Windthrow-generated tip-up mounds create contrasting regeneration niches for red oak and black cherry in a deer-browsed Carolinian forest

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Abstract

Carolinian old-growth forests in southwestern Ontario are among the most biodiverse ecosystems in Canada, yet regeneration of several canopy tree species is increasingly constrained by intense white-tailed deer browsing and changing disturbance regimes. Windstorms frequently uproot trees in this region, creating tip-up mounds that alter soil structure, drainage, and microtopography. These microsites may provide important opportunities for seedling establishment, but their role in forest regeneration remains poorly understood. This study examined how tip-up mound microsites differ from adjacent ground microsites in soil properties and how these differences influence seedling survival. A total of 84 tip-up mounds were sampled across several conservation areas in Hamilton, Ontario. For each mound, soil samples were collected from the mound top and adjacent forest floor and analyzed for soil moisture, pH, organic matter, and texture. Seedlings of two deer-preferred native species, red oak (*Quercus rubra*) and black cherry (*Prunus serotina*), were planted on mound tops and adjacent ground microsites, and their survival was monitored over the growing season. Ground microsites had significantly higher soil moisture and organic matter than mound tops, whereas mound tops were consistently drier. Seedling responses differed between species: red oak survival was higher on ground microsites, while black cherry survival was higher on mound tops. Logistic regression analyses indicated that soil moisture was the strongest predictor of seedling survival, with contrasting responses between the two species. These results suggest that tip-up mounds create distinct environmental conditions that selectively favor different regeneration strategies. As white-tailed deer browsing continues to suppress regeneration on the forest floor - particularly in areas of high deer activity and low wildlife species richness - while windthrow frequency rises under climate change, tip-up mounds are poised to become increasingly critical regeneration niches for species capable of establishing under drier, well-aerated microsite conditions.

Keywords: Tip-up mound, microsite, Carolinian forest, Soil texture, Soil organic matter, Soil pH, Soil moisture, Seedling survival, Red oak (*Quercus rubra*), Black cherry (*Prunus serotina*)

1.0 Introduction

Forest regeneration is fundamental to the long-term persistence and structural dynamics of temperate forests. However, successful recruitment of canopy tree species is increasingly constrained by interacting biotic and abiotic pressures. In many North American forests, intense herbivory by white-tailed deer (*Odocoileus virginianus*) has substantially altered understory composition and suppressed regeneration of preferred tree species (Côté et al., 2004; Patton et al. 2021, Don et al. 2024). At the same time, competition from understory vegetation and reduced light availability beneath closed canopies can further limit seedling establishment (Montgomery and Chazdon, 2001). While these drivers of regeneration failure are well documented, seedling success also depends strongly on the fine-scale environmental conditions encountered during establishment.

Microhabitat variation in soil properties, including moisture, aeration, nutrient availability, and organic matter content, can strongly influence early seedling survival and growth. Such environmental heterogeneity often interacts with species-specific physiological tolerances, resulting in differential regeneration success across microsites (Denney et al., 2020; García de Jalón et al., 2020). Consequently, small-scale disturbances that modify soil structure and microtopography can create regeneration opportunities within otherwise unfavorable forest environments.

Windstorms represent an important natural disturbance in many temperate forests. When trees are uprooted during windthrow events, the root plate lifts soil from the forest floor and forms elevated structures known as tip-up mounds, often paired with adjacent pits (Long et al., 1998). These features create pronounced microtopographic variation that can alter light availability, soil aeration, drainage, and organic matter distribution (Schaetzl et al., 1988). Because tip-up mounds are elevated above the surrounding forest floor, they may also reduce accessibility to large herbivores such as deer, potentially creating refuges for seedling establishment.

Previous studies have shown that mounds can function as localized regeneration sites by reducing competition and increasing light availability (Kern et al., 2019; Don et al., 2024). However, most research has focused on above-ground drivers of regeneration success, with comparatively less attention given to the role of below-ground environmental

conditions in shaping microsite suitability. In particular, few studies have directly compared soil attributes between mound and ground microsites while simultaneously evaluating their influence on seedling survival.

A key but rarely tested assumption in forest restoration and regeneration ecology is that undisturbed forest floor microsites represent a neutral or suitable baseline for seedling establishment. Many restoration efforts implicitly assume that planting directly into the forest floor provides appropriate conditions for regeneration (Bertacchi et al., 2016). However, long-term ecological changes-including fire suppression, canopy closure, and alterations to soil biota-may have modified forest floor conditions in ways that increasingly favor certain species while disadvantaging others. If so, disturbance-generated microsites such as tip-up mounds may provide critical opportunities for regeneration under contemporary forest conditions.

Differences in regeneration strategies among tree species may further influence how they respond to these microsite environments. For example, red oak (*Quercus rubra*) represents a relatively conservative regeneration strategy, capable of persisting in shaded understories through long-term advanced regeneration in compact and moist soils (Kuehne et al., 2014; Nosko et al., 2022). In contrast, black cherry (*Prunus serotina*) is a fast-growing, disturbance-adapted species that requires well-drained soils and higher light availability for successful establishment (Marquis, 1990; Jagodziński et al. 2019). These contrasting life-history strategies suggest that the two species may respond differently to the soil and microtopographic conditions present on tip-up mounds compared with adjacent ground microsites.

Carolinian forests in southwestern Ontario provide an ideal system to investigate these dynamics. Although they occupy less than 1% of Canada's land area, these forests support over 25% of the country's species at risk (Nature Conservancy Canada, 2025). This region also experiences the highest frequency of tornadoes in Canada (Public Safety Canada, 2020; Munoz and Anyomi, 2026), resulting in frequent windthrow events that generate tip-up mounds. At the same time, white-tailed deer densities in this region are estimated to exceed the ecological carrying capacity of the forest ecosystem (HCA, 2013), intensifying browsing pressure on regenerating tree species.

The goal of this study was therefore to evaluate how tip-up mound microsites influence soil properties and seedling survival in a deer-browsed Carolinian forest. Specifically, we aimed to 1) Compare soil properties - including soil moisture, pH, organic matter, and texture - between tip-up mound microsites and adjacent ground microsites. 2) Determine

how these microsite attributes influence the survival of red oak (*Quercus rubra*) and black cherry (*Prunus serotina*) seedlings. 3) Document wildlife presence and browsing activity using trail camera observations. By linking soil conditions, microsite type/position, and species-specific regeneration strategies, this study aims to clarify whether tip-up mounds function as ecological filters that favor certain tree species relative to the surrounding forest floor.

2.0 Method

2.1 Study Site

This study was conducted in old-growth Carolinian forest in Hamilton, Ontario. Carolinian old-growth forests, restricted to southwestern Ontario, cover less than 1% of the country's land area yet support over 25% of Canada's at risk species (Nature Conservancy Canada, 2025), including Eastern Flowering Dogwood (*Cornus florida*) and American Chestnut (*Castanea dentata*) among others. Many species occur at their northern range limit (Pedlar et al., 2024), making them especially vulnerable to environmental change. This high concentration of regionally unique and endangered species underscores the importance of targeted conservation and restoration efforts. Fieldwork was carried out within local conservation areas including Tiffany Falls Conservation area, McMaster Forest Nature Preserve, Borer's Falls Conservation area, Dundas Valley Conservation area, Rockcliff trails area and Mineral spring area (Figure 1), spanning upland and ravine habitats. Forest canopy within the Hamilton township is dominated by northern temperate species such as sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), shagbark hickory (*Carya ovata*), with scattered black cherry (*Prunus serotina*) and white ash (*Fraxinus americana*). Invasive species, notably garlic mustard (*Alliaria petiolata*) and common buckthorn (*Rhamnus cathartica*), occur throughout the region.

