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Detrimental impacts of flooding conditions on native tree recruitment but not on invasive plants

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A R T I C L E I N F O

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A B S T R A C T

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 point to the potential adverse effects novel flooding conditions could have on temperate forest recruitment dynamics and thus on future forest structure and composition, information that could be included in vegetation models of future forest performance as well as accounted for in the development of conservation and management plans.

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). By impacting recruitment, extreme events, such as heat waves, droughts, and flooding, may lead to rapid shifts in forest structure and composition (Grubb, 1977; Connell and Green, 2000; Weed et al., 2013). 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 (Hirabayashi et al., 2021; Kundzewicz et al., 2014), 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 during the flood; however, seedlings with much shorter roots may not (Glenz et al., 2006). Despite its potential impact, the effects of these flooding events are 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., 2023a, 2023b). 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 recruitment and thus forest dynamics (Kozlowski, 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

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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, total biomass, and also alter leaf nitrogen content, photosynthetic rate, and 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 novel 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 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, novel 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 several 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 (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., temporally exposed to high soil water levels) have an impact on tree seedling abundance and richness when compared to non-flooded areas? 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. Materials and methods

2.1. Study areas

We collected field data from temperate forests located at two different latitudes in Michigan's Lower Peninsula, USA (Appendix A Fig. A.1). 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; https://www.fema.gov/flood-maps/national-flood-hazard-layer) we considered the hydrologic flooding history of the area, including recent flooding in 2020, and excluded sites with historical seasonal or prolonged flooding. We selected seven forest forests of similar tree species composition, five in the south and two forests in the north (Appendix A Table A.1). 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). To reduce confounding factors affecting recruitment we then paired these areas with areas that were in close proximity, controls, with no

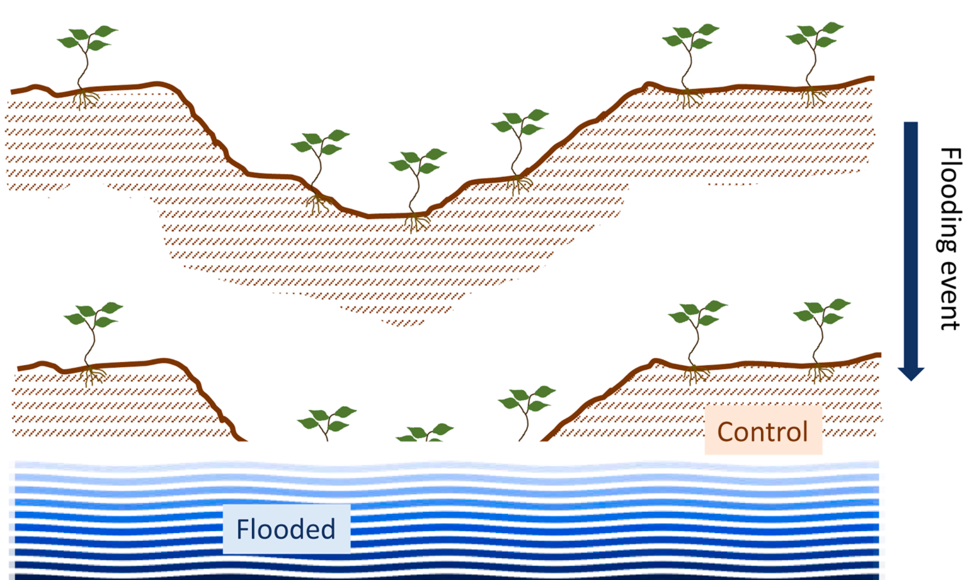

Fig. 1. Visualization of the topographic differences that could occur in forests and how these can lead to localized flooded conditions.

signs of flooding.

2.2. Data collection

Data collection took place in the summer of 2022 after spring seedling establishment. 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 and 5 pairs of transects per forest. We divided each transect into 1 m^2 plots, where we identified tree and other woody plant seedling species and recorded their abundances (number of seedlings/m^2). We focused on established plants, > 1 year old, that were 50 cm tall or lower; we did not record establishing seedlings, < 1 year old, which are easily recognized by their cotyledons and lack of lignified stems. We also outlined a perimeter around the transect stemming 10 m 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, cm^2/m^2) around each transect.

