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Urban Sprawl and Ecosystems — Can Nature Survive?

Daniel Czamanski[1], Itzhak Benenson[2], Dan Malkinson[3], Maria Marinov[4], Rafael Roth[5] and Lea Wittenberg[6]

[1] *Technion — Israel Institute of Technology; E-mail: danny@czamanski.com*
[2] *Tel Aviv University; E-mail: bennya@post.tau.ac.il*
[3] *University of Haifa; dmalk@geo.haifa.ac.il*
[4] *Technion — Israel Institute of Technology; E-mail: armarin@techunix.ac.il*
[5] *Technion — Israel Institute of Technology; E-mail: rothr@techunix.technion.ac.il*
[6] *University of Haifa; E-mail: leaw@geo.haifa.ac.il*

ABSTRACT

Contrary to the popular notion that the advancing frontier of urban development has been swallowing and destroying natural ecosystems we present evidence that the sprawl of cities creates ample open space in peri-urban areas. Traditional view of city–nature dichotomy and clear spatial separation should be substituted by a vision that reflects the complex spatial dynamics of city–rural–natural fabric with extended areas of overlap among them. We present a survey of the relevant research concerning urban and ecological systems spatial dynamics and conclude that nonregular, leapfrogging spatial expansion, characteristic of the majority of the modern western cities, may buffer between urban and intensively cultivated agricultural areas and counter their impacts on natural ecosystems. The wealthy sprawling suburbs provide essential habitats for native species and ensure their survival.

Keywords: Urban spatial dynamics; sprawl; landscape dynamics; urban ecology.

Classification: Urban economics, urban ecology

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1 INTRODUCTION

The urban population of the world has been increasing very rapidly in the past few decades. At the beginning of the 20th century, only 14 percent of humanity lived in cities. Today, the number of city dwellers has grown to about 50 percent. This means an almost fifteen-fold increase in the world's urban population, from 200 million in 1900 to 2.9 billion a hundred years later (United Nations, 2004). In many developing countries huge dense cities are draining the rural hinterland. In the more developed regions of the world there is undisputed evidence of processes of urban dispersal and sprawl.

During the last 100 years rural populations more than doubled, increasing from 1.4 billion to 3.2 billion (United Nations, 2002). The area occupied by agriculture, including arable land and permanent crops, has gradually been increasing since the beginning of the 20th century and today comprises roughly 11 percent of the total land area (FAO, 2007). Notably, the trend is different in developing and developed countries. Despite overall growth in agricultural area, in most developed countries the trend has been reversed, at least since the 1960s, and the amount of agricultural land is decreasing. In addition, in some areas of the United States and Western Europe, mainly in places that are proximate to the densely populated regions, there is evidence of land-use transition from agricultural land to natural open space. For example, in the Netherlands, land that is not economic in agricultural use is systematically being purchased by the government and left alone (Louw *et al.*, 2003).

It has become a popular notion that the advancing frontier of urban development has been swallowing and destroying natural ecosystems. There is evidence that in places where the islands of natural habitats survive, they are suffering from pollution, fragmentation, and constant interactions with humans (McKinney, 2002). Thus, often it is claimed that the never-ending expansion of urban and semi-urban land-uses leads to the disintegration and weakening of the adjacent ecosystems and their ultimate degradation (e.g., Paul and Meyer, 2001).

At the same time, there is a growing understanding that although urban areas are created by humans and for humans, they are also home to many plant and animal species that often display remarkable resilience to urban hazards. Species and communities undergo the necessary adjustments, adapt their spatial, temporal, and reproductive behavior to the new conditions and coexist comfortably, and even thrive, within the broader boundaries of cities (McGranaham *et al.*, 2005). These areas can provide nature-related amenities and cultural values, particularly if they are well managed. Moreover, there is much evidence that species richness and abundance in peri-urban areas is higher than in areas of rural monocultures.

This changed view of the urban boundary raises a serious challenge to both urban and ecological theory. Traditional view of the city–nature dichotomy with the prevalence of the city and clear spatial separation should be replaced by the gradient reflecting the city–rural–natural fabric with extended areas of overlap among them. The view of the complex spatial dynamics along this gradient is necessary for managing landscapes of each of the three main types and, especially for broad understanding how modern city really functions and evolves (Berkowitz *et al.*, 2003). The novel paradigm considers urban system as including areas and habitats suitable for native species and natural communities. The interface between urban and rural systems is of particular interest, and typical urban–rural gradients are characterized by various levels of heterogeneity, the latter being critical for persistence of ecological communities rather than individual species. Specifically, the dynamics of the ecosystems in and around urban areas is influenced by a rate of introduction of alien species, habitat diversity and fragmentation, human-induced habitat disturbances and many other factors (Rebele, 1994, Niemela, 1999).

Human and eco-systems along the urban–rural–nature gradient are all complex adaptive self-organizing systems in which structure and patterns at higher levels emerge from local behavior and interactions (Levin, 1998, Portugali, 2006). Heretofore, the questions concerning urban and natural system dynamics varied and were raised separately. The literature concerned with the spatial dynamics of urban systems is vast, as is the ecosystem literature. However, the typical questions asked regarding urban systems concern the temporal and spatial dynamics of the built-up area. In contrast, the typical questions asked regarding ecosystems concern the dynamics of its hierarchical structure and the ability to adapt to local and global environmental changes, along with issues concerning the spatial and temporal dynamics of species and communities. Seemingly urban system studies and ecological system studies take a complementary view of the landscape. Much too commonly the urban approach views the landscape as a matrix comprised of urban areas and a void among them, while the ecological point of view sees the urban areas as gaps within the matrix of natural areas. Rural systems are generally studied much less than urban or natural systems. It is our view that the time has come to study all three main land-use systems jointly. It is the purpose of this paper to present a detailed picture of the state of knowledge concerning the dynamic spatial behavior of urban systems and of the relevant ecological systems within the urban shadow and thus to provide a basis for a better understanding of the interaction among these systems. We compare and contrast among the approaches taken in urban system studies and ecological studies, in an attempt to bridge between the disciplines, and in the final section we synthesize among the emerging ideas and address direction for future investigation.

2 THE SPATIAL DIMENSION — ZONES AND BOUNDARIES

Cities, like other complex systems consist of many intertwined elements at various organizational levels. Their spatial evolution takes place at different timescales. Micro-patterns of houses, street segments and open areas exhibit fast dynamics measured in months and, mostly years, whereas macro-patterns of center-periphery gradient develop slower (Weidlich, 1999). The same is true for ecosystems — the local changes of species' abundance and communities' structure can take weeks, months or seasons, while it will take decades and sometimes centuries for an ecosystem to adapt to the environment, following a disturbance. Generally speaking, the dynamics of urban frontiers are thus the "fastest," comparing to the rest of the urban space, as consisting of interacting micro-structures of all three — urban, rural and natural — types. That is, at the boundary the time–space cross-derivatives are largest. In this paper, we choose to focus on the relatively short term timescales of years and few decades.

Conceptually, the dynamics at the boundary or at the frontier delimiting cities and their surrounding nonurban areas (henceforth "peri-urban dynamics") is just a particular case of general spatial dynamics of the landscapes. In what follows we define the peri-urban area as a zone of a varying width, from several to 10–20 kilometers wide. We focus on phenomena that occur within this geographical band at spatial resolutions that vary from the typical spaces between buildings to neighborhoods and blocks, and at temporal resolution of seasons, years, and decades.

In order to delimit the relevant region we rely on the existing knowledge about the urban frontier in the general terms of complex system theory. Here, we follow the somewhat ambiguous view that in order to decide whether some spatial unit belongs to the interface zone one has to know whether it is "essentially" influenced by/influences the processes on the "other side." That is, the very definition of the frontier is endogenous; it should be resolved together with the description of the dynamics of adjacent areas.

It is apparent that within many spaces surrounding urban areas human interference with the nature has become increasingly more frequent and significant, thus rendering such areas heterogeneous. The effects of human presence are felt in a variety of aspects and mediums, such as soil, waterways, and air, along roads and railways, power-lines and pipelines, often passing through areas of wilderness. In some cases the human presence is barely affecting the ecosystem. In other cases, despite the low frequency of human presence, the influence may be significant. It is quite likely that in many cases the full span of the human intervention is not completely understood.

Figure 1 displays a schematic typology of the zones along the urban — peri-urban — natural cross section. The urban core is the zone dominated by human presence, including all the associated human activities. The ecological systems inside the urban core are essentially man-made, such as the plant and animal communities related to parks and gardens, and consist of species which are able to cope and even benefit from human activities (omnivorous rodents, birds, etc.). The urban core is normally surrounded by peri-urban areas of lower intensity of human activities, such as rural suburbs. Peri-urban areas are characterized by lower density of human activities with patches of undisturbed natural habitats. As we move further away from the urban core, we generally encounter fewer islands of developed land. There is however, the difficult question of agricultural areas, where the physical human presence is relatively low, though the effects of human activities are often intensive and are extended over large contiguous areas. Such areas can be classified as nonurban anthropogenic landscapes. Finally, the areas where the human interference may be considered negligible are classified as natural areas. The various aspects of ecological adjustment dynamics in these different types of zones will be discussed below.

As we already stated, in recent years the general view of urban areas as sterile islands within the sea of natural systems is gradually changing. There is extensive and growing

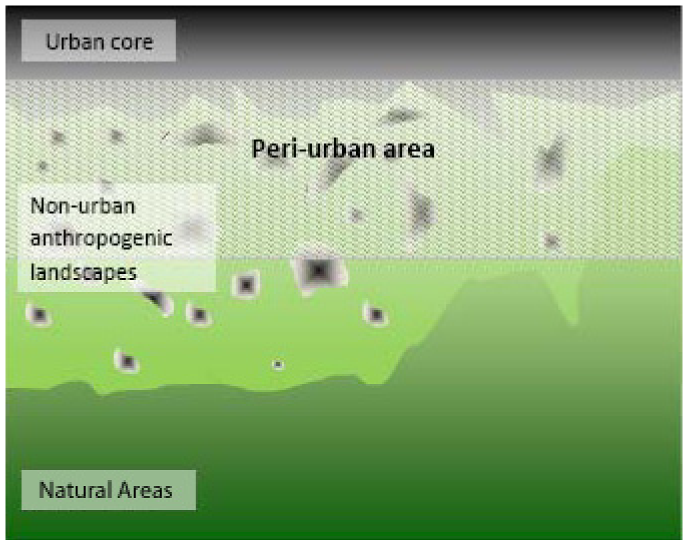

Figure 1. Schematic profile of the frontier as dependent on distance.

empirical evidence that many peri-urban areas, especially adjacent to high income low density residential areas, display greater biodiversity than many rural areas outside cities and can be compared favorably to natural habitats. This is partly due to the introduction of exotic (nonnative) species, and partly to the fact that such environments can support a wider range of species, providing favorable conditions such as food, water, shelter, and clean air. It is only natural that same characteristics that are preferred by humans in their living environment are also advantageous to many species of plants and animals.

Thus, the urban fringe becomes a pseudo-reserve where the anthropogenic influence may yield positive effects compared to the urban and agriculture landscapes that surround it. The wider the fringe, the lower the proportion of the built-up areas in it and the higher the socio-economic level of the population there, the higher is area's suitability for natural species and ecological communities. This is especially true for those species that are able to adapt and exploit the advantages of proximity to the human population.

