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Linked disturbance in the temperate forest: Earthworms, deer, and canopy gaps

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Abstract:

Despite the large body of theory concerning multiple disturbances, there have been relatively few attempts to test the theoretical assumptions of how and if disturbances interact. Of particular importance is whether disturbance events are linked, as this can influence the probability and intensity of ecological change. Disturbances are linked when one disturbance event increases or decreases the likelihood or extent of another. To this end, we used two long-term, multi-disturbance experiments in northern Wisconsin to determine whether earthworm invasion is linked to canopy gap creation and white-tailed deer browsing. These three disturbances are common and influential within North American temperate forests, making any interactions among them particularly important to understand. We expected both deer and canopy gaps to favor invasive earthworms, particularly species that live close to or on the soil surface. However, we found only partial support of our hypotheses, as both deer exclosures and canopy gaps decreased earthworms in each experiment. Further, earthworm density increased the most over time in areas far from the gap center and in areas with deer present. Deer exclosures primarily decreased *Aporrectodea* and *Lumbricus* species, while gaps decreased *Dendrobaena* and *Lumbricus* species. Our findings show that earthworm invasion is linked to deer presence and gap creating disturbances, which provides new insight towards multiple disturbance theory, aboveground-belowground dynamics, and temperate forest management.

Keywords: aboveground-belowground interactions, canopy gaps, invasive earthworms, linked disturbance, temperate forest, ungulates, white-tailed deer

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Introduction:

Our understanding of terrestrial disturbances is largely derived from researching individual phenomena (Turner 2010). Although single disturbance events can significantly impact ecosystems, their intensity may be dependent on the presence of other disturbances on the landscape (Foster et al. 2016; Johnstone et al. 2016). Disturbance events can be linked and increase or decrease the likelihood, intensity, or spatial extent of another (Buma 2015), such as blowdowns increasing wildfire intensity (Cannon et al. 2017). These linked disturbances can then compound, allowing an ecosystem little time for recovery between events and potentially sending it on a new developmental trajectory (Paine et al. 1998; Burton et al. 2020). As climate change increases disturbance frequency and duration, these interactions are expected to become more prevalent and influential in socio-ecological systems (Dale et al. 2001).

However, despite a well-established theoretical understanding of multiple disturbances and their potential consequences, there has been insufficient effort devoted to testing disturbance interactions relative to the effects of individual events (Graham et al. 2021). To this end, North American temperate forests are a relevant system to investigate disturbance interactions, given their ecological and functional importance (Landuyt et al. 2019). Three influential temperate forest disturbances are canopy gaps from treefall, white-tailed deer (*Odocoileus virginianus*) browsing, and European earthworm invasions (Frelich 2002; Bohlen et al. 2004b; Hanberry & Faison 2023). Each disturbance has unique and relatively well-understood individual effects on vegetation, but their long-term influence on one another is largely unknown, leaving a gap in our understanding of how common disturbances interact (Côté et al. 2004; Bohlen et al. 2004b; Muscolo et al. 2014).

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Canopy gaps can be created by windstorms, diseases, or tree harvest and often spur plant growth by increasing light availability in the understory. Gaps can also alter understory microenvironments, favoring certain plant species depending on location within or around the gap (Kern et al. 2013; VanderMolen et al. 2021). Canopy gap induced understory plant growth can then attract deer and increase browse pressure (Forrester et al. 2014). Over time, high browsing can transform the understory community of herbs and saplings, eventually leading to changes in succession and forest structure (Royo & Carson 2006; Royo & Carson 2022). Deer also indirectly change forest soil properties (Rooney & Waller 2001; Sabo et al. 2017), which can affect soil-dwelling fauna like earthworms.

Earthworms have long been recognized for their ability to transform soils (Darwin 1881). When introduced to formerly glaciated and earthworm-free landscapes in the Midwest U.S. earthworms function as a disturbance, causing significant losses in native plant biodiversity through soil mixing, consumption of seeds and litter, and alteration of soil chemical characteristics (Hale et al. 2006; Frelich et al. 2019). Earthworm impacts depend on the genera in question, as certain species occupy different soil niche spaces and can serve as an indicator of how an ecosystem is changing (Bottinelli et al. 2020). *Dendrobaena* species occupy the litter layer and do not impact soil or plant species (Hale et al. 2005b). *Aporrectodea* species occupy the first 15 cm of soil, are sensitive to soil chemical alterations, and can cause long-lasting changes in soil microbial communities (Bart et al. 2019), while *Lumbricus* species occupy multiple soil niche-spaces and can change soil faunal communities, nutrient levels, and seed communities (Cassin & Kotanen 2016).

There is limited and variable evidence regarding linkages among canopy gaps, deer, and invasive earthworms, despite each of their respective influences on the forest. Some studies link

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increased earthworm populations to deer presence, but this phenomenon has only been found in a handful of locations in the eastern United States (Davalos et al. 2015c; Cope & Burns 2019; Mahon & Crist 2019). Some hypothesize that deer create favorable soil environments for earthworms through increased soil heterogeneity from trampling or greater nutrient availability from deer waste (Davalos et al. 2015c; Cope & Burns 2019). Others have found no relationship between deer and earthworms (Shelton et al. 2014; Dobson & Blossey 2015). Thus, no conclusions can be made regarding this disturbance link's potential mechanisms or generalizability. Research on connections between canopy gaps and invasive earthworms is even more limited. Nachtergale et al. (2002) found that single-tree gaps decrease earthworm biomass through post-harvest soil disturbance, whereas Ganault et al. (2021) found that more open canopies may favor earthworms through abiotic factors.

To investigate whether influential temperate disturbances are linked, we tested how earthworm invasion is influenced by canopy gaps and deer in two long-term experiments in northern Wisconsin, USA. These experiments are unique in their factorial manipulation of dozens of large (>20-m) canopy gaps and deer exclosures over a decade and across a wide spatial scale. Since earthworms were already established at each experimental site, we could assess earthworm community variation across individual and combined gap creation and deer exclusion treatments. One site was surveyed for earthworms prior to experimental treatments, providing a baseline for us to test if earthworm density varied with disturbance treatments over 13 years. We hypothesized that increased earthworm biomass and density would be linked with deer presence and canopy gaps (H1 & H2) and that both disturbances would synergistically increase the biomass and density of all earthworm species (H3). In this scenario, increased vegetative biomass under a canopy gap would increase the number of deer, which would then

concomitantly increase earthworm populations through more favorable soil environments. Deer and canopy gaps likely affect the upper layers of soil, therefore we also expected earthworm species that reside on or near the surface to be particularly influenced by these disturbances.

