**Title:** Nuisance species compromise the carbon sequestration potential in an Eastern US temperate deciduous forest

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# Abstract

Temperate deciduous forests play a critical role in the global carbon (C) cycle, accounting for a substantial portion of the global forest C sink. The dominant view imbued in Earth System Models is that, at least within the eastern United States, the biome is likely to remain a C sink throughout the 21st century. However, these models do not incorporate nuisance species – *i.e.*, species whose local abundance has increased as a result of human activities and that are causing ecological harm. Nuisance species are known to increase tree mortality (*e.g.*, non-endemic pests and pathogens) and decrease recruitment (*e.g.*, deer and non-endemic plants) throughout the temperate deciduous biome, yet the net effect on current and future C cycling is unknown. Here, we use 15 years of detailed census data from a large (25.6 ha) forest dynamics plot in a Mid-Atlantic temperate forest, including a 4-ha deer exclosure, to understand how nuisance species are affecting C cycling. We show increased biomass mortality, a net reduction in aboveground C storage, and decreased abundance of canopy tree species in the understory. Under current trends this forest will continue to lose C sequestration capacity, indicating that the C sequestration of temperate deciduous forests is likely overestimated.

**Keywords**:

# 1 Introduction

The temperate forest biome plays a critical role in the global carbon cycle, accounting for almost half of the net global forest carbon (C) sink (Harris *et al.*, 2021), with deciduous forests representing a substantial portion of this, sequestering >300 Tg C yr-1 (Pugh *et al.*, 2019). Although currently a C sink, the future of the biome remains uncertain. The dominant view imbued in Earth System Models is that, at least within the eastern US, the biome is likely to remain a C sink for the remainder of the 21st century (Finzi *et al.*, 2020; Wu *et al.*, 2023), albeit with declining CO2 sequestration capacity (Ahlström *et al.*, 2012). Yet, global C models predict a wide range of future trajectories of CO2 sequestration (Ahlström *et al.*, 2012; Arora *et al.*, 2020), and current global C models do not represent some influential mechanisms (e.g., Fatichi *et al.*, 2014; Clark *et al.*, 2021). One mechanism that is not represented in global C models is the impact of nuisance species – i.e., endemic or non-endemic species that, as a result of human influence, have much greater abundance in an ecosystem than they did historically, resulting in undesirable ecological consequences (**refs?**). Similarly, the impact of nuisance species on forest carbon budgets is not considered in machine learning/niche models that seek to project future forest distribution and carbon stocks (**?** Wu *et al.*, 2023), nor in carbon offset projects (**???** **refs?**). This is problematic in that nuisance species – including non-endemic insect pests and pathogens, non-endemic plants, and over-abundant herbivores – are dramatically impacting carbon cycling in temperate deciduous forests around the world, as described below.

## 1.1 (paragraph on tree mortality from non-endemic pests and pathogens)

Non-endemic pests and pathogens have been important driver of mortality (Anderson-Teixeira *et al.*, 2021). These can reduce C and need to be considered in future climate change projections.

Fei *et al.* (2019)

Non-endemic pests and pathogens facilitate invasin of non-endemic plants (Guo *et al.*, 2023 and refs therein).

## 1.2 (paragraph on recruitment failure because of deer and non-endemic plants)

* white-tailed deer (*Odocoileus virginianus* ) is important endemic nuisance species, over-abundant because of human influence

McGarvey *et al.* (2013) Holm *et al.* (2013) Knauer *et al.* (2023)

The capacity to regenerate following disturbances, including ongoing gap formation through mortality of canopy trees, critically influences long-term forest dynamics. Regeneration depends first upon seed production and then upon seedling recruitment, survival, and growth into trees. When any one of these steps fails, the stage is set for disturbance to push forest ecosystems over a tipping point, whereby there is little chance that a forest will recover to it’s pre-disturbance state in the foreseeable future (**refs?**). Global change pressures can set the stage for such critical transitions by gradually shifting baseline conditions, making post-disturbance recovery unlikely despite the persistence of mature trees (Anderson-Teixeira *et al.*, 2013; McDowell *et al.*, 2020; **refs?**). In the mid-Atlantic region of eastern North America, forests face a severe “regeneration debt”, meaning that there are insufficient juveniles of current canopy tree species to replace the mature cohort when they eventually die (Miller & McGill, 2019; Miller *et al.*, 2023). Low juvenile abundance in the region is driven by a combination of over-abundant deer, competition with non-endemic species, and possibly climate change (Russell *et al.*, 2017; Miller & McGill, 2019; Gorchov *et al.*, 2021; Miller *et al.*, 2023). Deer are the biggest problem (Gorchov *et al.*, 2021). The juveniles that are present tend to represent a different, more mesophytic set of species (*Acer spp.*, *Fagus grandifolia*) than currently dominate much of the region (*Quercus spp.*, *Carya spp.*, Miller & McGill (2019); Nowacki & Abrams (2015)]–a dynamic driven by fire suppression and mesophication (**refs?**).

