Assessment of soil and tree carbon concentrations under varying levels of Chinese privet invasion

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Abstract

Invasive plant species are increasingly recognized for their capacity to alter ecosystem structure and function, yet their impact on carbon storage remains underexplored. This study investigates how Chinese privet (*Ligustrum sinense*), a widespread invasive shrub in the southeastern United States, may be influencing above- and belowground carbon in a secondary forest recovering from past agricultural use. We compared soil organic carbon (SOC) across three vegetation types (heavily invaded and uninvaded deciduous forest, and an adjacent loblolly pine stand) and tree biomass carbon at varying amounts of Chinese privet within a historic landscape in central Georgia. SOC was assessed at three depths (0-5, 5-10, and 10-15 cm) while tree carbon was estimated using structural measurements and species-specific allometric equations. Results showed that SOC was lowest in the invaded site, despite having similar soil texture and bulk density to uninvaded sites. The pine stand SOC was significantly lower than the uninvaded site, likely due to differences in litter inputs and disturbance history. Tree density and biomass carbon were significantly lower in privet-invaded areas compared to uninvaded sites. Overall, soil and tree carbon density were over 40% lower in the presence of Chinese privet. These findings suggest that Chinese privet may contribute to long-term reductions in both biomass and soil carbon pools by suppressing native woody regeneration and altering belowground processes. As

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forests play a critical role in carbon sequestration, understanding the indirect impacts of invasive species on carbon dynamics is vital for informing management and restoration strategies in disturbed landscapes.

Keywords: Carbon density, forest regeneration, carbon sequestration, tree density, organic carbon

Introduction

Understanding the role of terrestrial ecosystems in carbon sequestration is essential for mitigating climate change. According to the latest IPCC report, managed and natural terrestrial ecosystems absorbed approximately one-third of anthropogenic emissions between 2010 and 2019, acting as a significant carbon sink (Nabuurs et al. 2022). The IPCC also reaffirmed that human activities are the primary drivers of global climate change. To mitigate rising atmospheric carbon levels and their associated impacts, it is crucial to understand both the processes that remove carbon from the atmosphere and the interactions between carbon sinks and sources (Luo & Weng, 2011).

Carbon sequestration, the process of capturing and storing atmospheric carbon, occurs through both natural and anthropogenic mechanisms. Soil and plant biomass serve as key terrestrial carbon sinks. Plants absorb CO_2 from the atmosphere, storing it in their biomass for varying durations – months to years in herbaceous plants and centuries in woody plants such as trees (Keenan et al. 2016). Carbon enters the soil through root exudates and plant decomposition, contributing to soil organic matter, where it can remain sequestered for thousands of years before re-entering the atmosphere (Keenan and Williams 2018). Despite declining deforestation rates

and increasing forest growing stock globally, land-use changes – particularly deforestation – remain a major source of CO_2 emissions in the agriculture and forestry sectors (Shevliakova et al. 2013; Nabuurs et al. 2022). Other disturbances, such as shifts in plant community structure, species composition, and soil physicochemical properties, can also influence soil carbon storage. However, these impacts are more difficult to quantify and remain poorly understood (Raich & Schlesinger, 1992). Among these disturbances, invasive plant species are a particularly important but often overlooked factor.

Plant species introduced into new ecosystems often outcompete native vegetation for light, space, and nutrients. Their success is typically driven by rapid growth, high reproductive rates, and a lack of natural predators. As they establish, invasive species can significantly alter ecosystem structure and function, particularly by reducing native biodiversity. These changes are further intensified by climate change, which expands the range and impact of many invaders (Hubbard et al. 2024). Invasive plants have been shown to disrupt carbon and nitrogen cycling, reduce water availability, and suppress native regeneration, ultimately lowering ecosystem resilience (Cavaleri and Sack 2010; Jo et al. 2017). Because biodiversity supports ecosystem stability and enhances productivity, its loss diminishes the system's ability to withstand disturbances like drought, pests, or disease (Ehrlich et al. 1999). Moreover, ecosystems with greater plant diversity tend to store more carbon in both biomass and soils (Xu et al. 2020), suggesting that invasion-driven declines in diversity may impair carbon sequestration.

Reduced diversity and altered forest composition have measurable effects on productivity and biomass. Forests with a lower diversity of canopy trees typically exhibit lower aboveground biomass and productivity (Greene and Blossey 2012; Cai et al. 2016; Liu et al. 2018). Invasive woody shrubs, particularly those forming dense thickets, often exclude native tree seedlings and

saplings from the understory (Gorchov and Trisel 2003; Loewenstein and Loewenstein 2005). Over time, this shift suppresses forest regeneration and leads to structural changes—from tree-dominated to shrub-dominated systems. Empirical studies show that the biomass gained from invasive shrubs rarely compensates for the biomass lost when native trees are displaced (Brantley 2008; Trammell et al. 2012), potentially reducing the carbon storage capacity of invaded forests. These structural and compositional shifts raise important questions about how invasions influence not only aboveground biomass but also long-term soil carbon dynamics.

Soil carbon sequestration is promoted by traits that enhance soil carbon inputs through high primary productivity and traits that slow decomposition, such as litter quality, soil moisture, and temperature (De Deyn et al. 2008). Deforestation contributes to the increase in atmospheric carbon by removing the supply of detritus and enhancing decomposition rates, both of which significantly reduce soil organic carbon (SOC) (Nave et al. 2009). Woody invasive species in forests could mimic the impacts of deforestation because they reduce primary productivity (Brantley 2008; Trammell et al. 2012) and increase decomposition rates (Aragón et al. 2014; Woodworth et al. 2020). Studies show that many invasive species produce litter that has significantly lower C:N ratio and decomposes significantly faster than native species' litter (Mitchell et al. 2011; Trammell et al. 2012; Arthur et al. 2012). Nutrient poor litter has more recalcitrant forms of carbon which have a long residence time in the soil than the labile forms of carbon that are associated with nutrient rich litter (De Deyn et al. 2008). The increased presence of invasive species that produce high quality litter is likely to transform the litter pool composition by increasing the proportion of the labile carbon forms, subsequently affecting the soil carbon pool.