This relatively new phenomenon of recovering ecosystems may be termed the "third nature." It stands in sharp contrast to nature that exists in light of minimal human presence. It also stands in a stark contrast to urban systems that are in essence the "second nature." Third nature regions may offer simultaneously convenient habitats for variety of species as well as produce the much desired amenities that are evidently highly valued by the upper class households.[1]

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[1] There exists an extensive literature concerned with the valuation of natural environments. There are numerous reviews of this literature and we do not present it here.

In the following sections of the paper we first review the classical literature on urban spatial dynamics. We discuss the economic and noneconomic models of urban development. Thereafter we turn to the ecological side of the story. We present the review of empirical studies dealing with the ecosystems at the peri-urban frontier and their dynamics. We especially focus on the simulation models in both urban and ecological research that serve as powerful tools to unravel the mechanisms underlying the complex spatial dynamics of the systems. In the final section, we bring it all together and outline directions for further research.

3 WHAT DO WE KNOW ABOUT URBAN SPATIAL DYNAMICS?

In this section, we briefly discuss what is known about the changing perception of the spatial dynamics of urban systems. We present an overview of the theories and models within the framework of urban research that attempt to describe and explain the spatial form of urban areas and their evolution. We begin with a number of well-known classical theories that are at the basis of the main body of studies conducted in the field, such as bid-rent theory, the mono-centric city model and the theory of central places. We then proceed to review the more sophisticated economic models of developer and poly-centricity. Thereafter, we review the self-organization and noneconomic spatial approaches that made an important contribution to the understanding of dynamic urban systems in the past decade. We conclude this section with an overview of agent-based simulation models, some of which originated in natural sciences and similar in their approach to the ecological simulation models.

3.1 Classical Models

3.1.1 The Mono-centric City Model

The mono-centric city model is associated with the bid-rent theory, formulated by Alonso (1964) and originally proposed by von Thünen as early as 1826. The theory suggests a single-center city with concentric distribution of land uses and activities, where locations are determined as a result of competitive bidding. Alonso constructed the bid-rent curves for each land-use as decreasing away from the center, slopes reflecting the sensitivity of each land-use to accessibility.

The standard mono-centric city is envisaged as a circular residential area surrounding a central business district (CBD) in which all jobs are located. Households choose residential locations at different distances from the center and spend their exogenously determined income on apartment space, goods and transportation costs, or commuting costs. The model assumes a trade-off between utility gained from the size and location of residential lot and transportation costs that are incurred by traveling to the center (Mills, 1967, 1972, Muth, 1969). The mono-centric city model assumes a Pareto optimal equilibrium and much of the criticism is related to the fact that a static model is unable to capture the dynamic reality of a developing city (Anas *et al.*, 1998).

The bid-rent theory predicts the density gradient dropping monotonously away from the CBD, and as population and incomes grow, the city expands and tends to decentralize. This feature of the model has difficulty accounting for the fact that housing is durable and readjustments due to outward growth occur much too slowly to maintain the equilibrium state suggested by the theory.

In general, defining the local density $\rho(t, x, y)$, where t is time and x and y are location coordinates, can be rather complicated. In reality the density function displays discontinuities and often it is difficult to calibrate. In the past it was common to replace local density by a radial density at time t at a radial distance r from the center — $\rho c(t, r)$. Some researchers suggest that radial density may be assumed to decrease exponentially with distance from the center (Clark, 1951, Batty and Longley, 1994, Makse *et al.*, 1995), while others suggested applying more complex mathematical expressions (Krakover, 1983, 1985, Longley and Mesev, 1997). The choice of this kind of function implies some isotropy in the development of the city, clearly a questionable generalization. Essentially, the mono-centric city model portrays urban growth as a radial wave of development, crawling outwards from the center and swallowing up all the open spaces in its way.

The mono-centric city model has attracted much criticism in the past few decades. Its validity and its connection to modern cities have been questioned skeptically. Anas *et al.* (1998) assess that "…the monocentric model has been an excellent conceptual tool for thinking about an urban economy, particularly about the role of commuting costs. It facilitates accounting for general-equilibrium effects and it appears to identify some powerful determinants of urban structure. But it provides no more than a useful starting point in explaining the observed spatial structure of modern cities."

3.1.2 Theories of Central Places

Another well-known classical theory proposed by Christaller (1933) and Lösch (1940) offers an explanation for the spatial patterns of settlements, or central places that dispense goods and services to the surrounding markets. In spatial context, the theory of central places claims that the most efficient structure is accomplished by a series of hexagonal-shaped markets. The original version of the central place theory referred to towns serving a rural hinterland, but similar principles are applied to modern metropolitan areas. The patterns are explained by the notion of the hierarchy of centers, where goods and services of different order are available at different levels of the hierarchy.

The basic hierarchical structure of central places was empirically verified at a variety of geographical scales (Berry and Garrison, 1958, Davies, 1967). However, the evidence concerning the spatially regular pattern is rather contradictory (Clark, 1982, Guy, 1998). The most common criticism of the central place theory concerns the over simplistic assumptions of uniform, featureless space and identical players making single purpose trips to nearest centers (Kivell and Shaw, 1980). It is hardly surprising that areas, where spatial patterns consistent with the postulates of the central place theory were verified empirically, are usually uniform and lacking in physical irregularities (Munroe, 1999).

Another drawback of the central place theory was pointed out by Krugman (1996). It is its inability to demonstrate the mechanism by which the decisions of individuals on the micro-level would lead to the suggested spatial structure. The central place theory is also essentially limited for our purposes as disregarding the interaction between the growing built-up areas and the open spaces. This interaction is critical for description of the expanding urban frontier.

3.1.3 The Poly-centric City

A crude view of a metropolitan area may result in an ordered structure of center places. However, at a finer resolution the distribution of activities reveals irregularity and poly-centricity that depends on scale of observation.

Decentralization and suburbanization in most western countries has led to the emergence of multiple centers of urban activity away from the traditional CBD. Substantial empirical evidence exists in support of poly-centricity in the spatial structure of urban and metropolitan areas (Erickson, 1983, 1986, Bourne, 1989, Hartshorn and Muller, 1989, Heikkila *et al.*, 1989, McDonald and McMillen, 1990, Giuliano and Small, 1991, Shukla and Waddell, 1991, Garreau, 1992, Cervero and Wu, 1997, McMillen and McDonald, 1998).

Poly-centricity may be recognized by measuring various aspects of urban activity, such as, population and employment density, height of buildings, land value and firm location. Number of sub-centers is sensitive to the particular definition, and it usually involves minimum density or employment criteria. In their overview Anas *et al.* (1998) describe the three functional forms that generalize Alonso's (1964) mono-centric postulates to the poly-centric structure. These three forms are heavily discussed in literature and appear to be suitable for different cases in measurement of urban densities (Gordon *et al.*, 1986, Small and Song, 1994, Anas *et al.*, 1998).

Recent criticism of the poly-centric model stems from the fact that the employment has become increasingly dispersed and does not explain the formation of centers (Gordon and Richardson, 1996). Generally, as in the case of the mono-centric city, it appears that the mainstream poly-centric city models have come to a point where the real cities and metropolitan areas has become too complex and dynamic, for the models to keep up and provide an appropriate explanation. Just as the central places theory, poly-centric model disregards the complexity of urban frontier and thus has limited value for our purposes.

3.1.4 Dynamic Economic Models of Land Developers

The classical static economic models focused on the demand side of the housing market and ignored the supply side, the considerations of planners and developers and the characteristics of locations. The basic models assumed homogeneity of all parameters except one — the consumer's willingness to pay for houses' proximity to the center or multi-centers in the urban space (Alonso, 1964; Mills, 1967; Muth, 1969;

Wheaton, 1974). This simplistic assumption leads to a well-behaved pattern of concentric land-use circles around the city centers (CBD). The classical models lead to very superficial outcomes of continuous spreading of people, activities and buildings around the centers and supported rent gradient patterns.

One more basic limitation of the classical models is their inability to describe temporal dynamic processes in the urban space. These models ignored the durability characteristic of buildings and the main assumption was that buildings can be destructed and rebuild in a short time and without any limitations and costs. The early dynamic land-use models overcame part of the above limitations (Ohls and Pines, 1975, Anas, 1978, Brueckner, 1981a, 1981b, 1982, Mills, 1981, Fujita, 1982, Wheaton, 1982a, 1982b, Braid, 1988, 1990, Turnbull, 1988, Capozza and Helsley, 1989, 1990, Bar-Ilan and Strange, 1996). These models described the consequences of developers' decisions with the use of temporal profit functions. These functions represent the value of the cash flow of developers, consisting of capitalization of future rents with the deduction of capitalize future costs. The decision variables are timing, footprint area and building intensity or height of buildings. The models are different in their assumptions about the future: perfect or limited foresight of developers about future rents and uncertainties lead to variety of spatial outcomes. In the model outcomes, rent gradient and the continuous expansion are substituted by more realistic patterns and interesting anomalies: rents and heights decreasing in noncontinuous way, leapfrogging in the development process and even increasing rents and heights with distance from the CBD.

The new wave of urban economic studies focused on the supply side of the housing market (Sofer, 1994, Huriot and Thisse, 2000, Ginat, 2001, Glaeser and Kahn, 2003, Glaeser *et al.*, 2005, Glaeser and Ward, 2006, Czamanski and Roth, 2008). The approach in these studies considers much of the spatial–temporal evolution of cities to be the result of land developers' choices. In particular, the models concerning the decision developers make about the parcels of land to be developed and the intensity of development. Although developers are not the only actors in cities (there are also municipalities, resident households, firms, etc.), developer's behavior is assumed to reflect the dynamics and the main activities in the housing market. One of the critical variables in decision-making of developers is time. By means of these models it is possible to demonstrate that under certain market and spatial conditions the developer's behavior generates leapfrogging patterns, mainly during recession periods.

3.2 From General Complexity Theory to Urban Dynamics

3.2.1 Self-organization and New Economic Geography (NEG)

In the past decade models of self-organization have become increasingly popular in the study of urban systems (Krugman, 1996, Portugali, 1999). The elaboration of new scientific approaches based on such phenomena as bifurcations, self-organized criticality, deterministic chaos and self-similarity of urban patterns at different level of spatial hierarchy has generally emphasized the fact that exact prediction in complex socio-economic and socio-environmental systems is not possible.

In dynamic economic modeling the idea of self-organization was thoroughly explored by Krugman (1996). In his *Self Organizing Economy* he discusses the traditional theories (reviewed above) in light of the complexity theory. Krugman maintains that the interaction among economic agents in cities, and especially during periods of accelerated growth at the edge of urbanized areas, displays self-organized criticality, similar to land avalanches and earthquakes. The system that is developing in reaction to a certain set of factors along the steady trajectory, approaches the boundary of the trajectory basin of attraction. At this boundary, the system is sensitive to the minor factors whose influence was marginal till then. The system at this stage can be driven by positive feedbacks, and undergo bifurcations and other qualitative changes that can cause sudden and unexpected changes in system dynamics. Krugman (1996) illustrates the idea by several models of self-organizing city, in which the interaction between centrifugal and centripetal forces enable spatial structure described by Garreau in his *Edge Cities* — urban concentrations away from existing centers.

The Spatial Economy (Fujita *et al.*, 1999) which was published some years later discuss and reinterpret, in view of the theory of self-organization, a series of analytic results accumulated in the fields of economic geography and urban economics. The authors propose incorporating the economies of scale and the interaction between transport cost and factor mobility as well as the Dixit–Stiglitz model of monopolistic competition to create a new model of city formation. Their core-periphery model introduces a two-sector economy: An agricultural sector with constant returns to scale and without factor mobility and a manufacturing sector with increasing returns to scale and with factor mobility that are both modeled in a discrete location space.

