# Habitat structure: a fundamental concept and framework for urban soil ecology

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Urban Ecosyst (2007) 10:255–274
DOI 10.1007/s11252-007-0027-6

# Habitat structure: A fundamental concept and framework for urban soil ecology

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Published online: 26 June 2007


**Abstract** Habitat structure is defined as the composition and arrangement of physical matter at a location. Although habitat structure is the physical template underlying ecological patterns and processes, the concept is relatively unappreciated and underdeveloped in ecology. However, it provides a fundamental concept for urban ecology because human activities in urban ecosystems are often targeted toward management of habitat structure. In addition, the concept emphasizes the fine-scale, on-the-ground perspective needed in the study of urban soil ecology. To illustrate this, urban soil ecology research is summarized from the perspective of habitat structure effects. Among the key conclusions emerging from the literature review are: (1) habitat structure provides a unifying theme for multivariate research about urban soil ecology; (2) heterogeneous urban habitat structures influence soil ecological variables in different ways; (3) more research is needed to understand relationships among sociological variables, habitat structure patterns and urban soil ecology. To stimulate urban soil ecology research, a conceptual framework is presented to show the direct and indirect relationships among habitat structure and ecological variables. Because habitat structure serves as a physical link between sociocultural and ecological systems, it can be used as a focus for interdisciplinary and applied research (e.g., pest management) about the multiple, interactive effects of urbanization on the ecology of soils.

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**Keywords** Habitat structure · Urban ecology · Urban soils · Lawn · Mulches · Microclimate

## Introduction

Throughout history, describing and classifying habitats (or biomes) have been central endeavors for ecologists. Whatever the classification method (e.g., patches or gradients) and scale (e.g., local to continental), recognizing broad patterns of ecosystem and landscape structure is dependent upon differentiating various arrangements and compositions of abiotic and biotic physical matter. However, as McCoy et al. (1990) suggested after reviewing the literature, ecologists often take the underlying physical structure of nature for granted. Few research frameworks or agendas have been developed that explicitly include it as a central variable of interest (McCoy and Bell 1990, but see Tews et al. 2004). Nonetheless, the organization of physical material across space and time is important for ecologists to consider because it serves as the "stage" of the ecological theater.

The concept of habitat structure has been adopted to encompass the study of the effects of "the arrangement of objects in space" on ecological variables (Bell et al. 1990). Modified from Bell et al. (1990), habitat structure is defined as the amount, composition and three-dimensional arrangement of physical matter (both abiotic and biotic) at a location (Table 1). Previous research has shown that habitat structure is an important direct and/or indirect driver of many ecological patterns and processes. It can regulate community structure by providing resources (shelter, nutrients, nesting sites) and mediating interactions (predation, competition) for a diverse array of organisms in many ecosystem types (see reviews in Bell et al. 1990 and Tews et al. 2004). Ecosystem processes are influenced by habitat structure through its modification of environmental conditions and resource availability. Differences in habitat structures across space create landscape patterns, which in turn affect communities and ecosystem processes (Lovett et al. 2005). Because of its impact on variables across levels of ecological organization, habitat structure provides a useful multivariate concept that can help unify research and theories among ecological sub-disciplines (Bell et al. 1990; Wardle 2002; Lovett et al. 2005).

In particular, the concept of habitat structure is highly relevant to the emerging study of urban ecology. At its most fundamental level, urbanization is a process during which humans change the composition and arrangement of physical matter in the landscape by, for

**Table 1** Definitons of key terms related to the study of habitat structure. Modified from McCoy and Bell (1990) and Beck (2000)

| Key tems | Definitions |
|---|---|
| Habitat structure | The amount, composition and three-dimensional arrangement of biotic and abiotic physical matter within a defined location and time; refers to complexity and heterogenity of physical matter across horizontal and vertical physical space |
| Scale | Extent of spatial area, volume and/or timespan; refers to circumscription of location and time in which unit(s) of habitat structure is described |
| Complexity | The absolute amount of individual entities (components) of physical matter at a defined scale; refers to amounts of material, its surface area and surface area to volume ratio, i.e., the density of matter within a given volume |
| Heterogeneity | Variation of habitat structures within defined spatial or temporal scales; refers to numbers of different structures; location of change(s) in habitat structure is used to delineate boundaries around patches |

example, transforming forests and deserts into shopping malls and lawns. Because many types of habitat structure created in urbanized ecosystems do not exist in non-urban ecosystems, traditional ecological research frameworks and methods may not be fully relevant for approaching the study of urban ecology (Kaye et al. 2006). However, the concept of habitat structure is inherently broad and therefore facilitates comparison of the ecological characteristics of heterogeneous types of urban habitat structure with each other and those of non-urban ecosystems (Byrne 2006). In addition, the concept encourages fine-scale (i.e., cm to m), on-the-ground description of characteristics of the physical material at study sites rather than simply categorizing locations into generic types of land cover (e.g., urban green space) as is often done in coarse-scale, land cover mapping projects. For these reasons, among others, incorporation of habitat structure into urban ecology as a fundamental concept can help guide mechanistic research (sensu Shochat et al. 2006) about the multiple, interacting effects of urbanization on ecological variables.

Habitat structure is an especially useful concept for investigating relationships between the above- and belowground components of urbanized ecosystems. In general, very little is known about the effects of urbanization on the ecology of soils. However, as is true for all terrestrial ecosystems, soils in urbanized ecosystems provide a number of critical ecosystem services that should be conserved for both ecological and economic reasons (Wall 2004). Thus, a major challenge for urban ecologists is to generate basic data about the ecology of urban soils needed to help guide the management of urban ecosystem services (Kremen 2005). Habitat structure emphasizes the multivariate, ground-level, fine-scale perspective needed for developing questions and hypotheses about how human activities and sociocultural systems that dictate patterns of aboveground urban habitat structures affect belowground ecological variables.

The primary objective of this paper is to illustrate how habitat structure provides a fundamental concept for the study of urban soil ecology. This will be accomplished in three ways. First, published research about urban soils will be reviewed from the viewpoint of habitat structure to provide an overview of the current knowledge base. This review is divided into four sections (abiotic conditions, organisms, ecosystem processes and landscape patterns) which reflect the main foci of previous research. In addition to published studies, results from a recent field experiment that compared the above- and belowground ecological characteristics of four types of urban habitat structure (unmowed vegetation, lawn, bark and gravel mulches) are presented as a case study (Byrne 2006). Second, relationships between sociocultural variables and urban soil ecology will be discussed as they are linked via human management of aboveground habitat structure. Third, a synthetic conceptual framework with habitat structure as its conceptual core is presented as a tool to help guide the development of research questions about urban soil ecology. Overall, it is hoped that the review and framework stimulate interdisciplinary interest in, and research about, relationships among human creation and management of habitat structure and soil ecology in urbanized ecosystems.

