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Tree diversity promotes growth of late successional species despite increasing deer damage in a restored forest

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Abstract. The role of tree diversity in restored forests and its impact on key ecological processes like growth and resistance to herbivory has become increasingly important. We analyzed height growth and white-tailed deer *Odocoileus virginianus* browsing damage to saplings of 16 broadleaved tree species in a large-scale (13 ha) reforestation experiment in Maryland, USA, where we manipulated tree diversity in 70 1,225-m^2 plots. After four growing seasons, higher plot-level tree richness led to increased deer browsing damage (i.e., associational susceptibility). Despite increased deer damage to saplings in mixed plots, tree richness had no overall effect on sapling height growth. However, diversity–height relationships were related to species functional traits. Light demanding species with large leaves and faster growth rates had reduced heights in mixtures, whereas shade-tolerant, slower-growing species generally had either increased or unchanged height growth in diverse tree communities, likely related to increased canopy closure in mixtures relative to monocultures. We show that tree diversity can improve growth of late successional species despite exacerbated mammalian herbivore damage. By facilitating the establishment of species with a range of life-history strategies, increased tree diversity may enhance ecosystem multi-functionality in the early stages of forest restoration.

Key words: associational resistance; biodiversity–ecosystem functioning; diversity–herbivory relationship; diversity–productivity relationship; forest plantation; forest restoration; mixed forests; reforestation; sustainable forest management; TreeDivNet.

INTRODUCTION

Global momentum is growing around reforestation given its potential to mitigate climate change, provide habitat for biodiversity, and support human societies (Griscom et al. 2017, Bastin et al. 2019). Yet, many reforestation strategies focus on establishing monoculture plantations, despite burgeoning evidence that tree diversity is critical for forest sustainability (Verheyen et al. 2016, Paquette et al. 2018, Osuri et al. 2019), especially as it relates to forest productivity (Liang et al. 2016, Fichtner et al. 2018, Huang et al. 2018, Jactel et al. 2018). Moreover, tree diversity may help mitigate the negative impacts of herbivores (Jactel et al. 2017, Grossman et al. 2018), which often limit the reestablishment of new forests (McShea et al. 1997, Hackworth et al. 2018).

Plant–herbivore interactions are known to influence a range of ecosystem functions and services in forests including productivity, nutrient cycling, and community composition (Bagchi et al. 2014, Metcalfe et al. 2014). Mixed-species forests can promote associational resistance, whereby palatable trees surrounded by unpalatable heterospecific neighbors suffer less herbivore damage compared to trees in monocultures (Jactel and Brockerhoff 2007, Barbosa et al. 2009, Cook-Patton et al. 2014). However, evidence for associational susceptibility (i.e., increased herbivore damage in diverse mixtures relative to species-poor stands) has also been reported (Schuldt et al. 2010, Schuldt et al. 2015). Several explanations have been proposed to provide a mechanistic understanding of these conflicting diversity–herbivory relationships, including the resource concentration hypothesis (Root 1973), the nutrient balance hypothesis (Westoby 1978), and plant association theory (Barbosa et al. 2009, Ruttan and Lortie 2014).

Much of what we know about diversity–herbivory relationships in forest ecosystems comes from observational studies that are often limited by confounding factors such as environmental and management conditions (Nadrowski et al. 2010). In grassland ecosystems, controlled experiments have yielded valuable data and illuminated often complex plant–herbivore relationships

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(Haddad et al. 2011, Tilman et al. 2012). Until recently, however, experimental manipulations of tree species richness in forests have been rare. The recently established TreeDivNet global network of tree diversity experiments address this knowledge gap by evaluating a range of diversity-ecosystem function relationships in forests, including the assessment of herbivore damage over gradients of tree species richness (Verheyen et al. 2016, Paquette et al. 2018). A recent review of published TreeDivNet studies indicated no emergent pattern of diversity–herbivory relationships in experimental forests (Grossman et al. 2018). However, one shortcoming was that most experimental studies of tree diversity and herbivory investigated insect damage, with only three out of 36 studies investigating vertebrate herbivory, in large part because most tree diversity studies purposely exclude vertebrate herbivores to avoid browsing damage to saplings. This same focus on insect herbivores occurs in the broader tree diversity–herbivory literature (e.g., Jactel and Brockerhoff 2007, Vehviläinen et al. 2007, Castagneyrol et al. 2014, Guyot et al. 2016). Nevertheless, mammalian herbivores are often keystone species with disproportionate impacts on plant community structure and ecosystem function (Côté et al. 2004, Burkepile and Parker 2017, Averill et al. 2017). Indeed, overabundant mammalian herbivores are often cited as a reason for the failure of reforestation efforts (McShea et al. 1997, Hackworth et al. 2018), and potential tree damage and associated management costs (e.g., fencing, culling) are key considerations during the tree species selection and establishment phase in forest plantations. Thus, improved understanding of the impact of tree diversity on herbivory by generalist mammalian herbivores is required for enhancing future forest management.

While networks such as TreeDivNet have allowed for rigorous assessment of diversity-herbivory relationships in mixed stands, to our knowledge, in experimental forests, associational susceptibility of trees to browsing damage by large mammals has only been tested for moose *Alces alces* in relatively species-poor boreal forest stands (Vehviläinen et al. 2007, Milligan and Koricheva 2013). Here, we established a large-scale (13 ha) unfenced forest diversity experiment with 16 common tree species in temperate deciduous forests of eastern North America and analyzed white-tailed deer *Odocoileus virginianus* herbivory damage to 4-yr-old saplings. We tested tree species richness effects on herbivory and sapling height growth at the stand-level (1,200-m^2 plots) and at the local neighborhood spatial scale (19.6-m^2 subplots). Along with altering patterns of herbivory, tree diversity in young plantations can modify light availability, and species shade tolerance is an important trait for predicting the effect of tree diversity on sapling growth (Van de Peer et al. 2018). Therefore, we additionally tested whether tree richness effects on sapling height growth were related to traits associated with shade tolerance.

