

The Role of Flooded Soils on Tree Recruitment in Eastern Temperate Forests

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Abstract:

As a result of current climate change, flooding events are becoming more frequent and lasting longer, resulting in temporal floods in areas that have not historically experienced this disturbance. One critical aspect of forest dynamics that could be significantly impacted by increasing flooding is tree species recruitment. While adult trees may be able to survive temporary flooding, establishing seedlings with shallow root systems may not. A single flooding event could jeopardize decades of recruitment if seedlings are unable to survive the anaerobic conditions imposed by higher water levels. Despite the potential impact of flooding on forest dynamics, there is little information on seedling recruitment patterns after exposure to flooding.

To understand how flooding conditions could possibly be impacting forest recruitment, we conducted a field observational study across seven temperate forests. We gathered data on seedling abundance and diversity in areas with signs of recent flooding, as well as in nearby control (dry) areas. After controlling for the proximity of seed sources, our findings revealed a significant disparity between control and flooded plots in terms of seedling numbers and diversity, with control plots consistently exhibiting higher seedling abundance and species diversity. Decreases in seedling abundance ranged from 66% to 88%. This trend was consistent across most forests, except one with a historical prevalence of flooding. Species diversity was higher in control plots, with one or two species more. When comparing between native and invasive species, native seedlings tended to be more abundant in dry versus flooded plots, while invasive seedlings exhibited similar abundance under both conditions. These results document the adverse effects flooding conditions have on temperate forest recruitment dynamics, providing insights into how tree recruitment might be impacted by shifts in flooding patterns.

1. Introduction:

Climate change is predicted to drive changes in forest composition across ecosystems via both gradual and abrupt changes in growing conditions (Smith and Lazo 2001, Morin et al. 2018, Albrich et al. 2020). In particular, extreme events, such as heat waves, droughts, and flooding, may lead to rapid shifts in forest structure and composition (Weed et al. 2013, Fei et al. 2017), mostly acting via impacts in recruitment (Grubb 1977, Connell and Green 2000). One understudied extreme event that is likely to increase with global warming is flooding (Chappell 2006, Margrove et al. 2015, Rogger et al. 2017). Localized increases in flooding frequency and intensity have been broadly predicted across the globe (Kundzewicz et al. 2014, Hirabayashi et al. 2013), potentially creating a novel ecological filter at the recruitment stages. Due to their extensive root systems, adult trees may be able to survive the anaerobic conditions of the upper soil layers during the flood; however, seedlings with much shorter roots may not (Glenz et al. 2006; Fig. 1). Despite its potential impact, the effect of these flooding events is rarely accounted for when predicting future forest communities.

Models predicting future weather patterns indicate extreme precipitation events will increase, both in frequency and magnitude (Meresa et al. 2022). As a result, areas that historically did not undergo flooding as part of their natural disturbance regime may now experience it (Wang et al., 2023). This could lead to unadapted forest communities having to endure flooding conditions on a regular basis. Nevertheless, there is little information on how forests will respond to these shifts in the hydrological regime (Xu et al. 2018), even if flooding events can significantly impact forest dynamics if the recruitment layer is affected (Kozłowski 2002, Guilherme et al 2004, Myster 2007).

Individuals are most vulnerable to the impacts of flooding at the seedling stage since they do not have the physiological and morphological adaptations to withstand inundated conditions (Glenz et al., 2006, Da Silva et al. 2023). For example, due to the temporary lack of oxygen, flooding can detrimentally impact seedlings' height, stem diameter, and total biomass, altering leaf nitrogen content, photosynthetic rate, and even stomatal conductance (Martínez-Alcántara et al. 2012, Kreuzwieser and Rennenberg, 2014, Liu et al. 2014, Mozo et al. 2021). Studies in the Amazon comparing dry 'terra firme' and flooded areas saw evidence that periodic flooding negatively impacted tree recruitment (Polanía et al. 2020). However, studies in riparian zones point to both a negative impact of flooding on forest recruitment (Berthelot et al. 2014, Sarneel et al 2019) and a beneficial effect via facilitating the recruitment of flood-tolerant species (Rood et al. 1998). This flood tolerance has been attributed to traits like the ability to transpire during flooding and to dynamic root systems (Parolin and Wittman 2010, Kreuzwieser and Rennenberg 2014, Pan et al. 2022). Still, these tree species adapted to temporary waterlogging conditions may have to endure longer periods of flooding under climate change, and it is not entirely clear how changing flooding regimes will affect them (Niinemets and Valladares 2006, Gee et al. 2014, Saint-Laurent et al. 2019).

Over the years, tree populations accumulate a seedling bank ready to respond to openings in the canopy (Pakeman and Small 2005). However, we know little about the long-term consequences of changes in the seedling bank. If flooding affects the seedling layer (Ismail et al. 2009, Wang and Komatsu 2022) and flooding events become more prevalent in areas where tree species are not adapted to those conditions, then tree recruitment could be jeopardized (Lee et al. 2014). Furthermore, in forest communities facing flooding conditions, there will likely be intraspecific variation in how species respond and withstand such conditions (Rodríguez et al. 2020). A meta-analysis of the literature on this topic has shown that species like willows (*Salix spp*) are more successful in surviving and persisting in such environments, while other hardwood species and conifers are not as well adapted (Glenz et al. 2006). Moreover, European willows, which are pioneer floodplain species, have invaded riparian zones in South America by exploiting a vacant niche along rivers due to hydrological alterations (Lewerentz et al. 2019). Generalist forest species also seem to dominate flooded areas when compared to specialist species (Glaeser and Wulf, 2009). Therefore, flooding conditions could provide space for certain species to outcompete others at the recruitment stage (O’Briain et al. 2023). Understanding which species could or could not persist in flooding conditions will be critical to forecasting the structure and functioning of forests now exposed to flooding.

To better assess the potential impacts of flooding in temperate forest ecosystems, we conducted an observational study across forest stands. In a forest, there is often a level of topographic heterogeneity that, after intense precipitation events, can result in patches of localized flooding (Fig. 1). These areas can be used to make inferences about the effects of flooding on woody species recruitment and how it might compare to not flooded environments (Teodoro de Oliveira et al. 2014). After accounting for seed sources, we compared recruitment data between plots that did not show any indication of having been flooded vs. plots that have been recently flooded (Fig. 1). Our research was aimed at answering the following: 1) do flooded areas (i.e., high soil water levels) have an impact on tree seedling abundance and richness when compared to non-flooded environments? 2) do flooded areas differentially affect the recruitment of co-occurring tree species? Answering these questions will inform assessments of the impact of flooding on forest dynamics, information that could then be included in vegetation models of future forest performance as well as accounted for in the development of conservation and management plans.

2. Methods

Study Areas - We collected field data from forests located at two different latitudes in Michigan’s Lower Peninsula, USA (Fig. 2). The forests in northern latitudes are described as Laurentian Mixed Forests; the growing season is short relative to other areas, 122 days long, with snow being present on the ground throughout winter. At the southern latitude, Midwest Broadleaf Forests (McNab et al. 2007, Hatfield et al. 2015), the growing season period is around 173 days, and snow only covers the ground part of the winter. Using flood risk maps (Stay Dry v3.1 kmz, FEMA NFHL v3.2 kmz) we considered the hydrologic flooding history of the area and excluded sites with

historical seasonal or prolonged flooding when selecting sampling locations. We selected eight forest forests, six in the south and two forests in the north (Fig. 2, Appendix 1 Table S1). Two forests, the Goodrich Preserve and Horner Woods, spatially compose a continuous forest and, therefore, were analyzed as one, making a total of 7 forests for analysis. Within each forest, we visually assessed locations that had been recently flooded. We monitored for characteristics such as concave depressions and compressed litter layers as signs of recent and potential flooding (Fig. 1). We then paired these areas with control, no signs of flooding, and areas that were in close proximity to reduce confounding factors affecting recruitment.

