



Plant richness increases with surrounding habitat and management burns over 30-years in suburban forest understories

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ABSTRACT

Forests within and adjacent to cities are important habitats for native species and provide vital ecosystem services to cities and their residents. Herbaceous plants represent over 80% of all plant species in these forests, yet little is known about the long-term effects of management and landscape context on the understory of suburban forests. In this study, we used a 30-year dataset to fill this knowledge gap and evaluate the effect of prescribed burns on native forest herbs in suburban forest preserves of DuPage County, Illinois, USA. We also evaluated how the amount and configuration of forest habitat at multiple spatial scales affects native herb richness, gains, and losses in these forests over 30 years. We found that forests managed with prescribed burns increased in native herb richness over time, while unburned forests did not. Managed forests now have more native herb species than unburned forests. We also found that habitat amount in the surrounding landscape, but not the configuration of that habitat, had a positive effect on native herb richness and species gains over 30 years. Overall, we conclude that prescribed burns are effective in maintaining native forest herb richness in suburban forests. However, additional management actions such as seed augmentation may be required in areas with little surrounding forest herb habitat, as both overall richness and species gains over time are reduced in isolated forests.

1. Introduction

Forests in and around urban areas are increasingly recognized for their ability to maintain biodiversity, provide ecosystem services to urban residents, and contribute to the sustainability of cities (Duinker et al., 2015; Ives et al., 2016; Nesbitt et al., 2017). In North America, these forests may have an outsized importance for humans relative to their size, as over 80% of residents now live in urban areas (United Nations, 2018). Despite their importance and value, forests between the urban core and surrounding rural areas (i.e., suburban forests) are being threatened by urban land conversion, which has outpaced urban population growth in North America since 1970 (Güneralp et al., 2020). Furthermore, these forests have received limited research attention compared to both rural forests and more urban forests (Colgan et al., 2014).

Herbaceous plants ("herbs" from here forward) make up over 80% of plant species in temperate forests and thus are important to consider when attempting to conserve native species and maintain plant biodiversity (Gilliam, 2007, 2014; Pregitzer et al., 2021). The diversity of forest herbs is partially shaped by the heterogeneity of

microenvironments in the understory, including variation in light and soil (Hofmeister et al., 2009; Beatty, 2014). In urban forests, understory heterogeneity is also created by human disturbances. For example, Bhuiju and Ohsawa (2001) found that understory diversity in urban forests of central Japan is related to a combination of canopy disturbances from management activity and soil compaction from recreational activity. Human disturbances can also interact with non-human disturbances to impact understory heterogeneity and shape diversity; native herb richness was higher in areas cleared of downed and damaged trees after a stand-replacing windstorm than in uncleared areas in an urban forest of southern Italy (Teobaldelli et al., 2020).

For suburban forests, the process of urbanization itself, along with associated factors such as pollution and land use change, also shape forest herb diversity (Rogers et al., 2009; Allen et al., 2007; Breen et al., 2015). Air pollution decreases forest herb richness by increasing canopy defoliation, changing micro-environmental conditions in the understory and benefiting invasive species that outcompete natives (Allen et al., 2007). Past land uses also shape forest herb diversity. Forests on recently abandoned land are often dominated by early successional and invasive species in the understory, while forests that were abandoned earlier

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more closely resemble ancient forests (Breen et al., 2015). In time, as forest species accumulate in the understory, the herb community of these second growth forests may converge with those of ancient forests, but this process can take a century or more (Holmes and Matlack, 2018).

Plant diversity in urban and urbanizing landscapes is partially limited by recruitment events (Rogers et al., 2009; Piana et al., 2019). Recruitment limitations are broadly defined as the failure of species to add individuals to existing populations or to establish new populations in a landscape (Piana et al., 2019). Both within a community and between communities, recruitment can be limited by a lack of propagules and a lack of suitable sites Eriksson and Ehrlén (1992). Management actions focused on reducing invasive species directly affect the availability of suitable sites in the understory by introducing disturbances that alter the micro-environmental conditions, potentially aiding recruitment of herbs and increasing diversity (Bowles et al., 2007). But reducing invasive species does not increase the availability of native propagules arriving at newly available sites, and seed dispersal can be particularly limited in urban and suburban forests due to habitat fragmentation and isolation (Komuro and Koike, 2005; Lopez et al., 2018). Most forest herbs in eastern North America establish after a disturbance, are dispersed by ants, and lack specialized long-distance dispersal mechanisms (Whigham, 2004). Many depend on herbivory by white-tailed deer (*Odocoileus virginianus*) to disperse propagules over long-distances (Matlack, 1994; Myers et al., 2004; Vellend et al., 2006). White-tailed deer are expected to be especially important dispersers in fragmented landscapes; without deer, most forest herbs could only disperse a few meters from the parent plant and would be unable to recruit into a neighboring forested area (Matlack, 1994; Cain et al. 1998; Myers et al. 2004). In suburban landscapes, deer may be even more critical, as urbanization shifts the primary driver of diversity from local micro-environmental conditions in the understory to landscape factors that limit recruitment by reducing the availability of propagules (Rogers et al., 2009).

The amount and quality of habitat in the landscape directly affects the distribution and diversity of propagules that can disperse to sites in the understory. Species-area relationships predict that more habitat will lead to higher diversity, because more species can coexist in a larger area (Lomolino, 2000; Fahrig, 2013). In suburban landscapes, the amount of forest habitat directly affects species richness in the understory by altering plant recruitment, with Rogers et al. (2009) finding that sites with more forest habitat within five kilometers had higher colonization rates and lower extirpation rates than sites with less forest. The spatial arrangement (configuration) of habitat is also expected to affect diversity, but the extent to which configuration independent of habitat amount affects diversity is still a matter of debate (Fahrig, 2013; Hanski, 2015). The spatial scale at which landscape context affects biological responses, the ‘scale of effect’, is often not known, and cannot yet be predicted effectivity a priori, so multiple nested scales within a landscape need to be evaluated (Jackson and Fahrig, 2015; Miguet et al., 2016). Understanding the ‘scale of effect’ for suburban forests may be especially important for effective management, as the unique factors that shape plant communities in these landscapes may act at different spatial scales than in other landscapes (Aronson et al., 2016). For example, white-tailed deer have smaller home ranges in suburban landscapes as compared to rural landscapes (Cornicelli et al., 1996; Gaughan and DeStefano, 2005).

Management actions such as invasive species removal (Farmer et al., 2016; Johnson and Handel, 2016; Mattingly et al., 2016; Bierzychudek 2020), selective harvest of canopy trees Tessier (2010), herbivore exclusion (Faison et al. 2016), and prescribed burns (Heuberger and Putz, 2003; Bowles et al., 2007) can also shape forest herb diversity, but there is still uncertainty in the effect of these management actions in a suburban context (Pregitzer et al., 2021). Most previous studies of suburban forest management have focused on the effect of invasive species removal on the forest plant community (e.g., Farmer et al., 2016; Mattingly et al. 2016; Bierzychudek, 2020; Fuselier et al., 2017; Johnson

and Handel, 2016, 2019; Gharehaghaji et al., 2019; Bowles et al., 2007). This focus makes sense, as it is the most commonly conducted management activity in suburban forests in the United States (Pregitzer et al., 2021).

Another common management activity is prescribed fire, although this is less well-studied in suburban forests. Fire is particularly common in the prairie-forest interface of the American Midwest and is used to control woody invasive species including common buckthorn, *Rhamnus carthartica*, and bush honeysuckles, *Lonicera* spp. (Bowles et al., 2007; Meunier et al., 2021). Of the previous studies that considered the effect of prescribed management burns in suburban forests, only one study that we are aware of considered both a broad spatial (multiple forests) and broad temporal (multiple decades) scale (Gharehaghaji et al., 2019). But Gharehaghaji et al., (2019) focused exclusively on woody species and did not consider forest herbs. Previous studies of forest herbs were conducted at limited spatial scales or over shorter periods of time, usually considering only one forested area (e.g., Heuberger and Putz, 2003; Bowles et al., 2007; Mattingly et al., 2016) or ten years or less of data (e.g., Heuberger and Putz, 2003; Mattingly et al., 2016). A better understanding of the long-term effect of management actions in suburban forests is needed, as natural resource managers face unique challenges in these forests, including a prevalence of woody invasive species such as common buckthorn, *Rhamnus carthartica*, and frequent introduction of non-native species that may outcompete natives (Kurylo et al., 2007; Gaertner et al., 2017). No previous studies of management on forest herbs in suburban landscapes that we are aware of has considered the surrounding landscape context of the managed area.

In this study, we use a unique long-term dataset to investigate the effect of prescribed management burns and landscape context on the richness and turnover of native herbs. Studying 16 suburban forest preserves across DuPage County, Illinois, USA, we address three research questions:

1. Has the richness of native forest herbs changed over time, and do these changes depend on whether or not a plot was ever burned?
2. Which best explains current herb richness, species gains, and species losses over 30-years in the forest understory: whether the plot was burned, the amount of surrounding habitat, the configuration of that habitat, or a combination of these factors?
3. If habitat amount, habitat configuration, or both affect current species richness or turnover over 30 years, at which spatial scale do these have the biggest effect?