The goal of this study was to examine whether the presence of Chinese privet (*Ligustrum sinense* Lour.) is associated with differences in organic carbon densities within a regenerating forest. Specifically, we compared SOC concentrations between a severely invaded area and adjacent uninvaded areas. The study site, a former agricultural landscape, has undergone natural forest regeneration in recent decades and now contains a mosaic of native vegetation and numerous invasive species, including Chinese privet. Because privet litter decomposes more rapidly than native litter, we hypothesized that SOC concentrations would be lower in invaded areas. We also assessed tree biomass carbon (above- and belowground) under varying levels of Chinese privet and hypothesized that forest structural attributes such as tree density, biomass, and carbon storage would be lower in samples containing Chinese privet. While the study design was observational, our sampling approach allowed us to assess whether consistent patterns in carbon storage correspond with the presence or absence of this invasive shrub.

Materials and methods

Study site

The study was conducted at Andalusia, a historic property in Milledgeville, Georgia (33°07′30.77″ N, 83°16′03.56″ W), now managed by Georgia College & State University. Historically used for agriculture and timber, the site has undergone multiple disturbances, including cotton farming (1814–1931), cattle operations (1931–2003), and clear-cutting for timber (2009–2013). These land uses have resulted in heterogeneous vegetation and successional stages across the property. The climate is temperate, with hot, humid summers and mild, wet winters. Annual precipitation averages 116.4 cm, with peaks in February and lows in October. Soils range from sandy loam to clay loam.

Dominant native tree species include post oak (*Quercus stellata*), loblolly pine (*Pinus taeda*), mockernut hickory (*Carya tomentosa*), Carolina shagbark hickory (*Carya carolinae-septentrionalis*), and winged elm (*Ulmus alata*). Areas previously clear-cut are characterized by early successional species such as sweetgum (*Liquidambar styraciflua*) and shortleaf pine (*Pinus echinata*), alongside dense populations of the invasive shrub Chinese privet, particularly in disturbed zones. Chinese privet invasion in the study area can be broadly categorized into two invasion states. One state consists of older well-established and widely spaced individuals reaching up to 5 meters or more in height. There is a lower stem density but individuals have large basal diameters, and they often form a shrub-layer canopy that shades out understory vegetation. The second state consists of populations with numerous small-diameter shrubs growing in tight clusters. These clusters also limit the recruitment of other species due to their high stem density.

Soil sampling and analysis

Soil sampling was conducted between October and November 2023. Samples were collected from three distinct areas within the study site, selected to represent different vegetation types and invasion status, providing an opportunity to compare soil carbon dynamics under differing conditions. Two sampling blocks were located within a deciduous forest—one heavily invaded by Chinese privet and a nearby block that was relatively uninvaded. Chinese privet shrubs in the invaded block ranged from 3 m to 6 m in height and crown diameters averaging 5 m. The overstory canopy in this block was relatively open, with trees exhibiting visible signs of stress, and few or no other non-privet woody plants present in the understory. The uninvaded deciduous forest block, immediately adjacent to the invaded area, only had scattered small

individuals in the herb layer. This block featured a tall, closed-canopy overstory with a structurally intact understory composed of native herbs and shrubs. The third block was situated in a loblolly pine (*Pinus taeda*) stand, not as a control or reference, but to offer an alternative vegetation context that differs markedly in species composition, litter quality, and canopy structure. Including the pine stand allowed for a broader comparison of how different dominant vegetation types—deciduous hardwoods versus conifers—may influence soil carbon storage and other soil properties. Each sampling block encompassed an area approximately 0.10 ha.

Soil samples were strategically distributed within each block to maximize coverage of the area while accommodating natural obstacles such as roots and understory vegetation. The sampling unit was a 30 cm × 30 cm area where a soil sample was extracted and separated into three depth intervals: 0–5 cm, 5–10 cm, and 10–15 cm, not including the top organic layer. A total of 20 locations were sampled from each of the two deciduous forest blocks and 15 from the pine stand, resulting in 55 sampling locations overall and yielding 165 total samples for carbon analysis. Additionally, within each block, 10 undisturbed cores (15 cm depth) were collected using a soil corer to determine bulk density (n = 30). Soil samples were air-dried, ground with a mortar and pestle, and sieved through a 2 mm mesh. Standard soil analyses, including pH and most macronutrients (excluding nitrogen), were conducted by Clemson University's Agricultural Laboratory (Clemson, South Carolina).

Soil carbon was estimated at Georgia College & State University using the loss-on-ignition method (Rayment and Lyons 2011), with SOC calculated as 50% of the measured organic matter content (Pearson et al. 2007). A subset of samples (n = 99; 11 from each site, separated by depth) was sent to the University of Georgia's Agricultural and Environmental Services Laboratory (Athens, Georgia) for total carbon analysis using an elemental analyzer.

While the loss-on-ignition (LOI) method provides a reliable estimate of SOC and was used for the full dataset, elemental analyzers offer greater precision by directly measuring total carbon content. Including this additional analysis on a representative subset allowed us to assess the accuracy of LOI-derived SOC values and ensure consistency across methods.