MATERIALS AND METHODS

Experimental design

We conducted research at the BiodiversiTREE (SERC 2020) tree diversity experiment (Fig. 1), located in Maryland, USA (38°52' N, 76°33' W). BiodiversiTREE was established in spring 2013 on 13 ha of former cropland and is part of the TreeDivNet global network of tree diversity experiments (Ghent University Forest and Nature Lab 2011). The annual mean temperature of the site is 13.2°C; the average annual precipitation is 1,068 mm. In March and April 2013, 255 1-yr-old bare root, dormant seedlings per 16 tree species (total of 17,850 seedlings, Fig. 1) were planted into each of 70 35 × 35 m experimental plots (1,225 m^2). Our pool of 16 native broadleaf tree species represented most of the commonly occurring tree species in local forests based on basal area: *Acer rubrum*, *Carpinus caroliniana*, *Carya glabra*, *Carya tomentosa*, *Cornus florida*, *Fagus grandifolia*, *Fraxinus pennsylvanica*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Platanus occidentalis*, *Quercus alba*, *Quercus pagoda*, *Quercus rubra*, *Quercus velutina*, and *Ulmus americana*. Plants were sourced from a commercial nursery and averaged 0.38 m in height when planted. The experiment employs a classic biodiversity–ecosystem function manipulation, where we planted tree species into either monoculture plots (n = 2 plots per species), 4-species plots (n = 19), or 12-

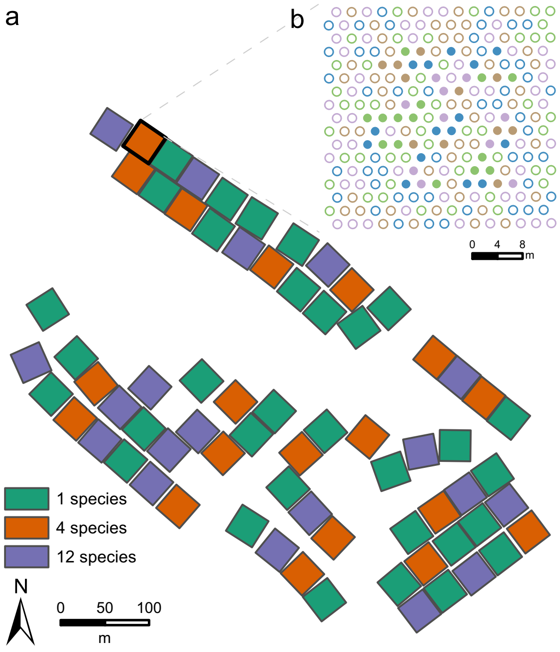

FIG. 1. Experimental design of the BiodiversiTREE forest diversity experiment. (a) Layout of plots, (b) layout of saplings within four-species mixtures (focal trees sampled for deer browsing and height estimates are solid points).

species plots (n = 19). We generated polyculture assemblages semi-randomly, adjusting compositions so that each combination occurred only once, and each species occurred with equivalent frequency across the entire experiment. Thus, differences among treatments are driven by species number and not species composition. Each 4-species polyculture received ~63 individuals per species; the 12-species polycultures received ~21 individuals per species. We randomly assigned the spatial location of each individual and planted them into an equidistant hexagonal grid with 2.4 m between trees (Fig. 1). Overall survival rate of saplings after 4 yr was 80%. The entire experiment has minor slope gradients (4.8° ± 1.93° [mean ± SD], full range = 0.03° to 13.25°), and consistent land-use history (continuously planted with corn *Zea mays* L. for at least the last 35 yr), providing relatively homogenous environmental and soil conditions across the site.

Data collection

In each plot, we randomly selected a subset of focal trees (n = 50 per plot, total n = 3,500) for measurements of deer browsing and growth. When selecting focal trees, we excluded the outer three rows of trees in each plot (7.2 m) to account for edge effects. Unlike many forest and grassland diversity–ecosystem function experiments (Grossman and Cavender-Bares 2019), the perimeter of the site was unfenced allowing access for mammalian herbivores. White-tailed deer were present at an average density of 20 deer/km^2 over the study period (J. D. Parker, *unpublished data*). In September/October 2016, after four growing seasons, we visually assessed sapling browse damage by estimating whether 0%, 1–25%, 26–50%, 51–75%, or 76–100% of branches exhibited evidence of deer browsing. Evidence of deer browsing included leaf removal, bite marks, damage to woody stems, and removal of terminal shoots. Although other mammalian herbivores are present at the study site (rabbits, voles, and groundhogs), white-tailed deer are the principal vertebrate herbivore at the site and their browsing damage is easily differentiated from the angular cuts produced by *Rodentia* species. When collecting deer browse damage estimates, we also collected height data for all living focal saplings, where height equaled the distance from the ground to the highest living apical bud. We focused on height measurements as our growth metric rather than diameter at breast height (DBH) because many saplings had not yet reached breast height. Sapling height increase was calculated as the change in height between planting in spring 2013 and data collection in September/October 2016 (four growing seasons).