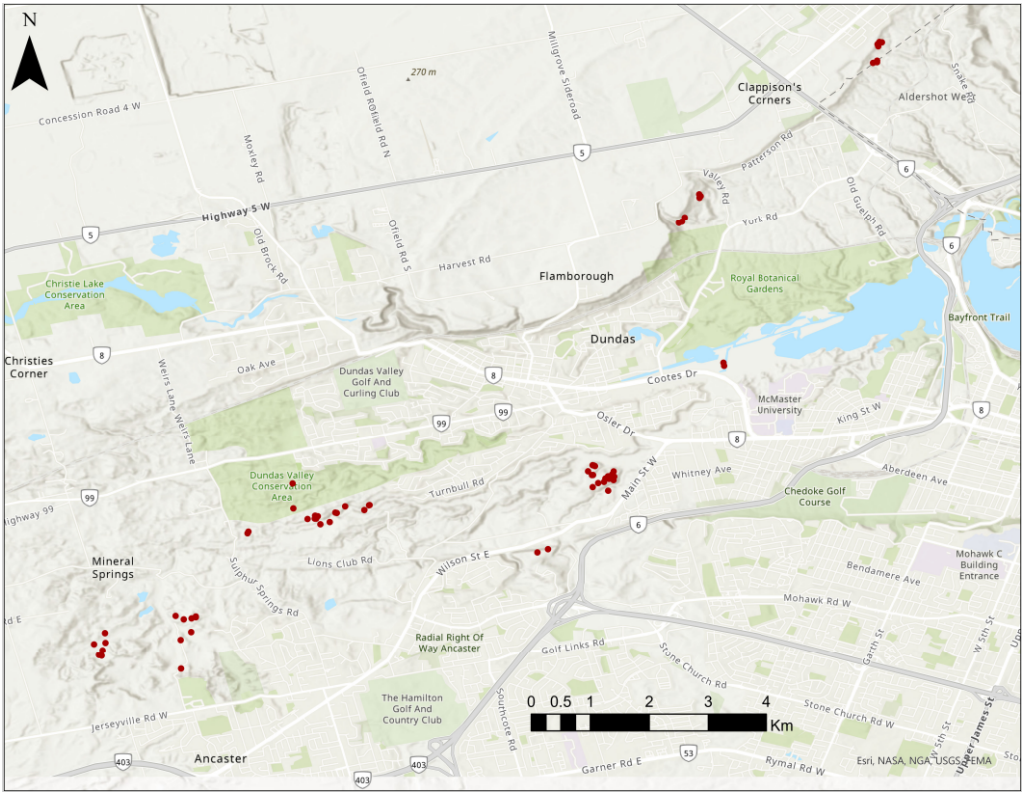


Figure 1. Location of tip-up mounds

2.2 Tip-up Mound Scouting

Field scouting was conducted to locate and assess tip-up mounds within the old-growth Carolinian forest in Hamilton which initially produced over 150 mounds and were then filtered to 84 mounds (Figure 1). To be considered suitable for inclusion; a) the mound had to be clearly detached from the pit, with no risk of the root plate tipping back into place - only fully uprooted and stable mounds were considered, b) the mound needed to be at least one meter in height from the base of the pit to ensure that it could potentially reduce access by deer browsing, c) there should be sufficient soil at the base of the uprooted tree to support the growth of seedlings. For each selected mound, GPS coordinates were recorded, and physical dimensions including mound height and width were measured.

2.3 Soil Sampling

For each selected mound, soil samples were collected from the mound top and from the nearby forest floor (ground) using a hand trowel to capture the environmental conditions directly experienced by young seedlings. Each soil sample was placed in a resealable ziplock bag, filling approximately 80 % of the bag's volume, then sealed, labeled, and

transported to the laboratory. Samples were stored in a refrigerator until subsequent analyses of soil organic matter (SOM), pH, moisture content, and texture.

2.4 Lab Analyses of Soil Samples

2.4.1 Soil moisture and organic matter

Soil moisture content was determined gravimetrically. For each sample, approximately 100 g of fresh soil was weighed and oven-dried at 105 °C for 24 h to remove water. The dried soil mass was recorded, and the gravimetric moisture content was calculated as:

$$\text{Moisture} = \frac{\text{Fresh mass} - \text{Dry mass}}{\text{Fresh mass}}$$

To quantify the proportion of organic matter in the soil, the dried soil samples, which contain both organic and inorganic components, were then placed into labeled ceramic crucibles and heated in a muffle furnace at 550 °C for approximately 3 hours to burn off all organic material (Hoogsteen et al. 2015). Their placement in the furnace was labelled on paper to keep track of them. After cooling for 1-2 hours, the remaining ash representing only the inorganic fraction was weighed again to obtain the ashed mass. The proportion of soil organic matter (SOM) was then calculated using the following equations:

$$SOM = \frac{Mass\ of\ dry\ soil - Mass\ of\ ashed\ soil}{Mass\ of\ dry\ soil}$$

2.4.2 Soil pH

Soil pH was measured using a pH probe calibrated using standard buffer solutions (pH 7.00 and pH 4.00). For each sample, 25 mL of deionized water was added to a 50 mL graduated cylinder, and soil was added gradually until the total volume reached 40 mL (≈1:1.6, v/v). Cylinders were sealed with Parafilm, shaken, and allowed to settle until two layers were visible, an upper layer (water solution) and a lower soil layer. The pH probe was carefully placed into the upper water layer without disturbing the soil layer, and readings were recorded once stable. Two replicate measurements were taken for each sample, and the mean pH value was calculated.

2.4.3 Soil Texture

Soil texture was determined using the mason jar sedimentation method. For each sample, a mason jar was filled to approximately half its volume with field-collected soil, after removing large stones and organic debris by hand. Deionized water was then added until the jar was nearly full, followed by approximately one tablespoon of powdered

dishwasher detergent to help disperse soil particles. The contents were thoroughly mixed using a large plastic stirring rod until all soil aggregates were fully broken apart and particles were suspended in the water. The suspension was then allowed to settle undisturbed for approximately two days, until three distinct layers formed including sand (bottom), silt (middle), and clay (top). Once the layers were clearly visible, the boundaries between layers were marked on the jar. The total height of the settled material and the height of each layer were then measured with a ruler. The percentage of sand, silt, and clay was calculated by dividing each layer's height by the total height of all layers. Soil texture class was determined by plotting these percentages on a standard USDA soil texture triangle.

2.5 Seedling Planting

Seedlings of two native tree species, Red oak (*Quercus rubra*) and Black cherry (*Prunus serotina*), both known to be highly preferred by deer (Barker, 2018), were sourced from Verbinnen's nursery (Dundas Ontario). Red oak seedlings were approximately 20 – 40 cm in height with a stem thickness of ~4 mm, while Black cherry seedlings were 10 – 20 cm tall with ~3 mm stem thickness. For each selected mound, one seedling was planted at the top of the mound and another in the nearby ground position, with species assigned randomly from the available stock rather than in controlled pairs. This design allowed independent evaluation of species responses to microsite conditions. In 11 mounds, more than one seedling was planted on top of the mound - these were treated as independent position-level observations in subsequent analyses. At the time of planting, all existing leaves were removed from each seedling, leaving only the terminal bud, so that the initial leaf count for all individual seedlings was zero.

2.6 Monitoring Seedling Survival

Following planting, seedlings were monitored two weeks after planting (first monitoring) and at the end of the summer (second monitoring). Seedlings were recorded as alive with leaves (green stem) and alive with no-leaf - both considered survivors, as both indicate the individual remained viable. Seedlings recorded as missing (absent from their planting location during monitoring) were excluded from calculations, as some may have been obscured by dense ground vegetation rather than dead or removed. Survival rate was calculated for all seedlings combined as the proportion of survivors (alive with leaves + alive with no leaf) relative to the total number of seedlings assessed (alive with leaves + alive with no leaf + dead).

2.7 Trail Camera Monitoring

To document wildlife presence and white-tailed deer browsing activities, 10-Browning

Strike Force FHDR motion-triggered trail cameras were installed next to tip-up mounds across the study area. Cameras were positioned with the tip-up mound as the primary focal point, while also including as much of the adjacent ground area as possible to capture a broader range of wildlife activity. This setup maximized the likelihood of detecting potential herbivores, while also documenting other fauna present in the vicinity. Camera was monitored every 2-weeks. Trail camera data covered June 20th to September 5th 2025 and were reviewed manually and with assistance from Grok 4 series AI model (xAI, 2025). Species richness was calculated as the number of unique species in an area.