We aim to fill a gap in the research literature by evaluating the effect of both management and landscape context on forest herbs across multiple suburban forests. This study will help natural resource managers in suburban landscapes better understand long-term effects of past management actions, and better plan future management actions.

2. Methods

2.1. Study area

This study was conducted in DuPage County, Illinois, USA, an urbanizing county in the Chicago metropolitan area with a population of 932,877 people (U.S. Census Bureau, 2021). DuPage County has a humid continental climate, with an average annual maximum temperature of 15° Celsius, average annual minimum temperature of 3.6° Celsius, and an average of 97.8 centimeters of precipitation a year (NOAA Climate Normals, Morton Arboretum, Lisle, IL 1961–2010).

Prior to European arrival, DuPage was inhabited by the Potawatomi people and primarily covered in tall grass prairie interspersed with oak (*Quercus* spp.) dominated forests, woodlands, and savannahs (Thomson, 1985; Bowles et al. 1994 & 1998; McBride and Bowles, 2001). Fire, set by the indigenous peoples and lightning, maintained these ecosystems, and forests and woodlands were generally restricted to firebreaks in the

landscape (Bowles et al., 1994 & 1998; McBride and Bowles, 2001). Public land surveys from the early 1800s indicate that approximately 20% of DuPage County was covered in wooded ecosystems (Bowles et al., 1994 & 1998; McBride and Bowles, 2001). These ecosystems were primarily forests with an average density of 125.4 trees/ha, with much of the remainder being woodland, with an average density of 70.3 trees/ha (Bowles et al., 1998; McBride and Bowles, 2001). White (*Q. alba*) and red oak (*Q. rubra*) were the dominant canopy species in these forests, with a lesser importance of bur oak (*Q. macrocarpa*) and hickory (*Carya spp.*), and an understory of hazel (*Corylus americana*) (Bowles et al. 1998; McBride and Bowles, 2001). Fire-intolerant and more mesic species such as elm (*Ulmus americana*), basswoods (*Tilia americana*), and maple (*Acer spp.*) were restricted to larger forests and areas along waterways that experienced both less frequent and less intense fires (Bowles et al., 1998). Much of the landscape was converted to farmland or forest through plowing or wildfire suppression (respectively) by 1850, before urban land development began in the 1920s (Thomson, 1985). The county rapidly urbanized during the 1950–1980s, and over 80% of DuPage is now considered developed (Thomson, 1985; Yang et al., 2018; Fig. 1). Prairies and forests are now restricted to public and private conservation areas, with wooded ecosystems comprising only about 8% of the county (Yang et al., 2018; Fig. 1).

All study locations are in forest preserves managed by the Forest

Preserve District of DuPage County and are in, or directly adjacent to (< 500 m), areas identified as forests and woodlands in the public land surveys prior to European arrival (Bowles et al., 1998). The tree canopy in these forests is primarily composed of native deciduous species, including white oak (*Q. alba*), red oak (*Q. rubra*), bur oak (*Q. macrocarpa*), wild black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), American elm (*U. americana*), sugar maple (*A. saccharum*), and basswood (*T. americana*) (Gharehaghaji et al., 2019).

The Forest Preserve District actively manages their forest preserves using a variety of techniques, including prescribed burns, woody brush removal, and limited herbicide application. Prescribed burns are conducted in fall or spring and focus on burning ecosystem units within the forest preserves. In addition, the white-tailed deer (*Odocoileus virginianus*) herd has been managed since 1993, with the goal of reducing the herd to 6–8 individuals per square kilometer before fawning. Deer density in DuPage County greatly exceeded this goal at the start of our study (>40 deer per square kilometer) but declined toward 4–6 deer per square kilometer by 1998 with intensive management (Etter et al., 2000). The deer population continued to decline through the remainder of our study (Illinois Department of Natural Resources, 2020). In this study, we focus explicitly on the effect of prescribed burns, as they are the most common and frequently applied management technique in these forests. We implicitly consider the effect of deer through our

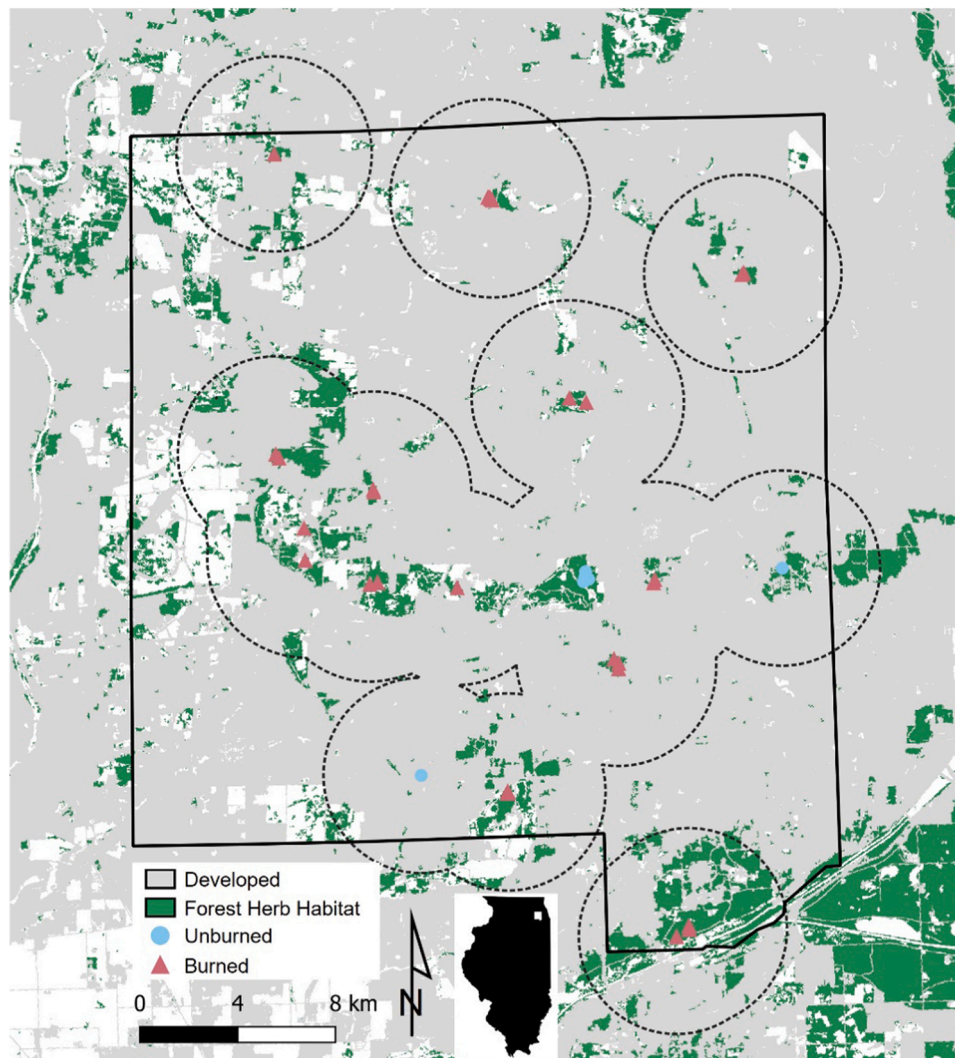


Fig. 1. Location of long-term monitoring plots in DuPage County, IL, USA. Plots managed with prescribed burns are represented with red triangles (△), unburned plots are represented with blue circles (○). The dashed buffer represents the area within four kilometers of the long-term monitoring plot. Developed land was identified from the NLCD developed land cover classes.

analysis of the surrounding landscape.

2.2. Plant sampling and classification

Vegetation data were collected by forest preserve staff in 34 long-term plots located within 16 forest preserves throughout the county (Fig. 1). Plots are approximately square, 0.45 ha in size, and are permanently marked in the field by painted trees and steel rods at all corners. Seven plots were established in 1986, 19 were added to the study by 1991, and 9 more were added by 1994. The understory community in each plot was surveyed at approximately 5-year intervals using 48, 0.25×0.25 m, quadrats placed randomly throughout the plot during the growing season. Understory surveys began in 1987, and initial surveys for all plots were conducted between 1987 and 1994. All vascular plants in the quadrats were identified to species.

In this study, we focused on native, herbaceous plant species, including all forbs, grasses, ferns, sedges, and non-woody vines. Species were considered native if the USDA Plants database identified them as such for the state of Illinois (USDA, 2021). While all plots were invaded by non-native species—garlic mustard, *Alliaria petiolata*, occurred in every plot, and woody invasives common buckthorn, *Rhamnus carthartica*, and bush honeysuckles, *Lonicera spp.*, were also common—fewer than three non-native herbaceous species were recorded on average in each plot (mean number of species = 2.15; range: [1,8]). Furthermore, there were few non-native herbaceous plant species across all plots and little variation between plots over the study period (Supplemental Fig. 1). We therefore did not analyze non-native species in this study.

