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The short-term and long-term effects of honeysuckle removal on canopy structure and implications for urban forest management

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ABSTRACT

Riparian forests across the continental United States are heavily invaded by Amur honeysuckle (*Lonicera maackii* (Rupr.)), an invasive shrub which suppresses native plants, homogenizes community structure and composition, and alters ecosystem processes. However, no studies have quantified the impacts of honeysuckle removal on forest canopy structure across the first decade of restoration. In this study we used a portable canopy LiDAR (PCL) to characterize the immediate (<1 year), short-term (1–2 years) and long-term (>10 years) impacts of honeysuckle removal on the horizontal and vertical complexity of canopy structure in 5 heavily invaded riparian forests in Ohio. Within two years of removal, forest canopies had a 40% reduction in canopy leaf volume, a greater average height of maximum canopy density, and increased aggregation of the remaining leaf area around trees than pre-removal conditions. Honeysuckle removal also prompted long-term (>10 years) increases in canopy structural complexity, but only in areas with initially high honeysuckle abundance and low native tree density. Honeysuckle cover had a much stronger influence on canopy structure than either its basal area or stem density. Our results suggest that removing honeysuckle from heavily-invaded stands can promote complex canopy structure over the long-term that is beyond the short-term accrual immediately following disturbance, but might depend on initial stand conditions.

1. Introduction

Urban riparian forests across the eastern United States are becoming increasingly vulnerable to urbanization, sea-level rise, and invasion by non-native plant species (Johnson et al (2020).). The loss of riparian forests is concerning because they provide critical ecosystem services, such as stabilizing streambanks, reducing runoff, lowering risk of floods, improving water quality, and harboring diverse and sometimes rare ecological communities (Macdonald et al., 2004). The recognition of the important roles played by riparian forests, in fact, led to their protection in many urban areas, especially in municipalities that were vulnerable to seasonal flooding. Unfortunately, most of these forests received little attention after protection, and the lack of management coupled with heavy deer browse facilitated invasion by non-native plants that have since dramatically altered their structure and function (McNeish and McEwan, 2016). Ecologists and land managers are now challenged to develop effective strategies to restore riparian forests and safeguard the ecosystem services they provide to human and non-human communities.

Amur honeysuckle (*Lonicera maackii* (Rupr.)) is an invasive shrub that dominates many forest understories in the central United States and is among the most widespread and problematic invasive plants in urban forests in the Eastern and Midwestern U.S. After its introduction from east Asia in the late 1800′s, *Lonicera maackii* has spread rapidly through native understories due to its competitive growth strategy, high plasticity, allelopathy, earlier bud break and longer leaf retention compared to native deciduous species, and ability to resprout after repeated cuttings (McNeish and McEwan 2016). Once established, honeysuckle can have a variety of negative impacts on native plants communities, such as suppressing plant recruitment, homogenizing communities in terms of

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structure and composition, and altering ecosystem processes (Collier et al., 2002; Hartman and McCarty, 2007; Hartman and McCarthy, 2008; Shields et al., 2015; McNeish and McEwan, 2016). Over time honeysuckle shapes canopy structure by affecting growth of overstory trees (Hartman and McCarty, 2007), the amount of canopy leaf material (Trammel et al., 2012), and species composition – all of which can alter the vertical compositional structure of the forest canopy (Hartman and McCarthy, 2008). Despite the known potential of honeysuckle to alter conventional, single dimensional attributes of physical forest structure (i.e., leaf area), we poorly understand its impacts on canopy structural traits (CST), such as vegetation density, height, arrangement, cover, and structural complexity (Fahey et al., 2019; Atkins et al., 2020).

Understanding the effects of honeysuckle on CST is ecologically important, as canopy structure is linked to ecosystem processes in temperate forests across the United States (Atkins et al., 2018b; Fahey et al., 2019). For example, work connecting CSTs to ecosystem function has provided empirical evidence that more complex forests tend to increase carbon sequestration (Fahey et al., 2015; Fotis et al., 2018; Gough et al., 2019) and are more efficient at resource acquisition and use (Hardiman et al., 2011; Atkins et al., 2018b). Canopy structure also affects light distribution and, accordingly, leaf morphology and physiology (Fotis and Curtis 2017). Over time, these changes potentially induce greater canopy 'exploration' by overstory trees that reduces forest productivity (Fotis et al., 2018). The impacts of structural changes can extend beyond plant communities and affect wildlife habitat (McCusker et al., 2010; Davis and Asner, 2014; DeJong 2020; Fotis et al., 2020). Therefore, understanding the drivers of CST, and the ways in which invasive species may affect them, should be a priority for forest management aimed at maximizing the ecological and functional value of forest ecosystems.

A rich body of literature shows that CSTs change through forest succession (Hardiman et al., 2013a, Hardiman et al., 2013b) and in response to disturbance (Fahey et al., 2015; Fahey et al., 2019; Atkins et al., 2020). Forest succession and disturbance shape the 3D structure of forest canopies directly by altering overstory leaf area and arrangement (Hardiman et al., 2013a; Atkins et al., 2020) and indirectly by altering stem numbers and size distributions (Fahey et al., 2015; Fotis et al., 2018; Fotis et al., 2020). For example, Fotis et al. (2018) found that forests with initially high stem densities and tree size heterogeneity were more structurally complex, and over a 7-year period, exhibited increases in open canopy space, height growth and interannual variability in CSTs as the canopy re-arranged itself. Honeysuckle abundance impacts recruitment of understory seedlings and saplings into the midcanopy (Hartman and McCarthy 2008) and may therefore be expected to indirectly impact long-term canopy structure by altering initial stand structure (i.e., stem density and tree size distributions), in addition to its direct influence on canopy leaf biomass and leaf area (Trammell et al., 2012). To date, no studies have quantified the immediate or long-term impacts of honeysuckle removal on CSTs, in part due to inaccessibility and logistical difficulties of measuring the 3D structure of forest canopies. However, recent advances in remote sensing, such as the portable canopy LiDAR (PCL), have now made it possible to measure and quantify the internal arrangement of leaves and empty space of entire canopies with high precision (Parker et al., 2004). As such, LiDAR may prove to be a rapid and relatively cheap method of quantifying the long-term impacts of honeysuckle removal on CSTs and forest function.

The first objective (Obj 1) of this study was to characterize the immediate (<1 year), short-term (1–2 years) and long-term (>10 years) impacts of honeysuckle removal on CST in 5 heavily invaded riparian forests in central Ohio using a portable canopy LiDAR (PCL). Because honeysuckle can comprise a large portion of canopy biomass and leaf area (Trammell et al., 2012), we hypothesized that:

- (H1) the immediate impact of honeysuckle removal is decreased leaf area, increased leaf clumping around trees, and a vertical shift in leaf material away from a bottom-heavy canopy towards a move even leaf distribution.
- (H2) long-term increases in canopy structural complexity following honeysuckle removal is a result of increased tree size heterogeneity (Fotis et al., 2020) as seedlings and saplings become recruited into the midstory (Hartman and McCarthy, 2008)
- (H3) initial differences in stand structure (i.e., tree density and tree size variability) resulting from varying honeysuckle abundance may alter the long-term (>10 yrs.) canopy structural successional trajectory of CST following removal of this invasive shrub, as initial stand structure can alter the temporal dynamics of canopy rearrangement over time (Fotis et al., 2018).

The second objective (Obj 2) of this study was to assess the utility of the PCL device as a rapid tool for identifying priority areas in need of invasive species management, as well as monitoring the impact of invasive species removal on canopy structure, by quantifying the degree to which different metrics of honeysuckle abundance (i.e., stem count, basal area, and cover) correlates with different CSTs. We hypothesize that:

- (H4) Honeysuckle cover will have the strongest impact on CSTs as it is likely to intercept more PCL lasers (and therefore impact structural metrics more) as compared to basal area and stem density, which are less likely to impact CSTs due to their mostly vertically orientation and smaller surface area.

2. Methods

2.1. Short-term experimental study site description

The five experimental restoration (ER) sites were located along riparian forests in the Scioto River Watershed in central Ohio, USA (Fig. 1a). The ER sites included Tuttle park (T_{ER}), Kenney Park (K_{ER}), Three Creeks Park (TC_{ER}), Casto Park (C_{ER}) and Wolfe Park (W_{ER}). These forests are comprised primarily of American Sycamore (*Platanus occidenta*lis L.), boxelder (*Acer negundo*), American elm (*Ulmus americana* L.), silver maple (*A. saccharinum* L.), sugar maple (*A. saccharum* Marshall), hackberry (*Celtis occidentalis* L.), eastern cottonwood (*Populus deltoides* Bartram ex Marshall), and black walnut (*Juglans nigra* L.). The understory consists of seedlings of the canopy species as well as Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim.), multiflora rose (*Rosa multiflora* Thunb.), spicebush (*Lindera benzoin* L.), and hawthorn (*Crataegus spp*.).