Data collection - Data collection occurred between the period of June 9th to July 28th, 2022, after the growing season. Within each sampled forest, we outlined transects, 4 m wide and 8-42 m long, in areas with signs of flooding and paired them with transects in control areas. For each forest, we collected data from multiple transects for each treatment for a total of 34 transects ranging between 2-5 pairs of transects per forest. We divided each transect into 1 m² plots, where we identified tree and other woody plant seedling species and recorded their abundances (number of seedlings/m²); plants were considered seedlings if they were 50 cm tall or lower. We also outlined a perimeter around the transect stemming 10 meters from its edges to gather data on adult tree basal area (a proxy for the abundance of seed sources) and richness (a proxy for the diversity of seed sources). In this area, we identified and measured the trunk diameter of all adult trees with diameters > 5 cm (diameter at breast height [1.35 m], dbh); we then used these measurements to calculate adults' basal area per unit of forest area (BA, cm²/m²) for each transect.

Environmental Variables - Since environmental conditions are known to affect tree recruitment in these forests (e.g., Lee and Ibáñez 2021, Ibáñez et al. 2017), we recorded soil moisture and light intensity within our transects at the time of the seedling sampling. We measured volumetric soil moisture content ($\frac{\text{volume of water (cm}^3\text{)}}{\text{volume of soil (cm}^3\text{)}}$) with a FieldScout TDR 350 soil moisture probe to quantitatively assess the differences in soil moisture-paired transects. We observed light availability for each subplot using a light meter probe to measure the light intensity (μmols/m²s). We measured light availability in the center of our plots at 50 cm above the ground to reflect light conditions for seedlings. Because environmental measurements were taken on different days across forests, to be able to make comparisons between paired transects, we standardized each forest's measurements independently (e.g., at 1 m² plot i standardized $\text{Light}_i = (\text{Light}_i - \text{meanLight}_{\text{forest}(i)}) / \text{SDLight}_{\text{forest}(i)}$).

Statistical Analysis - We first analyzed seedlings abundance, all tree species combined, as a function of being in control or flooded transects but also as a function of other factors affecting seedling density, i.e., adult tree density (BA, our proxy for seed sources), and standardized light intensity since light levels might have affected the establishment and early survival (Ibáñez and McCarthy-Neumann 2016). Each 1 m² plot i was modeled using a Poisson likelihood:

$$\text{Abundance}_i \sim \text{Poisson}(\lambda_i)$$

With process model:

$$\ln(\lambda_i) = \alpha_{forest(i),treatment(i)} + \beta_1 BA_i + \beta_2 light_i + \omega_i$$

Parameter ω was included to account for the overdispersion of the data (i.e., variance > mean). We analyzed seedling species richness (i.e., number of species) following the same approach but used adult tree species richness as a predictor instead of BA. We carried out a third set of analyses for species for which we had sufficient data across surveyed forests. These include two native species: *Acer rubrum* L., red maple, and *Acer saccharum* Marshall, sugar maple; one native genus, *Fraxinus* species, which included *Fraxinus americana* L., white ash, *Fraxinus nigra* Marshall, black ash, *Fraxinus pennsylvanica* Marshall, green ash, and *Fraxinus quadrangulate* Michx., blue ash; invasive buckthorns: grouped as *Rhamnus*, including *Frangula alnus* Mill., glossy buckthorn, and *Rhamnus cathartica* L., common buckthorn; and an invasive genus, *Lonicera* species, *Lonicera maackii* (Rupr.) Herder, Macks honeysuckle, *Lonicera tatarica* L., Tartarian honeysuckle.

Based on our ecological understanding of these systems, *A. rubrum* and those within the *Fraxinus* genus can recruit in areas under temporarily inundated conditions (Anella and Whitlow 1999, Anella and Whitlow 2000, Vreugdenhil et al. 2006). Meanwhile, species like *A. saccharum* do not survive in waterlogged areas long term (Carpenter and Mitchell 1980, Hauer 2021). *Lonicera* species are a genus of focus due to their capacity to become a matter of concern in disturbed waterlogged sites, specifically *L. Maackii* (Langley 2016). For the *Rhamnus* group, studies have reported *R. cathartica* individuals being able to tolerate flooding conditions and, to a certain extent, *F. alnus* being able to persist in these same environments as *R. cathartica* (Kurylo et al. 2015, Kalkman et al, 2019).

For each species, seedling abundance was analyzed as:

$$Species\ Abundance_i \sim Poisson(\lambda_i)$$

The process model is:

$$\ln(\lambda_i) = \alpha_{forest(i),treatment(i)} + \omega_i$$

All parameters were estimated from non-informative distributions, $\alpha_{*,*}, \beta_* \sim Normal(0, 1000)$, $\omega_* \sim Normal(0, \sigma^2)$, and $\frac{1}{\sigma^2} \sim Gamma(0.001, 0.001)$.

Analysis was conducted using OpenBUGS (version 3.2.3); for the analysis, we ran three MCMC chains for 10,000 iterations until convergence was reached. The posterior parameter means, standard deviations, and 95% credible intervals were then estimated across 50,000 iterations.

3. Results

In total, we surveyed 34 transects, 17 pairs across seven forests; transects ranged from 8 to 24 m in length, yielding 588 subplots for the analyses. Soil moisture comparisons between flooded and non-flooded transects in each forest show that flooded plots were more humid than control plots, with the average difference in soil moisture content being around 79% (Appendix 1 Table S1). Across control plots, abundance ranges between 0 and 72 individuals/m², with a mean abundance of 16.04 individuals/m². The range of species richness for control plots was between 0 and 8 species/m², with a mean richness of approximately 3.27 species/m². The range of abundance for flooded plots was between 0 and 25 individuals/m², with a mean abundance of 4.33 individuals/m². The range of species richness for flooded plots was between 0 and 6 species/m², with a mean species richness of approximately 1.48/m². Parameter values for all analyses can be found in Appendix 4 Table S3. Our abundance model had a goodness of fit (predicted vs. observed; R²) of 0.994, and the diversity model had an R² value of 0.44. For our species-specific models, the *Fraxinus* model had an R² value of 0.891, 0.944 for *A. saccharum*, and 0.99 for *A. rubrum*. For our invasive species, the *Rhamnus* model had an R² value of 0.993, while the *Lonicera* model had a value of 0.99 (Appendix Fig.5a-g).

Seedling abundance

Five out of the seven forests had significantly more seedlings per m² in the control plots than in the flooded plot (Fig. 3a). Decreases in seedlings abundance ranged between 31 % (back-transformed values) and 88.5%. Both basal area (BA) and standardized light were positively associated with higher seedlings abundance (coefficients mean±SD: 0.001±0.00005 for BA and 0.035±0.016 for light).