Equal proportions of the soil from all three depths were combined and thoroughly mixed. The composited samples were analyzed for soil particle size (texture) using the Buoycous method (Robertson et al. 1999). Samples collected for bulk density analysis were oven dried at 105°C for at least 48 hours until no further decrease in mass was detected. Bulk density (g/cm^3) was determined by dividing the dried weight of each sample (g) by its volume (cm^3). Soil carbon storage (density) for each sampling block was calculated as:

$$Carbon\ density\ (Mg\ ha^{-1}) = BD\ x\ depth\ x\ SOC\ x\ 100 \qquad [1]$$

where BD is average bulk density for that block and SOC was the mean percent averaged across all three depths in the block.

Vegetation sampling and analysis

Vegetation sampling was conducted between August and November 2024 using the point-centered quarter (PCQ) method along transect lines within the study site. Transect lengths ranged from 55 m to 110 m, depending on site characteristics. Transect locations were strategically selected based on the presence of Chinese privet ensuring representation of areas with no privet, moderate privet presence, and heavy privet infestation. A total of 10 transects were established, with sampling points spaced every 10 meters along each transect. This resulted in 87 total

sampling points, which were categorized into two groups: Privet-present samples– any amount of Chinese privet detected (n = 35) and privet-absent samples– Chinese privet was not present (n = 52). This sampling design allowed for a comparative analysis of vegetation structure and species composition in relation to Chinese privet presence.

At each sampling point, a perpendicular line to the transect was established, dividing the area into four quadrants. Within each quadrant, the distance to the nearest tree was measured and recorded in meters. Trees were identified to species level, and their diameter measured at 1.37 m height (referred to in this study as diameter at breast height – DBH). If a tree had multiple stems branching below the 1.37 m height, the DBH of each stem was recorded separately. Only individuals with DBH $\geq$ 5 cm were classified as trees. Individuals with DBH between 2 cm and 4.9 cm were recorded as saplings, with their distance from the sampling point also measured and recorded. A distance limit was applied to prevent double-counting of individual trees (Dahdouh-Guebas and Koedam 2006), as our goal was to describe local density near the sampling points rather than estimate the total forest density. This approach resulted in some quadrants lacking a recorded tree, which required a distance correction factor when calculating density.

For sampling points where Chinese privet was present**,** the measurement approach for Chinese privet shrubs differed from that used for trees. While tree density was determined by sampling the nearest tree in each quadrant, we specifically targeted the largest privet shrub within a quadrant, rather than the closest individual, and measured the basal diameter at the root collar (just above the soil surface where all stems join). This approach was chosen because basal area is strongly correlated with plant age and biomass, providing a more meaningful indicator of privet dominance over time. Additionally, Chinese privet frequently grows in dense clumps, particularly following disturbance, making individual counts less informative for assessing its

overall impact. By measuring the largest shrub, we ensured greater consistency across sampling points and captured a better representation of long-established privet individuals, which are more likely to influence forest structure and soil conditions.

Sample tree density was calculated following Dahdouh-Guebas and Koedam (2006) using the formula:

$$density\ (\#\ trees/m^2) = \frac{1}{d^2} x \frac{q_n}{q_t} \qquad [2]$$

where d is the average distance of all recorded trees within the quadrants, q_n is the number of quadrants containing a tree and q_t is the total number of quadrants. Trees were categorized into 5 cm diameter classes, including saplings (DBH <5 cm). The density of each size class was calculated using Equation 2, with d representing the average distance of all trees within a given size class and q_n denoting the number of quadrants containing trees of that class. These calculations were performed separately for privet-present and privet-absent groups. To facilitate comparisons between groups in light of sample size differences, density values were standardized by multiplying by 10,000 to express results as individuals hectare^{-1} (number of trees ha^{-1}). This enabled a comparative assessment of how Chinese privet presence correlates with overall forest structure.

Basal area of each sampled tree was calculated as:

$$Basal\ area\ (m^2) = \pi(\frac{DBH}{2})^2 \qquad [3]$$

For multi-stemmed trees, the basal area of individual stems was calculated separately and then summed to determine the total basal area per tree. For Chinese privet, basal area was calculated using the diameter measured at the root collar. Tree biomass was estimated using allometric equations developed for North American tree species (Jenkins et al. 2003; Pearson et al. 2007). Aboveground and belowground biomass were calculated for each tree as follows:

$$AGB\ (kg) = Exp^{(\beta 0 + \beta 1 lnDBH)} \quad [4]$$

$$BGB\ (kg) = Exp^{(-1.0587 + lnAGB + 0.284)} \quad [5]$$

where AGB is aboveground biomass; BGB is belowground biomass, *DBH* is the tree diameter measured at a height of 1.37 m; *Exp* is the exponential function; *ln* is the natural log base "e" (2.718282); and the parameters *β0* and *β1* are coefficients that vary by species groups and applied accordingly from (Jenkins et al. 2003). Total aboveground and belowground biomass for each tree was converted to carbon content (kg of carbon) by multiplying total biomass by the carbon-biomass coefficient of 0.50 (Pearson et al. 2007). The total tree carbon per sample was estimated by calculating the average carbon content of individual trees within each sample and multiplying it by the corresponding tree density (trees ha^{-1}). This allowed us to express tree carbon in units of kg ha^{-1}, facilitating comparisons between privet-present and privet-absent samples.

Statistical analysis

Statistical analyses were conducted in IBM SPSS Statistics (version 29). Multivariate analysis of variance (MANOVA) was initially considered to compare soil variables across the three forest stand types (pine, privet-invaded deciduous, and uninvaded deciduous). However, Box's test for equality of covariance matrices was significant ($P < 0.001$), indicating a violation of the assumption of homogeneity of variance-covariance structures. Additionally, sample sizes were unequal across groups further increasing the risk of biased results under MANOVA. Given these violations, separate one-way ANOVAs were conducted for each soil variable. When ANOVA results were significant, Tukey's HSD post hoc test was performed to determine pairwise differences between stand types.