In July 2018, four (18 × 32 m) permanent plots were established parallel to the riparian corridors at each ER site. In early August of 2018, 100% of honeysuckle shrubs were removed from half the plots in each site (hereafter referred to as removal plots) using a chainsaw/hand saw and a glyphosate herbicide (Roundup Pro, Monsanto MFG# MSR10317188) was applied as per the manufacturer label to honeysuckle stumps immediately upon removal to prevent regrowth. Honeysuckle was left intact in the other two plots (hereafter referred to as control plots) at each site. Control and removal plots within each site were further subdivided such that one received restoration plantings while the other did not. We did not analyze the effects of honeysuckle removal on the restoration plantings as this is an ongoing investigation of future studies.

Prior to honeysuckle removal, three 5 m radius subplots were established along the spine of each permanent plot ($n = 3$ per plot; $n = 12$ per site). Within each of these subplots, we measured the identity and diameter of each tree > 10 cm diameter at breast height (DBH; 1.37 m), inventoried woody saplings < 10 cm DBH by category (small [0.01–3.3 cm DBH], medium [>3.3–6.6 cm DBH], or large [>6.6–10 cm DBH]), and quantified honeysuckle cover within the 2–6 m strata using FIA canopy cover techniques (US FS 2011).

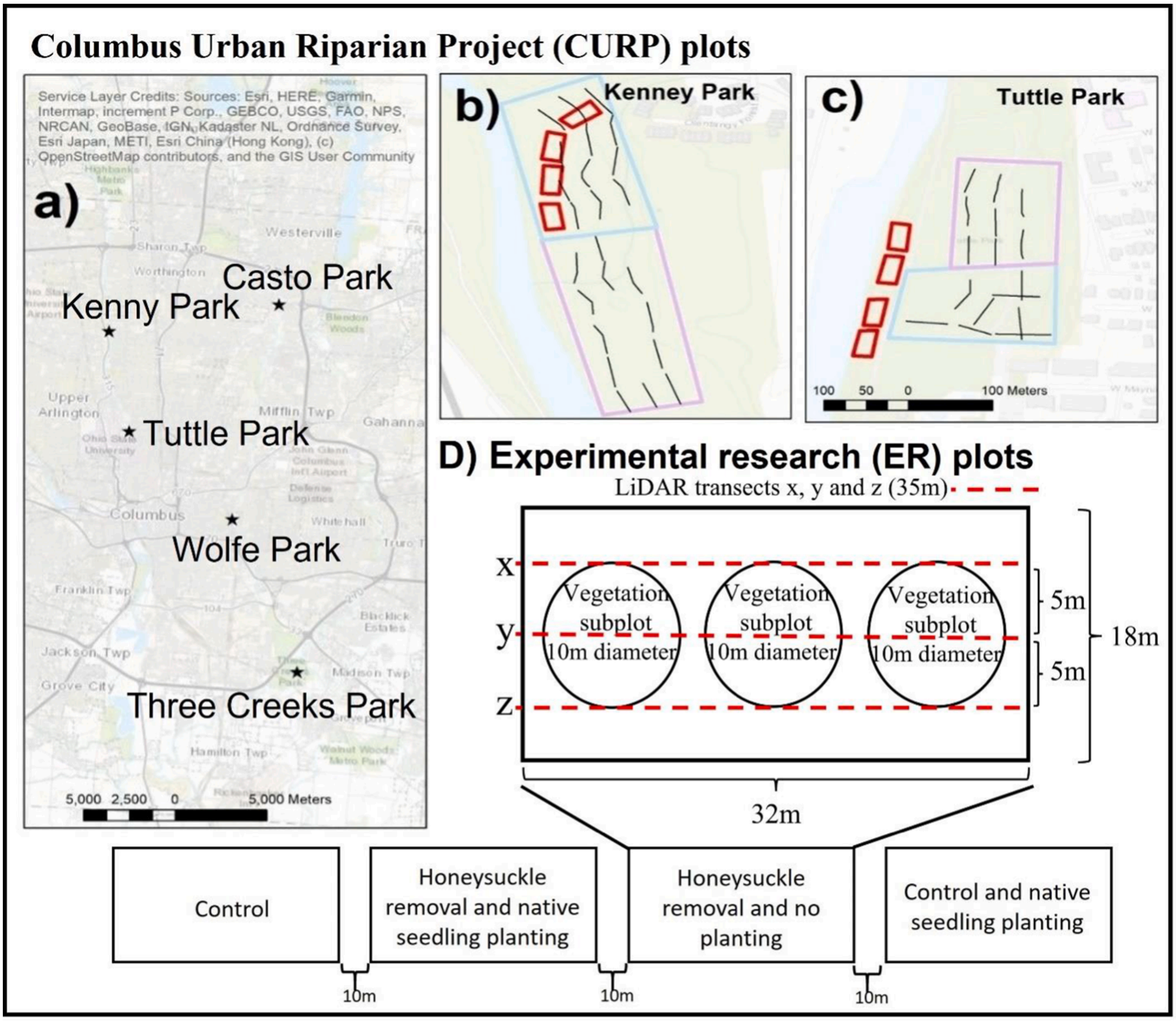

Fig. 1. a) Map showing the 5 experimental research (ER) sites established in 2018 along riparian forests in the Scioto River Watershed in central Ohio, USA. Representative sampling design for portable canopy LiDAR (PCL) transect placement at long-term Columbus Urban Riparian Project (CURP) plots at b) Kenny Park (K_{CURP}) and c) Tuttle Park (T_{CURP}). PCL data was collected along 40 m long transects (black lines), each with at least 10 m spacing between consecutive transects, for 12 control (no honeysuckle removal; light purple) and removal (honeysuckle removed; light blue) transects at K_{CURP} and 8 control and 8 removal transects at T_{CURP}. d) Four 18 × 32 m permanent plots were established within each ER site in July 2018 and honeysuckle was removed in early August of 2018 in two plots at each site. Within each ER plot, honeysuckle cover was visually estimated between 2 and 6 m from ground and all live stems were identified to species and their diameter at breast height (DBH) measured within 3, non-overlapping 5 m radius subplots spanning the plot. PCL data was collected along 3, 35 m long, parallel transects spaced 5 m apart, where the central PCL transect bisected the 5 m subplots. Note arrangement of Kenney and Tuttle ER plots (red rectangles) within the larger footprint of the two long-term CURP study sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. *Long-term experimental study site description*

Two of our ER study sites, T_{ER} and K_{ER}, were opportunistically embedded within a larger Columbus Urban Riparian Project (here after referred to as CURP with sites T_{CURP} and K_{CURP}; see Rodewald et al., 2013, Rodewald et al., 2014) in order to study the long-term effects of honeysuckle removal. In 2007, all honeysuckle stems were cut down using chainsaw/hand saws in plots located in the northern and southern portions of Kenney park ($K_{CURP\ removal}$) and Tuttle Park ($T_{CURP\ removal}$), respectively, such that half the plots remained controls with no removals ($K_{CURP\ control}$ and $T_{CURP\ control}$; Fig. 1b and 1c). In 2006, vegetation composition and stand structure (i.e., stem diameters) were measured at 5–8, 11.3 m-radius plots in the control and removal areas, for a total of 10–16 plots in each site (Rodewald et al., 2015). Control and removal plots were re-censused again in 2007, 2011, and 2019 after honeysuckle was cut down in the removal plots in 2007 (see Table 1). Within each plot, all woody plants > 3 cm DBH were counted, identified to species, and measured to nearest 0.5 cm DBH, whereby they were binned according to size: saplings (3 – 8 cm DBH), small trees (8.5 – 23 cm DBH), medium trees (23.5 – 38 cm DBH), and large trees (>38 cm DBH). Honeysuckle stems and basal area were also measured during each census period. We distinguish long-term data as those collected by Rodewald et al. (2013) in 2006 and onward at K_{CURP} and T_{CURP} from our short-term data which was collected in the 5 ER sites initiated in 2018.

2.3. *Stand structural metrics*

We calculated three metrics of stand structural characteristics based on stem size and spatial patterns for the ER sites using the 2018 census data and for the CURP sites using the 2006, 2007, 2011 and 2019 census data (see Table 1). The three stand structural metrics were standard deviation of DBH (Std_{DBH}), stem density ($Stem_{Den}$) and total tree basal

Table 1
Data collection in the short-term experimental research (ER) project initiated in 2018 and in the Long-term Columbus Urban Riparian Project (CURP) initiated in 2006 by Rodewald et al. (2013) and Rodewald et al. (2014). Table shows years that vegetation and portable canopy LiDAR (PCL) data was collected, whether honeysuckle was removed, and the sample sizes for each site. Honeysuckle was removed only once in each study (early August of 2018 for the ER study and in 2007 for the CURP study). ER vegetation data consisted of honeysuckle basal area, stem counts, cover (2–6 m), and all native tree stems > 10 cm DBH; CURP vegetation data consisted of honeysuckle basal area and stem counts, and all native tree stems > 10 cm DBH.