Skeptics argue that the NEG "… is neither that new, nor is it geography. Instead, it is a reworking (or reinvention) — using recent developments in formal (mathematical) mainstream economics — of traditional location theory and regional science" (Martin, 1998). We agree with this statement — both geographers and economists involved in the debate are concerned with the same issues of spatial dynamics: the distribution of economic activity, explanations for the processes of urban sprawl, regional inequalities, processes of decentralization, and suburbanization in cities. Despite the market progress in the development of spatial urban models, they are still reliant on simplistic assumptions and produce a rather generalized depiction of urban structure; their relation to the ex-urban area as to agricultural periphery and they focus on the processes at the city side of the urban boundary.

3.2.2 Fractals

What should be expected as the spatial pattern of a self-organizing city? Assuming that the forces shaping the city at different levels of urban hierarchy are similar, the resulting spatial pattern of the built-up area should be fractal, or should display self-similarity. In other words, the pattern of built-up and open areas in a city observed at a low resolution should be similar to that observed at a high resolution. Observed fractal characteristic of cities indicates that self-similarity is present at several hierarchical levels, at least at the typical resolutions of urban regions, census areas, neighborhoods, and surroundings of individual buildings.

The concept of self-similarity and fractals was introduced by Mandelbrot (1982) and results in "fractal dimension" — a noninteger number, between 1 and 2, that characterizes density of the built-up area in the city. Many researchers liked the idea that urban patterns might be described by one number and tested urban systems for the presence of fractality. In their book *Fractal Cities* Batty and Longley (1994) set out to conduct a comprehensive study of fractal geometry of cities and found that in fact many cities do display fractal characteristics. Batty and Longley report estimated fractal dimensions for many cities around the world, with the results in the range 1.55 to 1.93. The same interval was estimated by Frankhauser (1994) and Benguigui (1992, 1995). It is worth noting that their comparison of the maps of built-up area in London for each decade between 1820 and 1962, and of Berlin from 1875 to 1945, suggest that the fractal dimension has been increasing steadily over time. These findings suggest that the density of the built-up area in the city increases over time (Batty and Longley, 1994).

Despite the potential usefulness of the fractal dimension of urban areas as indicator of extant patterns of built-up and open areas, it should be used with care. First, not all cities are necessarily fractal. Benguigui *et al.* (2000, 2006) analyzed the fractal dimension of the Tel Aviv metropolitan between 1935 until 2000 and revealed that not every part of the metropolis can be represented, even approximately, by a fractal. Second, and more importantly, spatial patterns at different scales of resolution appear to be similar, despite the fact that the mechanisms that govern the creation of these patterns are different. The micro-processes that govern local land-use changes, land and dwelling prices and construction permits are significantly different from the macro-processes at large scales, including regional planning, regional economic base dynamics, the evolution of transportation infrastructure (Batty and Longley, 1994).

3.2.3 Diffusion, Percolation and Leapfrogging

Fractal patterns are the results among the "simplest" self-organizing structures. They can be considered as special outcomes of more general models that originate in physics. These models consider "particles" of the built-up area that occupy open urban space and, sometimes, "leave" it (i.e., are destroyed). These models include the Eden model (Vicsek, 1989), the diffusion limited aggregation (DLA) model (Witten and Sander, 1981, Batty and Longley, 1994), and correlated percolation model (Makse *et al.*, 1995). A detailed description and comparison between these models is given by Benguigui *et al.* (2000).

For example, Makse *et al.* (1995) propose a "correlated percolation model." In it the probability of constructing a new building is not constant but is correlated with the instantaneous density of the emerging clusters. It is shown that this model produces a good simulation of Berlin and London patterns from the middle of the 19th century and until today.

Percolation and DLA models represent a half-step toward the full representation of the dynamics of discontinuous urban patterns. Such patterns are generated fully by models of *leapfrogging*. For example, according to the *p*-model (Benguigui, 1995, 1998) the city is growing following developers' decisions to construct at a location that they "visited" several times. The intuition behind the model is that each visit represents a unit of time and provides a confirmation of the worthiness of construction at the particular location. In the *p*-model simulations the city starts with a well-developed center. Thereafter, secondary centers are generated, not adjacent to the initial center. Each of the centers continues to grow and generate new centers until they coalesce with each other or with the initial center.

Leapfrogging mechanisms can be identified by measuring population growth at various urban locations at a distance from the center of a metropolitan area. Recently several researches have performed such studies (Benguigui *et al.*, 2001a, 2001b, Heimlich and Anderson, 2001, Newburn and Berck, 2006). Leapfrogging results in spatial patterns that contain much open space that can be used for agricultural and/or natural areas. In the context of urban frontier, the study of clusters and leapfrogging is most attractive. It may thus provide more accurate description of the changing size and shape of the open spaces and the built-up areas.

3.2.4 The Problem of Urban Boundary

One obvious source of disparity between urban theory and practice is the lack of data that adequately represent urban spatial dynamics. Many researchers have recognized that the use of data delimited on the basis of municipal partitions leads to severe distortions, since their boundaries often are an anachronism and do not signify any actual spatial entities (Anas *et al.*, 1998, Benguigui *et al.*, 2006). This problem becomes especially important when the research follows metropolitan area over time. However, much of the research of urban systems is inevitably based on data aggregated into long-standing administrative units that might not be conducive to uncovering the true mechanisms of urban growth.

One way of getting around the problems is to focus on the data of real-world objects at their natural resolution, i.e., on the footprint of the building when studying the dynamics of built-up areas in cities, and then search for clusters of these basic objects (Schweitzer, 1997). The rigorous geometrical analysis of the clusters, their shapes and size distributions tells an entirely different story of evolution that can then be correlated to the historical trends in the development of the study area. Unlike the studies based on socio-economic data, analysis of urban clusters, especially in time, can lead to very general hypotheses concerning the formation of urban structures, their arrangement in space and of changes in their character and distribution over time (Benguigui *et al.*, 2006).

3.3 Urban Simulation Models

The use of high-resolution real-world data affords the extraction of a large number of empirical rules and laws underpinning our theories and models. The data-driven view of urban and ecological simulation modeling enables the use of empirically justified dependencies, even if their theoretical basis has yet to be developed. In urban and regional research simulation models are commonly based on cellular automata (CA) or multi-agent systems (MAS) principles and are applied to the explicit simulation of spatial systems in dynamic and high-resolution contexts (Torrens and O'Sullivan, 2001).

The general idea of CA models is associated with a view that space is partitioned into homogeneous cells, usually, but not necessarily, organized into square grid. Each cell is found in one of the predefined discrete states. In the classical version of cellular automata each cell has the capacity to process information from their surroundings, and the state of each cell changes automatically with time according to a set of rules, based on the information about its own state and the states of its neighbors. CA models are flexible and efficient abstractions that enable the construction of detailed, complex, dynamic models, well suited to handling geographic phenomena (Torrens and Benenson, 2005). Just as theoretical models, simulations help us to learn about the nature and dynamic behavior of the real-world systems and to find out how they are critically bounded (Engelen *et al.*, 1997). Also, they can be used for making predictions about the future of the spatial systems modeled.

From the early days of modern urban research CA simulations have been concerned with urban area only. While distinguishing between several states of urban lands and population, Lowry (1964) and Forrester (1969) combined the rest of the region into "unusable" lands that are the passive recipients of the consequences of urban processes. This view was shared by many since Forrester (1961) and Meadows *et al.* (1972). For two decades, the resolution of urban simulation models remained relatively high within cites and ignored processes outside the built-up area (Chapin and Weiss, 1962, Chapin and Weiss, 1965, Chapin and Weiss, 1968, Allen and Engelen, 1986, Putman, 1970, Batty, 1976, Tobler, 1970).

Despite this, the first generation of the simulation models pioneered several important approaches to modeling of the real-world cities. For example, Chapin and Weiss (1962), Steinitz and Rogers (1970), and Tobler (1970) were, first, to distinguish between the actual state of an urban cell and its potential for change that is later realized in case of sufficient demand. Second, the potential for changes is multi-dimensional and includes components for many urban and nonurban land-uses. Third, the model did not go beyond simple, usually linear and piecewise-linear dependencies of development potentials on environmental factors, just because, neither data nor theoretical justification existed for more complicated view.

A major step forward was made in the 1980s with the introduction of high-resolution CA models (Couclelis, 1985, Nakajima, 1977, Itami, 1988, Cecchini and Viola, 1990, 1992). These developments paved the way for acceptance of CA as a modeling tool, capable of explicit simulation of urban dynamics.

3.3.1 Land-use Transitions and Markov Field Models

Modeling land-use changes by means of probabilistic transitions of micro units from one state to another is associated with "Markov field" models (Conlisk, 1992). Markov models rely on estimates of transition probabilities and make them dependent on neighbors' states — assuming such dependence exists. The typical Markov model considers several discrete and easily recognized land-uses and a matrix of transition probabilities that are dependent on the state of the neighboring cells.

Statistical confirmation of the influence of neighborhood on cell land-use changes is of paramount importance, and has been demonstrated by several research projects. McMillen (1989) used the multinomial logit model and demonstrated that transitions between vacant, agricultural, and residential land-uses in fringe areas of Chicago depend on property size, distance from Chicago and nearby smaller towns, and characteristics of the quarter in which the property is located. De Almeida *et al.* (2003) demonstrated that distance to roads, industrial areas, as well as existence of subsidized dwellings and services, in the zone that a land unit is affiliated with, all influence land transitions in the Brazilian city of Bauru. Wu and Yeh (1997) regard factors of land-use change in Guangzhou, China and use logistic regression to represent transition from nonurban into urban land-use as a function of several groups of factors: characteristics of a land unit itself, fraction of neighbors of urban use, transport accessibility, potentials of employment, population, and investment, etc.

3.3.2 The Era of Cellular Automata

One of the earliest CA applications for real-world urban modeling is the constrained CA model of land-use dynamics by White and Engelen (1993). White and Engelen based their approach on the potential of a land cell to undergo a certain land-use transformation depending on the states of the cells' neighborhood. White and Engelen claim that at the resolution of homogeneous land units, the influence extends beyond a circle of the immediately adjacent cells. Based on this, the neighborhood is extended from a standard for CA 3×3 to 113 cells at a distance six or less cell units from the center. This extension is critical for representing interface dynamics. The characteristic size of the urban land unit is about 50×50 m. The sizes of nonurban land units vary, but they usually are larger. Thus the typical resolution of the land-use CA is usually no higher than 50 m and the six-cell distance is about 300 m, with an intuitive view of minimal width of the peri-urban zone.

"Constrained" CA of White and Engelen (1997) follows the basic principle that was first introduced by Chapin and Weiss (1968). The numbers N_i of cells that must have specific use S_i, $i = 1, \ldots, K$, at time step t is considered as an external parameter that determines the amount of the overall changes. Traditionally the demand comes from the urban land uses and is given in terms of dwellings, offices, commercial areas etc. For each land-use i the model determines the cells for which the potential for transformation into S_i is the highest, and distributes N_i among these cells. In this way, it is possible to distribute the demand for built-up uses among the land cells within the urban core and peri-urban belt.