Here, we use 15 years of detailed census data from a large forest dynamics plot including a 4-ha deer exclosure to test the following hypotheses: (1) C stocks have declined (-∆AGB) (2) canopy tree mortality and associated biomass loss are increasing, in large part due to non-endemic nuisance species (pests & pathogens) (3) recruitment (outside deer exclosure) and growth have not kept pace with tree mortality, implying that future mortality will result in substantial net biomass loss (regeneration debt)

# 2 Materials and Methods

## 2.1 Study site

*(describe location, forest type, etc)*

In addition to our consideration of the plot as a whole, we give special consideration to three portions of the plot, all upland forest (i.e., excluding low-lying areas around streams): (1) low deer, low non-endemic insects & pathogens (Fig. 1a)- 4 ha portion of upland forest in the SE quarter of the plot, fenced in YEAR and maintained with only occasional deer presence for the past ## years and with relatively low abundance of canopy species affected by non-endemic pests and pathogens; (2) high deer, low non-endemic insects & pathogens (Fig. 1b) - # ha of upland forest outside the deer exclosure with relatively low abundance of canopy species affected by non-endemic pests and pathogens; (3) high deer, high non-endemic insects & pathogens (Fig. 1c) - a # ha section of upland forest outside the deer exclosure with relatively high abundance of canopy species affected by non-endemic pests and pathogens. These areas were delineated as follows. Upland forest was defined according to topographic wetness index, originally calculated for the SCBI plot in McGregor *et al.* (2021). Vulnerability to non-endemic insects & pathogens was defined based on the abundance of canopy species affected by non-endemic pests and pathogens at the time of plot establishment (2008).



**Figure 1. Photos within the SCBI ForestGEO plot: (a) low deer, low non-endemic insects & pathogens, (b) high deer, low non-endemic insects & pathogens, (c) high deer, high non-endemic insects & pathogens**  *(add a map of the plot)* All photos taken September 2023 by K. Anderson-Teixeira.

## 2.2 Data collection

*(describe main census & years occurred)*

*(describe mortality census)*

*(describe invasive plants survey)*

*(describe seedlings survey, if used)*

## 2.3 Analyses

apply the metric of Miller *et al.* (2023) to determine imminent failure/ probable failure/ insecure/ secure?

# 3 Results

# 4 Discussion

Holtmann *et al.* (2021)

# 5 Conclusions (optional)

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# Conflict of Interest statement

The authors declare no conflict of interest.

# Authors’ contributions

*[Name of author 1] and [Name of author 2] conceived the ideas and designed methodology; [Name of author 1] and [Name of author 3] collected the data; [Name of author 2] and [Name of author 4] analysed the data; [Name of author 1] and [Name of author 4] led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.*

# References

**Ahlström A, Schurgers G, Arneth A, Smith B**. **2012**. [Robustness and uncertainty in terrestrial ecosystem carbon response to CMIP5 climate change projections](https://doi.org/10.1088/1748-9326/7/4/044008). *Environmental Research Letters* **7**: 044008.

**Anderson-Teixeira KJ, Herrmann V, Cass WB, Williams AB, Paull SJ, Gonzalez-Akre EB, Helcoski R, Tepley AJ, Bourg NA, Cosma CT, *et al.*** **2021**. [Long-Term Impacts of Invasive Insects and Pathogens on Composition, Biomass, and Diversity of Forests in Virginia’s Blue Ridge Mountains](https://doi.org/10.1007/s10021-020-00503-w). *Ecosystems* **24**: 89–105.

**Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH**. **2013**. [Altered dynamics of forest recovery under a changing climate](https://doi.org/10.1111/gcb.12194). *Global Change Biology* **19**: 2001–2021.

**Arora VK, Katavouta A, Williams RG, Jones CD, Brovkin V, Friedlingstein P, Schwinger J, Bopp L, Boucher O, Cadule P, *et al.*** **2020**. [Carbon concentration and carbon climate feedbacks in CMIP6 models and their comparison to CMIP5 models](https://doi.org/10.5194/bg-17-4173-2020). *Biogeosciences* **17**: 4173–4222.

**Clark JS, Andrus R, Aubry-Kientz M, Bergeron Y, Bogdziewicz M, Bragg DC, Brockway D, Cleavitt NL, Cohen S, Courbaud B, *et al.*** **2021**. [Continent-wide tree fecundity driven by indirect climate effects](https://doi.org/10.1038/s41467-020-20836-3). *Nature Communications* **12**: 1242.

**Fatichi S, Leuzinger S, Körner C**. **2014**. [Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling](https://www.jstor.org/stable/newphytologist.201.4.1086). *The New Phytologist* **201**: 1086–1095.

**Fei S, Morin RS, Oswalt CM, Liebhold AM**. **2019**. [Biomass losses resulting from insect and disease invasions in US forests](https://doi.org/10.1073/pnas.1820601116). *Proceedings of the National Academy of Sciences*: 201820601.