To quantify the relationship between diversity effects on sapling height growth and species shade tolerance, we recorded growth-related functional traits of our study species. We selected four functional traits related to growth-strategy and shade tolerance (Haase et al. 2015, Van de Peer et al. 2018); leaf area, leaf thickness, maximum height increase, and shade tolerance. To quantify leaf area, we collected 12 leaves per species (n = 4 per diversity treatments) and recorded surface area using a LICOR LI-3100C Area Meter. Leaf thickness was measured on leaves from the same plants using digital calipers. Maximum height was the greatest recorded height increase for each species in our experiment. Species shade tolerance (intolerant, intermediate, tolerant) was obtained from the PLANTS database (USDA 2015). To compare tree species palatability in our study with known palatability of species throughout their native range, we also obtained qualitative browsing mammal palatability (low, intermediate, high) information from the PLANTS database. Finally, we used hemispherical photography to assess the degree of canopy closure in our plot tree richness treatments. On uniformly overcast days, we recorded two photographs from non-overlapping locations near the center of each plot using an Olympus Stylus TG-4 digital camera (Toyko, Japan) and Bower Pro Digital HD MC fisheye lens (New York, USA). Tripod height was set to 0.7 m and photographs were processed for canopy closure using ImageJ software (National Institutes of Health, Bethesda, Maryland, USA).

Data analysis

Using our ordinal deer damage data, we used a cumulative link mixed model (clmm) within the ordinal R package (Christensen 2015) to test whether deer damage was related to species identity and plot tree species richness (fixed effects), including plot as a random variable (intercept). We also assessed effects of local neighborhood tree species richness on sapling deer browse scores using the same model structure. Local neighborhood tree species richness was defined as the richness of tree species in a circular plot of 2.5 m radius (19.6 m^2) around each focal tree, which incorporated all directly adjacent trees. For each species, we separately tested the effect of diversity (monoculture vs. mixture) on deer herbivory (cumulative link mixed models), again including plot as a random variable in species-specific models.

Next, we tested whether the effect of tree richness on deer herbivory was related to the palatability of co-occurring heterospecifics (i.e., associational effects). We first assigned each species with a relative browse palatability score P, defined as

$$P = \frac{P_i - P_{\overline{x}}}{P_{\overline{x}}}$$

where P_i is the average herbivory damage of species i in monoculture and P_x is the overall average damage score of all species in monocultures. Thus, values above zero indicate that species are consumed more than average, and values below zero indicate that species are consumed less than average. Then, for each species in each mixture plot, we quantified the average palatability of heterospecifics occurring in the same plot. Thus, plots containing highly preferred heterospecifics had high relative palatability, whereas plots with largely avoided heterospecifics had low relative palatability. We compared heterospecific relative palatability scores to the effect of diversity on deer damage for each species in each plot. We predicted that saplings growing in association with less palatable heterospecifics would receive less damage relative to monocultures (i.e., associational resistance), whereas saplings growing with highly palatability heterospecifics would receive more damage (i.e., associational susceptibility). The effect of diversity on deer browsing damage (ES_d) was calculated for each species in each mixture plot as

$$ES_d = \ln(d_{\text{mix}}) - \ln(d_{\text{mono}})$$

where d_{mix} is the mean damage in a mixture plot and d_{mono} is the overall mean damage of that species in monoculture. Positive ES_d values indicate that saplings had more damage in mixtures compared to monocultures, negative values indicate that saplings had less damage in mixtures, with zero values indicating no effect. We used linear mixed effect models (lmer in lme4, R Core Team; Bates et al. 2014) with restricted maximum likelihood (REML) to test whether the palatability of co-occurring heterospecifics predicted the effect of diversity on sapling herbivory ES_d, including species identity and plot as random variables.

To assess diversity effects on height growth, we used mixed-effects linear regression to test whether sapling height increase (log-transformed) was influenced by species identity and tree richness (plot and neighborhood), also including individual deer browse damage scores as a fixed predictor variable. For each species, we separately tested the effect of diversity (monoculture vs. mixture) height growth (mixed-effects linear regressions), again including plot as a random variable in species-specific models.

We used mixed-effects linear regression to test whether the effect of tree richness on sapling height growth (ES_h) was predicted by diversity-mediated patterns of deer browse (ES_d) and individual species functional traits, again including plot as a random variable (intercept). As a relative measure that allows for comparison across species, the effect of diversity on sapling height growth (ES_h) was calculated for each species in each mixture plot as the ln-transformed effect size

$$ES_h = \ln(h_{\text{mix}}) - \ln(h_{\text{mono}})$$

where h_{mix} is the mean height in a mixture plot and h_{mono} is the mean height in monoculture. Positive ES_h values indicate that saplings were taller in mixtures compared to monoculture, negative values indicate that saplings were smaller in mixtures, with zero values indicating no effect. The effect of diversity on deer browsing damage ES_d was calculated for each species in each mixture as previously described. To quantify variation in functional traits among species, we first performed a principal component analysis on our chosen plant functional traits (Appendix S1: Fig. S1, Table S1). Next, to reduce dimensionality of trait variables, we extracted Axis 1 of our PCA and included it as an additional fixed predictor variable in the model. Sixty-five percent of the variance in traits between species was explained by PCA axis 1, which was positively correlated with leaf area, maximum height, and shade tolerance. We additionally modeled the relationship between diversity-growth effects and each of our four functional traits individually using mixed-effects linear regressions. For all mixed models, significance of each variable was tested using likelihood-ratio tests of reduced vs. full models. Finally, differences in canopy closure in tree richness treatments were tested using a Kruskal-Wallis test. All statistical analyses were conducted using R software (version R 3.5.0; R Core Team 2017).