For each 0.45 ha plot, we identified the native species richness over all quadrats in each understory survey. We also determined the identity and number of species gained and lost over the 30 years of the study by comparing the species lists of the initial and most recent survey for each plot.

2.3. Characterization of the management regime

Burn management data were collated from notes by the burn chief who conducted each burn. These notes are preserved by the Forest Preserve District of DuPage County. We coded burn management as a binary variable (burned / unburned) because preliminary analysis showed an effect of burns for our sites over time but no difference between sites burned only once and those burned multiple times during the study (Supplemental Table 1 & 2). Long-term plots were considered burned if the ecosystem unit in which they are located was burned any time since 1986. This resulted in 28 plots that were burned and 6 plots that were not burned between 1986 and 2016. Burned plots experienced between 1 and 19 burns (Supplemental Fig. 2) over the 30 years, but most plots were burned at regular intervals every 3–5 years (mean 7.6 burns; median 7.5 burns; Supplemental Fig. 3), potentially limiting our ability to detect an effect of different burn frequencies.

2.4. Herb habitat & landscape patterns

Forest herb habitat surrounding each long-term plot was estimated using the National Land Cover Database (NLCD; Yang et al., 2018) and the land use database from the Chicago Metropolitan Agency for Planning (CMAP; Clark et al., 2016). We defined herb habitat as areas where conservation land use (from CMAP) and forest cover (from the NLCD) intersect; this allowed us to exclude areas with forest overstory but which are not considered forested natural areas, such as residential areas with substantial canopy cover. Forest cover included deciduous, evergreen, and mixed forests, as classified in the NLCD. We also included wooded wetlands as forest cover after reviewing NLCD forest cover in DuPage County and identifying several study sites that were classified as wooded wetland (Supplemental Table 3).

As the most relevant spatial scale for forest herb richness is not known, we measured forest herb habitat at 37 nested spatial scales

(0.3–4 km by 0.1 km increments) surrounding the plots. This range encompasses the average summer and fall home range and maximum dispersal distance of white-tailed deer in DuPage County, a main long-distance seed disperser of forest herbs in the region (Etter et al., 2002). The potential forest herb habitat at each spatial scale was mapped with ArcGIS 10.7 with the Spatial Analyst extension (ESRI, 2020) using circular buffers of corresponding radii around each plot center.

We determined the total amount and configuration of herb habitat at each spatial scale using FRAGSTATS 4.2.1 (McGarigal et al., 2012) using the ‘Class Area’ (CA, in hectares) metric and ‘Clumpiness Index’ (CLUMPY). The ‘Clumpiness Index’ ranges from -1 to 1 , with maximally disaggregated habitat having an index of -1 , maximally aggregated habitat having an index of 1 , and landscapes with randomly distributed habitat having an index of 0 . We selected the ‘Clumpiness Index’ as a measure of habitat configuration because it has low correlation with habitat abundance, unlike many other measures of configuration (Wang et al., 2014).

Of the 37 potential spatial scales considered for both habitat amount and configuration, we selected a smaller number of independent candidate spatial scales to include in the analyses. Following the methods of Martin and Fahrig (2012), we selected candidate scales using Spearman’s correlation between measures of habitat amount and configuration (individually) at adjacent spatial scales, starting at 0.3 km around the plot. Adjacent scales were compared, and the increment between compared scales was increased by 0.1 km (i.e. correlation between habitat amount at 0.3 km and 0.4 km, 0.3 km and 0.5 km, etc.) until the measure of habitat amount or configuration was no longer strongly correlated ($r < 0.7$). Spearman’s correlations were conducted using R (R Core Team, 2021).

2.5. Statistical analysis

Has forest herb richness changed over time, and do these changes depend on whether or not a plot was ever burned?

For the first research question, we constructed a single model a priori to investigate the effect of time, burn management, and the interaction of time and burn management on forest herb richness. This model included the fixed covariates *time* (in years since 1987; a continuous variable) and *burn management* (a categorical variable with two levels: burned and unburned) in the model. The interaction term *time x burn management* was also included. To incorporate the dependencies of multiple repeated surveys of a long-term plot and multiple plots co-occurring in the same preserve, we included *plot ID* as a random effect nested within the random effect *preserve*. We also included *year*, the year the plot was surveyed, as a random effect to account for potential variation between years and variation in which plots were surveyed each year.

Which best explains current herb richness, species gains, and species losses over 30-years in the forest understory: whether the plot was burned, the amount of surrounding habitat, the configuration of that habitat, or a combination of these factors?

For the second research question, we took an information theoretic approach with multi model averaging (Grueber et al., 2011). Current native herb richness, species gains, and species losses were modeled separately. We constructed 21 models for each response variable with different combinations of fixed covariates based on the following framework: management only, management + habitat amount, management + habitat configuration, and management + habitat amount + habitat configuration. All models included the fixed covariate *management* (a categorical variable with two levels: burn managed and unburned), as our initial analysis revealed that burns increased herb richness over time in these plots. Models with the covariate *habitat amount* (a continuous variable) and *habitat configuration* (a continuous variable) included the amount and configuration of habitat at each of

the selected candidate spatial scales, one model for each scale. We also considered a null model that only included random effects. The *habitat amount* and *habitat configuration* variables were standardized through mean centering and scaling by the standard deviation to aid in model convergence. Only *preserve* was included as a random effect in these models, as only the most recent survey or the change from the initial to the most recent survey were used and we did not need to account for repeated measures. We ranked candidate models by AIC scores adjusted for small sample sizes (AICc), and determined the top model set using 95% confidence of Akaike's weights (w_i ; Burnham and Anderson, 2002). If multiple models were included in the top model set, we used natural averaging to determine coefficient estimates to avoid shrinking the estimate towards zero (Grueber et al., 2011).

If habitat amount, habitat configuration, or both affect current species richness or turnover over 30 years, at which spatial scale do these have an effect?

To answer the third research question, we evaluated the top model set for all models considered for research question two. We determined which landscape covariates (habitat amount and habitat configuration) were retained within the top model set and at which spatial scale. We considered a covariate to have an effect on the response if the 95% confidence interval around the estimate of the multi model average did not overlap zero.

All statistical analyses for each research question were performed with R (R Core Team, 2021). GLMMs were constructed using the 'lme4' and 'lmerTest' packages (Bates et al., 2015; Kuznetsova et al., 2017). Model assumptions for each GLMM were evaluated visually by plotting residuals versus fitted values and all covariates. We conducted model rankings and multi model averaging using the 'AICcmodavg' and 'MuMin' packages (Mazerolle, 2020; Bartoń, 2020). Overall model fit for the first research question and the best model within the top set for the second question were evaluated using the 'MuMin' package (Bartoń,

2020).

3. Results

3.1. Native herb richness and turnover

Native herb richness recorded in DuPage forest plots ranged from 2 to 58 species per plot over the ~30 years of the study. Overall, FPDDC staff identified 213 native herbaceous species, including 163 forbs, 22 sedges, 18 grasses, 5 non-woody vines, and 5 ferns (Supplemental Table 4). Over the same ~30 years, plots gained 0–47 native herb species and lost between 0 and 17 species. The most common species gained across all sites were *Hackelia virginiana*, *Symphotrichum lateriflorum*, *Amphicarpaea bracteata*, *Carex rosea*, and *Ageratina altissima*, while the most commonly lost species were *Dentaria laciniata* and *Erythronium albidum*. Ninety-three species were only gained in burned sites, while two species, *Asclepias exaltata* and *Viola striata*, were gained only in unburned sites. Of the species that were uniquely gained in burned sites, the most common were *Hystrix patula*, *Solidago canadensis*, *Carex blanda*, *Leersia virginica*, and *Oxalis stricta*.

3.2. Herb habitat amount and configuration

Spearman's correlation for measures of habitat amount and configuration at adjacent spatial scales identified three independent scales for habitat amount (0.3 km, 0.9 km, and 3.4 km; Fig. 2A) and four independent scales for habitat configuration (0.3 km, 0.6 km, 2.7 km, and 3.3 km; Fig. 2B). Habitat amount within 0.3 km of the plots ranged from 4.0 to 28.1 ha (approximately 14–100% of the landscape, respectively), habitat amount within 0.9 km ranged from 4.9 to 178.9 ha (2–70% of the landscape), and habitat amount within 3.4 km ranged from 60.0 to 916.3 ha (2–25% of the landscape). Habitat surrounding the plots was largely aggregated at all spatial scales, with less variation in the

