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Changes in vegetation structure and composition of urban and rural forest patches in Baltimore from 1998 to 2015

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ABSTRACT

Urban forests often occur as highly fragmented patches with many non-native plant species, altered disturbance regimes, environmental pollutants, and uncertain trajectories of plant community composition. In 1998, the Baltimore Ecosystem Study, a U.S. National Science Foundation-funded Long-Term Ecological Research (LTER) program, established eight forested plots to investigate long-term impacts of urbanization on natural ecosystems. All plots were located in the Baltimore metropolitan area with four in urban forest patches and four in a rural forest. In 1998, these forest patches had closed canopies with well-developed tree, shrub and vine layers, and extensive herbaceous cover. The 1998 alpha diversity (species richness) was higher in urban plots than in rural plots, whereas both plot types had similar forest structure and a relatively small number of non-native species. In 2015, we resampled these plots to investigate changes in plant structure, composition, and diversity based on the abundance, cover, and size of plant species. Trees and vines experienced minimal structural changes in all the plots. Sapling, shrub, and herbaceous abundances all declined over time in the rural plots. In the urban plots, however, only the sapling and herbaceous layers experienced declines. Despite having fewer structural changes, urban plots showed a greater shift in species composition than did rural plots. As in 1998, alpha diversity was lower in the rural plots. Beta diversity (community dissimilarity) decreased among rural plots but remained nearly unchanged in the urban plots, whereas beta turnover (species turnover) was much higher in the urban plots. These data suggest that the urban plots may have divergent compositional trajectories from the rural plots, which may help urban forests retain structural similarities through functional redundancy.

1. Introduction

Conversion of forested areas to urban land-use yields isolated remnant forest patches surrounded by varying degrees of development (Pickett et al., 2008). Fragmentation influences urban forest regeneration and composition by altering seed availability, dispersal, and seedling establishment (Hobbs, 1988; Williams et al., 2009; Trentanovi et al., 2013). These patches are exposed to higher air temperatures, increased nitrogen deposition, altered hydrology, and higher atmospheric carbon dioxide levels than rural forests (Oke, 1982; Brazel et al., 2000; Savva et al., 2010). Such fragments are also characterized by reduced pollinator communities (Pauw, 2007), lower seed viability (Cheptou et al., 2008), and reduced genetic variation (Young et al., 1996). Further, plant assemblages in urban forests are influenced by the spread of horticultural species planted in neighboring residential and municipal areas (Swan et al., 2011; Groffman et al., 2014). Many of these non-native horticultural invaders outcompete native species for space and resources.

Diversity and cover of non-native colonizers vary with the degree of urbanization (Marzluff, 2008; Trentanovi et al., 2013). Whereas extreme urbanization may decrease alpha diversity due to inhospitable conditions (Trentanovi et al., 2013), species introductions under low to moderate urbanization can increase alpha diversity (Schwartz et al., 2006; McKinney, 2008 Kowarik, 2003; McDonnell and Hahs, 2008). By contrast, beta diversity among urban forest sites is typically decreased. This decrease may result from extirpation of native species through competition with non-native species or because native species do not tolerate stresses often associated with urban environments (Kühn and Klotz, 2006; Knapp et al., 2012). Distinct plant communities may thus homogenize through the ubiquitous gain of the same non-native species

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and loss of niche-specific and rare species (McKinney, 2004; Williams et al., 2009; Knapp et al., 2012).

Urbanization also tends to decrease phylogenetic and functional diversity (Knapp et al., 2012). Even with higher alpha diversity, urban forest communities have fewer lineages than rural forests (McKinney, 2006; Winter et al., 2009; Groffman et al., 2014). Urban homogenization can thus increase beta diversity on a regional scale as urban habitats diverge from neighboring rural habitats (McKinney, 2006). Evidence also suggests that plant species that thrive in urban environments have similar traits and life histories related to tolerance of such disturbances as forest fragmentation, altered biogeochemical cycles, and increased urban warming, thus limiting functional diversity as well (McKinney, 2006; Shochat et al., 2006; Grimm et al., 2008; Knapp et al., 2012; Groffman et al., 2014; Johnson and Swan, 2014).

Species composition is an integrative response variable of community assemblages (Dray et al., 2012) that is sensitive to local environmental conditions (Agrawal et al., 2007; Johnstone et al., 2016). For instance, floristic data have been extremely useful in assessing expansion of non-native plant species in urban systems (McKinney, 2006; Williams et al., 2009; Trentanovi et al., 2013) and have provided important insight on the challenges of certain forest species to regenerate without fire (Abrams, 1990; Arthur et al., 2012; Hutchinson et al., 2012). Community analysis provides information that alpha and beta diversity alone might mask by indicating which species are affected by changes in conditions. Combined analysis of diversity and composition provides an opportunity to quantify effects of disturbance on forest biodiversity, habitat structure, and the spread of non-native species. However, quantifying the rate or direction of change requires sampling the same communities over time. Only with long-term comparisons can we address important questions surrounding vulnerability versus resilience of urban plant communities (Turner et al., 2003).

We used eight permanent forest plots established in 1998 by the Baltimore Ecosystem Study (BES), a component of the U.S. National Science Foundation-funded LTER network (Groffman et al., 2006) to make such a comparison of changes in structure, diversity and composition of forests and the long-term impacts of urbanization on natural ecosystems. These plots were within the Baltimore metropolitan area; four rural plots were in Baltimore County and four urban plots were in Baltimore City. All plots were located in broadleaf eastern deciduous forests dominated by *Quercus* spp. and *Carya* spp. (Braun, 1950). All plots were similarly well developed with canopy and subcanopy tree layers, shrub and vine layers, and herbaceous cover (Groffman et al., 2006). In 1998, urban plots had higher alpha diversity than rural plots, and both plot-types had a relatively small proportion of non-native species. Structurally, shrub density was higher in the rural plots, but sapling, seedling, and herb density was higher in the urban plots. The authors attributed these differences to a greater canopy cover in the rural plots. They predicted that over time the structure and composition of the vegetation in the urban plots would diverge from the rural plots (Groffman et al., 2006). In 2015, we resampled the plots to test their predictions. Our central hypothesis was that species turnover would be greater in the urban plots than the rural plots due to increased amounts of non-native species and a concomitant decline in native species. We predicted this outcome based on assumptions that abiotic and biotic stresses, as well as sources of non-native propagules, may be higher in urban areas. Additionally, we anticipated community assemblages would change most markedly in the understory layers, given that the generation times of herbs, shrubs, and vines are generally shorter than the generation time of trees. The objective of this observational study was to identify trends or patterns in time and to infer information about cause and effect from observed correlations and naturally occurring events.

2. Methods

2.1. Site selection

All eight BES LTER permanent plots were located within the Gwynns Falls watershed in the Piedmont Plateau region of the Baltimore metropolitan area (Groffman et al., 2006). Within this watershed, plots were established in ~80 to 100 year old Northern Hardwood forests with > 80% continuous forest canopy (Groffman et al., 2006). The four rural plots were located within Oregon Ridge Park, approximately 16 km outside Baltimore City limits in Cockeysville, Maryland. Land-use in this area is primarily agriculture, recreational forests, and residential housing (Doheny, 1999). Oregon Ridge Park lies within 364 ha of continuous forest (Baltimore County EPS, 2007). This area was extensively logged in the 1800s to provide fuel for iron production, but forests have been allowed to regenerate since the early 1850s (Brooks et al., 1979). The four urban plots were divided equally between Leakin Park and Hillsdale Park, both located in Baltimore City. The National Land Cover Database classifies the area surrounding the parks as medium-density developed land (U.S. Geologic Survey 2011 edition, amended 2014). Forest structure in these city parks is considered relatively undisturbed (NRCS, 1998). Soils in all plots are a variety of loams (Table 1).

2.2. Plot Layout

Plot locations were selected in 1998 based on three subjective criteria: (1) Avoid obvious habitat boundaries, (2) Have consistent drainage, and (3) Maintain at least 80% continuous tree canopy (Groffman et al., 2006). The plots were originally sampled in June-August of 1998 and we resampled them in June-August of 2015 following protocols established in 1998 to allow comparison and reduce chances of difference resulting from sampling error. In 1998, plots were established by surveying boundaries to correct for slope and to achieve a 0.5 cm accuracy. Plot boundaries were permanently outlined with metal markers buried just below the soil surface. Six plots were 40 × 40 m (1600 m^2) whereas Hillsdale 1 and Hillsdale 2 were 30 × 30 m (900 m^2). Each plot was divided into a series of nested subplots organized in columns and rows, allowing for data collection appropriate to different vegetation layers (Fig. 1). Vegetation in the Oregon Ridge Park and Leakin Park plots was sampled for the complete 40 × 40 m plot in both 1998 and

Table 1
Locations, abbreviations, and soils series descriptions for the eight forest plots established for sampling by the Baltimore Ecosystem Study in 1998 (Groffman et al., 2006).