Methods:

Site Description

This study used two long-term experiments in Wisconsin, USA. The first experiment is the Managed Old Growth Silviculture Study (MOSS), which was established in 2007 and has three, ≈200 ha replicate sites located in the Northern Highlands American Legion State Forest (NH), the Flambeau River State Forest (FL), and the Chequamegon-Nicolet National Forest's Argonne Experimental Forest (AR) (Figure 1). The second experiment, 'The Flambeau Experiment' (FE), was established in 2006 and is in the northern portion of the Flambeau River State Forest (Figure 1). Stands at each site are representative of a maturing Great Lakes northern hardwood forest and are dominated by even-aged, second-growth sugar maple (*Acer saccharum*) with subdominant assemblages of intermediate shade-tolerant species such as white ash *(Fraxinus americana*), yellow birch (*Betula alleghaniensis*), and red oak (*Quercus rubra*) (Forrester et al. 2014; Fassnacht & Steele 2016). Soils differed among sites, with both Flambeau locations having silt loam over sandy loam soil, AR having sandy loam with high stone proportion, and NH having sandy loam soil over stratified outwash sand (Fassnacht et al. 2013). All sites in this study were separated by a maximum of 140 km across roughly the same latitude, with mean temperatures of ≈4.2° C and mean precipitation of ≈88.6 cm (Climate Normals 2006–2020; NOAA NCEI - Station USC00475516).

Managed Old Growth Silviculture Study (MOSS) – The MOSS experiment has several harvest-created canopy gap treatments across the three replicate sites that were established in the

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winter of 2007 and 2008 (for further detail regarding establishment see Fassnacht et al. 2013). We used the "Large Gaps" treatment, which consists of 16, 24-m diameter canopy gaps within a 48-ha stand at each site. One canopy gap could not be found at AR, leading to a total gap count of 47 across the three sites. Each gap contains a deer exclosure in one of four locations along a north-south gradient: the north transitional edge, the northern gap, the center gap, or the south transitional edge (Figure 1). All exclosures were established in summer 2007. Each fence is 5.25 x 5.25m wide and 1.5m tall, except for the north gap locations, which are longer (3.75 x 7.5m) to capture potential plant variation in this location of the canopy opening. Hereafter we also refer to exclosure treatments as "fenced" or "unfenced," with the latter signifying deer presence.

We sampled earthworms in August and September of 2019 in MOSS. In sites with a gap overhead, we placed one circular earthworm plot (0.07 m^2) in the center of exclosures and a paired earthworm plot 4.5 m away from the western or eastern edge of fencing (n = 47; Figure 1). We sampled inside and outside of 19 fences without a gap overhead across the three site's controls (AR [n=4]; FL [n = 4]; NH [n=11]). Prior to sampling, all litter in a plot was collected and searched for earthworms. Soil moisture and temperature were measured adjacent to the plot. We then poured a liquid mustard solution on the soil (40 g of powdered mustard to 3.8 L of water) and collected all earthworms that rose to the surface over 15 minutes (Hale et al. 2006). All earthworms associated with a single gap and exclosure were collected on the same day. Each earthworm that emerged from the soil was placed in 70% isopropyl alcohol for preservation. Isopropyl alcohol was replaced every three weeks for two months until earthworms were preserved. One earthworm sample within the control sites was lost due to the test tube cracking. Each earthworm was identified to species or genus and measured lengthwise. These lengths were input into Hale et al. (2004)'s allometric equations to estimate ash-free dry biomass (afdb).

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The Flambeau Experiment – The Flambeau Experiment (FE) is another long-term study that tests how forest structure influences fine-scale vegetation and soil processes (Forrester et al. 2012). The FE has 35, 80 x 80 m plots with seven fully replicated treatments. We used the canopy gap (n =5) and fenced canopy gap (n = 5) treatment's 22-m diameter gaps, which is similar to the gap sizes in the MOSS experiment (Figure 1). Gaps were established in January 2007. Each gap is surrounded by an uncut transitional edge that is the same radius as the gap itself (11-m) and an additional 5-m wide buffer area, which we used as a control. The fenced canopy gap plots are surrounded by an 80 x 80 m deer exclosure (2.1-m tall), which were established in fall 2007.

We sampled earthworms prior to gap and fencing treatments in late spring 2006, then sampled earthworms again 13 years after treatment in the fall of 2019. Earthworms were sampled along a north-south transect across each 22-m canopy gap, from the north buffer to the south transitional edge (Figure 1; n = 5 at each gap location). The 2019 earthworm sampling locations were approximately where earthworms were sampled in 2006. The only difference between sampling periods is that the 2019 north gap location was 1.5 m north of the 2006 north gap location. Earthworms were extracted, measured, and identified using the same methodologies as the MOSS experiment. Weather conditions between spring 2006 and fall 2019 were also consistent, with neither period experiencing drought, which reduces earthworm biomass (US Drought Monitor; Hale et al. 2006).

Statistical Methods

Across both MOSS and FE, earthworm biomass and density were used as the primary response variables in our study. Similar to Hale et al. (2005b) and Davalos et al. (2015c), species were binned according to the most common genera - *Dendrobaena*, *Aporrectodea*, and

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Lumbricus. Earthworms were grouped according to genera rather than functional group due to the current debate concerning this categorization framework (Chang et al. 2016; Bottinelli et al. 2020). Several *Dendrodrilus rubidus* specimens were found and binned with *Dendrobaena*, as both species are very similar in size and feeding patterns (Hale et al. 2005b). The genus *Octolasion* was present at some sites, but we did not have the statistical power to test if this genus varied with disturbance treatments. We also tested whether earthworm communities in 2019 varied with treatment using the 'adonis2' and 'betadisp' functions in the vegan package (Oksanen et al. 2022).

In MOSS, total earthworm biomass, total *Lumbricus* biomass, and total *Dendrobaena* biomass were either cube or square root transformed to meet the assumptions of a linear mixed effects model in the 'lme4' package (Bates et al. 2015). Our fixed effects were deer exclosures, gap presence, and their interaction. Our random effects structure for all MOSS models was location within a gap nested within gap number nested within site. Soil moisture and soil temperature were initially incorporated into models, but each of these variables had little influence on earthworm biomass and density. *Aporrectodea* biomass was analyzed using generalized linear mixed effects models (GLMM) in the 'glmmTMB' R package with a tweedie error distribution, which allows for zero-inflated, continuous data (glmmTMB; Brooks et al. 2017). Total and genera-specific earthworm densities were also tested using a GLMM with either a Poisson or negative binomial error distribution using the same model structure as above.