With several variations, the framework of constrained CA was successfully employed for simulating real-world dynamics of many cities, mostly in USA, Europe (Xie, 1996, Batty and Xie, 1997, White and Engelen, 1997, Engelen *et al.*, 2002, Barredo *et al.*, 2003), China (Li and Siu, 2001, Li and Yeh, 2000, Yeh and Li, 2001, 2002, Sui and Zeng, 2001), Australia (Bell *et al.*, 2000, Ward *et al.*, 2000a, Ward *et al.*, 2000b) and became a standard in urban CA modeling. The typical cell-size in these models is 100×100 — 250×250 m and six-cell neighborhood radius results in $\sim$0.5–1.5 km range of influence of the factors.

From the very beginning of the CA regional modeling era, the CA scholars realized the limitations of the short-range modeling and the need for distant action. The first to rise the challenge were Batty and Xie (Batty and Xie, 1994, Xie, 1996) who included into the model the interaction field $F(C)$ that is bigger than the neighborhood $N(C)$ and represents an intermediate urban scale between the neighborhood level and that of the city as a whole. They apply their model to description of the urbanization processes in a 20×20 km area around the city of Amherst (Buffalo metropolitan area) represented by means of a 600×600 grid of cells of the size of $1/3 \times 1/3$ km.

Another approach to the distant action was proposed by Keith Clarke and co-authors (Clarke, 1997; Clarke and Gaydos, 1998; Candau *et al.*, 2000) who have further explored a diffusion-based view of urban development. Clarke and colleagues proposed and built a general heuristic CA model called SLEUTH (Slope, Land cover, Exclusion, Urban, Transportation, and Hillshade). Developing the idea of the SLEUTH model that urban growth rates depending on the age of urban cluster, Candau *et al.* (2000) consider clusters of urban cells as Deltatrons, which act as self-existing urban entities growing on their edges. At each iteration a Deltatron cell ages by one unit of time, and, reaching a threshold age, a cell "dies" and can then be recruited as a seed for a new Deltatron. The Deltatron model has also been applied at a regional level (Hester, 1998), the most extensive being the Mid-Atlantic Integrated Assessment (MAIA) study area. MAIA includes seven states on the eastern coast of the United States: Delaware, Maryland, North Carolina, New York, Pennsylvania, Virginia, West Virginia, as well as the District of Columbia, and is designated by the Environmental Protection Agency for the implementation of research, monitoring, and assessment of ecological conditions there.

3.3.3 CA Models in 3D

It should not be surprising that consideration of biodiversity in and around cities needs to consider the 3D evolution of cities. Although most of CA models in 3D were developed in the natural sciences (Hua and Sprung, 1998, Siregar *et al.*, 1998, Hunt *et al.*, 2005 and others), there are also a few originating in the urban studies. The pioneering work of Semboloni in simulating the evolution of virtual cities (Semboloni, 1997, 2000a, 2000b) suggests that the 3D growth of cities results in spatial specialization in terms of types of land-uses. In Semboloni's models the weight of the neighboring land-uses in the development potential function for a given site dominates land-uses that do not already exist on the site. There is also some literature concerning visualization of cities in 3D (Batty *et al.*, 2000, Evans and Hudson-Smith, 2001, Benenson and Torrens, 2004, Maguire and Batty, 2005, Evans *et al.*, 2006). And yet, there is a paucity of simulation models that focus on the dynamics of the spatial distribution of high-rise buildings. One exception is the "Evo city" model of Austern *et al.* (2007). This model attempts to offer practical solutions and propose interesting ways to plan better cities in the future. The model is based on realistic economic considerations and influences and its outcome is the evolution of virtual city in 3D.

Another 3D simulation model is presented in Benguigui *et al.* (2008). With the use of simple means and intuitive mechanism this model proposes to explain the dynamics of heights observed in real cities. It presents a quasi-3D CA simulation model of cities. In this model 2D dynamics include a cell attribute that represents building height information. Dynamic processes are depicted using four parameters: initial building coverage, interaction with adjacent neighborhood, inertia, and noise. These parameters can assume simple economic interpretations, and combination of their values can generate interesting spatial results.

To conclude, development of simulation models has contributed a great deal to the understanding of urban spatial dynamics. Much progress has been made since the emergence of early CA models and the process is still under way. The models are able to reproduce both the mono-centric and the poly-centric structures, managed to grasp the variation in density and the complex spatial patterns of the multiple land-uses. Some of the more sophisticated models differentiate between the different types of "undeveloped" open spaces, such as natural versus agricultural. Despite their inability to predict future outcomes and few other limitations, the simulations are useful in defining the basic rules of land-use transition and in recognition of the factors effecting the urban growth. In some cases the connection between the simplistic behavioral mechanisms can be linked to spatial patterns on a macro level. It is clear however, that majority of the simulation models disregard the ecological aspects of development.

3.4 Modeling Sprawl

Urbanization and decentralization are occurring simultaneously in urban systems. On the one hand, in most developed countries cities are continuously growing at the expense of the periphery, thus causing more and more of the population and the activities to be located inside the urban area. This can be regarded as centralization of the system as a whole (Henderson *et al.*, 2001). On the other hand, the decentralization and suburbanization trends are taking place in many places, where the growth is characterized by low densities and noncontiguous development. The latter processes are associated with the concept of urban sprawl.

Most of the academic debate on the subject of sprawl revolves around its negative impacts of excessive costs on the economy (Ewing, 1997, Burchell *et al.*, 1998, Downs, 1998, Brueckner, 2000, Johnson, 2001). These include lack of exploitation of scale economies in public services, infrastructure and energy consumption, increased use of private vehicles, resulting in congestion and pollution. It is also claimed by opponents of sprawl that it causes further decline of central cities. Clearly, scattered and discontinuous urban development also causes irreversible changes in ecosystems, by reducing their total area and fragmenting them into separate systems, often lacking the critical mass for some species to survive.

Some researchers consider sprawl to be a mature stage in the evolution of a city toward a compact urban structure. Hall (1983) discusses sprawl in the context of a city passing from a condition of primary industrialization to absolute centralization, relative centralization, relative decentralization, and absolute decentralization. Thus sprawl is claimed to be characteristic of the latter two stages of an urban evolution process. In order to fully understand the phenomenon, there is generally a motivation to uncover the behavioral drivers or micro-motives. A simple and obvious explanation for the on-going and overwhelming sprawl processes is that it offers amenities people prefer and choose to pay for, whether or not planners and academics consider it to be sustainable (Morill, 1991). In addition to the standard life-style amenities, such as clean environment and proximity to open spaces, sprawl also offers the social benefits of safety and segregation from the lower income groups (Audirac *et al.*, 1990).

Although the reasons for sprawl are easily recognized, it is not so simple to quantify and measure sprawl. Torrens and Alberti (2000) provide a concise overview of the various aspects of sprawl and their measurement. Among other issues, they discuss the ecology of sprawl and ways of measuring its effect on the composition and spatial distribution of habitat patches.

Another very recent empirical work, performed by Frenkel and Ashkenazi (2008) applied various techniques of measuring sprawl to a series of land-use maps of urban settlements. The authors name five major groups of sprawl measures: growth rates, density, spatial geometry, accessibility, and aesthetic measures. The geometric measures, originate mostly from ecological research (McGarigal and Marks, 1995, Turner, 1989) or from fractal geometry (Batty and Longley, 1994). Some common measures of spatial geometry of sprawl include leapfrog or continuity measures (Galster *et al.*, 2001), measure of circularity (Gibbs, 1961), fractal dimension, and mean patch size, M (Batty and Kim, 1992, Batty and Longley, 1994, Benguigui, 1995, Torrens and Alberti, 2000, Herold and Menz, 2001).

Torrens (2006) demonstrates the application of a geographically derived automata methodology to the simulation of sprawl. He claims that the CA framework is particularly beneficial in modeling sprawl, since it allows for the description of system dynamics as a function of spatial interactions between mobile, agent-like entities and a static environment.

According to the author, the simulations yield evidence that sprawl is, to a certain extent, inevitable and is the likely end-state in the natural evolution of a city-system. Having said this, various potential options for managing sprawl are discussed. The results of the simulations suggest that sprawl might best be tackled geographically, by encouraging compact and sustainable clusters of leapfrog development in close proximity. Sprawl on the periphery of these clusters should serve as an in-fill mechanism rather than continuing on the periphery of a larger urban mass in an unsustainable fashion.

Yet, another agent-based model deals with measuring and simulating sprawl (Brown *et al.*, 2004). The authors present several scenarios of residential development at the rural–urban fringe to evaluate the effectiveness of a greenbelt located beside a developed area, for delaying development outside the greenbelt. Essentially, the aim of the model is to determine the width and location of the greenbelt that would slow or reduce sprawl. Here, as well as in many other studies, the sprawl is a presumed, if inevitable evil, in need of restraining and controlling by means of planning policies and regulation. The discussion of whether every type of sprawl is undesirable and what alternatives urban spatial processes may have to offer will be presented in the concluding section of the paper.

3.5 Key Features of Urban Spatial Structure

To sum up what is known about urban spatial dynamics, here are some key features:

(1) Urban spatial dynamics are discontinuous in space and nonuniform in time. As a result, precise descriptions based on a central principle, are elusive. Simple theories and models provide a very general depiction of the urban areas only. They disregard the essential processes occurring within the urban core and, especially, in the boundary zone.
(2) The very basic model of the city suggests a density gradient, steadily dropping with distance from the urban core. The classical models of urban growth describe an expansion wave of outward development. The majority of classical theories and models disregard the outlying nonurban land-uses completely.
(3) Urban systems are self-organizing, and urban growth is regulated by numerous feedback mechanisms, regulating the location, rate, and type of development. Methods and models, traditionally applied in analyses of physical systems, enable a vision of cities as self-organizing and give rise to the representation of discontinuities in spatial dynamics, sudden changes and criticality. These models generate great variety of urban patterns that reflect real-world cities better than classic models.
(4) An important consequence of self-organization is urban leapfrogging — the expansion of the developed area by a series of jumps, creating discontinuous spatial patterns. It also leads to irregularity of spatial growth and to self-similarity as indicated by estimated fractality and clustering.
(5) It has been shown that cities display clustering of built up areas, types of land-uses and functions. Analysis of anomalies in the evolution of clusters suggests that there is a relationship between cluster characteristics and socio-economic development. Clusters themselves possess irregular shapes and fractal dimensions.
(6) Leapfrogging and fractality lead to a stable fraction of open spaces within urban areas. These spaces — patches and narrow corridors are often regarded as undesirable waste of space and their benefits to the city dwellers are often underestimated.
(7) A city's spatial evolution is governed, among other things, by its characteristic time. This parameter represents the time from the acquisition of property rights in a plot of land by a developer and until the return on investment is realized. The city's characteristic time varies over time and over the city's geography. There is a need to study the time related aspects of urban evolution and its relation to biodiversity.

(8) The noncontinuous expansion of low density land-uses is generally defined as urban sprawl, which is considered undesirable and in need of regulation and limitation. Much attention is dedicated in academic literature to measurement of sprawl and to the policy measures to be taken in order to slow it down. It is recognized however, that sprawl is an inevitable, natural stage in the evolution of urban systems.
(9) The boundary zone of the intensive urban areas — the peri-urban fringe is of particular interest. It is in this zone that the interaction between urban uses and plant and animal species and communities is most significant and where the fastest processes of change take place. The discontinuous urban growth guarantees the fringe area of particular and essential width and extent. The processes taking place in the peri-urban fringe are generally understudied and in particular, have not been viewed in terms of their interactions with the communities and ecosystems within and adjacent to this area.