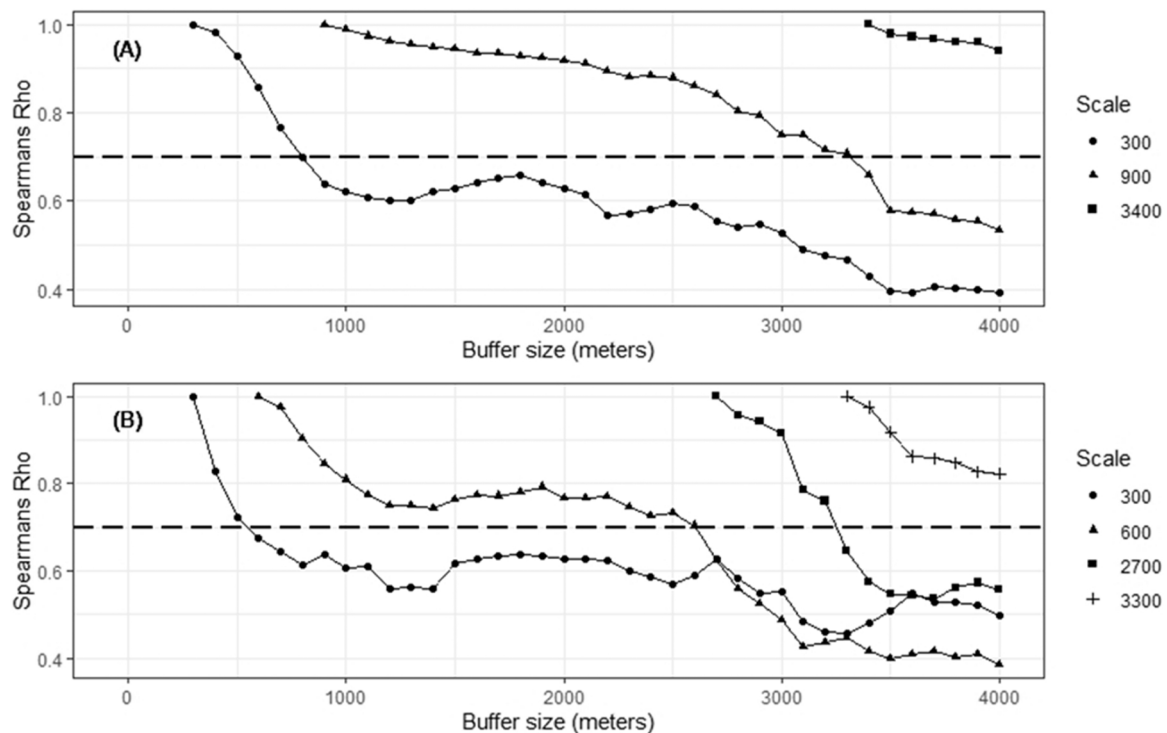


Fig. 2. Spearman's correlation between adjacent spatial scales for (A) habitat amount in hectares and (B) configuration measured with the 'Clumpiness Index'. Habitat amount at 0.3 kilometers from the site is highly correlated ($Rho > 0.7$) with habitat up to 0.9 kilometers from the site. Habitat amount at 0.9 kilometers is highly correlated with habitat up to 3.4 kilometers. Habitat configuration at 0.3 kilometers is highly correlated with habitat configuration within 0.6 kilometers of a site, which is highly correlated with habitat configuration up to 2.7 kilometers of the site. Habitat configuration within 2.7 kilometers is highly correlated with habitat configuration up to 3.3 kilometers of the long-term monitoring site.

‘Clumpiness Index’ between scales.

3.3. Native herb richness and burn management over time

Our analysis of change in species richness over time revealed a significant interaction between time and management. Generally, native herb richness increased over time in plots managed with prescribed burns but did not increase in unburned plots (Fig. 3; Table 1). The model explained 87% of the overall variation in herb richness, with fixed effects and their interaction explaining 12.3% of the variation. Model residuals indicated no problems.

3.4. Native herbs, burn management, & landscape context

Burn management and the amount of habitat in a 0.9 km radius were significant predictors of current herb richness and gains in herb richness over 30 years in the herb community (Fig. 4). No variables were significant predictors of native herb loss over 30 years. Habitat configuration was not a predictor of any response variable. Generally, burn managed sites currently have more native species than unburned sites (Fig. 4 & 5). Similarly, sites with more habitat within 0.9 km have more native species than plots with less habitat (Fig. 4 & 5). Burn managed plots, and those with more habitat within 0.9 km, also gained more herb species over 30 years (Figs. 4, 5, & 6).

The best model for current richness and species gains over 30 years explained 83% and 86% of the overall variation respectively, with fixed effects explaining 44% and 52% of the variation (Fig. 4). Model residuals generally indicated no problems, except for an outlier plot that only appeared in the subset of models that included both habitat amount within 3.4 km and habitat configuration within 0.6 km as fixed effects. We have no ecological reason to exclude this site from our analysis, and these models were not among the top models of the set.

4. Discussion

Our study shows that native herb richness increased over time with prescribed burns in suburban forests. Unburned plots gained significantly fewer species than burned plots over 30 years and also lost more species than burned plots over the same time, but this difference was not significant. Plots that have been burned at least once in the last 30 years now have more native herb species than unburned plots. We also found support that landscape context, specifically the amount of habitat within 0.9 km of a plot, influenced the number of species gained there. Together, these results suggest that prescribed burns have the potential

Table 1

Poisson GLMM indicates that native herb richness increased from 1987 to 2016 in burn managed plots but not in unburned plots in DuPage County, IL. Estimated value for $\sigma_{\text{Preserve}} = 0.199$, $\sigma_{\text{Plot}} = 0.456$, and $\sigma_{\text{Year}} = 0.148$.

Response	Predictor	Estimate	SE	z-value	P-value	R _m ² (R _c ²)
Richness	(Intercept)	2.79	0.26	10.87	< 0.01	0.12 (0.87)
	Burned	-0.16	0.28	-0.58	0.56	
	Time	-0.00	0.01	-0.52	0.61	
	Burned:	0.03	0.01	4.48	< 0.01	
	Time					

to increase native herb diversity anywhere in a suburban forest landscape, but areas with more habitat within 0.9 km may benefit most.

Increasing native herb richness is a goal of land managers and conservationists but should not be misinterpreted as a return of these forest understories to a pre-European condition. While we don't have information about the herbaceous plant species on the landscape prior to European arrival, contemporary forests in the American upper-Midwest are considerably different from the early forests (Fahey et al., 2012 & 2014) and are unlikely to return to their previous state, even with a return of burns (Nowacki and Abrams, 2008). As seen in other contemporary forests (e.g., Dzwonko and Loster, 1990), the composition and richness of forest herbs in DuPage County may differ from those in the ancient forests on this land. The current forests, like others in urban areas (e.g., Dresner et al., 2017, Kowarik et al. 2019, Solórzano et al., 2021), may be novel ecosystems, particularly due to the many non-native woody species that have become established within (Gharahghaji et al. 2019). However, increased native herb richness still benefits the forest community; forests with greater native herb richness and more native habitat specialists store more carbon, nitrogen, and phosphorus than forests with lower native herb richness, impacting nutrient cycling (Gerken Golay et al., 2016). Increased native herb richness can also lead to increased richness of arthropods and other wildlife that support other ecosystem services that benefit urban residents, such as pollination, pest control, and organic matter decomposition (Mata et al., 2021; Kotze et al., 2022). Finally, many native herbs have spring wildflowers that are of interest to hikers and naturalists, providing cultural ecosystem services as well (Graves et al., 2017). More research is needed to determine whether the increased richness is indicative of increasingly-healthy forest herb populations in the understory or whether it represents increased detection of relict native herbs populations in poor health that have yet to pay the extinction debt.

Our result of increased herb richness with management burns is in line with a systematic review by Eales et al., (2018), who found that

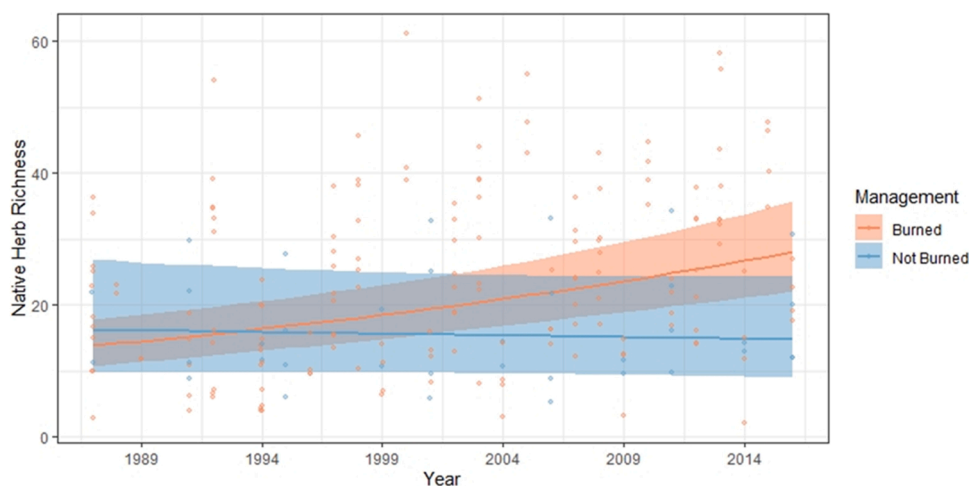


Fig. 3. Fit for the Poisson GLMM for native herb richness from 1987 to 2016. Shaded areas represent 95% confidence intervals. The overall model explained 87% of the variance in native herb richness, while fixed effects explain 12.3%.

