between- and within-subjects factors, respectively, and their interaction terms were also examined. Post-hoc comparisons were conducted with least significant differences tests. Because the number of sampling dates was unequal between the two years, a second GLM analysis was performed using the means across sampling dates within each year to test for differences between the years in activity-abundance levels and interactions between year and microlandscape pattern for each taxonomic group and total number of arthropods. For all these analyses, data were log-transformed to meet the assumptions of the GLM; untransformed data are presented in the figures. Block was included in all initial analyses but was never significant and was removed from final analyses. Significant differences were assessed at $P < 0.05$; however, differences that approached this significance level ($P < 0.1$) are denoted in the figures to indicate potentially important biological trends in the highly variable data. GLM analyses were conducted with Statistica 6.1 (StatSoft, Tulsa, OK).

**Results**

**Multivariate analyses.** The PCA analysis extracted two hypothetical axes that together explained 42.8% of the variation in the community-level arthropod data (after controlling for experimental block). Examination of the PCA biplot (Fig. 6-2) suggests that each of the axes seems to be associated with one of the series of microlandscape patterns (Fig. 6-1). Axis 1 (explaining 24.5% of the variation) largely reflects a gradient of increasing patchiness and heterogeneity in the landscape context of the central lawn patch (from left to right). The sample points of the microlandscapes containing only lawn (L) fall to the far left of the plot while the points for the microlandscapes with greater levels of habitat heterogeneity in the landscape context (3H and 9H) fall toward the right of the plot. Points representing the microlandscape with one unmowed patch in
the landscape context (1P) are located more centrally along Axis 1, reflecting the intermediate level of patchiness and heterogeneity in the landscape context of this microlandscape design. Three taxonomic groups (wasps, sminthurid collembola, Coleoptera) were disproportionately found in the 3H and 9H microlandscapes as compared to the L and 1P microlandscapes as indicated by the directions of their associated arrows. Three taxonomic groups (Orthoptera, Diplopoda, Isopoda) were found more often in the heterogeneous (3H, 9H) and plots containing only lawn (L) as compared to the microlandscapes with only unmowed patches (1P, 3P, 9P).
Axis 2 of the PCA (explaining 18.3% of the variation) appears to reflect the presence or absence of unmowed habitat patches in the landscape context (from bottom to the top of the axis). All the points for the microlandscapes with only lawn (L) fall toward the bottom of the axis whereas all the points associated with the microlandscapes containing unmowed patches in the landscape context (1P, 3P, 9P) are in the upper area of the biplot (Fig. 6-2). Four taxonomic groups (Diptera, Aranae, Entomobryomorpha collembola, ants) were disproportionatly found in the microlandscapes containing only unmowed patches (1P, 3P, 9P) as compared to lawn only plots (L) and the two heterogeneous microlandscapes (3H, 9H). Additionally, the points for the plots with only unmowed patches microlandscapes (1P, 3P, 9P) do not form distinct clusters, suggesting that the arthropod communities did not differ among these microlandscapes. However, it appears from the PCA biplot that these microlandscapes (1P, 3P, 9P) had different communities than those with greater habitat heterogeneity (3H, 9H). These interpretations of the two PCA axes are supported by the arrows associated with each of the microlandscape patterns that were passively (i.e., post-hoc) projected onto the biplot.

The two primary constrained axes extracted by the RDA analysis explained 74.3% of the arthropod community data with Axes 1 and 2 accounting for 45.3% and 29%, respectively. The Monte Carlo analyses showed that the arthropod communities from the lawn-only microlandscapes (L) differed significantly ($P = 0.002$) from the communities of all other microlandscape designs. The communities of the two heterogeneous microlandscapes (3H and 9H) differed significantly ($P \leq 0.02$) from each other and the communities of all the microlandscapes with only unmowed patches (1P, 3P, 9P) which did not differ from each other. The RDA biplot (Fig. 6-3) was almost identical to the PCA biplot in the direction of the arrows for the taxonomic groups and microlandscape patterns, thus supporting the interpretation of the PCA axes given above.

**Univariate analyses.** No consistent patterns in mean activity-abundance levels were found for any of the arthropod taxonomic groups among the microlandscape patterns or across the sampling dates (Fig. 6-4). Levels were highly variable among the sampling dates and within each of the microlandscape treatments (i.e., large standard errors around the means). In general, mean activity-abundance levels tended to be greater in the microlandscapes containing non-lawn habitat types than the lawn-only plots for certain taxonomic groups (e.g., Aranae, ants, wasps), especially on dates when activity-abundance levels were highest. However, significant differences ($P < 0.05$) in activity-abundance levels among the six microlandscape patterns were found only for total arthropods in June 2004 and Orthoptera in August 2003 and June and August 2004 (Table 6-1; see
Figure 6-3. Ordination diagram (biplot) from redundancy analysis (RDA) of arthropod activity-abundance levels averaged across seven sampling periods and constrained by microlandscape patterns as environmental variables. Labels of microlandscape arrows correspond to the microlandscape designs shown in Fig. 6-1.

Fig. 3-4 for differences among the microlandscapes). Although the effect of microlandscape pattern was significant for Coleoptera and Wasps in the GLM, no significant differences were detected in post-hoc analyses for these groups.

The effect of microlandscape pattern approached significance ($P = 0.06$) for Entomobryomorpha collembola but differences among the activity-abundance levels for this group were only marginally significantly different ($P = 0.07$) among the microlandscape treatments in June 2003 when mean levels were lower in the lawn only plots (L) than all the other microlandscape patterns. Similarly, differences in mean activity-abundance levels of sminthurid collembola were marginally significant ($P = 0.07$) for one sampling period (June 2004) when levels tended to be higher in the microlandscapes with 9 patches of unmowed habitat (9P). (The significant
Figure 6-4. Mean (± SE) activity-abundance levels of (A) total arthropods, (B) entomobryomorpha collembola, (C) sminthurid collembola, (D) Aranae, (E) ants and (F) Orthoptera, (G) Diplopoda, (H) Isopoda, (I) Hemiptera, (J) Coleoptera, (K) wasps and (L) Diptera in six microlandscape treatments that differ in the landscape context patterns around a central patch of lawn. Labels for each of the microlandscapes (e.g., L, 1P) correspond to the designs shown in Fig. 6-1. * denotes $P < 0.1$, ** $P < 0.05$ and *** $P < 0.01$ in least significant differences post-hoc comparisons.
Figure 6-4 continued.
Table 6-1  Univariate GLM results for mean activity-abundance levels of arthropods in six landscape treatments.