2.3. Environmental variables

Since environmental conditions are known to affect tree recruitment in these forests (e.g., Ibáñez et al., 2017; Lee and Ibáñez, 2021), we recorded soil moisture and light intensity within our transects at the time of the seedling sampling. We measured volumetric soil moisture content (%) with a FieldScout TDR 350 soil moisture probe to quantitatively assess the differences in soil moisture between paired transects. We recorded light availability for each 1 m^2 plot using a light meter probe to measure the light intensity (μmols/m^2s). 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 m^2 plot *i* standardized $\text{lightS}_i = (\text{Light}_i - \text{meanLight}_{forest(i)}) / \text{SDLight}_{forest(i)}$).

2.4. Statistical analysis

We first analyzed seedlings abundance, all woody 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). Differences in soil moisture between control and flooded are accounted by treatment level parameters, α, and the inclusion of transect level random effects did not improved the outcome of the model. Each 1 m^2 plot *i* was modeled using a Poisson likelihood:

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

With process model:

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

Parameter ω was included to account for the over dispersion 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, 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:

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

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 $\frac{1}{\sigma^2} \sim Gamma(0.001, 0.001)$.

Analyses were run in JAGS (Plummer, 2021) using the rjags package in R (R Core Team, 2021) (see Appendix B for JAGS code). 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

3.1. Overall trends

In total, we surveyed 34 transects, 17 pairs across seven forests; transects ranged from 8 to 24 m in length, yielding 588 1 m^2 subplots for the analyses. Soil moisture comparisons between flooded and non-flooded transects in each forest show that flooded plots had higher soil moisture content than control plots, with the average difference in soil moisture content being around 79% (Appendix C Table C.1). Across control plots, abundance ranges between 0 and 72 individuals/m^2, with a mean abundance of 16.04 individuals/m^2. The range of species richness for control plots was between 0 and 8 species/m^2, with a mean richness of approximately 3.27 species/m^2. The range of abundance for flooded plots was between 0 and 25 individuals/m^2, with a mean abundance of 4.33 individuals/m^2. The range of species richness for flooded plots was between 0 and 6 species/m^2, with a mean species richness of approximately 1.48/m^2. Parameter values for all analyses can be found in Appendix D Table D.1. Our abundance model had a goodness of fit (predicted *vs.* observed; R^2) of 0.994, and the diversity model had an R^2 value of 0.44. For our species/group-specific analysis an R^2 varied from 0.891 to 0.99 (Appendix E Fig. E.1).

3.2. Seedling abundance

Five out of the seven forests had significantly more seedlings per m^2 in the control plots than in the flooded plot (Fig. 2a). Decreases in seedlings abundance ranged between 31% and 88.5% (back-transformed values). Both basal area (BA) and standardized light were positively associated with higher seedlings abundance (coefficients mean ±SD: 0.0016±0.00005 for BA and 0.035±0.016 for light).

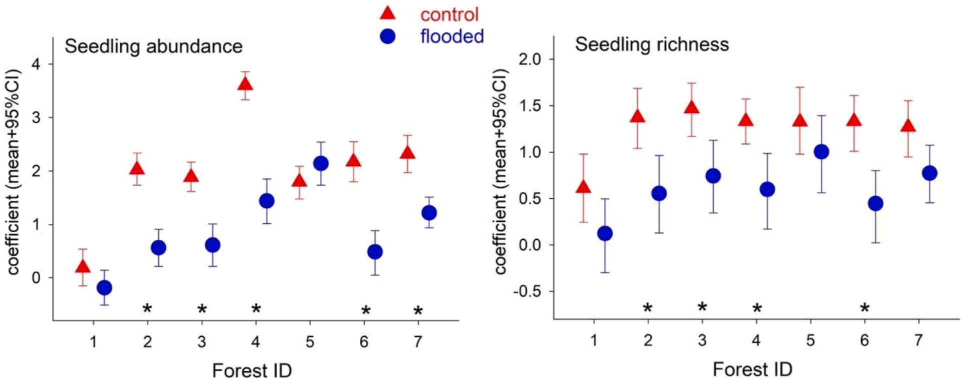

Fig. 2. Model coefficients associated with seedlings abundance (left pane) and seedling richness (right panes) across the surveyed forest in control (red triangles) and flooded (blue circles) plots. Asterisks indicate 95% credible intervals between the two treatments do not overlap.