Location	Plot ID	Soil Series
Oregon Ridge Park	Up 1	Glenelg- Fine-loamy, mixed, semiactive, mesic Typic Hapludults
Oregon Ridge Park	Mid 1	Glenelg- Fine-loamy, mixed, semiactive, mesic Typic Hapludults
Oregon Ridge Park	Up 2	Glenelg- Fine-loamy, mixed, semiactive, mesic Typic Hapludults
Oregon Ridge Park	Mid 2	Manor- Coarse-loamy, micaceous, mesic Typic Dystrudepts
Leakin Park	Leakin 1	Legore- Fine-loamy, mixed, active, mesic Ultic Hapludalfs
Leakin Park	Leakin 2	Occaquon- Fine-loamy, mixed, semiactive, mesic Inceptic Hapludults
Hillsdale Park	Hillsdale 1	Jackland- Fine, smectitic, mesic Aquic Hapludalfs
Hillsdale Park	Hillsdale 2	Legore- Fine-loamy, mixed, active, mesic Ultic Hapludalfs

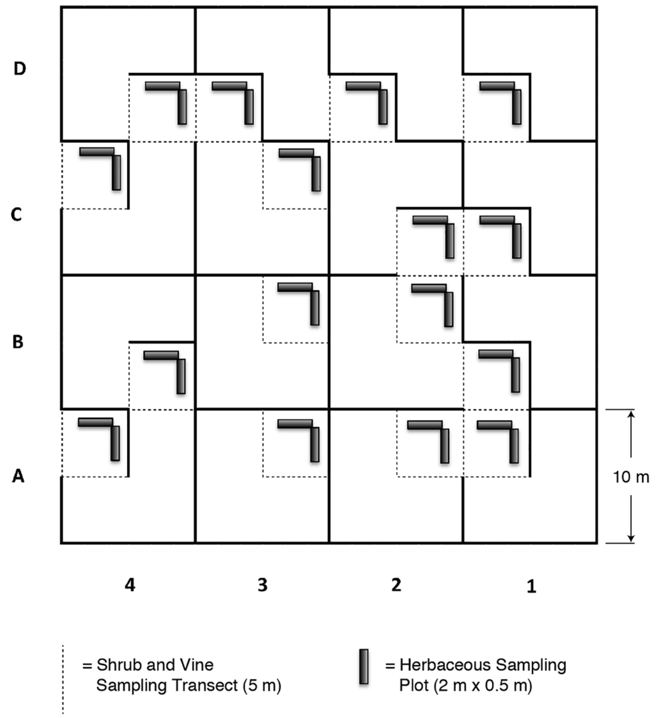

Fig. 1. Layout of plots. Alphanumeric boxes represent 10 × 10 m subplots used to sample trees and measure canopy cover. Within each 10 × 10 m subplot, the 5 × 5 m area marked by dotted and solid borders was used to sample saplings. Dotted lines represent transect lines used to measure shrubs and vines. The two perpendicular rectangles within each 5 × 5 m subplot show the placement of the 0.5 m quadrats used to sample herbs.

2015. However, data from one column and row (Fig. 1) were omitted from the six larger plots so that all sites had the same 900 m^2 area to allow comparison with the Hillsdale plots. In total, there were nine 5 × 5 m subplots with 18 quadrats in each 30 × 30 m plot (Fig. 1). The positioning of the subplots, transect lines, and quadrats was randomly selected once in 1998, then used across all plots. Resampling in 2015 used the same positioning of all subplot units.

2.3. Vegetation sampling methods

2.3.1. Tree layer

Trees were defined as individuals with a single primary stem from the base that reached a height of 137 cm with a diameter at breast height (DBH) ≥ 8 cm. All trees within the 900 m^2 plots were identified, counted, and DBH was measured (Fig. 1). Their location within the alpha-numeric space was noted for ease of relocation for resampling efforts. In 1998, all trees were permanently tagged with an identification number. In 2015, the tag number was recorded or a tag was added in the event that a tree transitioned from sapling to tree.

2.3.2. Sapling layer

Individuals of tree species as defined above that reached a height of 137 cm and measured < 8 cm DBH were considered saplings. All saplings within the nine 5 × 5 m subplots were counted (Fig. 1). DBH was measured to the nearest hundredths decimal place using General Ultratech digital calipers. As with the tree layer, saplings were tagged. In 2015, the 1998 tag number was recorded or a tag was added in the event of that a sapling transitioned from seedling to sapling.

2.3.3. Shrub and vine layer

Percent cover of shrub and vine species was recorded using a line-intercept method along two sides (lower and left) of the nine 5 × 5 m subplots (Fig. 1). Shrubs were defined as woody plants with multiple equally dominant stems from the base. Vines were defined as woody plants that grow by trailing or climbing on other plants. For each 1 m segment along the 10 m transects, the distance in contact with a vine or shrub species was recorded. To be recorded, shrubs and vines had to continuously intersect ≥5 cm of the line with no gaps. When measuring the same species, gaps less than 10 cm were recorded as continuous cover.

2.3.4. Herbaceous layer

Percent cover of each herbaceous species was estimated within each of the 18 2 × 0.5 m quadrats per plot (Fig. 1). As herbaceous vegetation can overlap, it was possible for cover to exceed 100%.

2.3.5. Canopy cover

Canopy gap percentage was estimated within each 10 × 10 m subplot to the nearest 5% (Fig. 1). At each subplot, three technicians estimated canopy gap independently and a final estimate of missing canopy was determined as a consensus value. The Forest Service's Forest Inventory Analysis (FIA) field manual was used to orient the field crew to different patterns and aggregations of canopy cover (U.S. Forest Service, 2005).

2.3.6. Species identification

The USDA-NRCS PLANTS database was used to determine non-native versus native status of all plant species to state level (USDA, NRCS, 2016). Voucher specimens were obtained for all identified species and are archived at the Norton-Brown Herbarium (MARY) at the University of Maryland, College Park. Specimens and material needed to confirm identifications were collected from outside the plots to prevent compromising the long-term study.

2.4. Analysis

2.4.1. Abundance and dominance

Abundance of each species within each layer was determined per plot. Relative abundance, the proportion of individuals of a particular species to the total number of individuals in a plot, was averaged by plot-type and year. Relative abundance of tree and sapling species was determined by standardizing to the number of stems per hectare. Percent cover per unit transect (10 m) was the abundance measurement used for the shrub and vine layers, averaged per plot and plot-type. Percent cover was also used to measure relative abundance of herb cover per quadrat (2 × 0.5 m), averaged per plot and plot-type. Relative non-native species abundance was the ratio of non-native species to native species cover per forest layer and per plot.

Changes in vegetation abundance across time were analyzed using effect size as measured by Cohen's *d* effect size metric. Effect size is an easily-interpreted scale based on comparing magnitudes rather than traditional statistical significance tests based on *p* values (Sullivan and Feinn, 2012). Effect size indices have the benefit of emphasizing the magnitude of the differences between groups without being confounded by sample size (Coe, 2002). Using Cohen's *d* allowed us to compare the change over time of species abundances in each forest layer, despite different sampling methods and the small number of plots. Effect sizes for differences between urban ($n = 4$) and rural ($n = 4$) plots across years were calculated by using the following equation:

$$d = \frac{[\text{Mean2015}] - [\text{Mean1998}]}{\text{StandardDeviation}_{pooled}}$$

The effect size of d is interpreted as small ($d = 0.2$), medium ($d \geq 0.5$), or large ($d = 0.8$), with value categories parameterized by the context of the data, i.e. other influencing variables such as the limitations of the experimental design (Sullivan and Feinn, 2012). Calculations of Cohen's *d* effect size were performed in the R statistical environment, version 2.4–6 (R Core Team, 2017), using the package effsize (Torchiano, 2017).

Relative dominance was the proportion of total basal area (cm^2/ha) of a species to the total basal area per hectare of all species within a plot group (n=4).

Data are stored on the LTER Network Data Portal and can be found by searching the Package ID knb-lter-bes.3300.110 or by the following URL link: https://doi.org/10.6073/pasta/67cd7c50ea5b87369c2b64-be62db366f.

2.4.2. Diversity

Alpha diversity, the number of plant species per plot, was averaged for the urban (n = 4) and rural (n=4) plots. Beta diversity was calculated as a monotonic transformation of the Jaccard index, a standardized scale from 0 to 1 of compositional similarity. This standardization allowed sites to be compared despite having used different methods of data collection at each forest layer. Beta diversity was calculated separately for the urban versus rural plots in 1998 and 2015 using the average pair-wise comparisons of distance for each group (Legendre and Cáceres, 2013). Beta diversity values were compared to determine the relative compositional dissimilarity between plot-type and survey year.

Turnover of species over time was determined by calculating beta turnover (β_T) as follows:

$$\beta_T = \frac{|g + l|}{2\bar{\alpha}}$$

where g is the number of species gained, l is the number of species lost, and $\bar{\alpha}$ is the average alpha diversity (McCune and Grace, 2002). β_T values were determined for each plot-type, with higher β_T values indicating more turnover across the sampling interval.