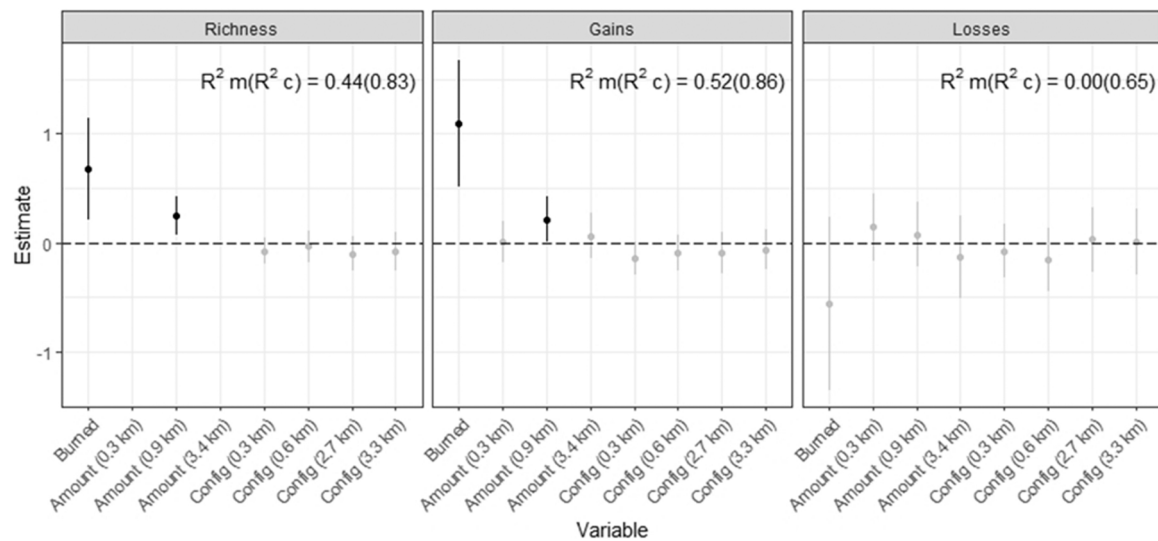


Fig. 4. Effects of prescribed burns and landscape context on native herb richness, species gains, and species losses over 30-years. Effect size estimates and 95% confidence intervals of variables are based on multi-model averages of GLMMs in the top model set (95% confidence of Aikake's weights). Variables that have an effect are in black, others that were included in the top model set but that do not have an effect are in grey. Marginal (R^2_m) and conditional (R^2_c) R^2 values are for the best (lowest AIC) model in the top model set.

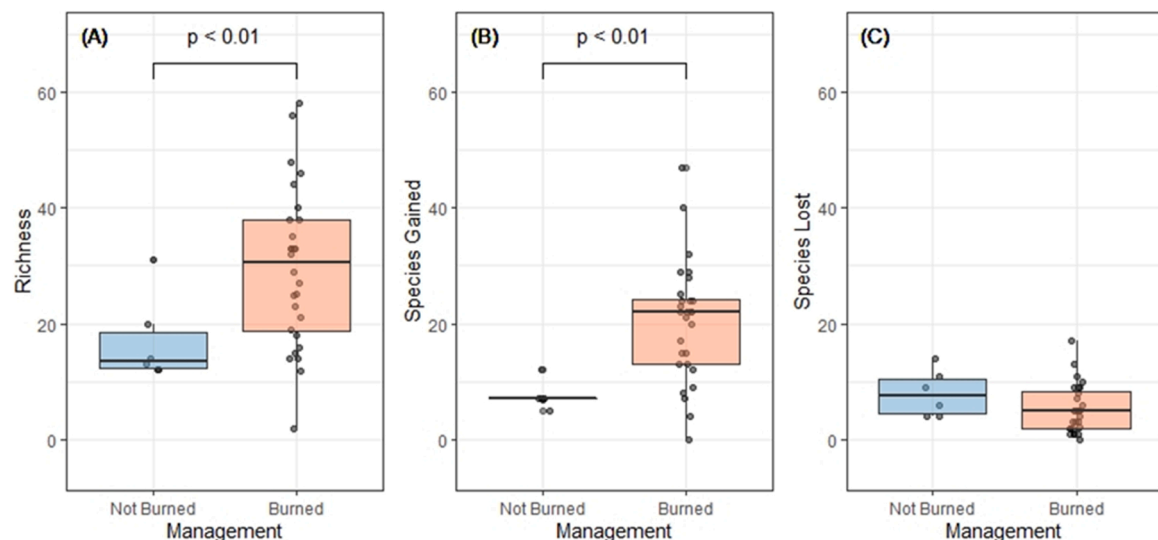


Fig. 5. (A) Current native herb richness in the understory of long-term monitoring sites that have been managed with prescribed burns or not managed over 30-years in suburban forests of DuPage County. (B) Number of native herb species gained over a ~30-year period in long-term monitoring sites that were burned and unburned. (C) Number of native herb species lost over a ~30-year period in burned and unburned sites. Brackets and p-values refer to prescribed burn management having an effect on the observed response when modelled with GLMMs. Prescribed burn management had no effect on the number of native herb species lost over the ~30-year period.

prescribed burns increased herb richness in broadleaf forests globally. Management burns impact forest herb richness through multiple potential mechanisms, including increased light and space in the understory and altered nutrient availability (Bowles et al., 2007; Taylor and Midgley, 2018). These changes can potentially enable relict native herb populations in the understory to expand into open microsites and become more viable. Holmes and Matlack (2018) suggest this mechanism to explain rapid increases of forest herbs in secondary forests growing on abandoned agricultural pasture in Ohio, USA. Unfortunately, light and nutrient levels in the understory were not measured in a consistent or comparable way in our study sites, limiting our insights into the effect of these variables. However, some species that were frequently recruited to burned plots do suggest that light may have increased. Calico aster, *Symphytotrichum lateriflorum*, and Canada

goldenrod, *Solidago canadensis*, which both recruited to at least half the burned sites during our study, are intolerant of shade and commonly occur in locations where light is a less limiting factor, such as open woodlands and savannas (USDA Plants; Wilhelm et al., (2017)). Not all species gained at burned sites, however, are shade intolerant. The common wood sedge, *Carex blanda*, and white grass, *Leersia virginica*, for example, were also commonly gained in burned sites, but are shade tolerant (USDA Plants). The mixture of shade tolerant and intolerant species gained at burned sites over time may reflect increased microsite heterogeneity with burns at a site, a key driver of understory herb diversity (Gilliam, 2007). Microsite heterogeneity can also be affected by burns through altered soil nutrients, such as nitrogen, which is known to affect herb richness (Hofmeister et al., 2009; Taylor and Midgley, 2018). Since management burns can alter microsite conditions in the

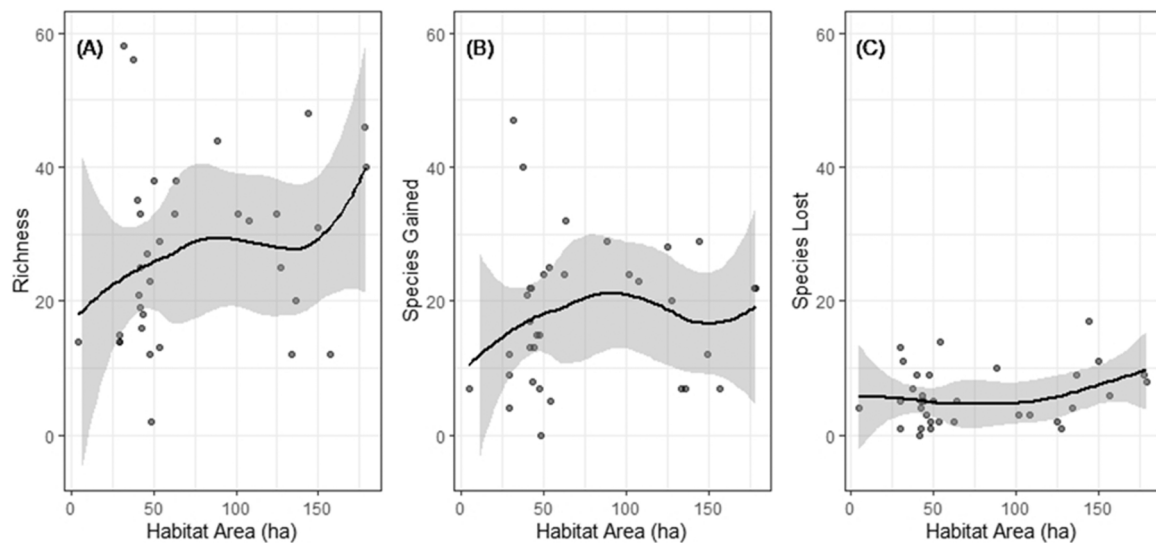


Fig. 6. (A) Current native herb richness and (B) the number of native forest herbs gained over a ~30-year period in the understory of long-term monitoring sites increases with the amount of forest herb habitat (hectares) within 0.9 km of the site. (C) Forest herb habitat (hectares) within 0.9 km of the long-term monitoring site does not affect the number of native herb species lost over a ~30-year period from the site. A loess smoothing function was applied to raw data to show the trend.

understory in multiple ways, further research on changes in life history and functional traits within the forest herb community is needed to better understand not just *if*, but *how and why* prescribed burns change herb richness in suburban forests.