For plant data analysis, the presence of a few unusually large trees skewed the data, necessitating a logarithmic transformation to improve normality assumptions (Wildi 2013). Levene's test was performed to assess variance equality in the log-transformed data. Welch's t-test was used for variables with unequal variances, while Student's t-test was applied to those with equal variance. The log-transformed means of sample tree density were compared between privet-present and privet-absent samples using a t-test. Basal area was standardized to enable comparison between privet-present and privet-absent samples by multiplying the average sample basal area (m^2) by the sample tree density (trees ha^{-1}), thus measuring basal area as (m^2 ha^{-1}). Doing this also incorporated differences in tree size which is not accounted for by tree density alone. The log-transformed basal area means were compared between groups. Similarly, average sample tree carbon was multiplied by sample tree density and the log-transformed means compared using a t-test. Additionally, for samples where privet was present, a linear regression analysis was performed to examine the relationships between privet basal area and DBH, tree density, tree basal area, and tree carbon.

Results

Soil

Results of the soil analysis showed that the three sites differed significantly in most of the chemical variables whereas the invaded and uninvaded sites did not differ in the physical characteristics (Table 1). The invaded forest block had the highest soil pH while the pine block was the most acidic. The pine stand block had the lowest mineral nutrient concentrations although phosphorus concentration did not differ significantly between samples. Soil particle size distribution showed that the invaded and uninvaded blocks did not differ from one another

whereas the pine stand had a significantly higher proportion of silt and lower proportion of sand than the other two blocks. The pine stand also had the highest soil bulk density while the other two had the same average soil bulk density. The LOI-derived SOC estimates were strongly correlated ($r = 0.96$, $P < 0.001$) with total carbon values obtained via elemental analysis, supporting the use of LOI in this study as a reliable method for estimating SOC. Results of SOC showed that concentrations within each block decreased significantly with depth (Fig. 1a). When compared between samples, the uninvaded site had significantly higher carbon concentrations at each depth. The invaded and pine sites did not differ in carbon concentrations in the top 5 cm (Fig. 1b), but the invaded site had significantly higher organic carbon in the middle and bottom depths than the pine site. There was no significant difference in total carbon in the middle and bottom depths between the pine and invaded sites. Soil carbon density was highest in the uninvaded site (56.6 Mg C ha^{-1}) followed by the pine stand (34.1 Mg C ha^{-1}) and the lowest was the invaded site (33.8 Mg C ha^{-1}).

Vegetation

Among the samples in which Chinese privet was present, a total of 12 species were recorded. Winged elm (*Ulmus americana*) was the species that occurred in the most quadrants (51%) and had the largest proportion of total stem basal area (37.6%). For the samples where privet was absent, 15 species were recorded and although winged elm occurred in the most quadrants (27%), loblolly pine (*Pinus taeda*) had the largest stem basal area proportion (20%) followed closely by Carolina shagbark hickory (*Carya carolinae-septentrionalis,* 17.8%). In both sets of samples, winged elm made up the largest percent of saplings (39% uninvaded, 46% invaded). Chinese privet shrub sizes varied from 3.4 cm diameter to 48 cm with an average diameter of 14.7 cm.

296 The tree size distribution showed a slightly better representation of trees in all class sizes
297 among the samples where Chinese privet was absent while the sapling (<5 cm) and 20.1-25cm
298 class sizes were poorly represented where Chinese privet was present (Fig. 2). A comparison of
299 tree size (mean tree diameter) showed no difference between samples with and without Chinese
300 privet (Fig. 3a, t = 0.027, P = 0.49) but the tree density was significantly lower among samples
301 where Chinese privet was present (Fig. 3b, t = 2.46, P = 0.008). Mean basal area (m^2 ha^{-1}) was
302 significantly greater in the samples without Chinese privet (Fig. 3c, t = 2.64, P <0.001). Also,
303 mean tree carbon was significantly lower (t=2.64, P =0.005) among the samples with Chinese
304 privet. The regression analysis showed a significant negative correlation between tree density
305 and privet basal area (Fig. 4) while DBH, tree basal area, and tree carbon were not significantly
306 correlated with privet basal area.
307
308 **Discussion**
309 At all three sites, the amount of soil carbon decreased significantly with increase in depth.
310 Soil samples collected from the uninvaded site had significantly higher soil organic carbon at all
311 three depths than both the pine stand and the invaded site. Overall, our estimated soil carbon
312 density at all three sites was much lower than the temperate forest average of 122 Mg C ha^{-1} in
313 soil (Lal 2005) or the 120 Mg C ha^{-1} estimate more specific to the southern region that includes
314 Georgia (Mckinley et al. 2011). This lower soil carbon density estimate is not unexpected given
315 the site's history of agricultural use. However, differences in carbon density between sites
316 suggest that accumulation is occurring at varying rates. SOC accumulation reflects the balance
317 between carbon inputs and losses during organic matter decomposition, a process influenced by a
318 complex interplay of biological, physical, and chemical factors. Soil texture, often used as a

proxy for these factors, can influence SOC through its effects on moisture retention and microbial activity (Luo and Zhou 2006). In this study, the invaded and uninvaded sites had similar proportions of sand, silt, and clay, as well as comparable bulk densities. In contrast, the pine site had a higher silt content and bulk density. Therefore, the lower SOC in the invaded samples is unlikely due to textural differences and may instead reflect changes in soil processes associated with Chinese privet invasion.

