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

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-rural 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.
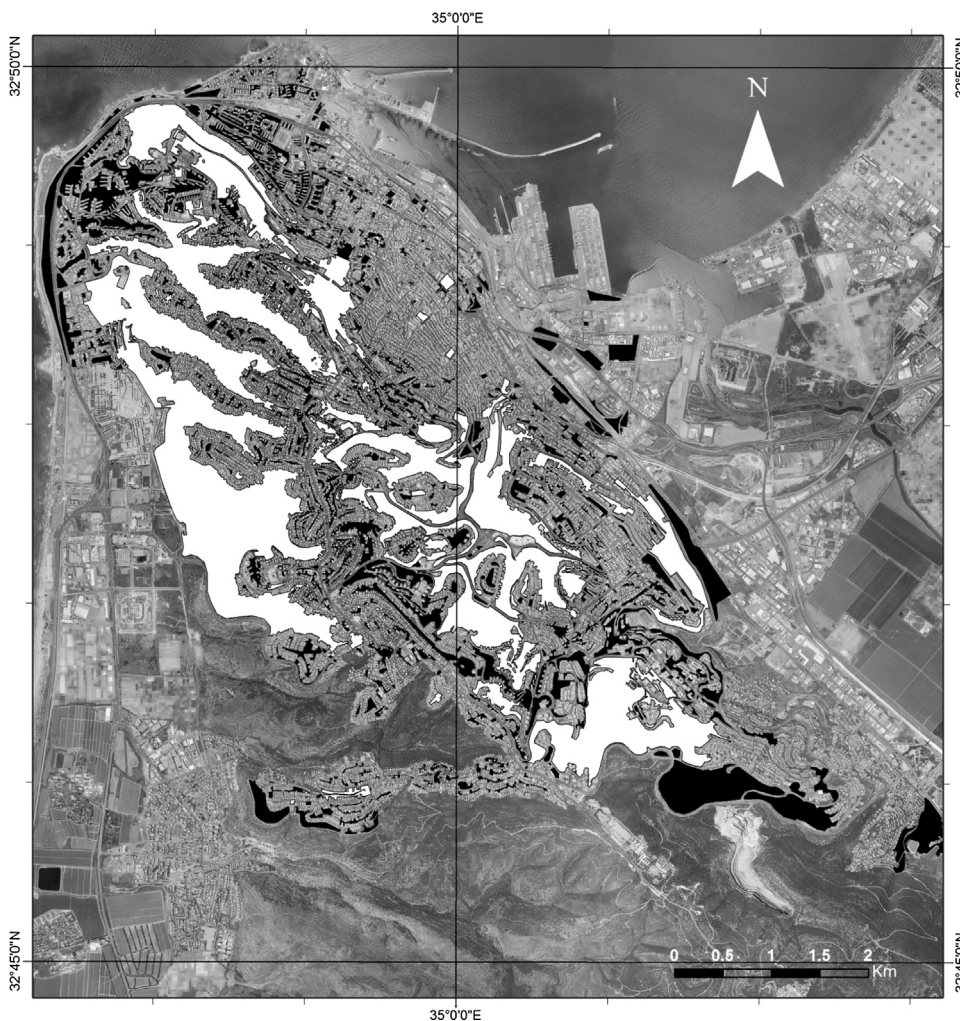
Fig. 1. Haifa and its open spaces. White polygons – sampled during the study, Black polygons-non-sampled patches.

approach follows Burnham and Anderson's (2002) model selection method by attempting to identify the model which best fits the data among a series of potentially explanatory models. Specifically, we studied only unmanaged, 'relict' open spaces, and assessed the role of patch spatial properties, and used the proportion of sealed surface around each patch as a proxy for the degree of urbanization. These variables were used to evaluate richness of native and non-native species.