RESULTS

Overall patterns of deer browsing and growth

Deer damage varied widely among species (LR stat = 1272.1, $P < 0.001$, Fig. 2; Appendix S1: Table S2) and generally reflected known palatability of species throughout their native range (Appendix S1: Table S1). *C. caroliniana* (58% ± 2% of branches browsed [mean ± SE]), *A. rubrum* (52% ± 2%), and *U. americana* (49% ± 2%) were highly browsed, whereas *C. tomentosa* (1% ± 0.5%), *P. occidentalis* (1% ± 0.3%), *L. styraciflua* (2% ± 0.6%), and *L. tulipifera* (2% ± 0.5%) were largely ignored (Fig. 2). Similarly, height growth differed markedly between species ($\chi^2 = 1888.4$, $P < 0.001$, Fig. 2; Appendix S1: Table S3). Average height increase after four growing seasons was highest for *P. occidentalis* (4.37 ± 0.12 m), *L. tulipifera* (1.67 ± 0.07 m), and *L. styraciflua* (1.66 ± 0.06 m), and lowest for *C. tomentosa* (0.05 ± 0.03 m), *C. glabra* (0.1 ± 0.04 m), and *U. americana* (0.22 ± 0.03 m). After four growing seasons, saplings exhibiting more extensive deer browsing damage had reduced height growth ($\chi^2 = 30.54$, $P < 0.001$, Fig. 2; Appendix S1: Table S3). For example, the average height increase of saplings with >75% of branches browsed was reduced by 38% relative to saplings with<25% of branches browsed. Fast-growing species such as *P. occidentalis, L. styraciflua*, and *L. tulipifera* received little browse damage, whereas species such as *C. caroliniana*, *U. americana*, and *A. rubrum* had low height increase coupled with a high incidence of deer browse (Fig. 2).

Diversity effects on deer browsing

Deer browse damage on saplings increased with higher plot tree species richness (LR stat = 5.46, $P = 0.019$,

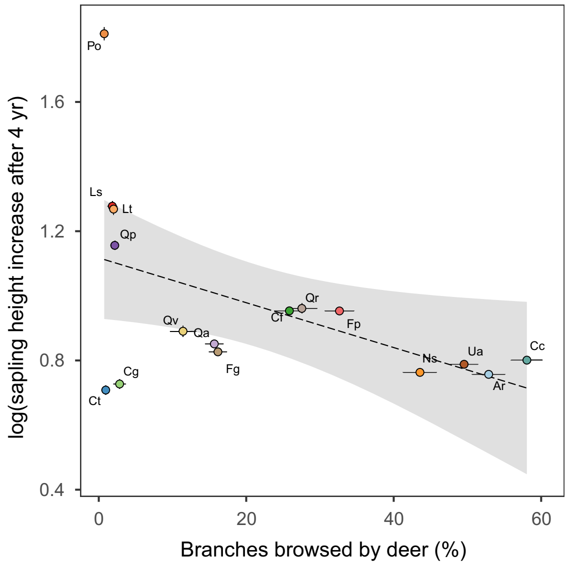

FIG. 2. Relationship between deer browse damage (mean ± SE) and sapling height increase (m; mean ± SE) of our 16 study species across all diversity treatments at the BiodiversiTREE experimental forest. Ar, *Acer rubrum*; Cc, *Carpinus caroliniana*; Cg, *Carya glabra*, 4; Ct, *Carya tomentosa*; Cf, *Cornus florida*; Fg, *Fagus grandifolia*; Fp, *Fraxinus pennsylvanica*; Ls, *Liquidambar styraciflua*; Lt, *Liriodendron tulipifera*; Ns, *Nyssa sylvatica*; Po, *Platanus occidentalis*; Qa, *Quercus alba*; Qp, *Quercus pagoda*; Qr, *Quercus rubra*; Qv, *Quercus velutina*; Ua, *Ulmus americana*.

Fig. 3a; Appendix S1: Table S2). Increasing neighborhood tree richness did not lead to significantly greater browse damage, despite a general trend of more damage in diverse neighborhoods (LR stat = 1.13, $P = 0.287$, Appendix S1: Fig. S2, Table S2). At the species level, 13 out of 16 species had greater deer browse damage in mixtures relative to their monocultures (Fig. 3b). Deer browse damage was significantly greater in mixed plots (i.e., associational susceptibility) for *L. styraciflua* (LR stat = 4.58, $P = 0.032$), *L. tulipifera* (LR stat = 4.22, $P = 0.039$), and *C. glabra* (LR stat = 7.82, $P = 0.005$, Appendix S1: Table S4), whereas no species had significantly less damage in mixtures compared to monocultures (i.e., associational resistance). The effect of diversity on sapling browse damage was not related to the palatability of co-occurring heterospecifics ($\chi^2 = 0.495$, $P = 0.464$, Fig. 4).

Diversity effects on height growth

Overall, height growth did not vary with tree richness at the plot ($\chi^2 = 1.697$, $P = 0.313$, Fig. 5a; Appendix S1: Table S4) or neighborhood ($\chi^2 = 0.263$, $P = 0.608$, Appendix S1: Fig. S3, Table S4) spatial scales. However, slower-growing species generally had similar or increased height growth mixtures compared to monocultures, whereas faster growing species had reduced height growth in mixture plots (Fig. 5b). For instance, *Q. rubra* had significantly reduced height increase in mixtures compared

