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Exploring the Urban Forest Herb Layer: A Patch-Size Perspective

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Introduction

As urbanization accelerates globally, with a projected 68% of the world's population residing in cities by 2050 (United Nations, 2018), human development continues to transform the natural landscape. Native forests are increasingly fragmented and overlaid with impermeable surfaces. Remnant natural areas within urban settings play a vital role in delivering ecosystem services and ameliorating some of the effects of anthropogenic climate change (Luck and Wu, 2002). These patches of forest grow in significance as cities expand around them (Hansen & Pauleit, 2014). Understanding these unique facets of the urban landscape is critical to maintaining and improving the vitality of cities. While significant effort and resources are dedicated to urban forests, we still possess a limited understanding of their communities and dynamics (Alberti 2005). For instance, the understory and herb layer is an essential part of forest ecology. The herbaceous community of rural forests can have a profound impact on the canopy, such as through its capability to filter the composition of regenerating forests through competition for soil nutrients (Lyon & Sharpe 2003) and light (Horsley 1993). The outcome of this competition on tree seedlings is species specific (George & Bazzaz 2003). The herbaceous layer can have other broad impacts on rural forest systems, through its outsized contribution to net primary productivity and carbon sequestration (Muller 1978, Neufeld & Young 2003), and its similarly disproportionate role in nutrient cycling (Muller 2003). Despite the important role that understory communities play in rural forests, there is little published literature on the ecology of the understory layer in urban forests outside of the realm of invasive species control.

The herb layer is understudied generally (Spicer et al. 2022), and there are even fewer studies that investigate herbs in urban forests. Notably, there are several rural to urban gradient studies that incorporate herbs, particularly along riparian corridors (Moffatt et al. 2004, Schwoertzig et al. 2016), roadways (Cochard et al. 2016), and within vacant lots (Blouin et al. 2019), though most of these examples are not explicitly focused on forested areas. While these types of studies characterizing plant communities along urban to rural or land use intensity gradients are inherently valuable for understanding how urban ecosystems broadly differ from rural ones, urban landscapes and their forests are

54   extraordinarily heterogeneous. They are split by development into remnant patches of various sizes, and

55   restoration or lot abandonment can allow previously developed areas to become regenerating forest

56   patches. Fragmentation such as this generates a unique matrix of community types which experience

57   different disturbance regimes (Pickett et al. 2001), degrees of edge effect (Murcia 1995), and limitations

58   on seed dispersal (Chazdon 2008).

59   There are few, if any, studies which investigate patterns of herb and understory diversity within

60   the context of urban forest patch size and land use history. Comparative research done in rural forests

61   likely does not describe the distinct communities found in urban forests, particularly when urban forests

62   possess such a level of heterogeneity even on local scales, with frequent anthropogenic disturbance

63   (Grimm et al. 2000) and greater pressure from invasive species (Cadotte et al. 2017). Previous research

64   (Doroski et al. 2022) demonstrates that the woody communities of urban forests may be more intact than

65   typically assumed, raising the possibility that the same holds true for the herbaceous layer. Any

66   management approach is contingent on understanding how various layers of the forest interact with one

67   another, and in urban forests, most questions regarding the herbaceous community remain important

68   knowledge gaps.

69   This study builds upon previous work done in New Haven's urban forest to further explore the

70   relationship between forest patch size and plant communities. The theory of island biogeography has been

71   used in previous research of urban forests to predict distribution of invasive plant species (Vidra and

72   Shear, 2008), and the richness and diversity of vascular plant species (Godefroid and Koedam, 2003).

73   Applying this framework to herb communities and their linkages with the mid and overstory across the

74   urban matrix can further our understanding of urban forests as ecological systems by revealing trends in

75   urban herbaceous communities in relation to patch size and anthropogenic disturbance, and through

76   identifying community features that may inform management of these crucial forested spaces.

77   In this study, we aimed to understand how understory plant communities (and their respective

78   functional groups) respond to patch size, land use history, disturbance, and woody plant communities

79   across an urbanized area. We evaluated the richness and diversity of understory vegetation between

80 different size classes of park. At a finer scale, we aimed to investigate changes in understory diversity and

81 community composition in response to a suite of local site features, in addition to the wider context of

82 patch size. We hypothesized that we would observe greater species abundance nearer to edges, as well as

83 a greater proportion of introduced species both near edges and throughout smaller patches. We also

84 expected that a higher degree of anthropogenic disturbance would be associated with the proportion of

85 introduced species. We investigated the relationship of the mid and overstory to the understory layer,

86 expecting to observe suppressed total abundance and richness of understory species under fuller canopy

87 cover (i.e greater basal area). Finally, we investigated the distribution and importance of several

88 introduced species of special interest, and their impacts on native herbaceous species.