P-values were determined by F-values computed from a one-way analysis of variance (ANOVA) for alpha diversity and beta diversity. Tukey's *post hoc* test was performed when a significant value ($p < 0.05$) was determined by ANOVA.

2.4.3. Species composition

Non-metric multidimensional scaling (NMDS) ordination as implemented in the vegan package (Oksanen et al., 2018) was used to measure compositional similarity among the plots. NMDS uses the pairwise dissimilarity of species composition to reduce dimensional space so that compositional changes can more easily be interpreted (Legendre & Legendre 2012). It is considered the most robust unconstrained ordination method as it makes none of the distributional assumptions that are common in other ordination methods (Minchin 1987; Ludwig and Reynolds, 1988).

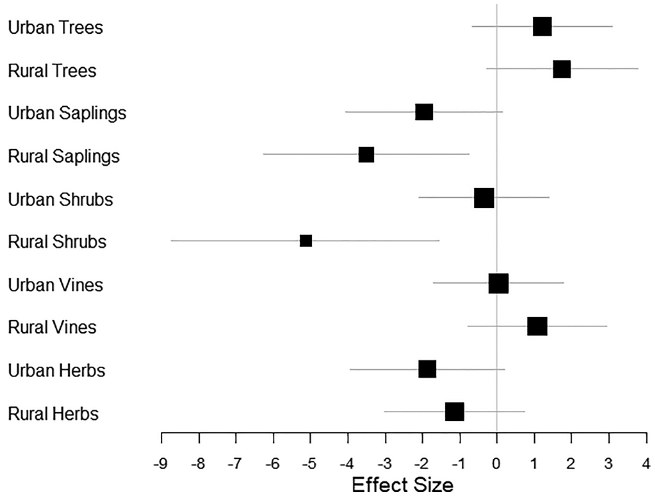

Fig. 2. Effect sizes (d) and 95% confidence intervals for changes in vegetation abundance between the 1998 and 2015 surveys. The scale of d is interpreted as a small ($d = (\pm)0.2$), medium ($d \geq (\pm)0.5$), or large ($d = (\pm)0.8$) effect size.

Plot points were based on relative abundance of species from all forest layers across both survey years. If a discrepancy in the identity of a species between survey years arose, we condensed those taxa to the genus level. We used Bray-Curtis dissimilarity, a semi-metric index of distance between site vectors (McCune and Grace, 2002), because it does not interpret shared absence of species in different sites as a similarity between those sites (Legendre and Gallagher, 2001). After twenty random starts, we examined both two (stress=0.078) and three (stress =0.050) dimensional solutions for NMDS and determined that a simpler two-dimension NMDS better represented the compositional pattern.

Minimum convex hull polygons defined by species scores (Eddy, 1977) were constructed around points represented by each plot-type and year. The relative size and position of the polygons within ordination space indicate compositional similarities or differences among vegetation communities within each plot-type and survey year.

3. Results

3.1. Abundance

Cohen's d effect size analysis indicated large changes in relative abundance of all vegetation layers except urban vines and shrubs between 1998 and 2015 (Fig. 2). These changes comprised increases in the abundance of trees in both the urban and rural plots but decreases in urban and rural saplings and herbs and rural shrubs (Fig. 2). Changes within each layer are detailed below.

The most abundant and dominant trees species in the urban 1998 plots were *Liriodendron tulipifera* followed by *Quercus alba*, *Cornus florida* and *Fraxinus pennsylvanica* (Fig. 3). In 2015, *L. tulipifera* remained the most abundant tree, however *Acer rubrum* surpassed *Q. alba* in abundance, *C. florida* declined greatly in abundance, and *F. pennsylvanica* became the most dominant species (Fig. 3). In the rural 1998 plots, *L. tulipifera*, *A. rubrum*, and *Q. alba* were the most abundant tree species, with *L. tulipifera* also being the most dominant followed by *Quercus rubra*, *Q. alba*, and *Q. velutina* (Fig. 3). *L. tulipifera* and *A. rubrum* remained the most abundant in 2015, but *Nyssa sylvatica* increased abundance while *Q. alba* decreased causing these two species to exchange their 1998 abundance rankings. Additionally, the dominance rankings of *Q. rubra* and *Q. alba* were swapped (Fig. 3). The urban and rural plots both had approximately 85% canopy cover in both 1998 and 2015 (data not shown).

Within the sapling layer, losses due to death far exceeded losses due to recruitment into the tree layer over the 17 years. More than 50% of all sapling species present in each urban plot and 33% of all sapling species present in each rural plot experienced a > 50% loss of individuals (Fig. 4a and b). Although both the urban and rural plots experienced large declines (Fig. 2), more individual saplings were lost in the urban plots than the rural plots (Fig. 4a and b).

In the rural plots, *N. sylvatica*, *Carya glabra*, and *Carya tomentosa* were the most retained sapling species (Fig. 4a). Each rural plot lost three to eight species as result of mortality of all individuals of a species while only a single previously unrecorded individual (*C. tomentosa*) was recruited into the tree layer in all the rural plots (Fig. 4a). In the urban plots, *A. rubrum*, *N. sylvatica*, and *Fagus grandifolia* were the most retained sapling species since 1998 (Fig. 4b). Each urban plot lost two to six species and three plots gained *A. rubrum*, *F. grandifolia*, and *C. tomentosa* individuals (Fig. 4b).

Reductions in *Viburnum acerifolium* abundance accounted for the decline in the rural plots (Figs. 2 and 5). Rural plots were dominated by *V. acerifolium* and *Vaccinium* spp. in 1998, but in 2015 the relative abundance of *V. acerifolium* declined by nearly 50% (Fig. 5a and c). Meanwhile, overall shrub cover in the urban plots did not change considerably (Fig. 2), but the abundance of *Lindera benzoin* increased from 69% in 1998 to 92% in 2015 (Fig. 5b and d).

Non-native species remained a generally low proportion of all vegetation layers except for vines (Table 2). Relative abundance of vine cover was consistent in the urban plots, but increased in the rural plots (Fig. 2).

3.2. Diversity

Alpha diversity of combined species presence/absence data from all forest layers was significantly greater in urban plots in both 1998 (F = 14.15, df = 3, $p < 0.044$) and 2015 (F = 14.15, df = 3, $p < 0.001$) (Table 3). Beta diversity significantly declined between 1998 and 2015 (F = 4.65, df = 3, $p < 0.36$) in the rural plots only (Table 3). Although many species were lost in the urban plots, enough species were gained to yield similar beta diversity over time (Table 3).

Most species lost from the rural plots were native, whereas gained species were mostly non-native (Table 4). Rural shrubs and trees lost the most species and vines gained the most. In the urban plots, turnover was greatest in the herb layer where nearly all lost species were native and both native and non-native species were gained (Table 4). All urban shrub species gained were native (Table 4).

3.3. Ordination

Non-metric multidimensional scaling (NMDS) showed that the plant community composition of urban and rural plots is quite different and that composition within plot types changed over time. The larger urban convex hull polygons signify greater differences in the species composition among the urban plots than among the rural plots in both years (Fig. 6). At the same time, we saw changes in the urban convex hull