Seedling richness

Overall richness was higher in control plots, statistically different in four out of the seven forests (Fig. 3b). Differences in the average number of species/m² between flooded and control range between 1 and 4 (back-transformed values in Fig. 3b). Adult richness was negatively associated with seedling richness (coefficient value[mean±SD]: -0.042±0.019), while higher light levels were positively associated with seedling richness (0.00012±0.00004)

Species-specific seedling abundance

When analyzing individual species or genera, abundance results were more variable (Fig. 4). Abundance of *A. rubrum* seedlings was higher in control plots in one of the four forests analyzed, for *A. saccharum*, the differences were statistically significant; abundance was higher in control plots, for two out of four forests. *Fraxinus* abundance was not different between treatments across six forests and higher under drier conditions in one forest. For the two invasive groups, *Rhamnus* and *Lonicera*, abundance was similar between treatments across forests.

4. Discussion

An increase in the frequency and magnitude of precipitation events is one of the forecasts associated with current climate change (Kundzewicz et al. 2014, Hirabayashi et al. 2013). Such events are likely to increase the area and duration of forest land exposed to flooding conditions. Although flooding may only be temporary, its effects on the recruitment layer could strongly affect the population dynamics of many tree species since seedlings may not be able to cope with anaerobic soil conditions.

In order to gain a more general understanding of how climate change-driven flooding may impact temperate forests, we studied temperate forest recruitment dynamics in flooded and non-flooded environments. We compared the abundance and richness of woody species between forest areas that have recently experienced flooded conditions and nearby areas that did not experience flooding. Our results show that, in forests that are outside the boundaries of experiencing regular or seasonal flooding regimes, flooding conditions were associated with a decrease in seedling abundance and richness. There were 66% to 88% decreases in abundance and 28% to 58% decreases in diversity across sites. Furthermore, native species were identified to persist more effectively in drier environments, while invasive species persisted similarly in both flooded and dry conditions. These associations and patterns suggest that the occurrence of flooding in forests where inundation does not commonly take place will likely have adverse effects on that forest's recruitment dynamics.

Global climate change is expected to alter forest dynamics either through abrupt or gradual changes in environmental conditions. These alterations will likely eventually lead to forest composition and structure changes (Smith and Lazo 2001, Kramer et al. 2020, Albrich et al. 2020). Despite its potential relevance to forest communities, there is little information on how these novel flooding events may affect forest recruitment patterns (Kramer et al. 2008, Evans et al. 2022). In this study, we observed how flooding conditions were a mechanism for these alterations as we documented reduced forest recruitment, in abundance and richness, across several temperate forests under flooded conditions. Recent research has pointed out that flooding could hamper forest recruitment dynamics when compared to drier environments (Saint-Laurent et al. 2019, Flores and Staal 2022). This may indicate that flooding is operating as an ecological filter at the community level in forest areas, especially in forests that do not experience a regular flooding regime (Polanía et al. 2020).

In our study, we also examined how temperate forest species may be performing in both environments and found that tree recruitment was more likely to be significantly more abundant and diverse in drier conditions. However, Eberwhite and Millennium Park showed either no significant difference or flooded environments had greater overall abundance (Figure 3a). For Millennium Park (Figure 1), the mean abundance in flooded plots was greater than that of control (dry), which, subsequently, the natural history of the location can explain. Millennium Park's soil

type and hydrologic history suggest that the environment has experienced an active flood regime. Thus, the forests would be more adapted to support flood-tolerant species that persist better in flooded soils (Appendix 1 Table S1). For Eberwhite woods, our research revealed the high presence of adult Elm (*Ulmus spp*) and species of Ash (*Fraxinus spp*), suggesting the soils at Eberwhite are regularly mesic, and these species are likely utilizing this recruitment niche through measurable recruitment abundance (Schwinning & Kelly 2013).

At the population level, we also examined how native and non-native species may be performing in both environments and found that native species were more likely to be significantly more abundant in drier environments. However, there were forests that did have mean abundances greater in flooded plots versus control for *Fraxinus spp* and *A. rubrum*. Notwithstanding, this can be attributed to the capacity of these species to adapt to flooding (Walls et al, 2005, Keller et al 2023). We can see this capacity through *Fraxinus*'s genus-level analysis (Fig. 4a). *Fraxinus* is considered to be a water-tolerant species, with species like *F. pennsylvanica* growing mainly in swamp-like environments. Species like *F. americana* and *F. nigra* have also been observed to persist in inundated conditions to some capacity as well (Robertson et al. 1978, Tardif and Bergeron 1999, Saint-Laurent et al. 2019). Thus, our results highlight this capability for *Fraxinus* species to be as abundant in inundated conditions as they are in drier conditions. A species-level analysis of *Acer* species also confirms well-known natural history features. Sugar maple, *A. saccharum*, was more abundant in drier conditions than flooded across all sites where they were present (Fig. 4b). This coincides with our understanding that this species does not tolerate waterlogged conditions effectively and will perform better in drier environments (Carpenter and Mitchell 1980, Hauer 2021). Red maple, *A. rubrum*, is believed to be able to survive and tolerate inundated environments where they are recruited (Anella and Whitlow 1999, Anella and Whitlow 2000); therefore, our findings support this notion. However, we did see environments where *A. rubrum* was more abundant in drier environments, although this could be due to localized competition or forest dynamics between generalist and specialist species (Glaeser and Wulf, 2009). This study supports that further investigation into species-level dynamics in relation to flooding conditions is required to garner a more effective understanding of this matter and determine whether these results can be replicated.

Our analysis of non-native species, in this case invasive, (*Lonicera spp*, *Rhamnus spp*), showed similar recruits in flooded environments as in the drier transects. This is in line with previous studies' conclusions of invasive species invading and out-competing other plant species in environments involving varying hydrological regimes (Lewerentz et al. 2019). This could indicate that novel flooding can pose as the catalyst for invasive seedling species to invade flooded environments through its disturbance (Orbán et al 2021). In addition, past studies suggest that flooded environments are able to maintain invasive populations due to decreased competition (O'Briain et al., 2023). In our case, the negative impacts we observed under flooding conditions on forest recruitment dynamics could take place via both a more detrimental

environment for seedling survival and higher competition by non-native species, imposing a notable threat to the persistence of native species in inundated-prone sites in the future.

Conclusions

It is at the seedling stage when plants are most vulnerable to environmental stressors (Harper 1977, Silvertown and Charlesworth 2001, Eriksson and Ehrlén 2008). As a result, patterns of tree seedling recruitment determine forest composition (Ribbens et al. 1994, Clark et al. 1999, Slik et al. 2008). Quantifying tree recruitment is thus essential to accurately predict future forest composition, structure, and function (Caspersun and Sapruff, 2005, Qiu et al. 2021, Wang et al. 2023). In the context of current climate change, the increasing incidence of extreme events is leading to novel environmental stressors, such as flooding events that may influence tree recruitment patterns (Menezes-Silva et al. 2019). In this study, we leverage the occurrence of flooded areas across seven temperate forests to assess the potential effects on tree seedling recruitment. From our analyses, we found that flooding conditions adversely impact tree recruitment. We observed that seedling abundance and biodiversity are lower under flooding conditions versus control, drier plots. In addition, these effects were more pronounced in native species than in invasive species. Overall, our results point out a detrimental effect of flooding in these forests that disproportionately affects native species over introduced ones. As extreme precipitation events become more common, tree seedling recruitment may be jeopardized in forests where flooding has not been part of the historical disturbance regime. The importance of forest recruitment processes and how flooding may affect these patterns could have significant implications for future forest compositions as they may shift to different structures due to flooding. Hereafter, studies could utilize field data from studies such as this to model changes to forests in relation to hydrologic and climatic regimes. Determining long-term changes that could occur due to flooding should be a research focus moving forward, as well as monitoring invasive species abundance in flooded areas for invasive management, as the dynamics observed in this study could have implications for future forest structure and composition predictions.