**Finzi AC, Giasson M-A, Plotkin AAB, Aber JD, Boose ER, Davidson EA, Dietze MC, Ellison AM, Frey SD, Goldman E, *et al.*** **2020**. [Carbon budget of the Harvard Forest Long-Term Ecological Research site: Pattern, process, and response to global change](https://doi.org/10.1002/ecm.1423). *Ecological Monographs* **90**: e01423.

**Gorchov DL, Blossey B, Averill KM, Dávalos A, Heberling JM, Jenkins MA, Kalisz S, McShea WJ, Morrison JA, Nuzzo V, *et al.*** **2021**. [Differential and interacting impacts of invasive plants and white-tailed deer in eastern U.S. forests](https://doi.org/10.1007/s10530-021-02551-2). *Biological Invasions* **23**: 2711–2727.

**Guo Q, Potter KM, Ren H, Zhang P**. **2023**. [Impacts of Exotic Pests on Forest Ecosystems: An Update](https://doi.org/10.3390/f14030605). *Forests* **14**: 605.

**Harris NL, Gibbs DA, Baccini A, Birdsey RA, Bruin S de, Farina M, Fatoyinbo L, Hansen MC, Herold M, Houghton RA, *et al.*** **2021**. [Global maps of twenty-first century forest carbon fluxes](https://doi.org/10.1038/s41558-020-00976-6). *Nature Climate Change*: 1–7.

**Holm JA, Thompson JR, McShea WJ, Bourg NA**. **2013**. [Interactive effects of chronic deer browsing and canopy gap disturbance on forest successional dynamics](https://doi.org/10.1890/ES13-00223.1). *Ecosphere* **4**: 1–23.

**Holtmann A, Huth A, Pohl F, Rebmann C, Fischer R**. **2021**. [Carbon Sequestration in Mixed Deciduous Forests: The Influence of Tree Size and Species Composition Derived from Model Experiments](https://doi.org/10.3390/f12060726). *Forests* **12**: 726.

**Knauer A, Betras T, Royo AA, Diggins TP, Carson WP**. **2023**. [Understory plant communities fail to recover species diversity after excluding deer for nearly 20 years](https://doi.org/10.1139/cjfr-2022-0234). *Canadian Journal of Forest Research* **53**: 379–390.

**McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, *et al.*** **2020**. [Pervasive shifts in forest dynamics in a changing world](https://doi.org/10.1126/science.aaz9463). *Science* **368**.

**McGarvey JC, Bourg NA, Thompson JR, McShea WJ, Shen X**. **2013**. [Effects of Twenty Years of Deer Exclusion on Woody Vegetation at Three Life-History Stages in a Mid-Atlantic Temperate Deciduous Forest](https://doi.org/10.1656/045.020.0301). *Northeastern Naturalist* **20**: 451–468.

**McGregor IR, Helcoski R, Kunert N, Tepley AJ, Gonzalez-Akre EB, Herrmann V, Zailaa J, Stovall AEL, Bourg NA, McShea WJ, *et al.*** **2021**. [Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest](https://doi.org/10.1111/nph.16996). *New Phytologist* **231**: 601–616.

**Miller KM, McGill BJ**. **2019**. [Compounding human stressors cause major regeneration debt in over half of eastern US forests](https://doi.org/10.1111/1365-2664.13375). *Journal of Applied Ecology* **56**: 1355–1366.

**Miller KM, Perles SJ, Schmit JP, Matthews ER, Weed AS, Comiskey JA, Marshall MR, Nelson P, Fisichelli NA**. **2023**. [Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks](https://doi.org/10.1002/eap.2837). *Ecological Applications* **33**: e2837.

**Nowacki GJ, Abrams MD**. **2015**. [Is climate an important driver of post-European vegetation change in the Eastern United States?](https://doi.org/10.1111/gcb.12663) *Global Change Biology* **21**: 314–334.

**Pugh TAM, Lindeskog M, Smith B, Poulter B, Arneth A, Haverd V, Calle L**. **2019**. [Role of forest regrowth in global carbon sink dynamics](https://doi.org/10.1073/pnas.1810512116). *Proceedings of the National Academy of Sciences* **116**: 4382–4387.

**Russell MB, Woodall CW, Potter KM, Walters BF, Domke GM, Oswalt CM**. **2017**. [Interactions between white-tailed deer density and the composition of forest understories in the northern United States](https://doi.org/10.1016/j.foreco.2016.10.038). *Forest Ecology and Management* **384**: 26–33.

**Wu C, Coffield SR, Goulden ML, Randerson JT, Trugman AT, Anderegg WRL**. **2023**. [Uncertainty in US forest carbon storage potential due to climate risks](https://doi.org/10.1038/s41561-023-01166-7). *Nature Geoscience*: 1–8.

# Data availability