

## Article

# Twenty Years of Urban Reforestation: Overstory Development Structures Understory Plant Communities in Lexington, KY, USA

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**Abstract:** Urban forests provide critical ecosystem services in an increasingly urbanized global landscape. The reforestation of undeveloped parcels and serially mowed grasslands can increase urban forest cover, but plant community development in planted urban forests is poorly understood. We conducted a study to elucidate the roles of time since tree planting, invasive species abundance, and other abiotic and biotic site-level factors in structuring understory plant communities within a 20-year chronosequence of planted urban forests in Lexington, KY, USA. We assessed the percent of groundcover of all understory species in fixed-radius plots on the site. Understory herbaceous plant communities demonstrated shifts from graminoid dominance to forb dominance over time, and plant communities in successively younger sites were increasingly dissimilar from that of the 20-year-old site. Invasive plant species were abundant, representing 21% of total groundcover across all surveyed plots, and became increasingly prevalent over time. Understory plant diversity was negatively associated with invasive species abundance. Overall, site factors, including time since planting, forest canopy closure, density of tree and shrub reproduction, and soil pH, accounted for much of the variability among understory communities. Understory plant communities across the chronosequence of planted sites demonstrated apparent structural shifts with overstory canopy development, but the increasing prevalence of invasive species and their negative impacts to plant diversity warrant future management to ensure the continuation of the desired successional trajectories.

**Keywords:** afforestation; reforestation; forest succession; rewilding; urban parks



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## 1. Introduction

The global population is becoming increasingly concentrated in urban areas, with 70% of the world's population [1] and 87% of the US population [2] expected to live in urban areas by 2050. Urban development is associated with a suite of negative ecological effects. Urbanization compromises soil [3,4], air [5], and water [6] quality, and elevates air [7] and water temperature [8]. Urban forests tend to be highly fragmented [9] and experience significant pressure from introduced species [10]. Urban wildlife populations often experience poor habitat quality [11] and connectivity [12], and have higher disease burden [13]. Due to impervious surface area, urban watersheds experience low infiltration and high surface runoff rates, increasing peak flow and reducing time to peak in urban streams [14]. Given the scope of these impacts and the increasing global significance of urbanization, it is imperative that we conduct new urban development more sustainably, and explore ways to improve and restore ecosystem health in existing cities.

One pathway to ecological restoration in urban areas is reforestation. Reforestation can occur naturally through the process of secondary succession, in which plant communities pass through a predictable sequence of seral stages on their way to the climax community, maintained by the given climatic and disturbance regimes [15]. In urban and peri-urban

areas, this process occurs in vacant or abandoned lots [16], or abandoned agricultural fields. In addition, this process can be accelerated by planting later-successional trees that would be typical of the climax community during the initial reforestation efforts [17]. However, given the various impairments characteristic of urban areas, planted urban forests may not follow the same developmental trajectory as planted forests in more rural spaces.

The Reforest the Bluegrass program (RTB), coordinated by the Lexington-Fayette Urban County Government (LFUCG) for over twenty years in Lexington, Kentucky, USA, is an example of an effort to augment ecological restoration through tree planting. As of 2020, LFUCG reports that the program has planted over 150,000 trees in 20 sites within the Lexington urban service boundary [18]. Lexington is situated within the Inner Bluegrass physiographic province of Kentucky, USA, characterized by rolling hills and fertile soils arising from Ordovician limestone [19]. Although much of the region has been developed for agricultural or urban/suburban land-use, the vegetation community typical of the region prior to European settlement was an open woodland, dubbed the Bluegrass Savanna. This woodland was dominated by trees, such as *Fraxinus quadrangulata* Michx. (blue ash), *Quercus macrocarpa* Michx. (bur oak), *Quercus muhlenbergii* Engelm. (chinkapin oak), and *Quercus shumardii* Buckland (Shumard oak), and is thought to have been maintained by fire and grazing [20]. Understory vegetation in these savannahs included rich canebrakes (*Arundinaria gigantea* [Walter] Muhl.), native warm-season grasses, and legumes that provided valuable forage for grazing animals, including *Bison bison* L. (American bison). After the exclusion of fire and the reduced importance of grazing by bison and other large ungulates, the abundance of these precolonial ecosystems has declined. In the absence of fire, fire-intolerant species are becoming increasingly important in forests across the eastern US, restricting recruitment of species less tolerant of shade, such as the once-dominant oaks (*Quercus* spp.) and hickories (*Carya* spp.) [21,22]. This background shift in the disturbance regime is further exacerbated by ongoing anthropogenic climate change [23] and various insect and disease outbreaks [24,25], which are expected to further alter the developmental trajectory of forests in the region.

Prior to tree planting, RTB sites were serially mowed urban grasslands, and, thus, understory plant communities began as open grassland/pasture, dominated by cool-season grasses and legumes. However, as trees formed a closed canopy upon entering the stem-exclusion stage of stand development, plant communities were expected to shift over time to shade-tolerant understory species characteristic of mature forests. However, while understories of intact forest remnants in the Inner Bluegrass are often quite diverse [26], it is unclear whether, and at what timescale, these diverse understory plant communities will recover on their own in planted forest sites. As Bartha et al. [27] noted, understory plant colonization rates decline after canopy formation in old field succession, potentially limiting the ability of passive restoration to support the recovery of native plant communities. Furthermore, as Oldfield et al. [17] describe, longer-term studies are critical to understand how plant communities develop in planted urban forests over time.

While not exclusively an urban problem, invasive plants tend to be particularly problematic in urban and periurban areas [28,29]. Many plants now considered invasive were once introduced intentionally as ornamentals or as street or other landscape trees [30]. In this region, *Pyrus calleryana* Decne. (Callery pear) and *Lonicera maackii* (Rupr.) Maxim. (Amur honeysuckle) are among the most common invasive woody plants and are associated with a host of ecological impacts [31,32]. While both *Lonicera maackii* and *Pyrus calleryana* are important in our study sites, this paper is focused on non-tree-forming and shrub-forming species, such as *Euonymus fortunei* [Turcz.] Hand.-Maz (purple wintercreeper) and *Alliaria petiolata* [M.Bieb.] Cavara and Grande (garlic mustard). Still available for sale in nurseries [33], *Euonymus fortunei* is a trailing vine that forms a dense mat on the forest floor. *Euonymus fortunei* possesses adaptations, such as extended phenology [34] and animal-assisted seed dispersal [35], that help it outcompete native flora [36]. Intentionally introduced as an herb in the 1800s, *Alliaria petiolata* produces allelopathic and anti-herbivory