<table>
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<th>Model term</th>
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<th>Sminthurid Collembola</th>
<th>Arane</th>
<th>Ants</th>
<th>Orthoptera</th>
<th>Diplopoda</th>
<th>Isopoda</th>
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Notes. A separate GLM analysis was conducted to test effects of year and year x habitat interaction because number of sampling dates was not equivalent between the two years of this study. Degrees of freedom for each model term are given as subscripts beside the "F" in the model term column. Significant P values (< 0.05) are shown in boldface type. Ento. denotes Entomobryomorpha.
microlandscape x date interaction (P = 0.0008) in the GLM permitted the post-hoc comparisons for this taxonomic group."

Differences among the sampling dates in activity-abundance levels were significant for nine of the 12 taxonomic groups examined (Table 6-1). Activity-abundance levels were higher for total arthropods and most taxonomic groups in June 2003 and June or August 2004. Interactions between sampling date and microlandscape pattern were significant only for sminthurid collembola and Orthoptera. The mean number of arthropods sampled over a 24 hour period (averaged across the sampling periods within each year) differed significantly between the years for seven taxonomic groups; however, no clear patterns in the effects of year on activity-abundance levels were apparent. No significant interactions between year and microlandscape patterns were detected for the activity-abundance levels for any taxonomic groups.

Discussion

Patchiness and heterogeneity are inherent properties of all landscapes, and all habitat patches are embedded in heterogeneous landscapes. A major challenge for ecologists is to investigate how patterns and processes across landscapes (i.e., regional variables) influence the local ecological dynamics within habitat patches (Ricklefs 1987, Mazerolle and Villard 1999, Lawton 2000, Turner 2005a, b). Although a foundational body of research has shown that variation in landscape context patterns generates differences in communities among patches of a focal habitat type (e.g., Donovan et al. 1997, Tscharntke et al. 2002, Elliott et al. 2002, Purtauf et al. 2005b), current understanding about relationships between landscape context patterns and local communities is limited by a paucity of studies, especially experimental ones. The current study was designed to generate new data about the effects of landscape context patterns on communities through the use of an experimental microlandscape system (EMS; Wiens et al. 1993) and represents a novel contribution to the study of the ecological effects of environmental heterogeneity.

Results from the multivariate analyses (Figs. 6-2, 6-3) clearly show that, on average, landscape context patterns differentially influenced the structure of ground arthropod communities within central patches of lawn, supporting the hypothesis guiding this study. It appears that habitat composition in the microlandscapes influenced the communities to a greater degree than the level of habitat patchiness or heterogeneity per se because the six microlandscape patterns were separated into three distinct groups in both ordination diagrams: microlandscapes containing 1) only lawn, 2)
lawn and unmowed patches and 3) lawn, unmowed and mulch patches. This suggests that the number of habitat patches within the landscape context may not influence the structure of local communities within a habitat patch as strongly as the habitat type(s) (and thus resources and environmental conditions) within the landscape. In this study, several taxonomic groups were disproportionately associated with either the microlandscapes containing unmowed patches or unmowed and mulch patches (see Fig. 6-2) which lends additional support to the conclusion that landscape composition may influence community responses to landscape patterns more than patchiness or heterogeneity levels. Although specific relationships between taxonomic groups and habitat types cannot be determined from this study, it is plausible that the results were strongly affected by the choice of habitat types used to create the microlandscapes and that different results would have been generated by microlandscapes with different habitat compositions. No studies were found in the literature that examined the relative influence of spatial patterns and composition of landscape context (and their interactions) on local communities. Clearly however, the effects of landscape context on local communities will be mediated by the influence of various habitat types on the abundances, distribution and behavior of organisms across landscapes, a topic that deserves greater research attention than it has previously been given (Johnson et al. 1992, Lima and Zollner 1996).

In contrast to the community-level results, few significant differences among the microlandscapes in mean activity-abundance levels for each taxonomic group were detected. Although these results might seem contradictory, the multivariate analyses were conducted using the mean activity-abundance levels over all the sampling periods. Thus, the community-level patterns were probably driven by the activity-abundance data from the sampling periods when the largest numbers of arthropods were collected (June 2003 and 2004, August 2004). (Temporal variation in arthropod activity-abundance levels is attributed to natural population fluctuations and will not be discussed further for brevity.) For these sampling periods (and others for certain taxa; see Fig. 6-4), the activity-abundance data show patterns more similar to those seen in the multivariate analyses and indicate potentially important ecological trends in the effects of landscape context patterns on arthropod activity-abundance levels. Specifically, for many groups (especially entomobryomorpha and sminthurid collembola, Araneae, ants, Orthoptera, wasps; Fig. 6-4) the highest mean activity-abundance levels occurred in microlandscapes containing patches of non-lawn habitat, with the highest levels often seen in the microlandscapes containing only unmowed patches. However, activity-abundance levels did not tend to be greater in microlandscapes with
greater number of habitat patches in the landscape context as hypothesized. Thus, results support the general conclusion that landscape context patterns containing non-lawn habitat tended to increase the activity-abundance levels of most taxa in the central lawn patch but that, as stated above, the response appears to have been mediated more by landscape composition than patchiness or heterogeneity level. In other words, arthropod communities and activity-abundance levels were generally similar among lawn patches adjacent to one, three or nine non-lawn patches with differences mediated by the type of non-lawn habitat. However, this general pattern was not consistent for all the taxonomic groups reflecting the suggestion made by others (e.g., Steffan-Dewenter et al. 2002, Burel et al. 2003, Dauber et al. 2003, Jeanneret et al. 2003) that responses to landscape context patterns will be taxon-specific and mediated by the trophic, behavioral and morphological (i.e., body size) characteristics of different organisms. Such analyses are beyond the scope of the current study because the finer-resolution taxonomic identifications needed for such analyses were not completed due to inclusion of more orders for community level analyses. Nonetheless, it is clear from this study that different groups of arthropods respond in different ways to landscape context patterns, perhaps due to differences in their resource (e.g., food, shelter) needs across space and time.

In addition to habitat composition of the microlandscapes and taxon-specific characteristics, three other factors may have influenced the results of this study. First, arthropod movement patterns and rates within each microlandscape plot could have been affected in different ways by the composition and arrangement of habitat patches (Johnson et al. 1992). In previous studies, the effects of landscape context on communities and animal abundances have been attributed to movement of organisms from the landscape context into the habitat under study (e.g., from forest patches into crop fields; e.g., Thies and Tscharntke 1999, Elliott et al. 2002, Steffan-Dewenter et al. 2002). However, it is possible that organisms emigrate from the focal habitat into the landscape context. In terms of the current study, arthropods may have moved from the central lawns into the non-lawn patches more readily than vice-versa, thus generating a negative relationship between activity-abundance levels in the central lawn patches and the number of non-lawn patches in their landscape contexts. Alternatively, more complex microlandscapes (i.e., with more non-lawn patches) may have reduced (or increased) the overall movement rates (e.g., distance covered in a day) of arthropods across the landscapes (i.e., due to variation in permeability of the boundaries between habitat types; sensu Stamps et al. 1987) and therefore reduced (or increased) the probability of their capture in pitfall traps in the central lawn. However, previous research has
shown that organisms’ movement rates differ among different habitat types and landscapes with different patterns (e.g., Johnson et al. 1992, Ricketts 2001, Haynes and Cronin 2003). Because arthropod movement patterns within and between the habitat types were not examined, it is unclear how differences in arthropod movements across the six microlandscapes may have influenced the ability of this study to detect the effects of landscape context.