2. Methods

2.1. Study area

The study was carried out in the relict open spaces of the city of Haifa. The city is located on the northern part of Mount Carmel and on the coastline of Haifa Bay, in the north-west of Israel. Mount Carmel rises to 480 m above the Mediterranean Sea (Fig. 1). Average annual rainfall varies with elevation, and is 550–800 mm. The average annual temperature is 19 °C. The majority of the soils are formed on carbonate sedimentary lithology, dominated by limestone and chalk-marls. The study was conducted in the part of the city located on the Mount Carmel ridge (64.54 km^2), where the average population density is 4102 people/km^2. Most of Haifa's remnant patches were planted with *Pinus halepensis*, *P. brutia, Eucalyptus camaldulensis* and other ornamental trees as part of the city design plan in the early 1930s and 1940s (Ben-Artzi 2004). At the turn of the 20th century, Mount Carmel was denuded of vegetation due to high intensity grazing and firewood felling. The grazing regime changed following the acquisition of the

land by settlers during the years following World War I. Haifa's western neighborhoods were built on the mountain plateau and then expanded to the steeper slopes. The streams were protected by city planners who wanted to keep them as green areas for the city's inhabitants.

For the purpose of this study classification of aerial orthophotos obtained during 2012 (RGB, 0.2 m resolution) were used to delineate Haifa's fringe, based on identification of the constructed areas line bordering the open areas at the outskirts of the city. The city is bordered to the west and southwest with large tracts of undeveloped maquis and planted pine forests, mostly in the Carmel National Park. To the east the study area was truncated by an industrial zone and by large intensively cultivated crop or fallow fields. From the open spaces listed in the city's municipal outline plan, we chose only patches of remnant vegetation—areas that have not been disturbed by development and are part of the green infrastructure of the city. Additionally, the images were classified and all areas dominated by vegetation cover and characterized with negligible sealed surface (e.g., paved paths, maintenance structures) were labeled as open space patches. Python scripting and ArcMap's Feature-Analyst (ESRI, 2013) were used for data preparation and analysis (Toger, Malkinson, Benenson, & Czamanski, 2015), and 124 m^2 was set as the lower limit of the area of identified open spaces. The area of each open-space patch and its distance from the border of the nearest neighbor was measured, as well as the distance to the urban fringe line. Patches were classified into three size categories: 0.2–1.6 ha (S), 1.6–35.5 ha (M), and > 35.5 ha (L) (Table 3); and three distance-to-fringe categories: ≤ 300 m, > 300 m–2000 m, and > 2000 m, yielding 9 size x distance classes. This definition of classes enabled us to select patches representing various size x distance combinations on a

Table 2
Habitat types recorded in the surveys.

Main vegetation structures
Slope aspect (north, south, east)
Grove of mono-specific planted trees
Flat area
Pile of construction debris
Maquis (chaparral)
Bare rock
Creek bottom
Cultivated area

Table 3
Study sites and species attributes.

	number of patches	Mean area (m^2)	Mean native species	Mean non-native species	Mean number of habitat types
Small patches	16	8792	71.1	10.2	2.8
Medium patches	17	90416	94.5	12.8	3
Large patches	8	828329	162.4	13.8	4.6

Table 4
Model List.

Model no.	Model	β_0
1	$\beta_0 area^{\beta_1}$	16.64
2	$\beta_0 [log_{10}(area)]^{\beta_1}$	0.742
3	$\beta_0 area^{\beta_1} \cdot e^{-\beta_2 \cdot log10(BD)}$	15.82
4	$\beta_0 [log_{10}(area)]^{\beta_1} \cdot e^{-\beta_2 \cdot log10(BD)}$	0.67
5	$\beta_0 \left(\frac{p}{A}\right)^{\beta_1}$	32.16
6	$\beta_0 \left(\frac{p}{A}\right)^{\beta_1} \cdot e^{-\beta_2 \cdot log10(BD)}$	19.14
7	$\beta_0 [log_{10}(area)]^{\beta_1} \cdot e^{\beta_2 BD} + \beta_3 e^{-\beta_4 NN}$	–
8	$\beta_0 Sealed25^{\beta_1}$	26.39
9	$\beta_0 \left(\frac{Area}{Sealed25}\right)^{\beta_1}$	16.67
10	$\beta_0 \left(\frac{Area}{Sealed25}\right)^{\beta_1} \cdot e^{-\beta_2 \cdot log10(BD)}$	23.74
11	$\beta_0 \left(\frac{Area}{Sealed25}\right)^{\beta_1} \cdot \#hbt^{\beta_2}$	15.35
12	$\beta_0 \left(\frac{Area}{Sealed25}\right)^{\beta_1} \cdot \#hbt^{\beta_2} \cdot e^{-\beta_3 * log10(BD)}$	15.68