For FE, we scaled 2006 and 2019 earthworm densities to a 1-m^2 area. The differences in earthworm density between 2006 and 2019 were then tested using GLMMs with year, gap location, and their interaction as fixed effects, or with year, fencing, and their interaction as fixed effects. Our random effects were gap location nested within plot number. Earthworm metrics

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from 2019 were tested as a function of deer exclosure, location within a gap, and their interaction, with plot number as a random effect. Significance within mixed effects models was tested with Type III ANOVA with a Kenward-Roger degrees of freedom adjustment and significance within generalized linear mixed effects models was tested using a Type III Wald Chi-Square test. All corresponding model assumptions were met and tested using the 'DHARMa' package (Hartig 2017). The 'emmeans' package was then used for pairwise analysis with a Bonferroni adjustment (Lenth et al. 2022). We report proportional differences between treatments based on untransformed means, but median values also showed similar patterns with disturbance treatment. We also report data to meet several minimum descriptive standards set by Buma (2021) to simplify integration into disturbance ecology related meta-analyses.

Results:

For this experiment we collected, measured, and identified nearly 2000 European earthworms. Population biomass and density varied by site, with the FE having the greatest earthworm biomass and density, followed by AR, then NH, and finally FL (Table 1). Species densities varied among sites, but all species aggregate biomass rankings were consistent among sites. *Lumbricus* had the highest biomass, followed by *Aporrectodea*, and then *Dendrobaena*. However, earthworm communities did not vary with disturbance treatments in either experiment (Appendix S1: Section S1 & S2). Between MOSS and FE, we found that deer and canopy gaps both influence earthworm density and biomass. Deer presence led to increased earthworm biomass and density, whereas canopy gaps led to decreased earthworm biomass and density.

Managed Old Growth Silviculture Study (MOSS)

Within MOSS, mean earthworm biomass was 21% lower in the fenced treatments ($F_{1,63}$ = 5.5, p = 0.02; Figure 2), while mean earthworm biomass was 62% lower under a canopy gap than

under a closed canopy ($F_{1,61.3}$ = 9.4, p = 0.003; Figure 2; Appendix S2: Section S1). Earthworm density had a similar trend with mean density being 17% lower inside of fencing (χ^2 = 4.6, df = 1, p = 0.03) and 8% lower under canopy gaps (χ^2 = 0.33, df =1, p = 0.56; Appendix S2: Section S2). No significant interactions were found between fencing and canopy gap presence, nor did earthworm biomass and density vary by location within the gap.

Each earthworm genus followed a similar response pattern to fencing and gap treatments, although certain genera were more strongly influenced by disturbance treatments than others (Figure 3; Appendix S2: Section S2 & S3). In fenced treatments, *Aporrectodea* mean biomass and density were 25% and 8% lower respectively (χ^2 = 4.2, df = 1, p = 0.04; χ^2 = 4.1, df = 1, p = 0.04), but canopy gaps had little influence on *Aporrectodea* biomass (χ^2 = 0.13, df =1, p = 0.71). Fencing and canopy gaps had an interactive effect on *Aporrectodea* density (χ^2 = 3.7, df =1, p = 0.05); Mean earthworm density was lower inside of fencing under a closed canopy (t = -2.0, df = 122, p = 0.04). Deer also influenced *Lumbricus* species, with fenced treatments leading to a 23% and 16% decrease in mean *Lumbricus* biomass and density respectively ($F_{1,63}$ = 6.0, p = 0.02; χ^2 = 2.1, df = 1, p = 0.15). Canopy gaps decreased mean *Lumbricus* biomass and density by 77% and 25% respectively ($F_{1,61.6}$ = 7.9, p = 0.006; χ^2 = 4.8, p = 0.03). Finally, deer fencing had no impact on *Dendrobaena* biomass or density, but gaps decreased mean *Dendrobaena* biomass by 33% ($F_{1,61.2}$ = 4.8, p = 0.03).

Flambeau Experiment

At FE, there was a significant interaction between the fencing treatment and year of sampling (χ^2 = 26, df =1, p < 0.0001); Therefore, the change in earthworm density in the fenced versus unfenced areas in 2019 from prior to initiation of fencing (in 2006) were different. Mean earthworm density strongly increased outside of fencing by 69% from pre-treatment conditions (*t*

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= -16.4, df = 88, $p < 0.0001$), while increasing by only 9% inside fencing (t = -7.79, df = 88, $p <$ 0.0001; Figure 4a). During this 13-year period, mean earthworm density increased the most under a closed canopy in the north buffer location (+62%; t = -14.6, df = 66, $p < 0.0001$), followed by the north transitional edge (+37%, t = -9.9, df = 64, $p < 0.0001$), then the south transitional edge location (+24%, t = -6.8, df = 64%, $p < 0.0001$), but stayed the same in the north gap location (t = -0.6, df = 64, p = 0.55; Figure 4b; Appendix S2: Section S5). In 2019, mean earthworm density and biomass were 22% and 24% lower in fenced treatments than unfenced treatments respectively (χ^2 = 10.6, df = 1, p = 0.001; $F_{1,8}$ = 1.9, p = 0.21; Appendix S2: Section S6). In 2019 we also found an interaction between fencing and gap location (χ^2 = 11.5, df = 4, p = 0.02), where mean earthworm density was 57% lower in the center of fenced gaps than the center of unfenced gaps (t = -3.3, df = 39, p = 0.002; Appendix S2: Section S7). In 2019, deer and canopy gaps in FE influenced earthworm species' density more than biomass. Mean *Aporrectodea* and *Lumbricus* density decreased by 30% and 23% respectively in fenced treatments (χ^2 = 4.0, df = 1, p = 0.05; χ^2 = 9.3, df = 1, p = 0.002; Appendix S2: Section S8). There was an interactive effect between gap location and exclosure on mean *Lumbricus* density (χ^2 = 15.0, df = 4, p = 0.005), which was lowest in the fenced center of a canopy gap compared to other gap locations (t = -3.0, df = 39, p = 0.004). *Lumbricus* mean density decreased by 65% respectively from the center of unfenced to fenced gaps. *Dendrobaena* did not respond to disturbance treatments.

