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Linking ecological and built components of urban mosaics: an open cycle of ecological design

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Summary

1. By the end of this decade, the majority of people will live in cities and suburban areas. Urban areas, including suburbs and exurbs, are expanding rapidly worldwide.

2. Plant ecology has largely ignored cities, or has primarily focused on the discrete urban green spaces within cities.

3. Plant ecology is increasingly engaging urban ecosystems as integrated natural-human systems, in which human agency is part of the complex of feedbacks.

4. Linking plant ecology with urban design (architecture, landscape architecture, civil engineering and urban planning) can help to integrate research and understanding of plants into the structure of cities, and to make use of urban design projects as ecological research tools.

5. *Synthesis.* A cycle of ecological design illustrates the linkage of plant ecological research with the ongoing transformation of urban systems by urban designers and civil society. Quality of life, human health, public appreciation of ecological processes in cities, and scientific understanding can all be enhanced by participating in a cycle of ecological urban design.

Key-words: architecture, city, design, development, ecosystem, experiment, planning, restoration, suburb, urban ecology.

Introduction

More than 50% of the Earth's residents will live in urban areas by 2010 (United Nations 2001). How will the science of plant ecology deal with this global trend? While most ecologists have focused on wild lands (Collins *et al.* 2000), several of the ecological pioneers investigated working landscapes (Watt 1960), or the vacant spaces of cities (Salisbury 1943). Indeed, Tansley (1935) called for attention to be paid to the role of humans in ecological processes when he introduced the ecosystem concept. Ecologists are beginning to address urban areas as complex ecosystems (Grimm *et al.* 2000; Cadenasso *et al.* 2006). What opportunities exist in ecology on the urban frontier?

Plant ecologists have examined plant community structure in certain cities, community dynamics on derelict land, and adaptation of plants to urban environments (Bornkamm *et al.* 1982; Sukopp 1990; Wittig 2005). However, plant ecology in cities, suburbs and the urban fringe has not taken human agency fully into account. How feedbacks operate between urban vegetation and plant species performance on the one hand, and human activities and social structures on the other, is a crucial issue for plant ecology in urban contexts.

In this essay, we highlight one way in which plant ecology can exploit and investigate the expanding urban ecosystem. We explore how plant ecology and urban design can intersect to improve ecological understanding and quality of life in the world's burgeoning settled areas. Urban design is a term used by architects, planners, landscape architects and civil engineers to label their cluster of professions. The call to connect ecology and the design realm in a better way has come from both ecologists (Palmer *et al.* 2004) and urban designers (Sukopp *et al.* 1995; McGrath *et al.* in press).

Plants in the structure and function of urban ecosystems

The first step in integrating plant ecology into design of cities is to make a structural assessment of urban areas. Like any ecological study, the understanding of urban ecological systems is concerned with structure, function, dynamics and their relationships. Urban structure includes the buildings and infrastructure; urban function includes delivery of

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resources and removal of wastes; and dynamics includes turnover in building stock and development of new transportation corridors, for example. However, beyond these obvious human features, plant ecological processes also play a role in the structure, function and dynamics of urban ecosystems. Vegetation, along with buildings and surfaces, is a principal element of urban structure (Ridd 1995). Plants contribute to the spatial structure of urban systems not only through their presence in parks and reserves, but also throughout the entire urban mosaic. In urban areas, the amounts, structure and condition of these three components (vegetation, buildings and surfaces) reflect human agency (Cadenasso *et al.* 2007).

One way in which understanding of the role of plants throughout urban systems is evolving is through improved classification of spatial heterogeneity in urban areas. Spatial differentiation in urban areas is a central concept in geography, social science and urban design (McGrath *et al.* in press). Spatial heterogeneity is also one of modern ecology's primary concerns (Hutchings *et al.* 2000). Many commonly used urban classifications have shortcomings as integrative tools. For instance, the system employed by the United Nations Food and Agricultural Organization (DiGregorio 1996) first distinguishes vegetated from non-vegetated areas on the coarse scale. This dichotomy segregates forest classes from settled land covers. In such classifications, urban areas are necessarily exclusive of natural areas.