stratified-random basis. Up to five open spaces were randomly chosen from each of these classes as study sites to ensure an equal sampling effort of all size–distance categories (Bastin & Thomas, 1999; Matthies, Ruter, Prasse, & Schaarschmidt, 2015). Nine habitats were identified in the 41 selected study sites, their categories are given in Table 2.

2.2. Data collection

The 41 sites were surveyed five times during the growing seasons (winter-spring) of 2011, 2013 and 2014, and all observed species were recorded. We repeated the process in order to obtain a complete representation of the plant species in each patch. Study sites were divided into dominant vegetation structures (habitat types) as they were surveyed (Table 2), by a single person throughout the duration of the study. Nomenclature of self-established native and non-native species followed Feinbrun-Dothan and Danin (1991), and nomenclature of invasive species followed (Dufour-Dror, 2012). Ornamental species were classified according to Roth Binyamini's Gardening site (http://www.ginatnoy.co.il/). Trees used for silviculture were retained in the analyses, as the vegetation had a semi-natural character, and it was not possible to distinguish between planted trees and natural occurrences.

2.3. Data analysis

We used the classified images to estimate patch size, patch perimeter, distance to the city boundary, distance to the closest neighboring patch, and the percentage of sealed area, a proxy for matrix properties, within radii of 25 m, 50 m, 75 m and 100 m around the patches. Another derivative of this analysis was area-perimeter ratio (A/P) which defines the proportion of the patch exposed to edge effect. The smaller the area, and the more irregular the perimeter, the larger is the proportion of patch exposed to these effects (Gonzalez et al., 2010; Stenhouse, 2004). The number of habitats within each patch was recorded during the field surveys. Exploratory linear regression analyses were conducted to individually identify the general relationships between the independent variables (patch size, no. habitats, distance to urban fringe, proportion of sealed area), and the dependent variables, namely: total number of species, native species, rare species and non-native species. To assess the relationship between patch size and the number of species we log-transformed patch size.

Following the exploratory analyses, a set of 13 non-linear regression

models (Table 5) was tested for the four species categories, by applying the Maximum Likelihood Estimate (MLE) approach (Burnham & Anderson, 2002). This approach entails the fit of a model to the data by numerically optimizing parameter values which minimize MLE values, and selecting the model which yields the lowest AIC value. Moreover, the models constructed enable one to assess mechanistic and functional relationships among the variables considered. The optimization was carried out using the Microsoft Excel optimization engine (Hobbs & Hilborn, 2006). The chosen optimization algorithm provides only local solutions, and lacks the functionality to search efficiently for global solutions. To overcome this problem each model was ran with several starting value combinations within the parameter space.

Three general families of models were assessed (Table 4). Models based on the analysis of patch size (Models 1–4), models based on area to perimeter ratio (A/P, Models 5–7), and models based on some combination of area and the proportion of sealed surface (Models 9–13). Each of the models incorporates to various degrees attributes associated with the three frameworks (URG, IBT, PM). Models 1 and 2 assess the relationships between patch size and the number of species. Models 3 and 4 add the effect of distance to the city boundary, and models 5–6 assess the role of the A/P. Model 7 incorporates the combined effects of patch size, distance to city boundary and distance to the nearest neighboring patch. Models 8–12 evaluate the effect of the proportion of the sealed surface around each patch, essentially representing the degree of urbanization in which the patch is embedded in. As the scale of 25 m yielded the best fit in the exploratory analysis (see Results), it was the only sealed surface predictor used. Model 8 is the simplest with respect to sealed surface, and Model 9 introduces the effect of patch size. The set of models (10–12) incorporate the ratio between the amount of sealed surface surrounding each patch standardized by patch size, and additional independent variables. Higher ratios suggest a stronger effect per patch unit area. Model 10 adds the effects of distance to city boundary, Model 11 adds to Model 9 the effect of the number of habitats found within each patch. Model 12 is similar to Model 11, and accounts for the number of habitats, as well as the distance to the city boundary. The proportion of sealed surface and patch properties represent functional relationships between these variables and species richness properties. The negative exponential function chosen to model the effects of distance from the city boundary or nearest neighboring patch represents a mechanistic relationship. This function is commonly used to model seed dispersal (Hovestadt, Bonte, Dytham, & Poethke, 2012), as it is assumed that the proportion of successful dispersers is constant over every distance unit traveled.