Using prescribed burns as a management tool comes with some challenges, especially in urban and suburban areas. For example, when conducting burns, the Forest Preserve District of DuPage County must carefully consider the proximity to roadways and developed land, along with current wind conditions, to minimize smoke drifting into roads, residential, or commercial areas. As a result, some areas are burned less frequently than desired by natural resource managers (S. Kobal, personal observation). Future climate change in the region may further restrict management burns; the region is predicted to warm and experience increased precipitation events during the dormant season when most management burns occur, potentially limiting the number of suitable days to conduct burns and reducing their effectiveness when they do occur (Hayhoe et al., 2010; Xue et al., 2022). However, despite these challenges, our results suggest that natural resource managers should consider using prescribed burns to maintain forest herb richness in suburban forests, especially in landscapes where fire is a historical disturbance.

We found that the amount of forest herb habitat within the landscape positively correlated with current herb richness and species gains over time, while the configuration of that habitat had no effect. Our results are in line with Rogers et al. (2009), who studied forest understory richness in southern Wisconsin, USA, and found that sites with more forest cover within five kilometers had higher rates of colonization and a lower rate of extinction over a 55-year period. The authors speculated that sites with more forest in the surrounding landscape were better able to recover species lost and add new species to the community when stochastic events opened new habitat in the understory (Rogers et al., 2009), perhaps due to greater habitat continuity (Wulf and Kolk, 2014). The surrounding landscape may be especially important for the initial colonization of sites after a disturbance, as the influence of landscape context may diminish over time with succession (Alexander et al., 2012). Other research has shown that areas with more habitat have higher population growth rates, and more viable populations, than areas with less habitat (Valdés et al., 2014). These populations may be more able to act as seed sources for neighboring habitat, as they have increased flowering and fruit production, likely due to increased pollination and outcrossing, and produce more seeds than populations with

less surrounding habitat (Valdés and García, 2011). Additional research that investigates the relationship between flowering, fruiting, and seed production of herb populations, and direct measures of species recruitment, is necessary to confirm that increased habitat improves recruitment in suburban forests.

In contrast to the amount of habitat, the configuration (i.e. the aggregation of habitat into continuous patches; fragmentation per se) of potential habitat around our study plots had no effect on the native herb richness observed there, or the number of native herbs gained and lost over 30-years. However, it is important to note that our study sites were not established in a way to capture a range of independent habitat amounts or configurations and the amount of habitat varied more between sites than configuration, potentially limiting our ability to detect an effect of configuration. The role of habitat configuration on species richness is still a matter of debate (Fahrig, 2013; Hanski, 2015). Fahrig (2013), in outlining the ‘habitat amount hypothesis’, argued that the configuration of habitat within a local landscape (fragmentation per se) plays little to no role in determining species richness at a site. This claim has been criticized (Hanski, 2015) and various studies have found mixed support for the importance of habitat configuration for species richness (Haddad et al., 2017 and references therein; Watling et al., 2020 and references therein). Nonetheless, our results are in line with a recent synthesis in which Watling et al. (2020) found a positive effect of landscape-level habitat amount and a negligible effect of habitat configuration on the species richness of eight taxonomic groups (including plants) across 35 studies.

We found the scale of effect for forest herb habitat to be between 0.9 and 3.3 km around our plots. We suggest that this distance reflects the mechanism by which seeds of native herbs disperse into our plots. Seeds of most forest herbs generally travel only a few meters from the parent plant if they are not attached to or eaten by white-tailed deer (Matlack, 1994; Vellend et al., 2004). However, there is increasing evidence that white-tailed deer are a generalist long-distance dispersal vector for forest herbs, dispersing seed hundreds to thousands of meters from the parent plant (Matlack, 1994; Vellend et al., 2004; Myers et al., 2004). Previous studies have shown that forest herb seeds ingested by deer are viable (Myers et al., 2004), and modeled seed shadows estimate that over 25% of the seeds ingested by deer are dispersed beyond 1 km, while few are predicted to be dispersed beyond 3 km (Vellend et al., 2003). These seed shadows suggest that deer are capable of dispersing seeds from populations within 0.9–3.3 km of our sites, our estimated scale of

effect. This range is well within the documented movement distances of white-tailed deer in DuPage County, who have a mean home range diameter of 0.9 km (Etter et al., 2002). The particular species gained at our sites over the 30-year period also suggest the movement of seed by deer or other wildlife. For example, stickseed, *Hackelia virginiana*, was the most commonly gained native herb species across all our sites. As its name suggests, it has barbed seeds that easily attach to wildlife. Furthermore, species such as Canada goldenrod, *Solidago canadensis*, and sedge species (e.g. curly-styled wood sedge, *Carex rosea*, and common wood sedge, *C. blanda*) were also commonly gained at our sites over 30-years and are known to be dispersed by white-tailed deer via endozoochory (Myers et al., 2004). Human hikers and mountain bikers may unintentionally disperse seeds over similar distances as deer (Ansong et al., 2015; Weiss et al., 2016; Pickering, 2022), particularly sticky seeds like *H. virginiana*, and particularly if hikers are going off-trail (Pickering, 2022), but these activities rarely disperse seeds beyond 20 m (Ansong et al., 2015; Weiss et al., 2016). We think it unlikely, therefore, that hiking or mountain biking are driving our observed scale of effect.

Deer are common in many suburban landscapes due to abundant forage and a lack of predators (Côté et al., 2004), and thus could potentially play an outsized role in the structure and regeneration of suburban forests. In addition to dispersal of native species, deer can suppress the regeneration of canopy trees through herbivory (Aronson and Handel, 2011), facilitate the spread of non-native and invasive species (Williams et al. 2008; Duguay and Farfaras, 2011), and shift the composition of the understory towards different plant growth forms (Faison et al., 2016). The ability of deer to benefit native species through dispersal is counterbalanced by their negative impact on plant populations through herbivory and depends on density of the deer (Vellend et al., 2006). The deer herd in DuPage County was intensively managed during our study, and reductions in deer density at the beginning of our study were associated with increased ground cover, plant height, and an increase in a number of native indicator species (Etter et al., 2000). Therefore, the potentially-positive impact of deer on herb richness in DuPage County likely depends on this intensive management.

To our knowledge, our study is the first to consider the effect of both a management action and landscape context on understory herbs in suburban forests over multiple decades and across multiple sites. For our analyses, we utilized an existing long-term monitoring dataset collected by a county forest preserve district. Similar datasets are regularly collected by government agencies across the United States but are currently underutilized in addressing ecological questions related to ecosystem management in urban and suburban landscapes (Pregitzer et al., 2021). However, this kind of dataset can come with challenges since the studies are rarely designed as controlled experiments. Agencies charged with managing forested natural areas are often restricted in where and when they can implement management actions, particularly in urban and suburban areas. Furthermore, funding realities can limit monitoring of these natural areas; over 90% of agencies reported funding and staff shortage as an important or very important challenge to accomplishing their mission (Pregitzer et al., 2021). For this reason, managed sites are more likely to be monitored compared to unmanaged sites, as agencies want to observe the outcomes of their management activities. This was the case with our dataset but can pose difficulties when trying to statistically evaluate the long-term effect of management. We therefore recommend that natural resource managers continue to invest in monitoring unmanaged natural areas in suburban landscapes, as these provide an important baseline for evaluating the impact of management actions on native species. This may be especially important for understory herbs, as these, unlike shrubs and canopy tree species, were not recorded in the public land survey, and do not have a comparable historic baseline for comparison. Natural resource managers can potentially supplement these structured biodiversity monitoring efforts with free, publicly collected, citizen science data to fill in any spatial or taxonomic gaps. We also suggest, as others have (e.g. Pregitzer

et al., 2021), that available monitoring data collected by local agencies be identified, analyzed, and synthesized, to provide greater insight into the effect of management practices not only within but across multiple cities. This will allow for a better understanding of the effect of management actions on native diversity, so we can better protect these valuable natural areas in urban and suburban landscapes.

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CRediT authorship contribution statement

PJ and EM contributed to the conceptualization of the study. SK and WL curated the vegetation survey data and management records. SK organized and collected the field data. PJ conducted all GIS work, analyses, and created the visualizations, along with drafting the manuscript. EM supervised the study and gave critical input in revising and editing the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2023.127955.