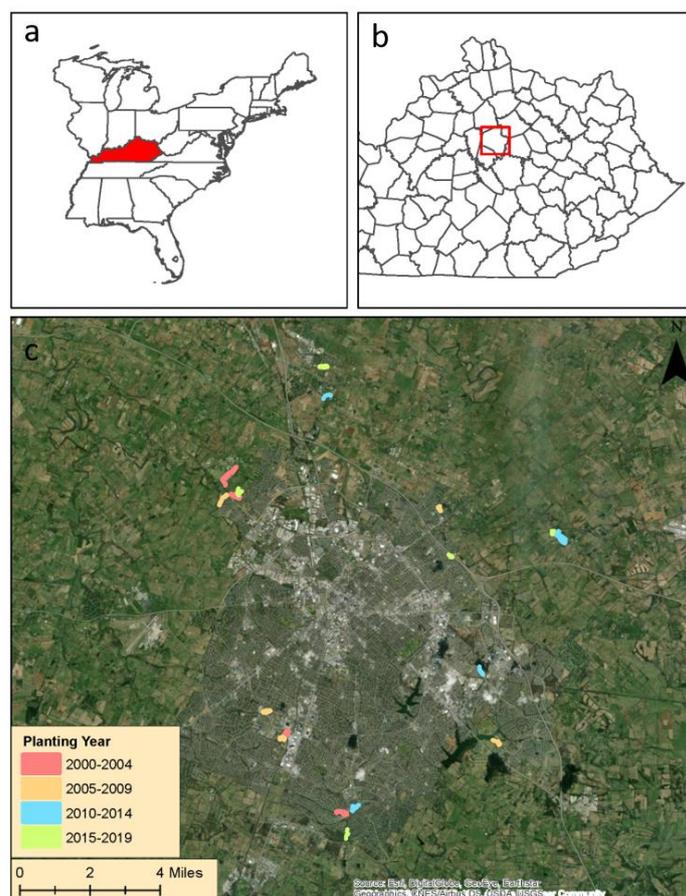
compounds and further benefits from the absence of natural predators, early phenology, and high reproductive output [37], which aid in its outcompeting of native flora [38].

Thus, while urban reforestation is of great interest for alleviating the negative ecological effects of urbanization, forest development on these sites over time is not well understood. Because urban forests are particularly vulnerable to invasive species, plant communities in planted urban forests may not develop similarly to non-urban sites, and ongoing management focused on understory plants may be required to assist community recovery. This study evaluated plant communities in planted forests in Lexington, KY, USA, focusing on three research questions: (1) to what extent does understory plant diversity change with the time since tree planting?; (2) how do non-native invasive species influence the structure of the understory plant community?; and (3) how do forest development and other site-level factors shape understory community assemblages? Plant communities were characterized by visually assessing groundcover of all plants not forming trees or shrubs in fixed-radius plots in each of the twenty planted urban forests planted between 1999 and 2019.

## 2. Materials and Methods

### 2.1. Study Sites

The urban forest sites surveyed during this study were planted as part of the RTB program and represent an annual chronosequence of forest ages planted between 1999 (Cold Stream Park) and 2019 (Masterson Station Park; Figure 1).



**Figure 1.** Reforest The Bluegrass planting sites in Lexington, KY, USA. (a) The location of Kentucky within the eastern USA; (b) the location of Fayette County within the eastern half of KY; (c) the distribution of Reforest The Bluegrass sites across the city of Lexington. Sites were planted annually between 2000 and 2019. Figure from Sena et al. (2021).

Because the Cold Stream site was recently disturbed as part of a stream restoration project, this site was excluded from our analysis, yielding 20 total sites representing continuous tree plantings from 2000 to 2019. Prior to planting, all sites were urban grasslands maintained by mowing, nearly all of which are within city parks managed by LFUCG. Planting approaches varied slightly over time. Earlier sites were located primarily in riparian and floodplain areas, and trees were planted in blocks of species based on site preferences: for example, *Taxodium distichum* (L.) Rich. (baldcypress) was planted nearest to streams, but upland *Quercus* spp. were planted in the more upland blocks. However, over time, planted sites expanded to more upland areas, and species were more evenly distributed across sites. All planted trees were native to Kentucky and were nursery-grown 1–0 bare-root seedlings. Trees were planted on 1.2 m × 1.2 m or 1.8 m × 1.8 m spacings, depending on the year. Volunteers planted trees using a tree spade or dibble bar, and weed-barrier mats approximately 1 m<sup>2</sup> were installed around the trees after planting to promote growth and survival.

## 2.2. Sampling

Permanent vegetation monitoring plots were established in all RTB sites in summer 2020. The number of plots established in each site was generally proportional to site area, but a minimum of 3 plots were established in each site (mean ± SD: 4.6 ± 2.5 plots; max = 9). Plot centers were located at least 19.8 m from one another and from the site edge to avoid edge effects. LFUCG has an active invasive species management program, and patches undergoing invasive species management were avoided to remove biases associated with management. Each monitoring plot featured a nested plot design in which a 0.008-ha circular plot was delineated to survey trees ≥ 2.5 cm diameter at breast-height (dbh) and a 0.002-ha circular plot was delineated to survey understory trees and shrubs < 2.5 cm dbh; both plots were concentric on the plot center. Woody plant data are available from Jacobs et al. [39]. To survey the herbaceous understory plant community, a 0.6-m × 0.6-m grid was randomly tossed 10 times within the 0.008-ha plot, avoiding overlapping. All plants present within the grid (excluding woody tree-forming and shrub-forming plants) were identified to the lowest taxonomic level possible according to Jones [40]; the abundance of each species present within a grid was visually estimated as the percent of groundcover in 5% intervals.

Composite soil samples, aggregated from five subsamples of the top 10 cm, were collected within each 0.002-ha plot. Soil samples were analyzed for pH [41], P [42], K, Ca, Mg, Zn [43], texture [44,45], total C [46], and total N (analyzed using a LECO combustion instrument) by the University of Kentucky Regulatory Services Soils Laboratory. The soil sampling and analytical methods, and the results, are described in Sena et al. [47]. Soil data are available from Jacobs et al. [48].

## 2.3. Statistical Analysis

### 2.3.1. Chronosequence Diversity Patterns

We calculated a series of alpha and beta diversity metrics to investigate patterns in the development of the understory plant community across the chronosequence of RTB planting sites. To compare diversity metrics among sites, we first performed rarefaction to account for differences in sampling intensity across sites. Rarefaction entailed drawing 10,000 bootstrapped resamples of the intensity of the least-sampled site from target datasets and calculating the metric of interest; the mean of the bootstrapped distribution was used as the rarefied estimate [49–51]. To evaluate temporal trends in alpha diversity, we first calculated rarefied estimates of species richness, the Shannon diversity index, and the Simpson diversity index for each plot; then, we evaluated the relationship of each metric with planting year using non-parametric Spearman rank correlations ( $\rho$ ) via functions in the *stats* package of the R programming language [52].