## Abiotic soil properties

At a basic physicochemical level, habitat structure dictates the abiotic environmental conditions at a location, including resource availability. In this section, the effects of habitat structure on abiotic soil properties will be considered in terms of soil temperature, physical and chemical properties and resource pools.

Alteration of macroclimate conditions by urbanization has long been recognized as the "urban heat island effect" in which densely urbanized environments have higher air temperatures than their surroundings (e.g., Bornstein 1968). Likewise, aboveground urban habitat structures mediate soil temperatures as determined by their interception and absorption of solar radiation and ability to transfer heat energy into the soil (Geiger et al. 2003). Thus, soils shaded from sunlight by trees and shrubs can generally be expected to remain cooler on average than those in locations without canopies such as lawns (Avondet et al. 2003; Geiger et al. 2003). Several studies have shown that belowground "heat islands" were created in soils directly beneath and surrounding pavement and gravel mulch layers, both of which transfer heat into the soil more effectively than organic detritus (Halverson and Heisler 1981; Celestian and Martin 2004; Montague and Kjelgren 2004; Mueller and Day 2005). For example, Byrne (2006) found that, during mid-day hours, gravel-covered soils were 8–20°C warmer than soils under bark mulch, lawns and unmowed old fields and that lawn and bark-covered soils became warmer than those under old fields (Fig. 1a). At night however, soil temperatures converged and became similar among the four types of habitat structure. Thus, soil temperatures across urbanized ecosystems may be characterized by high temporal variability and exhibit fine-scale spatial heterogeneity that reflects spatial patterns of aboveground habitat structure. Shochat et al. (2004) suggested that modified microclimate patterns within urbanized ecosystems might temporally shift, or even eliminate, seasonal dynamics of ecological patterns and processes as compared to those seen in non-urbanized environments. Testing this hypothesis remains a frontier in urban ecology because so few studies have examined the broader consequences of altered soil

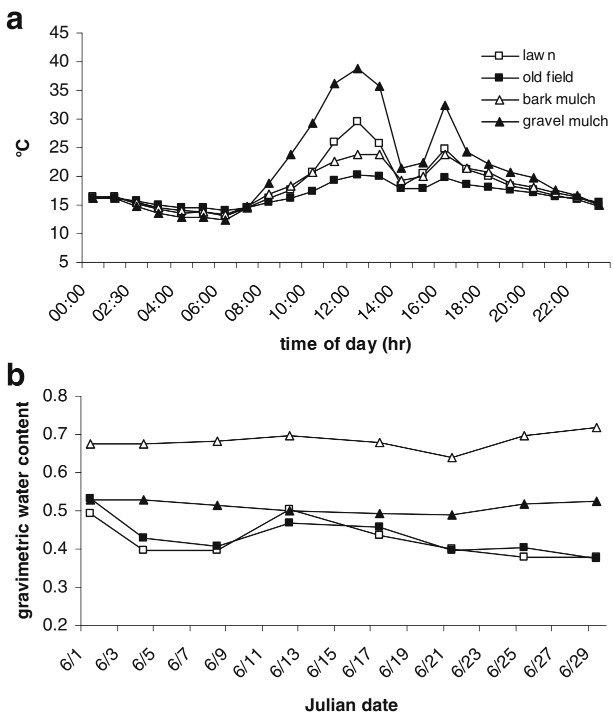


**Fig. 1** Abiotic microhabitat conditions in four types of urban habitat structure. **a** Mean hourly ground temperatures collected with dataloggers on June 1, 2004. Data are significantly different ($P<0.05$) at times of temperature divergence. From L.B. Byrne, unpublished data. **b** Mean gravimetric soil water content from the same habitat plots in June 2004. Bark mulch data differ significantly from all other habitats ($P<0.05$). From Byrne (2006). Data points for both variables are means from four replicated plots. SE bars and statistical differences among data points are not shown for visual clarity

(and air) temperature patterns for ecological variables in urbanized ecosystems and their soils.

Although human activities associated with urbanization often target manipulation of aboveground habitat structure, they usually result in concomitant alteration of the structure of soils and their chemical properties. Most dramatically, native soil profiles are disturbed through, e.g., removal, compaction or burial (Craul 1985; Lorenz and Kandeler 2005). Halverson and Heisler (1981) found that construction activities reduced the pH and increased the sand content in soils under asphalt. In addition, the bulk density, nitrogen (N) and organic matter content of urban soils can be altered by human activities, especially management of vegetation structure (Green and Oleksyszyn 2002; Pouyat et al. 2002; Hope et al. 2005; Kaye et al. 2005; Lorenz and Kandeler 2005). Scharenbroch et al. (2005) and Golubiewski (2006) found that age of landscapes (i.e., time since initial urbanization) was a significant predictor of many soil properties including organic matter content which increased with landscape age. However, as shown by Byrne (2006), soil properties can change quickly (e.g., within 16 months) after alteration of aboveground habitat structure (Figs. 1 and 2). Thus, the physicochemical characteristics of urban soils often exhibit higher

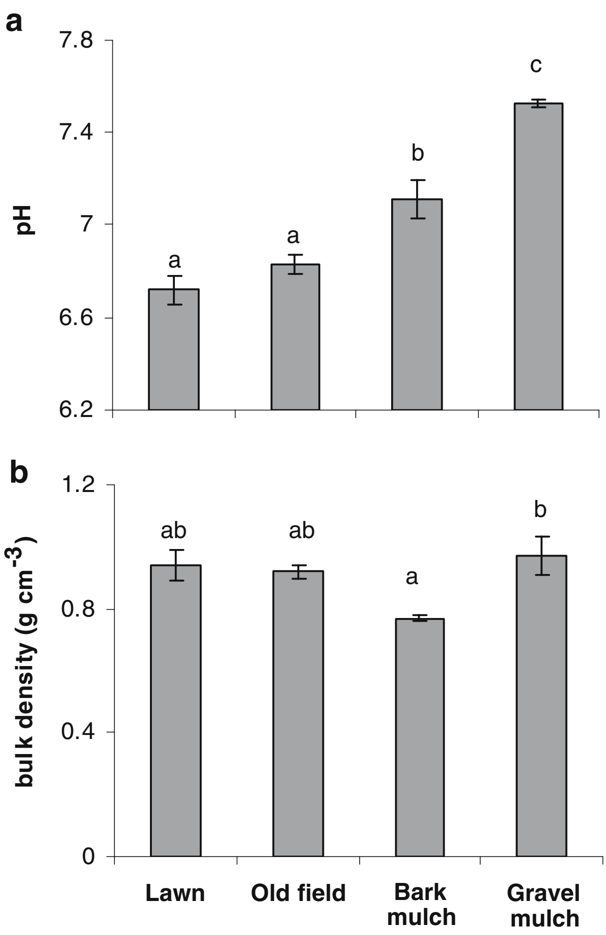


**Fig. 2** Soil properties under four types of urban habitat structure. **a** Mean (± SE) pH values of two sampling dates in 2004–2005. **b** Mean (± SE) soil bulk density of two sampling dates in 2004–2005. $N$=4 for each variable and habitat type. For both variables, means with different letters differ significantly ($P$<0.05) as analyzed with ANOVA. From Byrne (2006)