Soil pH is one significant difference observed in this study that could be attributed to the presence of Chinese privet. Soil pH plays a critical role in regulating soil respiration by influencing both microbial activity and key biochemical processes (Luo and Zhou 2006). Soil pH affects the solubility and availability of nutrients, enzyme activity, and microbial community composition, all of which can impact rates of organic matter decomposition and CO_2 production (Rousk et al. 2009). Microbial growth and activity tend to peak within an optimal pH range, with acidic conditions generally limiting microbial efficiency and reducing decomposition rates (Fierer and Jackson 2006). In contrast, higher soil pH, such as that observed in our invaded samples, can enhance microbial activity and enzyme function, potentially leading to increased carbon turnover and CO_2 release. This could explain the lower SOC in the privet invaded site, as microbial communities may be more active in decomposing organic material under higher pH conditions. Our findings align with previous studies that have also found significantly higher soil pH in association with invasive species (Ehrenfeld et al. 2001; Lobe et al. 2014; Hagan et al. 2014) potentially facilitating microbial processes that accelerate nutrient cycling in invaded ecosystems.

Differences in decomposition rates of plant litter may also contribute to the observed variations in SOC between sites. Decomposition is influenced by nitrogen (N) concentrations in

both soil and litter, with higher nitrogen levels generally accelerating decomposition (Luo and Zhou 2006). Chinese privet litter has a significantly higher N content and a lower C:N ratio compared to native litter, making it more readily decomposable and nutritionally superior for microbial decomposers (Mitchell et al., 2011; Weand, 2020; unpublished data). Numerous studies have demonstrated that litter from invasive species tends to decompose more rapidly than native litter, often due to elevated nitrogen content, lower lignin concentrations, or shifts in microbial communities that enhance breakdown rates. This pattern has been documented for Chinese privet (Mitchell et al. 2011; Bush et al. 2020; Weand 2020), *Lonicera maackii* (Trammell et al. 2012; Arthur et al. 2012), *Berberis thunbergii* (Ehrenfeld et al. 2001), and *Lonicera morrowii* (Ashton et al. 2005). The accelerated decomposition of invasive plant litter can result in reduced SOC accumulation, as carbon inputs from litter are rapidly mineralized rather than stabilized in the soil matrix. In our study, the lower SOC observed in privet-invaded sit may reflect these well-documented decomposition dynamics associated with differences in litter quality, as supported by both published research and our own unpublished findings.

The rate of organic matter breakdown is largely influenced by the composition of decomposer communities, which in turn can be shaped by shifts in soil properties associated with invasive species. For instance, a study examining microbial and arthropod decomposer abundances found significantly higher densities of bacteria, fungi, and arthropods colonizing litter from invaded forests compared to uninvaded sites (Woodworth et al. 2020). Similarly, Ashton et al. (2005) found that decomposition rates and nitrogen loss were significantly accelerated for both invasive species and closely related native species when placed in invaded sites, compared to uninvaded sites. Notably, because soil physiochemical properties in that study were similar between site types, the observed differences in decomposition rates were attributed

365 to differences in the decomposer community (Ashton et al. 2005). Mitchell et al. (2011) also
366 reported significantly higher microbial biomass in soils from severely invaded sites compared to
367 moderately invaded sites. Furthermore, other studies have demonstrated that microbial
368 community compositions associated with exotic invasive species differ significantly from those
369 in native ecosystems (Kourtev et al. 2002; Arthur et al. 2012). Given that Chinese privet invasion
370 is associated with increased nitrogen availability and altered soil pH—two key factors regulating
371 microbial community composition—it is plausible that microbial assemblages in invaded soils
372 differ from those in uninvaded soils, potentially accelerating decomposition rates and influencing
373 soil carbon dynamics.

374 While the specific mechanism responsible for lower SOC in the invaded site is unknown,
375 we presume that the faster litter decomposition of Chinese privet could be attributed to lower
376 C:N ratio and enhanced microbial activity. Consequently, the faster decomposition of privet-
377 derived litter likely reduces the accumulation of organic carbon in the soil, leading to the lower
378 SOC levels observed in our study. Mitchell et al. (2011) estimated that 30% privet in forest
379 litterfall can result in a 2.6-fold acceleration in forest floor carbon turnover. Experimental studies
380 are needed to determine the mechanisms for example, change in litter quality and/or quantity,
381 change in ground cover leading to more soil erosion, or change in microbial community and
382 decomposition rates, are responsible for changes in soil carbon storage

383 The overall findings of the tree data analysis supported our hypothesis that the presence
384 of Chinese privet would result in significant differences in the measured variables, including tree
385 density and carbon. Our results showed that on average, samples with and without privet had
386 trees of similar sizes as shown by the lack of difference in mean tree diameter. However, samples
387 that had privet had a significantly lower tree density. Additionally, there was a significant

388 negative correlation between privet basal area and tree density among samples in which privet
389 was present. We used basal area as a measure of privet cover because size is strongly correlated
390 with plant age and biomass (Atasoy 2017), providing a more meaningful indicator of privet
391 dominance over time.

392 The lack of difference in average tree size between privet-present and privet-absent
393 samples suggests that Chinese privet establishes beneath the canopy without significantly
394 impacting mature trees. However, despite this apparent coexistence, the significant reduction in
395 tree density, consistent with numerous other studies (Merriam and Feil 2002; Wilcox and Beck
396 2007; Hanula et al. 2009), highlights its severe impact on forest regeneration. Merriam and Feil
397 (2002) observed that where privet was present, native tree seedlings disappeared, but when privet
398 was removed, seedling density and species richness increased. They further projected that
399 understory plant populations would continue to decline due to seed bank exhaustion as privet
400 expanded. Native seedlings suppression was identified as one of the direct effects of about two
401 thirds of the at least 100 invasive shrubs, including Chinese privet, found in forests in the United
402 States (Boyce 2009).