Another factor related to movement rates that may have influenced the results of this study is the scale of the microlandscapes (i.e., 10 x 10m). Previous studies that have examined the effects of landscape context at much larger spatial scales (e.g., 50 to 200m) have concluded that the response of organisms to landscape context is scale-dependent with taxa responding differently to landscape structure at different scales of analysis (e.g., Steffan-Dewenter et al. 2002, Tscharntke et al. 2002). In the current study, microlandscape plots may have been too small to detect stronger effects of landscape context patterns if arthropods movement rates resulted in “well-mixed” communities within each microlandscape (i.e., differences in arthropod abundances among the habitat types were reduced by continual movement of arthropods between them). If true, this would limit the ability to extrapolate results from small-scale EMS studies to aid in the interpretation of ecological patterns at larger spatial scales as was suggested by Wiens et al. (1993) to be a strength of EMS studies. Future research is needed to increase understanding of how animal movements, habitat patch sizes and landscape context interact differently across spatial scales to determine the structure of local communities (Johnson et al 1992).

A third factor that may have affected the results of this study is the landscape context around the entire EMS and each individual microlandscape plot (Appendix A). A row of trees and a gravel road bordered two sides of the field. Internal to the EMS, each microlandscape was surrounded by plots of different composition (including plots used for the study of Chapter 5). These two factors may have contributed to the spatial variability seen among the activity-abundance levels for each microlandscape design (Fig. 6-4) which reduced the detection of more significant differences among the data (despite controlling for spatial variability by blocking replicated plots). As found in a study of landscape context effects on parasitism (Menalled et al. 1999), geographical location of study sites may exert stronger effects on results than the landscape pattern which a study was designed to examine. This is an important factor to consider during the formulation of future EMS studies.

The secondary objective of this study was to generate information about the potential of manipulating landscape patterns around lawns to increase the potential of conserving beneficial
arthropods in urbanized landscapes. Lawns are generally managed as large homogeneous patches that are highly suitable habitat for turfgrass pests but may be comparatively unsuitable habitat for beneficial arthropods (e.g., predatory spiders and ants and their alternative prey such as collembola). While many studies have been conducted about the effects of landscape context on arthropod communities and trophic interactions in agricultural ecosystems (e.g., Lys et al. 1994, Menalled et al. 1999, Tscharntke et al. 2002), few have examined how the design and management of urban landscape patterns impacts arthropods (McIntyre 2000). However, four recent studies have shown that increasing the heterogeneity of urban habitats in the landscape context can increase the abundance of predatory arthropods and rates of predation on arthropod pests in lawns and ornamental plants (Tooker and Hanks 2000, Bramen et al. 2002, Frank and Shrewsbury 2004, Rebek et al. 2005). Similarly, the results of the current study indicate that small (i.e., 3 x 3m) patches of unmowed habitat can increase the activity and abundance of beneficial arthropods in adjacent lawns (Fig. 6-4) and increase the potential for biological control of pests, thereby reducing the need for insecticide inputs. It is unclear from this study if the inclusion of bark and gravel mulches in urbanized landscapes might lead to increased or decreased arthropod activity-abundance levels because these habitat types were not present in any of the microlandscape designs in which unmowed habitat patches were absent (Fig. 6-1). However, results for some taxonomic groups from certain sampling periods (e.g., Aranae, ants, Coleoptera) suggest that increasing the habitat heterogeneity of the landscape context around lawns may limit the activity-abundance levels of arthropods in lawns as compared to areas surrounded by only unmowed patches. Future studies are needed to examine the mechanisms underlying the effects of landscape context patterns on arthropod communities, activity-abundance levels and their movement patterns between heterogeneous habitat types and the resulting consequences for food web dynamics that impact the potential for biological control of lawn pests (e.g., Frank and Shrewsbury 2004).

Conclusions

The effects of landscape patterns (i.e., habitat patchiness and heterogeneity) on ecological patterns and processes have received increasing research attention over the past two decades (Turner 2005a, b). Many studies have shown that landscape patterns surrounding a patch of habitat (i.e., the landscape context) can influence the presence and abundance of organisms within that patch (Mazerolle and Villard 1999). Most of these have focused on pre-existing landscapes dominated by forest fragments and agricultural fields (e.g., Donovan et al. 1997, Lindenmeyer et al.
1999, Menalled et al. 1999, Tscharntke et al. 2002) and few have utilized designed field
experiments to test hypotheses about the effects of landscape context on communities. Information
about the ecological effects of landscape context patterns is needed to inform the design and
management of landscapes in which the potential conservation of beneficial organisms is
maximized.

The current study presented results from a novel field experiment in which two series of
microlandscape patterns that differed in the number and composition of non-lawn habitat patches
around a central area of lawn were created (Fig. 6-1). The structure of ground arthropod
communities in the central area of lawn differed significantly among the microlandscape patterns
with those from microlandscapes composed only of lawn differing from those containing patches of
non-lawn habitat. Although few significant differences were detected among the microlandscape
patterns for arthropod activity-abundance levels, they tended to be higher in microlandscapes
containing non-lawn habitat patches for several taxa especially spiders, collembo, ants and
orthopterans. However, activity-abundance levels did not increase linearly with increasing
patchiness or heterogeneity in the landscape context across the series of microlandscape patterns.
Thus, the primary conclusions drawn from these results are that 1) landscape context influenced the
structure of arthropod communities and tended to increase their activity-abundance levels in central
patches of lawn, and 2) the habitat composition of the landscape context exerted a stronger
influence on the arthropod communities than the overall patchiness or heterogeneity. It is suggested
that the effects of landscape context in this study were driven largely by differences in patterns and
rates of arthropod movements among the microlandscape patterns. In addition, no consistent
patterns were seen among the taxonomic groups in the effects of microlandscape patterns on
activity-abundance levels (e.g., compare those of entomobryomorph and sminthid collembola),
which supports the conclusions made by others (e.g., Andrén 1994, Söderström et al. 2000, Steffan-
Dewenter et al. 2002, Jeanneret et al. 2003) that organism responses to landscape context patterns
are likely to be taxon specific and determined by the habitat and resource requirements of each
taxon.