To quantify the temporal divergence of herbaceous species assemblages across the range of forest ages, we calculated the pairwise Jaccard Distance between the species

observed in the 2000 planting site and those observed in each of the other planting sites. The Jaccard Distance is a measure of beta diversity and quantifies the dissimilarity in species assemblages between two communities, ranging from 0 (i.e., all species are common between the communities) to 1 (i.e., the communities have unique species). To characterize the extent of the relationship between the Jaccard Distance and the planting year, we regressed the Jaccard Distance by planting year using ordinary least squares simple linear regression, executed using functions in the R package *stats*. Year was centered and standardized to have a mean of 0 and standard deviation of 1 prior to modeling [53], and a probit transformation of the Jaccard Distance was performed to satisfy the model's normality assumption. We also fit models with second-degree and third-degree polynomial effects of year and compared all models via Akaike's information criterion, corrected for a small sample size ( $AIC_c$ ), using functions in the R package *MuMIn* [54] and residual standard error. Since the simple linear regression possessed the lowest  $AIC_c$  (year = 13.8, year 2 = 16.9, year 3 = 20.0) and lowest residual standard error (year = 0.3, year 2 = 0.31, year 3 = 0.31), we selected the simple linear regression as our final model. After validating the regression diagnostics of the final model, we evaluated the significance of the yearly effect and the amount of variation in the pairwise Jaccard Distances, controlled by net annual change via the coefficient of determination ( $R^2$ ).

Since changes in the dominance of plant functional groups are characteristic of forest succession, we analyzed temporal relationships in groundcover dominance among functional groups. We classified observed taxa into one of three functional groups: forbs, graminoids, and vines. Graminoids comprised the families *Cyperaceae* (sedges), *Juncaceae* (rushes), and *Poaceae* (grasses), while woody species with a vining habit were classified as vines. All other non-woody taxa were classified as forbs. Data on woody tree-forming and shrub-forming species were evaluated in Sena et al. [47], and were not collected in groundcover estimates. The groundcover percentage of each functional group was calculated by planting year, visualized, and evaluated for temporal relationships using Spearman rank correlations.

### 2.3.2. Invasive Plant Species Prevalence

During preliminary site surveys, we found that invasive plant species formed a large component of the understory in many RTB sites. To examine the importance and temporality of invasive species in the understory across the chronosequence, we calculated the percent of groundcover comprised by invasive species within each plot, and evaluated the Spearman rank correlation between planting year and percent invasive species. Further, we examined the influence of invasive species prevalence on local understory diversity. Since the relationship between invasive species prevalence and plant diversity appeared nonlinear, we modeled rarefied estimates of species richness, the Shannon diversity index, and the Simpson diversity index as the response variable in individual generalized additive mixed models, with the percent of invasive species as the explanatory variable using functions in the R package *mgcv* [55]. Planting year was included in all models as a random effect. For each response variable, we fit two models: a model with a linear effect of invasive species prevalence and a model that fit the effect of invasive species prevalence using a penalized cubic regression smoothing spline; smoothing parameters of splines were estimated using a generalized cross validation procedure. We calculated  $AIC_c$  to select the better model for each response variable. Models with a spline term for the effect of invasive species prevalence were the better supported models for all diversity metrics. After validating the regression diagnostics of the selected models, we evaluated the significance of the effect of invasive species prevalence on each diversity metric.

### 2.3.3. Nonmetric Multidimensional Scaling

To investigate the influence of site characteristics on the variation within the understory community, we performed nonmetric multidimensional scaling (NMDS). Importance values (IV) of each taxon were calculated by plot, per the following formula:

$$IV = \left( \frac{\text{Total groundcover of taxon in all grids}}{\text{Total plant groundcover in all grids}} + \frac{\text{Grids where taxon was present}}{10} \right) \times 100$$

Under this formulation, the range of possible IVs per plot is 0 to 200. The mean IV of each taxon was calculated by site to serve as the estimate of site-level importance. Taxa with mean IV < 10 were excluded from the analysis. Bray–Curtis distances were calculated from mean IVs of taxa at each site for use in NMDS. To select an appropriate number of NMDS axes, we performed ordinations with between two and five axes and selected the ordination with the minimum number of axes for which the stress < 0.2. For each ordination, we calculated linear and nonmetric fit statistics ( $R^2$ ) and visualized the correspondence of the observed dissimilarity and modeled ordination distance using Shepard diagrams. After selecting a final ordination, we calculated Spearman rank correlations to determine the association between continuous site covariates and NMDS axes, and performed a non-parametric analysis of similarities (ANOSIM) with 10,000 permutations, in order to evaluate differences among factor levels of categorical covariates. Site covariates included woody plant community metrics and soil characteristics, summarized in Sena et al. [47], and landscape metrics, including the topographic wetness index and the percent of developed landcover within 1 km of the planting sites (Table 1). Landscape metrics were derived using ArcGIS 10.7 (ESRI, Redlands, CA, USA), the National Elevation Dataset, and the 2019 National Land Cover Database (products courtesy of U.S. Geological Survey). Covariates demonstrating significant non-zero correlations with NMDS axes (continuous) or separation among factor levels (categorical) were considered important drivers of dissimilarity in understory community structure among sites. After selecting a subset of site covariates, we fit the continuous site covariates to the ordination to analyze linear relationships between covariates and NDMS axes. All analyses pertaining to NMDS were performed using functions in the R package *vegan* [56]. All statistical tests were performed at  $\alpha = 0.05$ .

**Table 1.** Descriptions and summary statistics of site covariates in Reforest The Bluegrass sites planted annually between 2000 and 2019 in Lexington, KY, USA. Methods describing the collection and analyses of these data are available in Sena et al. [47].