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90 2.   **Methods:**

91 *Site Description:*

92   New Haven is a city in southern Connecticut on the northern shore of the Long Island Sound. The

93 city covers 52.1 km^2, and currently houses a population of more than 135,000 people. New Haven

94 experiences a mean annual rainfall of 111.99 cm, and the average July and January temperatures are 24.0

95 and 0.8C, respectively (NOAA, 2018). It has a higher average canopy cover than most similarly sized

96 cities, at about 38% (Pelletier & O'Neil-Dunne, 2009).

97 The geology of the area is primarily glacial in origin, and it is characterized by glacial erratics, drumlins,

98 and trap rock ridges (Flint 1965), including the notable trap rock ridges of East and West Rock. However,

99 as New Haven is a built-up area, large portions are underlain with anthropogenic soil types, in addition to

100 its native inceptisols that are mostly Holyoke, Cheshire, and Hollis series soils, which result from

101 sandstone ablation till (NRCS, 2019). This study used plots from parks across New Haven and the

102 surrounding metropolitan area which were first established in 2018 (Doroski et al. 2019). We selected

103 plots for use in this study which occurred in parks with a forested area greater than 2 ha. A summary of

104 each park can be found in SI Table 1.

105 *Field Methods/procedures:*

106   We sampled 91 plots across 15 forested parks, though 1 patch (4 plots) were omitted from

107   analysis, leaving 87 plots across 14 parks (Figure 1). The plots were established in 2018 using a random

108   starting point and a sampling fraction of 1/10, so that the number of plots in each park was proportional to

109   the forested area, to capture heterogeneity in vegetation (Doroski et al 2019). When plots were

110   established, the centers were marked with painted iron rebar. We located the general area of the centers of

111   each plot using GPS coordinates in the mobile application Avenza, and then searched for the rebar. When

112   the rebar was no longer present, we used photos taken of each plot to find the approximate center. Once

113   we found the center, we followed the stratified sampling procedure used in Doroski et al 2019, which was

114   adapted from the Natural Areas Conservancy plots in New York City (Figure 2). We measured the

115   overstory trees greater than 5 cm DBH within a 10m radius, and midstory trees less than 5 cm in a 5m

116   radius. We identified each tree (including standing dead snags) to species when possible, or otherwise to

117   the genus.

118   For understory, we established 8 1m^2 subplots to uniformly sample the larger site. For each

119   cardinal direction, the bottom left corner of the subplots were situated 5m from the center, with the upper

120   left corner facing away from the center. For each ordinal direction, the subplot was situated extending

121   diagonally, with the innermost corner 7.5m from the center point. Within each understory subplot, we

122   assessed by eye the total ground cover of vegetation, live wood, coarse woody debris, leaf litter, soil, bare

123   rock, dumping (such as litter or landscaping waste), and impervious surfaces. For this measurement, totals

124   always equaled 100%. We identified and measured the percent cover of each species of plant present in

125   the plot. For most woody plants, we also counted the number of individuals and assigned a categorical

126   height class. Plants that were leaning, pinned, or fallen over were classified as their current height and not

127   their height if they were upright. Not all woody plants were tallied into height classes. Species of vines

128   and brambles for which individuals could be difficult to distinguish were omitted from height class

129   counts, but percent cover was still recorded (see SI table 2 for a list of species observed). The sum of

130   percent cover of each species of plant could exceed 100 within one subplot to fully account for species

131   which overlapped each other.

132   It was occasionally difficult to identify species of very small woody germinants, and nondescript,

133   out of flowering season herbs or graminoids. Some groups were routinely identified to a higher

134   taxonomic level (e.g. *Carex, Smilax, Vitis*), but in most cases, the narrowest identification possible was

135   made, often to genus, but occasionally higher (in the case of *Poaceae*). Percent cover of bryophytes was

136   typically recorded as a plant "species" (moss), but ultimately removed from analyses. We retained

137   *Dendrolycopodium obscurum* (flat-branched tree clubmoss), since it was a specific identifiable species

138   with a higher amount of structure. We did not record the occurrence of lichens on rock surfaces.

139   Finally, we measured the level of various forms of disturbance at each site, including cover of

140   trails, paths, impervious surfaces, and dumping, as well as signs of fire or hydrology. These

141   measurements were taken as a percentage of cover for the entire $314.16m^2$ site. For other indicators of

142   disturbance, such as cut stumps, and windthrown trees, we counted the number of each in the site. We had

143   one binary form of disturbance, for the presence or absence of signs of white-tail deer. However, white-

144   tail deer are extremely abundant in even small forest patches in the area, and we believe that nearly all

145   sites were impacted by them, regardless of obvious signs.