2.8 Statistical Analysis

2.8.1 Data Quality Review

Seedling survival at the end of the growing season was the primary response variable, as it reflected cumulative survival following planting. A total of 84 tip-up mounds were initially mapped and measured, each containing two microsite positions i.e. mound top and adjacent ground. Although this design would normally produce 168 position-level observations (84 × 2), the initial dataset contained 178 observations due to two factors: (1) some mound tops contained more than one planted seedling (+15 datapoints), and (2) five ground positions were shared by two adjacent mounds that were next to each other, resulting in one soil sample representing both mounds (a total of 5 datapoints). Data filtering was conducted at the microsite position level, meaning that if either the mound top or ground position lacked valid measurements, only that position was removed rather than excluding the entire mound. Of the initial 178 observations, 47 were excluded due to incomplete or unreliable data. These exclusions included: (1) positions where no seedlings were planted (n = 12), (2) missing soil samples (n = 13), (3) seedlings with undetermined survival status (n = 4), (4) unreliable soil organic matter measurements due to container damage during loss-on-ignition (n = 9), and (5) invalid soil texture classifications resulting from inconsistent duplicate measurements or non-classifiable inorganic material (n = 9). Following these exclusions, the final dataset consisted of 131 position-level observations used in subsequent analyses.

2.8.2 Comparison of microsite soil attributes

Differences in soil properties between mound-top and ground microsites were evaluated using appropriate statistical tests based on data distribution. Welch's *t*-tests were used to compare soil moisture and soil pH between microsite positions, as these variables satisfied assumptions of approximate normality but exhibited unequal variances. Soil

organic matter (SOM), which did not meet normality assumptions, was compared between microsites using a Wilcoxon rank-sum test.

2.8.3 Seedling Survival Analysis

Seedling survival was analyzed as a binary response variable (alive or dead at the end of the monitoring period). Survival patterns were first summarized descriptively by species and microsite position to identify general trends. To evaluate the drivers of seedling survival, we fitted a generalized linear model (GLM) with a binomial error distribution and logit link function. Predictor variables included soil moisture, soil organic matter, soil pH, soil texture, species identity, and microsite position (mound top vs ground), along with their interactions. Continuous predictors were standardized (centered and scaled), and categorical variables were coded using sum contrasts. Statistical significance of predictors was assessed using Type III likelihood-ratio χ^2 tests implemented in the *car::Anova* function in R. A set of 37 candidate models representing different combinations of microsite attributes and interaction terms was evaluated (Table S1). These models allowed testing hypotheses regarding the relative importance of soil properties and microsite position in determining seedling survival. The data shows that soil moisture is a critical driver of seedling survival. To further visualize survival responses along the soil moisture gradient, soil moisture values were divided into quartiles. Survival proportions were then calculated for each quartile by species and microsite position.

2.8.4 Environmental Drivers of Soil Moisture

To identify factors influencing soil moisture, we fitted a multiple linear regression model with soil moisture as the response variable:

[1] Moisture ~ SOM + Texture + Position + pH

Soil organic matter (SOM) and pH were treated as continuous predictors, while soil texture class and microsite position were treated as categorical variables. Model significance was evaluated using Type III ANOVA (*car::Anova*, type = 3). Effect sizes were quantified using partial η^2 (*effectsize::eta_squared*) and partial R^2 (*rsq::rsq.partial*).

The relationship between soil moisture and soil texture (ranked from coarse to fine) was evaluated using Spearman's rank correlation coefficient because visual inspection suggested a monotonic but potentially non-linear relationship.

The relationship between soil moisture and soil organic matter was further examined using a nonlinear saturating exponential model:

[2] Moisture = Asym × (1 − e^(−b × SOM))

where *Asym* represents the asymptotic maximum moisture and *b* represents the rate parameter. The model was fitted using nonlinear least squares (*nls*) in R, with starting parameter values selected based on exploratory analysis. Model fit was assessed using the coefficient of determination (R^2) calculated from residual and total sums of squares.

2.8.5 Wildlife Metrics

Wildlife species richness was calculated as the number of unique species detected per area. Total white-tailed deer detected by the cameras was also reported by area. The relationship between number of white-tailed deer detected and wildlife species richness was quantified using Spearman's rank correlation coefficient.

All statistical analyses were conducted in R Studio.

3.0 Results

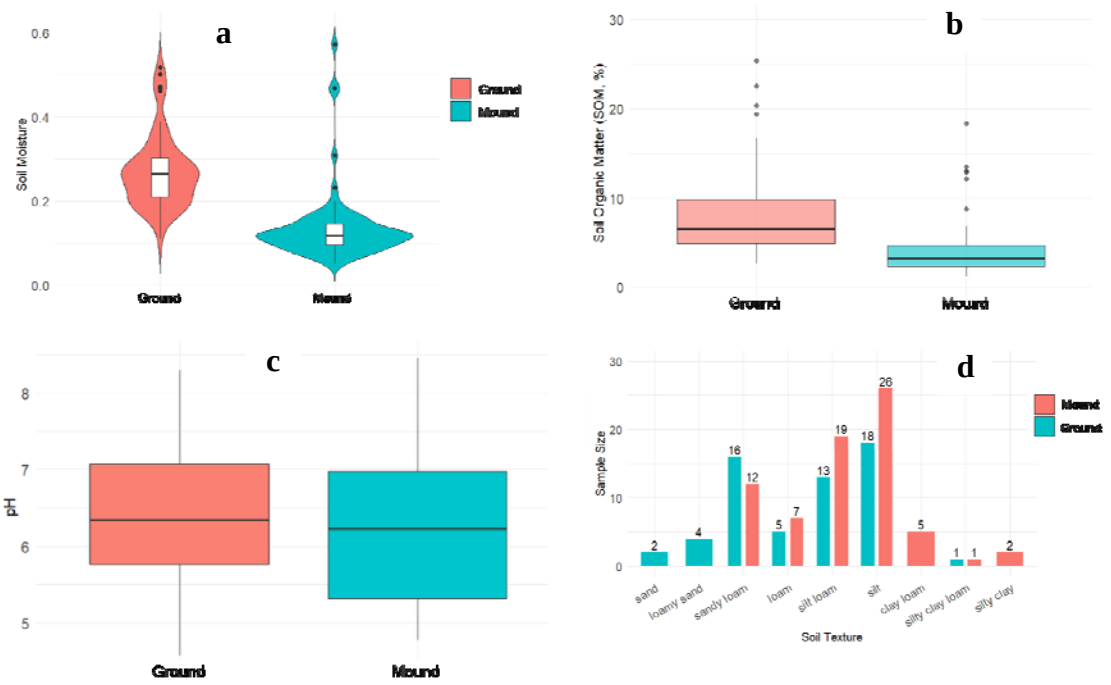
3.1 Differences in soil attributes between microsite positions

Soil moisture differed significantly between microsite positions (Welch's t-test: $t = 8.68$, $df = 124.21$, $p < 0.001$). Mean soil moisture was approximately twice as high in ground microsites (0.270 ± 0.087 SD, $n = 59$) compared with mound tops (0.137 ± 0.088 SD, $n = 72$). Median moisture values were 0.265 for ground microsites and 0.118 for mound tops. Interquartile ranges did not overlap (ground: 0.210–0.303; top: 0.095–0.145), indicating consistently wetter ground soils and consistently drier mound-top soils (Figure 2a).

Soil organic matter (SOM) was also significantly higher in ground microsites (median = 0.066, IQR = 0.050) than on mound tops (median = 0.033, IQR = 0.023; Wilcoxon rank-sum test: $W = 3452$, $p < 0.001$; Figure 2b).

In contrast, soil pH did not differ significantly between microsite positions (Welch's t-test: $t = 0.968$, $df = 128.97$, $p = 0.335$). Median pH values were 6.35 for ground microsites and 6.22 for mound tops (Figure 2c).

