



Comparison of decay rates between native and non-native wood species in invaded forests of the southeastern U.S.: a rapid assessment

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Abstract Invasive plants have the potential to affect decomposition both directly, by introducing novel substrates that may differ from native species in key structural or chemical properties, and indirectly through changes to soil properties and microbial communities. The relative importance of these two mechanisms is unclear, especially with regard to wood decomposition. To explore these questions, we used a novel method to rapidly assess the wood decay rates of 11 native and 11 invasive non-native angiosperm

species. The study was repeated at three pairs of sites, each consisting of an invaded and a relatively uninvaded forest. The invaded sites had either been colonized by a non-native grass (*Microstegium vimineum* (Trin.) A. Camus), a non-native woody shrub (*Ligustrum sinense* Lour.) or by multiple invasive species. After one year in the field, mass loss varied more than two-fold among the 22 wood species (24.2–52.3%). Wood origin (i.e., native or non-native) was only important at the *Microstegium* sites, with non-native species decomposing marginally faster than native species. Wood decomposed faster at both the *Ligustrum*-invaded and multiply-invaded sites than in their respective uninvaded sites but there were no differences between sites invaded or not by *Microstegium*. We detected positive relationships overall between mass loss and pH, K, P and NO_3^- , but invasion had no consistent effects on these soil properties. The results from this study show that the differences in wood decay rates between native and non-native species and the effects of invasion are highly idiosyncratic, with effects depending greatly on species and ecological context.

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Introduction

The invasion of non-native plant species is altering the composition and structure of forest ecosystems globally (Richardson and Rejmánek 2011; Vilà et al. 2011), but it remains poorly understood how these species will affect ecosystem processes, such as the decomposition of organic matter. Decomposition is a key process in carbon and nutrient cycles and is influenced by a wide variety of interacting biotic and abiotic factors, making it sensitive to changes in plant community composition and local climatic conditions (Bradford et al. 2014; Fukami et al. 2010). While much remains unknown about the relative importance of various factors, biotic factors, such as invasions of non-native plants, may exert a stronger effect on decay rates than the anticipated effects of climate change (Ashton et al. 2005). Invasive plants may affect decomposition through two potential mechanisms. The first is direct, and concerns differences between non-native and native plant species in structural or chemical properties of the decaying tissues that may affect decomposability. The second mechanism is indirect, and results from changes that non-native species exert on soil properties or taxa that modulate decomposition. While a number of studies have tested these mechanisms (hereafter referred to as “direct” and “indirect” effects) as they relate to leaf litter decomposition (Ashton et al. 2005; Jo et al. 2016), no studies have compared the wood decay rates of non-native versus native species nor investigated how invasion of non-native plants affects rates of wood decomposition. This is in part because wood decomposes very slowly and we lack methods to assess rates of wood decomposition rapidly. Indeed, traditional methods for studying wood decomposition are either limited to the early stages of the process, use a chronosequence approach or require a decade or more to complete (Bultman and Southwell 1976; Freschet et al. 2012, and references therein).

While plant traits often differ between non-native and native species (Ordonez et al. 2010; Van Kleunen et al. 2010) and there is a close connection between some traits (e.g., nutrient concentrations relative to carbon, lignin content, specific gravity, etc.) and decay rates (Cornwell et al. 2008; Mitchell et al. 2011; Weedon et al. 2009), there are few studies comparing the decay rates of non-native and native species. In some ecosystems, non-native leaf litter decomposes

faster than native leaf litter (Ashton et al. 2005; Ehrenfeld 2003), in part due to invasive species investing little in durable structures relative to many native species (Prescott and Zukuwert 2016). This generalization does not always hold true, however (Fernández and Aragón 2014; Jo et al. 2016). Moreover, the functional traits that predict decay rates of leaf litter may have little bearing on how quickly other plant parts, such as wood, decompose (Sun et al. 2018). Traits known to influence how quickly wood decomposes include the concentrations of N and C as well as C:N and wood density (i.e., specific gravity) (Héroult et al. 2010; Weedon et al. 2009) and all of these metrics have the potential to vary between native and non-native species. Although comparisons of nutrient concentrations between the wood of native and non-native species are lacking, previous studies have reported higher nutrient concentrations in the photosynthetic tissues of non-native plants (Sardans et al. 2017). In addition, because non-native plant species as a group grow faster than native taxa (Pattison et al. 1998; Van Kleunen et al. 2010) and faster growing species tend to produce less dense wood (Chave et al. 2009), it is plausible that non-native plants as a group are characterized by lower wood density and, as a consequence, promote faster wood decay rates.

Regarding the potential indirect effects of plant invasion on decomposition, an abundance of studies support the notion that nonnative plants can alter soil properties as well as microbial communities and these changes can affect decay rates. For example, many invasive plant species increase soil pH, water content, N mineralization and nitrification and phosphorus availability compared to uninvaded soil (Chapuis-Lardy et al. 2006; Ehrenfeld 2003; Ehrenfeld et al. 2001; Hawkes et al. 2005; Heneghan et al. 2006; McGrath and Binkley 2009; Rodgers et al. 2008; Sardans et al. 2017). These effects have been attributed to enhanced decay rates brought about by the relatively nutrient-rich plant tissues of invasive species (Rodgers et al. 2008; Sardans et al. 2017) as well as the release of secondary plant compounds that can have direct and indirect effects on soil chemistry. Changes in the composition of soil microbial communities following invasion can also have important implications for nutrient cycling and decay rates (Hawkes et al. 2005). Microbes and other soil organisms (e.g., mites, see McGrath and Binkley

(2009)) respond to increased nutrient availability and can be impacted by the secondary metabolites produced by many invasive plants (Cipollini et al. 2012). The effects of invasive plants on soil properties and microbial communities are known to vary greatly among and within species depending on soil conditions, interactions with other species and disturbance history (Dassonville et al. 2008; Kuebbing et al. 2014; Sardans et al. 2017).