levels of spatial and temporal heterogeneity than native soils (Craul 1985; Pouyat et al. 2002; Hope et al. 2005; Lorenz and Kandeler 2005) due to quickly changing human management regimes across time and space (e.g., in terms of disturbance and resource inputs). Therefore, it is critical for ecologists to measure as many soil variables as possible at all sites in urban studies to ensure that accurate conclusions are made about relationships among human activities, aboveground habitat structures and the structure and ecology of urban soils.

Habitat structure affects soil resource pools at a location in two ways: (1) directly when the habitat structure provides the resource (e.g., plants produce roots and litter) and (2) indirectly when it mediates resource availability through the biotic community (e.g., reduced litter availability due to consumption by abundant detritivores) or environmental conditions (e.g., higher soil temperatures increase water evaporation). In several studies, soil carbon pools were found to be greater in lawns than native (desert and shortgrass steppe) or other urban habitat types (old fields) due to the presence of vegetation (i.e., habitat structure) that had higher above- and belowground net primary productivity (NPP) (Green and Oleksyszen 2002; Byrne and Bruns 2004; Shochat et al. 2004; Kaye et al. 2005; Golubiewski 2006). In addition to management of plants, humans impact resource inputs to urban soils via removal or addition of materials (e.g., lawn clippings, leaves, mulches) on the soil surface. The type (organic or inorganic), quantity (i.e., density, Fig. 3a) and quality (N content) of managed surface materials can impact a wide range of soil variables. For example, soil water content can be increased by the placement of dense surface layers of material (i.e., mulches) which reduce evaporation rates (Fig. 1b; Byrne 2006). Soil moisture patterns across urbanized ecosystems are certainly also affected by the identities and density of plants which interact to drive local evapotranspiration rates (e.g., Eviner 2004). However, this topic remains almost entirely unexamined in urbanized ecosystems.

The availability of other resources (e.g., oxygen and N) in urbanized soils can also be affected by human management of aboveground habitat structure that alters soil water (Fig. 1b) and organic matter availability (Fig. 1b; Hope et al. 2005; Kaye et al. 2005; Byrne 2006). For example, when organic matter inputs are of low quality, as with bark mulch that has a high C-to-N-ratio (Fig. 3b), inorganic N may be removed from the soil solution by soil microbes (immobilization) to meet their N requirements as they decompose the mulch (Fig. 4a; Byrne 2006). This can reduce the availability of soil N for plants in areas covered with bark mulch, an indirect effect of habitat structure. In general, however, very little is known about relationships and feedback mechanisms among soil resource pools, habitat structure and ecosystems processes and services in urbanized ecosystems because so few studies have been conducted.

## Soil organisms

As is the case for abiotic conditions of urban soils, precious few studies have been conducted about the effects of urbanization on soil biota, especially studies comparing communities below different types of aboveground habitat structure. (More studies have compared the biota of urban versus rural forests but they fall outside the scope of this review.) Arthropods have been the focus of most research conducted to date and are therefore, by necessity, the main focus of this section and the landscape patterns section below.

In general, it has widely been shown that ground-dwelling and soil arthropods are strongly influenced by habitat structure (Bell et al. 1990; Langellotto and Denno 2004). In

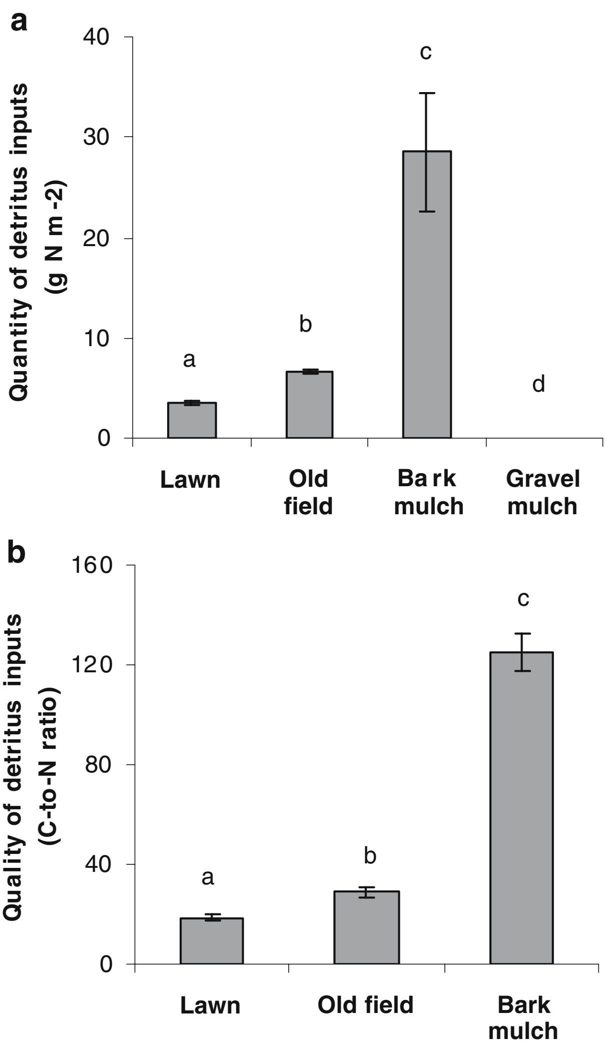


**Fig. 3** **a** Mean quantity of dead organic matter in the litter layer of four types of urban habitat structure collected in May 2005. **b** Mean (± SE) C-to-N ratios of dead organic matter from the litter layer in three types of urban habitat structure collected in May 2005. For both variables, $N$=4 per habitat and means with different letters differ significantly ($P$<0.05) as analyzed with ANOVA. From Byrne (2006)

an early urban ecology study, Nuhn and Wright (1979) concluded that the activity and abundance of ants across a heterogeneous urbanized landscape were determined by patterns of vegetation structure and microclimate. In addition, they found that soils beneath sidewalks were a common location for nests of certain species. Natuhara et al. (1994) reported that differences in the structure and composition of detritus layers among lawns, fields and forests in an urban park yielded differences in the species richness and abundance of soil mites and collembolans among the habitat types. More recent studies have also concluded that several habitat structure-related variables, rather than any one factor alone, interacted to drive patterns of ground and soil arthropod abundances and community structure across heterogeneous urbanized environments (Fig. 5a; McIntyre et al. 2001; Shochat et al. 2004; Byrne 2006).