References

- Alexander, H.M., Foster, B.L., Ballantyne IV, F., Collins, C.D., Antonovics, J., Holt, R.D., 2012. Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. *J. Ecol.* 100, 88–103.
- Allen, E.B., Temple, P.J., Bytnerowicz, A., Arbaugh, M.J., Sirulnik, A.G., Rao, L.E., 2007. Patterns of understory diversity in mixed coniferous forests of Southern California impacted by air pollution. *Sci. World J.* 7, 247–263.
- Ansong, M., Pickering, C., Arthur, J.M., 2015. Modelling seed retention curves for eight weed species on clothing. *Austral Ecol.* 40, 765–774.
- Aronson, M.F., Handel, S.N., 2011. Deer and invasive plant species suppress forest herbaceous communities and canopy tree regeneration. *Nat. Areas J.* 31, 400–407.
- Aronson, M.F.J., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P.S., Gilliers, S.S., Goddard, M.A., Hahs, A.K., Herzog, C., Katti, M., La Sorte, F.A., Williams, N.S.G., Zipperer, W., 2016. Hierarchical filters determine community assembly of urban species pools. *Ecology* 97, 2952–2963.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Bartoń, K. 2020. MuMin: Multi-model inference. R package version 1.43.17. (<https://cran.r-project.org/package=MuMin>).
- Beatty, S.W., 2014. Habitat heterogeneity and maintenance of species in understory communities. In: Gilliam, F.S. (Ed.), *The Herbaceous Layer In Forests Of Eastern North America*. Oxford University Press, New York, New York, USA, pp. 215–323.
- Bhujii, D.R., Ohsawa, M., 2001. Patch implications in the maintenance of species richness in an isolated forest site. *Biol. Conserv.* 98, 117–125.
- Bierzychudek, P., 2020. Passive recovery of an urban forest in the Pacific Northwest after removal of invasive plants. *Urban Ecosyst.* 23, 1023–1038.
- Bowles, M.L., M.D. Hutchison, J.L. McBride. 1994. Landscape pattern and structure of oak savanna, woodland, and barrens in northeastern Illinois at the time of European settlement. Pages 65–74 in *Proceedings of the north american conference on Barrens and Savannas*. Normal: Illinois State University.

- Bowles, M., J. McBride, L. Bell. 1998. Landscape Vegetation Pattern, Composition & Structure of Dupage County, Illinois, as Recorded by the US Public Land Survey (1821–1840). The Morton Arboretum/Ecological Services, Lisle, IL/Urbana, IL.
- Bowles, M.L., Jacobs, K.A., Mengler, J.L., 2007. Long-term changes in an oak forest's woody understory and herb layer with repeated burning. *J. Torre Bot. Soc.* 134, 223–237.
- Breen, D.B., Beauchamp, V.B., Koontz, S.M., Roberts, R.P., 2015. The influence of agricultural abandonment and the abiotic environment on the vegetation communities of a suburban deciduous forest. *Castanea* 80, 103–121.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed., Springer, New York.
- Cain, M.L., Damman, H., Muir, A., 1998. Seed dispersal and the holocene migration of woodland herbs. *Ecol. Monogr.* 68, 325–347.
- Clark, P., Brown, A., Drennan, J., Pedersen, E., Peterson, N., Prasse, M., Vernon, Z., Gable, A., 2016. Chicago Metropolitan Agency for Planning's 2013 land use inventory for Northeastern Illinois, version 1.0. Chicago Metropolitan Agency for Planning, Chicago, Illinois, USA.
- Colgan, C., Hunter, M.L., McGill, B., Weiskittel, A., 2014. Managing the middle ground: forests in the transition zone between cities and remote areas. *Landsc. Ecol.* 29, 1133–1143.
- Cornicelli, L., Woolf, A., Roseberry, J.L., 1996. White-tailed deer use of a suburban environment in southern Illinois. *Trans. Ill. State Acad. Sci.* 89, 93–103.
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol., Evol., Syst.* 113–147.
- Dresner, M., Van Winkle, J., Copp, F.S., 2017. Tree composition and abundance patterns differ in two watersheds of forest park, a large Pacific Northwest urban forest. *Arboric. J.* 39, 208–225.
- Duguay, J.P., Farfara, C., 2011. Overabundant suburban deer, invertebrates, and the spread of an invasive exotic plant. *Wildl. Soc. Bull.* 35, 243–251.
- Duinker, P.N., Ordóñez, C., Steenberg, J.W.N., Miller, K.H., Toni, S.A., Nitoslawski, S.A., 2015. Trees in Canadian cities: indispensable life form for urban sustainability. *Sustainability* 7, 7379–7396.
- Dzwonko, Z., Loster, S., 1990. Vegetation differentiation and secondary succession on a limestone hill in southern Poland. *J. Veg. Sci.* 1, 615–622.
- Eales, J., Haddaway, N.R., Bernes, C., Cooke, S.J., Jonsson, B.G., Kouki, J., Petrokofsky, G., Taylor, J.J., 2018. What is the effect of prescribed burning in temperate and boreal forest on biodiversity, beyond pyrophilous and saproxylic species? A systematic review. *Environ. Evid.* 7, 19.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- ESRI, 2020. ArcGIS Desktop: Release 10.8. Environmental Systems Research Institute, Redlands, California, USA.
- Etter, D.R., Van Deelen, T.R., Ludwig, D.R., Kobal, S.N., Warner, R.E., 2000. Management of white-tailed deer in Chicago, Illinois forest preserves. *Proc. Vertebr. Pest Conf.* 19, 190–196.
- Etter, D.R., Hollis, K.M., Deelen, T.R.V., Ludwig, D.R., Chelsvig, J.E., Anchor, C.L., Warner, R.E., 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. *J. Wildl. Manag.* 66, 500–510.
- Fahey, R.T., Bowles, M.L., McBride, J.L., 2012. Origins of the Chicago urban forest: composition and structure in relation to presettlement vegetation and modern land use. *Arboric. Urban For.* 38, 181–193.
- Fahey, R.T., Maurer, D.A., Bowles, M.L., McBride, J., 2014. Evaluating restoration baselines for historically fire-protected woodlands within a Northeastern Illinois Prairie Peninsula landscape. *Nat. Areas J.* 34, 166–177.
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663.
- Faison, E.K., Foster, D.R., DeStefano, S., 2016. Long-term deer exclusion has complex effects on a suburban forest understory. *Rhodora* 118, 382–402.
- Farmer, S., Ward, J., Horton, J., Clarke, D., 2016. Southern Appalachian urban forest response to three invasive plant removal treatments. *Manag. Biol. Invasions* 7, 329–342.
- Fuselier, L.C., Carreiro, M., Nason, L., 2017. Invasive species management impacts on native and nonnative ferns in an urban forest spore bank. *Castanea* 83, 28.
- Gaertner, M., Wilson, J.R., Cadotte, M.W., MacIvor, J.S., Zenni, R.D., Richardson, D.M., 2017. Non-native species in urban environments: patterns, processes, impacts and challenges. *Biol. Invasions* 19, 3461–3469.
- Gaughan, C.R., DeStefano, S., 2005. Movement patterns of rural and suburban white-tailed deer in Massachusetts. *Urban Ecosyst.* 8, 191–202.
- Gerken Golay, M., Thompson, J., Kolka, R., 2016. Carbon, nitrogen and phosphorus storage across a growing season by the herbaceous layer in urban and preserved temperate hardwood forests. *Appl. Veg. Sci.* 19, 689–699.
- Gharehaghaji, M., Kobal, S., Reklau, R., Minor, E.S., 2019. Management slows down invasion by non-native plants but does not prevent community change over 35 years in urban forests of the Midwestern USA. *For. Ecol. Manag.* 448, 424–431.
- Gilliam, F. (Ed.), 2014. The Herbaceous Layer in Forests of Eastern North America. Oxford University Press.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57, 845–858.
- Graves, R.A., Pearson, S.M., Turner, M.G., 2017. Species richness alone does not predict cultural ecosystem service value. *Proc. Natl. Acad. Sci.* 114, 3774–3779.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Güneralp, B., Reba, M., Hales, B.U., Wentz, E.A., Seto, K.C., 2020. Trends in urban land expansion, density, and land transitions from 1970 to 2010: a global synthesis. *Environ. Res. Lett.* 15, 044015.
- Hanski, I., 2015. Habitat fragmentation and species richness. *J. Biogeogr.* 42, 989–993.
- Heuberger, K.A., Putz, F.E., 2003. Fire in the suburbs: Ecological impacts of prescribed fire in small remnants of longleaf pine (*Pinus palustris*) sandhill. *Restor. Ecol.* 11, 72–81.
- Hayhoe, K., VanDorn, J., Croley II, T., Schlegal, N., Wuebbles, D., 2010. Regional climate change projections for Chicago and the US Great Lakes. *J. Great Lakes Res.* 36, 7–21.
- Hofmeister, J., Hošek, J., Modrý, M., Roleček, J., 2009. The influence of light and nutrient availability on herb layer species richness in oak-dominated forests in central Bohemia. *Plant Ecol.* 205, 57–75.
- Holmes, M.A., Matlack, G.R., 2018. Assembling the forest herb community after abandonment from agriculture: Long-term successional dynamics differ with land-use history. *J. Ecol.* 106, 2121–2131.
- Illinois Department of Natural Resources. 2020. White-tailed Deer Summary 2019–2020: DuPage County. Retrieved from (<https://www2.illinois.gov/dnr/conservation/wildlife/Pages/DeerHarvestSummaries.aspx>).
- Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrad, G.E., Bekessy, S.A., Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L.E., Kendall, D., 2016. Cities are hotspots for threatened species. *Glob. Ecol. Biogeogr.* 25, 117–126.
- Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? *Glob. Ecol. Biogeogr.* 24, 52–63.
- Johnson, L.R., Handel, S.N., 2019. Management intensity steers the long-term fate of ecological restoration in urban woodlands. *Urban For. Urban Green.* 41, 85–92.
- Johnson, L.R., Handel, S.N., 2016. Restoration treatments in urban park forests drive long-term changes in vegetation trajectories. *Ecol. Appl.* 26, 940–956.
- Komuro, T., Koike, F., 2005. Colonization by woody plants in fragmented habitats of a suburban landscape. *Ecol. Appl.* 15, 662–673.
- Kotze, D.J., Lowe, E.C., MacIvor, J.S., Ossola, A., Norton, B.A., Hochuli, D.F., Mata, L., Moretti, M., Gagné, S.A., Handa, I.T., Jones, T.M., 2022. Urban forest invertebrates: how they shape and respond to the urban environment. *Urban Ecosyst.* 1–21.
- Kowarik, I., Hiller, A., Planchuelo, G., Seitz, B., von der Lippe, M., Buchholz, S., 2019. Emerging urban forests: opportunities for promoting the wild side of the urban green infrastructure. *Sustainability* 11, 6318.
- Kurylo, J.S., Knight, K.S., Stewart, J.R., Endress, A.G., 2007. *Rhamnus cathartica*: native and naturalized distribution and habitat preferences. *J. Torre Bot. Soc.* 134, 420–430.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26.
- Lomolino, M.V., 2000. Ecology's most general, yet protean pattern: the species-area relationship. *J. Biogeogr.* 27, 17–26.
- Lopez, B.E., Urban, D., White, P.S., 2018. Nativity and seed dispersal mode influence species' responses to habitat connectivity and urban environments. *Glob. Ecol. Biogeogr.* 27, 1017–1030.
- Martin, A.E., Fahrig, L., 2012. Measuring and selecting scales of effect for landscape predictors in species-habitat models. *Ecol. Appl.* 22, 2277–2292.
- Mata, L., Andersen, A.N., Morán-Ordóñez, A., Hahs, A.K., Backstrom, A., Ives, C.D., Bickel, D., Duncan, D., Palma, E., Thomas, F., Cranney, K., 2021. Indigenous plants promote insect biodiversity in urban greenspaces. *Ecol. Appl.* 31, e02309.
- Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in Eastern North America. *Ecology* 75, 1491–1502.
- Mattingly, K.Z., McEwan, R.W., Paratley, R.D., Bray, S.R., Lempke, J.R., Arthur, M.A., 2016. Recovery of forest floor diversity after removal of the nonnative, invasive plant *Euonymus fortunei*. *J. Torre Bot. Soc.* 143, 103–116.
- Mazerolle, M.J. 2020. AICcmodavg: Model selection and multimodel inference based on (QAICc). R packages version 2.3–1. (<https://cran.r-project.org/package=AICcmodavg>).
- McBride, J.M. and M.L. Bowles. 2001. Vegetation pattern of DuPage and Will Counties at the time of European settlement. Pages 63–71 in Proceedings of the twelfth northern Illinois prairie workshop. College of Dupage, Glen Ellyn, IL.
- McGarigal, K., S.A. Cushman, E. Ene. 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at (<http://www.umass.edu/landeco/research/fragstats/fragstats.html>).
- Meunier, J., Holoubek, N.S., Johnson, Y., Kuhman, T., Strobel, B., 2021. Effects of fire seasonality and intensity on resprouting woody plants in prairie-forest communities. *Restor. Ecol.* e13451.
- Miguet, P., Jackson, H.B., Jackson, N.D., Martin, A.E., Fahrig, L., 2016. What determines the spatial extent of landscape effects on species? *Landsc. Ecol.* 31, 1177–1194.
- Myers, J.A., Vellend, M., Gardescu, S., Marks, P., 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139, 35–44.
- Nesbitt, L., Hotte, N., Barron, S., Cowan, J., Sheppard, S.R.J., 2017. The social and economic value of cultural ecosystem services provided by urban forests in North America: A review and suggestions for future research. *Urban For. Urban Green.* 25, 103–111.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- Piana, M.R., Aronson, M.F., Pickett, S.T., Handel, S.N., 2019. Plants in the city: understanding recruitment dynamics in urban landscapes. *Front. Ecol. Environ.* 17, 455–463.
- Pickering, C., 2022. Mountain bike riding and hiking can contribute to the dispersal of weed seeds. *J. Environ. Manag.* 319, 115693.
- Pregitzer, C.C., Charlop-Powers, S., Bradford, M.A., 2021. Natural area forests in US cities: opportunities and challenges. *J. For.* 119, 141–151.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<https://www.R-project.org/>).