In this study, we tested for both direct and indirect effects of invasion on wood decomposition using multiple native and invasive non-native wood (hereafter “non-native”) species occurring in the southeastern United States. We compared decay rates among these species at sites with variable invasion histories using a novel method for rapidly assessing decay rates. The southeastern U.S. provides a good opportunity for testing the impact of non-native species on decay rates because it has been invaded by numerous non-native plants including many woody trees and shrubs as well as a variety of grasses, vines and herbaceous plants (Miller 2003). We compared decay rates between invaded and uninvaded sites at three locations. The three invaded sites were (1) dominated in the understory by a non-native grass (*Microstegium vimineum* (Trin.) A. Camus), (2) dominated in the midstory by a non-native woody shrub (*Ligustrum sinense* Lour.) or (3) dominated at all forest layers by multiple species of non-native trees, shrubs and vines.

We hypothesized that invasive plants would accelerate decay rates through both direct and indirect effects. Regarding the direct effects, we predicted that non-native species would have lower specific gravity, higher N and lower C than native species and these differences would manifest in faster decay rates for non-natives. As for indirect effects, we predicted that invaded sites will have higher concentrations of soil nutrients including nitrate and ammonium as well as higher pH and these differences would correlate with faster decay rates in invaded than in relatively uninvaded sites.

Methods

Study sites and installation

The experiment was installed at three locations in northeast Georgia, with two sites per location (i.e., six sites in total), to compare rates of decomposition among forests with different invasion histories (Fig. 1, Online Resource 2). At each location there was a relatively invaded site and a relatively uninvaded site, hereafter referred to as invaded and uninvaded for simplicity although non-native plant species were present at all sites (Online Resource 3). At the “Stiltgrass” location, the forest floor at the invaded site was completely covered by the invasive annual grass, *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass), whereas this species was absent from the uninvaded site. The two sites consisted of mesic hardwood-dominated forests bordering Harris creek on the Oconee National Forest in Greene County and were separated by about 200 m. The “Privet” location consisted of two neighboring sites, approximately 100 m apart, within a mesic hardwood-dominated forest growing adjacent to the Oconee River in Greene County. The midstory of the invaded site was completely dominated by Chinese privet, *Ligustrum sinense* Lour., an invasive woody shrub. The privet at that site is well established, consisting of about 45 metric tons per ha (Hanula et al. 2011), and forms a dense midstory canopy that prevents the establishment of any other plants on the forest floor (Hanula et al. 2009). The uninvaded site was situated within an area from which all Chinese privet (*Ligustrum sinense*) had been removed from a ~ 4 ha area in 2005, followed by a single dormant-season application of 2% glyphosate in 2006. Although glyphosate can have short term effects on microbial biomass, soil respiration and other properties (Gaupp-Berghausen et al. 2015; Stratton and Stewart 1992), we do not expect this treatment to affect our results considering the applications took place nine years before this study began. Some privet regeneration had occurred within the cleared area but this consisted of small seedlings with negligible biomass and we do not expect below-ground roots to have remained nearly 10 years after the plants were originally cleared. The third location (“Multiple Species”) was in Clarke County where a gravel road separates a mostly uninvaded mature upland hardwood forest (> 100 years old) from a