Urban habitat types were used in this study to provide information about how urbanized
landscapes dominated by lawns can be managed to conserve beneficial arthropods. Data suggest
that incorporating one small (3m x 3m) patch of unmowed habitat into lawns can increase the
activity-abundance levels of beneficial arthropods such as predators and their alternative prey
within immediately adjacent lawn areas (i.e., within ~ 3 m). Additional studies are needed to
examine the underlying mechanisms of these patterns and to better understand how urban habitats provide suitable habitat for ground arthropods and influence the spatial patterns of their abundances and interactions. Because urbanized landscapes are characterized by high levels of habitat patchiness and heterogeneity, they are ideal systems with which to examine the influence of landscape context patterns on local communities. In addition, urban habitats provide ideal model systems because they are heterogeneous in resources and environmental conditions and are likely to differentially influence communities and movement of organisms. Increasing the use of urban landscapes and habitats in basic and applied landscape ecology research is likely to yield important, general insights into the ecological effects of environmental heterogeneity on ecological patterns and processes.

References


Chapter 7. Conclusions: Urban ecology at the aboveground-belowground interface

“Urban ecosystems are important for society, the future of the world and for the discipline of ecology. They are where important environmental problems and solutions are located and where new insights and concepts will be generated for the field of ecology.”
—Nancy Grimm (personal communication, April 3, 2006)

Introduction

I obtained the above quote from Dr. Grimm when I visited the University of Arizona to interview for a post-doctoral position in urban ecology. (At that time, Chapter 1, which opens with a quote from one of her articles, was finished and I thought it appropriate to obtain another quote from her with which to begin the final chapter.) The question I posed to her was: Why is urban ecology important? Her reply was inherently based on the recognition that the spatial extent of urbanized landscapes and numbers of humans inhabiting them are increasing around the world and that, consequently, the ecological impacts of urbanization are also becoming globally ubiquitous (U.N. 2003). Although many ecologists are embracing the study of urban ecology (as exemplified by those working at the University of Arizona whose research has been cited throughout this thesis), the number of urban ecologists remains small relative to the task at hand, i.e., generating the basic data about the ecology of urbanized ecosystems needed to guide the sustainable management of biodiversity and ecosystem services within them. This task inspired the primary objective for my thesis research: to examine how the creation and management of urban habitat types affects ecological patterns and processes at the aboveground-belowground interface.

When I returned to State College from Arizona, the plane I traveled on flew just west of my field site, close enough so that I could see the outlines of the experimental plots (Appendix A). From the air, they appeared to be extremely small and seemingly inconsequential within the expansive landscape surrounding them. Mirroring the question I asked Dr. Grimm, I wondered to myself: Why are these experimental field plots important to the science of urban ecology? In this concluding chapter, I attempt to provide some answers to this question by summarizing a few of the new insights generated by my research. In addition, I take the lead from Dr. Grimm’s quote and conclude with a brief discussion of my thesis’ relevance to the study of environmental problems and related management solutions associated with urbanization (specifically, the alteration of ecosystem services) and the broader discipline of ecology.
Ecological effects of mowing and mulching

In urbanized landscapes, especially residential ones, lawns and mulched gardens are among the most common types of habitat (or land cover) created and managed by humans. Often, these habitat types are managed for aesthetic (i.e., their visual appearance) rather than ecological purposes. In part, this is because so little is known about how urbanization and various urban habitat types affect ecological patterns and processes. Thus, in general, urban landscape managers do not know how various management practices compare in terms of their positive and negative environmental attributes (e.g., do they lead to higher or lower levels of nitrogen retention or biodiversity?). The research presented in this thesis has yielded new insights into how human management of urban landscapes (i.e., application of lawn chemicals and bark and gravel mulches, mowing of lawns and creation of landscape patterns) influences a wide range of ecological variables (microclimates, soil properties, biogeochemical cycles and invertebrate communities, summarized below). Therefore, results have application for informing the design and management of urbanized landscapes in which favorable biodiversity levels and ecosystem services are conserved.

Microclimates differed significantly among the four habitat types examined in this study especially during daytime hours when sunlight interacted with the material comprising them to generate variation in their ground temperatures (Chapter 3). Mulches were significantly warmer on the surface than lawns and unmowed habitat types; lawns were slightly warmer than unmowed habitats. Overnight, ground temperatures were cooler than during the daytime and became similar among the habitat types. Temperatures on the ground influenced the soil temperatures which exhibited similar patterns in daily temporal fluctuations and differences among the habitat types. Differences among the habitat types in ground and soil temperatures may have influenced rates of biogeochemical cycling and abundance of organisms (e.g., earthworms, arthropods) within them although additional research is needed to examine the details of such relationships.

In addition to soil temperature, differences were seen in other belowground variables among the habitat types (Chapter 3). Soils covered with bark and gravel mulches were consistently wetter than the vegetated plots due to the insulating effects of the mulch layers and absence of water uptake by plants. The lack of organic matter inputs into gravel plots resulted in lower levels of soil organic matter, soil aggregate stability, soil microbial biomass and earthworm densities as compared to the other habitat types. Bark mulch plots consistently had the largest earthworm populations (perhaps due to high soil moisture and organic matter inputs) which led to significantly lower soil bulk density compared to the other habitat types. Earthworm numbers were intermediate
and similar in unmowed and lawn habitats, except in 2005 (a drought year) when they decreased in lawns, apparently due to the interactive effects of warm and dry soil conditions.

Patterns of carbon cycling also differed among the habitats (Chapter 3). On average, fluxes of carbon dioxide from soils were greater from lawn and bark mulch plots than unmowed and gravel mulch plots, probably due to the influences of organic matter inputs in both and higher soil water content in bark-covered soils. Decomposition of oak leaves in litterbags was significantly faster in mulched plots as compared to vegetated plots probably due, in part, to warmer ground temperatures in those habitat types. Annual aboveground net primary productivity was similar between the lawn and unmowed habitat types (when measured with greater sampling intensity). Although lawns were highly productive because of densely growing plant species (e.g., dandelions, clovers) not found in unmowed habitat types, the amount of aboveground living and dead standing crop (i.e., plant biomass) was significantly greater in unmowed habitat plots. As compared to detritus in unmowed plots, the fragmented vegetation cut by mowing decomposed quickly in lawns thus reducing the amount of aboveground carbon stored in them.