4 BEYOND THE BUILT-UP ENVIRONMENT

Urban systems are only one of the three main components of the landscape. The other two are agricultural and natural ecosystems. From very general and casual spatial observation, agricultural systems are the successors of the urban ones. Examination of the general trajectories from city centers suggests out that city scapes are gradually substituted by agriculture and by natural systems further away. However, each pair of land-uses displays numerous interfaces and directly "competes for space" on the one hand, while being connected by numerous flows of energy, matter, and population on the other. Every model of landscape dynamics should explicitly define the city–agriculture–nature interactions.

As mentioned several times in the above sections, until mid 1990s attitude of urban modelers to agriculture and natural lands was very simple. Both types of land-uses were considered as "non-urban." The encroachment of cities and the transformation of such lands into urban uses are determined solely by urban needs and some direct or indirect "price" the city should pay for it. As is evident below, during the long history of its development ecological modeling was evolving in parallel to urban modeling. It focused on natural ecosystems while considering the urban uses as boundary conditions. Agriculture land-uses comprising up to 40 percent of the land area in many developed countries and steadily growing in most of Africa and Asia (FAO, 2007) are an essential part of the landscapes in the Western world. They fell "between the chairs" so to speak and did not attract much attention of modelers.

During the last decade this situation started to change. First, models that consider agriculture land-use dynamics began to appear. Usually models of this kind are limited to predefined boundaries of the farms and focus on the descriptions of crop dynamics within this area, too far from the goals of the current review. Second, explicit models of landscape dynamics that account for all three main types of land-uses at comparable levels of detail, at least with regard to spatial resolution and acting mechanisms, became one of the mainstreams of regional studies.

The interfaces between urban–rural, rural–natural, and urban–natural land-uses became a hot topic of the environmental modeling. Usually, the researchers consider either sufficiently large administrative area or water catchment area. The former is convenient for approaching collecting data on human activities, the latter for the description of the ecological natural process — and aim at representing the main processes that govern the land-use dynamics within each of three main land-uses and on the interfaces between them. The models are usually applied to either administrative area or river basins and usually aim at assessment of the development plans that regard these areas of their parts.

One of the pioneers in this respect is the Research Institute of Knowledge Systems (RIKS, www.riks.nl) that developed a software for high-resolution integrated modeling of socio-economic and land-use dynamics toward the 2000 (White *et al.*, 2000, White and Engelen, 2000, Engelen *et al.*, 2002, Oxley *et al.*, 2004, van Delden *et al.*, 2007) and from then on successfully implementing the software for assessment of the development plants at different scales, from the city of Dublin to the St Lucia island in Caribbean. The modeling environment accounts for 10 sub-models that simulate hydrology, human influences, crops, natural vegetation and climatic conditions and operate on different spatial and temporal scales. Many sub-models and, consecutively, numerous parameters make presentation of the model essentially problematic. After studying several applications of the models the authors claim that the contributions of actors and driving forces — political, economic and cultural, are of critical importance for model projections. This conclusion is supported in Schneeberger *et al.* (2007), who defined the relative importance of different actors and forces in the sequence of changes observed in northern fringe of the Swiss Alps during last 120 years. In the same venue, Bolte *et al.* (2007) compared different scenarios of actors' behavior aiming at conducting alternative futures analyses in the Willamette Basin, Oregon.

In order to work effectively with landscape simulation models one has to be an expert in the problems and development trends of the particular area being studied. Without such particular knowledge there is no basis to check the validity of the simulated results. Commonsense logic may lead to mistakes. The best practice in these cases is to define several scenarios of the landscape development, and then to investigate the sensitivity of the model dynamics to parameters for the scenarios (Hagen-Zanker and Lajoie, 2008), including sensitivity to changes in the spatial resolution of the model (Evans and Kelley, 2004). In this way the parameters that are important for the scenario can be revealed and their values can be checked more carefully. Investigations of this kind can be supported by clustering the observed land-use patterns into groups (Poudevigne and Alard, 1997, Kristensen *et al.*, 2004). In this way one can distinguish between more and less possible combinations of the parameters of the land-units.

Landscape simulation models explicitly consider agriculture as another important type of land-use that has been almost completely disregarded so far in this paper. Agriculture is often regarded as a buffer between the urban and the natural "worlds," under the assumption that it provides a suitable environment for the survival of native species, displaced by the sprawling cities. Costanza *et al.* (2002) presented an example of a comprehensive model framework that aims at comparing many scenarios to study the development of $\sim$ 2500 km^2 Patuxent River watershed in Maryland. The model integrates data over several spatial and temporal scales and investigates the effects of the spatial patterns of human settlements and agricultural practices on hydrology, plant productivity, and nutrient cycling in the landscape. The spatial resolution is variable, with a maximum of 200×200 m to allow adequate depiction of the pattern of ecosystems and human settlement on the landscape. The temporal resolution is different for various components of the model, ranging from hour in the hydrology component to a year in the land-use dynamics module.

After calibration, 18 scenarios of alternative land-use patterns and policies were compared. These scenarios include: (1) historical land-use in 1650, 1850, 1950, 1972, 1990, and 1997; (2) a "buildout" scenario based on fully developing all the land currently zoned for development; (3) four future development patterns based on an empirical economic land-use conversion model; (4) agricultural "best management practices" that lower fertilizer application; (5) four "replacement" scenarios of land-use change to analyze the relative contributions of agriculture and urban land-uses; and (6) two "clustering" scenarios with significantly more and less clustered residential development than the current pattern. As is often the case, the model dynamics display nonlinear dependence on parameters and one should interpret the results with great care.

Recently there are other simulation models that deal with urban–agriculture–natural interfaces. Bithell and Brasington (2008), for example present a modeling system to simulate land-use change by bringing together an agent-based model of subsistence farming, an individual-based model of forest dynamics and a spatially explicit hydrological model which predicts distributed soil moisture and basin scale water fluxes. Using this model they investigate how demographic changes influence deforestation and assess the impact of the demographic changes on forest ecology, stream hydrology, and changes in water availability.

To conclude, we consider the landscape simulation model as a working tool for the future studies of the Urban–Rural–Ecosystem interface.

5 URBAN AND PERI-URBAN ECOLOGIES

While urban studies investigate changes in the distribution of human population and activities, built-up patterns and urban land-uses, ecological research deals with similar issues pertaining to plant and animal species and communities, usually in their natural habitats. As will be detailed below, some of the ideas that have been considered by ecologists also parallel those ideas considered by urban system studies, such as the hierarchical structure of ecological systems, their spatial and temporal dynamics, species' and communities' succession.

The study of urban and natural ecosystems in isolation and conjointly requires conceptual as well as practical definitions of the boundaries of these systems. In the urban realm the unitary infrastructure elements, such as buildings, back yards, parking lots and industrial areas usually have sharp and well-defined boundaries (Alberti, 2005). This is true for a single patch or a single element. However, when higher order systems are perceived as a collection of such elements, identifying their precise boundaries becomes more complicated. On the gradient from city center to periphery the density of built areas decreases toward the outskirts, resulting in an increased average distance between constructed areas and higher variance of this distance. Consequently, defining urban areas and demarking their edges becomes dependent on the discipline's criteria and may be defined by political, social, physical, and structural characteristics or commuting radii (for example see Pickett *et al.* (2001)).

Ecosystem boundaries may be defined by watersheds, airsheds, the extent of animal movement among areas, and like the urban systems they may depend on the extent and resolution of the study area. In addition, due to the strong interactions among the elements of the system, and due to the fact that they are not readily decomposable as opposed to urban infrastructure, identifying the spatial boundaries of ecosystem becomes increasingly complicated (Urban *et al.*, 1987).

The effects of urban areas are not limited to, and do not cease at the physical boundaries of the cities. As it is well known, the activities of urban inhabitants as well as the air pollution emitted in urban areas may affect regions well beyond the city boundaries. This also holds true for water pollution. The interactions among urban and neighboring ecosystems are reciprocal as non-native species present in the urban systems, may invade the natural ecosystems, and vice versa (Godefroid and Koedam, 2003) (see Section 3.5).

McDonnell and Pickett (1990) propose to consider "ecological forcing functions" created by the growth of cities and human activities. Individual components as structures, physical and chemical environments, populations, communities, ecosystems, and human culture must be quantified to discover the ecologically important impacts of the urban development. Accordingly, within the urban setting, areas not intensively managed by people, such as parks, lakes, and streams are erroneously considered to be "natural" even when they include a variety of introduced as well as native species.

5.1 Urban Core to Periphery Gradients — The Ecological Aspect

Due to the difficulties in defining distinct boundaries to urban and natural ecosystems, a number of methods adopt a gradient analysis approach. Under this approach different indices are evaluated from the core of urban areas along a trans-section to rural areas. Luck and Wu (2002) for example, examined various landscape indices such as patch type percent cover, mean patch size, patch density, and patch size variability along such a gradient in the Phoenix urban–rural region. They contend that a single index is not sufficient to detect the spatial pattern of urbanization and that different land-uses (e.g. urban, natural, agriculture) may exhibit different "spatial signatures" (i.e., mean patch size, distance to closest neighbors, etc.). Comparing the spatial signatures among different urban–rural gradients may therefore provide insights to the extant urbanization processes.

The urban–natural array is often conceived as spatially structured and organized. The traditional "gradient paradigm" suggests that environmental variation is ordered in space and governs the corresponding structure and function of ecological systems. The "natural gradient" is a common approach among ecologists, applied to understand the relationship between environmental variation and ecosystems structure (McDonnell *et al.*, 1997). Recently, the gradient paradigm was adapted to urban environments (McDonnell and Pickett, 1990, McDonnell *et al.*, 1993). Urban areas in the United States typically consist of densely populated urban core surrounded by asymmetric rings of diminishing landscape modification (Dickinson, 1966, Forman and Godron, 1986). The resulting pattern of natural and human-modified ecosystems within a metropolitan area can be conceived as a simple gradient of land-uses coupled with a more complex gradient of urban effects (McDonnell and Pickett, 1990, McDonnell *et al.*, 1993).

In contrast to the densely populated highly modified urban core, natural areas are defined as ecosystems which persist primarily because of natural processes of plant establishment, water availability, nutrient cycling, and plant–animal interactions with minimal or limited human manipulation (McDonnell, 1988). Since the introduction of the urban–rural gradient concept by McDonnell and Pickett (1990), it has been widely used. In contrast to urban studies, ecological studies commonly observe such gradients from the opposite direction, namely as rural–urban gradients. There are several patterns that emerge from the related studies (Mckinney, 2002):

Physical gradient: A number of studies demonstrated increased physical changes, along the gradient, towards the inner core of the city. Examples are abundant and include soil chemical and physical properties (McDonnel *et al.*, 1997), soil and water pollution, heat island effects, etc. Physical changes also include the increase in impervious surfaces toward the inner city and other land-use transformation.

Habitat loss gradient: The physical changes produce a gradient of natural habitat loss toward the urban center that is replaced by four types of altered habitats: built habitats, managed vegetation spaces, ruderal vegetation, and natural remnant vegetation.

The increasing fragmentation of natural habitat by human disturbances tends to cause biodiversity changes and to reduce species richness providing the conditions for opportunistic species to gain dominance. This has been shown for many taxa including plants (Guntenspergen and Levenson, 1997), birds (Blair, 2001, Mortberg, 2001, Crooks *et al.*, 2004), butterflies (Blair and Launer, 1997), and insects (Niemela *et al.*, 2003). The issue of biodiversity in urban and peri-urban areas is discussed below in greater detail.