Habitat structure can also influence urban arthropod communities through top-down and bottom-up trophic mechanisms (Bramen et al. 2002; Shochat et al. 2004; Faeth et al. 2005).

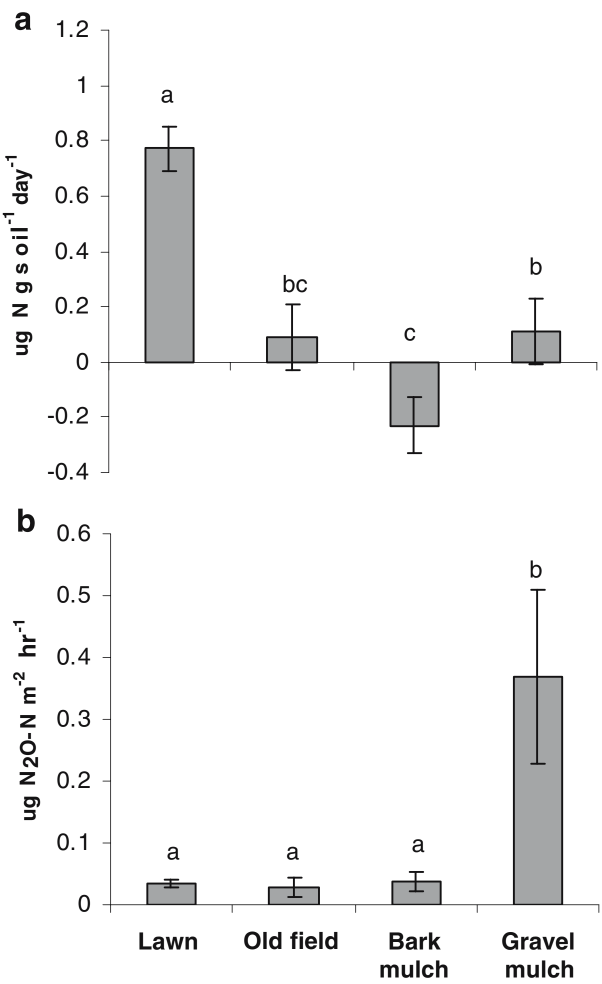


**Fig. 4** Net N mineralization and $N_2O$ flux from four urban habitat structures. **a** Mean (± SE) of net N mineralization rates from two field incubation periods in 2004 (June–September). **b** Mean (± SE) $N_2O$ flux from soil collected in static closed chambers in June 2004. $N$=4 for each habitat type. Means with different letters differ at $P<0.05$ as analyzed with ANOVA. From Byrne (2006)

For example, Byrne and Bruns (2004) found that certain collembolans were more abundant in lawns (managed without chemicals) than unmowed fields perhaps due to greater availability of mowed- clipping detritus in lawns, a bottom-up provision of resources. Alternatively, microclimate conditions mediated by habitat structure could promote top-down control of certain arthropods when predator numbers (e.g., spiders, beetles) increase in preferred habitats (Shochat et al. 2004; Faeth et al. 2005). Increased understanding of how above- and belowground food-webs (and linkages between them) are affected by urban habitat structures is needed to inform the design and management of urbanized landscapes in which beneficial predators are conserved and provide the ecosystem service of consuming pests (e.g., Bramen et al. 2002; see landscape patterns section below).

Another important issue related to arthropods, soils and habitat structure in urbanized ecosystems is the distribution and abundance of human disease vectors. For example, many studies in urbanized landscapes have reported that local tick abundance—and therefore probability of exposure to lyme disease—is affected by soil microclimate (especially humidity) which is largely determined by interactions among vegetation, detritus and soil

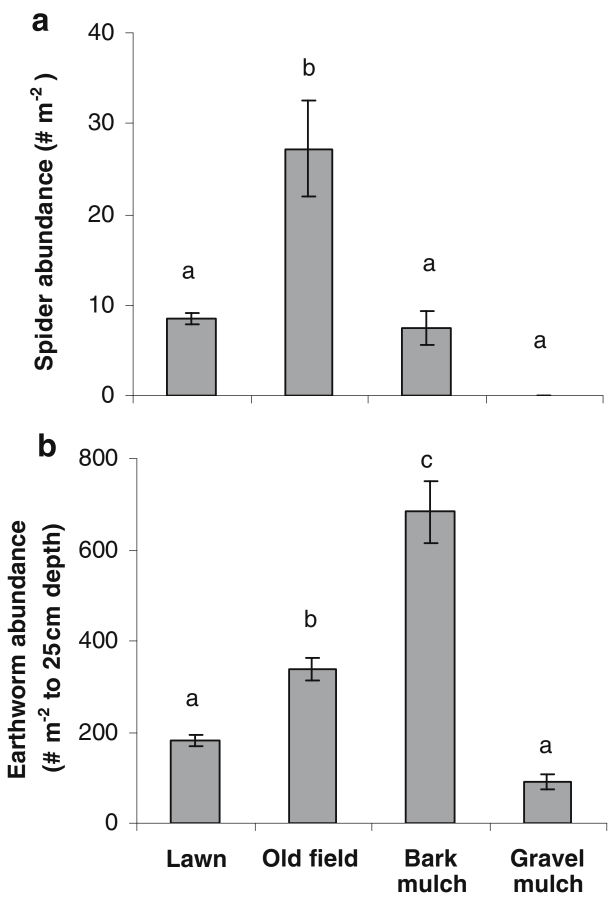


**Fig. 5** **a** Mean (± SE) spider abundances in four types of urban habitat structures. Spiders were collected by hand from 25 $cm^{-2}$ quadrats in September 2005. From L.B. Byrne, unpublished data. **b** Mean (± SE) earthworm abundances in four types of urban habitat structures averaged over six sampling dates 2004–2005. Earthworms were hand sorted from 25 $cm^{-3}$ soil samples. From Byrne (2006). For both variables, $N$=4 per habitat type and means with different letters differ significantly ($P$<0.05) as analyzed with ANOVA

structure (e.g., Ostfeld et al. 1996; Guerra et al. 2003). Such results can be communicated to the public using habitat structure as a focus because this concept provides a broad framework within which landscape management guidelines that aim to reduce the probability of disease exposure in urbanized ecosystems can be developed.