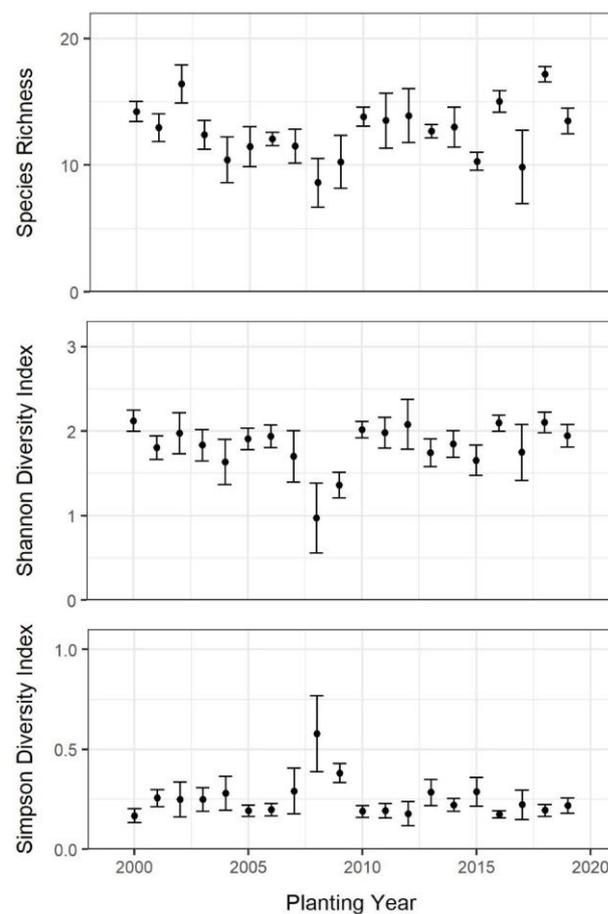
Covariate	Description (Units)	Mean $\pm$ SE (Extrema)
Basal Area	Basal area of plantation ( $\text{m}^2 \text{ha}^{-1}$ )	9.4 $\pm$ 0.9 (0, 39.9)
Carbon	Soil carbon concentration (%)	3.5 $\pm$ 0.1 (1.4, 6.7)
Calcium	Soil calcium concentration ( $\text{mg kg}^{-1}$ )	3126.9 $\pm$ 127.1 (918.5, 7024.0)
Canopy	Presence of open or closed canopy (Sena-et al., 2021)	-
Clay	Soil clay content (%)	15.0 $\pm$ 0.4 (0.6, 30.5)
Developed	Developed landcover within 1 km (%)	59.7 $\pm$ 0.03 (3.7, 98.6)
Magnesium	Soil magnesium concentration ( $\text{mg kg}^{-1}$ )	213.0 $\pm$ 6.9 (69.0, 497.5)
Nitrogen	Soil nitrogen concentration (%)	0.3 $\pm$ 0.01 (0.1, 0.6)
pH	Soil pH	5.6 $\pm$ 0.1 (4.0, 7.1)
Phosphorus	Soil phosphorus concentration ( $\text{mg kg}^{-1}$ )	161.8 $\pm$ 8.0 (16.5, 400.0)
Potassium	Soil potassium concentration ( $\text{mg kg}^{-1}$ )	149.3 $\pm$ 7.5 (42.5, 353.0)
Sand	Soil sand content (%)	16.4 $\pm$ 0.4 (9.0, 33.6)
Silt	Soil silt content (%)	68.6 $\pm$ 0.6 (41.0, 80.0)
TWI	Topographic wetness index	6.1 $\pm$ 0.02 (5.6, 6.7)
Woody Density	Density of woody stems with tree/shrub architecture ( $\text{stems ha}^{-1}$ )	3928 $\pm$ 3812 (0, 17,297)
Woody Height	Height of woody stems with tree/shrub architecture (cm)	98.8 $\pm$ 6.1 (0, 285)
Year	Year of tree planting	(2000, 2019)
Zinc	Soil zinc concentration ( $\text{mg kg}^{-1}$ )	6.2 $\pm$ 1.1 (1.1, 102.5)

### 3. Results

Across RTB sites planted between 2000 and 2019, we identified understory plants comprising 107 species, 92 genera, and 34 families. *Euonymus fortunei*, a non-native invasive species, was the most encountered species, accounting for 13% of total sampled ground-cover across all sites. *Festuca* spp. (fescue) and *Poa pratensis* L. (Kentucky bluegrass) were the second and third most encountered species, representing 7% and 6% of groundcover, respectively.

#### 3.1. Chronosequence Diversity Patterns

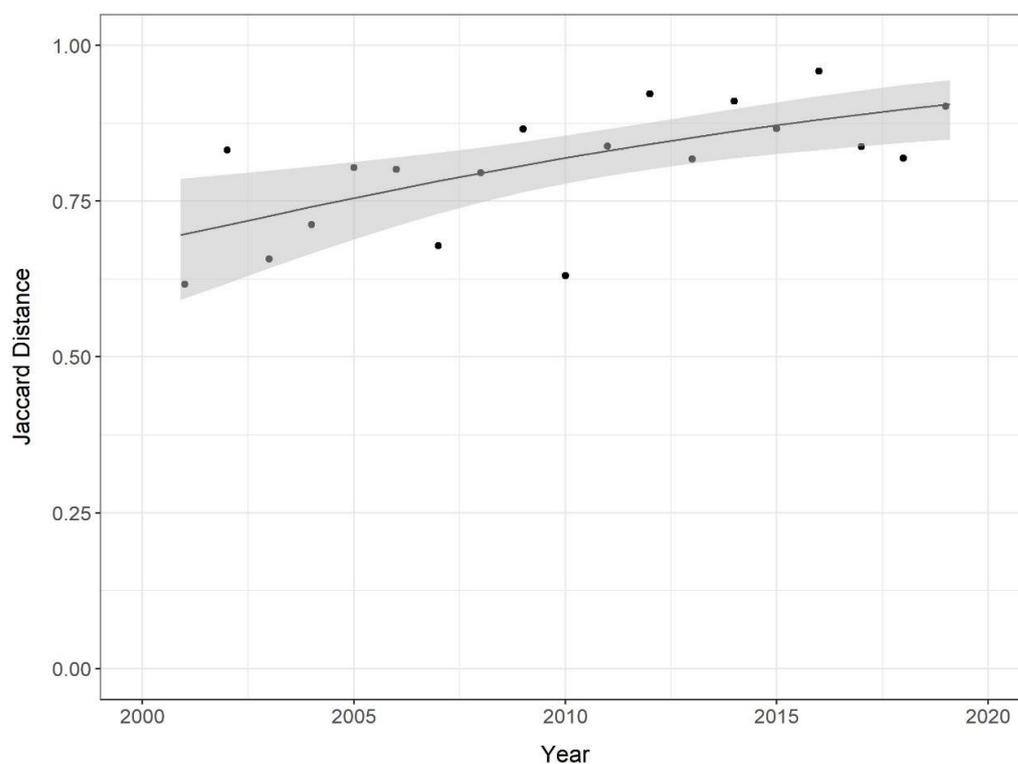
Among all sites, species richness was  $14.9 \pm 0.6$  species (mean  $\pm$  SE), and the mean Shannon and Simpson diversity indices were  $1.86 \pm 0.06$  and  $0.25 \pm 0.02$ , respectively. Spearman rank correlations of planting year with rarefied species richness ( $\rho = -0.04$ ,  $p = 0.67$ ), Shannon diversity index ( $\rho = -0.04$ ,  $p = 0.68$ ), and Simpson diversity index ( $\rho = 0.04$ ,  $p = 0.68$ ) indicated no evidence of temporal patterning in understory alpha diversity in RTB sites (Figure 2). Although alpha diversity was similar among sites, the diversity of the 2008 planting site was marginally lower than that of other sites, as evidenced by a lower mean Shannon index and higher mean Simpson index; this reduction in diversity resulted from the dominance of *Euonymus fortunei* in the understory of this site.