Short-term Experimental Research (ER) project initiated in 2018			
	Census dates		
	Early August 2018	Late August 2018	August 2019
Data collection in control plots with sample sizes	**ER Control Pre-disturbance plots**		**ER Control 1 yr. post-disturbance plots**
Honeysuckle removed ($n = 6$)	No	No	No
Vegetation data ($n = 6$)	Yes	No	Yes
PCL data ($n = 6$)	Yes	No	Yes
Data collection in treatment plots with sample sizes	**ER removal Pre-disturbance plots**	**ER removal Post-disturbance plots**	**ER removal 1 yr. post-disturbance plots**
Honeysuckle removed ($n = 6$)	No	Yes	No
Vegetation data ($n = 6$)	Yes	No	Yes
PCL data ($n = 6$)	Yes	Yes	Yes

Long-term Columbus Urban Riparian Project (CURP) initiated in 2006					
	Census dates				
	2006	2007	2011	2018*	2019
Data collection in control plots with sample sizes	**CURP Control**	**CURP Control**	**CURP Control**	**CURP Control**	**CURP Control**
Honeysuckle removed ($n=5$–8)	No	No	No	No	No
Vegetation data ($n=5$–8)	Yes	Yes	Yes	No	Yes
PCL data ($n=8$ Tuttle; $n=12$ Kenny)	No	No	No	Yes	No
Data collection in treatment plots with sample sizes	**CURP Treatment**	**CURP Treatment**	**CURP Treatment**	**CURP Treatment**	**CURP Treatment**
Honeysuckle removed ($n=5$–8)	No	Yes	No	No	No
Vegetation data ($n=5$–8)	Yes	Yes	Yes	No	Yes
PCL data ($n=8$ Tuttle; $n=12$ Kenny)	No	No	No	Yes	No

area divided by the number of trees (Ba$_{\text{Trees}}$). These metrics quantify aspects of tree size heterogeneity and successional stage of forest succession and are commonly used metrics of stand structure (Kuehne et al., 2015) or correlate well with PCL derived CST metrics used in this study (Fahey et al., 2015; Fotis et al., 2018; Fotis et al., 2020). Note that the stand structural variables described above are derived from tree stem measurements and are distinct from canopy structural metrics described in the next section, which are obtained from PCL measurements of canopy leaf arrangements.

2.4. *Canopy structural metrics*

Canopy structural metrics were measured and derived for the ER sites and the two CURP sites using a PCL device described by Parker et al. (2004), which has been used extensively to characterize broad scale classifications of CST in temperate forests of the United States (Atkins et al., 2018b; Fahey et al., 2020). For each ER plot, PCL data was collected along 3, 35 m long, parallel transects spaced 5 m apart, totaling 12 transects per site (Fig. 1d). PCL data was collected for control plots (ER$_{\text{control pre-disturbance}}$) and removal plots (ER$_{\text{removal pre-disturbance}}$) in early August of 2018 prior to honeysuckle removal, and re-measured again, immediately after disturbance in late August of 2018, for only the two plots where honeysuckle was removed (ER$_{\text{removal post-disturbance}}$). All PCL transects were then re-measured the following year during August of 2019 for both control plots (ER$_{\text{control 1 yr. post-disturbance}}$) and removal plots (ER$_{\text{removal 1 yr. post-disturbance}}$).

In 2018, we established additional PCL transects in the CURP sites. These transects followed an opportunistic sampling regime that differed from ER plots since we used an existing experimental design. For K$_{\text{CURP}}$, we set up three rows of parallel transects that spanned the site and bisected the control plots (no honeysuckle removal) and removal plots (honeysuckle removed) established during the Rodewald et al. (2014) study. We then collected PCL data in 40 m sections along each transect (comparable in length to ER treatments) leaving 10 m gaps between each consecutive section, resulting in a total of 12 transects for the control area (K$_{\text{CURP control}}$) and 12 transects for the removal area (K$_{\text{CURP removal}}$) (Fig. 1b). PCL collection sampling design differed at T$_{\text{CURP}}$ due to the non-symmetrical layout of the past treatments. This resulted in a total of 8, 40 m sections sampled in the control area (T$_{\text{CURP control}}$) and 8, 40 m sections located in the removal area (T$_{\text{CURP removal}}$) (Fig. 1c).

The PCL employs an upward-looking near-infrared pulsed laser distance measuring instrument (model LD90-3100VHSFLP; Riegl USA, Inc., Orlando, Florida, USA) to quantify the horizontal and vertical distribution of branch and leaf material along each transect. The spatial distribution of returns for each transect is partitioned into 1 × 1 m bins (Fig. 2) and processed with the forestr package in R (v. 3.5.0) to calculate the following 10 metrics of canopy structure described by Atkins et al. (2018a) from different taxonomic groups characterizing canopy cover and openness, arrangement, height, and heterogeneity: 1) *Vegetation area index* (VAI), the ratio of vegetation area of the canopy per ground area; 2) *sky fraction*, a measure of canopy gapiness proportional to the amount of empty horizontal area; 3) *clumping index*, a measure of vegetation dispersion from a random distribution where higher clumping results in more aggregated or grouped vegetation; 4) *porosity*, the percent of canopy space void of vegetation; 5) *maximum vegetation density* (mode.el), the average height of maximum canopy density; 6) *mean leaf height variance* (MHV), the vertical variability in VAI distribution; 7) *Gini coefficient*, a measure of vertical evenness of leaf distribution, whereby negative numbers indicate top heavy canopies, positive numbers indicate bottom heavy canopies, and 0 represents perfect evenness; 8) *Rugosity*, a measure of the horizontal variability of vertical variation in leaf area distribution, where higher numbers indicate more heterogeneity; 9) *Effective number of layers* (ENL), a measure of vertical connectivity, whereby ENL increases in taller stands with more even distributions of vegetation along the vertical profile; and 10) *Top Rugosity*, a measure of the canopy height variance of the canopy (see Table S1 for more detail).

2.5. *Honeysuckle abundance metrics*

Absolute and relative honeysuckle abundance metrics were calculated for each ER plot using the 2018 census data and CURP plots using

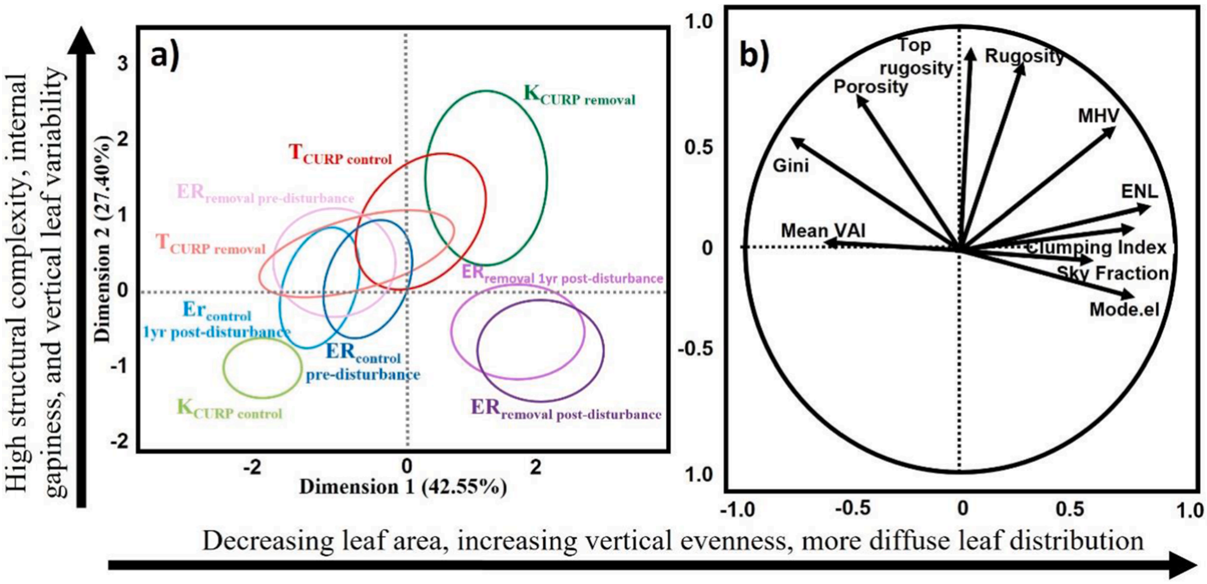

Fig. 2. Principal components analysis (PCA) showing a) 95% confidence ellipses characterizing differences in canopy structure among experimental research (ER) sites prior to disturbance in control plots ($ER_{control\ pre\text{-}disturbance}$) and removal plots ($ER_{removal\ pre\text{-}disturbance}$), immediately after honeysuckle removal ($ER_{removal\ post\text{-}disturbance}$), 1-year after removal for control ($ER_{control\ 1\ yr.\ post\text{-}disturbance}$) and removal plots ($ER_{removal\ 1\ yr.\ post\text{-}disturbance}$) and 10-years post removal for Tuttle control ($T_{CURP\ Control}$) and removal ($T_{CURP\ Removal}$) plots and Kenney control ($K_{CURP\ Control}$) and removal ($K_{CURP\ Removal}$) plots; and b) PCA axes describing relationships between environmental space defined by canopy structural traits. The first principal component (PC1) represents a gradient of decreasing canopy leaf surface volume, increasing vertical evenness, average height of maximum vegetation density and diffusivity in leaf spacing from negative to positive PC1 numbers. The second principal component (PC2) represents a gradient of increasing structural complexity, vertical leaf variability and internal canopy gapiness from negative to positive PC2 numbers.