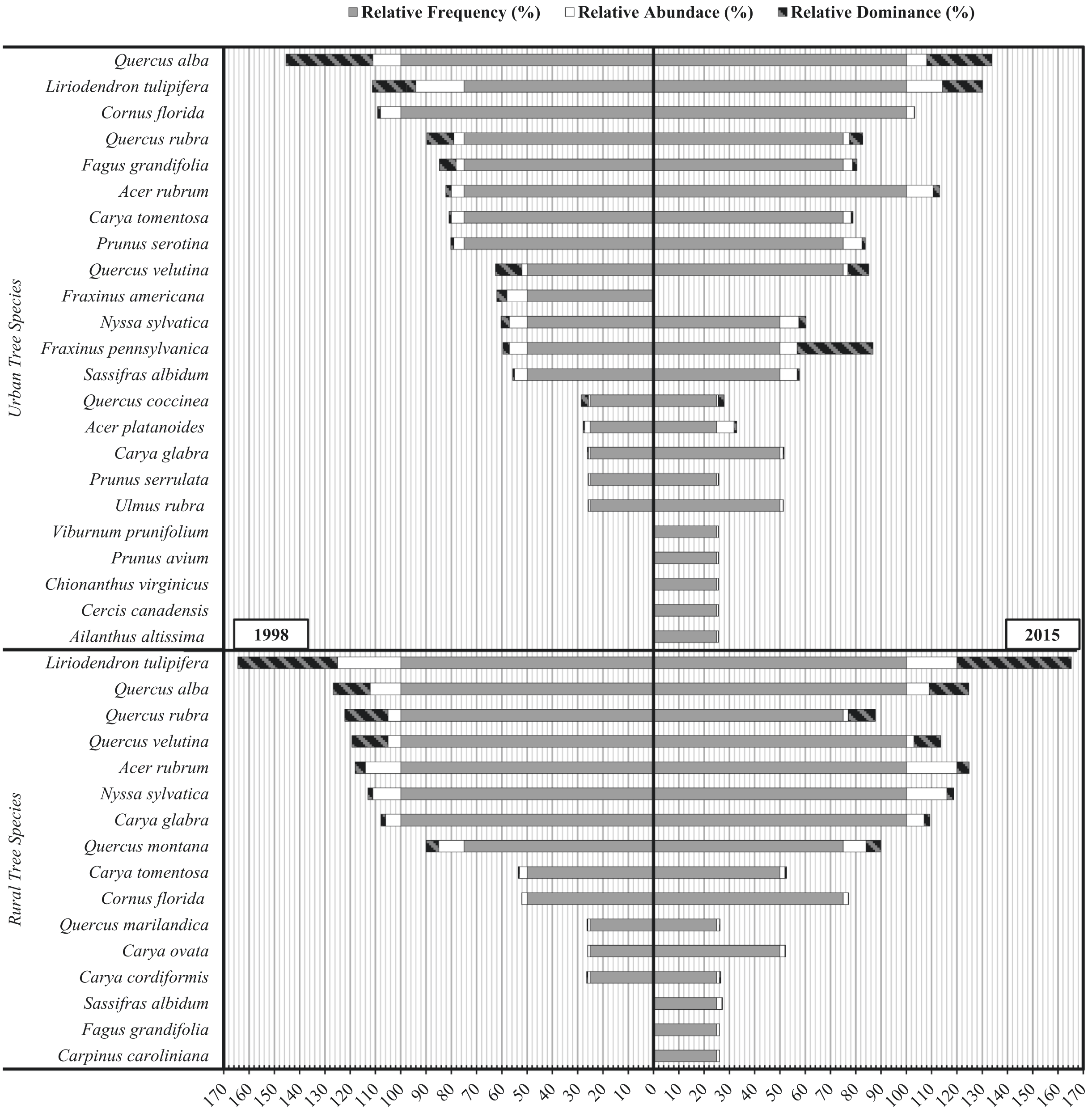

Fig. 3. Relative frequency, relative abundance, and relative dominance of tree species within the urban and rural plots between 1998 and 2015. Relative frequency was the percentage of plots a species was found in per group (n=4), relative abundance was the ratio of individuals of a species to all individuals found within a plot group (n= 4) per unit area (stems/ha), and relative dominance was the proportion of total basal area (cm^2/ha) of a species to the total basal area of all species within a plot group (n=4). The sum of all three values is the Importance Value (IV) for that species. Species are organized from largest to smallest IV in 1998 per plot group (n=4). Bars to the left of the vertical axis are the 1998 values and bars to the right are the 2015 values.

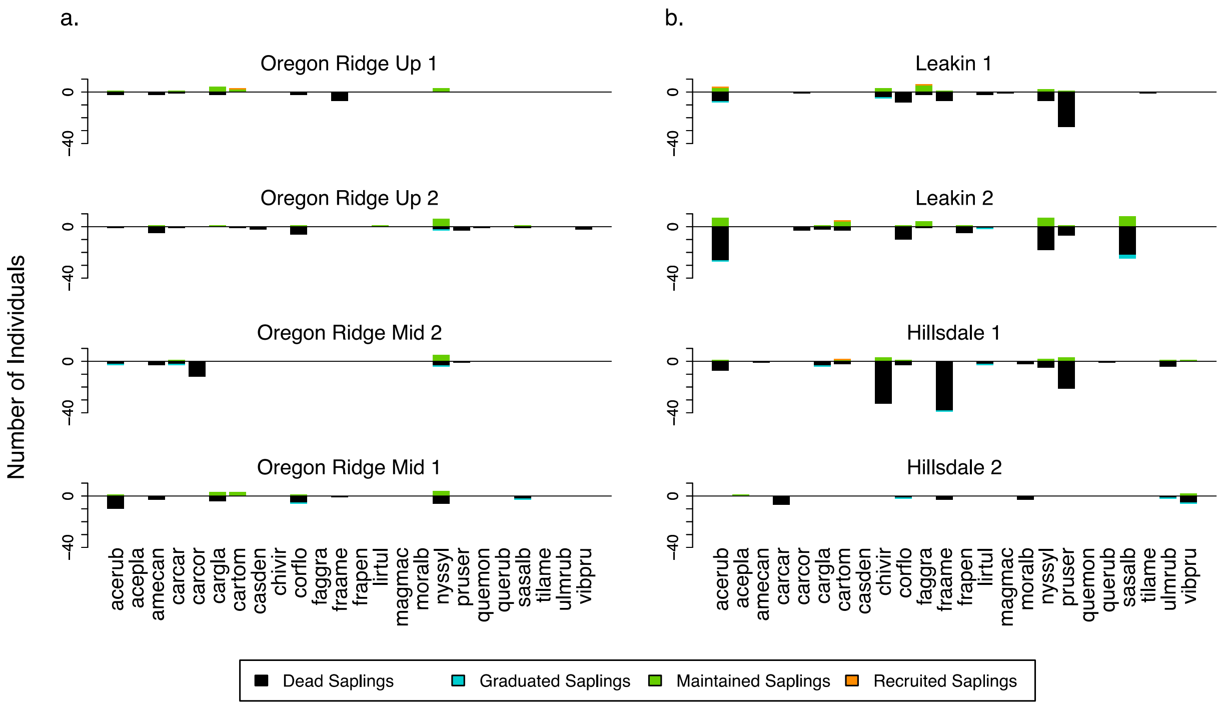

Fig. 4. Distribution of death, graduation, retention, and recruitment of saplings within rural (a) and urban (b) plots. Individuals missing from the plot or found as standing dead in 2015 were considered losses, as were individuals that graduated from the sapling layer into the tree layer. Individuals counted as saplings in both the 1998 and 2015 surveys were considered retained. Individuals recruited to the sapling layer after 1998 were considered gains. Each bar represents the gain or loss of individuals of a species. Bars are organized vertically with loss below the horizontal axis and gains and retention above. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix A.

volume between years. Reduced convex hull volume indicates homogenization of species assemblages across urban plots from 1998 to 2015 and this homogenization likely resulted from sapling losses (Fig. 4). Although the rural convex hulls had similar volumes between years, both are much smaller than the urban convex hulls indicating greater homogenization in the rural plots in both years. Additionally, shifts in the location of plots from different years in ordination space indicate that communities within each group have changed over time. The most apparent change was movement of 2015 urban and rural convex hulls towards the positive end of Axis 2 (Fig. 6). This upward shift was driven by species loss over time. For example, many of the species correlated with low values on Axis 2 were lost from many of the 2015 urban plots (Table 4). Axis 1 may have been driven by reduced relative abundances. Many species near 0.0 of Axis 1 are sapling species that experienced large declines (Figs. 4 and 6).

4. Discussion

We found critical changes to the structure, diversity, and composition of sapling and shrub layers over the 17 years since Groffman et al. (2006) described vegetation in these eight Baltimore forest plots. Plant species assemblages homogenized over time in the urban plots, yet alpha diversity and turnover was higher than the rural plots. Whereas introduced species accounted for elevated rates of turnover in the urban plots, we suggest alternative drivers for the structural and compositional changes found in both the urban and rural plots. It is important to note that in an observational study such as this, we can only make definitive statements about change over time. As we did not test for mechanisms in this study, we can only infer information about the causes of these changes from observed correlations, careful analysis of naturally occurring events, and other perceived changes that may have impacted the responses. Still, our results provide valuable insights regarding the effects of urbanization and the potential future trajectories of these vital communities.

4.1. *Marginal changes to the overstory establishment may be causing mesophication*

Mature trees are generally longer-lived and more resilient to disturbance than understory species. After reaching maturity, aboveground tree growth declines (Gower et al., 1996) but mortality tends to be low and driven by acute events (e.g. drought, fire, storms, pest and pathogen infestations, or human management practices). As there was no evidence of any major disturbance event in the plots, it was not surprising that only small changes were found in both the structure of the tree layer (Table 2) and the amount of canopy cover (~85% data not shown) within or among sites. Eighty-five percent canopy cover is typical for the region (Baltimore County EPS, 2007) and represents a “closed canopy” in this study.