Differences in nitrogen pools and fluxes among the four habitat types were probably caused by differences in the quality and quantity of their organic matter inputs, earthworms and soil moisture (Chapter 4). High temporal variability was seen in the nitrogen pools and fluxes in all the habitat types but variability was lowest in unmowed plots supporting the conclusion that mowing and mulching promote higher levels of inorganic nitrogen at certain times relative to those seen in unmanaged old fields. Particularly noticeable was an accumulation of nitrate in lawn and gravel-covered soils in 2005 when precipitation levels were low. Averaged across all sampling periods, net nitrogen mineralization rates were highest and positive in lawns, intermediate and close to zero in unmowed plots and negative in mulched plots. Laboratory measurements showed that mulch-covered soils had higher flux rates of nitrous oxide than vegetated soils. However, field measurements indicated that production of this greenhouse gas was only higher from gravel plots and that bark and vegetated plots had very low flux levels. It seems likely that earthworm activities and lower bulk density levels might have limited the production of nitrous oxide from bark mulch habitats under field conditions.

Arthropod communities and activity-abundance levels differed among lawn, unmowed and mulched habitat types (Chapter 5). However, few strong conclusions can be made from the current study about the relative preferences of any taxonomic groups for the habitat types because of temporal variability in the numbers of arthropods sampled from each habitat type. For example, the
highest mean activity-abundance levels of sminthurid collembola were seen in the unmowed, lawn and gravel plots during different sampling periods. However, multivariate analyses of arthropod communities suggested that most taxonomic groups were disproportionately found in lawns as compared to the other habitat types. Future studies are needed to better understand how interactions between resource availability, microclimates and trophic interactions differ among the habitat types to influence ground arthropod communities.

In a separate study (Chapter 6), arthropod communities and activity-abundance levels differed among patches of lawn that were surrounded by different levels of landscape heterogeneity (i.e., the number and composition of non-lawn habitat patches). Arthropod activity-abundance levels tended to be higher in experimental microlandscapes that contained patches of unmowed habitat than those containing only lawn or unmowed as well as mulch habitats. A key conclusion from this study is that the habitat composition of urbanized landscapes may drive the structure of arthropod communities at a location more than levels of habitat heterogeneity across landscapes. Results also suggest that one small patch (3 x 3m in this study) of unmowed habitat type can promote higher activity-abundance levels of beneficial arthropods (i.e., predators and their non-pest prey) in adjacent lawns (effects in this study seen within ~2m of unmowed patch) which might promote greater biological control of turfgrass pests. This is an especially important insight related to the conservation of beneficial arthropods in high-maintenance lawns where arthropod numbers can be reduced by pesticide applications. For example, in an observational study, it was observed that certain groups of collembola were less abundant in high-maintenance lawns as compared to low-maintenance lawns and unmanaged fields (Chapter 2). In light of the results from the arthropod studies presented in this thesis, it is apparent that abundances and distribution of arthropods across urbanized landscapes will be strongly influenced by human management of both local (i.e., lawn mowing, chemical and mulch applications) factors and regional (i.e., landscape context) land cover patterns.

**Managing ecosystem services in urbanized landscapes**

In an increasingly urbanized world, ecologists will be called upon to make recommendations about how environmental problems (e.g., nitrogen pollution, pest outbreaks) and ecosystem services (e.g., favorable regulation of inorganic nitrogen production, biological pest control) can best be managed in urbanized ecosystems (Kremen 2005, Kremen and Ostfeld 2005). Basic data about the ecology of common urban habitat types will be needed to ensure that recommendations are based on
reliable information rather than potentially-misguided guesswork about how urbanization and management of urban habitats influences ecological patterns and processes. Although a growing body of literature has reported such data (see references included in previous chapters), the studies included in this thesis are among the first comprehensive investigations about the effects of mowing and mulching on a wide-range of ecological variables. Certainly, more questions than answers have been generated by this thesis (a positive outcome), especially regarding the mechanisms driving the observed patterns and processes. Nonetheless, it is clear from the presented results that urban habitat types differ widely in their abilities to provide ecosystem services, especially regarding the regulation of carbon and nitrogen pools and fluxes. In addition, the habitat types may be associated with differences in arthropod communities that impact food web dynamics, and consequently, differentially affect the ability of arthropod predators to control arthropod pests and their associated economic and aesthetic damage within urbanized landscapes. Data such as those generated in this thesis can be used to engage urban landscape managers in discussions about how small-scale urban habitat management is related to broader ecological issues such as management of soils, biodiversity, carbon and nitrogen, all of which have relevance to management of ecosystem services. Ultimately, therefore, studies about the ecology of urban habitats may have their greatest impacts by helping to increase the ecological awareness of the public, i.e., through educational efforts focused on the ecology of the habitats and landscapes that surround people everyday (Berkowitz et al. 2003). It is hoped that the results and conclusions provided throughout this thesis provide foundational materials for developing future studies and educational programs that help improve both ecologists’ and the public’s understandings about relationships among urban landscape management, ecological variables, and ecosystem services.

**Broader relevance to the discipline of ecology**

Although my thesis primarily represents a contribution to the study of urban ecology, I conclude by proposing that my conceptual and methodological approaches have broader relevance to general ecological science. The concept of habitat structure provided a central theme for my work and I hope to have shown—especially through development of a new conceptual framework (Fig. 1-1)—that it provides a fundamental ecological concept that facilitates the comparison of ecological variables among locations that are distinguishable by the composition of the physical matter that comprises them. Although comparisons among habitat and ecosystem types has long been a central theme of ecology, I suggest that more explicit use of the habitat structure concept will encourage
fundamental and thorough description of habitat types (e.g., Appendix B) and spatial patterns of physical heterogeneity, especially subtle ones at fine-scales. Such descriptions should facilitate rigorous comparisons of ecological characteristics among urban and non-urban habitat types and, in turn, permit stronger evaluations of their relative abilities to provide ecosystem services.

Related to the concept of habitat structure, I also conclude that the core of my thesis work (Chapters 3-5) exemplifies a novel, multivariate approach to investigating relationships among above- and belowground patterns and processes at a location. I suggest that concurrent examination of many variables within each of the four habitat types enabled me to develop stronger insights, discussions, and conclusions about the data and their relationships than would have been possible if I had limited my thesis topic to only, e.g., soils, nitrogen, or carbon. This multivariate approach suggested the development of descriptive "ecological profiles" for each habitat type (Table 3-2). This profile framework might prove useful for developing mechanistic hypotheses about how variables interact with each other in different ways in distinctive habitat types to differentially drive the ecological patterns and processes within them.