the 2006, 2007, 2011 and 2019 data (see Table 1). Absolute honeysuckle abundance was calculated as honeysuckle stems per hectare ($H_{stems/ha}$) and honeysuckle basal area per hectare ($H_{ba/ha}$) for all individuals across the 3 ER subplots within each plot, and calculated for all individuals in a given 11.3 m radius plot for each plot in the CURP sites for each of the four census periods. Relative honeysuckle abundance was calculated relative honeysuckle stems ($H_{stems/\%}$) and relative honeysuckle basal area ($H_{ba/\%}$). The $H_{stems/\%}$ metric was calculated as the number of honeysuckle stems divided by the total stem count of all individuals (both woody saplings and trees > 10 cm DBH) and expressed as a percent. This was calculated for all individuals across the 3, 5 m radius subplots combined for ER plots and for all individuals in a given 11.3 m radius plot for the CRUB sites for each of the four census periods. Likewise, $H_{ba/\%}$ was quantified as the total honeysuckle basal area by the total basal area of all individuals and expressed as a percent. This was calculated for all individuals across the 3, 5 m radius subplots combined for ER plots and for all individuals in a given 11.3 m radius plot for the CRUB sites for each of the four census periods. Honeysuckle cover (H_{cover}) was additionally calculated for ER plots based on visual assessments of honeysuckle cover between 2 and 6 m averaged across the 3 ER subplots within each plot. H_{cover} could not be calculated for the CURP plots because data was not available.

2.6. Statistical analyses

To address our first two hypotheses of Obj 1, we first characterized the immediate (<1 year), short-term (1–2 years) and long-term (>10 years) impacts of honeysuckle removal on canopy structure using principal components analysis (PCA) to collapse all 10 PCL metrics into two synthetic predictor variables (PC1 and PC2) variables describing differences in canopy structure across sites prior to disturbance from those post honeysuckle removal and to differentiate short-term from long-term disturbance effects on canopy structure (See Table S2 for eigenvalues). Principal components analysis was performed on PCL metrics derived from the ER plots designated for honeysuckle removal prior to disturbance ($ER_{removal\ pre\text{-}disturbance}$), immediately after disturbance ($ER_{removal\ post\text{-}disturbance}$), and 1-year post honeysuckle removal ($ER_{removal\ 1yr.\ post\text{-}disturbance}$), on undisturbed ER control plots prior to honeysuckle removal ($ER_{control\ pre\text{-}removal}$) and undisturbed ER control plots 1-year post disturbance ($ER_{control\ 1yr.\ post\text{-}removal}$), and using the long-term CURP control ($K_{CURP\ control}$ and $T_{CURP\ control}$) and removal plots ($K_{CURP\ removal}$ and $T_{CURP\ removal}$) for > 10 year post disturbance effects. The degree of correlation (factor loadings) between CSTs, site and treatments with each axis can be found in Table S3. We used 95% confidence intervals around each treatment to highlight differences. To compliment the visual display of the PCA, we used a nonparametric permutation procedure (PERMANOVA) to test for differences in canopy structure across sites, treatments, and their interaction, based on Bray-Curtis distance measurements. Principal components analysis and graphs were created using the “Rcmdr” function in the “FactoShiny” package R software (Le et al., 2008) and PERMANOVA was performed using the adonis function in the vegan package of R.

A two-way analysis of variance (ANOVA) was used to test our third hypothesis of Obj 1 that differences in initial stand conditions in K_{CURP} and T_{CURP} can alter long-term (10 +) canopy structural successional pathways following honeysuckle removal. Initial stand conditions were entered as the dependent variables and defined as stand structure (Std_{DBH}, Ba_{trees}, $Stem_{Den}$), absolute honeysuckle abundance ($H_{stems/ha}$ and $H_{ba/ha}$), and relative honeysuckle abundance ($HA_{stem/\%}$ and $HA_{ba/\%}$) in 2006 before honeysuckle was removed. To determine whether initial stand conditions were different between CURP sites in 2006 (prior to honeysuckle removal), separate two-way ANOVAs were conducted on each metric of initial stand condition to compare means between K_{CURP} and T_{CURP} sites, and to test for within site differences between control plots and plots designated for honeysuckle removal in 2007 (i.e., removal plots), where site and treatment were considered independent variables. A Tukey’s post hoc test for all pairwise comparisons was conducted when main effects of site were significant. Normality and equal variance assumptions of the two-way ANOVA were determined for each metric using a Shapiro-Wilk test and Levene’s test of homogeneity of variance, respectively. Std_{DBH}, $Stem_{Den}$, and $Stem_{loss}$ met these assumptions, while Ba_{trees}, $H_{ba/ha}$, Ba_{loss} were log transformed and $H_{stem.ha}$ square root transformed, to meet normality and homogeneity of variance requirements. Statistical significance was considered at $\alpha < 0.05$. Effect size analysis was used to compare differences and magnitude of change in stand structure and honeysuckle abundance between control and removal plots within each site following honeysuckle removal in 2007 using Cohen's d. Effect sizes were calculated between group means for stand structural and honeysuckle abundance variables within each site across years 2006, 2007, 2011, and 2019, where an effect size (d) of $d < 0.2$ is considered a 'very small effect (vs)', 0.2–0.5 a 'small effect (s)', 0.5 represents a 'medium effect (m)', 0.8–1.0 a 'large effect (l)', 1.0–2.0 a 'very large effect (vl)' and > 0.2 a 'huge effect (h).'

(Cohen, 1988).

We used separate least squares regressions to test for correlations between honeysuckle abundance measurement(s) (i.e., stem/ha, basal area/ha and cover) and CSTs to address our Obj 2 of determining the utility of the PCL device as a rapid tool for assessing priority areas in need of invasive species removal and which honeysuckle metrics most strongly impact canopy structure.

3. Results

3.1. Short-term vs long-term changes in canopy structure following honeysuckle removal

Canopy structural complexity was similar between ER sites prior to disturbance and was significantly altered in the removal plots after honeysuckle was cut down (Fig. 2a). We summarized canopy structure using two synthetic predictor variables derived from collapsing 10 canopy structural metrics into two distinct principal components explaining ~ 70% of the variance. The first (PC1) and second principal components (PC2) explained 42.55% and 27.40% of the total variance in canopy structure, respectively, and were the two main axes used to characterize canopy structure across treatments and time periods (Fig. 3a). While principal components with Eigen values>1 are generally interpreted (PC3 had an Eigen value = 1.45), we did not consider PC3 to be ecologically important because it explained a minor proportion of variance (14%) in canopy structure compared to PC1 and PC2 (70%), and because treatment (honeysuckle removal) was not significantly correlated with this axis ($R^2 = 0.049$; p-value = 0.31; see Table S2).

Axis 1 was strongly related to CST metrics associated with the amount and arrangement of both leaf area and open space, and its vertical distribution within the canopy (Fig. 2b; see Table S3 for factor loadings). The first PC represents an axis of disturbance, whereby undisturbed forests (i.e., $ER_{control\ pre\text{-}disturbance}$, $ER_{control\ 1\text{-}yr\ post\text{-}disturbance}$, $ER_{removal\ pre\text{-}disturbance}$, and $K_{CURP\ control}$) were associated with negative values. Forests plots experiencing immediate disturbance ($ER_{removal\ post\text{-}disturbance}$), 1-year post honeysuckle removal ($ER_{removal\ 1yr.\ post\text{-}disturbance}$) and long-term (>10 years) impacts of honeysuckle removal ($K_{CURP\ removal}$) were significantly correlated with positive PC1 values (treatment: $p < 0.001$, $R^2 = 0.41$; site $p = 0.005$, $R^2 = 0.086$; See Table S3 for factor loadings); $T_{CURP\ control}$ and $T_{CURP\ removal}$ plots were the exception and were unrelated to PC1 and exhibited canopy structural characteristics intermediate of the disturbance gradient (Fig. 3a). Pre-disturbed canopies (negative PC1 values) had bottom-heavy leaf distributions (*Gini coefficient*: $p < 0.001$, $R^2 = 0.61$) and contained high quantities of leaf area (*mean VAI*: $p < 0.001$, $R^2 = 0.38$) (Fig. 2c; Fig. 3). Post-disturbance canopies (positive PC1 values) exhibited a vertical shift of vegetation density higher into the canopy (*mode.el*: $p < 0.001$, $R^2 = 0.67$) and a concomitant increase in leaf clumping ($p < 0.001$, $R^2 = 0.64$) and sky fraction ($p < 0.001$, $R^2 = 0.35$). Disturbed canopies also experienced a small increase in structural complexity (*Rugosity*: $p < 0.001$, $R^2 = 0.08$), both in terms of vertical connectivity (*ENL*: $p < 0.001$, $R^2 = 0.76$) and variability (*MHV*: $p < 0.001$, $R^2 = 0.51$).