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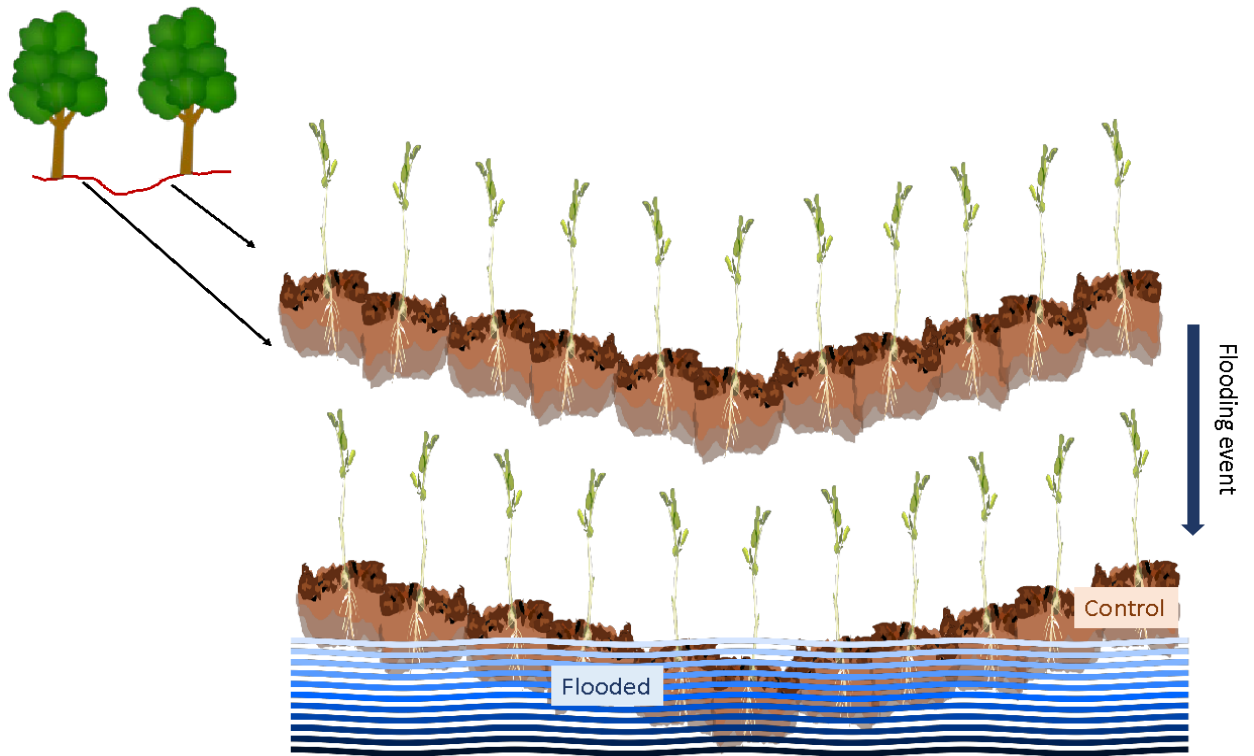


Figure 1. Visualization of the topographic differences that could occur in forests and how these characteristics can lead to localized flooded conditions.

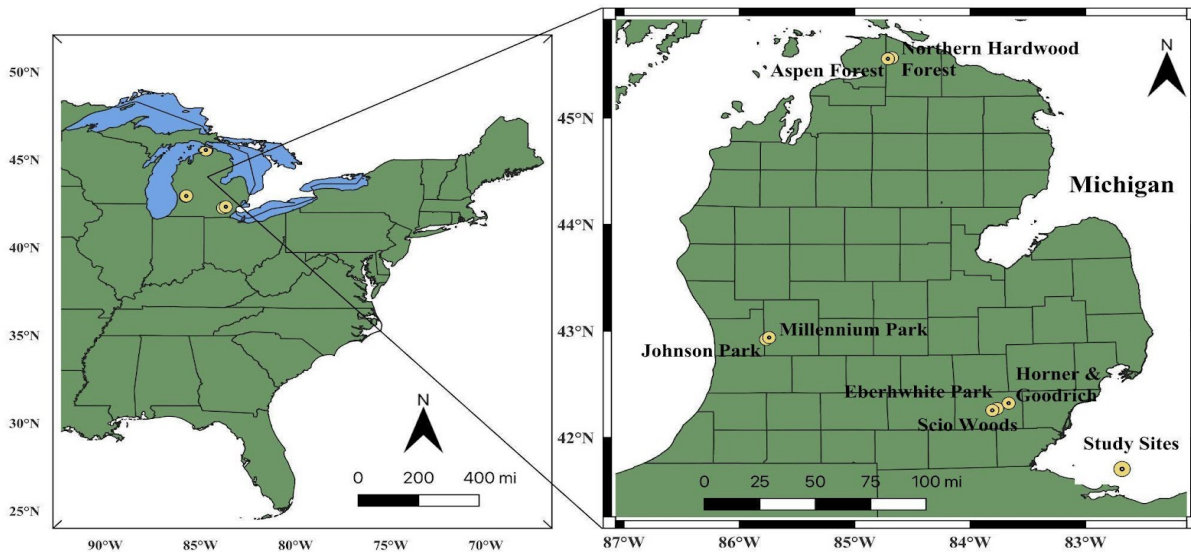


Figure 2. Map of the Eastern United States and the locations of Forests sampled in Michigan's lower peninsula. QGIS.org (2023). QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.org>

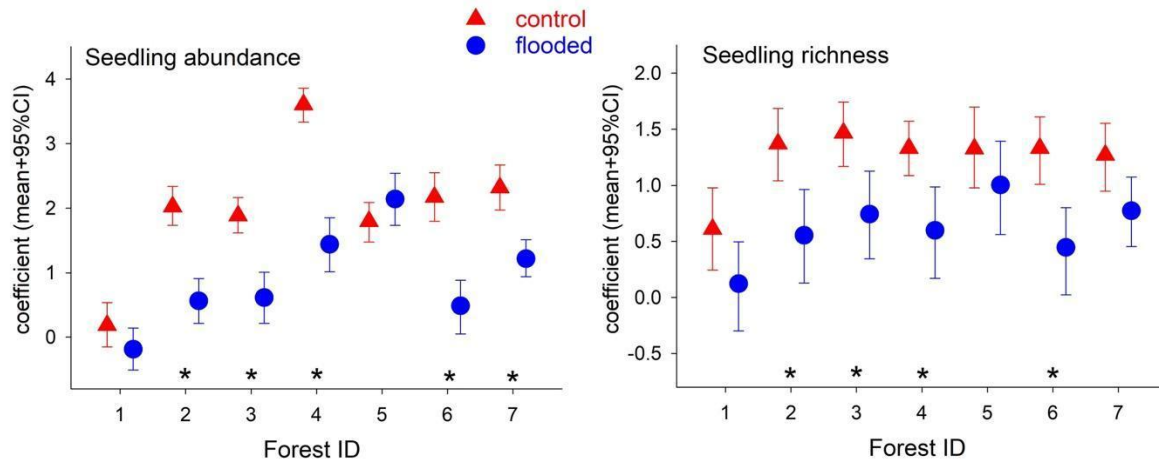


Figure 3. Model coefficients associated with seedlings abundance (left pane) and seedling richness (right panes) across the surveyed forest in control (red triangles) and flooded (blue circles) plots. Asterisks indicate significant differences between the two treatments.