**Figure 2.** Rarefied estimates (mean  $\pm$  95% CI) of species richness, the Shannon diversity index, and the Simpson diversity index of understory plant communities along the 20-year chronosequence of Reforest The Bluegrass plantings in Lexington, KY, USA.

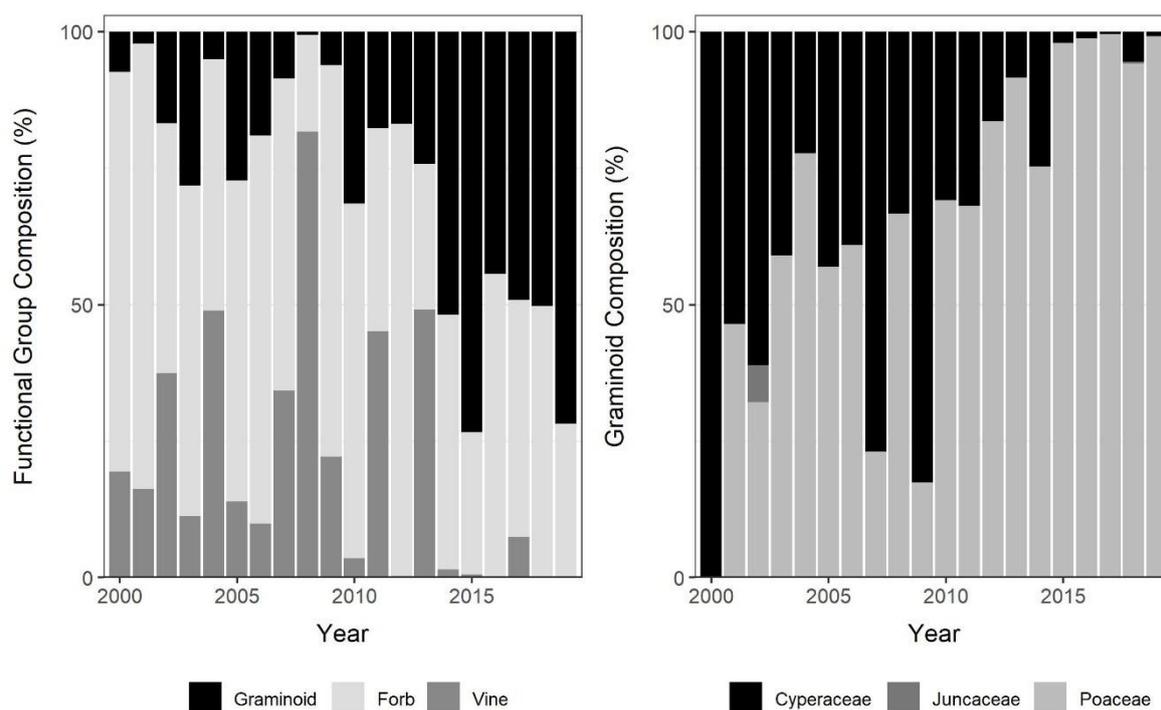
Conversely, a positive effect of planting year was apparent in the pairwise Jaccard Distance between the community assemblages in 2000 and those in successively younger planting sites ( $\beta_{\text{Year}} = 0.25$ ,  $p = 0.003$ ; Figure 3). This indicates that understory community composition is increasingly dissimilar, with an annual change in plantation age. The effect

of planting year accounted for nearly half of the variability in the pairwise Jaccard Distance of understory assemblages ( $R^2 = 0.42$ ). The mean Jaccard Distance between the assemblages of sites planted in 2000 and 2019 approached 0.9, identifying a near-complete disjunction of species compositions between the sites; the maximum observed pairwise Jaccard Distance was 0.96 with the 2016 planting site. Notably, the assemblages between the sites planted in 2000 and 2001 possessed a Jaccard Distance of 0.62, indicating only a 38% overlap in understory species between the two oldest planting sites.



**Figure 3.** Effect of planting year (regression mean  $\pm$  95% CI) on the Jaccard Distance between understory plant assemblages in the Reforest The Bluegrass site planted in 2000 (i.e., the oldest site) and in other planting sites. When the Jaccard Distance = 0, community assemblages are identical, while a Jaccard Distance = 1 indicates complete separation between the communities.

The relative composition of plant functional groups in RTB sites varied significantly with time. Graminoids were positively correlated with planting year ( $\rho = 0.73$ ,  $p < 0.001$ ), possessing the greatest percentage of groundcover in recent planting sites (Figure 4). Among the graminoids, the relative composition of *Poaceae* increased with planting year, while *Cyperaceae* was more abundant in older plantings; *Juncaceae* occurred in only three plots across two sites (2002 and 2018) and represented less than 5% of groundcover in these plots (Figure 4). In contrast to graminoids, forbs ( $\rho = -0.46$ ,  $p = 0.04$ ) and vines were negatively correlated with year ( $\rho = -0.6$ ,  $p = 0.006$ ; Figure 4), indicating an increased prevalence of both groups in older plantings. Species characterizing woody vines included *Campsis radicans* (L.) Seem. ex Bureau (trumpet vine), *Euonymus fortunei*, *Lonicera japonica* Thunb. (Japanese honeysuckle), *Parthenocissus quinquefolia* (L.) Planch. (Virginia creeper), *Toxicodendron radicans* (L.) Kuntze (poison ivy), and *Vitis* spp., although *Euonymus fortunei* comprised 87% of the group's coverage across all sites.