During the process of urbanization, humans often remove native vegetation and replace it with wholly new combinations of plant species (including many non-native ones) that might not otherwise co-exist (Whitney and Adams 1980; Hope et al. 2003; Thompson et al. 2003; Martin et al. 2004). A major frontier for urban soil ecology research lies in comparing the direct and indirect effects of heterogeneous urban plant communities (e.g., lawns, gardens) on soil organisms. Recent research about the influence of plant species identity and richness on soil biota (e.g., Korthals et al. 2001; Wardle 2002; Wolfe and Kilronomos 2005) suggests that human-designed plant communities may have unique and perhaps unexpected effects on urban soil biodiversity and, in turn, ecosystem processes and services. However, to date, relationships among human-designed urban floras, the patterns of habitat structure they create and soil organisms have not been widely investigated.

Likewise, the responses of most groups of soil biota to non-vegetation types of human-created urban habitat structure have not been studied. Thus, next to nothing is known about the diversity of life (or lack thereof) inhabiting soils beneath, e.g., mulched gardens, buildings, roads and parking lots. Byrne (2006) found that earthworm abundances decreased and increased in soils covered with gravel or bark mulch (but that lacked plants), respectively, as compared to their abundances in soils under lawns and unmowed old field vegetation (Fig. 5b). These results, as well as the ones summarized above for arthropods, indicate that human-manipulation of aboveground (plant and non-plant) habitat structure can strongly influence soil biota. Unfortunately, almost no other studies were found in the literature that reported comparisons of soil biota among different urban and non-urban habitat types. Thus, we remain a long way from understanding how the design and management of urbanized landscapes impact soil biodiversity.

## Ecosystem processes

Although ecosystem processes have rarely been examined in urbanized soils, foundational studies have appeared in recent years. As for soil abiotic conditions and organisms, rates of matter and nutrient transformations vary widely among urban and non-urban habitat types (Green and Oleksyszyn 2002; Milesi et al. 2003; Groffman et al. 2004; Scharenbroch et al. 2005; Kaye et al. 2004, 2005; Byrne 2006). Studies in arid biomes have shown that irrigated lawns have up to 2.5 and 10 times greater $CO_2$ and $N_2O$ flux from soils, respectively, than xeriscaped and native landscapes due to increased water inputs, NPP and microbial activity (Green and Oleksyszyn 2002; Kaye et al. 2004, 2005). Although certain urban habitat types may be highly productive, urbanization may reduce regional NPP rates as was observed in forested landscapes of the Southeastern United States (Milesi et al. 2003). Variability in NPP rates among different types of urban habitat structure (from zero in paved areas to very high in fertilized lawns) may in turn give rise to high spatial heterogeneity in the C pools and fluxes of urban soils (Pouyat et al. 2002; Byrne 2006).

Higher N inputs (e.g., from atmospheric pollution and lawn fertilizer) may also contribute to greater rates of NPP, C and N turnover and net N losses in urbanized ecosystems as compared to surrounding native ones (Baker et al. 2001; Groffman et al. 2004; Law et al. 2004; Hope et al. 2005). Yet, urbanized ecosystems have also been observed to retain large amounts of their N inputs (possibly in soils), upwards of 75% as observed in Baltimore, MD (Groffman et al. 2004). Because so few studies have been conducted to date, many opportunities exist for generating fundamentally new data about how urbanization affects rates of N turnover, accumulation and loss in urban soils at local scales and, in turn, contributes to altered patterns of N cycling at regional and global scales (Baker et al. 2001; Kaye et al. 2004, 2006).

The studies discussed above compared ecosystem processes between urbanized and non-urbanized ecosystems. Even fewer studies have compared them among soils beneath the different types of habitat structure that comprise urban landscapes. Scharenbroch et al. (2005) measured key ecosystem processes in urban soils from a range of habitats and ages and concluded that age of the urban environment greatly influenced soil C and N pools and fluxes. They observed that older urban soils had lower $CO_2$ flux and greater rates of N mineralization than more recently disturbed soils (Scharenbroch et al. 2005). As another example, Byrne (2006) observed significant differences in N mineralization rates and $N_2O$ flux among soils under lawns, old fields, and layers of shredded bark mulch and gravel mulch (Fig. 4). In this study, it was hypothesized that differences in N cycling among the four habitat types were driven by differences among them in soil abiotic conditions (Fig. 2), litter quantity (Fig. 3a) and quality (Fig. 3b) and earthworm abundances (Fig. 5b) (see Byrne (2006) for additional data about plant communities, C and N cycling). Significant differences in the soil properties and biogeochemical cycles among the experimental habitat structure plots studied by Byrne (2006) were observed within 16 months after their creation in a previously unmanaged old field. This suggests, in agreement with Scharenbroch et al. (2005), that urbanization and human management inputs can quickly change soil communities, resource pools and ecosystem processes. Given the high spatial and temporal heterogeneity of human activities in urbanized ecosystems, the search for general relationships between patterns of urban habitat structure and ecosystem processes may prove enormously challenging. Nonetheless, generating additional data about how various types of urban habitat structure affect ecosystem processes is critically needed to inform the development of landscape management methods that seek to conserve ecosystem services that, e.g., promote soil fertility in urbanized ecosystems (Wall 2004; Kremen 2005).

## Landscape patterns

In this section, two research topics related to landscape patterns and soil ecology that have been examined in urban ecosystems are discussed: landscape context and fragmentation.

The urban-rural (U-R) gradient approach has been used to investigate how different levels of urbanization (i.e., urban, suburban, rural) surrounding a focal study site (i.e., its landscape context) influence its ecology. Most U-R gradient research has focused on forests without comparing them to other habitat types. Nonetheless, discussion of these studies is included in this review because they illustrate the importance of including landscape context as a key variable of interest in urban soil ecology research.