Axis 2 was strongly related to CST metrics associated with leaf heterogeneity and arrangement (Fig. 2b; see Table S3 for factor loadings). $K_{CURP\ removal}$ plots were strongly associated with positive PC2 values while most treatments and time since disturbance sorted out along PC1 and were weakly correlated with axis 2 (treatment: $p < 0.001$, $R^2 = 0.156$; Site: $p < 0.001$, $R^2 = 0.22$; Fig. 3a). This second PC represents an axis of the potential long-term (>10-yr) successional trajectory in canopy structure following honeysuckle removal. Positive PC2 values are strongly associated with high structural complexity (*Rugosity*: $p < 0.001$, $R^2 = 0.71$) and surface topography (*Top.rugosity*: $p < 0.001$, $R^2 = 0.90$), vertical leaf variability (*MHV*: $p < 0.001$, $R^2 = 0.29$) and internal canopy gaps (*Porosity*: $p < 0.001$, $R^2 = 0.48$; Fig. 3b).

The PERMANOVA results showed that site, treatment, and their interaction, had a significant effect on canopy structure (p-values < 0.001 for all three comparisons). Canopy structure was impacted the most by treatment, which explained almost a quarter of the variance in canopy structure across sites and times ($R^2 = 0.24$), while site × treatment ($R^2 = 0.10$) and site ($R^2 = 0.16$) explained less variance.

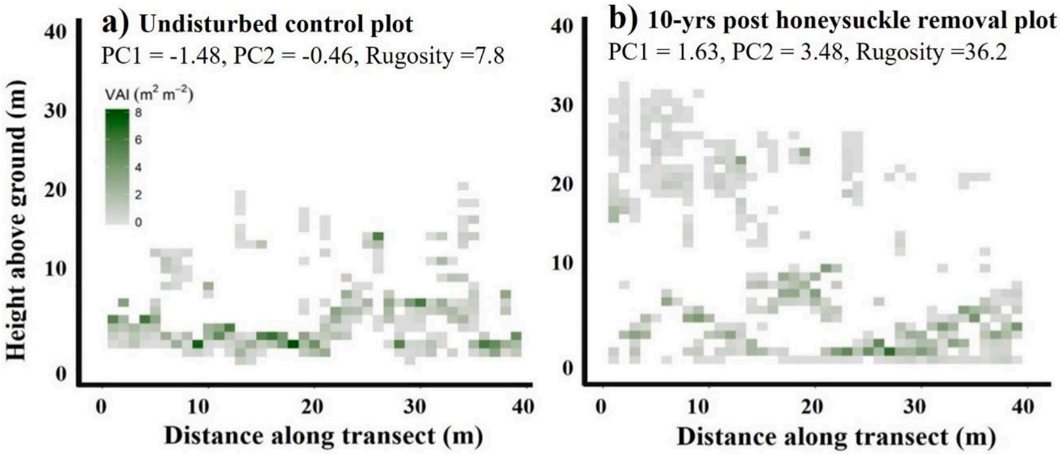

Fig. 3. Portable Canopy LiDAR (PCL) scan results visually highlighting extreme changes in canopy structure along the PC1 and PC2 gradient. The first PCL scan is a) a representative undisturbed control plot (highly negative PC1 and PC2 value) from the long-term Columbus Urban Riparian Project (CURP) at Kenny Park illustrating low canopy structural complexity prior to honeysuckle removal and b) a representative CURP plot at Kenney Park 10 + years post honeysuckle removal (highly positive PC1 and PC2 value) illustrating high canopy structural complexity. Greenscale shade ramp indicates vegetation area index (VAI) in 1 m vertical bins where darker green indicates more LiDAR returns (and foliage density). The y-axis illustrates height above ground surface, x-axis distance along transect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Initial stand conditions in the CURP sites

Relative and absolute honeysuckle abundance was significantly greater at K_{CURP} than T_{CURP} in 2006 before honeysuckle was removed but did not differ between the control and removal plots within either site prior to disturbance in 2007. The two-way ANOVA model showed significant differences between K_{CURP} and T_{CURP} sites with regard to honeysuckle basal area per hectare ($F_{1,23} = 18.07$, $p < 0.001$), honeysuckle stems per hectare ($F_{1,23} = 13.8$, $p < 0.001$), percent basal area lost ($F_{1,23} = 17.27$, $p < 0.001$) and percent stems lost ($F_{1,23} = 18.14$, $p < 0.001$). The interaction term between site and treatment was not significant with regards to absolute honeysuckle abundance metrics (honeysuckle basal area per hectare, $F_{1,23} = 2.87$, $p = 0.59$; honeysuckle stems per hectare, $F_{1,23} = 1.53$, $p = 0.70$) or relative honeysuckle abundance metrics (percent basal area lost, $F_{1,23} = 1.17$, $p = 0.75$; percent stems lost, $F_{1,23} = 2.47$, $p = 0.61$), indicating no difference in honeysuckle abundance between control and removal plots within either site prior to disturbance. The effect size (Cohens d) for mean differences in honeysuckle abundance between control and removal plots within K_{CURP} and T_{CURP} sites were similarly small in 2006, further corroborating no differences in honeysuckle abundance between treatments within either site prior to disturbance. The impact of honeysuckle removal was much larger in K_{CURP} plots than T_{CURP} plots following disturbance as indicated by larger effect sizes between control and removal plots for all honeysuckle metrics in K_{CURP} for each subsequent year after 2006 (Fig. 4). However, the effect size for all honeysuckle abundance metrics decreased between control and removal plots in 2019 relative to their 2007 and 2011 values for both sites, indicating some re-growth of honeysuckle 10 + years after removal (see Table S6 for Cohens d values).

Most stand structural features between CURP sites were similar in 2006 prior to disturbance but were significantly altered after honeysuckle was removed in 2007. The two-way ANOVA model showed significant differences in stem density between K_{CURP} and T_{CURP} sites ($F_{1,23} = 6.68$, $p = 0.01$) but no differences in the standard deviation of DBH ($F_{1,23} = 0.31$, $p = 0.58$) or the basal area/number of trees ($F_{1,23} = 2.106$, $p = 0.12$) in 2006. The interaction term between site and treatment was not significant with regards to stand deviation of DBH ($F_{1,23} = 0.45$, $p = 0.51$) or basal area/number of trees ($F_{1,23} = 0.18$, $p = 0.67$), indicating that stem size variation and average tree size were no different between sites, or between treatments within sites, prior to honeysuckle removal. The effect size for mean differences in standard deviation in DBH and basal area/number of trees between control and removal plots at K_{CURP} and T_{CURP} were similarly small in 2006 (Fig. 5), further corroborating no difference in these measures of stand structure between treatments within either site prior to disturbance. However, there was a medium effect size for stem density ($d = 0.55$) for K_{CURP} plots in 2006, suggesting that the stem density of native plants might have been somewhat higher in control plots than removal plots prior to honeysuckle removal. The effect sizes for basal area/number of trees and stem density did not change much for 2007, 2011 and 2019 for either site, indicating that honeysuckle removal did not alter these stand metrics over time.

