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Research Paper

From rural-urban gradients to patch – matrix frameworks: Plant diversity patterns in urban landscapes

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A B S T R A C T

Studies have attempted to disentangle the relationships between urban properties and species richness patterns by studying them within the urban-rural gradient context, the Island Biogeography framework, or the patch-matrix approach. We compared and contrasted these frameworks, to highlight their attributes. We assessed the role of patch properties and matrix characteristics, in light of these approaches, to identify the relative roles of different drivers in dictating urban plant species richness patterns.

Vegetation surveys were conducted in 41 open space patches within the city boundaries of Haifa, Israel. Plants were classified into three categories: rare, native and non-native. Patch properties, distance to nearest neighboring patch, distance to city boundary, within patch heterogeneity and percentage of sealed surface buffering the patch were evaluated in relation to species richness. Non-linear regressions indicated that total, rare and native species richness were best explained by a combination of patch area, sealed surface and patch habitat heterogeneity. Non-native species richness was best explained indirectly by the proportion of sealed surface. No clear cut distinctions between the three frameworks were observed. The results point to the existence of non-linear interactive relationships between the drivers and species richness, which depend on patch and urban matrix properties, particularly on degree of urbanization. We conclude that patch-matrix mechanisms interact with the urban-rural gradient approach to determine plant richness patterns in urban landscapes. Additionally, the degree of urbanization is differentially associated with richness patterns, where rare and native species are negatively associated with it, and non-native species are positively associated with urbanization.

1. Introduction

Urbanization and the human alteration of landscapes significantly modify biotic communities at various scales, and change resource availability and the ability of organisms to move across the landscape. The process of urbanization and the structure of cities have produced diversity of habitats influenced, modified and maintained by humans. Urban habitats have many similar ecological characteristics, and are influenced by similar drivers, such as the prevalence of disturbed and artificial soils, irrigation and fertilization in parks and gardens, and urban habitat diversity, even in different biogeographic regions (Grapow & Blasi, 2002; Lososová et al.,2012; Vitousek, Mooney, Lubchenco, & Melilo, 1997). The similarity in conditions may cause uniformity of the urban floras, but many studies report that disturbed sites (Angold et al., 2006; Niemelä, 1999a; Tilman & Lehman, 2001) and urban parks contain the highest species richness (Nielsen, van den Bosch, Maruthaveeran, & van den Bosch, 2014). Urban open space patches are extremely diverse, and include relict patches of undisturbed remnant vegetation, municipal parks, cemeteries, vacant lots, gardens, landfills, and other forms of open spaces (Breuste, Niemelä, & Snep, 2008; Bolund & Hunhammar, 1999). These various categories of urban open spaces may be distinguished by the degree of direct human intervention. Municipal parks are commonly characterized by active maintenance and management, whereas human intervention is commonly the least in relict patches. This study focuses exclusively on flora richness patterns in relict patches within the urban matrix. In many urban areas, the spatial patterns of such patches are highly dynamic, influenced by urban growth and sprawl. Urban landscapes are considered to be extremely fragmented habitats (Bolund & Hunhammar, 1999; Elmqvist, Alfsen, & Colding, 2008; Wadduwage, Millington, Crossman, & Sandhu, 2017), and these patterns are perpetuated by continuous development and sprawl (Irwin & Bockstael, 2007).

Nielsen et al. (2014), in their review of urban park studies, list the factors commonly studied to predict richness patterns, which include: patch size and isolation, patch diversity, patch age, matrix properties, and the urban—rural gradient. Patch size and isolation are essentially

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the foundations of the Theory of Island Biogeography (MacArthur & Wilson, 1967) and meta-population theory (Hanski, 1991). Urban open spaces are commonly viewed as limited in size, occluded within the built-up matrix, and are separated from each other by harsh and often inhospitable sealed and developed areas. Some studies indicate that such patches behave as small island habitats with restricted biodiversity and impoverished wildlife components (Helden & Leather, 2004; Johnson, 2001). In contrast, however, other studies point to high species richness values in urban areas, particularly of flora (Knapp, Kühn, Schweiger, & Klotz, 2008). Additionally, it has been demonstrated that the urban matrix is not a homogeneous hostile environment, and organism movement is correlated with the degree of urbanization (Caryl, Thomson, & Ree, 2013, Jha & Kremen, 2013). Similarly, with respect to the theory of Island Biogeography, the open spaces located closer to the rural areas or urban fringe may be associated with higher probabilities of species colonization or organism settlement from nearby semi-natural habitats. In addition, the patches embedded within the city are exposed to increased invasion by non-native species from the surrounding urban matrix. Many studies describe species-richness patterns, framed within various hypotheses that have been proposed and adopted to explain urban species-richness patterns. The three dominant patterns are the urban-rual gradient (URG) approach (McDonnell & Pickett, 1990), the framework of the Island Biogeography Theory (IBT; MacArthur & Wilson, 1967), and the patch-matrix/landscape fragmentation perspective (PM), which embodies the IBT (Laurance, 2008). We compare and contrast these perspectives, and outline their expected predictions.