Many finer scale ecological classifications within urban areas continue this approach of separating the anthropogenically constructed, paved or denuded sites from those occupied by vegetation (Klotz 1990). While they may do so to help protect green spaces in cities (Sukopp *et al.* 1995), they still obscure the joint role of human agency and vegetation processes in urban mosaics (Cadenasso *et al.* 2007).

The fact that urban covers are complexes of three elements (vegetation, surfaces and buildings) suggests that a different classification strategy is appropriate. Cadenasso *et al.* (2007) have devised a classification that discriminates patch types on the basis of the combined cover of the three major elements of urban cover. This reconceptualization of urban land covers assumes that the cover and type of vegetation, building and ground surface *jointly* define the spatial heterogeneity of human settlements. This new model of integrated urban land cover sets the stage for improved linkage between urban design and plant ecology.

Existing vs. designed urban structure

Two perspectives on urban vegetation are possible. One deals with urban vegetation as it exists. This helps elucidate the role of vegetation in the ecological services in urban systems (Bolund & Hunhammar 1999; Grimm *et al.* 2000; Pataki *et al.* 2006; Troy *et al.* 2007).

In contrast, a new alternative approach focuses on how new or altered vegetation can contribute to improved ecological services in the future. Using this approach, plant ecologists can become involved in work examining how the vegetation component of urban patch types, spread throughout the urban ecosystem, can improve ecological function by design. Acknowledging the role of design in the urban mosaic allows plant ecologists to consider new urban vegetation as a tool to enhance the environmental goods and services it provides and supports throughout the metropolis, and not just in designated reserves. Ecologists, urban designers and psychologists have recognized the beneficial effects of vegetation in cities, suburbs and towns (Spirn 1984; Sukopp 1990; Frey 1998; Kuo et al. 1998). The opportunity exists to combine the growing knowledge of the role of vegetation in cities, towns and suburbs with the work of urban designers. Urban designers work to imagine what the city can be, and express their vision in architectural, infrastructural and landscape designs, and in plans scaled from the neighbourhood to the region. Is it possible to develop a model that integrates urban design with the knowledge and concerns of plant ecologists? How can plant ecology become better integrated with the creative thinking and work of urban design?

Three main ecologically orientated goals may be achieved in urban areas. First, plant ecology can contribute to increased understanding of the structure and function of urban ecosystems. In spite of the large number of effects that have already been documented, there remains much opportunity for better understanding of the ways in which plants contribute to functions such as C sequestration, nutrient retention and maintenance of biodiversity. Furthermore, the ways in which plants and vegetation influence human actions and decision-making are open questions. How ethnicity and lifestyle, property regimes, social norms and economic factors influence the structure and function of the vegetation component of cities are also active areas of research (e.g. Grove et al. 2005, 2006a,b; Troy et al. 2007). Temporal lags and the role of history in the interaction between these various social and vegetational factors are also important (Cadenasso et al. 2006).

The second goal is to increase the ecological function of urban areas. For example, storm water quality may be improved and its volume reduced by increasing permeability of urban surfaces or by restoring urban streams and riparian zones (Groffman et al. 2003). Similarly, improving microclimate, and thus reducing cooling and heating demands, can be achieved through the presence of trees (Nowak et al. 2002). Particulate pollution can be reduced by the presence of mature tree canopies (McPherson et al. 1997). These examples indicate how ecological processes acting in cities can reduce the work required of engineered structures and petroleum powered processes in maintaining local environmental quality. A third goal is to increase the benefits to humans of the vegetation component of urban areas. These may include such social benefits as reduction in conflict (Kuo & Sullivan 2001), provision of a focus for neighbourhood revitalization (Burch & Grove 1993), or promotion of human health (Hill 2001; Northridge et al. 2003).

These points suggest that explicit incorporation of plant ecology into the work of urban design may yield benefits both to local urban residents and to people and systems 'downstream', in terms of water, air and pollution flows. Benefits may also accrue to ecology itself as a result of using designed areas as experimental comparisons or as areas for ecological monitoring. Developing partnerships with urban designers to exploit design projects as venues for rigorous ecological experiments can extend the sites that are available for research in urban areas, alert urban dwellers and policy makers to locally relevant ecological knowledge, and serve as locations for engaging with primary and secondary education (Felson & Pickett 2005).