403 Studies assessing forest structure after disturbances reinforce the suppressive effects of
404 privet. Following a hurricane-induced disturbance, Turner et al. (2022) found no increase in
405 regenerating individuals even after ten years, with tree density and basal area remaining low due
406 to persistent privet cover. In contrast, Hudson et al. (2014) documented significant differences in
407 plant communities just five years after privet removal. Although removal had no effect on
408 canopy tree growth, the shrub layer in treated areas was dominated by early successional woody
409 saplings with minimal privet reinvasion. This contrast suggests that privet removal facilitates
410 regeneration, whereas its continued presence prevents forest recovery, even after natural

411 disturbances. Over time, this disruption of forest succession could have profound consequences.
412 As canopy trees decline due to natural disturbances or senescence, the absence of native saplings
413 will leave a regeneration gap, which privet is well-positioned to exploit. Without intervention,
414 this process could further reinforce privet dominance, fundamentally altering long-term forest
415 dynamics.

416 The significance of tree density differences extends to biomass and carbon storage.
417 Privet-present samples had significantly lower total tree carbon, reinforcing concerns about long-
418 term forest carbon dynamics. Our estimated average tree carbon density (above and
419 belowground) for privet-absent samples (115 Mg C ha^{-1}) aligns closely with the temperate forest
420 average of 96 Mg C ha^{-1} (Lal, 2005). When adjusted to aboveground carbon alone, our estimate
421 is 93 Mg C ha^{-1}, higher than the regional average of 70 Mg C ha^{-1} reported by McKinley et al.
422 (2011). In contrast, the aboveground tree carbon density in privet-invaded samples (55 Mg C
423 ha^{-1}) was considerably lower than both estimates, highlighting the potential long-term impact of
424 regeneration failure.

425 While many studies have examined the structural effects of invasive shrubs on forests,
426 significant gaps remain in understanding their indirect impacts, particularly on SOC. Boyce
427 (2009) outlines a range of indirect effects of invasive shrubs in U.S. forests, including changes in
428 soil nitrogen, alterations in soil pH, and effects on soil biological activity. However, changes in
429 soil carbon density remain understudied. Given our findings, this aspect warrants further
430 investigation. Because our study was observational and involved separate soil and plant
431 sampling, we cannot establish a causal relationship between privet presence and lower soil
432 carbon density. Nevertheless, our results suggest that this potential impact of Chinese privet—
433 and invasive shrubs more broadly—deserves more attention in future research.

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Consent to participate:

Not applicable

Consent for publication:

Not applicable

Availability of data and materials:

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request

Code availability:

Not applicable

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582 **Table 1** Comparison of soil physical and chemical properties between sites. All values are means
583 (±1STD), and significances are shown by a letter exponent - different letter exponents indicate
584 significant mean differences between groups ($\alpha = 0.05$).

Soil variable	Uninvaded	Invaded	Pine stand	P-value
Soil pH	5.54 (0.37)^{a}	6.03 (0.32)^{b}	4.96 (0.18)^{c}	<0.001
Phosphorus (ppm)	7.45 (2.7)	8.05 (9.7)	5.20 (1.6)	0.38
Potassium (ppm)	72.4 (15.2)^{a}	46.4 (13.9)^{b}	33.8 (8.9)^{b}	<0.001
Calcium (ppm)	898 (362)^{a}	1071 (549)^{a}	260 (70)^{b}	<0.001
Magnesium (ppm)	189.8 (42.4)^{a}	119.9(29.8)^{b}	60.2±19.3^{c}	<0.001
Total base saturation (%)	59.9 (10.2)^{a}	71.4 (11.7)^{b}	40.5 (7.0)^{c}	<0.001
Bulk Density (g cm^{-3})	1.38 (0.06)^{a}	1.38 (0.07)^{a}	1.55 (0.11)^{b}	<0.001
Clay (%)	3.2 (0.5)	3.1(0.8)	3.0 (0.9)	0.98
Silt (%)	11.9 (1.2)^{a}	12.7 (2.3)^{a}	15.4 (2.3)^{b}	0.001
Sand (%)	85.1 (1.5)^{a}	84.2 (2.0)^{a}	81.6 (2.0)^{b}	<0.001

585
586

Fig. 1 Mean percent soil organic carbon. **(a)** Comparison between sites, separated by depth; **(b)** Comparison by depth within each site. Error bars represent ± standard error. Different letters denote significant mean differences between groups ($\alpha = 0.05$).

Fig. 2 Distribution of trees by DBH class (5 cm intervals). **(a)** Trees from samples without Chinese privet; **(b)** Trees from samples with Chinese privet present.

Fig. 3 Box plots showing the distribution of vegetation metrics between sites. **(a)** No significant difference in average DBH ($P = 0.49$); **(b)** Significant difference in tree density ($P = 0.008$); **(c)** Significant difference in total tree basal area ($P = 0.001$); **(d)** Significant difference in tree carbon ($P = 0.006$).

Fig. 4 Regression analysis showing a significant negative correlation between privet basal area and tree density.