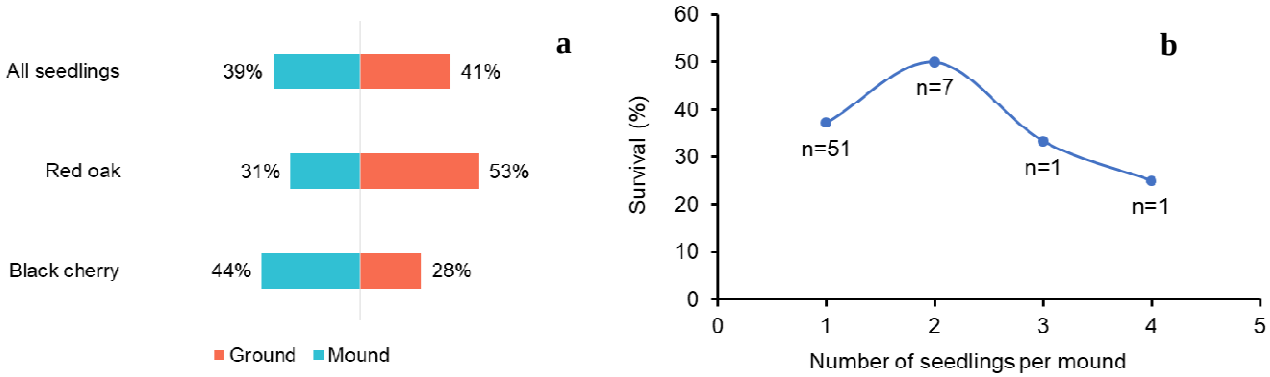
Soil texture differed between microsite positions, with finer-textured soils more common on mound tops and coarser-textured soils more frequent in ground microsites (Figure 2d).



303 Figure 2. a) soil moisture by microsite type (position), b) SOM by microsite type, c) soil
304 pH by microsite type (position), d) distribution of soil texture and by microsite position.

305 *3.2 Seedling survival dynamics*

306 Across both species combined, seedling survival was 39% on mound tops (*n=72*) and 41%
307 on ground microsites (*n=59*) (Figure 3a). Species responses differed between microsite
308 positions. Black cherry showed higher survival on mound tops (44%, *n* = 43) compared
309 with ground microsites (28%, *n* = 29). In contrast, red oak survival was higher on ground
310 microsites (53%, *n* = 30) than on mound tops (31%, *n* = 29) (Figure 3a). Seedling
311 survival also varied slightly with the number of seedlings planted per mound. Mounds
312 with one seedling (*n* = 51) had a mean survival rate of 37%, whereas mounds with two
313 seedlings (*n* = 7) showed a higher survival rate (50%). Mounds containing three (*n* = 1)
314 or four seedlings (*n* = 1) showed lower survival rates of 33% and 25%, respectively
315 (Figure 3b).



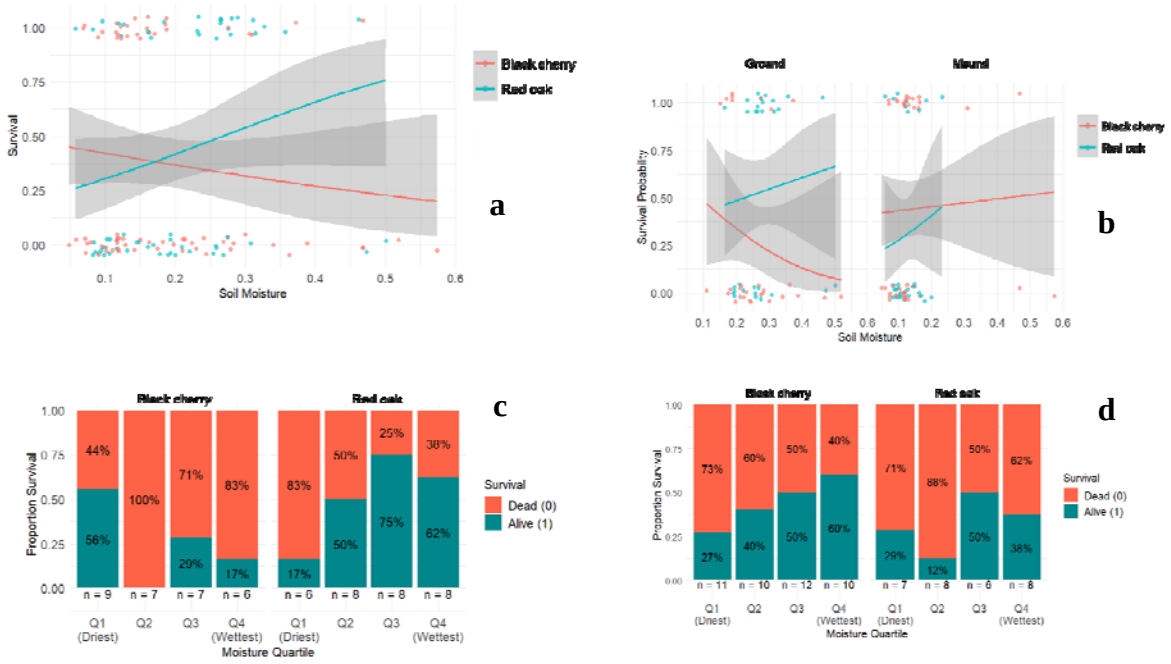
316 Figure 3. Seedling survival by a) species type (Red oak vs. Black cherry) and microsite
317 position (mound vs. ground), b) the number of seedlings planted per mound.

318 *3.3 Effects of microsite attributes on seedling survival*

319 Generalized linear modeling indicated that soil moisture was a significant predictor of
320 seedling survival ($p = 0.030$), with a strong interaction between moisture and species
321 identity (Species × Moisture, $p = 0.019$; Table S1).

322 Red oak survival probability increased with increasing soil moisture, whereas black
323 cherry survival probability decreased as soil moisture increased. These contrasting
324 responses were evident across microsite positions. Because mounds were consistently
325 drier than ground microsites (Figure 4b), predicted survival probabilities differed
326 accordingly between positions.

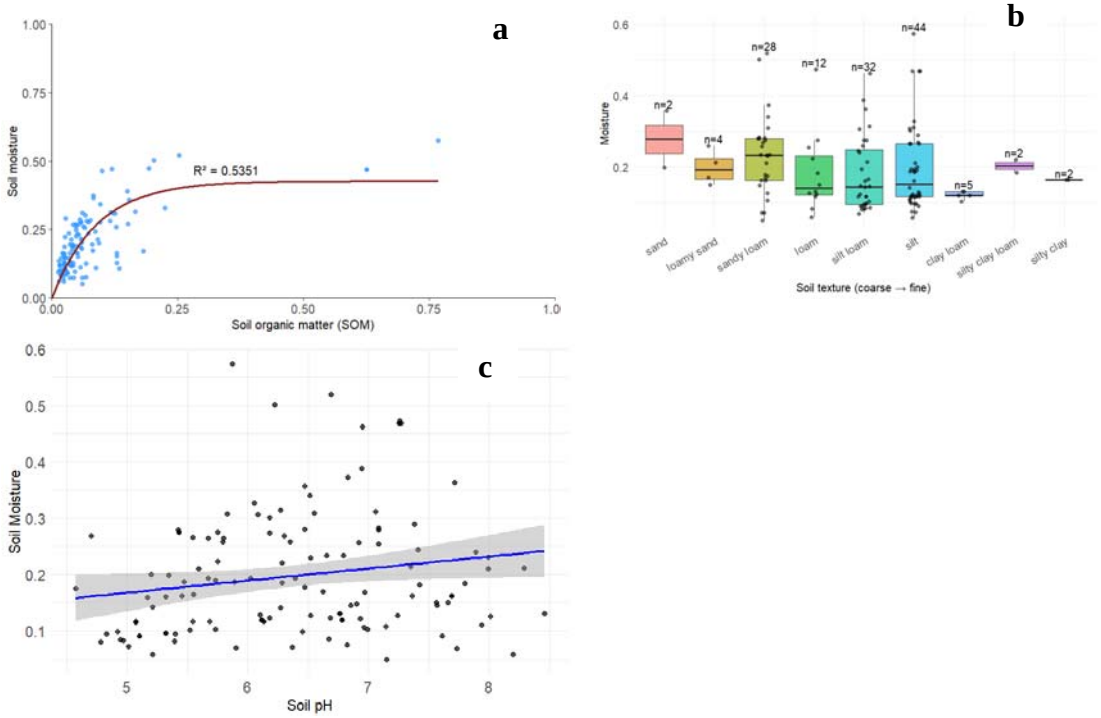
327 Quartile analyses further illustrated these patterns. With ground microsites (Figure 4c),
328 black cherry survival was highest in the driest quartile (Q1: 56%) and declined in wetter
329 quartiles (Q2: 0%, Q3: 29%, Q4: 17%). In contrast, red oak survival was lowest in the
330 driest quartile (Q1: 17%) and increased in wetter quartiles (Q2: 50%, Q3: 75%, Q4: 62%).
331 With mound microsites (Figure 4d), black cherry survival increased with increasing
332 moisture, rising from 27% in the driest quartile (Q1) to 60% in the wettest quartile (Q4).
333 Red oak survival was lowest in the drier quartiles (Q1: 29%, Q2: 12%) and higher in
334 wetter quartiles (Q3: 50%, Q4: 38%).