5.2 What are Urban and Peri-urban Ecologies?

Intra and inter-species competition, predation, parasitism and several other types of interactions (facilitation, symbiosis, etc.) dictate the dynamics of ecological systems. Their rates, magnitudes, manifestation, and relative importance differ among the various systems and depend on species characteristics, energy fluxes and nutrient availabilities within each ecosystem. To identify the result of human presence and activities within urban ecosystems and along the urban–rural gradient, Pickett *et al.* (1997) suggest that social and behavioral aspects of human activity should be incorporated, in contrast to natural ecosystems in which the human aspect is usually implicitly addressed. As will be detailed below, the landscape structure and spatial distribution of the built-up versus natural elements, is a seminal system driver in urban and human dominated ecosystems.

Ecosystems transformed by human activities are also termed "cultural ecosystems" and are characterized by urban and agriculture landscapes. Such systems are evidently not self-sustaining and are characterized by input of energy, materials, and nutrients from anthropogenic sources. Human activities determine their structure and functional organization (Brussard *et al.*, 1998). The rate and magnitude of ecological succession depends, besides environmental conditions, on the degree of human intervention. Cramer *et al.* (2008) argue that an ecosystem subject to anthropogenic effects passes two transition thresholds: a biotic and an abiotic one. With the strengthening of these effects the system first passes the biotic threshold: the biological properties of the system are essentially affected, while manipulations only of the vegetation are required to restore the system, as the physical properties of the system are still intact. When the abiotic threshold is crossed, physical intervention is required to restore the system to its natural state.

Due to the gradual and fuzzy nature of the transition from natural to anthropogenic environment (the growth of built-up areas, for example), it is virtually impossible to define a boundary or a threshold beyond which "natural" ecosystems[2] become "urban" ecosystems. The place of a certain ecosystem on the natural-urban continuum is usually defined based on species diversity and abundance, both clearly associated with human presence. Clergeau *et al.* (1998) indicate that in Québec bird abundance was highest in the most urbanized plots studied, and that only three species (house sparrows, European starling, and rock dove) accounted for more than 50 percent of the observed birds. Hence abundance of some species may serve as indicators for higher degrees of urbanization. Another possible approach is to estimate the ratio of natural vs non-native species. Threshold values remain the key problem of such approaches. In addition, the ecosystem structure may be affected by the social welfare of the human population. Rapoport (1993) reports that in Bariloche, Argentina, for a given housing density, the number of exotic species was higher in affluent compared to less affluent neighborhoods. These findings are similar to the ones obtained in the Phoenix metropolitan area, as described by Hope *et al.* (2003).

Is the degree of human influence the key difference between urban and natural ecosystems? Several urban ecologists agree (Sukopp and Numata, 1995, Walbridge, 1997), but others suggest that differentiation should be based on ecological processes and not on urban characteristics. Trepl (1995) proposed three main properties distinguishing urban landscapes from rural ones: (a) fragmentation and interconnectivity, (b) succession, and (c) invasion by alien species. These properties may be evaluated independently of the urban properties, and thus may serve as an alternative approach to distinguish between urban/rural ecosystems.

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[2] Since the effects of human activities are global, and extend well beyond the boundaries of particular ecosystems, then practically, strictly speaking, there are no "natural" ecosystems.

The identification of ecosystems within an urban environment entails further difficulties. It is possible to view the city as one ecosystem or as several separate ecosystems within the urbanized space, such as trees lawns, parks, lakes or seas, urban forests, wetlands and streams (Bolund and Hunhammar, 1999). We support the view of Rebele (1994), who argues that the important thing is not the mere use of the term ecosystem, but the way in which it is used.

5.3 Spatial Ecological Patterns in Urban/Peri-urban Systems

Ecological studies recognize the spatial heterogeneity of the environment. Levins (1969) was the first to introduce the term "meta-population," suggesting that populations may be viewed as a composite of several sub-populations, each occupying a distinct patch in space. Following the recognition and incorporation of spatial structure into ecological models, Holt (1985) and Pulliam (1988) introduced the concept of sink–source populations. In some patches the conditions are sufficient to sustain individuals, but not the population, i.e., reproduction rates are lower than mortality rates. Such populations are considered to be sink populations. In source populations conditions are favorable and a surplus of individuals is produced. A fraction of the dispersing individuals may successfully arrive at the sink populations, and their immigration serves to demographically sustain these populations. This concept is especially important for urban–rural landscapes, where the urbanized areas may serve as sink patches for the species that cannot self-sustain under strong anthropogenic influence.

Harveson *et al.* (2004), for example, studied the population dynamics of the endangered Florida Key Deer (*Odocoileus virginianus clavium*). They demonstrated that the deer populations of south Big Pine Key, which is densely developed, are at risk of extinction if incoming dispersal were to be eliminated from north Big Pine Key. Sink–source relationships are an extreme example of population dynamics at the landscape or meta-population scale.

In other cases species may be able to successfully reproduce in urban areas, but the urban landscape may not be sufficient to sustain populations which are large enough to be considered viable. Research indicates that medium and large-sized carnivores are more sensitive to urbanization. Riley *et al.* (2003) studied coyote (*Canis latrans*) and bobcat (*Lynx rufus*) populations in peri-urban areas in southern California, and found that home-range sizes were positively associated with the degree of urbanization. In spite of the increased prey availability in these areas, they postulated that the larger home ranges (i.e., lower densities of bobcats and coyotes) result from lower availability of den locations, and increased human activities. In addition, the behavior of wildlife species may notably change in urban areas (Ditchkoff *et al.*, 2006). Riley *et al.* (2003) show changes in the activity times of the individual animals occupying the increasingly urbanized areas: more frequent during the night hours, compared to the "rural individuals." Needless to mention, that studies on large predators in completely urbanized areas are lacking, due to the fact that they are rarely found in such habitats.

In contrast to the observed decrease of predator densities in urban and peri-urban areas, other species tend to be strongly affiliated with human presence and activities.

Scenes of piazzas and city squares with a plethora of rock doves (*Columba livia*) are common and familiar. News reports of municipalities requesting the assistance of citizens in eradicating rat (*Rattus rattus*) populations are all too common.[3] These are examples of species which have well adapted to human presence, and in conjunction with the lack of natural predators may become over-abundant (Vuorisalo *et al.*, 2003). In addition, in urban areas people actively enhance habitat quality by providing bird food and artificial nesting boxes. According to the 1996 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation approximately 54×10^6 Americans actively fed birds. According to a 2002 US Fish and Wildlife survey Americans spend annually over 2.03 billion dollars on packaged bird food, and over 730 million dollars on bird boxes and artificial nests.

Such activities do not benefit all species uniformly, and as a result the species community structure in urban and peri-urban areas is altered compared to the natural ones. While wildlife in the urban settings may be a source of aesthetic value and local recreation, the increasing abundance of these populations may lead to human–wildlife conflicts. Consequently, wildlife related disease may be of higher prevalence in urban areas compared to neighboring rural areas (Ditchkoff *et al.*, 2006).

5.4 Dispersal in the Urban-rural Landscape

Movement and dispersal of individuals between suitable habitat patches is essential for a variety of causes: search for more ample food resources, search for a breeding mate, avoidance of inbreeding and others. Assessment of the degree to which a landscape is fragmented due to urbanization, however, is species specific, and therefore scale dependent. Landscapes may be viewed as suitable patches surrounded by a hostile matrix (Forman, 1995), although the binary model of suitable/nonsuitable landscape structure does not depict reality adequately.

The physical characteristics of the landscape may affect the mobility of the organisms and their displacement speed (Baguette and Van Dyck, 2007). For example, predation risk and movement speed through orchards may be different than that in meadows, particularly for ground-dwelling species.

Intuitively, the dispersal of organisms with flying capabilities should be affected to a lesser degree by the urban landscape, compared to ground dwelling organisms. Evidence, however, suggests that this is not always the case. Hodgson *et al.* (2007) investigated the movement of bird species across habitat edges interconnecting bushland and suburban housing developments of different densities in Australia. They found that insectivore species tended to cross less into urbanized areas compared to omnivores and nectarivores. They reasoned that this may be due to either differential behavioral response to the physical structure in the urbanized systems or in response to differences in forage availabilities. Similar results have been observed in flying insect populations by Bhattacharya *et al.* (2003), who experimentally moved bumblebees among forage patches. The results

[3] In 2005, for example, the Government of Hong Kong requested the assistance of the citizens in capturing rats, in attempts to eradicate a rat infestation.

indicated that the bumblebees were able to fly over roads and railroads, but they were reluctant to do so. Evidently, some species avoid movement into and over the urbanized patches or human constructed elements, hence perceiving them as nonpreferred elements in the landscape matrix.

Dispersal corridors were suggested to alleviate the reluctance of species to cross urban landscapes. Dispersal corridors may be defined as landscape elements connecting patches of suitable habitats, which enhance individual's movements among them and increase their survival probabilities (Vos *et al.*, 2002). Examples of corridors may include stretches of riparian zones, fencerows, underpasses and tunnels beneath highways, or any other distinct feature in the landscape providing cover or enhancing dispersal. Dispersal corridors are species and scale dependent. A strip of riparian vegetation, for example, which may facilitate movement of a bear across the landscape, may be sufficiently large to provide a living habitat for a warbler. The importance of the landscape corridors is still being debated, however, as experimental studies provide inconclusive evidence (Beier and Noss, 1988, Haddad *et al.*, 2000).

Experimental studies point out the importance of dispersal corridors in the landscape matrix. Haddad *et al.* (2003) compared movements of organisms between patches connected with corridors to isolated patches. They analyzed movements of organisms from different taxa, ranging from dispersal of plant species, through insects to rodents. Altogether 10 species were studied, which all dispersed in higher rates among corridor connected patches. In addition, the movement rates among connected patches were 67 to over 400% higher compared to nonconnected patches. Other studies present similar results, in which corridors facilitate movement among patches (e.g., Haas, 1995, Mech and Hallett, 2001), but in others results are not conclusive. Experimental studies investigating rodent movements across the landscape (e.g. Bowne *et al.*, 1999, Mabry and Barrett, 2002) suggest that movement of the individuals among patches that were not connected by corridors was much higher than expected, and accounted for a significant proportion of dispersal movements.

5.5 Biodiversity in Urban Landscapes

Recognition and awareness of the need to protect biodiversity has become part of mainstream ecology during the 1980s (Ehrlich and Ehrlich, 1981, Wilson and Peter, 1988). Since then much attention has been given to the causes of biodiversity loss, the ecological, social and economical importance of maintaining biodiversity, and the ethical responsibilities of humans to maintain it. Consequently, attention has been given to the investigation of biodiversity in urban systems. The studies addressing these issues provide mixed results that depend on the taxa and on the life-history patterns of the species studied. Roy *et al.* (1999) analyzed vegetation species richness in Britain, comparing among urbanized and rural areas. They concluded that increased urbanization does not reduce overall species richness of plants. The proportion of alien (non-native) species increased significantly with the increase in urban densities, resulting in a loss of the native species. These trends are expected in human managed gardens and parks with many exotic (non-native) species.