An open cycle of ecological urban design

To explore the potential social and scientific benefits of linking ecology with urban design, we present a synthetic framework. We use Baltimore, Maryland, USA, as an example. The cycle begins with a practical motivation: the health of the Chesapeake Bay, on which Baltimore is located. The Bay is classified as 'threatened waters' by the Clean Water Act of 1972. The seven states in the Chesapeake watershed must reduce nitrate, phosphate and sediment pollution to the Bay by 40% before 2011 (Koroncai *et al.* 2003). While controlling point source pollution has been used for a long time in an attempt to achieve that goal, given the slow progress in pollution mitigation, increasing attention is being paid to nonpoint sources of pollution.

One way to reduce non-point loading of nitrate to the streams draining into the Chesapeake Bay is to improve riparian ecosystem function. Based on knowledge from agricultural and wild landscapes, it was originally assumed that urbanized riparian systems might contribute substantially to improving Chesapeake Bay water quality. Recent findings in Baltimore that urban and suburban riparian zones often do not function to convert nitrate pollution to harmless nitrogen gas (Groffman et al. 2003) have stimulated managers to look to the larger watersheds as sites for pollution mitigation (Pickett et al. 2007). In addition, experience with urban tree planting as a technique to improve neighbourhood environmental quality and social cohesion (Grove et al. 2005) suggests that both environmental and social goals can be advanced by enhancing tree canopy cover beyond the riparian. This then becomes the entry point for a cycle unifying urban design and ecology (Fig. 1).

The second step is to examine the relationship between the structure of the urban landscape, particularly its vegetation component, and the nitrate conversion of that landscape. The land cover existing at the beginning of the study can be quantified using the integrated land cover classification described earlier and its functioning relative to nitrate yield can be measured (e.g. Cadenasso *et al.* 2007). Also included in this step is an assessment of household characteristics that affect nitrogen management (Law *et al.* 2004). This model represents time 1.

The next step is to identify management practices or structural modifications that might improve the ability of the landscape to reduce nitrate loss downstream. Engineers and environmental managers are especially likely to have pertinent suggestions (Pickett *et al.* 2007).

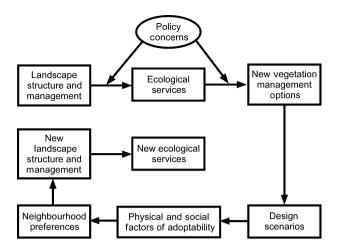


Fig. 1. The open cycle, or spiral, of ecological urban design as exemplified by the policy motivations, and relationships between plant ecological, physical, management, design, social and democratic states and activities. The oval shows the policy motivations, noting that they can affect the vegetation and landscape itself, or the ecological services that emerge from that landscape. The second line shows the relationships between vegetation structure and function, its impact on ecosystem services, and the expert local knowledge of best management practices to achieve the ecosystem services and facilitate social benefits. The bottom line involves the creative work of designers as informed by plant ecological knowledge, and filtered through social and geographical measurements that suggest where designs may best be situated in the landscape. Those opportunities are further filtered by the desires and needs of specific neighbourhood communities. The spiral ends in a new landscape model based on installing acceptable designs in the urban mosaic, and predicting any alteration of the ecosystem service based on the new landscape mosaic that results. Each step of this generalized framework is explained in the text using the example of an ecological design response in the Baltimore, Maryland, metropolitan area to improve water quality in the Chesapeake Bay.

Once a suite of environmental mitigation methods is articulated, urban designers can evaluate potential sites and generate new designs that include nitrate and storm water retention. We expect that vegetation structure and phenology will be important features of such designs. The tools and approaches that urban designers use include green roofs, bioswales, rain gardens, and the configuration of impervious vs. permeable and vegetated surfaces. European designers have pioneered many of these tools (European Commission 1996; Beatley 2000) that can be employed in the design cycle elsewhere.