Discussion:

Our results support the idea that common and influential disturbance events can be linked to one another, shedding new light on disturbance dynamics in temperate forests. Using northern Wisconsin's forests as a study system, we found that fencing out white-tailed deer and creating

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canopy gaps decreased earthworm biomass and density (Figure 5). These patterns were maintained across two separate experiments that differed in spatial scales, with FE exclosures being 230 times larger than MOSS exclosures. The consistency of our results highlights the potential ubiquity of earthworm invasion being linked to deer and canopy gaps in temperate deciduous forest landscapes. Given each disturbance's power to shape the function, composition, and structure of a stand, the links we found have important implications for contemporary forest ecology and management.

H1: Deer increase invasive earthworms

Although most research concerning ungulate herbivores relates to their strong influence on vegetation (Côté et al. 2004), increasing focus is being placed on indirect effects of ungulates on invertebrate communities (Bernes et al. 2018) and soil properties (Ohira et al. 2022). Our finding that deer can increase earthworm populations aligns with several studies throughout the eastern United States (Davalos et al. 2015c; Cope & Burns 2019; Mahon & Crist 2019) and provides a deeper understanding of the relationship between deer and invasive earthworms. In particular, we found that ambient deer populations lead to greater earthworm densities over time (in comparison to fenced treatments) and that certain earthworm genera are more likely to be influenced by deer.

Our finding that earthworm densities increased the most over time outside of fencing and increased slightly inside of fencing differs from both Davalos et al. (2015c) and Mahon and Crist (2019), who found that earthworm density generally decreases inside of fencing with time. These differences among studies could be due to the timing of earthworm invasion (i.e. how long after initial invasion that earthworms were sampled). In addition, Davalos et al. (2015c) found lower *Aporrectodea* density with fencing treatments but were unsure of whether this was due to

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confounding effects. Our study supports this result and points to several potential mechanisms that have not been adequately tested when evaluating deer and earthworm linkages. Since Aporrectodea are particularly influenced by deer in our study and receive most of their nutrients from the soil, the mechanism driving increased earthworm biomass and density with deer presence could be due to altered soil properties. One potential mechanism is that deer are indirectly increasing belowground microbial biomass as plants reallocate nutrients to their roots to compensate for losses in foliar tissue (Bardgett & Wardle 2003; A'Bear et al. 2014). Increased soil microbial biomass would then favor a microbe-feeding group like *Aporrectodea*. The second potential mechanism is that deer reduce the density and diversity of plants aboveground, which then reduces soil nutrient uptake outside of exclosures, thereby favoring increased earthworm biomass and density (Bardgett & Wardle 2003). The third and fourth potential mechanisms are that deer are directly increasing earthworm populations by transporting earthworm cocoons with their hooves or by increasing soil nitrogen through fecal and urinary inputs, although deer-mediated increases in nitrogen would likely be heterogeneous and operate at scales of 1-20 m (Murray et al. 2013). Since direct aboveground and belowground relationships between trophic levels are rare, the first two indirect mechanisms seem most likely (Bardgett & Wardle 2003).

The management and ecological implications of deer increasing invasive earthworms may be substantial, as deer and earthworms both function as a disturbance and an ecological engineer (Fisichelli et al. 2013; Hanberry & Faison 2023). Individually, overabundant deer and earthworms reduce forest biodiversity and structure (Frelich et al. 2019; Reed et al. 2022). However, these linked disturbances may have a compounding effect on ecosystem nutrients and vegetation, leading to understory dominance of ruderal species and altered successional trajectories (Powers & Nagel 2009). In a recent study showing how combined deer and

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earthworms can change ecosystems, Mahon et al. 2020 found that deer increased earthworm populations, which then increased leaf litter decomposition rates and changed soil nutrient dynamics. However, more research is needed on the combined effects of earthworms and deer, considering their many indirect effects on ecosystems (Rooney & Waller 2003; Frelich et al. 2019).

H2: Canopy gaps decrease invasive earthworms

Our initial hypothesis that gaps increase invasive earthworms was not supported, as canopy gaps decreased earthworm biomass and density. This is likely due to closed canopies having nutrient-rich tree leaf litter, which serves as shelter and food for earthworms (Mathieu et al. 2010). Further, our finding that *Lumbricus* and *Dendrobaena* population biomass increased under a closed canopy points to leaf litter quality as a driving force in determining earthworm populations (Suárez et al. 2006). Additionally, a lack of recent soil disturbances in the closed canopy treatments may favor earthworms (Nachtergale et al. 2002).

Earthworm densities also differed among specific gap locations. Over time, earthworm densities increased the most in locations further from the gap center and the least underneath an open canopy. There are several potential reasons gap location may cause earthworm densities to vary. Canopy gap edges may have more deer browsing pressure and preferable abiotic soil conditions, which would then increase the number of earthworms (Burton et al. 2021). It is also possible that differences in earthworm density are caused by earthworms slowly migrating outwards from gap centers and into the surrounding forest, as Hale et al. (2005) showed that earthworms can move several meters per year in the right conditions. However, since the total number of earthworm cocoons is far greater than the total number of earthworms at any given time (Butt 1992; Fernández et al. 2010), it is more likely that environmental conditions under a

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canopy gap are influencing the rates of mortality and recruitment of hatchlings rather than leading to mass-migration of earthworms. Reductions in hatchling success would then lead to differential earthworm biomass and density in certain areas over time. In addition, Aporrectodea species have been shown to burrow downwards with adverse environmental conditions (Perreault & Whalen 2006; Nuutinen & Butt 2009), which would likely reduce their movement laterally into the forest. Therefore, we believe that these gap and fence treatments are primarily influencing the population growth of earthworms rather than their dispersal. Assuming that canopy gaps decrease earthworm populations, our results suggest that efforts to increase canopy complexity towards old-growth structure may have benefits that extend beyond increased plant biodiversity and could slow earthworm invasion. Nevertheless, how canopy gaps and increasing canopy complexity effects earthworm migration and reproduction requires more research.