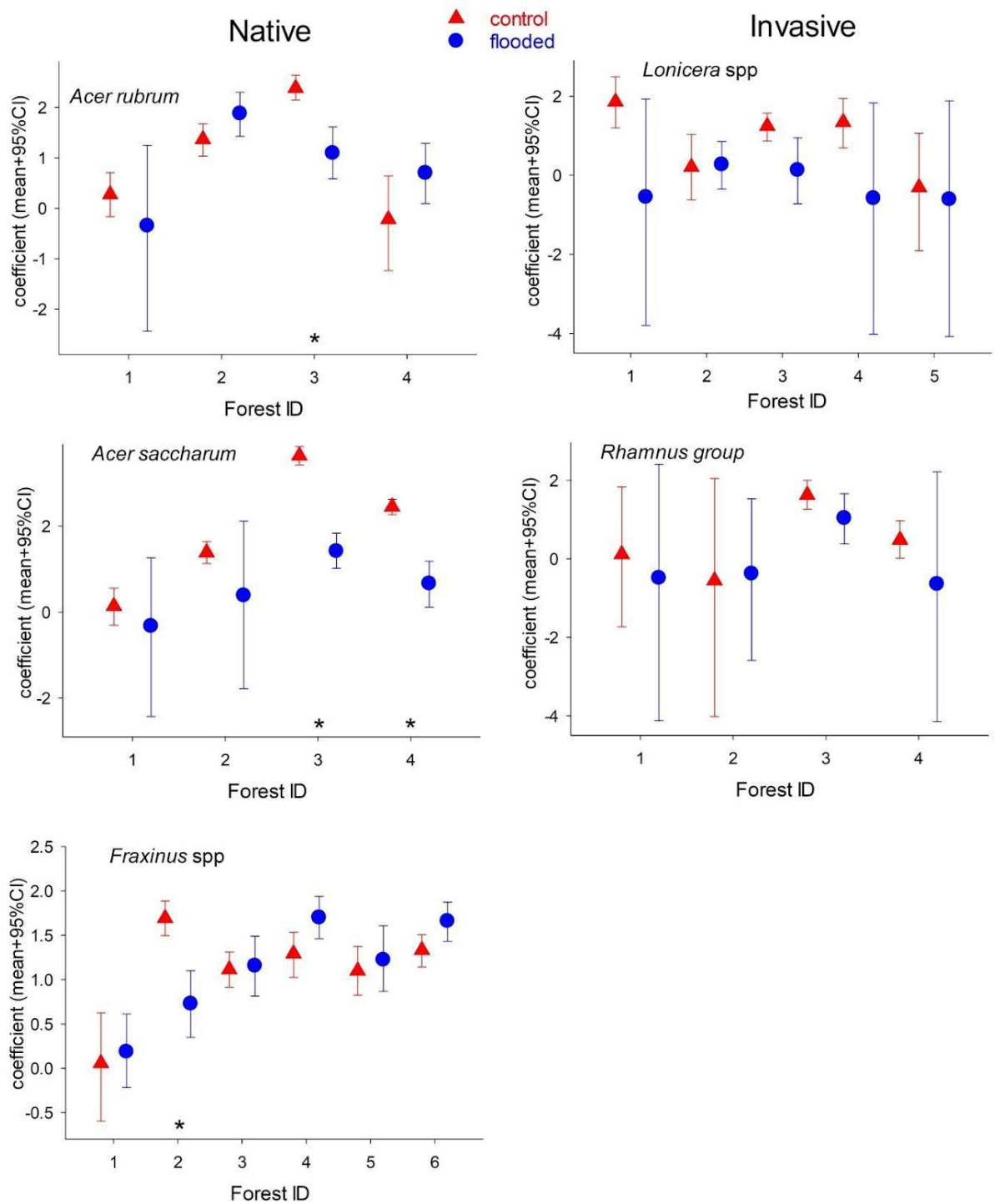


Figure 4. Species, genus, or group level analyses of seedlings abundance of native and invasive woody plants. Asterisks indicate a significant difference in the number of seedlings between the two treatments (control: red triangles; flooded: blue circles).

Supplemental Information

Appendix 1 – Information on the forests sampled in this study.

Table S1. Location, climate, forest and soil type, flood risk, and forest stand area surveyed.

<u>Forest</u> N: north S: south	<u>Latitude</u> <u>N</u> <u>Longitude</u> <u>W</u>	<u>Climate</u>	<u>Forest</u> <u>Type</u>	<u>Soil Type</u>	<u>Flooding</u> <u>Risk</u>	<u>Forest</u> <u>Stand</u> <u>Area</u>
<i>S:Eberwhite Woods</i>	42.27, -83.76	Hot-summer humid continental	Oak, Hickory, Elm, Ash	Loamy soils underlain by sand & gravel	No measurable flood risk	31 Acres
<i>S:Scio Woods</i>	42.26, -83.81	Hot-summer humid continental	Oak, Hickory, Maple, Beech	Loamy soils underlain by sand & gravel	No measurable flood risk	90 Acres
<i>S:Goodrich Preserve</i>	42.32, -83.67	Hot-summer humid continental	Oak, Hickory, Maple, Beech	Loamy soils	Low to Moderate Flood risk	45.2 Acres
<i>S:Horner Woods</i>	42.32, -83.67	Hot-summer humid continental	Oak, Hickory, Maple, Beech	Loamy soils	Low to Moderate Flood risk	98.6 Acres
<i>S:Millennium Park</i>	42.94, -85.74	Warm-summer humid continental	Maple-Ash	Clay dominated Soils	High risk	1,400 Acres
<i>S:Johnson Park</i>	42.92, -85.77	Warm-summer humid continental	Maple-Beech, Oak	Wet Organic & Loamy Soils	Low to Moderate risk	160 Acres
<i>N:Aspen Forest</i>	45.56, -84.72	Warm-summer humid	Maple-Beech	Sandy soils	Low to Moderate risk	117 Acres

		continental				
<i>N:Hardwood Forest</i>	45.56, -84.68	Warm-summer humid continental	Maple-Beech	Sandy soils	Low to Moderate risk	190 Acres

Appendix 2. Summary statistics for soil moisture and seedlings abundance and richness data.