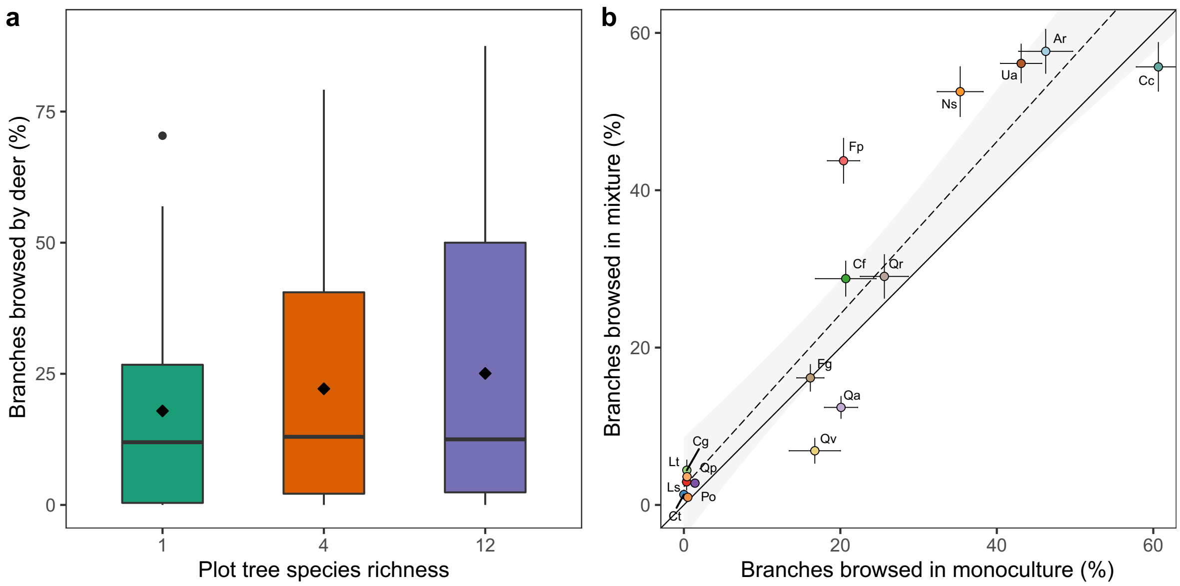

FIG. 3. (a) Average sapling deer browse damage in plots containing 1, 4, or 12 tree species at the BiodiversiTREE experimental forest. Box plots indicate the upper and lower quartiles and vertical lines indicate values within 1.5 times above the interquartile range. Horizontal lines within boxes represent median values and black diamonds indicate group means. (b) Species-level responses (mean ± SE) of deer browsing damage to tree species mixtures. In panel b, values above the solid 1:1 line indicate increased herbivory damage in mixtures relative to monocultures (i.e., associational susceptibility) and values below the 1:1 line indicate reduced damage in mixtures relative to monocultures (i.e., associational resistance). Species identity is indicated by color. Species codes are as described in Fig. 2 caption.

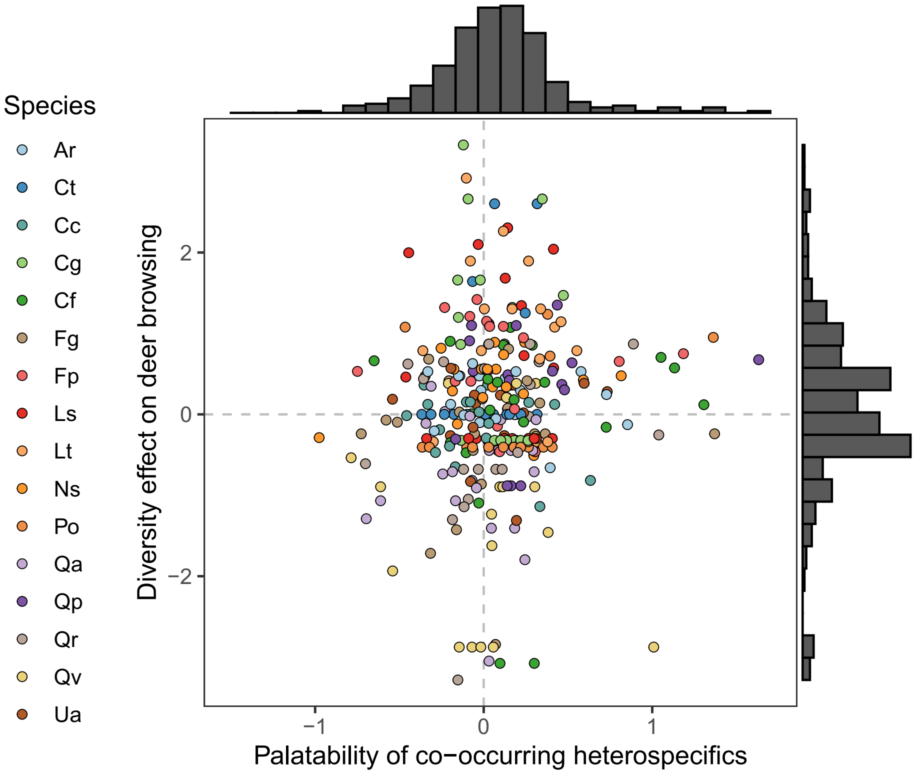

FIG. 4. Relationship between the effect of tree diversity on sapling browse damage and the palatability of co-occurring heterospecifics in mixture plots. For each species in each mixture, diversity effect values represent ln-transformed effect sizes, calculated as the natural log of average sapling browse damage divided by the overall average browse damage of that species in monoculture. Positive diversity effect values indicate that saplings are more susceptible to damage in mixtures compared to monocultures, negative values indicate that saplings are less susceptible in mixtures, with zero values indicating no effect. Species identity is indicated by color. Species codes are as described in the Fig. 2 caption.

to monocultures ($\chi^2 = 4.629$, $P = 0.031$, Fig. 5b; Appendix S1: Table S4).