Fig 1

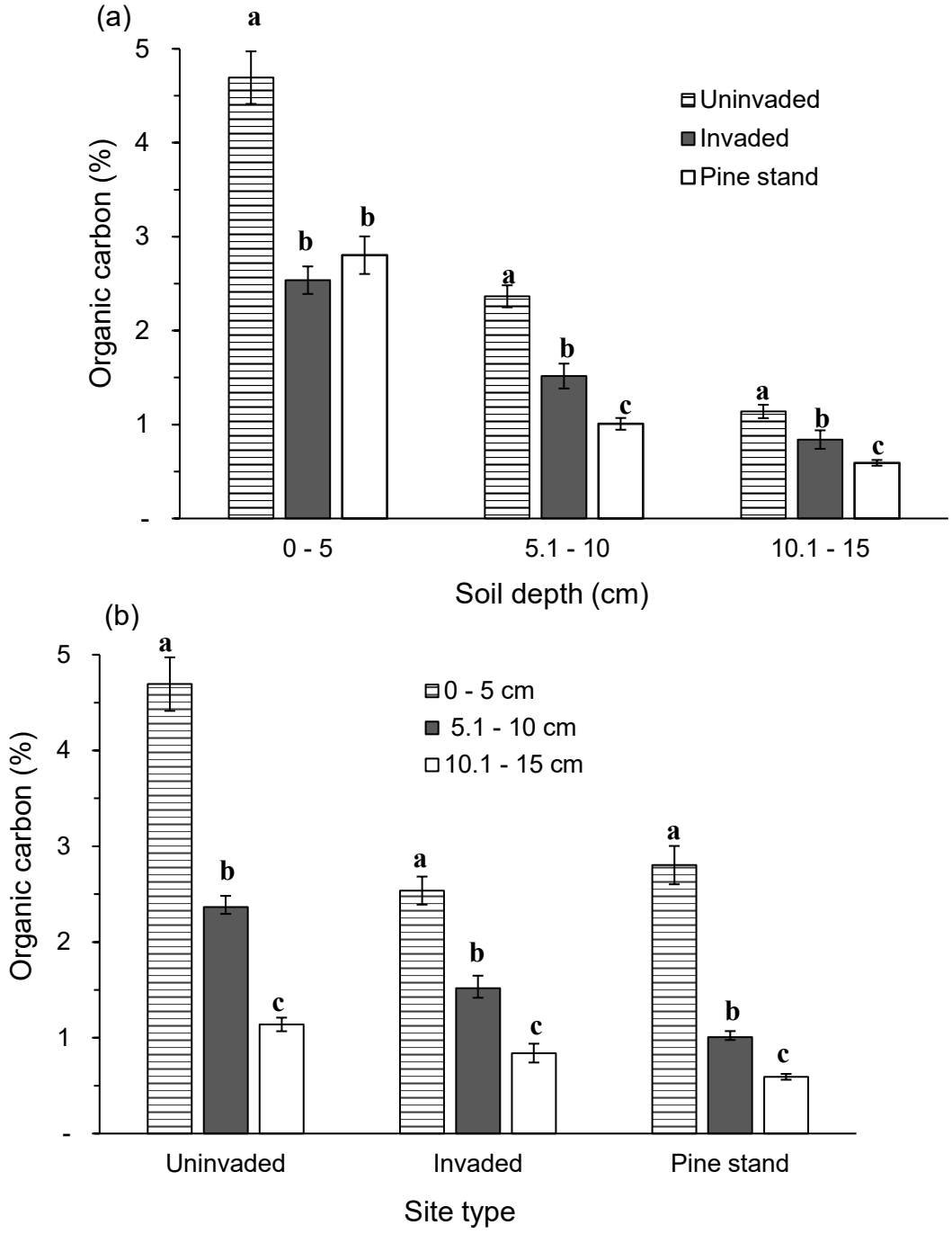

(a)
Organic carbon (%)
5
4
3
2
1
-
a
b
b
a
b
c
a
b
c
Uninvaded
Invaded
Pine stand
0 - 5
5.1 - 10
10.1 - 15
Soil depth (cm)
(b)
Organic carbon (%)
5
4
3
2
1
-
a
b
c
a
b
c
a
b
c
0 - 5 cm
5.1 - 10 cm
10.1 - 15 cm
Uninvaded
Invaded
Pine stand
Site type

Fig 2

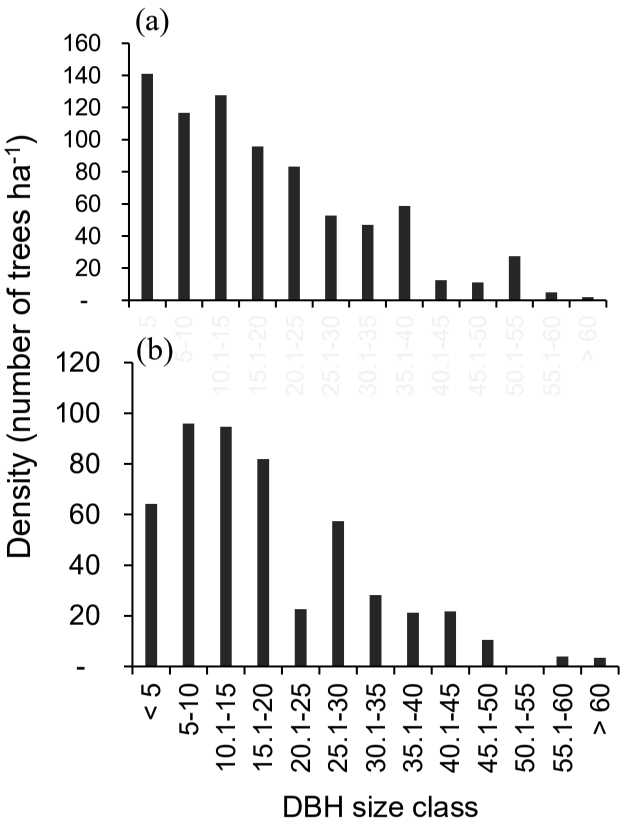

(a)
160
140
120
100
80
60
40
20
-
(b)
120
100
80
60
40
20
-
Density (number of trees ha-1)
< 5
5-10
10.1-15
15.1-20
20.1-25
25.1-30
30.1-35
35.1-40
40.1-45
45.1-50
50.1-55
55.1-60
> 60
DBH size class