Good designs are only a starting point for altering an urban mosaic. The geographical and social template into which these designs might fit is an additional filter in the process of improving the ability of a landscape to reduce nitrate pollution. Geographers and social scientists can evaluate spatial and social opportunities and constraints for realizing the ecologically motivated designs (Troy *et al.* 2007). They can evaluate how this node in the cycle of ecological urban design narrows or shapes the kinds of designs that can be used. As a result of such analyses, specific geographical and social settings can be identified in which designs aimed at reducing nitrate yield might be applied. The next link in the cycle is to interact with specific neighbourhoods and communities that satisfy the physical needs for new designs in order to determine what ecological designs the residents prefer. Focus groups or community meetings can be used to elicit responses about the designs. These meetings can be used to choose a subset of designs that specific neighbourhoods would consider. Urban design has been developing a democratic, participatory style for a long time (Hester 2006).

The specific designs can then be inserted into appropriate locations in the original land cover model, and a new map can be generated to represent the landscape cover configuration at some future time when the potentially retentive designs might be built. This event marks time 2. Given the relationships between the elements of landscape configuration and nitrogen dynamics discovered in empirical, small watershed studies (e.g. Cadenasso *et al.* 2007), and hydrological modelling of specific cover types, a new model of nitrogen dynamics at time 2 can be generated. This completes the cycle. However, the cycle is not strictly closed, because the landscape at time 2 is different from that at time 1.

The ecological design cycle: a summary

Urban design, plant ecology, hydrology, the knowledge of managers and policy makers, and the desires of neighbourhood residents are combined to generate a new mosaic of vegetation, buildings and surface covers. To the extent that the new landscape differs from the original one, the cycle is open. Such an open cycle (or perhaps better, an open spiral) suggests the opportunity for improving the quality of the local environment and the water quality downstream, based on the interaction of design and plant ecology in the context of ecosystem function and incorporating the input of managers (Fig. 1).

This spiral suggests hypotheses for testing and thus motivates ecological research in urban systems. It suggests that all designs, whether intentionally ecological or not, can be evaluated for their contribution to, or deduction from, ecological functioning in urban areas. The environmental services and variables that are affected by any given ecological design should be quantified. There is an urgent need to understand ecologically the individual and incremental impacts of urban design.

There are other benefits of integrating ecology with design via the design cycle. It brings plant ecology into the city as a whole (Felson & Pickett 2005), rather than only into the obvious locations of parks, remnant natural areas, or urban forests. It provides an opportunity to educate the public and policy makers about the ecological processes on which their settlements depend. Ecological design may provide examples of semi-natural or ecologically functional systems as educational tools for schools. Presenting statistically well-conceived design projects and controls can educate urban dwellers about experiments as an important component of the scientific process (Felson & Pickett 2005). If ecological urban designs succeed in engaging the public, the designs can justify and exemplify bringing plant ecology to bear in the process of community decision making.

There are also direct benefits to science. Incorporating ecological processes in designs and monitoring the results provides ecologists with many more potential research sites in and around cities than focusing on dedicated green space alone would suggest. Urban design often reflects the fine-scale, ecologically relevant spatial heterogeneity that is expressed in new integrated land cover models (Cadenasso *et al.* 2007). Finally, the ecological urban design cycle helps integrate plant ecology with other sciences, including social and biogeochemical disciplines. The growing linkage of design with public health concerns may provide an additional bridge between ecology and the fields of human health (Northridge *et al.* 2003). Human behaviour and exposure to environmental hazards and amenities influence health in cities. Ecological design can accommodate these concerns as well as ecosystem functions.

Linking plant ecology with so many different perspectives, kinds of expertise, and motivations in the cycle of design is challenging. However, it is also an opportunity to use plant ecology to learn new things about urban ecosystem function, and about conservation and vegetation management in urban areas. If an ecological urban design cycle can contribute to improving the quality of life in cities, it may help prevent suburban sprawl, with its pressure on the natural habitats ecologists prize so dearly. Both urban and wild systems share concepts and theories and stand to benefit by engaging the urban design professions in an adaptive cycle.