H3: Connections among canopy gaps, deer, and invasive earthworms

Earthworm biomass and density are likely a product of net interactions between canopy gaps and deer, wherein gaps decrease earthworms and deer increase earthworms (Figure 5). Our interpretation of results is benefitted by considering these disturbances through a "press-pulse" lens. Many studies on disturbance linkages are focused on combinations of high-severity, short-duration pulse events, such as fire and blowdowns (Cannon et al. 2017, Jentsch and White 2019). Although these pulse-pulse disturbance interactions can quickly and dramatically change landscapes, their influence can hinge on the severity of existing press disturbances (Bergstrom et al. 2021). A press disturbance, such as species invasion or deer browse, operates continuously on a system from year to year and is not temporally confined (Lake 2000). Our work suggests that press disturbances can be linked with other press or pulse disturbances, which can have particularly long-lasting effects on ecosystem structure and function (Ratajczak et al. 2017).

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Our study shows that the intensity and extent of one press (earthworm invasion) can be linked to another press disturbance (deer herbivory). This implies that disturbances can also potentially be "unlinked" and indirectly controlled to maintain ecological structure and function. Similar to targeting climate-mediated positive feedback loops, by identifying and breaking the links between influential disturbances we may be able to slow ecosystem degradation. This strategy may be particularly important when trying to control influential press disturbances that seem impossible to manage, such as invasive earthworms. In temperate forests, deer can be a dominant press disturbance that are seemingly linked to the extent and intensity of other disturbances across a wide spatial scale. By reducing deer populations or fencing out deer from target areas, by proxy we may be able to better control "unmanageable" disturbances such as invasive earthworms over the long term. In places where deer management is culturally sensitive or not preferred (Cambronne 2013), canopy gap creation through group selection harvesting may be a more feasible way to take advantage of disturbance links and slow earthworm invasion. Thus, by identifying and targeting a suite of linked press and pulse disturbances, we may be able to make or break links to control certain undesirable disturbances, save management time and effort, and discover new connections within disturbance ecology.

Future Research & Conclusions

Our work provides evidence of links between canopy gaps, deer, and invasive earthworms, but future research should explicitly address the mechanisms behind these disturbance links, such as changes in soil nutrients, microbial biomass, or litter quality. By identifying how aboveground disturbances are linked to belowground disturbance we will gain a deeper understanding of ecosystem function, biodiversity, and restoration (A'Bear et al. 2014). Researchers should also evaluate if deer and canopy gaps can influence other important soil-

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dwelling fauna, such as *Amynthas* species, a group of earthworms that are likely to be a highly damaging wave of disturbance that many temperate forests will face (Chang et al. 2021). Lastly, future work should test whether deer concentrate at gap edges and if this microsite preference facilitates an increase in invasive earthworms.

Our work highlights the importance of linked disturbances and our limited knowledge regarding how a belowground disturbance may be connected to aboveground disturbances. Deer, canopy gaps, and invasive earthworms are likely to become more frequent with a changing climate, which would make their linkages more important to understand in order to conserve soil communities and ecosystem processes (Park et al. 2014; Fisichelli & Miller 2018). Therefore, our understanding of disturbance theory will be incomplete without greater effort to understand disturbance's linked nature and its potential influence on forest ecology and management. To this end, reduced deer populations and strategic tree harvesting could be a means to take advantage of disturbance links and slow earthworm invasion.

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Conflicts of Interest:

The authors declare no conflicts of interest.

Author Contributions:

All authors contributed to project design, development, and editing. SPR and LMP did field work. SPR did lab work, analyses, and writing.

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Table 1: Genera-specific mean earthworm density and biomass by experimental site

Site	Mean Earthworm Density (# / m^2)				Mean Earthworm Ash-Free Dry Biomass (g / m^2)			
	Aporrectodea	***Dendrobaena***	***Lumbricus***	**Total**	***Aporrectodea***	***Dendrobaena***	***Lumbricus***	**Total**
AR (MOSS)	47.0	85.7	80.1	212.8	2.1	0.4	3.2	5.7
FL (MOSS)	8.6	25.7	27.5	61.8	0.1	0.1	1.1	1.3
NH (MOSS)	29.7	51.1	44.2	125.0	0.7	0.2	1.9	2.7
The FE	50.9	29.7	112.0	192.9	2.0	0.2	3.9	6.1

Abbreviations: AR = Argonne Experimental Forest; FL = Flambeau River State Forest; NH = Northern Highlands American Legion State Forest; MOSS = Managed Old Growth Silviculture Study; The FE = The Flambeau Experiment

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FIGURE CAPTIONS:

Fig. 1 Map of N. Wisconsin, USA with depictions of canopy gap and earthworm sampling design. Gold stars represent the MOSS experiment, where earthworms were sampled inside and outside of small fences underneath a canopy gap (n=47). The green star represents the Flambeau Experiment, where earthworms were sampled along a north-south transect across a fenced (n=5) or unfenced gap (n=5) in both 2006 and 2019. Sampling points along this transect extended from the north buffer (25-m from gap center), to the north transitional edge (16-m from gap center), to the north gap (7-m from gap center), to the gap center, to the south transitional edge (16-m from gap center). Map adapted from Fassnacht et al. 2013.

Fig. 2: Earthworm biomass decrease with deer fencingand decreased with gap creation, while earthworm density decreased with fencing but was not influenced by gaps (Appendix S2: Section S1). Diamonds are means, while bold horizontal lines are medians.

Fig. 3: Larger earthworm genera were influenced by deer fencing and gap creation. *Aporrectodea* and *Lumbricus* biomass decreased inside of fencing, while *Lumbricus* biomass decreased with gap creation (Appendix S2: Section S2). All genera follow a pattern of lower biomass inside of fencing and decreased biomass under a canopy gap. Photos by Samuel Reed.

Fig. 4: A) From pre-treatment (2006) to 13 years post-treatment (2019), earthworm density increased by 69% in unfenced treatments, while earthworms only increased by 9% in fenced treatments (Appendix S2: Section S7). **B)** Earthworm density also increased the most over 13 years in the north buffer location (+62%) (Appendix S2: Section S8). These results indicate that deer and closed canopies favor earthworm populations.

Fig. 5: Diagram showing how earthworms are linked to disturbance treatments in our study: **A)** Deer presence under a closed canopy leads to the highest earthworm biomass and density **B)** Fencing out deer decreases earthworm biomass and density; **C)** Gap creation substantially decreases earthworm biomass and density; **D)** Deer presence and canopy gaps cause the lowest earthworm biomass and density. Created with BioRender.