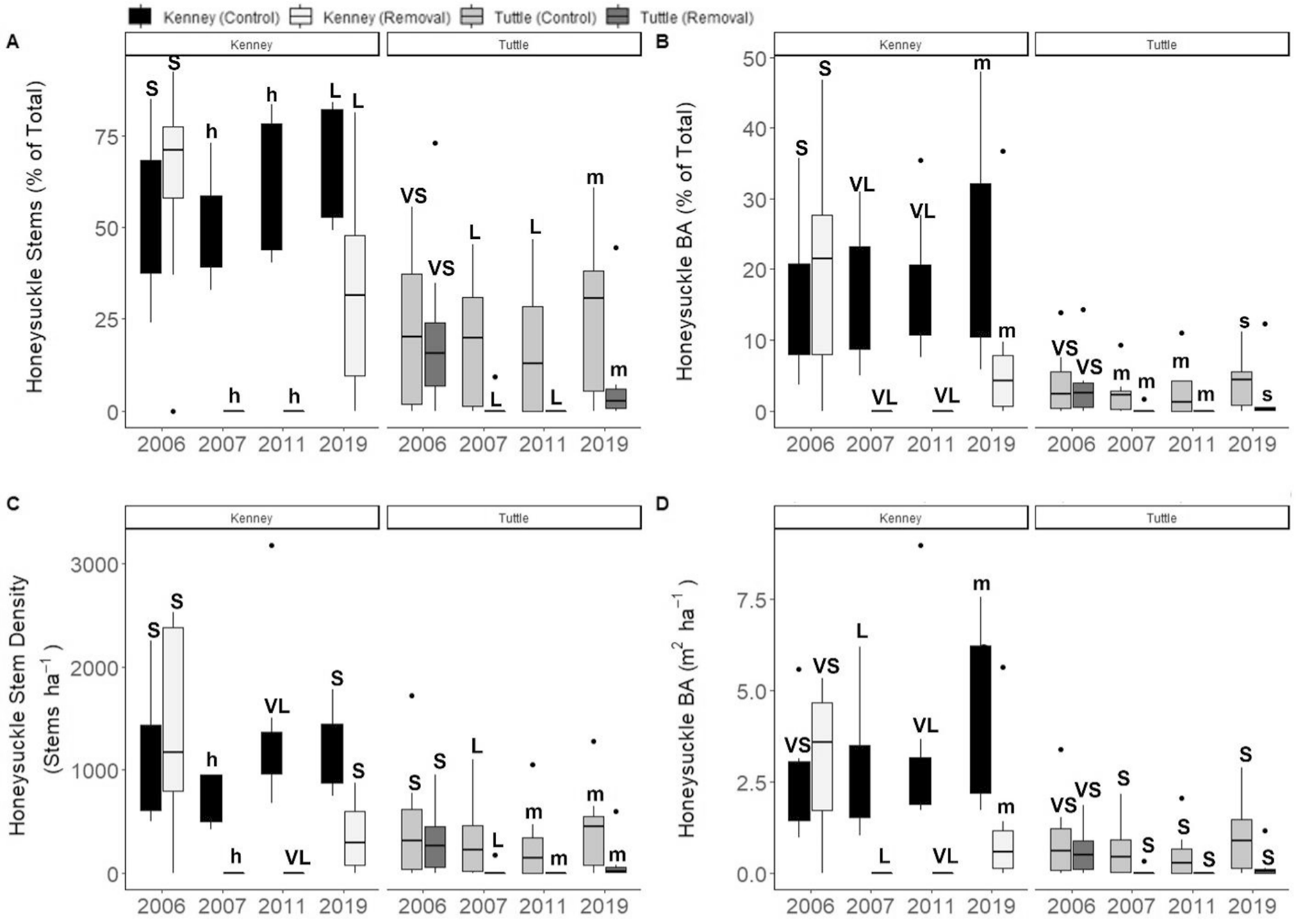

Fig. 4. Effect size analysis comparing differences in a) percent honeysuckle stems b), percent honeysuckle basal area (BA) c), honeysuckle stems ha^{-1} and d) honeysuckle basal area (m^2 ha^{-1}) between control and removal plots prior to honeysuckle removal (2006) and post honeysuckle removal (2007, 2011 and 2019) for Kenny park (K_{CURP}) and Tuttle park (T_{CURP}) sites. The magnitude of removal effects on mean honeysuckle abundance between control and honeysuckle removal plots within sites was measured for each year using Cohen's d of effect size (d), where $d < 0.2$ is considered a 'very small effect (vs)', 0.2–0.5 a 'small effect (s)', 0.5 represents a 'medium effect (m)', 0.8–1.0 a 'large effect (l)', 1.0–2.0 a 'very large effect (vl)' and > 0.2 a 'huge effect (h).'.

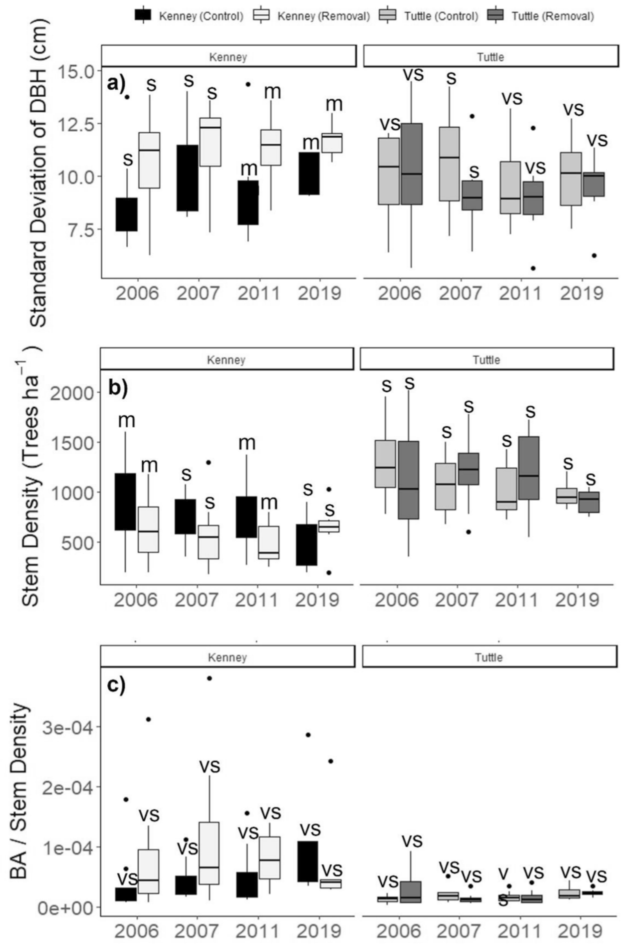

Fig. 5. Effect size analysis comparing differences in a) standard deviation of DBH, b) stem density (stems ha^{-1}) and c) basal area/number of trees between control and honeysuckle removal plots prior to honeysuckle removal (2006) and post honeysuckle removal (2007, 2011 and 2019) for Kenny park (K_{CURP}) and Tuttle park (T_{CURP}) sites. The magnitude of removal effects on mean stand structure between control and removal plots within sites was measured for each year using Cohen's d of effect size (d), where $d < 0.2$ is considered a 'very small effect (vs)', 0.2–0.5 a 'small effect (s)', 0.5 represents a 'medium effect (m)', 0.8–1.0 a 'large effect (l)', 1.0–2.0 a 'very large effect (vl)' and > 0.2 a 'huge effect (h)'.

However, the effect size for standard deviation of DBH increased from small in 2006 ($d = 0.44$) and 2007 ($d = 0.34$) to medium in 2011 ($d = 0.60$) and 2019 ($d = 0.67$) for K_{CURP}, indicating that honeysuckle removal caused a small increase in tree size variability over time at this site (see Table S6 for Cohens d values).

3.3. Relationships between honeysuckle abundance and canopy structural traits

Honeysuckle cover had a much stronger influence on canopy structure than either basal area or stem density. Honeysuckle cover was correlated with 4 of 10 CSTs. In general, canopies with higher honeysuckle cover had a lower average height of maximum canopy density (*Mode.el*: $p = 0.008$, $R^2 = 0.36$), less vertical connectivity (*ENL*: $p = 0.001$, $R^2 = 0.47$), was more densely packed (*Sky fraction*: $p = 0.04$, $R^2 = 0.23$) with fewer leaves concentrated around trees (*Clumping index*: $p = 0.003$, $R^2 = 0.41$), and trended towards more bottom-heavy leaf distributions (*Gini coefficient*: $p = 0.06$, $R^2 = 0.18$) with greater leaf area (*mean VAI:* $p = 0.06$, $R^2 = 0.20$). The amount of honeysuckle basal area per hectare and honeysuckle stems per hectare had a weaker effects on canopy structure, influencing only 1 of 10 CSTs for honeysuckle basal area and 2 of 10 CSTs for honeysuckle stems. Canopy structural complexity decreased with increasing honeysuckle basal area per hectare (rugosity: $p = 0.015$, $R^2 = 0.28$) and honeysuckle stems per hectare (rugosity: $p = 0.004$, $R^2 = 0.36$). Canopies with higher honeysuckle basal area per hectare trended towards a lower outer surface topography (*TOC*: $p = 0.07$, $R^2 = 0.16$) and those with greater honeysuckle stems per hectare had less vertical connectivity (*ENL*: $p = 0.05$, $R^2 = 0.18$).

4. Discussion

4.1. Short-term responses of canopy structure to honeysuckle removal

Honeysuckle removal caused immediate (<1 year) and short-term (1–2 years) changes in the amount and arrangement of both leaf area and openness, as well as the vertical distribution of the canopy, all of which supported our first hypothesis. Canopy structural characteristics among ER sites were similar prior to honeysuckle removal in early August of 2018 and remained similar the following year in undisturbed plots (Fig. 2a). After honeysuckle removal, canopies exhibited a 40% reduction in canopy leaf surface volume (i.e., ~40% more PCL derived laser pulses passed through canopies; measured as sky fraction), a clustering of remaining leaf area around trees, and an overall shift in the average height of maximum canopy density as leaf arrangement trended towards a more even vertical distribution (Fig. 3b; Fig. S1). Trammel et al. (2012) also reported that honeysuckle similarly dominated leaf area in the canopy, comprising up to one-third of total canopy leaf area as estimated with leaf litter traps. The changes in canopy structure observed across our ER removal sites are akin to other pulse disturbances (i.e., high pressure, short-term disturbances) caused by fire, ice, and deer herbivory, which reduce canopy VAI and cause remaining leaves to be highly aggregated and clustered around trees (Atkins et al., 2020; Reed et al., 2021). These short-term changes in canopy structure resulting from honeysuckle removal may affect seedling recruitment and growth by opening the understory and increasing light (Sweeney et al., 2002; Hartman and McCarthy, 2004; Trammell et al., 2012).