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References

- Beatley, T. (2000) Green Urbanism: Learning from European Cities. Island Press, Washington, DC.
- Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. Ecological Economics, 29, 293–301.
- Bornkamm, R., Lee, J.A. & Seaward, M.R.D. (1982) Urban Ecology. Blackwell Science, Oxford.
- Burch, W.R. Jr & Grove, J.M. (1993) People, trees, and participation on the urban frontier. Unasylva, 44, 19–27.
- Cadenasso, M.L., Pickett, S.T.A. & Grove, J.M. (2006) Dimensions of ecosystem complexity: heterogeneity, connectivity, and history. *Ecological Complexity*, 3, 1–12.
- Cadenasso, M.L., Pickett, S.T.A. & Schwarz, K. (2007) Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. *Frontiers in Ecology and Environment*, 5, 80–88.
- Collins, J.P., Kinzig, A., Grimm, N.B., Fagan, W.F., Hope, D., Wu, J. & Borer, E.T. (2000) A new urban ecology. *American Scientist*, 88, 416–425.
- DiGregorio, A.F.A.O. (1996) Land cover classification: a dichotomous, modular-hierarchical approach. Sustainable Development, Food and Agriculture Organization of the United Nations, Rome.
- Eurpean Commission (1996) European Sustainable Cities Report. Directorate General XI, Environment, Nuclear Safety and Civil Protection, Brussels.

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- Felson, A.J. & Pickett, S.T.A. (2005) Designed experiments: new approaches to studying urban ecosystems. *Frontiers in Ecology and Environment*, 3, 549– 556.
- Frey, J. (1998) Comprehensive biotope mapping in the city of Mainz a tool for integrated nature conservation and sustainable urban planning. *Urban Ecology* (eds J. Breuste, H. Feldmann & O. Uhlmann), pp. 641–647. Springer-Verlag, New York.
- Grimm, N.B., Grove, J.M., Redman, C. & Pickett, S.T.A. (2000) Integrated approaches to long-term studies of urban ecological systems. *Bioscience*, 50, 571–584.
- Groffman, P.M., Bain, D.J., Band, L.E., Belt, K.T., Brush, G.S., Grove, J.M., Pouyat, R.V., Yesilonis, I.C. & Zipperer, W.C. (2003) Down by the riverside: urban riparian ecology. *Frontiers in Ecology and Environment*, 1, 315–321.
- Grove, J.M., Burch, W.R. Jr & Pickett, S.T.A. (2005) Social mosaics and urban community forestry in Baltimore, Maryland. *Communities and Forests: Where People Meet the Land* (eds R.G. Lee & D.R. Field), pp. 249–273. Oregon. State University Press, Corvallis.
- Grove, J.M., Cadenasso, M.L., Burch, W.R. Jr, Pickett, S.T.A., O'Neil-Dunne, J.P.M., Schwarz, K., Wilson, M.A., Troy, A.R. & Boone, C. (2006a) Data and methods comparing social structure and vegetation structure of urban neighborhoods in Baltimore, Maryland. *Society and Natural Resources*, 19, 117–136.
- Grove, J.M., Troy, A.R., O'Neil-Dunne, J.P.M., Burch, W.R. Jr, Cadenasso, M.L. & Pickett, S.T.A. (2006b) Characterization of households and its implications for the vegetation of urban ecosystems. *Ecosystems*, 9, 578–597.
- Hester, R.T. (2006) Design for Ecological Democracy. MIT Press, Cambridge. Hill, K. (2001) Design and planning as healing arts: the broader context of health and environment. Ecology and Design: Frameworks for Learning (eds)
- K. Hill & B.R. Johnson), pp. 203–214. Island Press, Washington, DC. Hutchings, M.J., John, E.A. & Stewart, A.J.A., eds. (2000) *The Ecological*
- Consequences of Environmental Heterogeneity. Blackwell Science, Malden. Klotz, S. (1990) Species/area and species/inhabitants relations in European
- cities. Urban Ecology: Plants and Plant Communities in Urban Environments (eds H. Sukopp, S. Hejny & I. Kowarik), pp. 100–112. SPB. Academic Publishers, The Hague.
- Koroncai, R., Linker, L., Sweeney, J. & Batuik, R. (2003) Setting and allocating the Chesapeake Bay basin nutrient and sediment loads: the collaborative process, technical tools, and innovative approaches. US Environmental Protection Agency, Annapolis.
- Kuo, F.E., Macaicoa, M. & Sullivan, W.C. (1998) Transforming inner-city landscapes: trees, sense of safety, and preferences. *Environment and Behavior*, 30, 28–59.
- Kuo, F.E. & Sullivan, W.C. (2001) Aggression and violence in the inner city: effects of environment via mental fatigue. *Environment and Behavior*, 33, 543–571.
- Law, N.L., Band, L.E. & Grove, J.M. (2004) Nitrogen input from residential lawn care practices in suburban watersheds in Baltimore County, MD. *Environmental Planning and Management*, 47, 37–55.