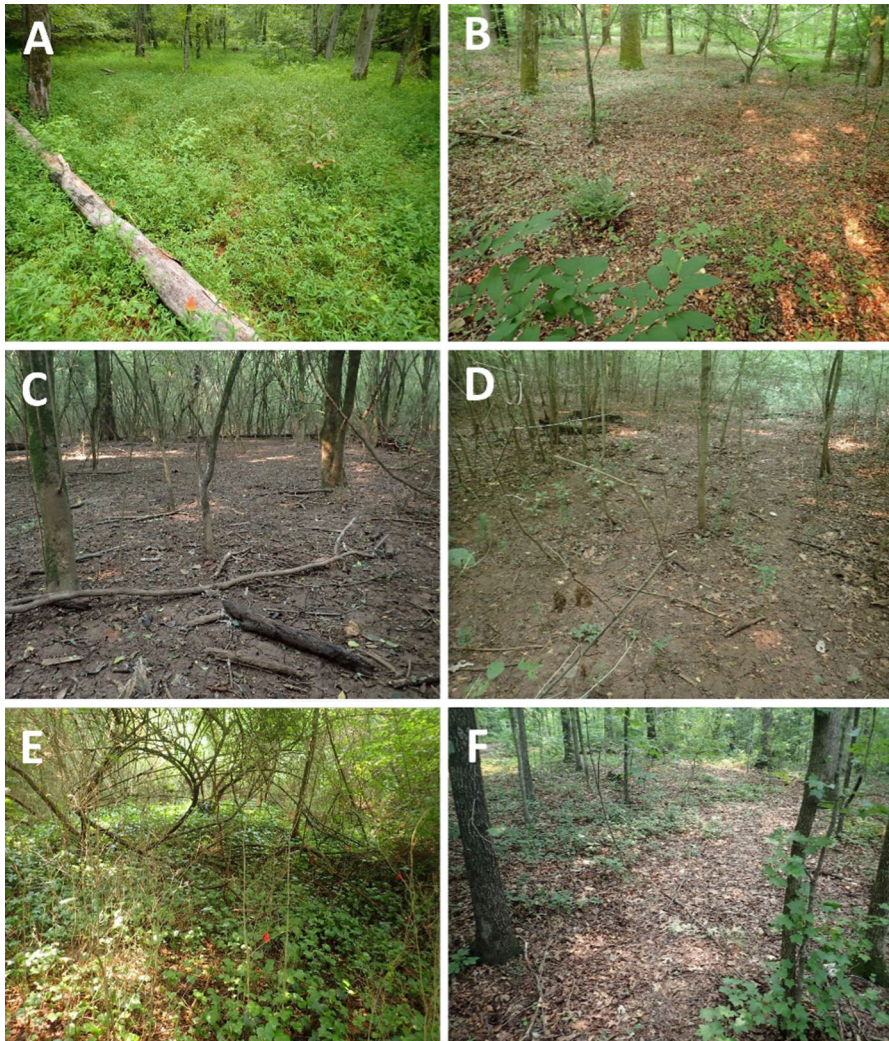


Fig. 1 Sites invaded (a) and uninvaded (b) by *Microstegium*; invaded (c) and uninvaded (d) by *Ligustrum*; and invaded (e) or uninvaded (f) by multiple invasive species

regenerating and highly invaded forest (< 40 years old based on available aerial images), which consisted almost entirely of non-native species (Online Resource 3). These sites were separated by about 50 m. Whereas the paired sites at the Stiltgrass and Privet locations were carefully selected to minimize any differences in forest age or disturbance, an important consideration (Sokol et al. 2017), the Multiple Species sites differed greatly in age and disturbance history. This was done intentionally to determine how decomposition rates differ between natural forests and the “invasional meltdown” scenario commonly seen on highly disturbed sites. Thus, by design, we were less able to isolate the effects of

invasion from disturbance history at the Multiple Species location than at the other two locations.

A 23×5 m rectangular grid was established at each site, resulting in 115 grid cells. Each grid cell received one core (see section below) from one of the 115 sampled trees (i.e., five trees from each of the 23 species), with the positions chosen randomly. The cores were individually enclosed within nylon mesh sleeves (0.3 mm openings) which were sewn shut along the long edge and stapled shut at the ends. It was necessary to use fine mesh in this study given the small size of the tree cores, i.e., to avoid the loss of small wood fragments. On 16–18-March-2015, one sleeved core was placed in contact with the mineral soil at the

center of each grid cell and secured in place with a tent peg passing through an attached loop of fishing line. Once in place, each core was covered in litter that had been removed to expose mineral soil.

Tree cores

Tree cores collected from healthy trees were used to rapidly assess decay rates in this study. Increment borers were used to collect the cylindrical cores of wood, 0.4 cm in diameter, from 22 (11 native, 11 non-native, see Online Resource (1) genera of woody angiosperms occurring widely across the southeastern United States. We also collected cores from a native gymnosperm, *Pinus taeda* L., to facilitate comparisons with the existing decomposition literature from the region. This species was excluded from the main analyses, however, as gymnosperms are known to decompose more slowly than angiosperms due to various structural and chemical differences (Weedon et al. 2009). All cores were collected in the fall (September–October 2013–2014) and only plants ≥ 19 cm in diameter and growing in forested areas were included in the study. Cores were collected from five trees of each species (115 trees in total) with 7–8 cores collected from the base of each tree, in a closely-grouped vertical row 0.5–1.5 m above ground. Immediately after collection, the outer 2 cm of each core was removed (because this area is sometimes damaged during coring) and a 10-cm section of the remaining piece was retained for use in the study. The volume of each 10-cm section was determined to the nearest 0.01 ml using the volume displacement method, followed by a determination of dry weight to the nearest 0.01 g (dried at 60 °C until no further weight loss was detected). These measurements were used to calculate the specific gravity (dry mass/fresh volume) of each core, a potentially important explanatory variable that is positively correlated with wood moisture (Hérault et al. 2010). Six cores from each tree were used in the decomposition experiment while the remaining one or two cores were dried and ground in a Wiley mill for determination of N, C and C:N. These samples were submitted to the Yale Analytical and Stable Isotope Center (YASIC) where they were analyzed using a Costech ESC 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, CA, USA) interfaced with a Delta Plus Advantage

isotope ratio mass spectrometer (Thermo, Bremen Germany).

Data collection

Mass loss

To assess relative rates of decomposition between native and non-native wood species and between invaded and uninvaded sites, cores were collected from all locations after one year in the field on 17-Mar-2016. Both Stiltgrass sites and both Privet sites had experienced flooding over the winter months and the cores at these sites were buried under ~ 1 –3 cm of sediment. Upon returning to the lab, all cores were stored in the freezer until further processing. Each core was removed from the mesh sleeve and rinsed over a 63-micron screen. Cores were individually placed into small paper bags and dried at 60 °C until no further mass loss was observed. Wood mass loss was calculated for each core using the following equation: [(initial dry mass – final dry mass)/ initial dry mass].

Soil properties

To understand how soil properties varied among the six sites, five samples of mineral soil were collected to a depth of 10 cm at each site in July 2015, one from the center and four from the corners of each 23 × 5 grid. The samples were submitted to the Agricultural and Environmental Services Laboratories at the University of Georgia to be analyzed for pH, mineral concentrations and other properties. Minerals (P, K, Ca, Mg, Zn, Mn) were extracted in Mehlich I solution and analyzed using an Inductively Coupled Plasma Spectrometer. Nitrate (NO_3^-) was extracted in 2 M KCl and analyzed using continuous-flow calorimetry (Perstorp Analytical Enviroflow). Ammonium (NH_4^+) was extracted in 2 M KCl and analyzed using a photometric analyzer (LabMedics Aquakem). Finally, organic matter was determined by the “loss on ignition” method in which samples were heated for 3 h at 360 °C with the results reported in percent by weight.