4.2. Long-term responses of canopy structure to honeysuckle removal

Data from the CURP study suggests that honeysuckle removal may cause additional long-term increases in canopy structural complexity in some cases but might be dependent on initial stand conditions (see section 3.3 below for more detailed explanation). The undisturbed $K_{CURP\ control}$ plots had similar structural complexity to our ER control plots (i.e., negative PC1 values) and weak correlations with PC2, suggesting similar starting points in canopy arrangement prior to any disturbance (Fig. 3a). Upon honeysuckle removal, the ER removal plots showed an immediate, but small, increase in structural complexity that was sustained the following year, while K_{CURP} plots showed much higher increases in structural complexity with time since disturbance as indicated by their location in the upper right quadrant of ordination space (Fig. 2; Fig. 3b). This additional accumulation of structural complexity in K_{CURP} plots was likely the direct result of the disturbance, as both the relative and absolute honeysuckle abundance did not differ between control and removal plots prior to cutting down honeysuckle (i.e., small effect sizes), but large differences were observed post-removal (i.e., large effect sizes; Fig. 4). Importantly, structural changes in K_{CURP} removal plots also suggest that canopies with honeysuckle removed do not return to pre-disturbance canopy characteristics despite some honeysuckle regrowth (Fig. 4), but rather, continue to accumulate structural complexity beyond the immediate changes observed in our ER plots.

Results from K_{CURP} provide support to our second hypothesis that the long-term increases in canopy structural complexity observed following honeysuckle removal in K_{CURP} may have resulted from recruitment of seedlings and saplings into the midstory. Differences in tree size heterogeneity began to increase in the K_{CURP} removal plots in 2011 compared to K_{CURP} control plots (a couple years after honeysuckle was removed) and remained more variable 10-years post-disturbance (i.e., an increase in the effect sizes), suggesting that suppressed seedlings and saplings might have begun growing into the mid-canopy space during that time. Previous studies demonstrate greater canopy structural complexity in forests with higher tree size variability resulting from more vertical heterogeneity in leaf distribution (Fahey et al., 2015; Fotis et al., 2018; Fotis et al., 2020). This may explain the increase in rugosity and higher variability of the outer canopy surface topography (i.e., top rugosity: TOC) in K_{CURP} removal plots, while T_{CURP} removal plots, which experienced no divergence in tree size heterogeneity following disturbance, did not accumulate canopy structural complexity.

4.3. *Initial stand conditions impact long-term canopy structural pathways*

Initial stand conditions at T_{CURP} likely caused the long-term canopy structural trajectory to differ from K_{CURP} following disturbance, lending support to our third hypothesis. While pre-disturbance stand structure did not differ substantially between CURP sites, K_{CURP} did have higher initial honeysuckle abundance and somewhat lower stem densities of native plants than T_{CURP} (Fig. 4 and Fig. 5). The initially lower honeysuckle abundance at T_{CURP}, and the weaker response to the removal treatment (i.e., lower effect sizes; Fig. 4), may explain why canopy structure did not change much between control and removal plots over the decade following the disturbance event; this site did not experience as large of a disturbance, and therefore, 're-shuffling' of the canopy. Furthermore, the lower effect size at T_{CURP} may be a consequence of relatively greater recreational use compared to K_{CURP}, which receives the least human use among the five ER sites (Smith-Castro and Rodewald 2010). Though we lack trail use data at Tuttle park, it was the second most urban of 25 CURP sites, is bisected by a paved bike path, and has many unofficial walking trails (Rodewald and Shustack, 2008). The high human disturbance and potential trampling of the understory at Tuttle may therefore have lowered honeysuckle abundance and the ability of native seedlings and saplings to emerge into the midcanopy when honeysuckle was removed. The lower tree density at K_{CURP} could be the result of higher initial honeysuckle abundance, which may have reduced tree recruitment and regeneration of saplings into the mid-canopy layer (Hartman and McCarthy, 2008; Trammell et al. 2012). Higher shrub densities have been shown to increase tree mortality and tree spacing over time (Donato et al., 2012). The more sparsely-spaced trees at K_{CURP} could result in more empty canopy space following honeysuckle removal and might explain the long-term increase in porosity (positive correlation with PC2 axis) post-disturbance (Fig. 2b). Long-term legacy effects of deer browsing can similarly cause greater tree spacing by creating a recalcitrant understory of unpalatable hay-scented fern that increases canopy porosity and leaf clumping between trees as a result of reduced stem density (Reed at el., 2021). Fotis et al. (2018) also found that areas with low stem densities had more open space devoid of leaves within canopies. If the internal canopy porosity created by honeysuckle removal was not uniformly spaced, it would increase the horizontal heterogeneity in understory gaps and leaf clumping, and partially explain the observed increase in canopy rugosity over time. This is supported by Fotis and Curtis (2017), who found higher rugosity in canopies with greater porosity. T_{CURP} may have lacked this response due to a canopy that was more densely packed with non-honeysuckle leaf material prior to disturbance and did not have the empty space needed for canopy 'exploration' (Fotis et al., 2018).

4.4. *Relationships between honeysuckle abundance and PCL-derived CSTs*

Our results show that the PCL device might be a useful tool for restoration projects aimed at rapid identification of sites that could exhibit large responses in canopy structural changes following honeysuckle removal, and would therefore benefit the most from, such interventions. Each method of quantifying honeysuckle abundance (i.e., stems count, basal area and cover) requires different amounts of effort and resources, and has varying degrees of correlation with canopy structure, and presumably, potential impacts on restoring ecosystem functions upon removal. We suggest rapid visual assessments of honeysuckle cover as a good candidate variable to quickly quantify areas that would benefit most from honeysuckle removal due to the strong degree of correlation that its cover had with canopy structure (i.e., 4 of 10 CSTs were correlated, and 2 CSTs were marginally insignificant). Furthermore, local assessments of honeysuckle leaves can be easily observed in spring and fall due to its earlier bud break and longer leaf retention compared to native deciduous species (McEwan et al., 2009; Trammell et al., 2012; McNeish and McEwan, 2016), while larger scale assessments of cover can be conducted using aerial remote sensing techniques during the fall (Wilfong et al., 2009). We suggest however, that honeysuckle stem count and basal area are not a good candidate when resources are limited as it is time consuming and labor intensive, and further, had limited to no association with CSTs in our study. The vertical orientation and low surface area of honeysuckle stems (Deering and Vankat, 1999) may minimize laser interceptions and could explain the lack of correlation with PCL derived canopy structural metrics. Altogether these results suggest that control efforts may be more successful and economical if they focus on populations before they become well established and form an integral part of the forest canopy, and potentially influencing its future structural/successional trajectory.

5. Conclusions

The short-term structural changes following honeysuckle removal in ER plots are both ecologically and functionally meaningful. While the immediate changes were not the result of instantaneous canopy growth, the relative re-arrangement of interstitial canopy space and vertical distribution of the remaining canopy leaves may alter wildlife habitat (McCusker et al., 2010; Davis and Asner, 2014; DeJong 2020; Fotis et al., 2020) and immediately impact leaf morphology, physiology, and forest productivity through changes in light distribution (Fotis and Curtis, 2017; Fotis et al., 2018). Removing this exotic-invasive shrub also significantly reduced canopy leaf volume which may aid restoration management aimed at enhancing seedling recruitment of planted and/or naturally regenerating vegetation (Hartman and McCarthy 2008, Trammel et al. 2012). Furthermore, honeysuckle removal has the potential to increase the long-term canopy structural complexity beyond the short-term accrual immediately following disturbance. Work linking canopy structural complexity to ecosystem function has provided empirical evidence that more complex forests tend to be more productive (Fahey et al., 2015; Fotis et al., 2018; Gough et al., 2019) and are more efficient at resource acquisition and use (Hardiman et al., 2011; Atkins et al., 2018b).

Overall, our results suggest that removing honeysuckle in other heavily invaded riparian forests has the potential to restore ecosystem function and improve wildlife habitat within a decade of treatment. However, results in the CURP sites demonstrated multiple pathways of structural succession following honeysuckle removal that may depend on initial stand conditions (i.e., stem density of native plants and honeysuckle abundance) and these differences may influence how ecological networks are restored (Rodewald et al., 2015). Therefore, understanding initial conditions should be considered during forest management aimed at restoring canopy structural complexity of forests following thinning-from-below silviculture treatments (Kuehne et al., 2015). More long-term (>10 yrs.) studies of honeysuckle removal are needed to understand why only some forests diverge in their structural successional trajectories after removal of this invasive shrub. Nonetheless, the PCL device may provide a valuable tool in forest management aimed at rapid assessment of areas that would benefit most from honeysuckle removal and in monitoring the structural changes following its removal.