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147   *Statistical Analysis*

148   From our data, we built an understory species matrix for use in analyses, and an associated set of

149   environmental characteristics, in addition to a complete list of observed species, their nativity status in

150   Northeastern America, and their functional groups (Tree sapling, shrub, vine, herb, and graminoid). We

151   ultimately removed 4 plots from this dataset, constituting all of the plots from one park, due to concerns

152   about management activities in the park (evidence of targeted removal of trees and introduced species,

153   and landscaping).

154   Analyses were conducted using the statistical freeware R (version 3.6.3**;** Bates et al. 2017; R Core

155   Development Team, 2018). We used Vegan and BiodiversityR to construct species accumulation curves

156   and to calculate chao estimates, diversity, species richness, abundance, and evenness for different growth

157   forms, plant native status, and park size classes.

158   We built linear models to assess the relationship between these diversity measures and site

159   characteristics (Forested area size, distance of a plot to an edge, and basal area of overstory trees). We

160   used hierarchical, linear mixed-effects models for this set of analyses to account for potential spatial

161   autocorrelation associated with park-level characteristics. Specifically, we assumed a common slope for

162   the random effects and included 'park' to represent different intercepts. We included interior or edge

163   status of plots as a binary (0=interior and 1=edge) predictor, and included basal area of overstory trees,

164   total forested patch size, and an index generated from anthropogenic forms of disturbance as continuous

165   predictors. To further explore trends in understory diversity, we selected abundant introduced species of

166   interest to use as predictors of native herb diversity measures in similar linear models. To permit

167   comparison of the effect sizes of the predictor terms in each model, predictor variables were standardized

168   by centering (the binary predictor) and by dividing by two standard deviations (the continuous predictor),

169   following Gelman (2008).

170   We note that we did not use model selection nor rely on statistical significance and multivariate

171   analyses for our causal inference. Instead, we relied primarily on evaluating standardized coefficient

172   estimates (i.e., conditional effect sizes) considering published evidence of edge effect and patch size on

173   species diversity. We report p and R^2 values in our tables, given their value in indicating the precision of

174   effect size estimates, but in the text focus on coefficient estimates.

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176   **3.   Results**

177   We measured 165 species of plants in the understory across 87 plots. A species accumulation

178   curve suggests that effort was sufficient to get a comprehensive sampling of species present (Fig. 3). To

179   assess the diversity of understory plants across the city, we calculated the Shannon diversity index,

180   richness, abundance, and evenness (Table 1). We calculated these same measures for subsets of the full

181   dataset, including park size, and edge or interior status of plots, as well as plant nativity and different

182   plant functional groups (tree, shrub, herb, and vine). Small parks demonstrated a marginally higher mean

183   Shannon diversity and richness, and considerably higher understory abundance than large parks. Both size

184   classes showed similar evenness. Edge plots show larger Shannon diversity, abundance, richness, and

185   evenness than interior plots. Native species had a much greater Shannon diversity, richness, and evenness

186   than introduced species, which had a slightly higher mean abundance. Of the plant functional groups,

187   herbs had the greatest Shannon diversity and richness, while shrubs and vines were the most abundant.

188   Trees had the greatest evenness.

189   Total understory diversity, abundance, richness, or evenness were not well explained by

190   environmental characteristics. Some variables were statistically significant, but the overall ability of the

191   models to fully capture and explain the complexity of understory diversity was limited. The R-squared

192   values, which reflect how well a model fits the observed data, were relatively low. Despite this general

193   trend, there were several relationships of note, particularly in regard to the basal area of overstory trees,

194   which had a negative effect on abundance and richness of herb (-27.79 ± 13.87 and 1.4 ± 0.5,

195   respectively) and vine species (-45.15 ± 19.71 and -0.65 ± 0.37, respectively), as well as on introduced

196   plants as a whole. The index of anthropogenic disturbance had a large effect on the abundance of herb

197   species (-27.91 ± 15.11) and the richness of vine species (-0.74 ± 0.4), but not on the diversity measures

198   of introduced species specifically.