As forest canopies close, reduced evapotranspiration leads to increasing soil moisture. Nowacki and Abrams (2008) termed this component of forest succession *mesophication*. Without regular disturbance, such as the pre-settlement fire intervals that promoted fire-adapted pioneer species (Nowacki and Abrams, 2008; Hanberry et al., 2012), mesophication produces feedback loops that facilitate establishment of mesophytic species (Barnes et al., 1998; Kreye et al., 2013). Mesophication thus shifts forest composition from shade-intolerant and xeric species, such as *Quercus* spp. and *Carya* spp., to species more tolerant to lower light and mesophytic habitats, such as *A. rubrum* and *N. sylvatica* (Abrams, 2003; Nowacki and Abrams, 2008; Burgess et al., 2015). Indeed we observed increased abundances of *A. rubrum* and *N. sylvatica* and decreased abundances of most *Quercus* and *Carya* species in the sapling layer (Fig. 4). This suggests that *Quercus* spp. regeneration may be reduced in these sites, an observation consistent with the literature on this topic for the past three decades (e.g. Abrams, 1990, 2003). The leaves and acorns of *Quercus* spp. are a valuable food source for many native insects, birds, and mammals (Baltimore County EPS, 2007) and loss of these species could have compounding effects on ecosystem functioning such as food web dynamics.

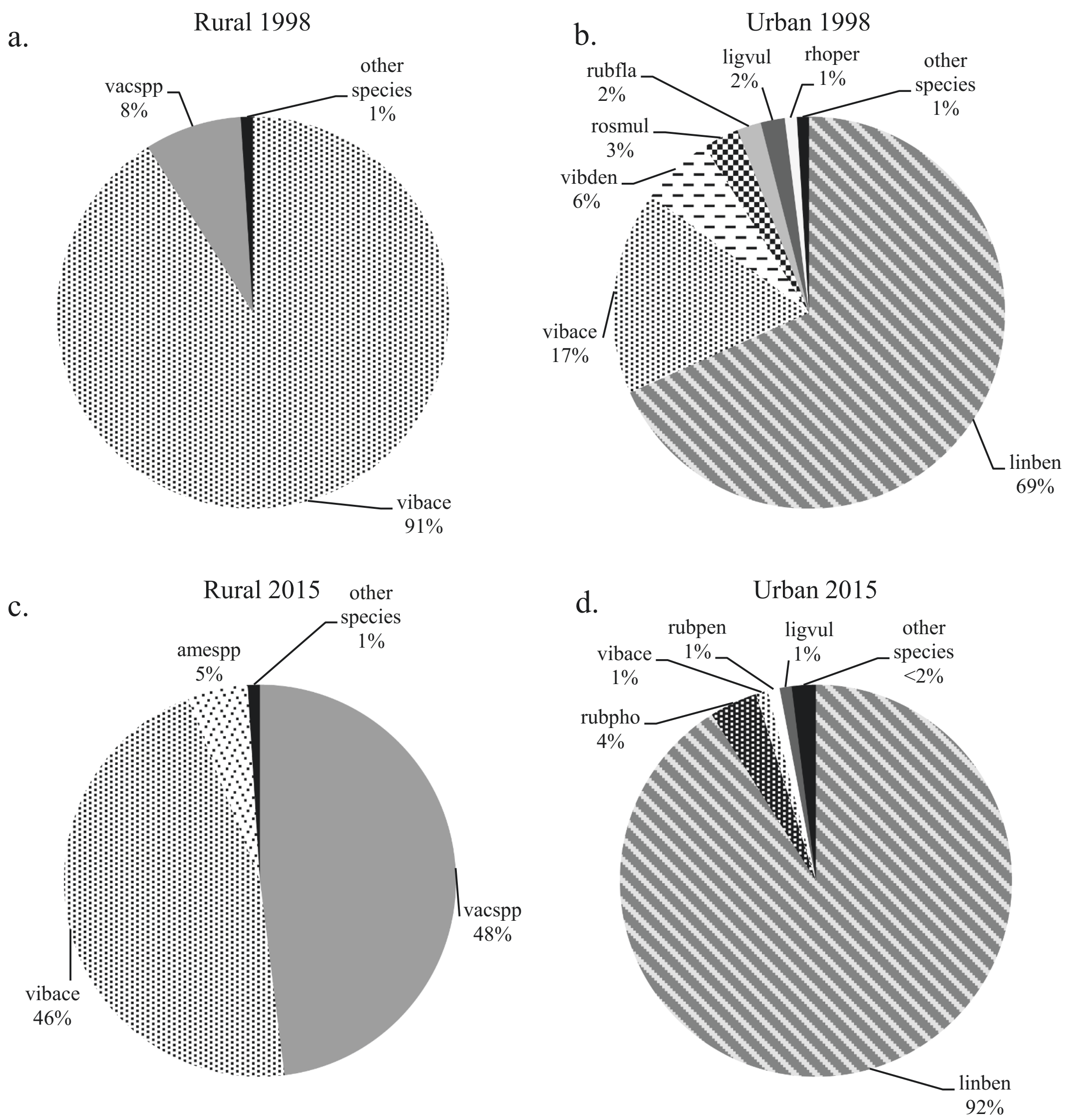

Fig. 5. a-d. Relative proportion of shrub species in each plot-type and sampling year. Percentages were calculated as the proportion of a species measured in cm of cover. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix A.

Quercus spp. not only regenerate more in burned gaps, but repeated burnings reduce the frequency of *A. rubrum* regeneration (Hutchinson et al., 2012). In the majority of Maryland, the pre-settlement fire-return interval was between 7 and 12 years (Frost, 1998). The current fire return interval has greatly increased as wildfires are highly controlled in most areas. In 2015, the Maryland Forest Service reported that only 105 ha of Maryland forest burned, and no prescribed burns were implemented (Maryland Forest Service, 2015). It has been well established (e.g. summarized by Brose et al., 2014) that periodic controlled forest burnings incorporated into management plans can enhance establishment and maintenance of *Quercus* spp. and *Carya* spp. dominated forests. We suggest that absence of fire may also contribute to reduced regeneration of *Quercus* spp. and *Carya* spp. at our sites.

4.2. Potential drivers of structural and compositional change

Declines in understory vegetation abundance as observed in this study (Fig. 2 & Table 2) have typically been linked with limited canopy openness (Nowacki & Abrams, 2008; Hanberry et al., 2012; Hutchinson et al., 2012), disease and infestation (Gottshalk, 1990, Ayres & Lombardero, 2000; Flower et al., 2013), or deer herbivory (Tilghman, 1989; Stromayer & Warren, 1997; Horsley et al., 2003; Côté et al., 2004; McGarvey et al., 2013). Our plots had consistently high canopy cover across survey years yet we found no major increase in abundance of shade-tolerant understory species (Fig. 4 & Table 4); in fact we found the opposite, with substantial decreases in many shade tolerant sapling and shrub species (Figs. 4 and 5; Table 4). Because a closed-canopy was established prior to the 1998 survey, land-use history coupled with the demise of fire, herbivory, and disease infestations, as well as other weather-related drivers, have all likely contributed to the observed changes in understory vegetation.

Although the impacts of disease and infestations may be dramatic in some instances, they frequently affect only a few species. For example, dogwood anthracnose (*Discula destructiva*) on *C. florida*, emerald ash borer (*Agrilus planipennis*) on *F. americana*, and gypsy moth (*Lymantria dispar dispar*) on *Quercus* spp., all may have reduced survival and regeneration of these species in our plots. In 2006 gypsy moths were reported in eight stands at Oregon Ridge Park, with complete defoliation and subsequent death of all *Quercus* spp. within one stand (Baltimore County EPS, 2007). Our closest rural plot was located over 700 m from the decimated stand. Additionally, the stand reported to have complete *Quercus* spp. death was only a small portion (8 ha) of Oregon Ridge's 362 ha of continuous forest and was reforested shortly after the infestation with several native species of *Quercus* and *Carya*.

Table 2
Occupancy, density, and relative proportion of non-native species organized by forest layer. Values are the mean (± SE) for each group (n = 4) rounded to adjust for sampling precision. Occupancy was defined for trees and saplings as basal area (m^2/ha), for shrubs and vines as percent cover per transect (10 m), and for herbs as percent cover per quadrat (1 m^2). Density values were only provided for trees and saplings, as they were the only layer with count data. The relative proportion of non-native species is the percent abundance for trees and saplings and percent cover for vines, shrubs, and herbs.