Fig. 3

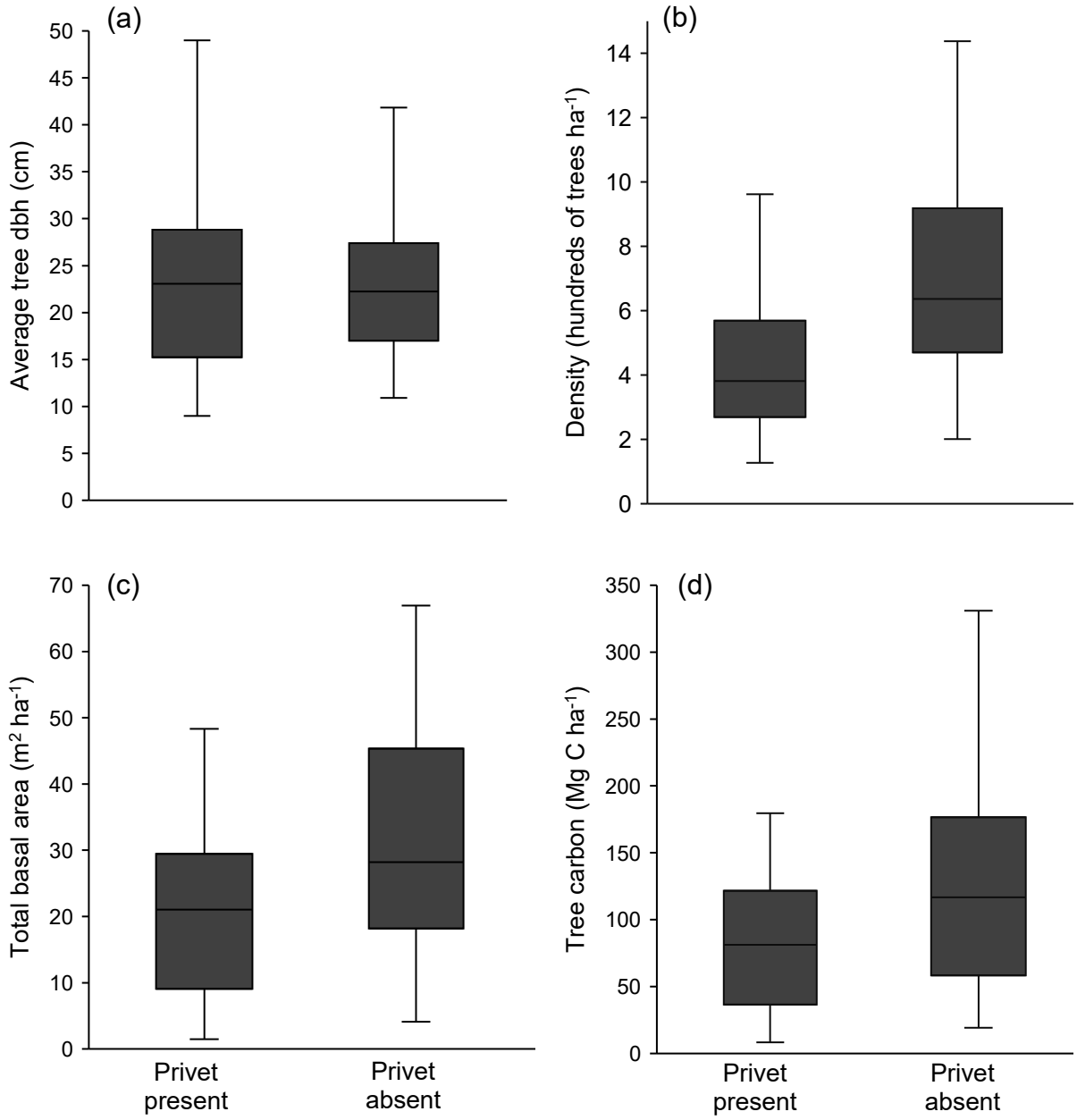
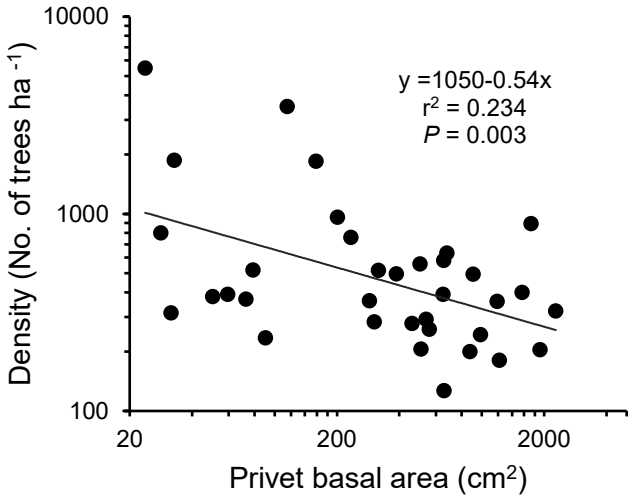

(a)
Average tree dbh (cm)
0
5
10
15
20
25
30
35
40
45
50
(b)
Density (hundreds of trees ha-1)
0
2
4
6
8
10
12
14
(c)
Total basal area (m2 ha-1)
0
10
20
30
40
50
60
70
Privet present
Privet absent
(d)
Tree carbon (Mg C ha-1)
0
50
100
150
200
250
300
350
Privet present
Privet absent

Fig. 4


10000
1000
100
Density (No. of trees ha -1)
y =1050-0.54x
r2 = 0.234
P = 0.003
20
200
2000
Privet basal area (cm2)