199   The proportion of introduced species present in the community was significantly related to the

200   edge or interior status of a plot, the size of a park, and signs of anthropogenic disturbance, when these

201   variables were individually assessed with a t-test (p=0.013, <0.001, 0.009, respectively). When tested

202   together in a linear model, the size of the park was the most important for increasing the proportion of

203   introduced species (0.19 ± 0.06), where smaller parks had a larger proportion. Importantly, however, the

204   total abundance of native plants in the understory had no relationship to that of introduced plants (p=

205   0.24). Plant functional groups responded to these variables to different extents. T-tests for each variable

206   were highly significant for the proportion of introduced herbs and the proportion of introduced shrubs. On

207   the other hand, the only variable significant for the proportion of introduced vines was disturbance (p=

208   0.02), and none were significant for tree seedlings. When variables were assessed together in a linear

209   model for each functional group, only the proportion of introduced shrubs was well explained by the plot

210   variables. Anthropogenic disturbance was the most important, increasing the proportion of nonnative

211   shrubs (0.27 ± 0.11), followed by the park size class (0.18 ± 0.09).

212   Rank abundance plots (Fig. 4) demonstrate that total understory cover across the city was heavily

213   driven by several of the most abundant species. The species observed with the greatest abundance was

214   multiflora rose (*Rosa multiflora*) followed by winged euonymus (*Euonymus alatus)*, greenbriar (*Smilax*

215   *spp.*) and common ivy (*Hedera helix*). Notably, the high abundance of some species was driven

216   overwhelmingly by just a few sites. For instance, the most abundant species, multiflora rose, was present

217   in 30 plots, but a full 90% of its abundance is attributable to 10 plots, and another abundant introduced

218   species, common ivy, occurred in 14 plots, but 90% of its abundance was due to just three. One native

219   herb species, wild sarsaparilla (*Aralia nudicaulis*), owes 86% of its abundance to a single plot. Many of

220   the most abundant native species in the understory are also widespread, i.e. they have a less skewed

221   distribution of their abundance. However, some introduced species, namely oriental bittersweet (*Celastrus*

222   *orbiculatus)* and winged euonymus, also follow this pattern (Fig. 5).

223   The communities of large and small parks differed, as did the communities of plots with evidence

224   of anthropogenic disturbance compared to those without. The presentation of the communities of different

225   understory functional groups was complex. Notably, the shrub communities of disturbed plots and small

226   parks resemble each other closely in regards to the most abundant shrub species of each respective group

227   (namely, multiflora rose, winged euonymus, and mapleleaf viburnum (*Viburnum acerifolium*). Large

228   parks share high shrub cover of winged euonymus and mapleleaf viburnum, but multiflora rose is very

229   rare by comparison. Large parks also had higher abundance of Japanese barberry (*Berberis thunbergii)*

230   and lowbush blueberry (*Vaccinium angustifolium*), which are both mostly associated with disturbed sites,

231   but were very rare in small parks. All but one species of vine were found in disturbed sites, and most

232   vines were more abundant in disturbed sites, except for common ivy, which was also almost exclusively

233   found in small parks. As such, the undisturbed plots of small parks contained the largest amount of

234   common ivy. Like the ivy, there are a few other individual species that drive much of the difference

235   between large and small parks. For instance, Japanese knotweed (*Polygonum cuspidatum*), the most

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236   abundant herb in small parks (due partially to its large size), is entirely absent from large parks, and garlic

237   mustard, the second most abundant in small parks, is relatively rare in large parks. Other herb species

238   which are fairly abundant in large parks are comparatively rare or absent in small parks, such as New

239   York fern (*Thelypteris noveboracensis*), Hay-scented fern (*Dennstaedtia punctilobula*) and Japanese

240   stiltgrass (*Microstegium vimineum*). There are a number of rare herb species found in low abundance in

241   just one large park plot. There were many more species of herbs in disturbed sites, and in greater

242   abundance, across both park size classes. Despite the differences in large and small parks, some herbs

243   were found in abundance across both, including white wood aster (*Eurybia divaricata*), Solomon's seal

244   (*Polygonatum sp.*), and goldenrod (*Solidago spp.*). See Tables 3, 4 and 5, for full summaries of herb,

245   vine, and shrub species abundance across size class and disturbance strata.

246

247   **4.   Discussion**

248   Research into urban understory plant communities has predominantly focused on comparisons to

249   rural forest types. Urban forests contend with unique disturbance regimes and landscape fragmentation

250   relative to rural forests, and their understory communities likely reflect these environmental drivers.