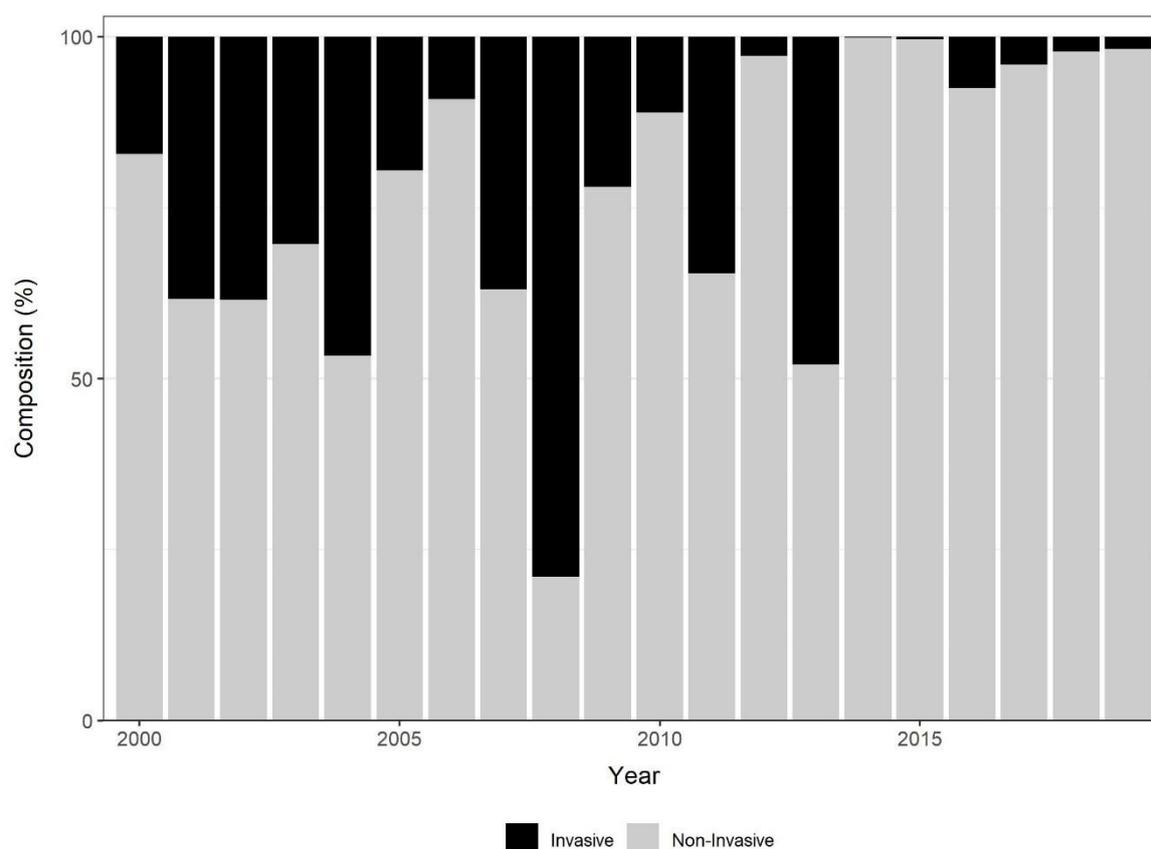


**Figure 4.** Composition (%) of plant functional groups and graminoids by family along the 20-year chronosequence of Reforest The Bluegrass plantings in Lexington, KY, USA.

### 3.2. Invasive Species Prevalence

We identified six non-native invasive species occupying understory communities in RTB sites: *Alliaria petiolata*, *Euonymus fortunei*, *Lespedeza cuneata* (Dum. Cours.) G. Don (sericea lespedeza), *Lonicera japonica*, *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass), and *Sorghum halepense* (L.) Pers (Johnsongrass). These species accounted for 21% of total groundcover across all sites. *Euonymus fortunei* and *Alliaria petiolata* comprised 68% and 27% of the invasive component, respectively. The importance of invasive species in the understory decreased with planting year ( $\rho = -0.56$ ,  $p < 0.001$ ), and increased markedly at the onset of canopy closure (2013; Figure 5). Between 2000 and 2013, understory composition of invasive species generally ranged from 25% to 50%. The species importance varied across the chronosequence, according to shade tolerance: *Sorghum halepense* was most abundant in years  $\geq 2016$ , but was replaced in older plantings largely by *Alliaria petiolata* and *Euonymus fortunei*.

Generalized additive mixed models identified a significant nonlinear effect of invasive species prevalence on species richness, the Shannon diversity index, and the Simpson diversity index (Table 2). Invasive species prevalence comprised more than 50% of the variability in the Shannon and Simpson diversity indices (Table 2). All metrics indicated a general reduction in alpha diversity in the understory community, with an increased prevalence of invasive species (Figure 6). Diversity was highest when invasive species comprised  $< \sim 25\%$  of groundcover, remaining largely stable over this interval; however, diversity declined rapidly with a greater prevalence of invasive species.



**Figure 5.** Composition (%) of non-native invasive species along the 20-year chronosequence of Reforest The Bluegrass plantings in Lexington, KY, USA.

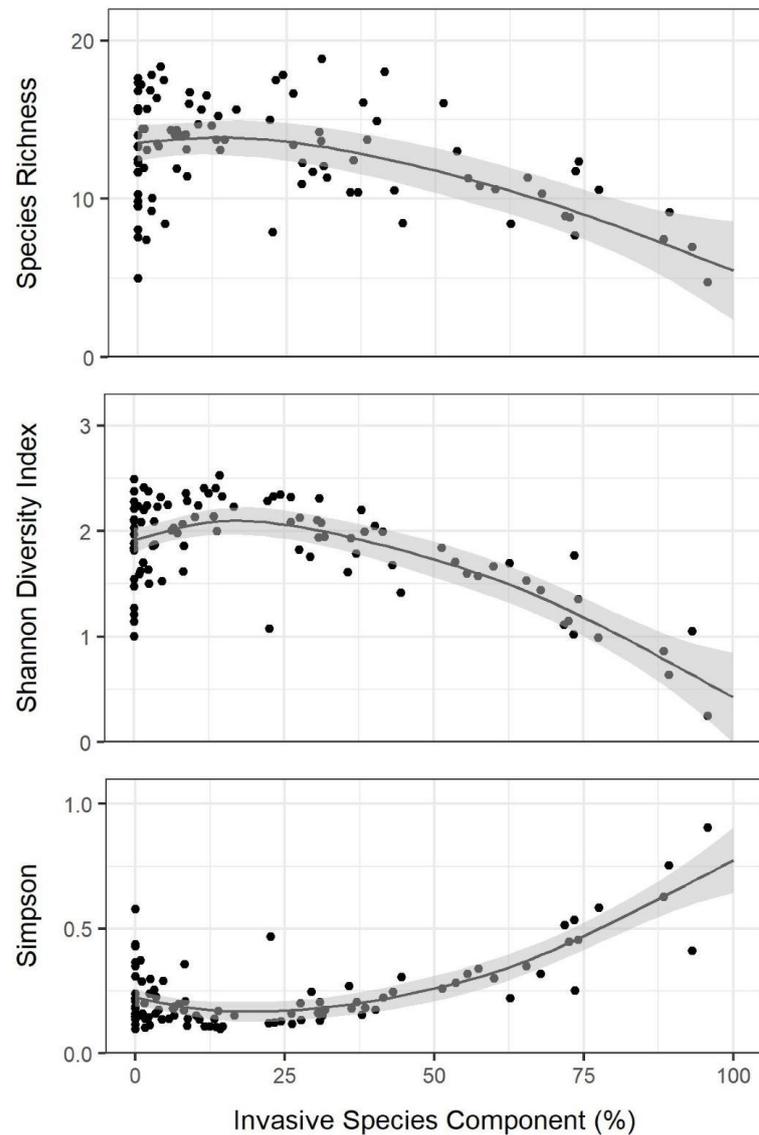
**Table 2.** Fit statistics of generalized additive mixed models with alpha diversity metrics as the response variable and a smoothing spline effect of percent groundcover occupied by invasive species in Reforest the Bluegrass planting sites in Lexington, KY, USA. EDF = effective degrees of freedom of the smoothing spline; F = F test statistic used in an approximate hypothesis test for the significance of the effect of invasive species component, and  $p$  =  $p$ -value of F test;  $R^2$  is the coefficient of determination.