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Figure 1

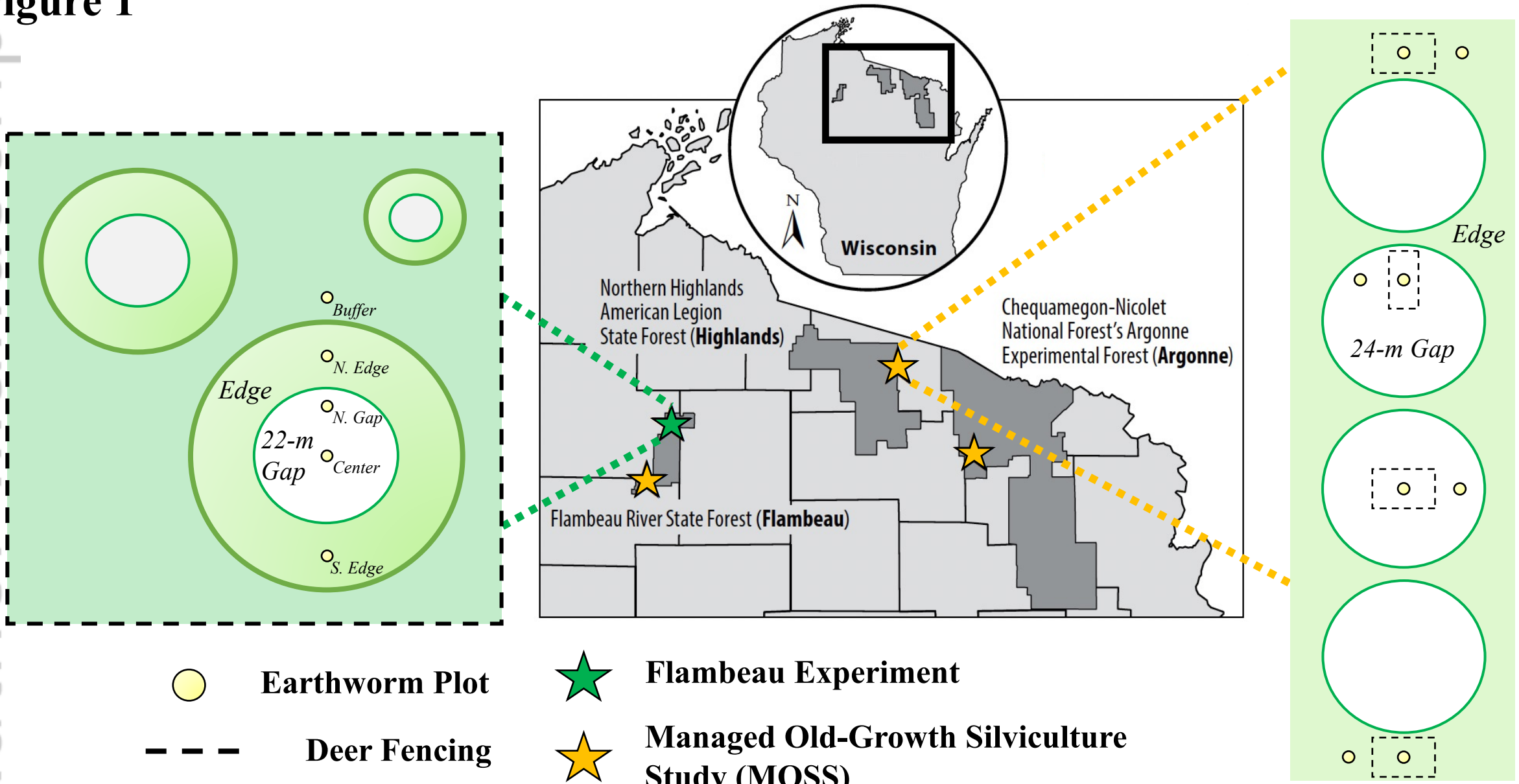

Figure 2

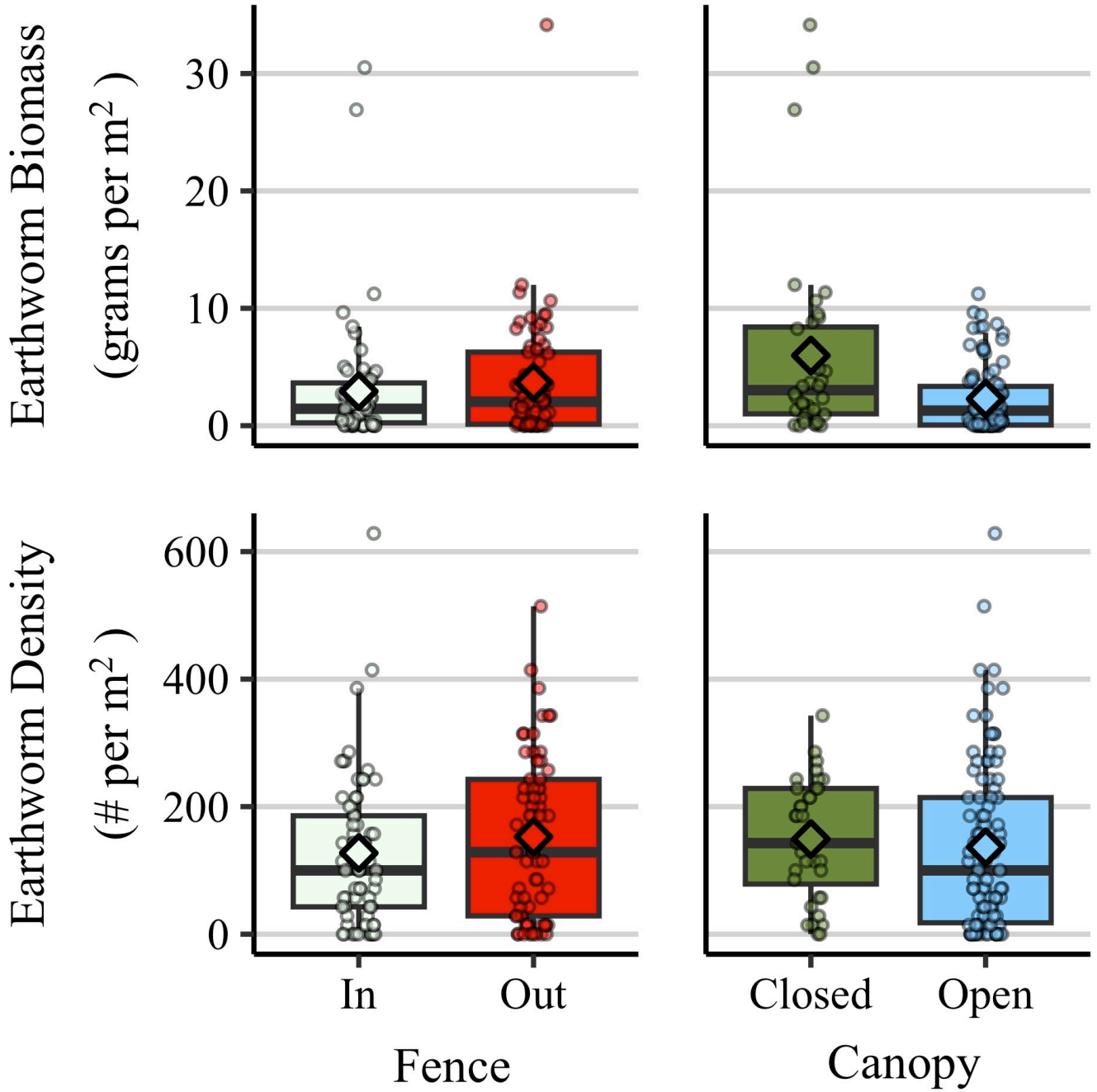