The most well characterized U-R gradient to date consists of oak forests located in New York City, NY and suburban and rural Connecticut (McDonnell et al. 1997). Numerous abiotic and biotic variables, and ecosystem processes in the soil and leaf litter were found to differ along this U-R gradient. For example, urban forests exhibited 2–3°C higher average monthly soil temperatures (from 1985–1991), higher soil heavy metal concentrations and lower leaf litter biomass than rural sites (McDonnell et al. 1997). Abundances of soil mites and collembolans and fungal growth rates on leaf litter were lower in the urban sites during certain seasons and were negatively correlated with soil heavy metal concentrations (McDonnell et al. 1997). In contrast, non-native earthworms were found to be more abundant in the urban forests (McDonnell et al. 1997). Differences in the abiota, biota and leaf litter chemistry along the U-R gradient appear to influence variability in C and N pools and fluxes among the forest patches (McDonnell et al. 1997; Carreiro et al. 1999; Zhu and Carreiro 2004). The mechanistic relationships between these observations and urban habitat structure patterns in the forests' landscape contexts are not well understood. However, the lesson to be learned from this and other gradient studies (e.g., Avondet et al. 2003; Pavao-Zuckerman and Coleman 2005) is that spatial patterns of habitat structure in a study site's landscape context can strongly impact the ecology of its soil, possibly to a greater degree than the characteristics of its own habitat structure.

The ecological effects of landscape context have also been studied in urban ecosystems in relation to the conservation of beneficial ground-dwelling and soil arthropods. Although urban landscapes generally have high spatial heterogeneity, the diversity of plant species and their habitat structural complexity can be reduced locally resulting in large patches of homogeneous microclimate and resource availability (e.g., in expansive lawns). If numbers of predatory arthropods are reduced in structurally simple landscapes, outbreaks of lawn and garden pests (e.g., soil grubs) can occur (Shrewsbury et al. 2004). Manipulating patterns of habitat structure provides a way to conserve natural enemies that can help keep pest numbers in check (i.e., the goal of conservation biological control). For example, increasing the diversity of flowering plants in urbanized landscapes might provide favorable habitats and resources for predators and parasitoids and increase their abundances (Bramen et al. 2002; Shrewsbury et al. 2004; Rebek et al. 2005). Alternatively, small patches (e.g., 3×3 m) of unmowed vegetation or mulch that have dense and complex detritus layers can provide refugia for predatory arthropods (e.g., spiders, ants) in highly managed lawns and, in turn, increase their overall activity levels across urbanized landscapes (Byrne 2006). These perspectives reflect the utility of using habitat structure as a focus for discussing applied ecological problems and their solutions in urbanized ecosystems.

Another landscape-scale topic that has been investigated in urbanized ecosystems is the effects of habitat fragmentation on ground arthropod communities. Several studies found that arthropod communities were affected by the patch sizes of urban habitats in conjunction with shifts in plant species composition at patch edges (Faeth and Kane 1978; Miyashita et al. 1998; Bolger et al. 2000; Gibb and Hochuli 2002). In general, island biogeography theories have been supported in urban ecology studies with positive relationships observed between species richness and patch size (Faeth and Kane 1978; Miyashita et al. 1998; Bolger et al. 2000). However, taxon specific responses have been observed to be more variable with some species persisting in small fragments but not larger ones and vice versa (Gibb and Hochuli 2002). Miyashita et al. (1998) observed that spiders' body sizes influenced, in part, which species persisted in urban forest patches of different sizes, e.g., larger species were absent from small patches. Bolger et al. (2000) emphasized that time since initial fragmentation was an important factor that influenced arthropod communities in the patches they examined. Results from these studies suggest that many factors alone, or in combination, can affect arthropod communities in highly fragmented urbanized landscapes. Habitat structure provides a central concept for approaching the description of urban landscape patterns and investigating their effects on the distribution and movement of soil organisms across urbanized ecosystems.

## Sociocultural variables and urban soil ecology

The multivariate literature review presented above illustrates that habitat structure provides a useful perspective from which to examine the effects of human management of urbanized landscapes on urban soil ecology. In addition, habitat structure is highly relevant to the study of urban ecology in general because creation and maintenance of desired habitat structures is often a key objective of human urban landscape management activities. Following this, indirect relationships between variables associated with human sociocultural systems (e.g., wealth, politics, values) and urban soil ecology can be considered because sociocultural variables influence human landscape management activities that drive patterns of urban habitat structure and, consequently, belowground variables.

Although examination of relationships between sociocultural and ecological variables is a central goal of urban ecology research (e.g., Pickett et al. 1997; Grimm et al. 2000; Hope et al. 2003), few, if any, of the studies discussed above attempted to link sociocultural variables with ecological patterns in urban soils. However, a small but growing body of aboveground-centered research has revealed that the structure of urban plant communities is significantly related to sociocultural variables such as household income and lifestyle behavior (Hope et al. 2003; Martin et al. 2004; Grove et al. 2006). In other words, as Whitney and Adams (1980) stated, "Urban plant communities are as much a product of the cultural environment as they are a part of the physical landscape (p. 446)." For example, in

Phoenix, AZ, Martin et al. (2004) found positive relationships between family incomes and plant species richness in residential landscapes, suggesting that wealth might enable people to create more structurally diverse gardens. Often, urbanized landscapes are managed to visually convey information about the wealth and aesthetic sensibilities of the property owners, as when lawns are managed with chemical inputs and raked free of leaves (Nassauer 1995; Law et al. 2004; Byrne 2005). An exciting interdisciplinary opportunity for urban ecologists is to examine the degree to which sociocultural variables that drive human management of urbanized landscapes might explain some of the fine-scale spatiotemporal heterogeneity of ecological patterns and processes in urban soils. Habitat structure will certainly help in this endeavor because it provides the physical and conceptual link needed to concurrently examine the sociocultural and ecological variables associated with a location, as illustrated in the conceptual framework introduced below.

## Habitat structure conceptual framework

The primary premise of this article is that habitat structure provides a useful concept for organizing the multivariate study of the direct and indirect effects of urban habitat structure on the ecology of urban soils. As such, habitat structure was used as a starting point from which to create a conceptual framework (Fig. 6) that can facilitate the development of questions and hypotheses for urban soil ecology research. Although several conceptual frameworks have previously been proposed to guide urban ecologists (Pickett et al. 1997;