Table S2. (a) Cumulative comparisons of soil moisture (Volumetric soil water content = $\frac{\text{volume of water (cm}^3\text{)}}{\text{volume of soil (cm}^3\text{)}}$), (b) Abundance (number of individuals per plot), and (c) species richness (number of species per plot).

a. Soil Moisture

<u>Treatment</u>	<u>Minimum</u>	<u>Maximum</u>	<u>Std. Deviation</u>	<u>Mean</u>	<u>Mean Percent Difference</u>
Flooded	40.50	82.20	8.76	55.96	79%
Control (Dry)	4.10	47.00	12.37	24.26	

b. Abundance

<u>Treatment</u>	<u>Minimum</u>	<u>Maximum</u>	<u>Std. Deviation</u>	<u>Mean</u>	<u>Mean Percent Difference</u>
Flooded	0	25.00	5.32	4.33	114.9%
Control (Dry)	0	72.00	14.94	16.04	

c. Species Richness

<u>Treatment</u>	<u>Minimum</u>	<u>Maximum</u>	<u>Std. Deviation</u>	<u>Mean</u>	<u>Mean Percent Difference</u>
Flooded	0	6	1.20	1.48	17.57%
Control (Dry)	0	8	1.65	3.27	

Appendix 3. Model code for the seedling abundance analysis.

OpenBUGS model code for the seedling abundance analysis, code for species richness, and species-specific analyses is similar to this one.

```
model{
  for(i in 1:N){
    #likelihood
    NoSlings[i]~dpois(lambda[i])
    #predicted
    NoSlings.pred[i]~dpois(lambda[i])
    #process model

log(lambda[i])<-alpha[forest[i],treat[i]]+beta[1]*BA[i]+beta[2]*lightS
[i]+omega[i]
    #overdispersion term
    omega[i]~dnorm(0,tau)
  }

#priors
for(i in 1:7){ #number of forests
  for(t in 1:2){ #number of treatments
alpha[i,t]~dnorm(0,0.0001)
  }
dif[i]<-alpha[i,1]-alpha[i,2] #differences between treatments
}
for(i in 1:2){beta[i]~dnorm(0,0.0001)}
tau~dgamma(0.01,0.01)
}
```

Appendix 4. All analysis parameter values

Table S3. Parameters' posterior means, SD, and 95% credible intervals from the abundance and richness data analyses. Different letters indicated statistically significant differences (95% CI do not overlap) between control and flooded plots in each forest. Bold parameters indicate statistically significant coefficients (95% CI does not overlap with zero) of the covariates.

All species abundance, parameter :

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile	
1	flooded	$\alpha_{1,control}$	-0.190575	0.1652397	-0.507957072	0.140149705	a
1	control	$\alpha_{1, flooded}$	0.187304	0.1803553	-0.150717489	0.538440666	a
2	flooded	$\alpha_{2,control}$	0.56596	0.1843194	0.21382788	0.908534675	a
2	control	$\alpha_{2, flooded}$	2.026329	0.1582078	1.7320285	2.337965383	b
3	flooded	$\alpha_{3,control}$	0.612765	0.2028012	0.21578107	1.007009105	a
3	control	$\alpha_{3, flooded}$	1.887687	0.1404863	1.617037246	2.165472186	b
4	flooded	$\alpha_{4,control}$	1.435829	0.2169112	1.014564576	1.851098758	a
4	control	$\alpha_{4, flooded}$	3.601693	0.1382247	3.335376506	3.860433226	b
5	flooded	$\alpha_{5,control}$	2.14191	0.2037038	1.73365695	2.543920937	a
5	control	$\alpha_{5, flooded}$	1.793828	0.1538227	1.476186891	2.088934319	a
6	flooded	$\alpha_{6,control}$	0.476359	0.2150394	0.051086462	0.886219009	a
6	control	$\alpha_{6, flooded}$	2.173198	0.1872985	1.797354503	2.550615515	b
7	flooded	$\alpha_{7,control}$	1.220121	0.1462501	0.939331204	1.512666505	a
7	control	$\alpha_{7, flooded}$	2.322888	0.1814949	1.973775799	2.670428104	b
	Basal Area	β_1	0.00016	5.11E-05	5.44E-05	0.000259324	
	Light	β_2	0.035004	0.0169303	0.001438269	0.067856739	
	Overdispersion	$1/\sigma^2$	0.490494	5.3325958	0.413397023	0.59385988	

Richness:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile		
	1	flooded	$\alpha_{1,control}$	0.1118371	0.2088799	-0.29871911	0.496806803	a
	1	control	$\alpha_{1,flooded}$	0.6105974	0.1874597	0.244883455	0.978409511	b
	2	flooded	$\alpha_{2,control}$	0.5535315	0.2134407	0.130024064	0.962749991	a
	2	control	$\alpha_{2,flooded}$	1.367371	0.1654329	1.041752132	1.684478708	b
	3	flooded	$\alpha_{3,control}$	0.7433839	0.2050922	0.345697943	1.12802551	a
	3	control	$\alpha_{3,flooded}$	1.4626515	0.1445043	1.168513227	1.742403042	b
	4	flooded	$\alpha_{4,control}$	0.592385	0.2099925	0.171701768	0.986745292	a
	4	control	$\alpha_{4,flooded}$	1.3288007	0.1252057	1.087808606	1.572132269	b
	5	flooded	$\alpha_{5,control}$	0.9984942	0.2139504	0.56253903	1.393630791	a
	5	control	$\alpha_{5,flooded}$	1.3296008	0.1863599	0.977568501	1.697552645	a
	6	flooded	$\alpha_{6,control}$	0.4386456	0.1973797	0.022607235	0.800698513	a
	6	control	$\alpha_{6,flooded}$	1.3258088	0.1571253	1.009674394	1.609843384	b
	7	flooded	$\alpha_{7,control}$	0.7675728	0.1617378	0.45500518	1.074366787	a
	7	control	$\alpha_{7,flooded}$	1.2671404	0.1555739	0.948243997	1.55394944	b
		Adult richness	β_1	-0.048602	0.0192005	-0.08577018	-0.012992619	
		Light	β_2	0.0001283	4.48E-05	3.98E-05	0.00021682	
		Overdispersion	$1/\sigma^2$	0.0056371	0.0102266	0.002298972	0.019741939	

Acer rubrum seedling abundance:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile
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3	flooded	$\alpha_{3,control}$	-0.34574477	0.928709624	-2.437424933	1.246810817	a
3	control	$\alpha_{3, flooded}$	0.273095289	0.227916201	-0.167018842	0.709143894	a
5	flooded	$\alpha_{5,control}$	1.879568164	0.221876747	1.428908561	2.303665188	a
5	control	$\alpha_{5, flooded}$	1.369685923	0.164151653	1.037476092	1.67707819	a
6	flooded	$\alpha_{6,control}$	1.096710125	0.269413631	0.585179956	1.612404477	a
6	control	$\alpha_{6, flooded}$	2.382180668	0.124140444	2.148193814	2.637379628	b
7	flooded	$\alpha_{7,control}$	0.701541604	0.305443803	0.094665036	1.290656284	a
7	control	$\alpha_{7, flooded}$	-0.21877694	0.48062685	-1.235910859	0.641973466	a
	Overdispersion	$1/\sigma^2$	0.515079378	2.791779788	0.366129635	0.749914283	