McGrath, B.P., Cadenasso, M.L., Grove, J.M., Marshall, V., Pickett, S.T.A.

& Towers, J., eds (in press) *Designing Urban Patch Dynamics*. Columbia University Graduate School of Architecture, Planning and Preservation, New York.

- McPherson, E.G., Nowak, D., Heisler, G., Grimmond, S., Souch, C., Grant, R. & Rowntree, R. (1997) Quantifying urban forest structure, function, and value: the Chicago urban forest climate project. *Urban Ecosystems*, 1, 49–61.
- Northridge, M.E., Sclar, E.D. & Biswas, P. (2003) Sorting out the connections between the built environment and health: a conceptual framework for navigating pathways and planning healthy cities. *Journal of Urban Health*, 80, 556–568.
- Nowak, D.J., Crane, D.E. & Dwyer, J.F. (2002) Compensatory value of urban tees in the United States. *Journal of Arboriculture*, 28, 194–199.
- Palmer, M., Bernhardt, E., Chornesky, E., Collins, S., Dobson, A., Duke, C. et al. (2004) Ecology for a crowded planet. Science, 304, 1251–1252.
- Pataki, D.E., Alig, R.J., Fung, A.S., Golubiewski, N.E., Kennedy, C.A., McPherson, E.G., Nowak, D.J., Pouyat, R.V. & Romero Lankao, P. (2006) Urban ecosystems and the North American carbon cycle. *Global Change Biology*, **12**, 2092–2102.
- Pickett, S.T.A., Belt, K.T., Galvin, M.F., Groffman, P.M., Grove, J.M., Outen, D.C., Pouyat, R.V., Stack, W.P. & Cadenasso, M.L. (2007) Watersheds in Baltimore, Maryland: understanding and application of integrated ecological and social processes. *Journal of Contemporary Watershed Research and Application*, **136**, 44–55.
- Ridd, M.K. (1995) Exploring a V–I–S (vegetation–impervious surface–soil) model for urban ecosystem analysis through remote sensing: comparative anatomy for cities. *International Journal of Remote Sensing*, 16, 2165–2185.
- Salisbury, E.J. (1943) The flora of bombed areas. Proceedings of the Royal Institution of Great Britain, 32, 435–455.
- Spirn, A.W. (1984) The Granite Garden: Urban Nature and Human Design. Basic Books, New York.
- Sukopp, H. (1990) Urban ecology and its application in Europe. Urban Ecology: Plants and Plant Communities in Urban Environments (eds H. Sukopp, S. Hejny & I. Kowarik), pp. 1–22. SPB. Academic Publishers, The Hague.
- Sukopp, H., Numata, M. & Huber, A. (1995) Urban Ecology as the Basis of Urban Planning. SPB Academic Publishing, The Hague.
- Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology*, 16, 284–307.
- Troy, A.R., Grove, J.M., O'Neil-Dunne, J.P.M., Pickett, S.T.A. & Cadenasso, M.L. (2007) Predicting patterns of vegetation and opportunities for greening on private urban lands. *Journal of Environmental Management*, 40, 394–412.
- United Nations (2001) *Demographic Yearbook*. United Nations Statistics Division, New York.
- Watt, A.S. (1960) The effects of excluding rabbits from acidophilous grassland in Breckland. *Journal of Ecology*, 48, 601–604.
- Wittig, R. (2005) The origin and development of the urban flora of Central Europe. Urban Ecosystems, 7, 323–329.
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