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Figure 3

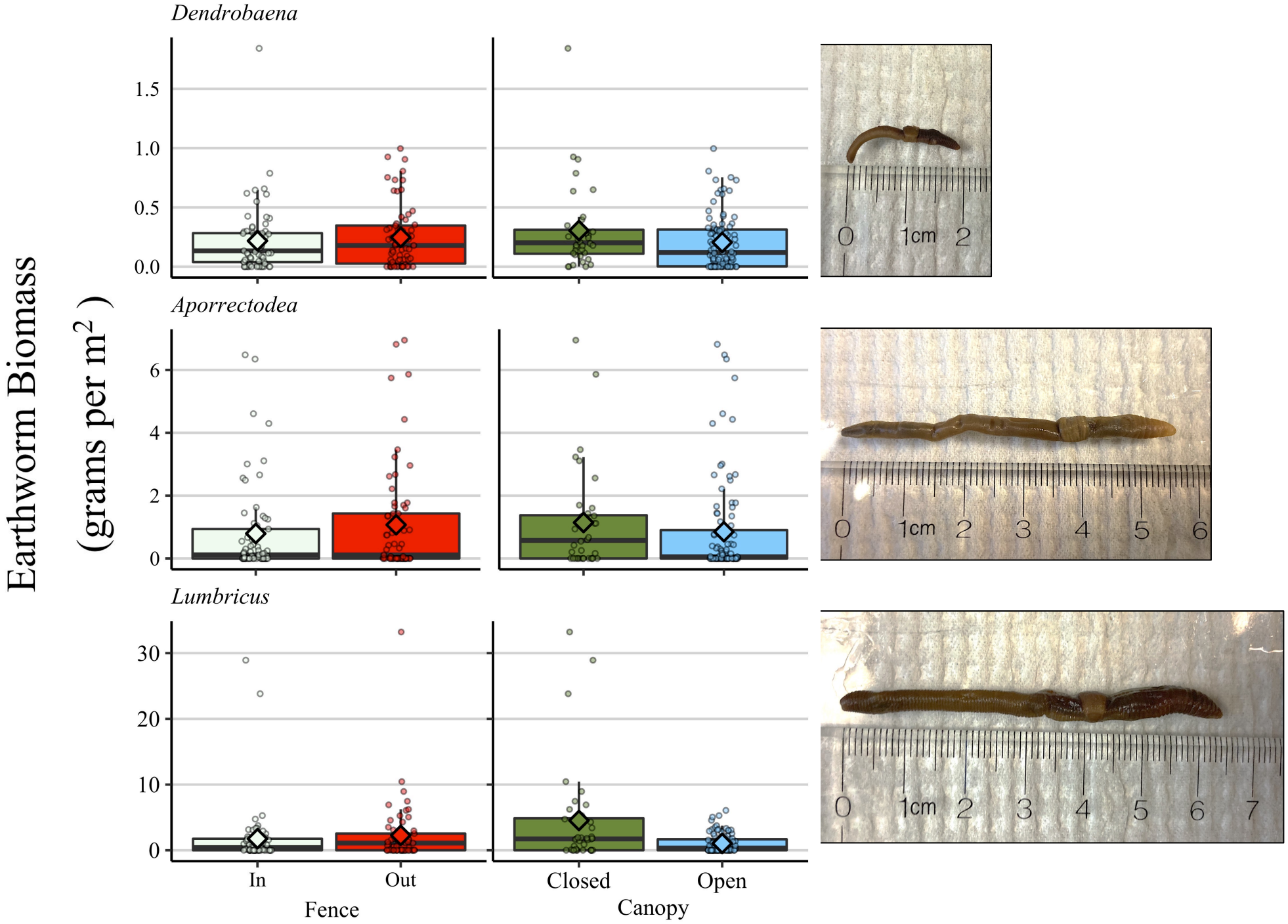
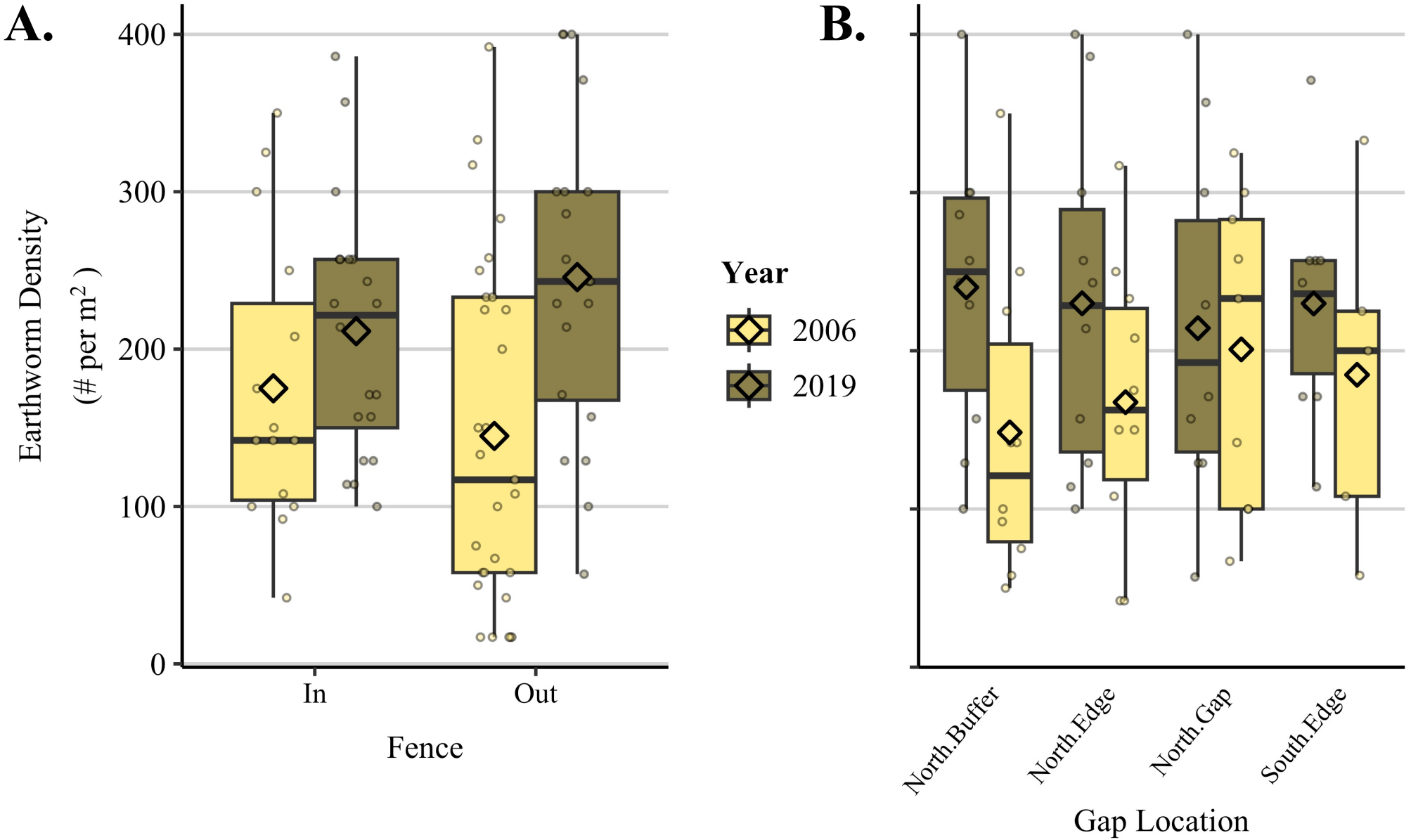