251   Using an observational study design, we described the diversity of the understory in urban forested

252   patches, and examined whether patch size was linked to changes in understory community composition or

253   measures of diversity. We expected that we would observe greater plant abundance nearer to edges,

254   which we did. However, the statistical relationship between abundance of both understory plants as a

255   whole, and for different functional groups, and the edge or interior status of a plot, was not very strong,

256   with the exception of vine species richness. Instead, abundance was more strongly predicted by the basal

257   area of a plot, and in the case of herbs, by the amount of anthropogenic disturbance. This dovetails with

258   another of our hypothesis concerning the suppression of abundance in areas with higher basal area, which

259   did hold true across most groups, affecting herbs, vines, shrubs, particularly introduced species of these

260   groups. In addition, the richness of herbs and vines (but not shrubs) were suppressed under high basal

261   area. The proportion of introduced species as a whole was best predicted by the size of a forested patch,

262 but this relationship was modified by the functional class of plant. Shrubs were the only functional group

263 where the proportion of introduced species was strongly related to multiple site environmental factors

264 (edge, patch size, disturbance), while herbs and vines had less clear, weak relationships.

265   These findings are, in some respects, surprising, particularly the seeming unimportance of edge or

266 interior status of a plot for all but vine species. Our findings can be further contextualized by the analysis

267 of understory community composition, which showed that there is a considerable amount of overlap

268 between large and small park communities. Large parks did have more species, which can likely be

269 partially explained by large parks also having a wider range of habitat types by virtue of their larger size

270 and greater landscape range (e.g. ridgetop sites). While there is much overlap in the communities, there

271 are important differences as well, with specific species occurring with much greater abundance in one

272 patch size and not the other.

273   There is also the interesting phenomenon of very large proportions of abundant introduced

274 species coming from relatively few sites, creating an illusion of widespread dominance, when it is

275 actually narrow hyper-dominance. This is the case for multiflora rose and common ivy, which both had

276 extraordinarily high abundance in a few sites, and are notably both found almost exclusively in small

277 parks. They are not broadly characteristic of small parks, which have varied and diverse communities

278 overall, but they are highly characteristic of some sites within small parks, which frequently also have

279 multiple other introduced species present. Meanwhile, there are several introduced species which are

280 distributed across park size, whether plots were along an edge or interior. These include Japanese

281 honeysuckle, winged euonymus, and oriental bittersweet. It is not surprising that introduced species are so

282 frequent in the understory of New Haven's urban forests, given the fragmented and anthropogenic

283 landscape. It is surprising, however, that the understory communities of large parks and small parks

284 would be so difficult to disentangle. We had expected that small parks would be more uniformly

285 degraded, and instead found that besides a few outlying plots, they were fairly similar in some respects to

286 large parks.

287   Our findings can inform management of urban forests in several ways. Firstly, we show that the

288   quality of the understory layer can vary widely in smaller forested areas, in ways which are partially

289   explained by disturbance and edge proximity. Areas of small parks can resemble the communities of

290   larger parks, particularly when they are interior or undisturbed. This indicates that small parks are not

291   inherently degraded and are likely worth the investment of management for biodiversity and ecosystem

292   services. Secondly, the link between basal cover and reduced richness of introduced species, while

293   unsurprising, confirms that focusing management efforts on canopy gaps and/or managing for dense

294   canopy cover by protecting existing trees (such as through de-vining stewardship) could be an effective

295   way to reduce the forest health threats posed by some introduced species. However, other introduced

296   species, like winged euonymus, are widespread in the understory in interior and undisturbed areas of

297   forest, and where it occurs in high abundance, few other species of shrub grow. Shrubs are a major

298   component of the understory and midstory that can influence biogeochemical cycling and recruitment.

299   Winged euonymus currently grows beneath both disturbed and intact native forests in New Haven parks,

300   with no relationship to basal area, and may change their future trajectories. It is important to further study

301   the role that widespread and abundant introduced shrubs are playing in woody seedling recruitment and

302   understory dynamics within urban forests, and also to assess their potential to spread to rural forests.

303   Understanding how heterogeneity within the urban forest matrix may affect understory

304   communities can contextualize urban forests generally and improve our ability to manage these forests in

305   a changing environment. The understory is a crucial but understudied component of urban forests, and our

306   research begins to fill this knowledge gap by interrogating the role of plot-specific environmental factors

307   in understory diversity and composition. Our patch framework had limited capacity to predict trends in

308   overall measures of diversity but did reveal some key similarities and differences in the understory

309   communities of urban forest patches across New Haven, such as the widespread prevalence of winged

310   euonymus, and comparatively narrow range of other introduced species. These findings are particularly

311   important for prioritizing further research into the function of the understory in urban forests, and how

312   composition interacts with functionality. Our results add to a growing body of literature on urban forests

that highlight the complexities driving community composition, and the need to assess urban forests

independently of rural baselines.

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