In addition, the use of urban habitat types for this study provided a novel context for testing the generality of ecological theories and principles. While my work did not invalidate any long-standing ecological ideas, it did show that the urban habitat types had unique ecological profiles which gave rise to potentially unexpected results. For example, general ecological theory would predict high nitrous oxide production from soils covered with bark mulch because of their high soil moisture content which would promote the anaerobic process of denitrification. However, this pattern was not observed in field measurements, perhaps because the high density of earthworms reduced the availability of nitrate or anaerobic microsites (by increasing soil pore spaces) for denitrifying bacteria. A major challenge for urban ecologists is to evaluate the applicability of ecological ideas developed from non-urban ecosystems to understanding urbanized ecosystems and, where needed, modify them so that they can encompass urban habitats or develop new theories and concepts based on novel urban ecology data (Kaye et al. 2006). As more urban ecology studies are conducted, it seems likely that they will be increasingly integrated into the broader purview of ecological science (i.e., they will be discussed more often in introductory textbooks and included in requests for grant proposals) for the benefit of both ecological science and society.

Finally, the topics encompassed by the chapters of my thesis reflect my (and others') belief that ecologists need not become specialists within any particular sub-discipline of ecology to conduct meaningful research. As my interdisciplinary conceptual framework (Fig. 1-1) and chapter
titles show, I have purposefully integrated ideas from many subjects into my thesis including those from soil, community, ecosystem and landscape ecologies. In this regard, I have been influenced by contemporary writings (e.g., Wardle 2002, Naeem 2002, Polis et al. 2004, Lovett et al. 2005) which advocate the dissolution of historical barriers between ecological sub-disciplines to allow for the synthesis of seemingly disparate topics. Similarly, my interests in exploring the effects of aboveground habitat management on belowground variables mirrors current perspectives that aboveground and soil ecological systems influence each other and should be studied in concert (e.g., Wardle 2002, Wardle et al. 2004, Bardgett et al. 2005). Although others might argue that I have short-changed myself by not becoming an "expert" on a more narrow research topic (although have I become an “expert” on the four habitat types?), I maintain that the breadth of research methods, cited literature and perspectives from across ecological sub-disciplines included in my thesis represents an important, valid and necessary approach to graduate training. Just as experts are needed to guide developments in any research field, broadly-trained scientists are needed to help integrate concepts developed by experts and promote synthetic, interdisciplinary understanding of, e.g., relationships between social and ecological systems (Pickett 1999, Kinzig 2001). Although I certainly do not claim to have achieved any rigorous level of interdisciplinary (or even disciplinary) synthesis in my thesis, I do feel that it represents a coherent body of research that accurately reflects my broad interests in, and knowledge about, the diversity of topics within the science of ecology.

As my graduate training nears its end with the composition of these final sentences, I will conclude by expressing four of my hopes regarding the longer-lasting effects of my thesis research. First, I hope that the work, especially when published in peer-reviewed journals, is widely read and respected by my peers. Second, I hope that the propositions I have made about the relevance of my research to ecological science and the design and management of urbanized landscapes are true, at least in some small ways. This would be confirmed if the ideas embodied in my work influence other ecologists (i.e., they cite my work) and urban landscape managers (i.e., they consider the ecology of urban habitats in their management decisions). Third, (and most importantly?), I hope that the completion of this research provided me with the skills needed to end my career as a student and enter the "dark-side" of academia (i.e., where pursuing grant monies and tenure become paramount). In other words, I hope I have gained the credentials needed to convince others to employ me so that I may continue my pursuit of an academic research and teaching career in ecology, the discipline about which I have become increasingly passionate during my enjoyable
graduate school years. Therefore, my fourth hope is that my passion for ecology has been effectively conveyed throughout this thesis.

References


Appendix A. Aerial photographs of experimental field

**Figure A-1.** Aerial photo of part of Penn State University’s Agricultural Experimental Research Station showing location of field where experimental urban habitat structure plots were located.

**Figure A-2.** Aerial photo of experimental field and surrounding landscape features where experimental urban habitat structure plots were created at the Penn State University Agricultural Research farm. Area encompassed by all 32 plots is 0.84 ha (8400 m²).
Figure A-3. Layout of experimental plots at field site. Treatments (urban habitat structure plots or microlandscape designs) are designated by labels as designated above and are grouped into four blocks by dashed lines which separate each group of treatments for each block. Each plot was separated from other plots, areas of unmowed habitat type, road and hedgerow by at least 3m of mowed lawn. Not to scale.

Habitat structure plots used for Chapters 3, 4, 5 (see Appendix B for images):
- L = mowed vegetation (lawn)
- U = unmowed vegetation
- B = shredded bark mulch
- G = gravel mulch

Microlandscape plots used for Chapter 6 (see Fig. 6-1 for designs):
- 1P = 1 unmowed patch
- 3P = 3 unmowed patches
- 9P = 9 unmowed patches
- 3H = 1 unmowed patch, 1 bark mulch and 1 gravel mulch patch
- 9H = 1 unmowed patch, 1 bark mulch and 1 gravel mulch patch
Appendix B. Photographs and descriptions of four habitat types

Figure B-1. Soil-litter-vegetation profiles of the (A) lawn, (B) unmowed, (C) bark mulch and (D) gravel mulch habitat structures used in this study. (A) The litter layer in unmowed plots consisted primarily of light-colored dead orchard grass leaves and stems that fell to the ground at the end of each growing season. It had a low bulk density (i.e., litter was not compacted), was 5-10 cm thick and completely covered the soil surface between dense clumps of living orchard grass. Areas between orchard grass clumps (~50% of the surface area) were sparsely populated by Kentucky bluegrass and herbaceous plants. (B) In lawns, ~95% of the soil surface was covered by plants. The litter layer was thin to non-existent and was composed of small plant pieces (mowed clippings) and plant material that died below the mowing height. Less than 5% of the mineral soil surface was not covered. (C) Shredded bark mulch formed a dense layer of material comprised of a heterogeneous mix of bark ranging in size from 5cm long to very fine dust. Bark was very dark brown when first applied but faded to a lighter brown as it slowly decomposed. Bark at the top of the layer dried out quickly after rains and remained dry while bark in contact with the mineral soil generally remained wetter. 100% of mineral soil in the bark mulch plots was covered by bark mulch. (D) 100% of the soil surface was covered by limestone gravel rocks in gravel mulch plots. Other than sparse growth of plants, organic matter was absent in the gravel plot because very little entered or remained in them throughout the experiment.
Appendix C. Equations used for calculation of aboveground net primary productivity

Table C-1. Table of published formulas and their modifications used to calculate aboveground net primary productivity (ANPP) in lawns and unmowed habitats in this study.