The model selection approach facilitates comparison among models,

and selecting the model and parameter values which best fit the data. Further, it is possible to calculate the Akaike weight of each model, which ascribes the relative likelihood of each of the tested models (Wagenmakers & Farrell, 2004). A model's weight is calculated by measuring the distance of the ith model AIC value in relation to the best fit model:

$$L(\Delta ri) = e^{-0.5*(AICi - \min(AIC))} \tag{1}$$

The relative weight of each model, i.e., the relative likelihood of obtaining the model from among the available models, may be assessed by:

$$Wr = \frac{L(\Delta ri)}{\sum_i^r L(\Delta ri)}. \tag{2}$$

Wr ranges from 0 to 1, and provides a means to compare the likelihood of a model. The higher the *Wr* of a model, the higher is the relative support for the model. The quality of fit of models cannot be compared among the various classes of analysis (total, native, non-native) using the MLE approach. However, within each class, comparisons among the fit of the models can be made, and *Wr* provides the means to compare the relative fit of the models with respect to a given dependent variable. I.e., a comparison of a specific model fit (AIC value) between the classes, e.g., Model 1 of the native species and Model 1 of the non-native species, is meaningless. Comparing the ranking of the models, however, is a means of assessing the relative importance of the various independent variables and their functional relationships. For each of the four species groups, the three top fitted models are presented.

3. Results

A total of 392 species of vascular plants belonging to 87 families were recorded in the 41 study sites. Of these, 53 species were non-native to the region (13.7%), comprising 43 invasive species, agriculture and ornamental, and 10 non-Mediterranean planted species. The non-native flora was dominated by species of neotropical origin. The highest number of species recorded in a single patch was 261, found in a 48.7-ha patch located in the middle of the urban area. Seven different sub-habitat types were found in this patch. The lowest number of species, 34, was found in a homogeneous patch, consisting of a single habitat type 14.2 ha 'flat area' (Table S1). The total mean number of species (native and non-native) in the small patches was 81, in the medium size patches it was 107, and in the large patches it was 176 (Table 3).

Of the observed species, 19 were the most abundant, with frequencies higher than 80%, most of which were woody. Several non-native species, such as *Oxalis pes-caprae* and *Dodonaea viscosa* were also observed at high frequencies, 93% and 78% respectively. Of the native species, three – *Pistacia lentiscus, Sonchus oleraceus,* and *Urospermum picroides* – were found in all 41 sites. The least abundant species – those that appeared only in one to three sites of the study sites – were either listed in the Israeli Red List of species, or were non-native.

The relationship between the total number of species and patch size was significant ($R^2 = 0.34$, $p < 0.001$), and so was the relationship between the number of native species and patch size ($R^2 = 0.32$, $p = 0.0001$). This relationship may be observed in Map S1, where the large patches are characterized by high total species counts. This relationship also holds for the rare species (Map S3). In contrast, the relationship between non-native species and patch size was not significant ($R^2 = 0.08$, $p = 0.064$, see Map S2). A linear regression assessing the relationship between the number of species and distance from the city boundary was found to be insignificant for all the species classes (Fig. 2). The distance from the patch to the urban area fringe-line was also examined, but did not yield any significant relationships for any of the vegetation classes.