Hope *et al.* (2003) addressed a similar question regarding vegetation species richness, but rather than correlating it with the urban–rural gradient, assessed the effects of socio-economic welfare and found that socio-economic factor is positively correlated with vegetation species richness. Once again, the increase in species richness in this research was associated with an increase in alien species and a decrease in the proportion of the native ones. Ecologists are particularly concerned with the trend of loss of the native and invasion of exotic species, which can be observed along urban–rural gradient. For example, in Berlin, Sukopp *et al.* (1979) documented an increase from 28% to 50% in alien species along a transect from the city's suburbs to the center. In a longer term, approximately 180 plant species became locally extinct in Munich, Germany during the last 100 years (Duhme and Pauleit, 1998). Drayton and Primack (1996) suggest that mechanisms such as soil trampling, development of trail systems in urban parks and fires may accelerate the invasion of exotics species. They report that 155 of the plant species recorded in an urban park in Boston were absent in 1993, and 64 species were new.

In avian communities two general types of species richness responses to the urbanization gradient have been reported. First, several studies describe a negative correlation between urbanization and total species richness. Clergeau *et al.* (1998) compared bird diversities along urban–rural gradients in Quebec, Canada, and Rennes, France. These cities share similar urban characteristics, but are located in different climatic areas. In both cases bird species richness declined with increased urbanization, and this decline has been repeatedly observed in other studies (e.g., Melles *et al.*, 2003). The second type of response reported in the literature entails a peak in species richness in the urban outskirts, rather than in the rural areas. Blair (1996), for example, surveyed the avian community along an urban–rural gradient in Santa Clara County, California. He classified the landscape to six categories, ranging from most urban to natural: business district, office park, residential, golf course, open-space recreation, and a reserve. The highest number of species observed was in the golf-course habitat (28 species). At the open-space recreation area 21 species were observed, similarly to the number of species observed in the reserve. In the residential area 16 species were observed, and the lowest number observed was eight at the business district. Similar findings were reported by Crooks *et al.* (2004). Such findings have also been reported for other taxa, such as mammals (Racey and Euler, 1982), butterflies (Blair, 2001), and lizards (Germaine and Wakeling, 2001). The difference in the patterns may be attributed to the fact that in arid and semi-arid areas, as in Southern California, human presence enriches and diversifies the environment, providing for higher species richness. It is argued that mild human interference promotes increased environmental heterogeneity in addition to improved conditions such as water, food, and nutrients (McKinney, 2002).

In addition, in many cases human activities in the city centers provide ample resources for the species that have adapted for this type of environment. Studies along a rural–urban gradient in New York indicate, for example, that both the abundance and biomass of earthworms increased in urban forests compared to rural forests by more than an order of magnitude (McDonnell *et al.*, 1997). With respect to bird and mammal species, Shochat *et al.* (2006) suggest that there is an inverse relationship between number of species and the density of individuals along the urban–rural gradient. At city centers the number of species is lower, compared to the rural areas, but the number of individuals is higher.

Hope *et al.* (2003) point out, however, that such studies have been traditionally carried out along urban rural gradients, that do not necessarily correspond to the gradient of ecologically important factors. They suggest considering a wider range of gradients, that are nested within the urban–rural gradient, such as resource availability, disturbance, cultural, and socio-economic characteristics of the neighborhood.

Succession is another fundamental ecological process that can be essentially altered following human development in peri-urban areas. Succession is defined as a predictable replacement of a set of species by a different one over time. Biodiversity, in a long run, is evidently related to succession. It has been suggested by Hansen *et al.* (2005) that the response of biodiversity to changes in peri-urban areas may last several decades. Consequently, positive or negative effects of human activities on the ecosystem may not be noticed or evaluated in the short term.

To summarize the relationships between urban development and ecological systems it is important to note that the fundamental processes driving the latter are similar, be it in an urban, peri-urban or a natural landscape. However, due to the intense intervention of humans in urban and peri-urban systems, the rates and predominance of different processes change. Finally, this review has strictly touched upon the relationships of urban-ecological systems, and did not address tangent fields such as environmental quality and landscape aesthetics.

5.6 Ecological Models

Ecological systems are complex and as in many other fields of research dealing with complexity, a considerable effort was invested in modeling. The initial models of ecological systems were restricted to temporal modeling and ignored spatial patterns of species and communities. The first models of population and community dynamics were carried out by Lotka (1925) and Volterra (1926). Both independently developed a set of coupled nonlinear differential equations, to describe the temporal characteristics of interacting predator and prey populations. This approach has been extended to species competing for limited resources, and to systems with $n > 2$ species.

The first notable effort was carried out by MacArthur and Wilson (1967), who introduced the Theory of Island Biogeography. Within the framework of this theory MacArthur and Wilson implicitly considered the spatial relationships between islands on which species can exist, surrounded by a hostile environment. They argued that the number of species expected to be found on such islands depends on the distance to the closest mainland, and the sizes of the mainland and the island. Accordingly, the equilibrium number of species is a function of natural extinction and colonization processes. The closer the islands–mainlands and the larger their sizes, the higher the equilibrium number of species on the island is expected to be. Hence, this approach laid the foundation for considering patch size, connectivity and hostility matrices and the effects of these parameters on species distribution. Just as the original urban models, MacArthur and Wilson (1967) focus on equilibrium distribution of species and did not investigate the convergence to equilibrium.

Ideologically similar model for a single species was provided by Levins (1969), who introduced the idea of a metapopulation as a set of N habitat patches suitable for population and characterized by extinction and colonization probabilities. Levins' model predicts the proportion, N^*, of habitats occupied by the subpopulations, and assumes equal dispersal and equal local dynamics within the patches, but lacks explicit spatial structure. However, it was a major foundation and advancement in the incorporation of spatially structured populations.

More recent approaches synthesize implicitly or explicitly between the concept of Island Biogeography and metapopulations and represent spatial distribution of suitable habitats explicitly. In addition, explicit consideration of local dynamics and dispersal success has also been incorporated. Hanski (1998) divides spatial ecological models into three general categories: (1) landscape ecology models where the entire landscape is considered, commonly its spatial structure is quantified, but the dynamics of populations are usually ignored; (2) metapopulation models explicitly addressing species dynamics while considering different spatial patterns of habitat distribution, and overlooking the background matrix which exists among the patches; (3) "theoretical models" investigating short-term interactions among individuals, and the emergent patterns which arise from these interactions. These models commonly ascribe a homogeneous landscape over grid surfaces, and assume the CA approach presented in previous sections.

Another prominent feature of ecological models is scale. As we have already stated, ecological processes are scale-dependent. In order to model spatial patterns at a certain scale, relevant factors should be considered (Levin, 1992). Ecological models attempt to predict the dynamics of systems at scales ranging from internal changes in an individual, as a result of host-parasitoid interactions, to global climate models impacts on ecological systems. Urban–rural interactions focus on intermediate scales, where landscape models are commonly applied. An example of extremely high resolution models is the CA model of Köchy and Tielbörger (2007) which uses a 2 cm cell size and an extent of 1 m^2 to model dynamics of herbaceous vegetation in daily increments. At the other extreme, Pearson *et al.* (2002) used a grid based model, with a resolution of 5 km, to model the effects of climatic changes on the distribution of plant species in Great Britain.

Complex models of interrelationships between species dynamics and emerging landscape patterns, e.g., between grazing and vegetation patterns, are still lacking. Grazing may generate spatially heterogeneous vegetation patterns, which in turn may affect the grazing regimes. Farnsworth and Anderson (2002) applied diffusion models to simulate the effect of animal foraging behavior on vegetation cover and the reciprocal response of the animals to the emergent vegetation spatial patterns.

Typically, landscape changes are represented by the Markov models. In such models the status of a land parcel changes based on a set of predefined rules and dependent of its state at a previous time-step, similar to the approach applied to urban models and described in Section 3.3. However, despite evident common background and methodological similarity, these two disciplines have not been participating in a dialog, but rather viewing the other discipline as a confounding variable at best. Ecological models consider urbanization processes as ones, which consume natural areas, while urbanization models consider open areas as areas waiting to be converted. Ecologists for example, lack the understanding of the effects of different policies on land use changes, and how these may affect the long term dynamics of the landscape (Bockstael, 1996). On the other hand, many development decisions fail to account for the decreased biodiversity and abundance, quality of air and water, pollution and loss of esthetic value, due to the destruction of natural habitats.

The spatial resolution and temporal scales of urban and ecological models overlap, but are not identical. Vermaat *et al.* (2005) review and compare among spatial economic models and landscape ecological ones, and demonstrate that the cell size and the extent modeled in ecological models are typically smaller when compared with the ones used in the spatial economic models. Apparently, the next phase of modeling ought to consider bridging the gap between the two disciplines, in order to investigate the consequences of the interrelationships to landscape changes.

Some rare exceptions to the ecology–urbanization dichotomy exist, however. The research conducted by Costanza *et al.* (2002) presented in Section 4, presents an integrated ecological and economic modeling approach. The model attempts to explain the long term changes of the landscape while explicitly considering effects on the hydrology, vegetation productivity and nutrient cycling in the watershed. The land-use changes are based on an economic model which considers factors such as selling price of the land unit, distance to recreation areas, employment centers, infrastructure and other economic drivers which may affect land-use transition probabilities. Due to the magnitude of processes considered, several modules were developed, each operating in different spatial and temporal resolutions. This modeling approach currently seems to be a rare exception in which an attempt was made to bridge between the two disciplines.

5.7 Key Features of Ecological Systems in the Urban Setting

1. Parallel to urban systems identification of ecosystem boundaries are fuzzy. Consequently, the ecological scientific discourse is concerned with the processes along the urban–rural–natural gradient.
2. The spatial arrangement of natural patches has critical implications to the dynamics of flora and fauna populations. Ecological corridors serve as important conduits for the landscape matrix of species movements.
3. Species response to human presence is differential. Some species are strongly affiliated with human activities and thrive in areas dominated by human presence. Other species are extremely sensitive to anthropogenic intervention, which may result in their local extinction.
4. For some species, the biomass and abundance of individuals peak in urban areas due to the ample sources of food and water. Species richness generally increases with increasing distance from urban centers and may be highest in peri-urban areas, due to the presence of both native and introduced species.
5. Ecological and urban models apply similar approaches based on scale, hierarchy, and spatial interactions, but lack operational interaction.

5.8 Where Do We Stand and Where Do We Go From Here?

The main purpose of this survey is to shed light on the existing knowledge concerning the joint evolution of urban and natural systems and on the character of their dynamic coexistence. This perspective is especially important for understanding the developments at the urban fringe. While the literature on the various aspects of the dynamics of urban and ecological systems is extensive, the two disciplines appear to be developing almost independently of each other. The study of the dynamics and evolution of the urban–rural–natural land-use triad has yet to be launched.

As a first approximation we propose to base such studies on three broad categories of landscapes:

1. Build up areas that include dwelling, commerce, office, and industrial areas.
2. Rural areas with significant agriculture use.
3. Open/natural areas where human intervention is negligible.

In this section, we present the main issues that are perplexing and that are suggested by this survey.