Response Variable	EDF	F	$p$	$R^2$
Species Richness	2.6	16.9	<0.001	0.22
Shannon Diversity Index	3.4	31.9	<0.001	0.52
Simpson Diversity Index	3.5	41.6	<0.001	0.6

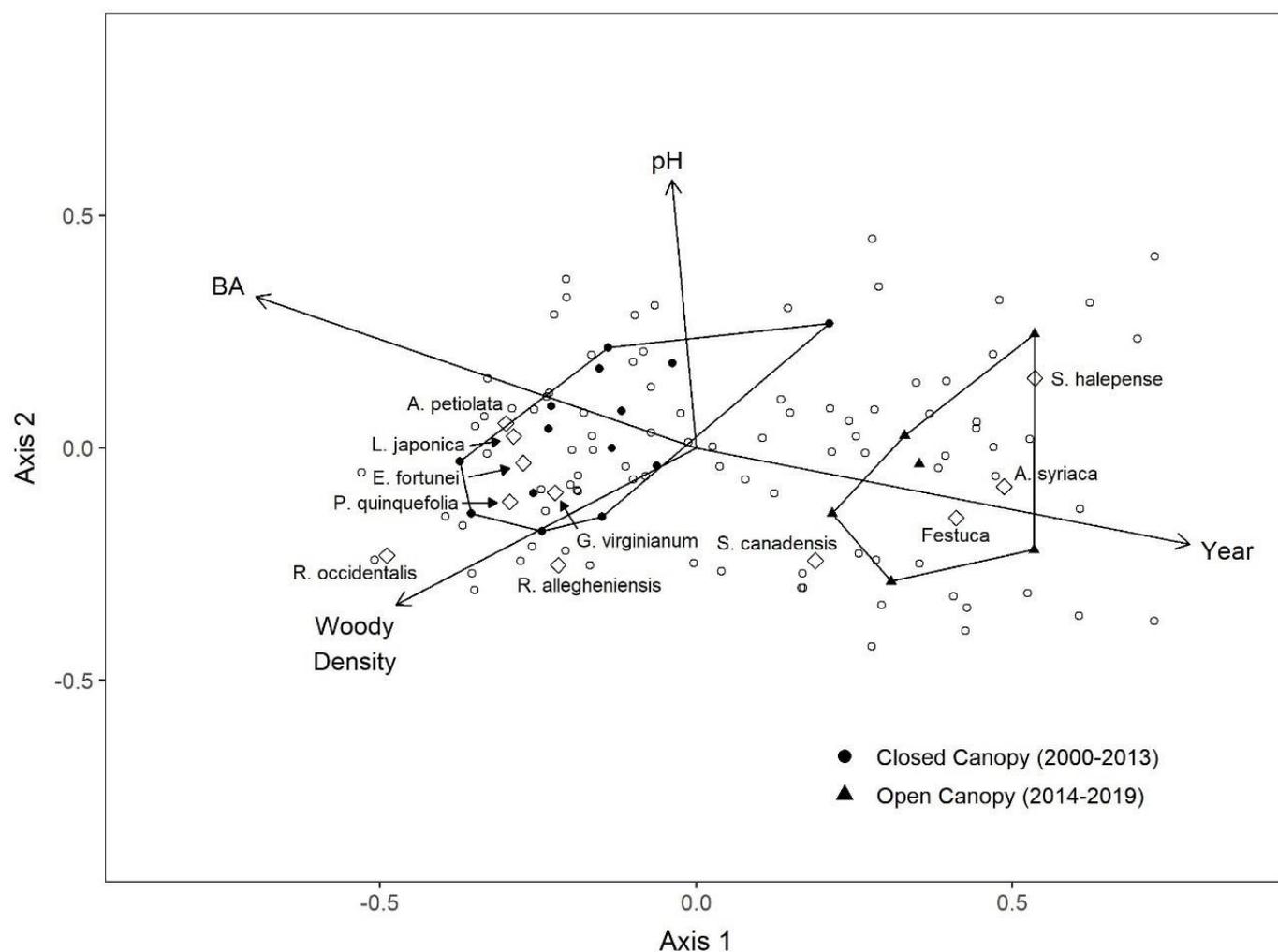
### 3.3. NMDS

After performing NMDS ordinations with 2–7 axes, the ordination with two axes presented an acceptable stress value (0.14) and fit (linear  $R^2 = 0.91$ , nonmetric  $R^2 = 0.98$ ); we evaluated this ordination for relationships with site covariates (Figure 7). Understory communities diverged significantly between sites with open and closed forest canopy (ANOSIM  $R = 0.85$ ,  $p < 0.001$ ). Significant non-zero Spearman correlations were found between NMDS axes and four site covariates: planting year ( $\rho = 0.75$ ,  $p < 0.001$ ), overstory basal area ( $\rho = -0.65$ ,  $p = 0.002$ ), and understory woody plant density ( $\rho = -0.64$ ,  $p = 0.002$ ) were correlated with axis 1, while soil pH ( $\rho = 0.52$ ,  $p = 0.02$ ) was correlated with axis 2 (Table 3). Fitting vectors for these covariates to the ordination revealed that these effects were linear (Table 4). The effects of planting year and overstory basal area identified the same site-level effect, evidenced by the near-opposite orientations of their respective vectors (Figure 7). An examination of the selected species on the ordination plot identified patterns in group divergence. Grassland species, such as *Asclepias syriaca* L. (common milkweed),

*Festuca* spp., *Solidago canadensis* L. (goldenrod), and *Sorghum halepense* were indicative of new plantings with little to no accumulation of overstory basal area. Brambles (*Rubus* spp.) characterized sites transitioning between open and closed canopy, possessing high woody tree densities in the understory, while species occupying forests, such as *Geum virginianum* L. (cream-colored avens) and *Parthenocissus quinquefolia*, were indicative of older planting sites (Figure 7). Three prevalent invasive species—*Alliaria petiolata*, *Lonicera japonica*, and *Euonymus fortunei*—were found typically in closed canopy sites, with relatively high basal areas and low to moderate understory woody densities.



**Figure 6.** Nonlinear effect (regression mean  $\pm$  95% CI) of invasive species prevalence on species richness, Shannon diversity index, and Simpson diversity index of understory plant communities within Reforest The Bluegrass planting sites in Lexington, KY, USA.