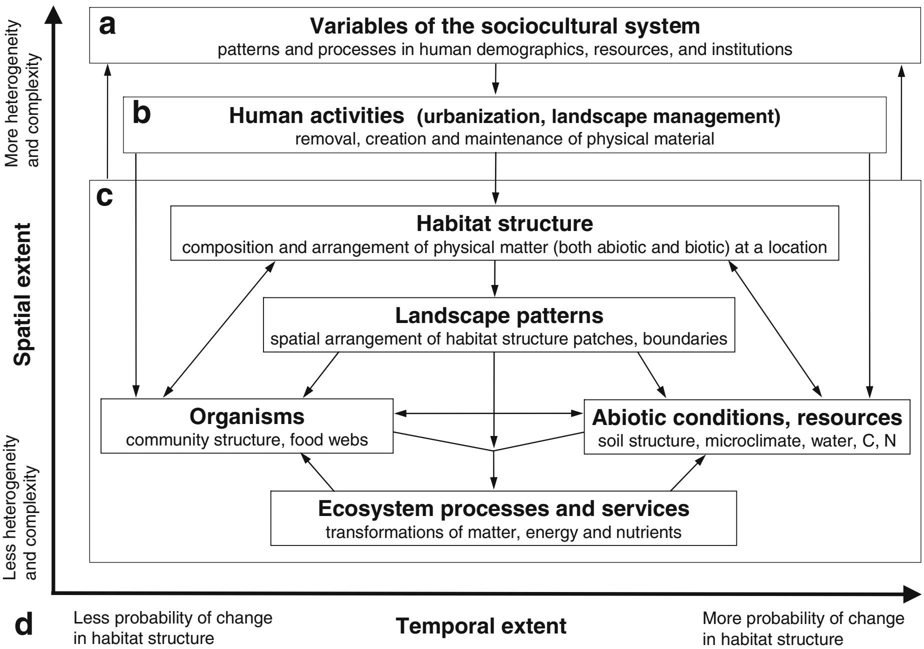


**Fig. 6** A conceptual framework using habitat structure as a central concept to illustrate relationships among **a** sociocultural variables, **b** human activities and **c** ecological variables. **d** Examination of the variables and their relationships can be examined across spatial and temporal scales. See text for further discussion. Modified from Byrne (2006)

Grimm et al. 2000; Alberti et al. 2003), none have explicitly incorporated habitat structure as a fundamental ecological concept. The framework presented here is not meant to replace the others. Rather, adopting habitat structure as an organizing focus generates an alternative framework that is more suitable for fine-scale (i.e., cm to m), on-the-ground approaches to soil ecology research. Such approaches are needed to help reveal soil ecological patterns within heterogeneous urbanized landscapes that might be missed using broader-scale frameworks (e.g., that emphasize patch dynamics) and methodologies (e.g., mapping of land cover at coarse scales). However, the framework was designed to be flexible and broad such that it can be used in any study where habitat structure is a variable of interest (including those of non-urban ecosystems).

The organizing backbone of the framework is sociocultural variables (Fig. 6a) driving human activities (e.g., construction, gardening; Fig. 6b) that modify habitat structures which influence other ecological variables (Fig. 6c). Sociocultural variables that influence human activities have been discussed previously (Pickett et al. 1997; Grimm et al. 2000; Law et al. 2004; Byrne 2005) and could be readily adapted into the framework; they are not discussed further because they are not a primary focus of this article. However, the framework does highlight the importance of human activities as a mechanistic link connecting sociocultural and ecological variables, a point often ignored or underemphasized in previous discussions of urban ecology (but see Grimm et al. 2000). Although subtle, explicit recognition of this linkage is necessary to more fully understand how sociocultural variables are translated through human activities into patterns of habitat structure and, in turn, other ecological variables.

Habitat structure is an appropriate vantage point from which to examine other ecological variables because it is the physical stage on which they interact. In the habitat structure framework (Fig. 6), four main components of ecological systems are included following the topics used to organize the urban soil ecology literature review: abiotic conditions and resources, organisms, ecosystem processes and landscape patterns. A number of basic questions can be asked about the relationship between each of these and habitat structure, exemplifying its power as an integrating concept for general ecological research in addition to urban soil ecology studies. What are the abiotic conditions and resource pools generated by the habitat structure? How does the habitat structure affect the abundance and interactions of organisms? How are ecosystem processes affected by habitat-structure mediated variables? How do the landscape patterns created by heterogeneity of habitat structures across space affect the movement of organisms and nutrients?

For soil ecologists, these questions can be rephrased to help examine relationships between aboveground habitat structure and belowground ecology. For such questions, it is critical to bear in mind (as shown in the literature review sections) that habitat structure may have both direct and indirect effects on many soil variables. This can be illustrated in the framework by connecting habitat structure to any of the four other ecological components directly or indirectly through another component. For example, habitat structure can influence local abundances of soil arthropods (e.g., collembolans) directly by providing surface areas over which they can move and hide from predators. Indirect effects of habitat structure on soil arthropods would occur when the structure creates favorable microclimates or provides food resources. Countless such relationships could be described for any combination of variables while using habitat structure as a common focal point.

In most urban ecology studies, habitat structure is an essential a priori consideration because study locations (e.g., forests, lawns, streams) are chosen (or created) based on physical structures and/or the spatial context of structures surrounding them (e.g., as in riparian zones and U-R gradients). A general description of the structures within and around study sites is usually included in most research articles (as exemplified by McIntyre et al. 2001) and may be sufficient for many research objectives. However, more rigorous and detailed examination of the effects of habitat structure on ecological variables requires making the habitat structure concept and framework more operational. Specifically, three key dimensions of habitat structure should be considered when adopting it for studies of soil ecology in urban (and non-urban) ecosystems: heterogeneity, complexity and scale (McCoy and Bell 1990).

Heterogeneity refers to “kinds of structures” (McCoy and Bell 1990, p 18) and is generated by differences in the composition (i.e., physicochemical structure) and/or arrangement (i.e., distribution in space) of matter among locations (Table 1). Thus, two discrete locations will be heterogeneous in habitat structure if 1) the arrangement of matter having the same composition differs between them or 2) one location contains matter of different composition than the other. In contrast, complexity refers to “amounts of structure” (McCoy and Bell 1990, p 18) and is generated by the numbers, or volume, of distinct, individual entities (e.g., blades of grass, walls) at a location (Table 1). Surface area of material is a key feature of habitat structure complexity that dictates the space over which organisms, nutrients and energy can interact (Beck 2000). Generally, a location with a greater number of distinct structures can be expected to have more surface area and higher complexity. Note, however, that two habitats with similar amounts of matter may differ in complexity if the number of distinct structures comprising one habitat is larger than in the other and therefore the habitats differ in their surface areas. For this reason, the surface area-to-volume ratio can be an appropriate description of habitat complexity.

In measurements (or general descriptions) of habitat structure, caution must be taken to not confuse complexity with heterogeneity (McCoy and Bell 1990; Beck 2000). These properties can vary independently of each other and differentially affect ecological variables. In many studies, complexity and heterogeneity have been confounded, thus lessening their value for providing insight into how different dimensions of habitat structure influence organisms and ecosystem processes (McCoy and Bell 1990; Beck 2000). (Reviewing methods for measurement of complexity and heterogeneity is outside the scope of this paper; see Bell et al. 1990; Beck 2000; and Tews et al. 2004 for additional discussion.) As is true for the ecological literature at large (McCoy and Bell 1990), the urban soil ecology papers reviewed above have not discussed the relative influence of the complexity versus heterogeneity of habitat structure on ecological variables. A major challenge for future habitat structure research will be to operationalize these concepts further so that their relative effects on urban soil ecology can be discerned.