Vegetation layer	Plot group	Occupancy (m^2/ha), (% cover/transect), or (% cover/quadrat)	Density (stems/ha)	Non-native species (%)
Tree	Urban 1998	0.28 ± 0.06	333 ± 38	1
	Rural 1998	0.32 ± 0.05	291 ± 15	0
	Urban 2015	0.35 ± 0.06	403 ± 14	10
	Rural 2015	0.31 ± 0.06	372 ± 29	0
Sapling	Urban 1998	0.0049 ± 0.0009	1006 ± 280	5
	Rural 1998	0.0039 ± 0.0006	381 ± 50	0
	Urban 2015	0.0032 ± 0.0013	206 ± 76	8
	Rural 2015	0.0026 ± 0.0003	119 ± 16	0
Shrub	Urban 1998	32.6 ± 16.5		5
	Rural 1998	46.4 ± 6.2		0
	Urban 2015	22.2 ± 12.4		5
	Rural 2015	1.3 ± 0.6		0
Vine	Urban 1998	14.7 ± 11.5		53
	Rural 1998	1.2 ± 0.4		0
	Urban 2015	15.3 ± 1.8		91
	Rural 2015	8 ± 4.1		18
Herb	Urban 1998	8.9 ± 2.5		0
	Rural 1998	4.8 ± 1.6		0
	Urban 2015	2.3 ± 0.2		10
	Rural 2015	1.9 ± 0.8		0

Table 3
Diversity metrics for all species organized by plot-type and year. Total species (γ) is the sum total of all species within a group (n = 4). Alpha diversity (α) is the mean alpha diversity per group. Beta diversity (β) is the average pair-wise comparison of the inverse of the Jaccard similarity index within each group. Species lost and species gained were summed per group. Turnover since 1998 (β_T) is the absolute value of species lost and gained divided by the product of average alpha diversity and two (McCune & Grace 2002). Different letters for column values of alpha and beta diversity indicate a statistically significant difference ($p < 0.05$) as determined by ANOVA with Tukey's *post hoc* test.

Plot group	Total species (γ)	Alpha diversity (α)	Beta diversity (β)	Species lost since 1998	Species gained since 1998	Turnover since 1998 (β_T)
Urban 1998	73	41 ± 3.08^A	0.42 ± 0.06^A			
Rural 1998	46	30.75 ± 0.63^B	0.57 ± 0.03^B			
Urban 2015	69	39.5 ± 2.87^A	0.42 ± 0.03^A	20	16	0.44
Rural 2015	40	21.75 ± 2.39^B	0.43 ± 0.03 ^{A}	11	5	0.26

Therefore, we find it unlikely that this instance of gypsy moth infestation had a long-term effect on oak reproduction in our plots. No known gypsy moth outbreaks have occurred in the parks containing the urban plots. Dogwood anthracnose, generally associated with the Appalachian Mountains, has a range that includes Baltimore City and County (Stolte et al., 2012), though no official impact surveys have been conducted to our knowledge. Similarly, emerald ash borers have been identified in the Baltimore metropolitan area, and although no survey on the impact on *Fraxnius* spp. abundance has been conducted yet, we saw little evidence during our survey in 2013. Since that time, the impact of this invasive insect has spread dramatically and it is expected to negatively impact *Fraxinus* spp. in both urban and rural settings (Flower et al., 2013). As declines in abundance of *Quercus* spp., *C. florida,* and *F. americana* were concurrent with declines in several other species not likely affected by these disease and infestation events, it is likely that other factors also contributed to the changes we observed.

White tailed deer (*Odocoileus virginianus*) are considered keystone herbivores (Rooney, 2001). Deer browse on plants within reach, such as herbs, seedlings, shrubs, and saplings. The immense impact of deer on eastern U.S. forest density and structure has been well documented (Augustine and Frelich, 1998; Stromayer and Warren, 1997; Rooney, 2001; Rooney and Waller, 2003; Côté et al., 2004; Long et al., 2007; McGarvey et al., 2013; Begley-Miller et al., 2014). Over-browsing results in forest stands devoid of understory plants and overrepresented by mature trees, as smaller stems are consumed (Tilghman, 1989; Stromayer and Warren, 1997; Côté et al., 2004; McGarvey et al., 2013). Although deer are generalist feeders, some plant species, such as *Microstegium vimineum and L. benzoin*, are unpalatable to deer, while others, like *Rosa multiflora* and *Berberis thunbergii*, are well-protected with thorns and are avoided by deer, contributing to the selective proliferation of these species in forest communities subject to heavy browsing (Rawinski, 2008, Averill et al., 2016). In this manner, deer browsing directly modifies forest understory structure and composition (McShea et al., 1997; Rooney and Waller, 2003; McGarvey et al., 2013). Our plots, particularly the rural ones, had understory structures that support characteristics of an over-browsed understory, with reduced sapling, shrub, and herb abundances (Fig. 2). Since declines were noted in species susceptible to deer browsing, such as saplings of *Quercus* spp. (Coblentz, 1970), *F. americana* (Gottschalk and Marquis, 1982), and *Prunus serotina* (Arnold and Welch, 1996) (Fig. 4), as well as shrubs of *V. acerifolium* (Kribel et al., 2011) and *Vaccinium* spp. (Rawinski, 2008) (Fig. 5), we believe that browsing was a major factor leading to the changes we observed in the forest understory.

Interestingly, the mean abundance of urban saplings was nearly two-thirds greater than rural saplings in 1998 (Table 2). Deer browsing likely reduced sapling abundance in the rural plots prior to 1998, and deer populations have since expanded into urban plots, affecting saplings in those areas as well. Although it is unknown whether deer occur at similar densities in the urban and rural parks, overabundance of deer is an increasing concern throughout Maryland. In 1998, the deer population was estimated to be just under 250,000 statewide (Maryland Department of Natural Resources, 2009). In 2015, the deer population in Maryland was 214,000 (Maryland Department of Natural Resources, 2016). The deer population in both years was much greater than

Table 4
Species lost and gained to the urban and rural plot groups between 1998 and 2015 organized by vegetation type. Native species are identified with an *.

		Species Lost	Species Gained
Rural	_Tree/sapling_	_Castanea dentata_* _Fraxinus americana_* _Prunus serotina_* _Viburnum prunifolium_*	None
	Shrub	_Ilex verticillata_* _Rhododendron periclymenoides_* _Vaccinium angustifolium_* _Vaccinium stamineum_* _Viburnum dentatum_*	_Rosa multiflora_
	Vine	None	_Celastrus orbiculatus_ _Lonicera japonica_ _Toxicodendron radicans_*
	Herb	_Goodyera pubescens_* _Tipularia discolor_*	_Microstegium vimineum_
Urban	_Tree/sapling_	_Amelanchier candensis_* _Carpinus caroliniana_* _Carya cordiformis_* _Fraxinus americana_* _Magnolia macrophylla_* _Morus alba_ _Tilia Americana_*	_Ailanthus altissima_ _Cercis canadensis_* _Prunus avium_
	Shrub	_Rhododendron periclymenoides_* _Vaccinium_ sp.* _Viburnum dentatum_*	_Euonymus americanus_* _Vaccinium pallidum_* _Vaccinium corymbosum_*
	Vine	_Toxicodendron radicans_*	None
	Herb	_Actaea alba_* _Aralia nudicaulis_* _Collinsonia canadensis_* _Dennstaedtia punctilobula_* _Hepatica americana_* _Lycopus virginicus_* _Sanicula canadensis_* _Sanicula gregaria_* _Thalictrum dioicum_*	_Alliaria petiolata_ _Botrychium virginianum_* _Dioscorea villosa_* _Duchesnea indica_ _Erechtites hieraciifolius_* _Geranium_ sp. _Hackelia virginiana_* _Kummerowia striata_ _Polygonum cespitosum_ _Viola_ sp.

175,000, the number considered moderate (Brian Eyeler, Maryland Department of Natural Resources, personal communication). We regularly observed deer browsing the urban and rural plots, and evidence of browsing was extensive.

4.3. Consequences of understory shifts towards shade-tolerant and unpalatable species

Regeneration of tree species suggests that the forest canopy will be composed of more shade-tolerant species in the future. The prolific reproduction of *A. rubrum*, *N. sylvatica*, and *F. grandifolia* is consistent with numerous other studies reporting *Quercus* spp., *Carya* spp., and *L. tulipifera* replacement by more shade-tolerant and later successional species, changes driven by reductions in canopy disturbance (Abrams, 1990; Abrams, 1998; Nowacki and Abrams, 2008; Dawson, 2010; Hanberry et al., 2012; Hutchinson et al., 2012; McGarvey et al., 2013; Desprez et al., 2014). When canopy disturbance is low, the opportunity for overstory species that rely on periodic breaks in the canopy to regenerate is reduced (Runkle, 1982; Augspurger, 1984; Brokaw, 1987). In our plots, shade-intolerant *L. tulipifera* and intermediately shade-tolerant *Quercus* spp. (Burns and Honkala, 1990) were the most common sapling species in 1998, but were absent from that layer in 2015. Prolonged canopy closure combined with deer browsing likely contributed to the decline of these species. The absence of *Quercus* spp. and *L. tulipifera* in the sapling layer indicates that the regenerated canopy will look quite different in the next century if the closed canopy persists. If, however, disturbance opens the canopy, propagules of current canopy trees could germinate and grow to fill gaps or other seedlings that are shade-intolerant and survive the disturbance could reach canopy levels.