Acer saccharum seedling abundance:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile	
1	flooded	$\alpha_{1,control}$	-0.323791577	0.911238975	-2.42854421	1.262418095	a
1	control	$\alpha_{1, flooded}$	0.140983315	0.226189999	-0.304564614	0.56039	a
2	flooded	$\alpha_{2,control}$	0.390662517	1.004323696	-1.784276792	2.119496779	a
2	control	$\alpha_{2, flooded}$	1.385924884	0.13047339	1.128954624	1.639835666	a
4	flooded	$\alpha_{4,control}$	1.420849283	0.212451724	1.01976117	1.835997418	a
4	control	$\alpha_{4, flooded}$	3.638955425	0.107340719	3.425668683	3.848149922	b
7	flooded	$\alpha_{7,control}$	0.665941523	0.272138274	0.110882484	1.18600314	a
7	control	$\alpha_{7, flooded}$	2.449115484	0.090465906	2.268240211	2.625413536	b
	Overdispersion	$1/\sigma^2$	0.321663262	1.860719469	0.233595813	0.459846577	

Fraxinus spp seedling abundance:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile	
					-0.21755995		
1	flooded	$\alpha_{1,control}$	0.187312397	0.212121682	9	0.612178692	a
					-0.59705751		
1	control	$\alpha_{1, flooded}$	0.055749371	0.315785367	2	0.626779305	a
2	flooded	$\alpha_{2,control}$	0.727948973	0.19691238	0.347639194	1.099914902	a
2	control	$\alpha_{2, flooded}$	1.692138761	0.098402088	1.496721487	1.88768807	b
3	flooded	$\alpha_{3,control}$	1.156883538	0.172348517	0.812595168	1.488730673	a
3	control	$\alpha_{3, flooded}$	1.114329308	0.10229906	0.913379667	1.312013015	a
5	flooded	$\alpha_{5,control}$	1.701418116	0.12318557	1.461927455	1.939310239	a
5	control	$\alpha_{5, flooded}$	1.292094027	0.128665027	1.022914746	1.534916588	b
6	flooded	$\alpha_{6,control}$	1.223926947	0.191086201	0.866092866	1.606847561	a
6	control	$\alpha_{6, flooded}$	1.100111322	0.141287743	0.823216687	1.372689348	a
7	flooded	$\alpha_{7,control}$	1.661655003	0.108424522	1.431875036	1.874469468	a
7	control	$\alpha_{7, flooded}$	1.331666674	0.097773978	1.142483433	1.50786061	b
	Overdispersion						
	n	$1/\sigma^2$	0.20965769	1.200045431	0.150326231	0.292287944	

Lonicera spp seedling abundance:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile	
1	flooded	$\alpha_{1,control}$	-0.547187 076	1.4674723 68	-3.800046 846	1.9284571 06	a
1	control	$\alpha_{1, flooded}$	1.8569469 98	0.3355430 45	1.2005557	2.4911225 33	a
2	flooded	$\alpha_{2,control}$	0.2723655 6	0.3097110 15	-0.351448 591	0.8552624 97	a
2	control	$\alpha_{2, flooded}$	0.2094641 63	0.4222588 28	-0.622425 293	1.0333264 59	a

3	flooded	$\alpha_{3,\text{control}}$	0.1324832 47	0.4312828 63	-0.721097 456	0.9470511 32	a
3	control	$\alpha_{3,\text{flooded}}$	1.2462269 88	0.1795973	0.8651459 58	1.5744825 82	b
6	flooded	$\alpha_{6,\text{control}}$	-0.581780 533	1.4820493 25	-4.021587 386	1.8294413 11	a
6	control	$\alpha_{6,\text{flooded}}$	1.3434085 78	0.3114591 07	0.6939441 84	1.9403470 29	a
7	flooded	$\alpha_{7,\text{control}}$	-0.608354 156	1.4885843 6	-4.080096 429	1.8814340 63	a
7	control	$\alpha_{7,\text{flooded}}$	-0.306199 217	0.7704883 3	-1.912691 381	1.0636990 86	a
	Overdispersion	$1/\sigma^2$	0.5592177 04	2.2340788 31	0.3543978 01	0.9239289 9	

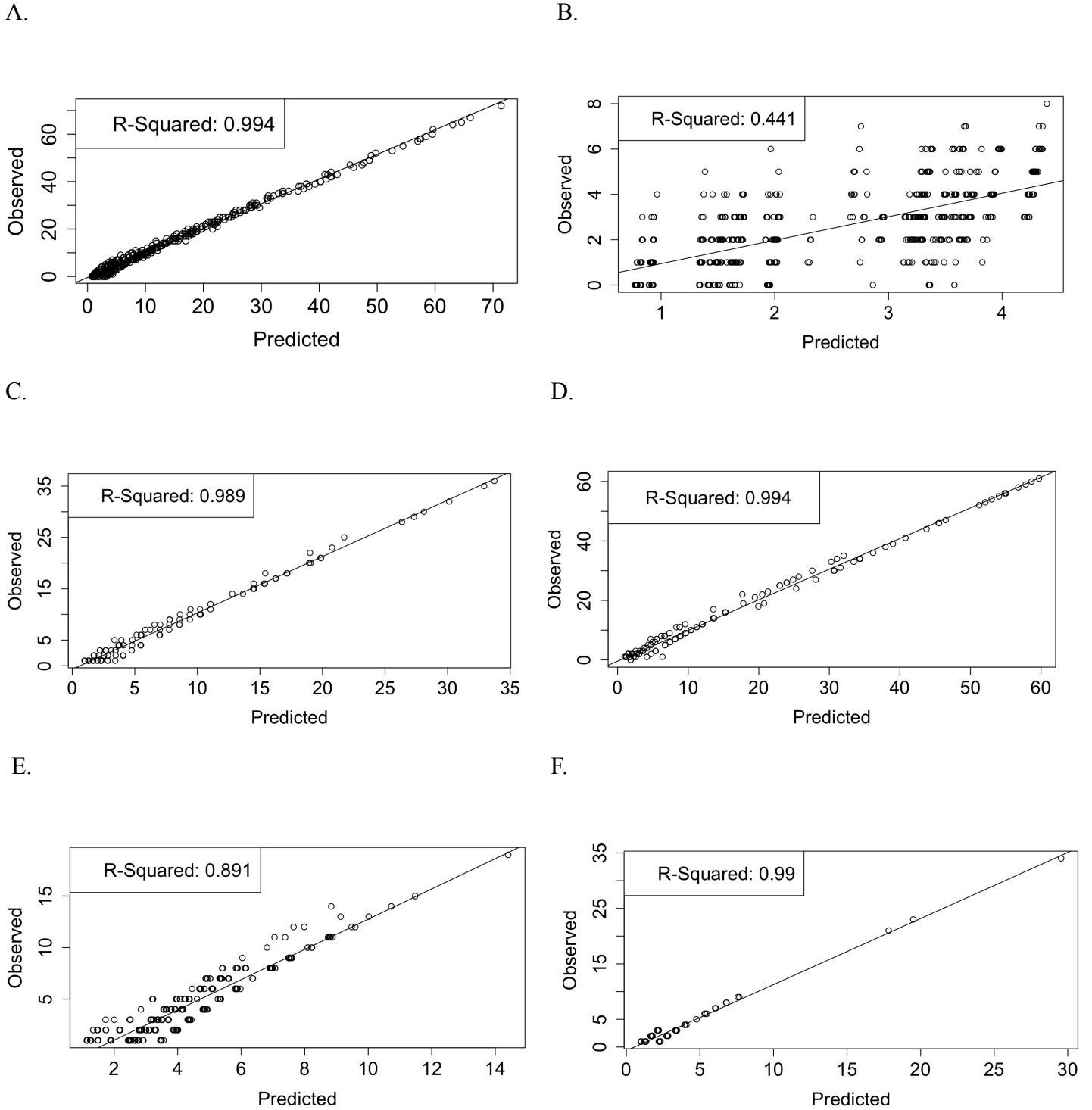
Rhamnus group seedling abundance:

Forest	treatment	parameter	mean	SD	2.5 % quantile	97.5 % quantile	
				1.5790250		2.4051254	
1	flooded	$\alpha_{1,\text{control}}$	-0.4893203	7	-4.1257472	5	a
1	control	$\alpha_{1,\text{flooded}}$	0.1136616 5	0.9055542 1	-1.73139	1.8296508 7	a
2	flooded	$\alpha_{2,\text{control}}$	-0.3764618	4	-2.5916625	1	a
2	control	$\alpha_{2,\text{flooded}}$	-0.5524682	2	-4.0219648	4	a
3	flooded	$\alpha_{3,\text{control}}$	1.0352792 1	0.3171919 8	0.3802513 1	1.6546879 1	a
3	control	$\alpha_{3,\text{flooded}}$	1.6262972 4	0.1917746 3	1.2600797 2	1.9982058 9	a
5	flooded	$\alpha_{5,\text{control}}$	-0.6403351	4	-4.1475225	7	a
5	control	$\alpha_{5,\text{flooded}}$	0.4811033 7	0.2515095 9	0.0148689 8	0.9710430 7	a

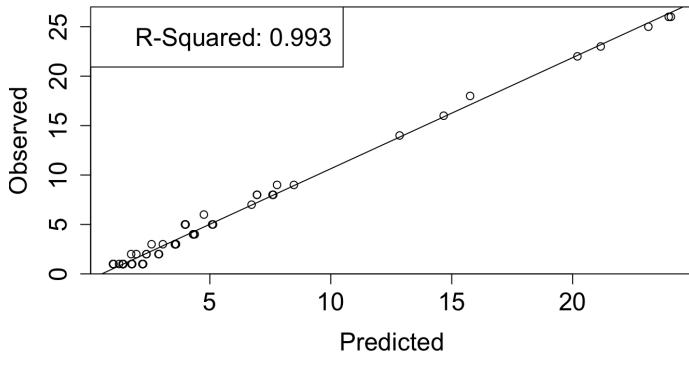
Overdispersion	$1/\sigma^2$	0.7799550	0.5028830	1.3690184	
n		4	3.1051924	7	7

Appendix 5. Goodness of fit.

Figure S1. Predicted vs. Observed plots for the overall analyses of seedlings abundance (a), richness (b), and the analyses of specific species, genera, and groups, (c) *A. rubrum*, (d) *A. saccharum*, (e) *Fraxinus*, (f) *Lonicera*, and (g) *Rhamnus*.



G.



Appendix 6 Total Seedling and Adult Species Abundance

Table S4. Cumulative (a) Seedlings and (b) Adult Species observed and their abundances across all sites.

A.

<u>Common Name</u>	<u>Scientific Name</u>	<u>Seedling Abundance</u>
1. Ash group	<i>Fraxinus americana</i> , <i>Fraxinus nigra</i> , <i>Fraxinus pennsylvanica</i>	1456
2. Red Oak Group	<i>Quercus sect. Erythrobalanus</i>	77
3. White Oak Group	<i>Quercus sect. Leucobalanus</i>	48
4. Bitternut Hickory	<i>Carya cordiformis</i>	36
5. Pignut Hickory	<i>Carya glabra</i>	13
6. Shagbark Hickory	<i>Carya ovata</i>	84
7. Sugar Maple	<i>Acer saccharum</i>	2359
8. Black Maple	<i>Acer nigrum</i>	4
9. Red Maple	<i>Acer rubrum</i>	387
10. Norway Maple	<i>Acer platanoides</i>	25
11. Striped Maple	<i>Acer pennsylvanica</i>	27
12. Choke Cherry	<i>Prunus virginiana</i>	207
13. Black Cherry	<i>Prunus serotina</i>	54
14. American Elm	<i>Ulmus americana</i>	41
15. Siberian Elm	<i>Ulmus rubra</i>	1
16. Dogwoods	<i>Cornus spp</i>	25
17. Serviceberrys	<i>Amelanchier spp</i>	173
18. American Basswood	<i>Tilia americana</i>	8
19. Yellow Birch	<i>Betula alleghaniensis</i>	1
20. Aspens	<i>Populus grandidentata</i> , <i>Populus deltoides</i>	3
21. Ironwood	<i>Ostryaya virginiana</i>	186
22. Musclewood	<i>Carpinus caroliniana</i>	40
23. Beech	<i>Fagus grandifolia</i>	32

24. Witch-hazel	<i>Hamamelis virginiana</i>	31
25. Winterberry	<i>Ilex virginiana</i>	12
26. Multiflora rose	<i>Rosa multiflora</i>	2
27. Northern Hackberry	<i>Celtis occidentalis</i>	1
28. Hawthorn	<i>Crataegus spp</i>	8
29. Viburnum	<i>Viburnum spp</i>	10
30. Gray alder	<i>Alnus incana</i>	60
31. European Spindle tree	<i>Euonymus europaeus</i>	2
32. Black locust	<i>Robinia pseudoacacia</i>	3
33. Honeysuckles	<i>Lonicera spp</i>	1433
34. Buckthorns	<i>Rhamnus spp</i>	386

B.

<u>Common Name</u>	<u>Scientific Name</u>	<u>Adult Abundance</u>
1. Ash group	<i>F. americana, F nigra, F pennsylvanica, Fraxinus quadrangulata</i>	65
2. Red Oak Group	<i>Quercus sect. Erythrobalanus</i>	94
3. White Oak Group	<i>Quercus sect. Leucobalanus</i>	68
4. Bitternut Hickory	<i>Carya cordiformis</i>	30
5. Pignut Hickory	<i>Carya glabra</i>	64
6. Shagbark Hickory	<i>Carya ovata</i>	85
7. Sugar Maples	<i>Acer saccharum, Acer saccharum var. nigrum</i>	490
8. Red Maple	<i>Acer rubrum</i>	156
9. Striped Maple	<i>Acer pennsylvanica</i>	9
10. Black Cherry	<i>Prunus serotina</i>	18
11. American Elm	<i>Ulmus americana</i>	76
12. Siberian Elm	<i>Ulmus rubra</i>	2
13. Dogwoods	<i>Cornus spp</i>	3
14. Serviceberries	<i>Amelanchier spp</i>	9
15. American Basswood	<i>Tilia americana</i>	50
16. Yellow Birch	<i>Betula alleghaniensis</i>	15
17. Aspens	<i>P. grandidentata, P. deltoides</i>	42
18. Ironwood	<i>Ostryaya virginiana</i>	237
19. Musclewood	<i>Carpinus caroliniana</i>	16
20. Beech	<i>Fagus grandifolia</i>	63
21. Witch-hazel	<i>Hamamelis virginiana</i>	2
22. Hawthorns	<i>Crataegus spp</i>	37
23. Viburnums	<i>Viburnum spp</i>	10

24. Gray alder	<i>Alnus incana</i>	60
25. Honeysuckles	<i>Lonicera spp</i>	50
26. Buckthorns	<i>Rhamnus spp</i>	13