Data analysis

To look at relationships among wood properties, Pearson’s correlations were calculated among specific gravity, N, C and C:N. To study the relationships

between mass loss and each wood property, we conducted mixed linear models using SAS 9.4 (SAS Institute 2013) with species as a random effect and the wood properties partitioned into between (i.e., average values by species) and within species (i.e., deviations from species means by tree) components. Because we only had a single value for initial N and C from each tree, we averaged specific gravity and mass loss data over cores (and hence over sites) for each tree prior to this analysis. Using these same average values, differences in wood properties between native and non-native species were tested using mixed models in which origin was included as a fixed effect and species within origin as a random effect. To help interpret our mass loss results, we also tested these models with species within origin treated as a fixed effect to limit our inference to only those species included in this study. Finally, a mixed model analysis was applied to decay rates for individual cores for each location separately to test for the effects of origin, invasion (i.e., invaded or uninvaded) and the origin \times invasion interaction. Species within origin, tree within species and the invasion \times species within origin interaction were included as random effects in this model.

Soil properties (pH, Ca, K, Mg, Mn, P, Zn, NH_4^+ , NO_3^- and organic matter) were compared among the six sites using the GLM procedure of SAS and Tukey's Honest Significant Difference post-hoc test. We also used orthogonal contrasts to specifically compare these metrics between invaded and uninvaded sites at each location. To examine how soil properties varied among the six sites, we conducted nonmetric multi-dimensional scaling using PCORD (McCune and Mefford 2011). The data for each soil property were relativized by maximum prior to this analysis. We then performed PERMANOVA followed by pairwise comparisons to test for significant differences in soil properties among sites. After calculating mean values for mass loss and soil properties by site (since soil samples were collected from just five positions within each site), the effect of each soil property on mass loss was assessed using separate mixed effects models in SAS with location treated as a random effect. To examine the relationship between the overall soil profile and mass loss, we also included the average values for axes 1 and 2 as predictors in the same model. In all analyses, P -values < 0.05 are considered significant while those < 0.1 are reported here as marginally significant.

Results

Wood properties

Wood properties varied widely among the 115 trees sampled (Table 1), with up to a 3.3-fold difference in average specific gravity (range: 0.21–0.69), a 6.5-fold difference in N (range: 0.04–0.26), a 1.1-fold difference in C (range: 40.54–46.40) and a 6.0-fold difference in C:N ratios (range: 171.56–1021.79). After limiting the dataset to angiosperms (i.e., *Pinus taeda* excluded), there were no significant correlations among average specific gravity, N, and C, although there was a marginally significant negative correlation between N and C ($r = -0.17$, $P = 0.07$). There was also no significant correlation between specific gravity and C:N. There were no significant differences in specific gravity ($F_{1,21} = 0.05$, $P = 0.8$), N ($F_{1,21} = 1.2$, $P = 0.3$), C ($F_{1,21} = 0.7$, $P = 0.4$) or C:N ($F_{1,21} = 1.4$, $P = 0.2$) between native and non-native species in mixed linear models in which species was included as a random effect. However, when we limited our inference to just the species used in this study by including species within origin as a fixed rather than a random effect, there were significant differences between non-native and native wood species in N ($F_{1,92} = 27.3$, $P < 0.0001$) and C:N ($F_{1,92} = 51.7$, $P < 0.0001$) with non-native species being characterized by higher N and lower C:N. There was also a marginally significant difference in C ($F_{1,92} = 3.6$, $P = 0.06$), with C being higher for non-native than native species.

Decay rates

Decay rates were compared using percent mass loss data after one year in the field. Including *P. taeda*, mass loss varied up to 4.6-fold among trees (range: 13.35–61.05%) and 2.8-fold among tree species (range: 18.4–52.3%) (Fig. 2). Ignoring species effects, there were significant correlations between mass loss and specific gravity ($r = -0.32$, $P < 0.001$), N ($r = 0.19$, $P = 0.05$), C ($r = -0.34$, $P < 0.001$) and C:N ($r = -0.22$, $P = 0.02$) but only C was a significant predictor of mass loss based on mixed models with species included as a random effect. More specifically, C explained a significant amount (24.6%) of between-species variation in mass loss ($F_{1,20} = 6.51$, $P = 0.02$) but was not a significant