Changes in understory composition often result from browsed plants having reduced growth, fecundity (Augustine and Frelich, 1998), and survivorship (Long et al., 2007). Browsing limits the capacity for growth and reproduction, ultimately lowering the relative abundance of palatable species (Rooney, 2001). We suggest that the major structural (Fig. 2) and compositional (Fig. 5) changes in the shrub layer are also the result of preferential deer browsing. *V. acerifolium*, an important species to both plot-types in 1998, has been previously reported to be preferentially browsed by deer (Kribel et al., 2011). The relative proportion of *V. acerifolium* declined in both plot-types (Fig. 5), yet the rural plots experienced much greater overall structural declines (Fig. 2). The structural resilience of the urban shrub layer despite *V. acerifolium* losses is explained by proliferation of *L. benzoin* (Fig. 5d), a species avoided by deer due to the biochemical composition of its leaves and twigs (Rawinski, 2008). A shift from a *V. acerifolium* to a *L. benzoin* dominated shrub layer was also found in a study in neighboring Washington, D.C., that reported deer negatively impacted all major woody species, with the exception of *L. benzoin* and *F. grandifolia* (Rossell et al., 2007).

A forest health assessment conducted in Maryland noted that without controls of the local deer population or increased canopy openness, *Quercus* spp. reproduction will not be possible (Baltimore County EPS, 2007). Although it has been well established that *Quercus* spp. are being replaced by *A. rubrum* and *L. tulipifera* in forests throughout the Eastern United States (Abrams, 1998; Abrams, 2003; Horsley et al., 2003; Fei et al., 2011; Arthur et al., 2012; Dey, 2014), few studies have addressed whether urban forests are also experiencing this phenomena. Our study provides evidence that urban forests are also at risk of losing *Quercus* spp. dominance.

4.4. Resilient diversity in urban plots

The higher alpha diversity in urban plots in both survey years (Table 3) is in part consistent with findings that increased diversity is due to the naturalization of escaped non-native species (Kowarik, 2003; Schwartz et al., 2006; McDonnell and Hahs, 2008, McKinney, 2008). In our case, however, 50% of the species gained in the urban plots were native to the area (Table 4). Perhaps a better explanation for the relatively higher alpha diversities of the urban plots stems in part from loss of species from all plots (Fig. 6; Tables 3 and 4). We suggest that loss of understory species is the result of intense long-term browsing of palatable species, a finding echoed in numerous other studies (Frelich and Lorimer, 1985; Tilghman, 1989; Abrams, 1998; Rooney and Waller, 2003; Rooney and Waller, 2003; Côté et al., 2004; Begley-Miller et al., 2014; Bradshaw and Waller, 2016).

It has been proposed that small isolated forest fragments may be hyper-dynamic due to high species turnover from species loss coupled with influxes of species migrating from forest edges (Laurance, 2002). We suggest such a dynamic occurred in the urban plots, as these plots were located closer to forest edges than were the rural plots. As is typical in urban forests, the proportion of non-native species in the herb and vine layers of the urban plots was higher than in the rural plots (Table 2). As new species were added in the urban plots, beta diversity was maintained and beta turnover increased (Table 3). At the same time, beta diversity significantly declined over the sampling interval in the rural plots (Table 3), suggesting that species lost from the rural plots were unique to an individual plot, while species gained or retained were similar across all rural plots.

We found it interesting that homogenization of community composition was more apparent in the rural plots, given this process has been more typically linked with urban areas (Schwartz et al., 2006; McKinney, 2008; Groffman et al., 2014). Perhaps the ecological filtering effects of deer are more acute in areas with lower levels of migrating species, and greater exposure to non-native species, common in urban areas, may allow urban forests to maintain diversity despite deer

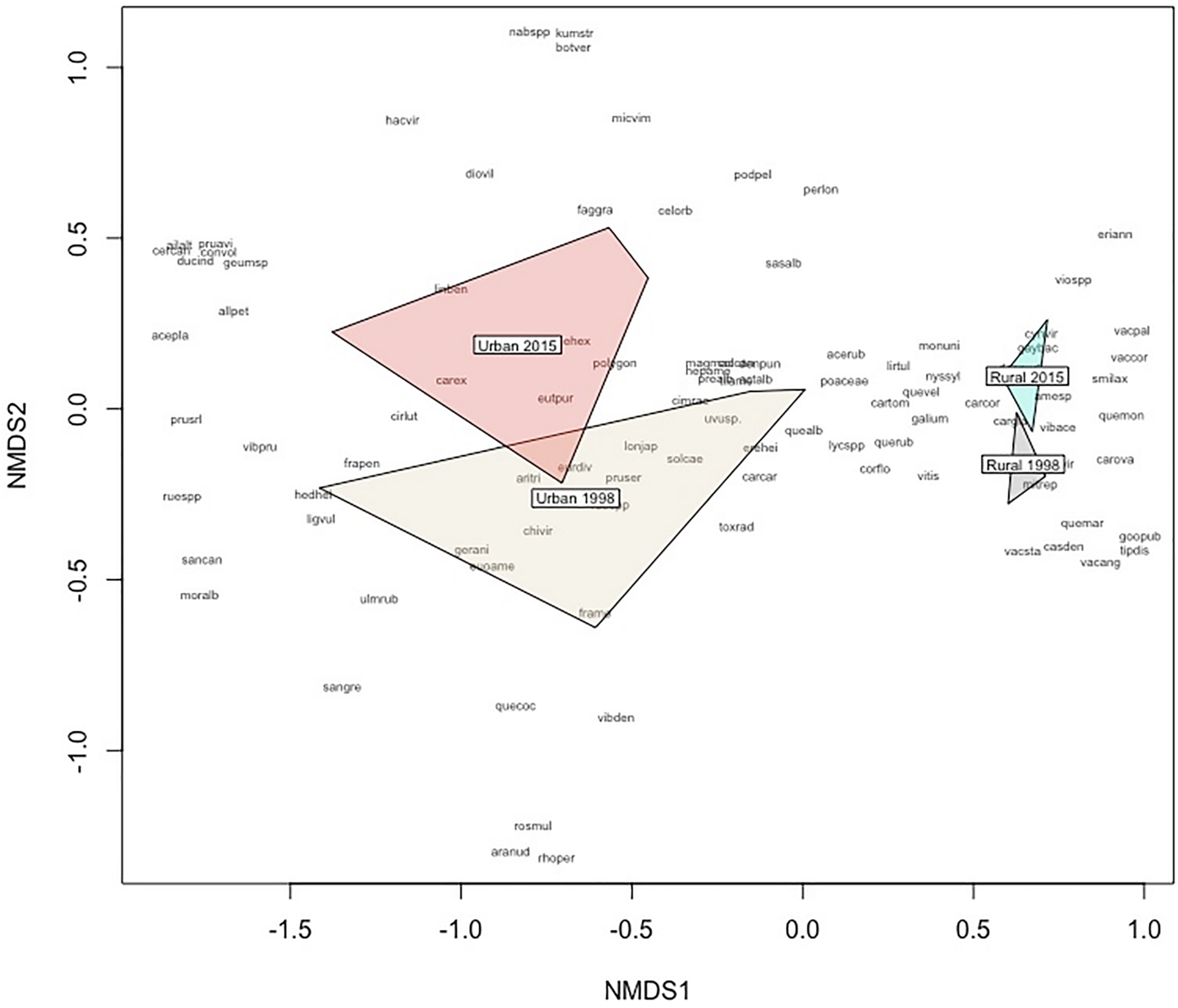

Fig. 6. Non-metric multidimensional scaling (NMDS) of the entire plant community composition. Convex hulls envelop points for the urban and rural plots in 1998 and 2015. Plot points are based on Bray-Curtis distance, calculated using relative abundance data for 98 taxa. The distance between the points represents compositional similarity, with closer points being more similar than points further apart. Stress value = 0.078. Species labels are the first three letters of the genus followed by the first three letters of the specific epithet. A species code key can be found in Appendix A.

browsing, infestation, and high canopy cover.

5. Conclusions

Our comparison of data from long-term plots showed that species turnover in the urban plots was nearly twice that of the rural plots. Turnover has important implications for the resilience of ecosystems (Allen et al., 2005). When species are lost and turnover is low, forest plant communities may become locally and regionally homogenized (Groffman et al., 2014; La Sorte et al., 2014). In this study, we suggest that presence of unpalatable species and higher exposure to novel species may allow urban forests to maintain diversity. Apart from sapling decline, overall plant abundance was more stable in the urban plots. The ability of an ecosystem to be structurally resilient due to high amounts of turnover suggests a functional role for diversity (Folke et al., 2004). Contrary to expectations, our results suggest that urban forests may be more resilient to environmental stress than rural forests.