Figure 4



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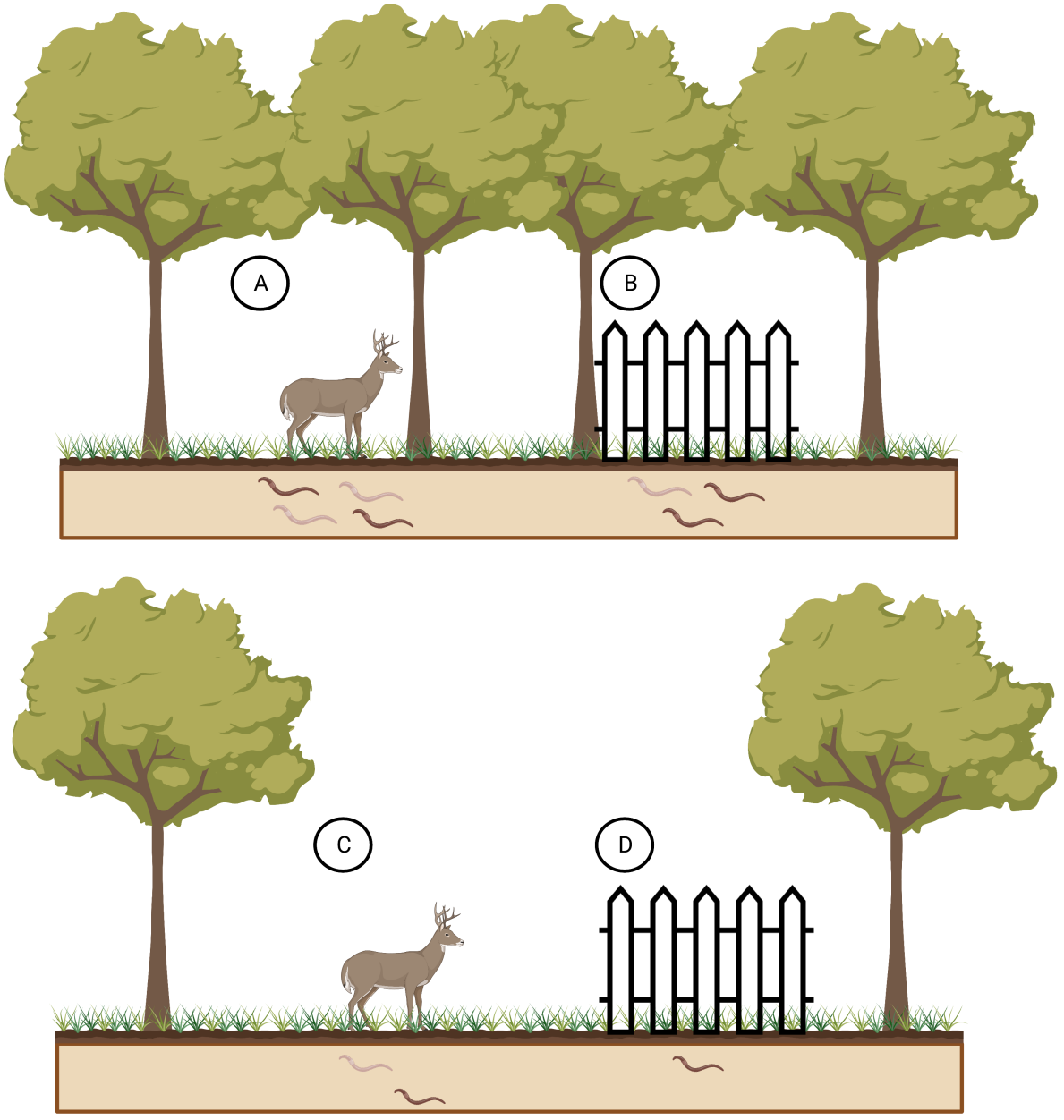
Figure 5