**Figure 7.** Ordination via nonmetric multidimensional scaling (NMDS) of mean importance values of understory taxa in Reforest The Bluegrass planting sites in Lexington, KY, USA. Open circles (○) identify observed taxa. Important taxa are illustrated with an open diamond (◇) and labeled. Convex hull polygons distinguish clusters of sites with open and closed forest canopy. Continuous covariates with significant associations to NMDS axes are depicted as vectors. *A. petiolata* = *Alliaria petiolata*; *A. syriaca* = *Asclepias syriaca*; *E. fortunei* = *Euonymus fortunei*; *Festuca* = *Festuca* spp.; *G. virginianum* = *Geum virginianum*; *L. japonica* = *Lonicera japonica*; *R. allegheniensis* = *Rubus allegheniensis*; *R. occidentalis* = *Rubus occidentalis*; *S. canadensis* = *Solidago canadensis*; *S. halepense* = *Sorghum halepense*; *P. quinquefolia* = *Parthenocissus quinquefolia*.

**Table 3.** Spearman rank correlations (*p*-value) between NMDS axes and site covariates in Reforest The Bluegrass sites planted between 2000 and 2019 in Lexington, KY, USA. Correlations significantly different from 0 are in bold.

Covariate	Axis 1	Axis 2
Basal Area	<b>−0.65 (0.002)</b>	0.21 (0.37)
Carbon	0.1 (0.69)	−0.16 (0.5)
Calcium	0.09 (0.71)	0.36 (0.12)
Clay	0.21 (0.37)	0.04 (0.87)
Developed	−0.24 (0.3)	0.22 (0.34)
Magnesium	−0.07 (0.76)	−0.28 (0.23)

**Table 3.** Cont.

Covariate	Axis 1	Axis 2
Nitrogen	0.09 (0.7)	−0.17 (0.47)
pH	0.08 (0.72)	<b>0.52 (0.02)</b>
Phosphorus	−0.1 (0.68)	0.03 (0.89)
Potassium	−0.14 (0.57)	−0.24 (0.31)
Sand	0.34 (0.15)	0.18 (0.44)
Silt	−0.2 (0.39)	−0.11 (0.63)
TWI	0.36 (0.12)	−0.13 (0.59)
Woody Density	<b>−0.64 (0.002)</b>	−0.18 (0.45)
Woody Height	−0.21 (0.37)	0.04 (0.62)
Year	<b>0.75 (0.0002)</b>	−0.12 (0.62)
Zinc	−0.3 (0.19)	0.39 (0.09)

**Table 4.** Vectors and linear fit statistics of significant continuous site covariates ( $p < 0.05$ ), with axes from nonmetric multidimensional scaling (NMDS) of mean importance values of herbaceous taxa in Reforest The Bluegrass planting areas, Lexington, KY, USA.

Covariate	Axis 1	Axis 2	$p$	$R^2$
Basal Area	−0.906	0.423	<0.001	0.591
pH	−0.066	0.998	0.033	0.333
Planting Year	0.967	−0.256	<0.001	0.652
Understory Density	−0.814	−0.580	0.029	0.339

#### 4. Discussion

Although alpha diversity of the understory community was similar among planting years, temporal shifts in community composition were apparent: recently planted sites were dominated by graminoids, but forbs and vines became more important with increased time since planting. These shifts in understory herbaceous plant communities followed anticipated successional trajectories, from dominance by shade-intolerant to shade-tolerant species, as reported in studies of forest regeneration from clearcuts or old fields [27,57] or in the reforestation of other disturbed landscapes [58]. Templeton et al. [59] reported higher rates of herbaceous species turnover in urban forests than rural forests, which they attributed to interactions between deer browse and high intensities of forest fragmentation. However, the herb layer in planted urban forests has not yet been well documented in the literature: for example, Doroski et al. [60] studied a planted forest in New York City but focused on woody plant recruitment, rather than herbaceous species. Our study provides the first documentation of shifts in herbaceous plant communities, corresponding to secondary succession in planted urban forests. Ongoing monitoring will be necessary to characterize how these communities continue to develop over time, especially as the tree and shrub layers continue to develop.

Invasive species were abundant in RTB sites, comprising 21% of total groundcover. These findings are consistent with the literature, which generally reports significant invasive species pressure in urban and peri-urban forests [17,61,62]. The most common invasive plants in the herb layer of our sites were *Euonymus fortunei* and *Alliaria petiolata*, which are common in forests across the region and are known to negatively affect natural regeneration and recruitment [36,37,63]. Importantly, these problematic invasive species tended to increase in importance in our sites after canopy closure, a critical time period for colonization of native shade-tolerant species. Furthermore, the alpha diversity of understory plants declined as invasive species prevalence increased, suggesting that invasive species may be suppressing recruitment or otherwise reducing colonization and establishment success on these sites. The removal of invasive species, coupled with replacement plantings, can support the recovery of diverse understory plant communities [36,64–66]. LFUCG began removing *Lonicera maackii* and *Pyrus calleryana* from select RTB sites in 2017 (Nathaniel

Skinner, personal communication). While we avoided sampling patches undergoing invasive species management for this study, future work should stratify sampling by invasive species management activities to evaluate how management influences forest development over time. In addition, our results suggest that management targeting *Euonymus fortunei* and *Alliaria petiolata* in addition to problematic tree and shrub species is essential. Ongoing monitoring will be necessary to evaluate the role of continued invasive species management on both herbaceous and woody plant communities within these sites.

NMDS showed a clear separation between understory herbaceous plant communities in open-canopy and closed-canopy sites. This separation aligns with the observed community shifts from dominance by graminoids to dominance by forbs over time since planting. Furthermore, NMDS identified the soil pH as a key site factor, structuring plant communities across these sites. Soil pH is a critical determinant of plant nutrient availability and can exert a profound influence on plant community structure and composition, especially in the restoration of degraded lands [67]. Urban soils are highly heterogeneous and exhibit complex effects of prior management [68]; these, and other legacy effects of human activity, structure plant communities [69,70]. This study documents soil pH as a key determinant of understory plant community structure in planted urban forest sites. The ongoing management of planted sites, as well as selection and planning for planting future sites, should consider soil pH and other soil chemical characteristics to ensure that planted species are tolerant of the soil conditions.

Overall, this study documents herbaceous plant community development in planted urban forests across a chronosequence of ages, between 1 and 20 years. Interestingly, these sites developed successional, as would be expected in a naturally regenerating forest in this region. Herbaceous plant communities were structured by forest overstory development (i.e., formation of a closed canopy and associated shading of the understory), as well as by the abundance of invasive species and soil chemical characteristics. These factors further demonstrate the importance of canopy closure, invasive species, and edaphic conditions in regulating the dynamics of understory herbaceous plant communities; they further underline the critical role of management in structuring ongoing planted forest development. Continued research on these sites will be necessary to understand how plant communities develop into the future, especially as influenced by management activities, such as the removal of *Lonicera maackii* or *Pyrus calleryana*. With careful planning and coordination, management on these sites can be structured in a way to support a more experimental, rather than observational, study in the future.

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