335 Figure 4. Seedling survival by a) species and soil moisture, b) species, soil moisture and
336 microsite type/position. Survival by species and moisture quartile for c) ground
337 microsite/position, d) mound microsite type/position

338 *3.4 Environmental drivers of soil moisture*

339 Soil moisture increased nonlinearly with soil organic matter (SOM), explaining 53.5% of
340 the variance in moisture (r=0.665, Figure 5a). This suggests that higher organic matter
341 content contributes to increased water retention in ground microsites. Microsite
342 type/position also had a strong effect on soil moisture ($p < 0.001$), with ground microsites
343 consistently wetter than mound microsite (Figure 2a). Soil moisture showed a weak but
344 significant negative correlation with soil texture fineness (Spearman's $\rho = -0.18$, $p =$
345 0.040; Figure 5b). Coarser soils were associated with higher moisture values. This
346 relationship likely reflects the co-variation between soil texture and SOM across
347 microsites rather than a direct causal relationship between texture and moisture. Soil pH
348 showed a weak but significant positive relationship with soil moisture ($\beta = 0.021$, $R^2 =$
349 0.032, $p = 0.039$; Figure 5c).



350 Figure 5. Variation in soil moisture by a) soil organic matter (SOM), b) soil texture, and c)
351 soil pH.

352 *3.5. Wildlife activity*

353 Wildlife species richness ranged from 2 to 7 across conservation area and the number of
354 white-tailed deer detected ranged from 11 to 385. Conservation areas with relatively low
355 wildlife species richness recorded higher white-tailed deer numbers (*rho=-0.66, p>0.05*).
356 White-tailed deer observed has various fur coloration and pattern (Figure S1). A young
357 white-tailed deer is often seen with an adult browsing typically during the day (Figure
358 S2). A mature male deer (buck) is typically seen browsing at night alone (Figure S3).
359 Coyotes and racoons were seen mostly at night across the conservation areas (Figure S4).
360 Wild turkeys and some bird species were also observed by the mounds during the day
361 (Figure S5).

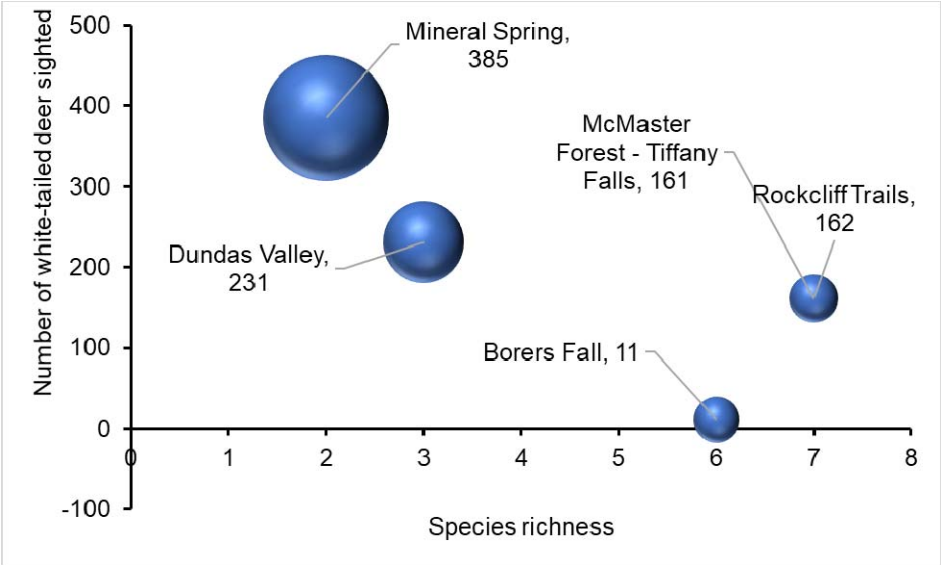


Figure 6. Number of white-tailed deer (detected by trail camera) by the wildlife species richness. The size of the bubble refers to the duration of monitoring which ranged from 20 to 56 days (June - September 2025).

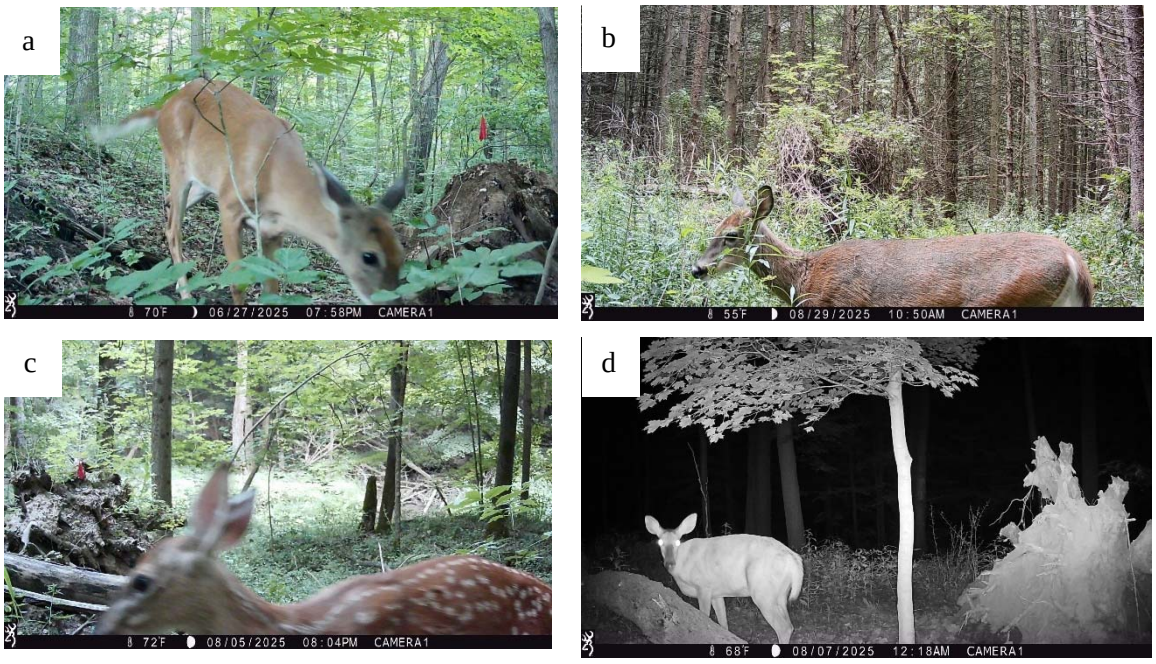


Figure S1 a) smooth shiny brown fur of white-tailed deer browsing at Borer's fall conservation area, Hamilton, Ontario. b) A reddish-brown fur of deer (*Odocoileus virginianus*) detected at the Mineral spring area, Hamilton, Ontario. c) White-tailed deer with smooth reddish-brown fur and white spots detected at the Dundas valley conservation area. d) White-tailed deer at McMaster Forest Nature Preserve -Tiffany falls conservation area suspected to be leucistic (appearance may be due to night vision)