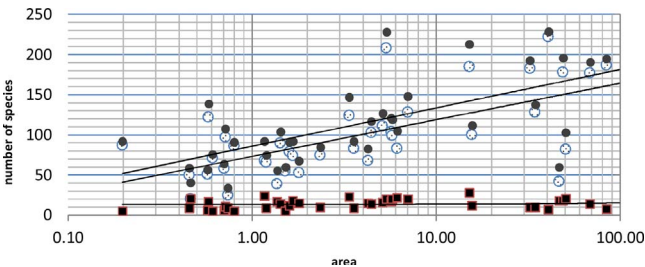The analyses of the relationship between the number of species and

Fig. 2. The relationship between patch size and species richness of the three vegetation classes, full-squares: number of non-local species found in a patch, full-circles: total species, empty-circles: local species. Note log(area) scale.
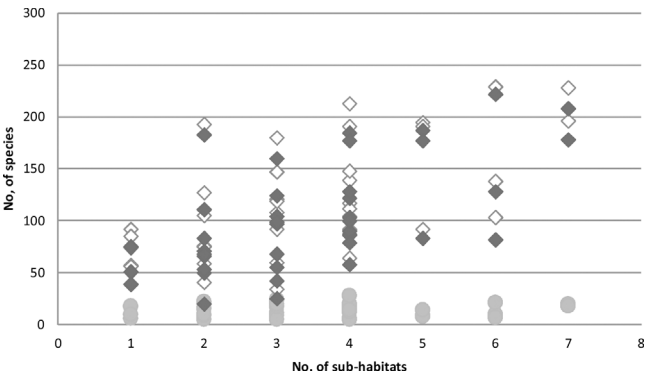

Fig. 3. The relationship between habitat heterogeneity and species richness of the three vegetation classes. Total species (empty-square), native species (full-square) and non-native species (full-circle). Total species richness ($R^2 = 0.45$), local species ($R^2 = 0.41$), non-native species ($R^2 = 0.0017$).

the number of habitat types within the patches exhibited similar patterns to those of the correlations with patch size. The total number of species ($R^2 = 0.32$, $p < 0.001$) and the number of native species ($R^2 = 0.30$, $p < 0.001$) were found to be correlated with the number of habitats, whereas the number of non-native species was found not to be correlated ($R^2 = 0.08$, $p = 0.075$) (Fig. 3).

The last exploratory set of the linear regression analyses evaluated the relationship between the number of native species and the proportion of sealed surface surrounding each patch. The analysis was conducted at four spatial scales of increasing buffer distances around each patch. Buffer rings of 25 m, 50 m, 75 m and 100 m were constructed and regressed against the number of native species. The results indicate that the 25 m buffer was most strongly correlated with the number of native species, and that the relationship weakened as the scale of the buffer ring increased, becoming insignificant at 100 m (Table 5). The relationship was negative at all scales, indicating that the number of species declined with increased surface sealing.

Considering non-native plant richness patterns (Table 6c), Model 5, which considered only the A/P ratio, best explained the data. The Akaike weight of Model 5 was $Wr = 0.448$, indicating that the other models, which were based on alternative processes, had little explanatory power. Adding distance to city boundary weakened the model (Model 6), but this class of models still out-performed the models which were based on patch size (Models 1–4), and on the proportion of

Table 5
R^2 relationship between buffer scale and species richness.

Buffer scale (m)	Adjusted R^2	p value
25	0.69	0.8×10^{-12}
50	0.66	0.6×10^{-11}
75	0.6	0.13×10^{-9}
100	-0.015	0.53

Table 6
MSE and AIC values of the different vegetation categories: a) all species, b) native species, c) non-native species, Rare species. BD – distance of patch to urban fringe-line, NN – distance to nearest neighbor, #hbt – number of habitats in a patch, Sealed25 – proportion of sealed surface in a buffer 25 m around the patch. * – no convergence of the model to an optimal solution.