Table 1 Mean ± SE ($n = 5$) wood properties and decay rates by tree species

Species	Origin	C (%)	N (%)	C:N	Specific gravity	Mass loss (%)
<i>Acer negundo</i> L	Native	44.8 ± 0.3	0.145 ± 0.0114	319 ± 29	0.384 ± 0.010	28.1 ± 2.2
<i>Ailanthus altissima</i> (P. Mill.) Swingle	Non-native	43.5 ± 0.3	0.107 ± 0.013	428 ± 42	0.536 ± 0.003	47.5 ± 4.0
<i>Albizia julibrissin</i> Durazz	Non-native	43.8 ± 0.7	0.136 ± 0.006	325 ± 18	0.478 ± 0.018	49.4 ± 1.5
<i>Betula nigra</i> L	Native	44.7 ± 0.3	0.085 ± 0.003	531 ± 17	0.500 ± 0.013	41.6 ± 1.5
<i>Broussonetia papyrifera</i> (L.) L'Hér. Ex Vent	Non-native	43.7 ± 0.5	0.208 ± 0.020	218 ± 20	0.546 ± 0.014	42.3 ± 1.9
<i>Celtis laevigata</i> Willd	Native	43.2 ± 0.3	0.175 ± 0.013	252 ± 17	0.507 ± 0.017	52.3 ± 0.6
<i>Cinnamomum camphora</i> (L.) J. Presl	Non-native	44.4 ± 0.2	0.074 ± 0.004	609 ± 31	0.455 ± 0.010	44.5 ± 3.0
<i>Firmiana simplex</i> (L.) W. Wight	Non-native	44.0 ± 0.2	0.152 ± 0.014	301 ± 29	0.379 ± 0.031	47.2 ± 1.0
<i>Fraxinus pennsylvanica</i> Marsh	Native	44.2 ± 0.3	0.114 ± 0.008	397 ± 33	0.503 ± 0.026	39.5 ± 3.0
<i>Juglans nigra</i> L	Native	43.9 ± 0.2	0.089 ± 0.003	495 ± 22	0.575 ± 0.020	40.5 ± 2.5
<i>Ligustrum sinense</i> Lour	Non-native	43.8 ± 0.2	0.141 ± 0.005	311 ± 10	0.634 ± 0.021	47.2 ± 2.5
<i>Liquidambar styraciflua</i> L	Native	43.3 ± 0.3	0.060 ± 0.002	721 ± 29	0.528 ± 0.011	49.9 ± 3.9
<i>Liriodendron tulipifera</i> L	Native	43.4 ± 0.2	0.109 ± 0.003	400 ± 12	0.401 ± 0.010	51.5 ± 3.0
<i>Melia azedarach</i> L	Non-native	44.5 ± 0.1	0.077 ± 0.004	585 ± 30	0.497 ± 0.009	27.1 ± 2.1
<i>Paulownia tomentosa</i> (Thunb.) Sieb. & Zucc. Ex Steud	Non-native	45.0 ± 0.2	0.075 ± 0.003	604 ± 21	0.240 ± 0.009	47.3 ± 3.6
<i>Pinus taeda</i> L	Native	45.0 ± 0.1	0.050 ± 0.003	903 ± 48	0.499 ± 0.014	18.4 ± 1.8
<i>Platanus occidentalis</i> L	Native	44.2 ± 0.3	0.083 ± 0.005	544 ± 35	0.495 ± 0.018	42.9 ± 2.1
<i>Prunus serotina</i> Ehrh	Native	44.8 ± 0.2	0.062 ± 0.001	720 ± 19	0.614 ± 0.016	30.7 ± 2.4
<i>Pyrus calleryana</i> Decne	Non-native	45.4 ± 0.3	0.094 ± 0.002	483 ± 10	0.653 ± 0.011	36.9 ± 1.8
<i>Quercus nigra</i> L	Native	42.6 ± 0.6	0.097 ± 0.007	446 ± 28	0.626 ± 0.009	32.7 ± 2.4
<i>Triadica sebifera</i> (L.) Small	Non-native	43.7 ± 0.1	0.103 ± 0.004	427 ± 15	0.472 ± 0.014	50.9 ± 2.4
<i>Ulmus parvifolia</i> Jacq	Non-native	45.1 ± 0.2	0.086 ± 0.004	532 ± 27	0.668 ± 0.009	24.2 ± 1.0
<i>Ulmus rubra</i> Muhl	Native	43.9 ± 0.3	0.087 ± 0.007	519 ± 41	0.540 ± 0.012	42.9 ± 3.1

predictor of within-species variation ($F_{1,87} = 0.42$, $P = 0.52$). The only other wood property that was marginally significant was specific gravity, which explained a considerable amount (14.6%) of between-species variation in mass loss ($F_{1,20} = 3.43$, $P = 0.08$) but negligible within-species variation ($F_{1,87} = 0.05$, $P = 0.8$).

We tested the effects of origin and invasion for each location separately. At the Privet location, there was a significant effect of invasion ($F_{1,21} = 21.8$,

$P < 0.0001$) while origin and the origin × invasion interaction were both nonsignificant (Fig. 3b). Similarly, at the site with multiple invasive species, the effect of invasion was also significant ($F_{1,21} = 89.0$, $P < 0.0001$), with greater mass loss in the invaded site, but there was also a significant interaction between origin and invasion ($F_{1,21} = 4.7$, $P = 0.04$) (Fig. 3c), where mass loss tended to be higher for native than non-native species at the uninvaded site, while the opposite pattern was observed at the invaded

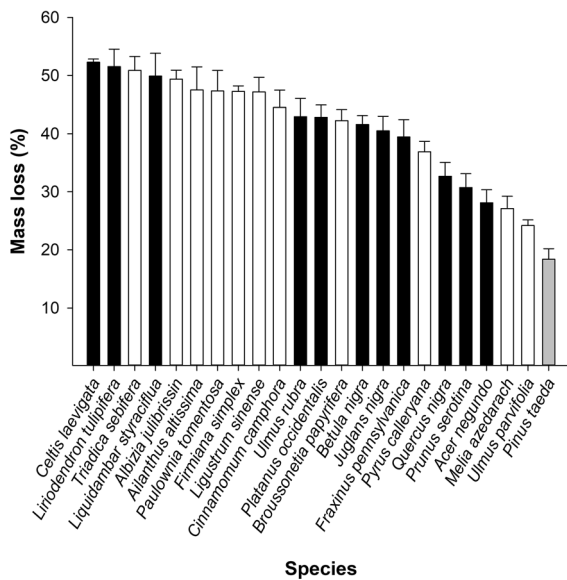


Fig. 2 Mean \pm SE ($n = 29$ – 30) percent mass loss for the 11 non-native (white bars) and 11 native tree (black bars) angiosperm species after one year in the field. Note: results for *Pinus taeda* (grey bar), a gymnosperm, are included here for comparison but are not included in the main analysis

site (Fig. 3c). Finally, at the Stiltgrass location, origin had a marginally significant effect ($F_{1,21} = 3.15$, $P = 0.09$), with mass loss being greater for non-native than native species, whereas invasion and the origin \times invasion interaction were nonsignificant (Fig. 3d).