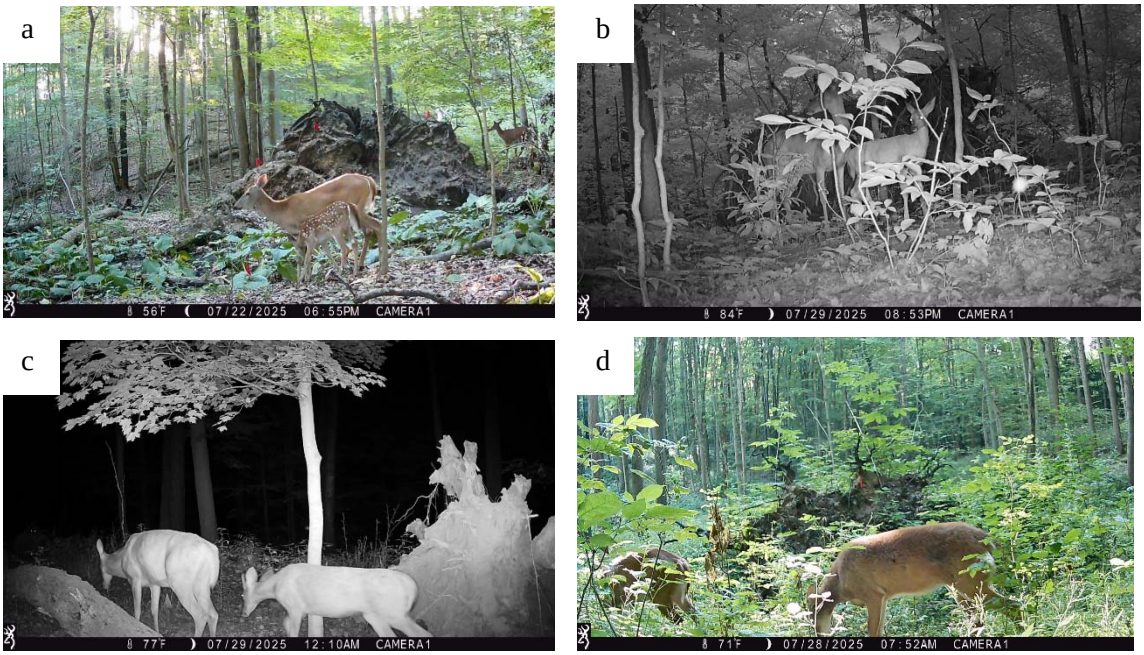


Figure S2 a) A young deer and likely mother (*Odocoileus virginianus*) detected at the Mineral spring area, Hamilton, Ontario. b) White-tailed deer (*Odocoileus virginianus*), likely mother and young detected at the Rockcliff trails area, Hamilton, Ontario. c) A young and adult white-tailed deer (*Odocoileus virginianus*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario. D) A young and adult white-tailed deer (*Odocoileus virginianus*) detected at the Dundas valley conservation area, Hamilton, Ontario.

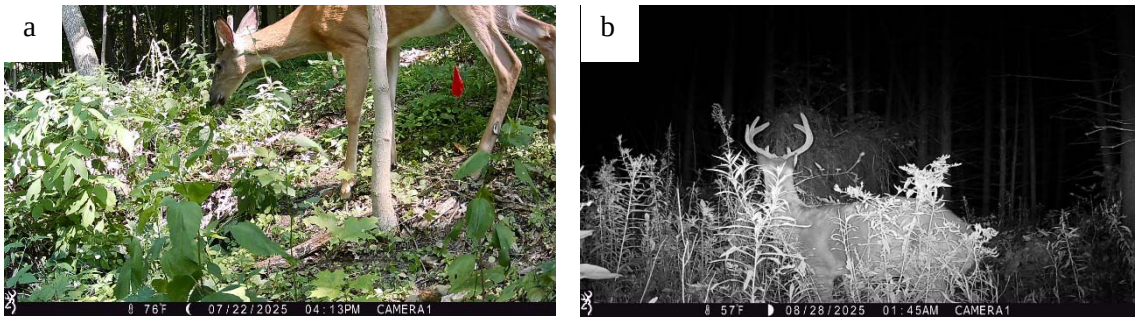


Figure S3 a) A young buck (*Odocoileus virginianus*) browsing at the Tiffany Falls conservation area in Hamilton, Ontario. b) A mature buck detected at the Mineral spring area, Hamilton, Ontario.

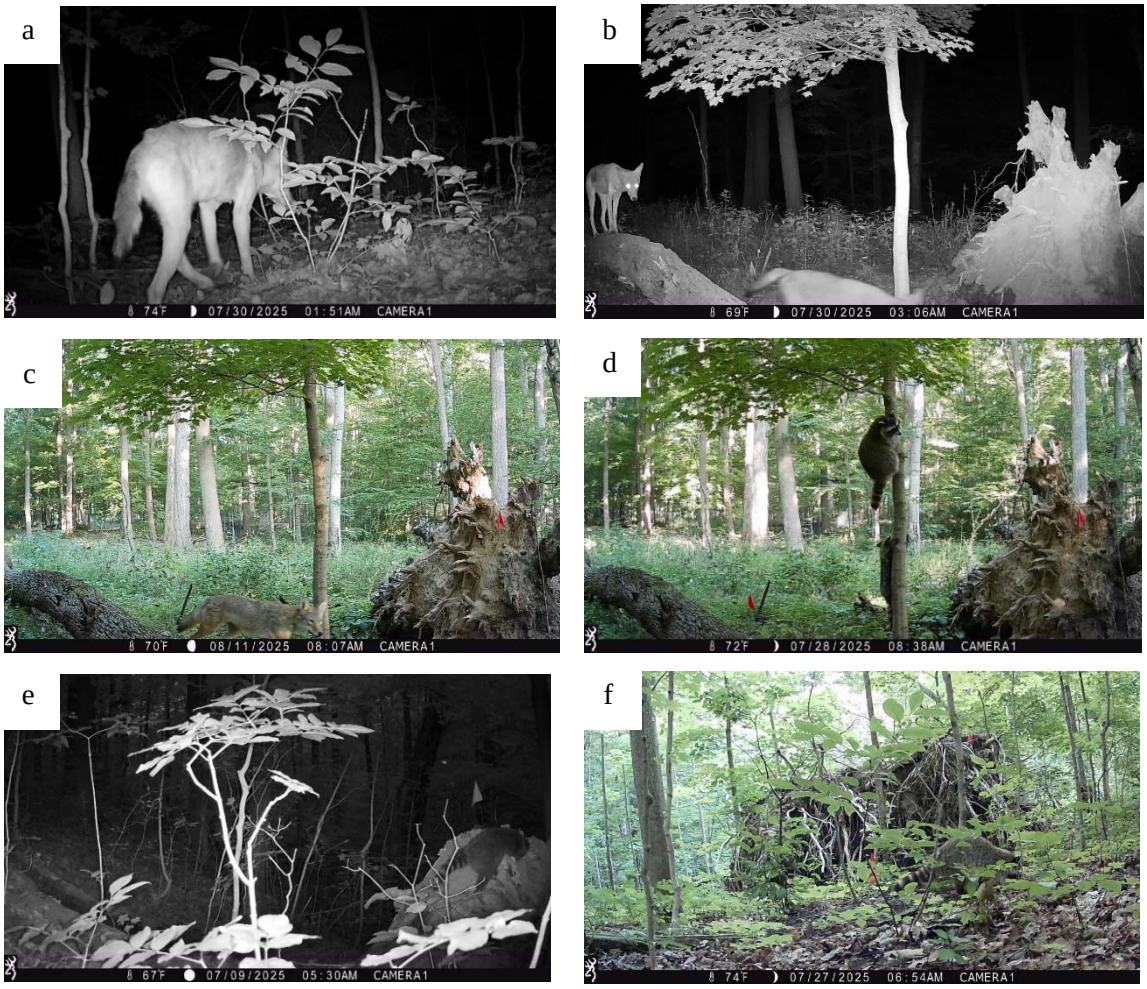


Figure S4 a) A coyote (*Canis latrans*) detected at the Rockcliff trails area, Hamilton, Ontario, b) two coyotes (*Canis latrans*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario, c) a coyote (*Canis latrans*) detected during the day at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario. d) two racoons (*Procyon lotor*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario, e) Raccoon (*Procyon lotor*) detected at the Borer's fall conservation area, Hamilton, Ontario, f) Raccoon (*Procyon lotor*) detected at the Rockcliff trails area, Hamilton, Ontario.