<table>
<thead>
<tr>
<th>Method</th>
<th>Published formula</th>
<th>Modification for lawn</th>
<th>Modification for unmowed habitat</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual ANPP =</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Falk (1980)</td>
<td>$\sum$ grass clippings + (max. standing crop of stubble $\times$ stubble turnover)</td>
<td>N/A</td>
<td>N/A</td>
<td>Requires data on stubble turnover; Few values of this parameter have been published. Falk (19080) reported values of 0.67 and 0.65. The mean of these were used for calculations in this report.</td>
</tr>
<tr>
<td>From Scurlock et al. (2002)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Max. Aboveground Living Standing Crop $+$ $\sum$ grass clippings $+$ Value of Standing Crop at First Sampling of Season</td>
<td></td>
<td></td>
<td>Not an accurate estimate of ANPP when more than one peaks of living biomass are observed within one year.</td>
</tr>
<tr>
<td>2</td>
<td>Max. Aboveground Living Standing Crop $+$ Max. Standing Dead Biomass $^#$ $+$ $\sum$ grass clippings $+$ Value of Standing Crop at First Sampling of Season</td>
<td></td>
<td></td>
<td>Requires separation of standing dead biomass from living. If this value is not available then ANPP will be the same as for method 1.</td>
</tr>
<tr>
<td>3</td>
<td>Max. Aboveground Living Standing Crop $-$ Minimum Aboveground Living Standing Crop Biomass $+$ $\sum$ grass clippings</td>
<td></td>
<td>N/A</td>
<td>Subtraction of minimum standing crop assumes that this biomass was produced in the previous year. This assumption may be tenable for lawns in some locations but is violated for unmowed vegetation that dies to the ground over the winter. We assumed the latter for our study and did not apply this method for unmowed habitats.</td>
</tr>
<tr>
<td>4</td>
<td>$\sum$ Positive Differences in Aboveground Living Standing Crop Between Sampling Dates $+$ $\sum$ grass clippings $+$ Value of Standing Crop at First Sampling of Season</td>
<td></td>
<td></td>
<td>This method is highly sensitive to the number of samples collected with more samples yielding a more accurate ANPP estimate.</td>
</tr>
<tr>
<td>5</td>
<td>$\sum$ Positive Differences in Aboveground Living Standing Crop Between Sampling Dates $+$ Simultaneous Positive Differences in Standing Dead $+$ $\sum$ grass clippings $+$ Value of Standing Crop at First Sampling of Season</td>
<td></td>
<td></td>
<td>Requires separation of standing dead biomass from living. If this value is not available then ANPP will be the same as for method 4.</td>
</tr>
<tr>
<td>6</td>
<td>$\sum$ Positive Differences in Aboveground Living Standing Crop Between Sampling Dates $+$ Simultaneous Positive Differences in Standing Dead $+$ Simultaneous Positive Differences in Dead Standing Crop (Litter) $+$ $\sum$ grass clippings $+$ Value of Standing Crop at First Sampling of Season</td>
<td></td>
<td></td>
<td>This is the only method to consider changes to the dead biomass as litter. If living and dead standing crop increase, it is assumed that there was simultaneous production and death of plant biomass during the sampling interval. The biomass entering the dead standing crop pool should therefore be included as part of the ANPP.</td>
</tr>
</tbody>
</table>

$^\#$ Stubble is the living standing crop below mowing height in lawns. Standing dead biomass is the biomass of dead vegetation that has not entered the litter layer on the soil surface. Dead standing crop is the dead biomass on the soil surface (i.e., litter).
Appendix D. Hourly data points for soil and surface temperatures in four habitat types (legend on next page)
Appendix D. (continued from previous page)

**Figure D-1.** Daily patterns in hourly surface and soil temperature fluctuations in four urban habitats and air temperatures over four successive dates. (A) Surface temperatures for April 22-25, 2004. (B) Soil temperatures (5 cm depth) for April 22-25, 2004. (C) Surface temperatures for July 15-18, 2004. (D) Soil temperatures for July 15-18, 2004. Data shown are means of four replicated plots per habitat except for bark which has only three replicates for April surface temperatures and July surface and soil temperatures. SE bars are only shown for daily maxima and minima temperatures (except for July 16) for visual clarity but are generally small (range of 0 to 4.2) and therefore are not visible at all data points. See Fig. 2 in text for information about statistical analyses.
Appendix E. Relationships among surface, soil and air temperatures in four habitat types using weekly and monthly means (legend on next page)

A. 

- **Lawn**
  - $y = 0.7281x + 10.992$
  - $R^2 = 0.67$  $P=0.00$
- **Unmowed**
  - $y = 0.9219x + 5.4627$
  - $R^2 = 0.70$  $P=0.00$
- **Bark**
  - $y = 1.4301x + 7.9991$
  - $R^2 = 0.56$  $P=0.00$
- **Gravel**
  - $y = 1.2106x + 14.025$
  - $R^2 = 0.65$  $P=0.00$

B. 

- **Lawn**
  - $y = 0.6318x + 12.285$
  - $R^2 = 0.77$  $P=0.00$
- **Unmowed**
  - $y = 0.8679x + 6.3018$
  - $R^2 = 0.72$  $P=0.00$
- **Bark**
  - $y = 1.2507x + 9.9594$
  - $R^2 = 0.63$  $P=0.00$
- **Gravel**
  - $y = 1.2042x + 13.494$
  - $R^2 = 0.87$  $P=0.00$

C. 

- **Lawn**
  - $y = 1.059x - 4.7706$
  - $R^2 = 0.68$  $P=0.00$
- **Unmowed**
  - $y = 0.8462x - 0.306$
  - $R^2 = 0.82$  $P=0.00$
- **Bark**
  - $y = 2.4203x^{0.5971}$
  - $R^2 = 0.38$  $P=0.00$
- **Gravel**
  - $y = 0.5745x^{0.0113}$
  - $R^2 = 0.82$  $P=0.00$

D. 