As we hope was demonstrated in this review, the predominant view of the trans-section that begins in the center of the city and goes outside has essentially evolved during last half of a century. Figure 2 presents a traditional "Classical City" view introduced by the urban theories of 1950s–1960s. Based on stylized facts these theories suggest that the city boundary is a narrow belt and an outer area is used for agriculture. Close to the city boundary the fraction of the cultivated land is close to 100 percent, gradually decreasing with distance from the city. On the city side boundary, there are species associated with human society only (e.g., flies, mosquitoes, or pigeons). These are associated with negative ecological impacts. On the rural side, the agricultural areas serve as an ecological sink, or as a dispersal corridor for migrating species. As the fraction of uncultivated area increases with distance from the city boundary it is capable of supporting more and more endemic species, with species diversity and abundance growing proportionally. Ecological theory adds to this that species richness grows slower than abundance with distance. This is due to essential vulnerability of some of the species to the presence of man. Further away from the city, uncultivated area eventually reaches 100 percent and the species abundance and richness become maximal.

Modern cities are much more complex than this mono-centric model suggests. Numerous observations of urban footprints, such as that of Tel Aviv presented in Figure 3, confirm empirically that cities are not mono-centric and that cities do not evolve as a wave of expansion. Urban expansion is discontinuous in space and in time.

The "Sprawling City" is illustrated in Figure 4. This illustration represents the state-of-the-art view of urban and ecological research. With increasing distance the proportion of open areas increases and agricultural areas dominate. Further away from the city, natural ecosystems take over. Consequently, we argue that species diversity will be higher in such landscapes, compared to mono-centric city landscapes.

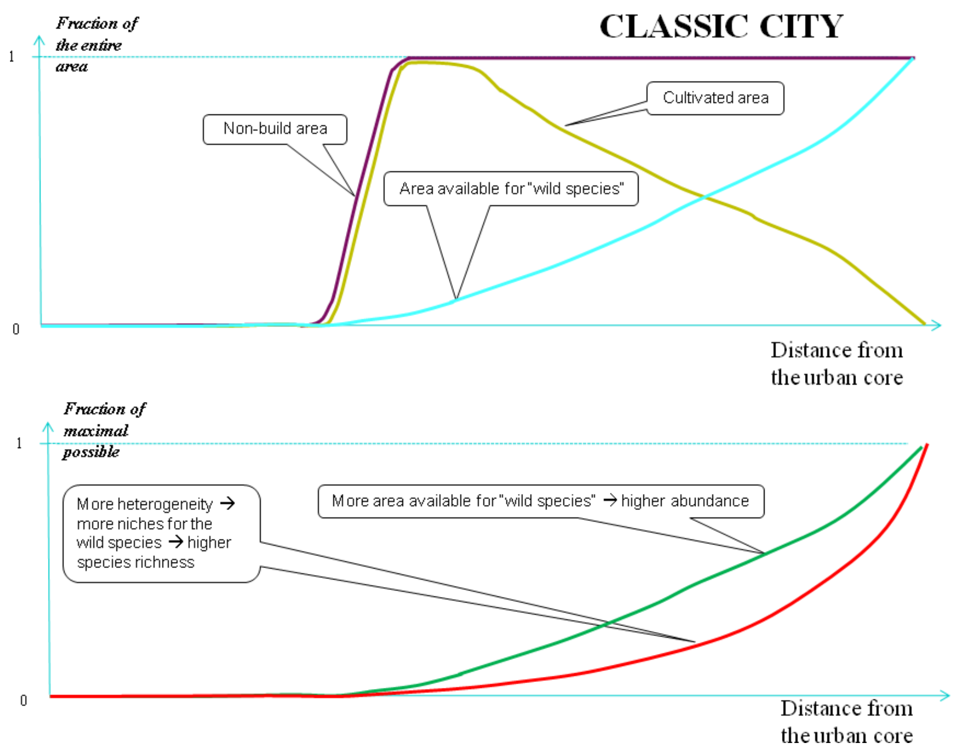

Figure 2. Land uses (upper diagram) and biodiversity (lower diagram) at various distances from the urban core in the classic city.

The essential feature of the modern city is heterogeneity. Even the very dense center of modern cities contains "green areas" that serve for temporary, and sometimes even permanent, use by few wild species that can coexist with humans (e.g., squirrels or deer). Further away from the city center and in the context of the wealthier neighborhoods there are more and larger "green" patches. The possibility of dispersal among these areas results in a variety of species and communities and the necessity for explicit accounting for the tight interactions between the urban and ecological dynamics in our attempts to understand and model landscape dynamics.

We consider especially important the low-density residential neighborhoods. In contrast to extensive pasture-type agriculture, these neighborhoods "repel" intensive agriculture from the nearby land. This is due to the negative economic impact on the neighborhoods due to low esthetic value, lack of trees, machinery and pesticides involved, etc. The economics forces instigate widening of this belt of uncultivated lands that inevitably may become suitable habitat for endemic species. The land use dynamics enforces a positive feedback in this case: more sprawl-more pseudo-natural fringe areas, that raises the value of the already existing and of the nearby lands yet

Figure 3. The urban footprint of Tel Aviv metropolitan area.

available for low-density construction. As a by-product, these "sprawl-adjacent" areas become peri-urban wildlife reserves that supply sufficiently connected heterogeneous and "protected" habitats.

Species abundance and richness peak within the sprawl-adjacent urban belt. Beyond it we approach agricultural land-uses. Agriculture land-uses are the buffer between the urban and the natural "worlds." The habitats of the majority of species are incompatible with intensive agriculture, whose goal, by definition, is to minimize impacts and damages caused by nonagricultural species and thus to maximize crop production. Species abundance and richness drops at some distance beyond the fringe of sprawling neighborhoods and remains low until beyond the belt of intensive agriculture. As the natural landscapes

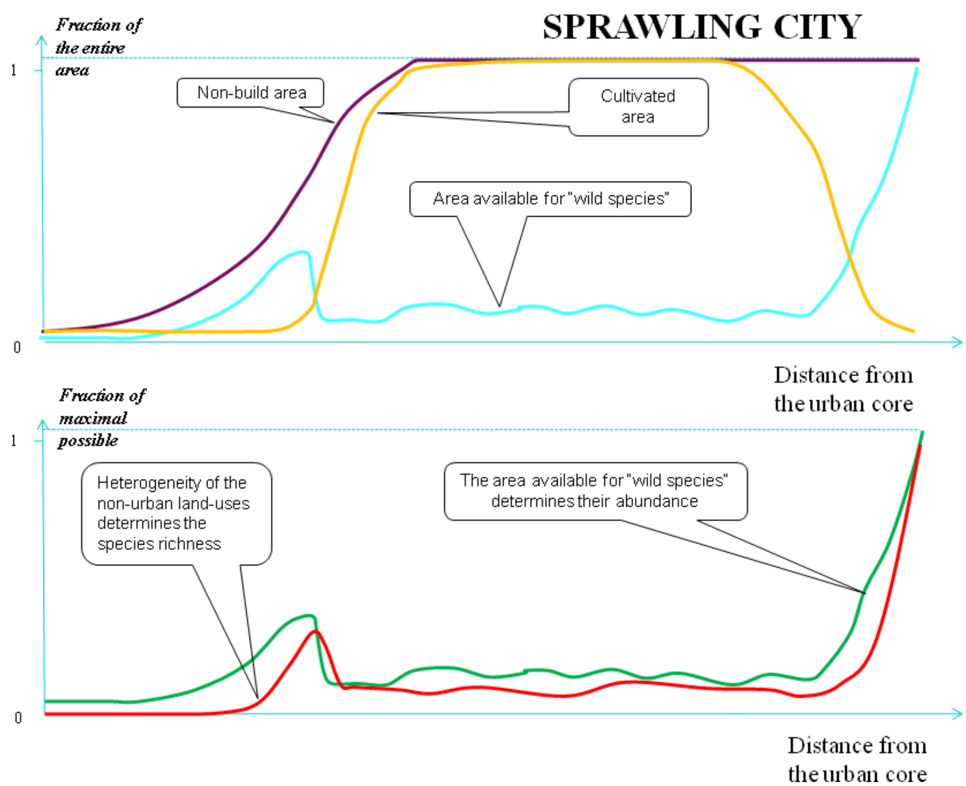

Figure 4. Land uses (upper diagram) and biodiversity (lower diagram) at various distances from the urban core in the sprawling city.

become more and more abundant species richness increases respectively. It is our view that species' richness peaks in peri-urban areas and is associated with increased human induced environmental heterogeneity and diversity. It should be emphasized that maximization of the number of species is not the ultimate goal of environmental normative theory. The ultimate objective is to maintain the value and functioning of the environment by protecting the endemic species communities.

It appears to be in consensus that in most developed countries urban sprawl is inevitable and so is the direct harm it perpetuates on the natural systems. However, it may be true that the sprawling city is not the monster it was made out to be. If managed with care and with better understanding of the complex interactions taking place in the fringe zone, the peri-urban areas may serve as "third nature" reserves for many native species. The noncontinuous piecemeal pattern of development with patches and corridors of open spaces, linking the peri-urban areas to the outlying natural spaces, may provide the conditions for "symbiotic" existence of man and the nature.

Accordingly, developers and environmentalists should seek practices that minimize damage to the endemic flora and fauna communities and ecological processes, while accommodating for and optimizing the inevitable alterations caused by human presence. Synthesizing between the state-of-the-art urban sprawl and ecological knowledge and models may provide sound insights into the dynamics of the fringe areas. The urban leapfrogging is not incompatible with the ecological demand of habitants' quality and connectivity. The guidelines for large scale development policies should be matched to the small scale policies that address the single household, particularly those located at the edge of urban sprawl. Urban planners should consider maintaining or replicating the spatial footprint formed by modern sprawling cities in order to sustain this phenomenon. Further, the urban green areas should be viewed as complementing the natural areas located in the rural areas (Lehvavirta, in press), and planners should not view them solely as facilities for raising the well being of the human residents. Such areas, including golf courses, back yards, city parks and other facilities, should be allowed to undergo natural succession processes. At least to some extent this would alleviate the negative impacts of urban development.

The discussion presented here is based on the fundamental perception that the demand for developed land at the city's edge will ultimately take place, even when opposed by planning authorities. Refraining from any development might be preferred management option for natural ecosystems but seems unrealistic. We claim that the negative effects of development may be alleviated by a better understanding of the role of the urban fringe, and its dynamics. The third nature reserve — urban fringe — is self-organizing dynamic entity, as it may move along the distance axis with time, following changes in the proportion of build up and open lands. Attempts to reconcile urban dynamics with ecosystem conservation ought to recognize that these, dynamic in space and time systems, become the valid landscape component that should not be lost in larger spatial scales.

We thus suggest that nonregular, leapfrogging spatial expansion, characteristic of the majority of the modern western cities, may serve as a buffer between urban and intensively cultivated agricultural areas and counter their impacts on natural ecosystems. As has been repeatedly demonstrated the low density sprawling suburbs provide essential habitats for endemic species and ensure their survival.

To test these ideas and to provide a basis for the management of sprawl there is a need for dynamic models of the landscape that are based on the models presented in Section 4 of this review and explicitly incorporate the experimental views of urban and ecology dynamics along with small-scale agriculture economics. The fundamental building blocks of such models include a representation of the economics of agro-production, a land-use dynamics module that incorporates economic and lifestyle factors and that focuses on sprawl and a representation of wildlife dynamics. The economic drivers affect and ultimately determine the land use that in turn affects the species habitats in the landscape. The driver of the model is the interaction between urban morphology dynamics, that determines sizes and shapes of open spaces, and the economics that determine the extent and nature of sprawling built-up areas, the feasibility of agriculture and regulatory reactions that govern interactions among these three components. In addition, species composition affects changes in land-use structure by influencing economic processes and policy regulations. Together these interactions determine the prospects and resilience of the third nature within the urban realm.

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