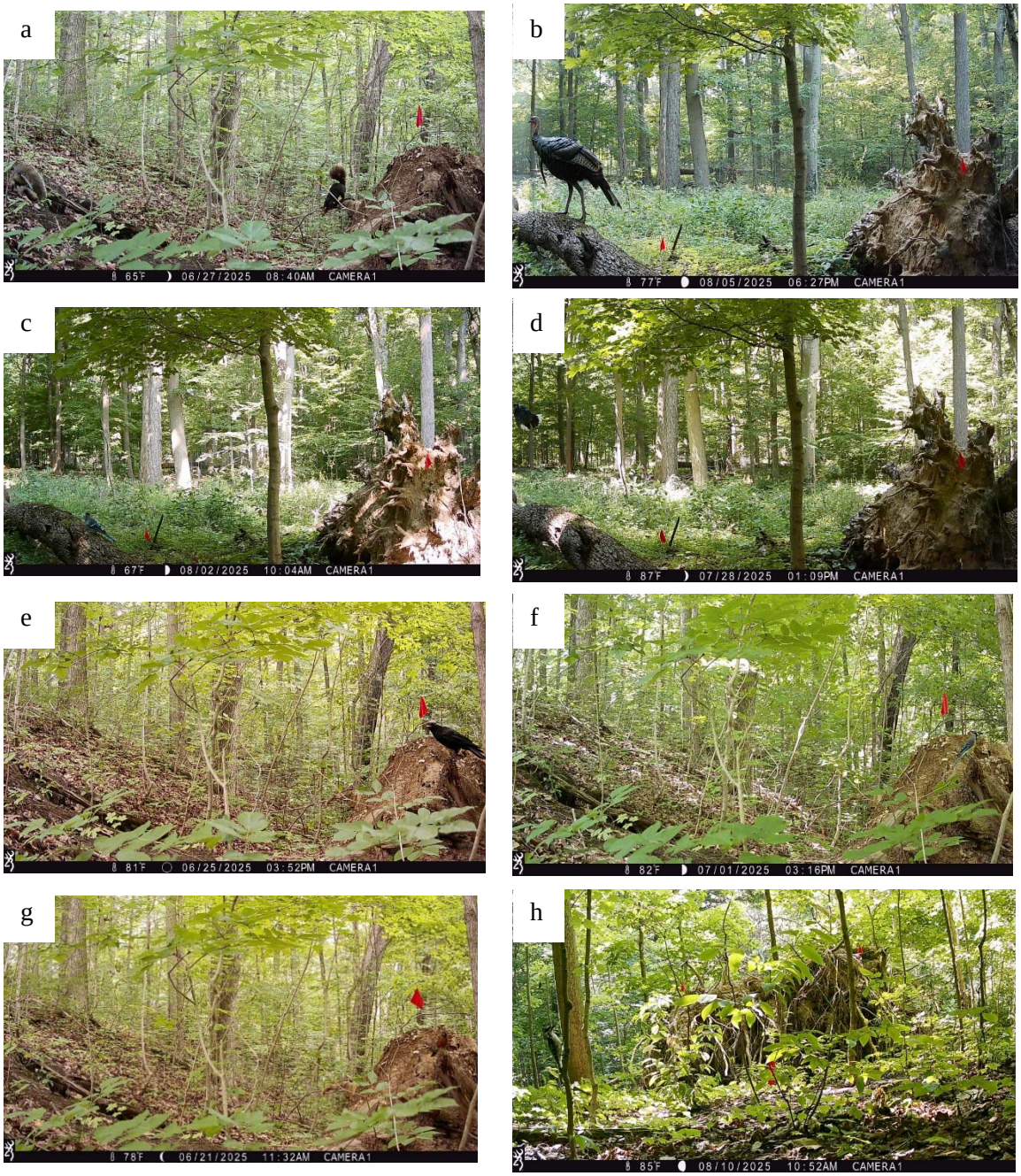


Figure S5 a) eastern gray squirrel of both black and grey coloration (*Sciurus carolinensis*) were observed everywhere. b) A wild turkey (*Meleagris gallopavo*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario, c) a downy wood pecker *(Dryobates pubescens*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario, d) an eastern king bird (*Tyrannus tyrannus*) detected at the McMaster Forest Nature Preserve (Tiffany Falls Conservation area), Hamilton, Ontario, e) American crow (*Corvus brachyrhynchos*) detected at the Borer's fall conservation area, Hamilton, Ontario. f) Blue jay (*Cyanocitta cristata*) detected at the Borer's fall conservation area, Hamilton,

Ontario, g) American robin (*Turdus migratorius*) detected at the Borer's fall conservation area, Hamilton, Ontario, h) a downy wood pecker *(Dryobates pubescens*) detected at the Rockcliff trails area, Hamilton, Ontario. Please note that the quality of photos is not the best for accurate identification of bird species.

4.0 Discussion

This study examined soil attributes across more than 80 microsites created by tree uprooting (tip-up mounds) compared with adjacent ground microsites and evaluated their influence on seedling survival during the unusually warm summer of 2025 in a Carolinian old-growth forest in Hamilton. Our results show that soil moisture was the strongest predictor of seedling survival, with significant interactions between moisture, species identity, and microsite position. Although treefall disturbances generate distinct microtopographic environments, their ecological effects appear to operate primarily through differences in moisture availability. These moisture conditions interact with species-specific physiological tolerances, producing contrasting survival patterns for red oak and black cherry.

4.1 Moisture as the primary driver of microsite effects

The contrasting survival patterns of red oak and black cherry across mound-top and ground microsites can largely be explained by differences in soil moisture and species-specific responses to these gradients. Ground microsites were consistently wetter than mound tops, exhibiting nearly twice the mean moisture content and a broader moisture range (Figure 2a), whereas mound tops were relatively dry due to their elevated and exposed position. Red oak survival increased with increasing moisture, consistent with its known tolerance of moist soils (e.g. Sander, 1990; Kuehne et al., 2014; Nosko et al., 2022). In contrast, black cherry survival declined as moisture increased on ground microsites, suggesting sensitivity to oxygen limitation or waterlogging in compacted soils. When examined within each microsite type, these species-specific responses become clearer. On wetter ground microsites, conditions aligned with oak's moisture preferences, producing higher oak survival and lower cherry survival. Conversely, the drier mound-top microsites provided relatively more favorable conditions for cherry while limiting oak survival (Figure 4a, 4b).

Quartile analyses further illustrate these dynamics. On ground microsites (Figure 4c), black cherry-often described as drought-tolerant (Barkley, 2007) - achieved its highest survival in the driest soils (Q1, 56%), whereas red oak survival in these soils was only 17%, indicating vulnerability to desiccation stress. Oak survival increased substantially in

wetter ground soils, reaching up to 71% in Q3, while cherry survival declined under these wetter conditions. On mound tops, however, black cherry survival increased with moisture, reaching 60% in the wettest quartile (Q4). This pattern suggests that moisture itself is not inherently detrimental to cherry seedlings. Rather, cherry appears sensitive to oxygen limitation associated with poorly aerated soils, a condition common on the compacted forest floor. Physiological studies indicate that oxygen limitation under waterlogged conditions can impair black cherry performance (Wang et al., 2023). Tip-up mounds provide well-drained and aerated soils, allowing oxygen to remain available in the rooting zone even when moisture increases. Under these conditions, cherry seedlings can benefit from both water availability and adequate aeration. Red oak, meanwhile, maintained relatively low survival across all moisture levels on mound tops (≤50%). Because mound tops are generally drier than ground microsites, they rarely provide the higher moisture conditions that favor oak survival. These findings indicate that microsite effects arise largely from moisture regimes created by microtopography rather than microsite position alone. The unusually warm summer of 2025 may have contributed to the contrast.

4.2 Life-history strategies and species responses to tip-up mounds

Red oak and black cherry represent contrasting regeneration strategies that strongly influence their responses to microsite conditions. Oak seedlings grow slowly and allocate early resources toward deep and robust root systems rather than rapid above-ground growth. This strategy allows oak to persist in shaded understories as part of advanced regeneration (Dillaway and Stringer 2006, Nosko et al., 2022), where seedlings remain suppressed until canopy openings permit accelerated growth. Black cherry follows a contrasting strategy. It is a fast-growing, shade-intolerant species that relies on rapid establishment following disturbance (Marquis, 1990). Its fine root system requires well-aerated soils, and its growth is closely tied to light availability. Consequently, cherry performs poorly in compacted and shaded ground soils but thrives in disturbed microsites that provide aeration, moisture, and increased light. Although black cherry is frequently described as drought-tolerant, its apparent advantage in drier soils may partly reflect avoidance of oxygen limitation in compacted ground soils rather than a direct preference for drought conditions. Tip-up mounds expose loose mineral soil, reduce litter layers, and open canopy gaps, creating conditions that closely match the ecological requirements of this disturbance-adapted species. Red oak seedlings, in contrast, showed higher survival on ground microsites, particularly in wetter soils (Figure 4c). This pattern reflects oak's conservative life-history strategy. Oaks tolerate low light and higher soil moisture, often

persisting for extended periods beneath closed canopies. However, their survival declined on mound tops, likely because these elevated microsites lack sufficient moisture for early establishment.