a) All species

Model no.	Model	β_0	β_1	β_2	β_3	MLE	AIC	Wr
11	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}\cdot\#hbt^{\beta_2}$	15.35	0.14	0.188	–	−209.18	424.36	0.573
12	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}\cdot\#hbt^{\beta_2}\cdot e^{-\beta_3*log10(BD)}$	15.68	0.15	0.13	−0.028	−209.35	426.69	0.178
9	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}$	16.67	0.15	–	–	−211.97	427.94	0.095

b) Native species

Model no.	Model	β_0	β_1	β_2	β_3	β_3	MLE	AIC	Wr
11	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}\cdot\#hbt^{\beta_2}$	12.55	0.166	0.0909	–	–	−206.11	418.23	0.405
9	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}$	13.20	0.171		–	–	−207.49	418.99	0.277
12	$\beta_0\left(\frac{Area}{Sealed25}\right)^{\beta_1}\cdot\#hbt^{\beta_2}\cdot e^{-\beta_3*log10(BD)}$	12.96	0.163	0.094	$-9.99*10^{-5}$	–	−206.10	420.20	0.151

c) Non-native species

Model no.	Model	β_0	β_1	β_2	β_3	β_3	MLE	AIC	Wr
5	$\beta_0\left(\frac{P}{A}\right)^{\beta_1}$	2.55	−0.525		–	–	−154.37	312.74	0.448
6	$\beta_0\left(\frac{P}{A}\right)^{\beta_1}\cdot e^{-\beta_2\cdot log10(BD)}$	2.94	−0.51	−0.04	–	–	−154.18	314.36	0.198
4	$\beta_0[log_{10}(area)]^{\beta_1}\cdot e^{-\beta_2\cdot log10(BD)}$	1.058	$6.47*10^{-5}$	−0.752	–	–	−155.35	316.69	0.062

d) Rare species

Model no.	Model	β_0	β_1	β_2	β_3	β_3	MLE	AIC	Wr
5	$\beta_0\left(\frac{P}{A}\right)^{\beta_1}$	2.55	−0.525		–	–	−154.37	312.74	0.448
6	$\beta_0\left(\frac{P}{A}\right)^{\beta_1}\cdot e^{-\beta_2\cdot log10(BD)}$	2.94	−0.51	−0.04	–	–	−154.18	314.36	0.198
4	$\beta_0[log_{10}(area)]^{\beta_1}\cdot e^{-\beta_2\cdot log10(BD)}$	1.058	$6.47*10^{-5}$	−0.752	–	–	−155.35	316.69	0.062

sealed surface (Models 9–13).

Model 11, which considered the proportion of sealed surface, patch size and the number of habitats, best explained the distribution of the native species (Table 6b). In general, this family of models, based on the relationship of richness patterns with sealed surface and patch size, outperformed the two other families of models. In this case, the Akaike weight of Model 11 was *Wr = 0.40*, indicating the dominance of this model. Model 10, which accounted only for sealed surface and patch size, obtained a *Wr = 0.27*, and Model 12, which incorporated the effects of distance from the city boundary, had the third highest Akaike weight value (*Wr = 0.15*). The area/sealed surface ratio contributed highly to the performance of this set of models; and the number of habitats marginally added to the improvement of their fit. The total number of species exhibited similar trends to those of the native species (Table 6a), due to the dominance of the native species in the observations. As in the native species case, the best model explaining the total number of species in each patch was Model 11, with *Wr = 0.57*. Again, once the area/sealed surface ratio was introduced, this family of models

outperformed the others. Model 12, which accounted for the number of habitats, as well as the distance from the city boundary, had the second-best fit. The sequence of models best explaining species richness patterns of the rare species (Table 6d) was identical to the set of models explaining the richness patterns of the total number of species (Models 11, 12, 9 in the respective order).

4. Discussion

With the increasing prevalence of urban areas and urbanization processes, interest has been devoted to better understand the drivers dictating species richness and diversity patterns in disturbed environments (Tscharntke et al., 2012). McDonnell and Hahs (2013) point out the need to address more explicit and question-driven properties of urban environments to gain better understanding of the mechanisms generating the observed response patterns. Many studies investigate the role of the driving factors independently, e.g., the rural–urban gradient, concepts and derivatives of the theory of Island Biogeography, patch-

matrix properties, and others. In this study we investigated the role of attributes of the various frameworks, and applied semi-mechanistic considerations to evaluate the non-linear relationships between urban landscape properties and vegetation richness patterns. Richness was assessed in Haifa's non-managed open spaces, i.e., in abandoned, relict or uncultivated patches.