Finally, we analyzed the relationship between mass loss and soil properties, averaged by site, with location included as a random effect. There were significant and positive relationships between mass loss and pH ($F_{1,2} = 75.1$, $P = 0.01$), K ($F_{1,2} = 24.2$, $P = 0.04$), P ($F_{1,2} = 24.4$, $P = 0.04$) and NO_3^- ($F_{1,2} = 129.3$, $P < 0.01$). There were no significant relationships between mass loss and values for either of the NMDS axes (results not shown).

Soil

All soil variables differed significantly among the six sites. At the Privet location, only Mn differed between the invaded and uninvaded sites, being significantly higher in the latter (Table 2). All ten variables differed significantly between the invaded and uninvaded sites at the Multiple Species location. Values for seven of them (pH, Ca, K, Mg, P, Zn, NO_3^-) were greater in the

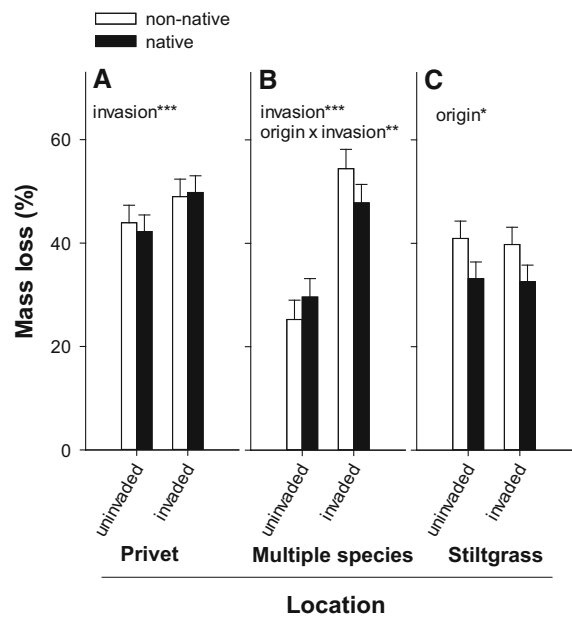


Fig. 3 Percent mass loss (LS-means \pm SE) for non-native (open bars) vs. native wood (closed bars) species placed in uninvaded and invaded sites at three locations. The individual locations included sites invaded by *Ligustrum* (a), multiple plant species (b) or by *Microstegium* (c). Although all six sites were invaded to some extent by non-native plants, they are labelled here as uninvaded or invaded for simplicity. Asterisks next to significant effects indicate the level of significance: $P < 0.1^*$, $P < 0.05^{**}$, and $P < 0.01^{***}$. Invasion refers to whether the sites were invaded or uninvaded and origin distinguishes between non-native and native wood species

highly invaded site than the uninvaded site whereas the opposite was true for Mn, NH_4^+ and organic matter (Table 2). Five of the variables differed between the two Stiltgrass sites (Ca, Mg, Mn, NH_4^+ and organic matter), with values for all of them being higher in the invaded site. NMDS yielded a two-dimensional solution with a final stress of 8.94. It is clear from the ordination that combined soil properties varied greatly among locations (Fig. 4) and this is supported by PERMANOVA which indicated all but one of the pairwise comparisons among the six sites were significantly different. The non-significant pairwise comparison in that analysis was between the two sites at the Privet location.

Table 2 Mean \pm SE ($n = 5$) soil characteristic for the various sites

	Location: privet		Location: multiple species		Location: stiltgrass	
	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded	Invaded
	pH	5.99 \pm 0.10 a $F_{1,24} = 1.09, p = 0.3073$	6.18 \pm 0.07 a	4.70 \pm 0.05 b $F_{1,24} = 26.43, p \leq .0001$	5.65 \pm 0.20 a	6.03 \pm 0.11 a $F_{1,24} = 0.32, p = 0.574$
Ca (ppm)	1594.60 \pm 163.92 a $F_{1,24} = 0.18, p = 0.6778$	1701.00 \pm 137.11 a	131.00 \pm 20.14 c $F_{1,24} = 17.61, p = 0.0003$	1192.60 \pm 299.15 ab	668.60 \pm 127.80 bc $F_{1,24} = 8.89, p = 0.0065$	1422.60 \pm 200.12 ab
K (ppm)	62.82 \pm 3.09 b $F_{1,24} = 1.47, p = 0.2379$	95.66 \pm 18.04 ab	99.90 \pm 20.79 ab $F_{1,24} = 5.45, p = 0.0282$	163.26 \pm 37.02 a	57.34 \pm 7.91 b $F_{1,24} = 0.1, p = 0.7567$	65.84 \pm 2.79 b
Mg (ppm)	219.84 \pm 11.80 a $F_{1,24} = 0.46, p = 0.5059$	232.04 \pm 8.36 a	68.58 \pm 10.67 b $F_{1,24} = 6.52, p = 0.0175$	114.70 \pm 12.88 b	119.74 \pm 18.96 b $F_{1,24} = 48.92, p \leq 0.0001$	246.10 \pm 11.44 a
Mn (ppm)	102.50 \pm 5.43 a $F_{1,24} = 11.1, p = 0.0028$	80.04 \pm 5.36 b	64.88 \pm 5.32 bc $F_{1,24} = 26.56, p \leq .0001$	30.14 \pm 2.32 d	29.18 \pm 5.79 d $F_{1,24} = 8.87, p = 0.0065$	49.26 \pm 3.31 cd
P (ppm)	5.54 \pm 0.63 a $F_{1,24} = 0, p = 0.9749$	5.65 \pm 1.06 a	4.05 \pm 0.14 a $F_{1,24} = 8.24, p = 0.0084$	13.62 \pm 5.56 a	6.51 \pm 0.15 a $F_{1,24} = 0.04, p = 0.8451$	7.17 \pm 0.95 a
Zn (ppm)	10.62 \pm 0.21 a $F_{1,24} = 0.22, p = 0.6447$	9.44 \pm 0.33 a	3.50 \pm 0.63 ab $F_{1,24} = 6.08, p = 0.0212$	9.71 \pm 4.29 a	1.53 \pm 0.28 b $F_{1,24} = 0.38, p = 0.543$	3.09 \pm 0.18 ab
NH ₄ ⁺ (mg/kg)	8.08 \pm 0.96 b $F_{1,24} = 1.52, p = 0.2297$	10.96 \pm 0.68 ab	16.13 \pm 2.90 a $F_{1,24} = 14.57, p = 0.0008$	7.21 \pm 2.06 b	5.55 \pm 1.50 b $F_{1,24} = 6.06, p = 0.0214$	11.30 \pm 0.38 ab
NO ₃ ⁻ (mg/kg)	13.42 \pm 1.66 a $F_{1,24} = 1.54, p = 0.2266$	16.91 \pm 1.56 a	0.50 \pm 0.12 b $F_{1,24} = 40.28, p \leq .0001$	18.34 \pm 4.22 a	2.82 \pm 0.53 b $F_{1,24} = 0.17, p = 0.683$	3.98 \pm 0.65 b
Organic matter (%)	8.14 \pm 0.33 ab $F_{1,24} = 0.28, p = 0.6007$	8.77 \pm 0.51 ab	9.59 \pm 1.67 a $F_{1,24} = 10.06, p = 0.0041$	5.87 \pm 0.47 bc	2.58 \pm 0.58 c $F_{1,24} = 5.09, p = 0.0334$	5.23 \pm 0.62 bc