4.3 Tip-up mounds as ecological filters

Our findings suggest that tip-up mounds function as ecological filters (Keddy, 1992) that selectively favor species possessing certain functional traits. Although red oak and black cherry coexist within the same forest, they exhibit contrasting ecological strategies. Cherry is a disturbance-adapted species requiring high light, loose soils, and effective drainage, whereas oak is a slower-growing species capable of persisting in shaded, compacted, and moist environments. Tip-up mounds modify several environmental factors simultaneously. They increase light availability, improve soil aeration through loosened soil structure, and enhance drainage due to their elevated position (Lutz 1940; Yoshida, 2021). These changes alleviate many of the establishment constraints faced by cherry while simultaneously removing the stable moisture conditions that benefit oak. This relationship is illustrated in our conceptual model, which frames tip-up mounds as environmental filters that promote disturbance-adapted species while disadvantaging more conservative species. By linking disturbance characteristics such as aeration, drainage, and light availability to species' functional traits, this framework provides a testable approach that may apply across different disturbance contexts and forest types.

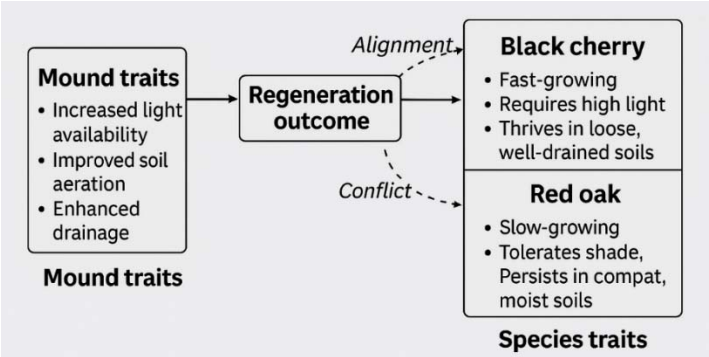


Figure 7. A conceptual framework of tip-up mounds as an environmental filter

4.4 Changing forest floor conditions as long-term environmental filters

Our findings raise the possibility that modern forest floor conditions may increasingly constrain regeneration for certain species. Much of the literature on regeneration failure has focused on external pressures such as deer browsing or invasive species, implicitly assuming that the forest floor itself remains suitable for seedling establishment. However, long-term ecological changes may have altered these conditions in ways that influence

regeneration dynamics. Decades of fire suppression, canopy closure, and earthworm invasion have been associated with increased soil compaction, higher moisture retention, and reduced aeration in many temperate forests (Frelich et al., 2006; Nowacki and Abrams, 2008; Tsogbadrakh et al., 2024). These changes may lead to chronically low oxygen availability in the rooting zone, particularly in undisturbed ground microsites. For species such as black cherry that require well-drained and aerated soils, these conditions may limit successful establishment even when other pressures such as herbivory are absent. At the same time, these altered soil conditions may favor species that tolerate shaded, compacted, and moist environments. In this study, red oak showed higher survival on ground microsites, particularly under wetter conditions, reflecting its ability to persist in low-light understories and soils with reduced aeration. Such conditions may therefore act as environmental filters that selectively favor species possessing traits suited to shaded and mesic environments. Similar shifts in forest composition have been documented across eastern North America, where mesic species have increased while disturbance-adapted or drought-tolerant species have declined (Woodbridge et al., 2022). In this context, contemporary forest floors may increasingly function as long-term environmental filters that shape regeneration patterns and influence future community composition. If these conditions persist over time, forest understories may continue to shift toward species that match the prevailing environmental constraints, reinforcing the decline of species such as black cherry in undisturbed ground microsites.

4.5 Wildlife dynamics

High numbers of white-tailed deer recorded in several conservation areas further emphasizes the importance of elevated microsites such as tip-up mounds, which may partially reduce access by herbivores and thereby increase seedling persistence.

5.0 Conclusion

Taken together, our results indicate that regeneration in this forest is shaped by two contrasting environmental filters associated with microsite conditions. Tip-up mounds favor species that require well-drained and aerated soils, such as black cherry, whereas the surrounding forest floor characterized by higher moisture, greater compaction, and persistent shading favors species tolerant of these conditions, such as red oak. These contrasting microsites create distinct regeneration niches, illustrating how small-scale disturbances restructure regeneration dynamics through their effects on soil moisture and microenvironmental conditions. From a restoration perspective, these findings challenge the common assumption that planting directly into undisturbed forest floor soils is universally suitable for seedling establishment. Instead, disturbance-generated microsites

such as tip-up mounds may provide critical opportunities for regeneration by creating environmental conditions that align with the ecological requirements of certain species. More broadly, our results highlight how microtopographic variation and species functional traits interact to shape regeneration patterns in temperate forests experiencing high browsing pressure and changing disturbance regimes.

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Supplementary documents

Table S1. Seedling survival candidate models

Model	k	AIC	DeltaAIC	BIC
Survival ~ Moisture_c:Species	3	177.6133	0	186.2389
Survival ~ Species:Position	5	178.5693	0.956021	190.0701
Survival ~ Species * Position	4	178.5693	0.956021	190.0701
Survival ~ pH_c	2	178.9725	1.359179	184.7229
Survival ~ Moisture_c:Species:Position	5	179.3041	1.690823	193.6801
Survival ~ Moisture_c * Species	4	179.3651	1.751825	190.8659
Survival ~ SOM_c	2	179.6418	2.0285	185.3922
Survival ~ Species	2	179.6782	2.064919	185.4286
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Species + Moisture_c:Position	8	179.7747	2.161396	202.7763
Survival ~ Moisture_c	2	179.8745	2.261192	185.6249
Survival ~ Position	2	179.9563	2.342952	185.7066
Survival ~ pH_c + Species	3	180.755	3.141748	189.3806

Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Position + Species:Position	8	180.8008	3.187541	203.8024
Survival ~ pH_c:Species	3	180.8339	3.220649	189.4595
Survival ~ SOM_c + Species	3	181.3647	3.75137	189.9903
Survival ~ Moisture_c + Species	3	181.5731	3.959837	190.1987
Survival ~ Moisture_c:Position	3	181.6032	3.98986	190.2288
Survival ~ SOM_c:Species	3	181.6172	4.003898	190.2428
Survival ~ Species + Position	3	181.6559	4.042646	190.2815
Survival ~ Moisture_c + Position	3	181.8744	4.261143	190.5
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Species:Position	7	182.284	4.670703	202.4104
Survival ~ pH_c * Species	4	182.5885	4.975212	194.0893
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Species	7	183.2554	5.642088	203.3818
Survival ~ Moisture_c * Species + Position + pH_c + SOM_c	7	183.2554	5.642088	203.3818
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Position	7	183.2682	5.654891	203.3946
Survival ~ Moisture_c * Position + Species + pH_c + SOM_c	7	183.2682	5.654891	203.3946
Survival ~ SOM_c * Species	4	183.3158	5.702494	194.8166
Survival ~ Moisture_c + Species + Position	4	183.5697	5.956352	195.0704
Survival ~ Moisture_c * Position	4	183.5991	5.985809	195.0999
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Species + Species:Position	8	184.0397	6.426412	207.0413
Survival ~ Moisture_c * Species * Position	8	184.4637	6.850412	207.4653
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c	6	184.8499	7.236574	202.1011
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Species + Moisture_c:Position + Soil.Texture	16	191.0244	13.41114	237.0276
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Species:Position + Soil.Texture	15	191.9977	14.38441	235.1257
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Species + Soil.Texture	15	194.0934	16.48015	237.2214
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Moisture_c:Position + Soil.Texture	15	194.1215	16.50819	237.2494
Survival ~ Moisture_c + Species + Position + pH_c + SOM_c + Soil.Texture	14	195.3754	17.7621	235.6282

657