Initially, we examined the linear relationships between various patch properties and richness properties. Similarly to observations in other studies, patch size was a significant factor explaining richness patterns of native species and the total number of species (Dunstan & Johnson, 2006; Honnay, Endels, Vereecken, & Hermy, 1999; Matthies et al., 2015; Munguía-Rosas & Montiel, 2014). Due to the dominance of the proportion of native species present in the patches, the total number of species and the number of native species exhibit similar relationships throughout the various analyses. In contrast, the response of non-native species does not exhibit similar relationships. With respect to the distance of patches from the city boundary, the results do not conform to those commonly reported in the literature. No correlation was found between distance and species richness patterns, in contrast to results reported by Godefroi and Koedam (2003). This might be a consequence of the fragmented structure of Haifa's built-up area, and the penetration of finger-like open spaces into the urban fabric of the city. Native and total species richness were also found to be positively correlated with habitat diversity. This observation agrees with other reported studies. For example, Deutschewitz, Lausce, Kuhn, and Klotz (2003) and Wania, Kuhn, and Klotz (2006) also found similar relationships between habitat diversity and species richness. The last set of exploratory analyses evaluated the relationship between the proportion of sealed surface around each open area patch and species richness patterns, thus evaluating the role of the degree of urbanization. Of the exploratory analyses, the proportion of sealed surface was the best predictor for species richness, explaining almost 70% of the variation when considering a buffer at a scale of 25 m (Table 4). To date, few studies have investigated the relationship between the proportion of sealed surface and species richness properties at such high spatial resolutions. Albrecht and Haider (2013) found a similar relationship when evaluating sealed surface proportion at a scale of 1 km^2. They suggest that increased sealed surface produces higher thermal stress, reduced habitat availability and increased fragmentation, which result in lower numbers of species. This may not be the case in our study, as sealed surface was measured at higher spatial resolutions, in a buffer surrounding each of the patches. Accordingly, we suggest that in relation to the present study, increased sealed surface i.e., urbanization intensity, may reduce patch connectivity, resulting in lower richness values.

Following the exploratory analyses, we compared various non-linear models, in light of the URG, IBT and PM frameworks, identifying which combination of drivers best explained the observed data. The results do not provide a clear-cut distinction among them. Similar patterns were observed for the rare, native and total number of species. The top models explaining the distributions of non-native species were starkly different from the other groups of species, reflecting on different mechanisms dictating their patterns, namely patch geometry. Assessing combined and interactive effects of the various framework attributes indicated that in the case of total, native and rare native species numbers the interactive effects of matrix properties and patch size (Model 9) laid the foundation for the models best explaining richness patterns. This model suggests that the proportion of sealed surface buffering the patch, per unit area of the patch, is an important factor. The best model in these three categories was Model 11, which also incorporated within habitat heterogeneity, i.e., the number of habitat types, pointing to the importance of habitat diversity in increasing species numbers (Garden, McAlpine, & Possingham, 2010; Matthews, Cottee-Jones, & Whittaker, 2014; Rudd, Vala, & Schaefer, 2002). It thus seems that the PM framework weighs heavily in driving the observed richness patterns, and that rare species respond to these drivers similarly to all species combined.

This highlights the importance of the degree of fragmentation and urbanization in dictating species richness, as is highlighted by many studies (Clark, Reed, & Chew, 2007; Dolan, Moore, & Stephens, 2011; Lee, Ding, Hsu, & Geng, 2004; McKinney, 2008). Moreover, this also reflects the quality and degree of resistance of the landscape matrix as a factor influencing richness. Additionally, these results point to the importance of interactive effects of urbanization with patch size. The smaller the patch, the greater are the effects. The patch selection processes ensured that we studied all patch size classes at all distance combinations from the city boundary, and thus our results were not confounded by a skewed selection of the distribution distances or sizes. When considering the rare and the total number of species, the second-best model was the one which also accounted for the distance from the city's boundary line (Model 12). This points to the importance of directionality, attributes of the rural–urban gradient and IBT frameworks. Considering only native species, the second-best model was Model 9.