- Rogers, D.A., Rooney, T.P., Hawbaker, T.J., Radeloff, V.C., Waller, D.M., 2009. Paying the extinction debt in southern Wisconsin forest understories. *Conserv. Biol.* 23, 1497–1506.
- Solórzano, A., Brasil-Machado, A., Ribeiro de Oliveira, R., 2021. Land use and social-ecological legacies of Rio de Janeiro's Atlantic urban forests: from charcoal production to novel ecosystems. *R. Soc. Open Sci.* 8, 201855.
- Taylor, Q.A., Midgley, M.G., 2018. Prescription side effects: Long-term, high-frequency controlled burning enhances nitrogen availability in an Illinois oak-dominated forest. *For. Ecol. Manag.* 411, 82–89.
- Teobaldelli, M., Cona, F., Stinca, A., Saulino, L., Anzano, E., Giordano, D., Migliozi, A., Bonanomi, G., D'Urso, G., Mazzoleni, S., Saracino, A., 2020. Improving resilience of an old-growth urban forest in Southern Italy: Lesson (s) from a stand-replacing windstorm. *Urban For. Urban Green.* 47, 126521.
- Tessier, J.T., 2010. Effect of forest harvest on the vegetation of an urban park. *Northeast. Nat.* 17, 273–284.
- Thomson, R.A., 1985. *DuPage Roots*. DuPage County Historical Society, Wheaton, Illinois, USA.
- United Nations, Department of Economic and Social Affairs, Population Division. 2018. *World urbanization prospects: 2018 revision*. New York, United Nations.
- U.S. Census Bureau. 2021. *2020 census of population and housing*. Retrieved from (<https://www.census.gov/quickfacts/fact/table/dupagecountyillinois#>).
- USDA, NRCS. 2021. *The PLANTS Database* (<http://plants.usda.gov>). National Plant Data Team, Greensboro, North Carolina, USA.
- Valdés, A., García, D., 2011. Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb: Landscape change affects plant reproduction. *J. Appl. Ecol.* 48, 1422–1431.
- Valdés, A., García, D., García, M.B., Ehrlén, J., 2014. Contrasting effects of different landscape characteristics on population growth of a perennial forest herb. *Ecography* 37, 230–240.
- Vellend, M., Gardescu, S., Marks, P.L., Myers, J.A., 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139, 35–44.
- Vellend, M., Knight, T.M., Drake, J.M., 2006. Antagonistic effects of seed dispersal and herbivory on plant migration. *Ecol. Lett.* 9, 319–326.
- Vellend, M., Myers, J.A., Gardescu, S., Marks, P.L., 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84, 1067–1072.
- Wang, X., Blanchet, F.G., Koper, N., 2014. Measuring habitat fragmentation: an evaluation of landscape pattern metrics. *Methods Ecol. Evol.* 5, 634–646.
- Wating, J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L. M., Fang, R., Hamel-Leigues, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L., 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecol. Lett.* 23, 674–681.
- Weiss, F., Brummer, T.J., Pufal, G., 2016. Mountain bikes as seed dispersers and their potential socio-ecological consequences. *J. Environ. Manag.* 181, 326–332.
- Whigham, D.F., 2004. Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol. Syst.* 35, 583–621.
- Wilhelm, G., Rericha, L., Lowther, M.M., 2017. *Flora of the Chicago Region: A Floristic and Ecological Synthesis*. Indiana Academy of Science, Indianapolis.
- Williams, S.C., Ward, J.S., Ramakrishnan, U., 2008. Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. *For. Ecol. Manag.* 255, 940–947.
- Wulf, M., Kolk, J., 2014. Plant species richness of very small forests related to patch configuration, quality, heterogeneity and history. *J. Veg. Sci.* 25, 1267–1277.
- Xue, P., Ye, X., Pal, J.S., Chu, P.Y., Kayastha, M.B., Huang, C., 2022. Climate projections over the Great Lakes Region: using two-way coupling of a regional climate model with a 3-D lake model. *Geosci. Model Dev.* 15, 4425.
- Yang, L., Jin, S., Danielson, P., Homer, C., Gass, L., Bender, S.M., Case, A., Costello, C., Dewitz, J., Fry, J., Funk, M., Granneman, B., Liknes, G.C., Rigge, M., Xian, G., 2018. A new generation of the United States national land cover database: requirements, research priorities, design, and implementation strategies. *ISPRS J. Photogramm. Remote Sens.* 146, 108–123.