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Appendix A. Species List

Code	Scientific Name	Common Name
ACEPLA	*Acer platanoides* L.	Norway maple
ACERUB	*Acer rubrum* L.	Red maple
ACTALB	*Actaea alba* Elliott	White baneberry
AILALT	*Ailanthus altissima* (Mill.) Swingle	Tree of heaven
ALLPET	*Alliaria petiolata* (M. Bieb.) Cav.& Grande	Garlic mustard
AMEARB	*Amelanchier arborea* (Michx. f.) Fernald	Common Serviceberry
AMECAN	*Amelanchier canadensis* (L.) Medik.	Canadian serviceberry
AMESPP	*Amelanchier* sp.	Serviceberry
ARANUD	*Aralia nudicaulis* L.	Wild Sarsaparilla
ARITRI	*Arisaema triphyllum* (L.) Schott	Jack in the pulpit
ATRSPP	*Atrichum* sp.	Moss
BERTHU	*Berberis thunbergii* DC.	Japanese barberry
BOTVIR	*Botrychium virginianum* (L.) Sw.	Rattlesnake fern
CARAMP	*Carex amphibola* Steud.	Eastern narrowleaf sedge
CARBLA	*Carex blanda* Dewey	Eastern woodland sedge
CARCAR	*Carpinus caroliniana* Walter	American hornbeam
CARCOR	*Carya cordiformis* (Wangenh.) K. Koch	Bitternut hickory
CAREX	*Carex* sp.	Sedge
CARGLA	*Carya glabra* (Mill.) Sweet	Pignut hickory
CAROVA	*Carya ovata* (Mill.) K. Koch	Shagbark hickory
CARTOM	*Carya tomentosa* (Lam.) Nutt.	Mockernut hickory
CASDEN	*Castanea dentata* (Marshall) Borkh.	American chestnut
CELORB	*Celastrus orbiculatus* Thunb.	Oriental bittersweet
CERCAN	*Cercis canadensis* L.	Eastern redbud
CHIVIR	*Chionanthus virginicus* L.	White fringetree
CIMRAC	*Cimicifuga racemosa* L.	Black bugbane
CIRLUT	*Circaea lutetiana* L.	Broadleaf enchanter's nightshade
COLCAN	*Collinsonia canadensis* L.	Northern horse-balm
CONVOL	*Convolvulaceae* sp.	Morning glory
CORFLO	*Cornus florida* L.	Flowering dogwood
CYNVIR	*Cynoglossum virginianum* L.	Wild comfrey
DENPUN	*Dennstaedtia punctilobula* (Michx.) T. Moore	Eastern hayscented fern
DESNUD	*Desmodium nudiflorum* (L.) DC.	Nakedflower ticktrefoil
DIOVIL	*Dioscorea villosa* L.	Wild yam
DUCIND	*Duchesnea indica* (Andrews) Teschem.	Indian strawberry
EREHEI	*Erechtites hieraciifolius* (L.) Raf. ex DC.	American burnweed
ERIANN	*Erigeron annuus* (L.) Pers.	Eastern daisy fleabane
EUOALT	*Euonymus alatus* (Thunb.) Siebold	Burningbush
EUOAME	*Euonymus americanus* L.	Bursting-heart
EUOSPP	*Euonymus* sp.	Euonymous
EURDIV	*Eurybia divaricate* (L.) G.L. Nesom	White wood aster
EUTPUR	*Eutrochium purpureum* (L.) E.E. Lamont	Sweetscented joe pye weed
FABSPP	*Fabaceae* sp.	Bean
FAGGRA	*Fagus grandifolia* Ehrh.	American beech
FRAME	*Fraxinus americana* L.	White Ash
FRAPEN	*Fraxinus pennsylvanica* Marshall	Green ash
GALCIR	*Galium circaezans* Michx.	Licorice bedstraw
GALIUM	*Galium* sp.	Bedstraw
GAYBAC	*Gaylussacia baccata* (Wangenh.) K. Koch	Black huckleberry
GERSPP	*Geranium* sp.	Geranium
GEUCAN	*Geum canadense* Jacq.	White avens
GEUMSP	*Geum* sp.	Avens
GOOPUB	*Goodyera pubescens* (Willd.) R. Br.	Downy rattlesnake plantain
HACVIR	*Hackelia virginiana* (L.) I.M. Johnst.	Beggarslice
HEDHEL	*Hedera helix* L.	English ivy
HEPAME	*Hepatica americana* (DC.) Ker-Gawl.	Round-lobed hepatica
ILEOPA	*Ilex opaca* Aiton	American holly
ILEVER	*Ilex verticillata* (L.) A. Gray	Winterberry
KUMSTR	*Kummerowia striata* (Thunb.) Schindl.	Japanese clover
LIGVUL	*Ligustrum vulgare* L.	European privet
LINBEN	*Lindera benzoin* (L.) Blume	Northern spicebush
LIRTUL	*Liriodendron tulipifera* L.	Tuliptree
LONJAP	*Lonicera japonica* Thunb.	Japanese honeysuckle
LYCSPP	*Lycopus* sp.	Clubmoss
LYCVIR	*Lycopus virginicus* L.	Virginia water horehound
MAGMAC	*Magnolia macrophylla* Michx.	Bigleaf magnolia
MEDVIR	*Medeola virginiana* L.	Indian cucumber
MICVIM	*Microstegium vimineum* (Trin.) A. Camus	Japanese stiltgrass
MITREP	*Mitchella repens* L.	Partridgeberry
MONUNI	*Monotropa uniflora* L.	Indianpipe
MORALB	*Morus alba* L.	White mulberry
NABSPP	*Nabalus* sp.	Rattlesnakeroot
NYSSYL	*Nyssa sylvatica* Marshall	Blackgum
PARQUI	*Parthenocissus quinquefolia* (L.) Planch.	Virginia creeper
PERLON	*Polygonum cespitosum* Blume var. *longisetum* (Bruijn) A.N. Steward	Oriental lady's thumb
PHEHEX	*Phegopteris hexagonoptera* (Michx.) Fée	Broad beechfern

POACEAE	*Poaceae* sp.	Grass
PODPEL	*Podophyllum peltatum* L.	Mayapple
POLYGON	*Polygonatum* sp.	Solomon's seal
PREALB	*Prenanthes alba* L.	White rattlesnakeroot
PRUAVI	*Prunus avium* L.	Sweet cherry
PRUSER	*Prunus serotina* Ehrh.	Black cherry
PRUSRL	*Prunus serrulata* Lindl.	Japanese flowering cherry
QUEALB	*Quercus alba* L.	White oak
QUECOC	*Quercus coccinea* Münchh.	Scarlet oak
QUEMAR	*Quercus marilandica* Münchh.	Blackjack oak
QUEMON	*Quercus montana* Willd.	Chestnut oak
QUERUB	*Quercus rubra* L.	Northern red oak
QUEVEL	*Quercus velutina* Lam.	Black oak
RHOPER	*Rhododendron periclymenoides* (Michx.) Shinners	Pink azalea
ROSMUL	*Rosa multifora* Thunb.	Multiflora rose
ROSSPP	*Rosaceae* sp.	Rose
RUBFLA	*Rubus flagellaris* Willd.	Northern dewberry
RUBPEN	*Rubus pensilvanicus* Poir.	Pennsylvania blackberry
RUBPHO	*Rubus phoenicolasius* Maxim.	Wine raspberry
RUBPUB	*Rubus pubescens* Raf.	Dwarf red blackberry
RUBSPP	*Rubus* sp.	Blackberry
RUESPP	*Rue* sp.	Rue
SANCAN	*Sanicula canadensis* L.	Canadian blacksnakeroot
SANGRE	*Sanicula gregaria* E.P. Bicknell	Common blacksnakeroot
SASALB	*Sassafras albidum* (Nutt.) Nees	Sassafras
SMILAX	*Smilax rotundifolia* L.	Roundleaf greenbrier
SOLCAE	*Solidago caesia* L.	Wreath goldenrod
THADIO	*Thalictrum diocicum* L.	Early meadow-rue
TILAME	*Tilia americana* L.	American basswood
TIPDIS	*Tipularia discolor* (Pursh) Nutt.	Cranefly orchid
TOXRAD	*Toxicodendron radicans* (L.) Kuntze	Eastern poison ivy
UKNSPP	*Unknown species*	
ULMRUB	*Ulmus rubra* Muhl.	Slippery elm
UVUSES	*Uvularia sessilifolia* L.	Sessileleaf bellwort
UVUSP.	*Uvularia* sp.	Bellwort
VACANG	*Vaccinium angustifolium* Aiton	Lowbush blueberry
VACCOR	*Vaccinium corymbosum* L.	Highbush blueberry
VACPAL	*Vaccinium pallidum* Aiton	Blue Ridge blueberry
VACSPP	*Vaccinium* sp.	Blueberry
VACSTA	*Vaccinium stamineum* L.	Deerberry
VIBACE	*Viburnum acerifolium* L.	Mapleleaf viburnum
VIBDEN	*Viburnum dentatum* L.	Southern arrowwood
VIBPRU	*Viburnum prunifolium* L.	Blackhaw
VIOHIR	*Viola hirsutula* Brainerd	Southern woodland violet
VIOSPP	*Viola* sp.	Violet
VITAES	*Vitis aestivalis* Michx.	Summer grape
VITRIP	*Vitis riparia* Michx.	Riverbank grape
VITSPP	*Vitis* sp.	Grape

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