In contrast to the rare, native and total number of species, the richness patterns of non-native species were best explained by patch geometry attributes (P/A) – Model 5 ($Wr = 0.965$). The next best model was model 6, which also accounts for the distance from the city boundary. Intuitively, this value manifests the edge effect. Generally speaking, edges result in increased species richness, attributed to spill-over from adjacent habitats, increased habitat heterogeneity at the edges, or increased resource availability (Ries & Sisk, 2004), Thus we hypothesized that the higher the ratio, i.e., the higher perimeter per unit area, the higher the number of non-native species that will be observed. This is assuming higher spill-over rates from neighboring cultivated parks and gardens, and increased opportunities for this species group to penetrate the patches. In contrast to expectations, however, the fit obtained was reciprocal to the expected one. In our case, there is a negative correlation ($\beta_1 = -0.525$) between increasing perimeter to area unit and species richness. A closer examination of the data reveals that in the case of Haifa, the A/P ratio is positively and strongly correlated with the proportion of sealed surface around the patch ($p < 0.001$, $R^2 = 0.58$). This suggests an indirect relationship between high A/P ratios, which are associated with high sealed surface, and a higher amount of non-native species. Higher sealed surface is commonly interpreted to be indicative of more intensive urbanization, and hence the higher number of non-native species.

Kopel, Malkinson, and Wittenberg (2015) previously studied the properties of the vegetation communities of Haifa, with respect to age and time since construction disturbance at edges of the patches. They found that time has a degradation effect on the species diversity, and older sites were populated by a higher number of exotic species than the younger ones. Likewise, it may be hypothesized that given enough time, time-delayed colonization will take place in the urban open space patches of the study. In a sense, this is the reciprocal process to the 'extinction debt', which refers to time-delayed extinction in patches after they have been fragmented and isolated within the landscape (Tilman et al., 1994; Tilman, 1994).

5. Conclusions

No one single set of variables described richness patterns well, when exploring the patterns of native species and non-native species richness, nor did the explanatory variables fall exclusively into one of the frameworks investigated. The preliminary regression analysis highlighted the significance of the proportion of sealed surface in dictating richness patterns, i.e., the role of the matrix. Thus, the results of this study suggest that the dominant drivers explaining species-richness patterns are associated with the PM framework. However, distance from the city boundary, an attribute of the URG and the IBT frameworks, is also important, but to a lesser extent. Seemingly, this suggests that these frameworks complement each other. The results should be interpreted in light of the morphology of the city. Haifa belongs to a class of cities where fingers of natural areas penetrate into the city. In contrast to

other cities, Haifa lacks a well-defined urban structure. McDonnell and Hahs' (2008) review indicates that a peak in richness values at the fringe of cities is found in many studies, highlighting the importance of directionality. Such a peak is clearly an emergent property of the URG framework. Perhaps the absence of such a peak could be explained by the morphologies of cities, as in the case of the city of Haifa which lacks a traditional core-fringe structure. Nonetheless, some resemblance to other, traditionally structured, cities exists. Matthies et al. (2013) compared between Hannover, a traditional European city, and Haifa. In both cities the proportion of sealed surfaces were similar – 53% in Hannover and 51% in Haifa. Further, in both cities patch area was an important predictive driver, whereas distance from city edge was not. Nonetheless, given the results of the current study, we suggest that directionality be incorporated into PM models when considering species richness patterns in urban landscapes, particularly when considering the location of the patch in relation to the city's border. We note, however, that it is likely that the findings of the study are more relevant to taxa such as plants, which are passive dispersers. As such, individuals do not select movement direction or distance, and seeds are randomly dispersed, which is a fundamental assumption of biogeographic theories (Hubbell, 2001).

Plant species richness in the urban environments depends on the city's green infrastructure quality. This is comprised from the quality of each individual patch, and the matrix properties, as expressed by the proportion of sealed surface in this study. The analysis revealed that native plant species were directly associated in a negative manner with increasing urbanization. In contrast, non-native species richness patterns were positively associated, in an indirect manner, with increasing urbanization.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2017.09.021.

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