The effect of diversity on sapling height growth was not related to diversity-mediated deer browsing ($\chi^2 = 2.287$, $P = 0.131$, Fig. 6a; Appendix S1: Table S5). For example, species such as *A. rubrum*, *N. sylvatica*, and *C. tomentosa* had increased height growth in mixtures despite also having increased deer browse damage (Fig. 6a). Instead, diversity effects on height growth were strongly related to species functional traits ($\chi^2 = 55.02$, $P < 0.001$, Fig. 6b; Appendix S1: Table S5). For species with traits indicative of late successional tree species (e.g., slow growth rates, shade tolerance), height increase tended to be greater in mixtures compared to monocultures. In contrast, height growth of species with early successional traits (e.g., fast growth rates, light demanding) tended to be negatively impacted by diversity (Fig. 6b). For example, *P. occidentalis*, *L. tulipifera*, and *L. styraciflua*, all light-demanding species with rapid growth rates, had reduced height growth rates when surrounded by heterospecifics compared to conspecifics. Considered individually, leaf area ($\chi^2 = 63.28$, $P < 0.001$), maximum sapling height growth ($\chi^2 = 82.53$, $P < 0.001$), and shade tolerance ($\chi^2 = 41.01$, $P < 0.001$) were all independently related to the growth response of saplings in mixtures (Appendix S1: Fig. S4). Finally, increasing tree richness increased canopy closure ($\chi^2 = 10.67$, $P = 0.004$, Fig. 7). Average canopy closure increased from 15% ± 5% (mean ± SE) in monocultures to 16% ± 4% in 4-species polycultures and 24% ± 4% in polycultures (Fig. 7).

DISCUSSION

Using data from an early-stage tree restoration experiment, we show that tree species richness has positive or neutral effects on height growth of shade-tolerant species despite increasing herbivory damage by white-tailed deer. Our results support recent evidence suggesting that tree species richness increases sapling damage from ungulate herbivores in young forests (Vehviläinen and Koricheva 2006, Milligan and Koricheva 2013, Muiruri et al. 2015). However, herbivory is only one potential limit on tree growth, and tree diversity can enhance stand growth in other contexts (Fichtner et al. 2018, Jactel et al. 2018). We found that, for slow-growing and shade-tolerant species, the negative impacts of increased deer browsing in mixtures were likely buffered by positive effects of increased canopy closure in mixtures

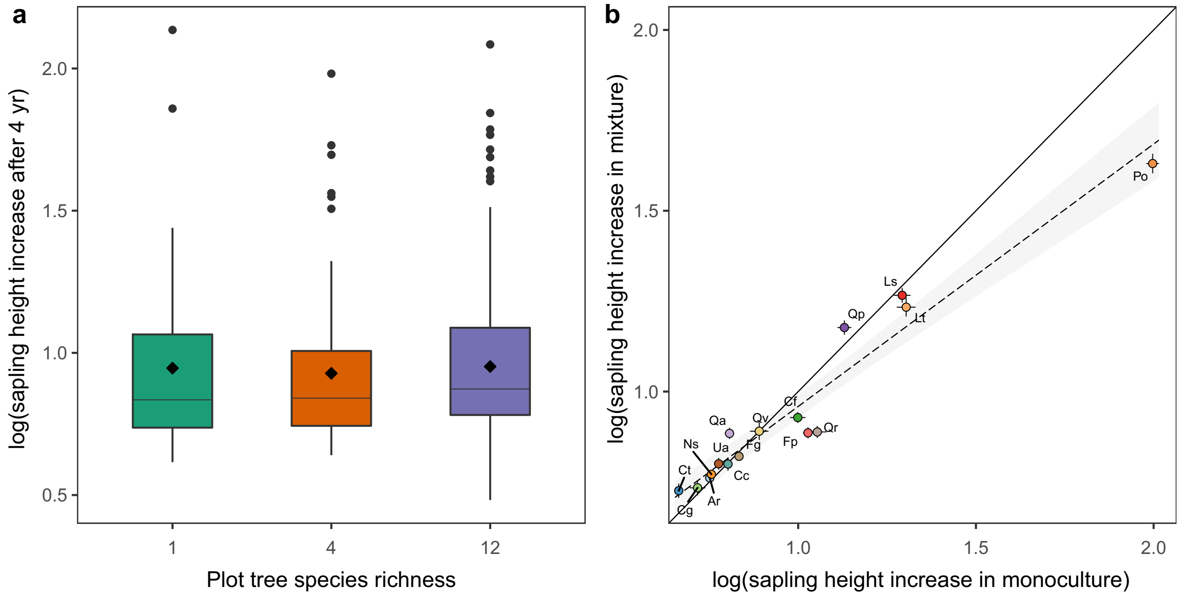

FIG. 5. (a) Average log-transformed sapling height growth increment (measured in m) after 4 yr in plots containing 1, 4, or 12 tree species at the BiodiversiTREE experimental forest. Box plots indicate the upper and lower quartiles and vertical lines indicate values within 1.5 times above the interquartile range. Horizontal lines within boxes represent median values and black diamonds indicate group means. (b) Species-level log-transformed sapling height growth increment (mean ± SE; measured in m) in monoculture and mixed plots. In panel b, values above the solid 1:1 line indicate increased height growth in mixtures relative to monocultures and values below the 1:1 line indicate reduced height growth in mixtures relative to monocultures. Species identity is indicated by color. Species codes are as described in the Fig. 2 caption.

relative to monocultures. Thus, diversity–herbivory relationships need to be integrated with other key ecosystem functions such as biomass and/or productivity.

Tree richness and deer browsing damage

Experimental evidence from boreal forests has indicated that browsing damage by ungulate (moose *Alces alces*) herbivores may be greater in species-rich tree communities compared to monocultures (Vehviläinen and Koricheva 2006, Milligan and Koricheva 2013, Muiruri et al. 2015). Our study in a diverse temperature deciduous forest experiment provides further support for this observation as increased tree richness was associated with greater sapling damage by white-tailed deer. In our study, herbivory by deer was not mediated by palatability of co-occurring heterospecifics. Some of the most preferred species in monocultures, such as *U. americana* and *A. rubrum*, received more damage in mixtures, even when surrounded by less palatable neighbors, indicating that tree richness alone may be a more important driver of deer browse damage compared to the palatability of neighboring trees. The nutrient balance theory (Westoby 1978), or dietary mixing, suggests that diverse plant communities will suffer more damage as herbivores seek to achieve a balanced nutrient intake. For mammalian herbivores, species-rich tree communities can be more nutritionally beneficial compared to single-species or species-poor stands (Westoby 1978). Large-bodied herbivores often switch between forage species because nutritional requirements cannot be met by a single plant species (Westoby 1978). Additionally, foraging on a range of plant species may be a behavioral mechanism to avoid the accumulation of potentially harmful plant secondary metabolites (Foley and Moore2005).