Within each row, means with different letters next to them are significantly different as determined by Tukey's studentized range test. Results for orthogonal contrasts are given below means for each pair of sites at each location. Significant differences are indicated in bold

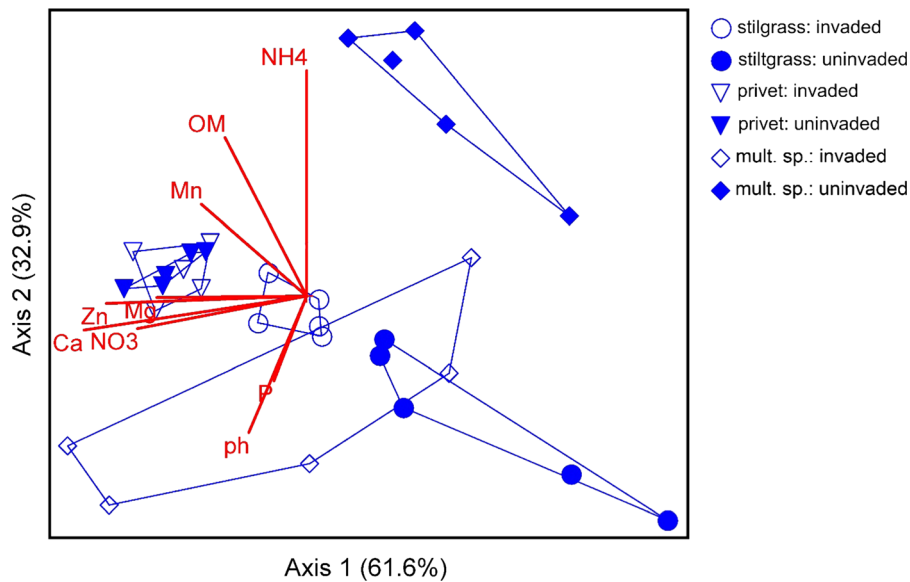


Fig. 4 Ordination from nonmetric multidimensional scaling for soil profiles as measured at five positions at each of the six sites. Circles, triangles and diamonds represent the Stiltgrass, Privet and Multiple Species locations, respectively

Discussion

Here we assessed the direct and indirect effects of invasive plants on wood decomposition in southeastern U.S. forests. We tested direct effects by comparing wood traits and decay rates between native and non-native species of woody angiosperms, and we investigated indirect effects by comparing decay rates under three different invasion histories.

Regarding direct effects, we found decay rates varied widely among the 22 angiosperm species included in this study (Fig. 2) and this variability was driven in part by interspecific differences in wood properties, most notably C. We found limited support for our first hypothesis, that non-native wood species would decompose faster than native species. Only at the Stiltgrass location did we observe this pattern, and the difference was only marginally significant (Fig. 3). At the Multiple Species location, we observed a significant interaction between origin and invasion, where mass loss tended to be higher for native than non-native species at the uninvaded site, while the opposite pattern was observed at the invaded site. Finally, at the Privet location, origin had no significant effect on decay rate. These results suggest that differences in decay rates may exist between native and non-native wood species under some conditions, possibly driven by differences in wood properties.

Nevertheless, our findings are largely consistent with those of Jo et al. (2016) who reported no differences in leaf and root decomposition rates between 42 native and 36 non-native plant species. Indeed, non-native species were among both the fastest (e.g., *Triadica sebifera* (L.) Small and *Albizia julibrissin*) and slowest (*Ulmus parvifolia* Jacq. and *Melia azedarach*) decomposing species in this study (Fig. 2).