3.3. Seedling richness

Overall richness was higher in control plots, statistically different in four out of the seven forests (Fig. 2b). Differences in the average number of species/m^2 between flooded and control ranged between 1 and 4 (back-transformed values in Fig. 2b). 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)

3.4. Species-specific seedling abundance

When analyzing individual species or groups, abundance results were more variable (Fig. 3). Abundance of *A. rubrum* seedlings was higher in control plots in one of the four forests analyzed, for *A. saccharum* 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 (Hirabayashi et al., 2021; Kundzewicz et al., 2014). 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 soils. To gain a more general understanding of how climate change-driven flooding may impact temperate forests, we leveraged topographic differences within forests and studied recruitment dynamics in flooded and non-flooded patches. 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 66–88% decreases in abundance and 28–58% decreases in diversity across sites. Furthermore, native species were found 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 novel flooding events in forests where inundation does not commonly take place will likely have adverse effects on the forest's recruitment dynamics.

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), indicating that flooding could operate 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). Despite its potential relevance to forest communities, there is little information on how novel flooding events may affect forest recruitment patterns (Evans et al., 2022; Kramer et al., 2008). In this study, we observed how flooding conditions were a mechanism shaping recruitment patterns as we documented reduced forest recruitment, in abundance and richness, across several temperate forests in plots with signs of flooding. However, two of the surveyed forests, showed either no significant difference or flooded environments had greater overall abundance (Fig. 3a, forests 1 and 4). In the first forest, our research revealed the high presence of adult Elm (*Ulmus spp*) and species of Ash (*Fraxinus spp*), suggesting the soils at this site are regularly mesic, hosting species adapted to higher water levels (Schwinning and Kelly, 2013). In the second forest the mean abundance in flooded plots was greater than that of control (dry). Even if we selected forest outside flooding zones, in a post field survey information gathering, we found out this particular stand has experienced an active flood regime (Appendix A Table A.1), and as with the previous one hosted more flood tolerant tree species, mostly of the genus *Fraxinus*. Still, overall, we found that across different forests common species tree recruitment was more likely to be higher and more diverse in plots that did not show signs of flooding.

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 abundant in drier environments. However, there were forests that did have mean abundances greater in flooded versus control plots for *Fraxinus spp* and *A. rubrum* (Fig. 3), all species with the capacity to grow under flooding conditions (Walls et al., 2005; Keller et al., 2023). *Fraxinus* is considered to be a water-tolerant species, with species like *F. pennsylvanica* growing mainly in swamp-like environments. *Fraxinus americana* and *F. nigra* have also been observed to persist in inundated conditions to some capacity (Robertson et al., 1978; Tardif and Bergeron, 1999; Saint-Laurent et al., 2019). Thus, our results highlight the potential for *Fraxinus* species to be as abundant in inundated conditions as they are in drier conditions. Red maple, *A. rubrum*, has also been shown to be able to survive and tolerate high soil moisture environments (Anella and Whitlow, 1999, 2000). However, we did see environments where *A. rubrum* was more abundant in drier environments showing the great range of conditions this species can thrive (Barnes and Wagner, 2004). Sugar maple, *A. saccharum,* however, was more abundant in drier, but still mesic, than flooded conditions across all sites where it was present (Fig. 3b). This coincides with our understanding that this species does not tolerate waterlogged conditions (Carpenter and Mitchell, 1980; Hauer, 2021).

Our analysis of non-native species, in this case invasive, (*Lonicera spp*, *Rhamnus spp*), showed similar recruits in flooded environments as in