In contrast to findings of associational susceptibility of tree species to mammalian herbivore damage, early assessments of diversity–*insect*-herbivory relationships in forests generally confirmed findings from grassland and crop systems; tree diversity promotes resistance to insect damage to plant tissues (Jactel and Brockerhoff 2007). Differences in diversity effects on vertebrate and insect herbivores may be related to differences in foraging strategies and herbivore specialization. Jactel et al. (2017) for example propose that the likelihood of associational resistance varies along gradients of herbivore selectivity and spatial extent. In our study, although browse damage by deer tended to increase with increasing local neighborhood tree richness, diversity–herbivory effects were more strongly related to plot-level tree richness. Thus, increasing neighborhood diversity could result in reduced herbivory by specialized insect herbivores with smaller range sizes, but increasing stand-level tree diversity may result in increased damage by generalist mammalian herbivores with larger range sizes.

While other studies from young planted forests have also reported associational susceptibility to mammalian herbivory in mixtures (Vehviläinen and Koricheva 2006,

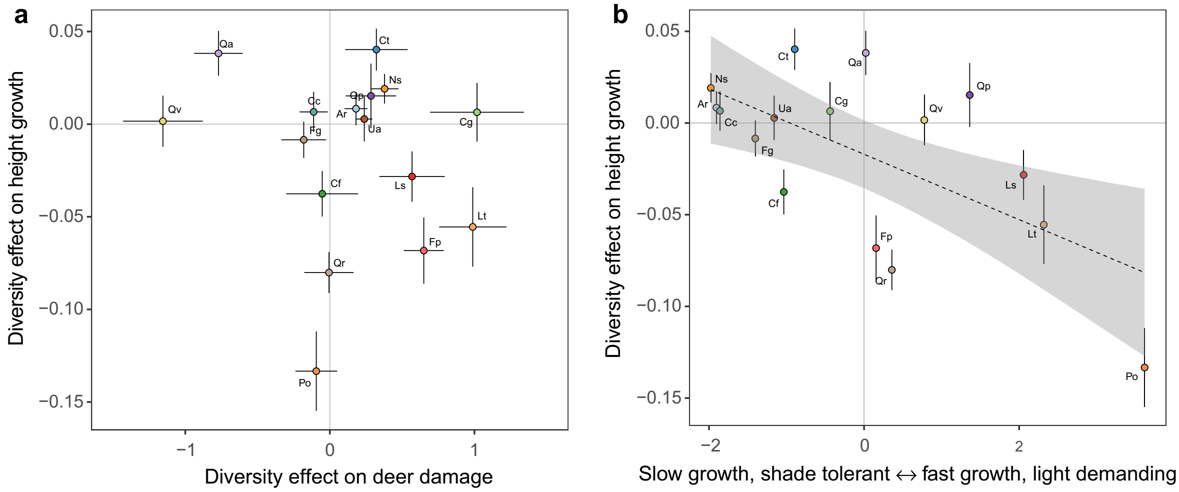

FIG. 6. Relationship between the effect of tree diversity (monoculture vs. mixture) on sapling height growth (mean ± SE) and (a) diversity effects on deer browsing (mean ± SE) and (b) species functional traits. Diversity effects on height growth values represent ln-transformed effect sizes ES$_h$, calculated as the natural log of sapling height growth in mixtures divided by the average herbivory damage in monoculture – ES$_h$ = ln(h_{mix}) − ln(h_{mono}), where h_{mix} is the mean height in a mixture plot and h_{mono} is the mean height in monoculture. Positive ES$_h$ values indicate that saplings were taller in mixtures compared to monoculture, negative values indicate that saplings were smaller in mixtures, with zero values indicating no effect. Similarly, the effect of diversity on deer browsing damage (ES$_d$) was calculated for each species in each mixture as ES$_d$ = ln(d_{mix}) − ln(d_{mono}), where d_{mix} is the mean damage in a mixture plot and d_{mono} is the mean height in monoculture. Positive ES$_d$ values indicate that saplings had more damage in mixtures compared to monocultures, negative values indicate that saplings had less damage in mixtures, with zero values indicating no effect. In panel b, “Slow growth, shade-tolerant↔fast growth, light demanding” represent values from the main axis of a principal component analysis of growth and shade tolerance related functional traits (leaf area, leaf thickness, maximum height, shade tolerance) of our study species, which was extracted to reduce dimensionality of trait variables. Thus, species grouped together share similar growth and shade tolerance related functional traits. Species identity is indicated by color. Species codes are as described in Fig. 2 caption.

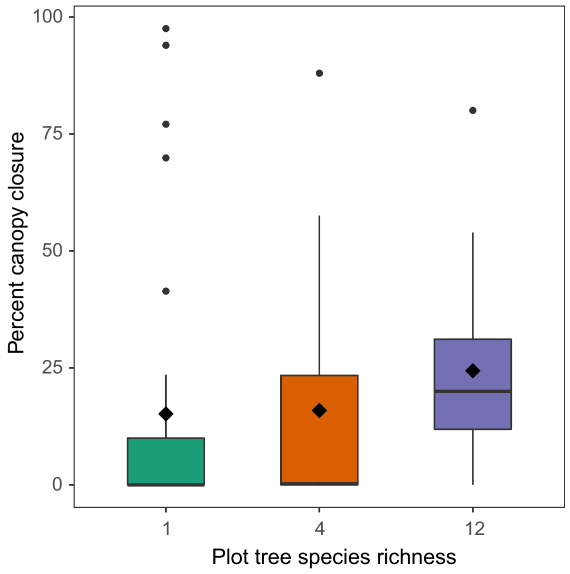

FIG. 7. Changes in percent canopy closure with increasing plot-level tree species richness. Box plots indicate the upper and lower quartiles and vertical lines indicate values within 1.5 times above the interquartile range. Horizontal lines within boxes represent median values and black diamonds indicate group means. In both monocultures and four-species polycultures the median value for canopy closure was 0.