We first address the URG framework. Within this framework many studies demonstrate that species-richness values peak at the fringe or suburban areas of the cities (McDonnell & Hahs, 2008). Richness patterns associated with urban gradients vary with the taxa studied; where some taxa exhibit the highest richness outside the urban areas, and some in peri-urban neighborhoods (Breuste et al., 2008; McDonnell & Hahs, 2008). Explanations for this include two processes which operate in conjunction. Firstly, many of these studies depict this gradient as associated with decreasing sealed or impervious surfaces from the urban center towards the fringe of the city (McKinney, 2002), implicitly relating to matrix properties and degree of urbanization. Thus it is assumed that the proportion of open spaces, parks and gardens increases towards the outskirts of the city, resulting in a decreasing degree of urbanization. Assessing landscape structure from the perspective of the URG approach reveals that along a gradient of increasing urbanization, patch density generally increases, whereas patch size and landscape connectivity decrease (Luck & Wu, 2002). Secondly, two contrasting species-richness gradients exist, interacting to form a peak in richness values. The first relates to human commensal species, which are tightly associated with human activities, termed urban exploiters by McKinney (2002). Such species are most abundant and thrive in the core of urban areas, and decrease towards the fringe. The second gradient is associated with rural regions which provide a pool of species, and a decreasing number of species as one penetrates into the central parts of cities. Hence, directionality is inherent to the rural-urban framework.

The Theory of Island Biogeography has also been adopted as a framework to study richness patterns in urban environments. Urban areas may be viewed as spatial systems of isolated islands, and in urban terms – patches embedded within the hostile urban matrix (Davis & Glick, 1978). The two fundamental parameters on which the IBT is founded are the size of the island, and the distance from the pool of species. Larger patches are expected to support a larger number of species; and patches closer to the fringe of the city are also expected to support larger numbers, being closer to the presumed rural pool source when applied to urban environments. Thus the IBT also implies a notion of directionality, with decreasing richness values in the core parts of the urban areas. Many studies followed the island biogeography framework and constructed species-area curves to describe and predict the relationship between species diversity and patch sizes in modified landscapes. This approach is based on knowledge of pre-disturbance species richness. Angold et al. (2006), for example, examined the effects of habitat fragment size and connectivity upon the ecological diversity and individual species distributions. They found that although patch size is positively correlated with diversity and richness of the patch, the location of the patch in the landscape in relation to its neighbors was of secondary and minor significance. While several studies adopted the IBT framework (Faeth & Kane, 1978; Marzluff, 2008), Niemelä (1999b) points to its shortcomings in urban landscapes. He argues that in urban landscapes there is no clear mainland serving as a pool source, and that the urban matrix is not as hostile as the oceanic matrix surrounding true islands.

In attempts to overcome the constraints of the IBT, the patch–matrix, or landscape fragmentation framework, has been adopted (Haila, 2002; Laurence, 2008). With respect to urban landscapes Williams et al. (2009) and Zipperer, Wu, Pouyat, and Pickett (2000) point to the need to consider inter- and intra-patch heterogeneity, patch properties, patch location in relation to other patches, the degree of connectivity, which is matrix-dependent, and the dynamics of the patches. Whereas in the IBT patch size is considered, a much broader set of patch attributes is considered under the patch–matrix framework, including patch geometry and other physical properties. Many studies have been conducted in natural systems in an attempt to evaluate the role of patch and network properties on species diversity. The more structurally complex, larger, older, and less isolated a patch is, the more likely it is to be functional and species rich (Cornelis & Hermy, 2004; McKinney, 2006; Werner, 2011). Further, fragmented patches in the city may behave differently, as they may depend on other adjacent patches for availability of resources (Tilman, 1994; Tilman, May, Lehman, & Nowak, 1994). Urban matrix properties are commonly addressed by quantifying the proportion of built lands around the open space patches as a proxy (Bräuniger, Knapp, Kuhn, & Klotz, 2010; Smith, 2007; Tonietto, Fant, Ascher, Ellis, & Larkin, 2011). In contrast to the URG and IBT approaches, however, the PM framework does not explicitly consider directionality and the presence of species pool sources. Table 1 summarizes the key attributes of each of these approaches, showing that there is no clear-cut distinction between them.

The three frameworks discussed above can be used to evaluate factor, or combination of factors, drive species richness patterns in urban environments. Accordingly, we framed a series of models, incorporating features from these frameworks, in an attempt to evaluate their relative importance. We hypothesized that if richness patterns are associated with distance from the urban fringe, then this would support the IBT or the URG frameworks. If patch size is a dominant factor, this would support the IBT or the patch–matrix framework. Evidence supporting the importance of patch geometry, distance to nearest neighbors and matrix properties will support the patch–matrix framework. To test these hypotheses a series of non-linear regression models was constructed and the models' performance were compared. This

Table 1
Central features of the rural-urban gradient, IBT and patch–matrix frameworks which dictate species-richness patterns.

	Rural-urban gradient	IBT	Patch-matrix/landscape fragmentation
species pool source	+	+	−
directionality	+	+	−
patch size	−	+	+
patch properties (excluding size)	−	−	+
matrix properties/patch connectivity	−*	−	+

* – matrix properties, however, are indirectly considered by the location of the patch along the gradient.