CRediT authorship contribution statement

Alexander Fotis: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. **Charles E. Flower:** Conceptualization, Investigation, Project administration, Methodology, Supervision, Writing – review & editing. **Jeff W. Atkins:** Formal analysis, Software, Writing – review & editing. **Cornelia C. Pinchot:** Investigation, Methodology, Writing – review & editing. **Amanda D. Rodewald:** Investigation, Methodology, Writing – review & editing. **Stephen Matthews:** Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120251.

References

Atkins, J.W., Bond-Lamberty, B., Fahey, R.T., Haber, L.T., Stuart-Haëntjens, E., Hardiman, B.S., LaRue, E., McNeil, B.E., Orwig, D.A., Stovall, A.E.L., Tallant, J.M., Walter, J.A., Gough, C.M., 2020. Application of multidimensional structural characterization to detect and describe moderate forest disturbance. Ecosphere 11 (6). https://doi.org/10.1002/ecs2.v11.610.1002/ecs2.3156.

Atkins, J.W., Fahey, R.T., Hardiman, B.H., Gough, C.M., 2018a. Forest canopy structural complexity and light absorption relationships at the subcontinental scale. Journal of Geophysical Research: Biogeosciences 123 (4), 1387–1405.

Atkins, J.W., et al., 2018b. Quantifying vegetation and canopy structural complexity from terrestrial LiDAR data using the forestr r package. Methods in Ecology and Evolution 9, 2057–2066.

Cohen, J., 1988. Statistical Power Analysis for the Behavioral Sciences. Erlbaum Associates, Hillsdale, NJ.

Collier, M.H., Vankat, J.L., Hughes, M.R., 2002. Diminished plant richness and abundance below Lonicera maackii, an invasive shrub. American Midland Naturalist 147 (1), 60–71.

Davies, A.B., Asner, G.P., 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology and Evolution 29 (12), 681–691.

Deering, R.H., Vankat, J.L., 1999. Forest colonization and developmental growth of the invasive shrub Lonicera maackii. American Midland Naturalist 141 (1), 43–50.

DeJong LN (2020) Impacts of Amur Honeysuckle (Lonicera maackii) Removal on the Composition of Avian Assembledges in Rural Riparian Forests.

Donato, D.C., Campbell, J.L., Franklin, J.F., Palmer, M., 2012. Multiple successional pathways and precocity in forest development: Can some forests be born complex? Journal of Vegetation Science 23 (3), 576–584.

Fahey, R.T., Atkins, J.W., Gough, C.M., Hardiman, B.S., Nave, L.E., Tallant, J.M., Nadehoffer, K.J., Vogel, C., Scheuermann, C.M., Stuart-Haëntjens, E., Haber, L.T., Fotis, A.T., Ricart, R., Curtis, P.S., Penuelas, J., 2019. Defining a spectrum of integrative trait-based vegetation canopy structural types. Ecology Letters 22 (12), 2049–2059.

Fahey, R.T., Atkins, J.W., Campbell, J.L., Rustad, L.E., Duffy, M., Driscoll, C.T., Fahey, T. J., Schaberg, P.G., 2020. Effects of an experimental ice storm on forest canopy structure. Canadian Journal of Forest Research 50 (2), 136–145.

Fahey, R.T., Fotis, A.T., Woods, K.D., 2015. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock – hardwood forests. Ecological Applications 25 (3), 834–847.

Fotis, A.T., Morin, T.H., Fahey, R.T., Hardiman, B.S., Bohrer, G., Curtis, P.S., 2018. Forest structure in space and time: Biotic and abiotic determinants of canopy complexity and their effects on net primary productivity. Agricultural and Forest Meteorology 250-251, 181–191.

Fotis, A.T., Curtis, P.S., 2017. Effects of structural complexity on within-canopy light environments and leaf traits in a northern mixed deciduous forest. Tree Physiology 37, 1426–1435.

Fotis, A.T., Patel, S., Chavez, A.S., 2020. Habitat-based isolating barriers are not strong in the speciation of ecologically divergent squirrels (Tamiasciurus douglasii and T. hudsonicus). Behavioral Ecology and Sociobiology 74, 1–14.

Gough, C.M., Atkins, J.W., Fahey, R.T., Hardiman, B.S., 2019. High rates of primary production in structurally complex forests. Ecology 100 (10). https://doi.org/10.1002/ecy.v100.1010.1002/ecy.2864.

Hardiman, B.S., Gough, C.M., Halperin, A., Hofmeister, K.L., Nave, L.E., Bohrer, G., Curtis, P.S., 2013a. Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. Forest Ecology and Management 298, 111–119.

Hardiman, B., Bohrer, G., Gough, C., Curtis, P., 2013b. Canopy structural changes following widespread mortality of canopy dominant trees. Forests 4 (3), 537–552.

Hardiman, B.S., Bohrer, G., Gough, C.M., Vogel, C.S., Curtis, P.S., 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. Ecology 92 (9), 1818–1827.

Hartman, K.M., McCarthy, B.C., 2007. A dendro-ecological study of forest overstorey productivity following the invasion of the non-indigenous shrub Lonicera maackii. Applied Vegetation Science 10 (1), 3–14.

Hartman, K.M., McCarthy, B.C., 2008. Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (Lonicera maackii). Journal of the Torrey Botanical Society 135 (2), 245–259.

Hartman, K.M., McCarthy, B.C., 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (Lonicera maackii). Restoration Ecology 12 (2), 154–165.

Kuehne, C., Weiskittel, A.R., Fraver, S., Puettmann, K.J., 2015. Effects of thinning-induced changes in structural heterogeneity on growth, ingrowth, and mortality in secondary coastal Douglas-fir forests. Canadian Journal of Forest Research 45 (11), 1448–1461.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25, 1–18.

Macdonald, E., Burgess, C.J., Scrimgeour, G.J., Boutin, S., Reedyk, S., Kotak, B., 2004. Should riparian buffers be part of forest management based on emulation of natural disturbance? Forest Ecology and Management 187 (2-3), 185–196.

McCusker, C.E., Ward, M.P., Brawn, J.D., 2010. Seasonal responses of avian communities to invasive bush honeysuckles (Lonicera spp.). Biological Invasions 12 (8), 2459–2470.

McEwan, R.W., Birchfield, M.K., Schoergendorfer, A., Arthur, M.A., 2009. Leaf phenology and freeze tolerance of the invasive shrub amur honeysuckle and potential native competitors. Journal of the Torrey Botanical Society 136 (2), 212–220.

McNeish, R.E., McEwan, R.W., 2016. A review on the invasion ecology of Amur honeysuckle (Lonicera maackii, Caprifoliaceae) a case study of ecological impacts at multiple scales. Journal of the Torrey Botanical Society 143 (4), 367–385.

Parker, G.G., Harding, D.J., Berger, M.L., 2004. A portable LIDAR system for rapid determination of forest canopy structure. Journal of Applied Ecology 41 (4), 755–767.

Rodewald, A.D., Kearns, L.J., Shustack, D.P., 2013. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. Biological Conservation 160, 32–39.

Reed, S.P., et al., 2021. The long-term impacts of deer herbivory in determining temperate forest stand and canopy structural complexity. Journal of Applied Ecology 1–10.

Rodewald, A.D., Rohr, R.P., Fortuna, M.A., Bascompte, J., Ings, T., 2014. Community-level demographic consequences of urbanization: An ecological network approach. Journal of Animal Ecology 83 (6), 1409–1417.

Rodewald, A.D., Rohr, R.P., Fortuna, M.A., Bascompte, J., 2015. Does removal of invasives restore ecological networks? An experimental approach. Biological Invasions 17 (7), 2139–2146.

Rodewald, A.D., Shustack, D.P., 2008. Urban flight: Understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. Journal of Animal Ecology 77 (1), 83–91.

Service USF (2011) Forest Inventory and Analysis National Core Field Guide Volume I: Field Data Collection Procedures for Phase 2 Plots, Version 5.0. 310.

Shields, J.M., Jenkins, M.A., Saunders, M.R., Gibson, K.D., Zollner, P.A., Dunning, J.B., 2015. Influence of Intensity and Duration of Invasion by Amur Honeysuckle (Lonicera maackii) on Mixed Hardwood Forests of Indiana. Invasive Plant Science and Management 8 (1), 44–56.

Smith-Castro, J.R., Rodewald, A.D., 2010. Effects of recreational trails on Northern Cardinals (Cardinalis cardinalis) in forested Urban Parks. Natural Areas Journal 30 (3), 328–337.

Sweeney, B.W., Czapka, S.J., Yerkes, T., 2002. Riparian forest restoration: Increasing success by reducing plant competition and herbivory. Restoration Ecology 10 (2), 392–400.

Trammell, T.L.E., Ralston, H.A., Scroggins, S.A., Carreiro, M.M., 2012. Foliar production and decomposition rates in urban forests invaded by the exotic invasive shrub, Lonicera maackii. Biological Invasions 14 (3), 529–545.

Wilfong, B.N., Gorchov, D.L., Henry, M.C., 2009. Detecting an Invasive Shrub in Deciduous Forest Understories Using Remote Sensing. Weed Science 57 (5), 512–520.