Milligan and Koricheva 2013), some studies from natural forests have linked tree diversity with associational resistance (Cook-Patton et al. 2014). Indeed, Cook-Patton et al. (2014) found that tree mixtures in 1-m^2 plots received less deer browsing damage than single-species plots. Although this study was carried out in the same region using many of the same tree species as our experiment, their study had much lower densities of deer (3–8 individuals/km^2 compared to 20 individuals/km^2 in our study; J. D. Parker, *unpublished data*) and utilized much smaller plots (1-m^2 plots with 15 saplings vs. 1,200-m^2 plots with 255 saplings in BiodiversiTREE) planted into an existing secondary forest with a well-developed overstory (vs. the creation of stands in open habitat in the BiodiversiTREE experiment). Thus, diversity–herbivory relationships are possibly related to local herbivore densities, plot spatial scale, and the landscape context of the study. Furthermore, whether effects of tree richness on mammalian herbivory are consistent across newly restored forests vs. natural forests remains unclear.

Tree richness and sapling height growth

In contrast to recent studies documenting overyielding of tree mixtures in planted forest experiments (Fichtner et al. 2018, Van de Peer et al. 2018), we found no overall increase in sapling height in diverse plots and local neighborhoods relative to single-species plots. Instead, after four growing seasons, the strength and direction of tree richness effects on sapling height were related, to some extent, to diversity-mediated deer browsing, but particularly to species growth and shade tolerance traits. Increased deer damage to fast-growing, light demanding species like *F. pennsylvanica*, *L. tulipifera*, and *L. styraciflua* in mixture plots was associated with reduced height increases. In contrast, despite increased deer browsing damage in mixtures, slow-growing, shade-tolerant species had either comparable or increased height in mixtures relative to monocultures, likely benefitting from the increased canopy closure in diverse plots. Thus, even accounting for associational susceptibility to herbivore damage, increasing diversity may nonetheless still lead to increased growth and productivity via complementarity and selection effects (Loreau and Hector 2001). Numerous studies have now documented positive effects of tree diversity on overall productivity (Liang et al. 2016, Fichtner et al. 2018, Jactel et al. 2018, Huang et al. 2018), suggesting that the impacts of tree diversity on herbivory damage should be viewed in combination with the effects of tree diversity on other key ecosystem functions such as biomass and/or productivity.

Rather than increasing growth in mixed plots due to diversity-related facilitation, early successional species in our study tended to have reduced height increases in diverse plots compared to monocultures. For fast-growing, light demanding species, high *intraspecific* competition for light in monocultures may drive fast rates of stem elongation and mediate height–stem-diameter relationships (Van de Peer et al. 2017). For these same species, less intense *interspecific* competition for light in mixtures may lead to differing allometry, with saplings potentially allocating resources to stem diameter increases rather than height (Setiawan et al. 2017). Given the young stage of the experiment, we focused on sapling height increase rather than DBH as a proxy for growth. While this allows us to evaluate diversity effects on stem elongation, future measurements of other facets of sapling growth, such as stem diameter increases, may reveal more information regarding diversity–productivity relationships.

CONCLUSIONS

Experimental forests are often fenced to exclude large mammalian herbivores that may cause widespread mortality of saplings during the initial establishment phase. While management strategies such as fencing may ensure acceptable survival rates, they may obscure potentially important diversity–herbivory relationships that could guide global reforestation efforts. Our study demonstrates that increasing tree species richness in young plantation forests does not necessarily enhance resistance to damage by herbivores, and that consideration of multiple factors including tree species selection and knowledge of the principal types of herbivores is required for effective management. If for example, generalist mammalian herbivores are known to cause major losses and limit establishment, intimate mixtures may in fact lead to greater overall stand damage and management such as fencing may be required. Fencing, however, may not be practicable or financially feasible in large-scale reforestation efforts, such as those proposed in the Bonn Challenge (Molin et al. 2018). Castagneyrol et al. (2014) propose that mixing phylogenetically distant species, such as broadleaved and coniferous species, promotes associational resistance, although this remains to be experimentally tested for mammals. In our study, all 16 tree species were native broadleaves, and deer showed clear preferences among species, but all species received at least some level of herbivory. It remains unclear whether the associational susceptibility reported in our study would persist if mixtures incorporated more phylogenetically distant and highly unpalatable conifers. Moreover, despite associational susceptibility to herbivore damage, increasing diversity may nonetheless still led to increased productivity via complementarity effects associated with shade tolerance (Loreau and Hector 2001). More broadly, by facilitating shade-tolerant and late successional species, tree diversity may enhance ecosystem multifunctionality in early-stage plantation forests. For example, when compared to species-poor tree communities, species-rich forests are known to enhance a range of forest ecosystem services (Gamfeldt et al. 2013). Thus, by promoting growth of tree species with a range of life-history strategies (i.e., early, intermediate, and late successional species), increased tree richness in young planted forests may help regulate decomposition rates, pathogen damage, disturbance resistance, and animal diversity across multiple trophic levels (Van Der Plas et al. 2016). In light of the growing contribution of restorations and plantations to the global forest resource, such multifunctionality in planted forests is key to meeting sustainability targets.

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Devaney, J. D. Parker, J. Pullen, S. Cook-Patton, and K. Burghardt led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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