Evidence in support of indirect effects was also mixed. Although we found higher decay rates in the sites invaded by privet and by multiple species than in their respective uninvaded sites, *Microstegium* had no detectable effect on wood decomposition. The differences in soil properties detected in this study cannot fully explain these patterns. At the Privet location, for example, wood decomposed faster in the invaded site than in the uninvaded site even though soil profiles did not differ between those sites. By contrast, there was no difference in decomposition between the two sites at the Stiltgrass location despite large differences in soil profiles between those sites. Although invasion by privet, stiltgrass or multiple species had no consistent effects on soil properties that could then be used to explain decay rates, we did detect positive relationships between mass loss and pH, K, P and NO_3^- . These findings are largely in line with past studies, e.g., P is important in governing decay rates (Zechmeister-Boltenstern et al. 2015) and pH affects

microbial abundance and activity (Bååth and Anderson 2003). Additions of NO_3^- have previously been shown to stimulate wood decomposition (Allison 1965) although N is known to sometimes inhibit microbial activity, especially in wood and other recalcitrant substrates with high C:N ratios (Fog 1988).

Other effects of invasive plants not measured in this study may also have affected decay rates. For example, Chinese privet is known to produce a higher quality litter than many native species, characterized by less lignin, more nitrogen and lower C:N (Mitchell et al. 2011). Moreover, Mitchell et al. (2011) showed that as the proportion of litter consisting of privet increases, the decay rate of litter also increases. Although the decay rates of each species of litter present in these mixed litter bags were not assessed, it is known that recalcitrant litter types can decompose faster when mixed with more labile substrates (Gartner and Cardon 2004). While these studies focus on litter rather than wood decomposition, it nevertheless seems plausible for wood imbedded within a litter layer including privet to similarly decompose more quickly. The presence of privet may help explain decomposition patterns observed at both the privet and Multiple Species locations considering that about 75% of the invaded site at the latter location was covered by privet (Online Resource 3).

Similar to privet, stiltgrass is also expected to produce high quality litter compared to native litter sources and these inputs have been linked to increased loss of soil organic carbon (Strickland et al. 2010). However, unlike sites invaded by privet, we did not observe an increase in wood decomposition at sites invaded by stiltgrass. This seeming discrepancy may be indicative of the variable effects observed for stiltgrass invasion on soil organic carbon. That is, stiltgrass invasion has both been observed to decrease and increase soil organic carbon depending on the specific effect the invasion has on site temperature and active microbial biomass (Strickland et al. 2011). Our findings suggest that for this particular site, stiltgrass invasion did not stimulate increased wood decomposition, but may at other sites. Additionally, unlike privet, stiltgrass is an annual species, and has been shown to increase inputs of labile carbon compounds via root exudation (Bradford et al. 2012). This shift in carbon inputs leads to increased rates of carbon cycling in soils and may also shift soil microbial

communities towards copiotrophs that specialize on labile resources (Warren et al. 2011). If this is the case, and soil communities exhibit 'preferential substrate utilization', then communities associated with our stiltgrass plots may utilize high-quality (i.e. stiltgrass litter and/or root exudates) carbon sources before the utilization of low-quality (i.e. wood) carbon sources (Fontaine and Barot 2005).

We observed the biggest difference in decay rates between invaded and uninvaded sites at the Multiple Species location, where a total of twelve species were present in the invaded site. While these results may be due in part to differences in disturbance history between the two sites (Sokol et al. 2017), they may also reflect the effects of multiple interacting invasive species. The presence of multiple invaders can have non-additive effects on soil properties key to decomposition. Kuebbing et al. (2014), for example, found plots containing two invasive shrubs (*Lonicera maackii* and *Ligustrum sinense*) to have three times higher potential β -glucosidase (a cellulose-degrading enzyme) activity compared to uninvaded soils. Kuebbing and Bradford (2019) also found the addition of litter types to have non-additive positive effects on decomposition and this non-additivity was highest when trait differences among the litter types were large. Such effects may have contributed to the high rates of decomposition observed at the site invaded by multiple species in this study.

In addition to the effects of plant invasion on decomposition differing among species, the effects of individual invasive plant species often vary depending on local soil conditions as well as the extent of invasion (Hulme et al. 2013). In Europe, for instance, Dassonville et al. (2008) found invasive plants to have a positive impact on topsoil nutrient concentrations on sites with low initial nutrient concentrations but saw negative impacts when initial nutrient concentrations were high. Similarly, the effects of invasive plants on nutrient cycling can be positive or negative depending on where a site falls along the precipitation gradient (Ehrenfeld 2003; Scott et al. 2001). Invasion impacts are also known to interact with anthropogenic disturbance. For example, Sokol et al. (2017) found logging to amplify the effects of *Microstegium vimineum* on soil microbial biomass and pH and that these effects varied with time. Logging had dampening, negating and reversing effects on other soil properties in the same study. It is clear from such findings that many

factors will need to be taken into consideration before we can make reliable predictions about the effects of individual invasive species on decomposition.

Conclusions

Our results indicate that wood traits and decay rates are highly variable for both native and non-native wood species. The effects of plant invasion on decay rates and soil properties were similarly idiosyncratic. Despite these inconsistencies, we observed significant effects of invasion status and wood origin at individual locations, underscoring the complexity of the relationships between decomposers, plant traits, soil properties and invasion history. Because our study was established within a small area at each site, we caution against making broad generalizations about the effects of *Ligustrum*, *Microstegium* or multiple species on decay rates or soil properties. Indeed, much more work will be needed to verify these patterns and to understand the mechanisms behind them. Our method of using tree cores to rapidly assess relative decay rates was quite effective, allowing us to test these questions after just one year in the field. While this method may have great utility in studies focused on microbial decomposers, it is less suitable for studies including invertebrates as most taxa will be excluded by the fine mesh used to enclose the cores. Future research comparing the activities of invertebrates among native and non-native wood species would be of great interest given the importance of these organisms to decomposition (Ulyshen 2016) and the high degree of host specificity exhibited by some taxa (Ulyshen et al. 2018). In addition, the effects of invasion by non-native plants on detritivores and other soil invertebrates important to decomposition (Lobe 2012; Bush et al. in press) is another important consideration for future research.

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