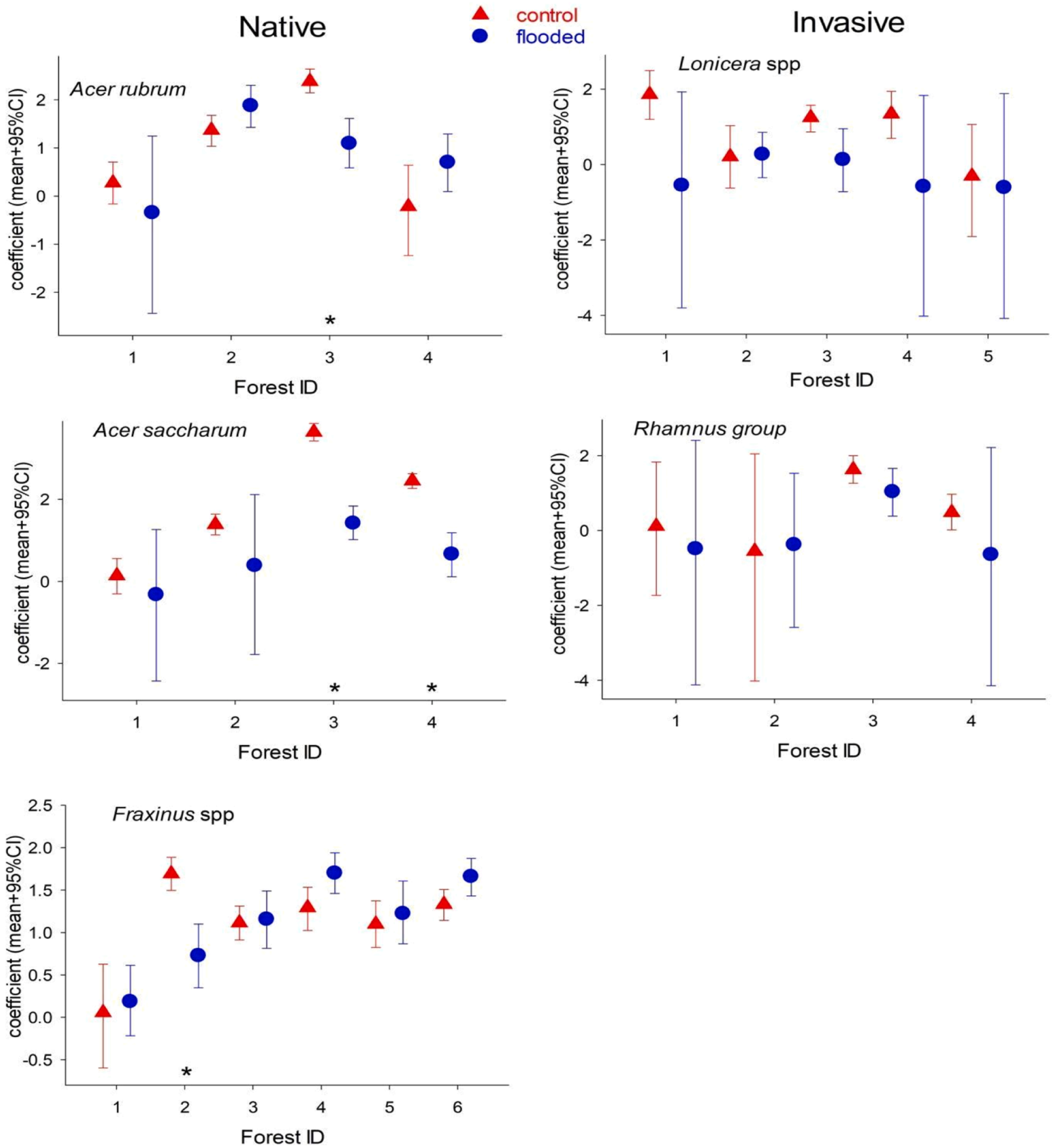

Fig. 3. Species, genus, and group level analyses of seedlings abundance of native and invasive woody plants. Asterisks indicate 95% credible intervals between the two treatments do not overlap.

the drier transects. This is in line with previous studies' conclusions of invasive species invading and outcompeting other plant species under varying hydrological regimes (Lewerentz et al., 2019). This could indicate that novel flooding can pose as a catalyst for invasive seedling species to hold into forested areas (Orbán et al., 2021). In addition, past studies suggest that flooded environments are able to maintain invasive populations due to decreased native 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 native seedling survival and higher competition from non-native species.

5. Conclusions

Global climate change is expected to alter forest dynamics either through abrupt or gradual changes in environmental conditions. These alterations could eventually lead to forest composition and structure changes (Smith and Lazo, 2001; Kramer et al., 2020; Albrich et al., 2020). It is at the seedling stage when plants are most vulnerable to environmental stressors (Harper, 1994; 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 (Caspersen and Saprunoff, 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, seedling abundance and richness were 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 and may cause flooding events, tree seedling recruitment may be jeopardized in forests where flooding has not been part of the historical disturbance regime.

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CRediT authorship contribution statement

Ines Ibanez: Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Ezekiel J. Herrera-Bevan:** Writing – review & editing, Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data have been made publicly available in an open repository: http://doi.org/10.6073/pasta/c59a863a9d9976b7bb22264f87bcbe2c.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121886.

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