- **Lawn**
  - $y = 1.3002x - 10.165$
  - $R^2 = 0.67$  $P=0.00$
- **Unmowed**
  - $y = 0.9359x - 2.2514$
  - $R^2 = 0.84$  $P=0.00$
- **Bark**
  - $y = 1.0922x^{0.8275}$
  - $R^2 = 0.37$  $P=0.00$
- **Gravel**
  - $y = 0.1922x^{1.3617}$
  - $R^2 = 0.94$  $P=0.00$
Appendix E. (continued from previous page)

Figure E-1. Relationships among mean surface and soil daytime temperatures (11:00 to 17:00) in four urban habitats and air temperature averaged across weeks and months. Regressions between (A) weekly mean daytime air and surface temperatures, (B) monthly mean daytime air and surface temperatures, (C) weekly mean daytime surface and soil temperatures, and (D) monthly mean daytime surface and soil temperatures. Data points for habitat surface and soil temperatures are means of four replicated plots. Letters next to regression lines represent first letter of habitat type for the respective regression equations. Within each graph, habitat names with different letters have significantly different ($P \leq 0.05$) regression equations with GLM analyses.
Appendix F. Aboveground living biomass in lawns and unmowed habitats

![Graph showing living standing crop in lawns and unmowed habitats over time]

**Figure F-1.** Mean (± SE) living standing crop m⁻² in lawn (squares) and unmowed (diamonds) in 2004 and 2005. Means with different letters are significantly different ($P < 0.05$) with Tukey’s post hoc comparisons.
Appendix G. Estimates of lawn and unmowed aboveground net primary productivity from different calculations

Figure G-1. Annual aboveground net primary productivity (ANPP) for lawn and unmowed habitats in 2004 and 2005 calculated with methods described in Appendix C and modified from Falk (1980) and methods 1-6 described in Scurlock et al. (2002). Methods 1&2 and 4&5 differ only by inclusion of standing dead biomass in calculation. The paired methods provide the same ANPP estimates when standing dead biomass is not separated from the living standing crop as for this study. Falk's method was designed for lawns and is not appropriate for unmowed habitats because it includes estimation of stubble (the biomass below mowing height) turnover rate which is not applicable to unmowed vegetation. Method 3 of Scurlock et al. (2002) is not appropriate for calculating unmowed ANPP because it requires subtraction of the minimum value of living standing crop. For calculations, it was assumed that unmowed vegetation begins growing from zero living biomass each year and therefore the minimum standing crop value should be included as a contribution to ANPP.
Appendix H. Hourly ground temperatures in four habitat types during ground arthropod sampling periods.

Figure H-1. Mean hourly ground temperatures during three arthropod sampling periods. Standard error bars are only shown for selected data points (mid-day temperatures) for visual clarity. Mean temperatures with different letters differ significantly ($P < 0.05$) with least significant differences post-hoc comparisons.
Appendix I. Results from GLM analyses of activity-abundance levels for six arthropod groups in four habitat types.

Table I-1. Results of univariate GLM analyses for mean activity-abundance levels of arthropods in four habitat types.

<table>
<thead>
<tr>
<th>Model term</th>
<th>Diplipoda</th>
<th>Isopoda</th>
<th>Hemiptera</th>
<th>Orthoptera</th>
<th>Wasps</th>
<th>Diptera</th>
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<tbody>
<tr>
<td>Habitat</td>
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<tr>
<td>$F_{3,12}$</td>
<td>6.08</td>
<td>17.96</td>
<td>224.49</td>
<td>11.41</td>
<td>2.58</td>
<td>6.7</td>
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<tr>
<td>$P$</td>
<td>0.009</td>
<td>&lt; 0.001</td>
<td>0.00</td>
<td>&lt; 0.001</td>
<td>0.1</td>
<td>0.007</td>
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<tr>
<td>Sampling Date</td>
<td></td>
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</tr>
<tr>
<td>$F_{2,24}$</td>
<td>3.63</td>
<td>11.28</td>
<td>55.36</td>
<td>17.31</td>
<td>69.97</td>
<td>46.47</td>
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<tr>
<td>$P$</td>
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<td>&lt; 0.001</td>
<td>0.00</td>
<td>&lt; 0.001</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Year</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>$F_{1,12}$</td>
<td>23.05</td>
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<td>7.55</td>
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<tr>
<td>$P$</td>
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<td>0.11</td>
<td>0.3</td>
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<tr>
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<tr>
<td>$F_{6,24}$</td>
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<td>2.52</td>
<td>3.66</td>
<td>0.79</td>
</tr>
<tr>
<td>$P$</td>
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<td>0.1</td>
<td>&lt; 0.001</td>
<td>0.05</td>
<td>0.01</td>
<td>0.58</td>
</tr>
<tr>
<td>Habitat x Year</td>
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<tr>
<td>$F_{3,12}$</td>
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<td>2.29</td>
<td>0.57</td>
<td>6.2</td>
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<td>1.48</td>
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<tr>
<td>$P$</td>
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<td>0.13</td>
<td>0.64</td>
<td><strong>0.008</strong></td>
<td>0.08</td>
<td>0.27</td>
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</tbody>
</table>

Notes. Date x Year and Habitat x Date x Year interactions are not shown because sampling dates differed between years and therefore these are not valid interaction terms. Degrees of freedom for each model term are given as subscripts beside the "F" in the model term column. Significant $P$ values (< 0.05) are shown in boldface type.
Appendix J. Temporal patterns of activity-abundance levels of six arthropod groups in four habitat types.

Figure J-1. Mean (± SE) activity-abundance levels for (A) Diplopora, (B) Isopoda, (C) Hemiptera, (D) Orthoptera, (E) Wasps and (F) Diptera in four habitat types over six sampling period. Means with different letters for a given sampling period differ significantly (P <0.05) with least significant differences post-hoc comparisons. Results of GLM analyses are presented in Appendix I. Although the effect of habitat type was not significant for wasps, the habitat x date interaction term was significant for this taxon which permitted for post-hoc comparisons to be made among the habitat types for each sampling period.
Vita

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Education
B.A. in Ecological Artistry, May 2000, Hiram College, Hiram, OH, summa cum laude
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Grants
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2003 Competitive Student Research Grant, Penn State College of Agricultural Sciences
2003-05 Pennsylvania Space Grant Consortium Fellowship
2004 Research grant, Penn State Center for Environmental Chemistry and Geochemistry
2004-05 National Science Foundation Doctoral Dissertation Improvement Grant

Selected Scholarly Awards (all at Penn State University)
2002 First prize, biological sciences division, College of Ag. Sciences poster exhibition
2003 Brian Horton Memorial Award, Ecology Program
2004 Ralph Mumma Graduate Student Award, Department of Entomology
2004 First prize, natural sciences division, Graduate School Research Exhibition
2006 Third prize, biological sciences division, College of Ag. Sciences poster exhibition

Publications


Selected Oral Presentations
2004 City collembolan, country collembolan: A tale of lawn and garden landscape ecology. In symposium on urban soil ecology, Ecological Society of America (ESA) meeting, Portland, OR.
2005 Carbon and nitrogen cycling in urban habitats. Soil Ecology Society meeting, Argonne, IL.
2005 Effects of landscape pattern on arthropod communities. ESA meeting, Montreal, Canada.
2006 The ecology of mowing and mulching: communities and ecosystem processes in urban habitats. ESA meeting, Memphis, TN.

Teaching Experience (both at Penn State)
2003-05 Teaching assistant and laboratory instructor, Soil Ecology (w/ M.A. Bruns), 3 semesters
2004 Laboratory instructor, Introductory Soils, 1 semester