As emphasized by many of the studies discussed in the literature review, another important consideration for all habitat-structure studies is scale, both temporal and spatial. A key advantage of the habitat structure concept is its flexibility for use at a wide-rage of scales (e.g., meters and patches to kilometers and biomes). The definition adopted in this paper (Table 1) is intentionally silent about appropriate scales of study but emphasizes that the spatial and temporal extents must be defined for each unit (or type) of habitat structure examined. It is important to explicitly describe the extent of each study site because the complexity and heterogeneity of habitat structures will change with increasing spatial and temporal scales. As in all ecological studies, the extent of area and time encompassed by research on urban habitat structures should be relevant to specific objectives and the organisms and processes under investigation (McCoy and Bell 1990). However, as discussed in the landscape patterns section, the spatial scale of most studies should be large enough to include some consideration of the landscape context around study sites because of potential influences of the surrounding habitat structures on the ecology of the study sites of interest.

Because defining spatial and temporal scales of study are critical to the working definition of habitat structure, they are incorporated into the conceptual framework as axes along which ecological variables can be placed to facilitate generation of hypotheses about them (Fig. 6d). Although the study of landscape patterns and ecosystem processes inherently include time and space dimensions, placing these and other variables within a matrix of smaller or larger scales suggests a range of alternative hypotheses that can be developed about how dynamics of sociocultural and ecological systems change together or independently through time and space (Pickett et al. 1997; Grimm et al. 2000). Investigating the variability in relationships between ecological and sociological systems across a wide-range of temporal and spatial scales is a frontier for urban ecology in general and specifically for understanding the ecology of urban soils (Kaye et al. 2004).

A final issue related to urban habitat structure that has not yet been addressed concerns the ways in which human activities may indirectly affect habitat structure without direct modification of physical matter. In particular, such activities include those that involve inputs of chemicals (e.g., pollution or lawn fertilization) or organisms into the environment (e.g., introduction of non-native or biological control species). In the conceptual framework, these are illustrated by arrows connecting human activities (Fig. 6b) to the organisms and abiotic conditions (Fig. 6c). Chemical and organism inputs by humans may or may not be intentional or intended to affect habitat structure. For example, inputs of heavy metal into soils from industrial or transportation activities and invasions of non-native earthworms are not intentional but may alter patterns of habitat structure, perhaps in undesirable ways (e.g., increasing or decreasing litter decomposition rates; McDonnell et al. 1997). In contrast, fertilizer and pesticide inputs into lawns are intentional and directed toward maintaining habitat structure (i.e., grasses) in desired forms (i.e., green, one species; Law et al. 2004; Byrne 2005). In turn, such management practices indirectly influence soil organisms and abiotic variables through their direct effects on the habitat structure. Although such relationships appear complex at first, the habitat structure conceptual framework (Fig. 6) provides an effective roadmap for guiding discussion and interdisciplinary analyses about relationships among sociocultural variables, human management of habitat structure and a wide range of above- and belowground ecological variables.

## Conclusions

A key challenge for urban ecologists is to tease apart the relative contributions of sociocultural versus biophysical factors as drivers of ecological patterns and processes (Grimm et al. 2000; Hope et al. 2003). Habitat structure is a useful concept for addressing this challenge because it focuses attention on a variable (i.e., physical matter) that is simultaneously related to both sociocultural and ecological systems. The objective of many human landscape management activities in urbanized ecosystems, which are influenced by sociocultural variables, is to create and maintain desired types of habitat structure (e.g., lawns, roads). In turn, patterns of habitat structure affect many other ecological variables (Bell et al. 1990). Thus, habitat structure provides a physical and conceptual link between sociocultural and ecological variables that can be exploited as a fundamental theme for urban ecology research (Byrne 2006).

Specifically, the study of urban soil ecology can be facilitated by the fine-scale, on-the-ground multivariate perspective emphasized by the habitat structure concept. The review of urban soil ecology research presented in this paper illustrates the multivariate ways in which heterogeneous habitat structures influence the abiotic conditions, resource pools, organisms and ecosystem process in the soils of urbanized ecosystems. Key insights emerging from the review of this research suggest the following opportunities for studying urban soil ecology:

- Because very little research has been conducted about urban soil ecology, endless opportunities exist to develop observational and experimental (especially factorial) studies that tease apart the direct and indirect effects of urban habitat structures on soil ecological variables.
- Habitat structure provides a link between sociocultural and ecological variables and between above- and belowground habitats. Thus, it can be used as a focus for exploring relationships between sociocultural variables and patterns of urban soil ecology. However, this research opportunity is challenged by the high level heterogeneity in types of urban habitat structure and reasons why humans manage urbanized landscapes which may make discovery of general relationships difficult.
- Ecological characteristics of urban soils can change quickly after alteration of aboveground habitat structure (Byrne 2006) and may differ widely among soils of different ages (e.g., Scharenbroch et al. 2005). Investigating details about the temporal patterns of change in urban soils is an open frontier for future research.
- Research about urban soil ecology is needed at the fine scales relevant to human management of backyards in order to address applied questions related to managing pest populations (e.g., herbivores, disease vectors) and soil processes that provide urban ecosystem services. Habitat structure provides a framework for developing easy-to-understand landscape management guidelines.
- Relationships between soil ecological variables and human-created urban plant communities as well as non-vegetation types of urban habitat structure remain almost wholly unexamined but may yield unexpected and important insights.

A main conclusion from the review of the urban soil ecology literature is that there is currently a dearth of knowledge about how soils are influenced by urbanization and human management of urbanized landscapes. Although habitat structure is largely underappreciated and underutilized in the broader ecological community, it provides a useful concept for elucidating direct and indirect relationships among sociocultural and ecological variables that interact to determine the ecological characteristics of soils at a given location. A conceptual framework based on the concept of habitat structure has been presented to facilitate the development of interdisciplinary questions and hypotheses about the ecology of urban soils.

It is hoped that this article has succeeded in illustrating that habitat structure provides a fundamental concept and framework for the study of urban soil ecology and, thus, has inspired others to begin the important task of improving our understanding of how human creation and management of different types of urban habitat structure impact the ecology of soils. Such research is critically needed to inform the design and management of urbanized landscapes in which favorable levels of soil biodiversity and ecosystem services are conserved.

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