The Effects of *Pteridium aquilinum* (Bracken fern) on Understory Microclimate and Seedling Success in Temperate Forests

By

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Ecology and Evolutionary Biology
at The University of Michigan
April 2025

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Acknowledgments

This project is my love letter to science, it's the culmination of late nights and early mornings, endless reading and writing, and pure willpower (this took tremendous amounts of it). The past two years have been invaluable, and this journey has been amazing because of all the wonderful people in my life. To my advisor, Aimée Classen, I am forever grateful to you; thank you for taking me into your lab and constantly reminding me that science is a continuous learning process. To my fellow Classen (and Sanders) lab members: Brenda, Olivia, Isabel, Karin, Emma, Julia, Kate, Anna, and Peter—working alongside such amazing people has been a transformative experience for me; thank you for your assistance with fieldwork, R coding, and everything in between. To my committee members, Inés Ibáñez and Mia Howard, thank you for your guidance and advice, it helped shape this project. To my frontiers cohort, Denise, David, and Yamile: Thank you. It has been a pleasure to learn and grow with you all. Thank you to George Kling for always being willing to talk science and have a heart-to-heart. Thank you to the Frontiers admin: Liliana Cortés-Ortiz, Justin Hopper, Gideon Bradburd, and Rory Walsh. To the UMBS staff: Candice Everett, Jumanah Saadeh, Jason Tallant, Helen Habicht, Adam Schubel, and Sherry Webster, thank you. To all of my mentees, Amy, Ada, Catherine, Max, Kayenne, Khylie, Lamees, and Lena—you made my first experiences as a teacher and a mentor very special, so thank you. To my many lovely friends, but especially Alyssa, Savannah, Jodi, Dani, Askya, Angie, Cheyenne, Ariel, and Manar, you all reassured me that I could do this, and it turns out you were right—thank you; I love you guys. To my family, the McCloud Clan, I love you all; I am so thankful for your unwavering support. Lastly, I thank those who financially supported this research: the UMBS Graduate Student Fellowship, the Rackham Research Grant and Rackham Merit Fellowship, and the EEB Block Grant.

Abstract

Understories influence biodiversity and ecological processes and are a defining element of forest ecosystems, as they can contain up to 90% of plant species in temperate forests. Bracken Fern (*Pteridium aquilinum*) often dominates forest understory communities globally, including those in Northern Michigan. Dominant understory species affect ecosystems proportional to their high abundance. To explore how bracken fern impacts microclimate, plant diversity, and seedling success, I asked two overarching questions: (1) how does natural variation in density of a dominant species impact understory abiotic conditions and plant diversity? (2) How does the cover and removal of a dominant species affect seedling survival and success? I established a bracken fern removal experiment in three forests at the University of Michigan Biological Station (UMBS). I paired plots where the bracken fern cover was left intact (natural) with plots where the bracken fern cover was removed (removal), across a gradient of bracken fern densities (0, 25, 50, 75 100% cover). Soil moisture and temperature varied across the gradient of bracken fern density in natural plots. At peak growing season, soil moisture variation was the highest in 50% natural plots. We did not detect a significant difference in seedling survival across the gradient of bracken fern density in either natural or removal plots. Seedling leaf area, specific leaf area, and leaf carbon-to-nitrogen ratios were not significantly affected by the removals. In 75% natural plots exclusively, removal had a negative effect on seedling green leaf % N. Our results highlight that dominant understory species differentially influence understory microclimate and seedling traits in temperate forests, but their impact is not proportional to cover. Instead, bracken fern cover may be both facilitative and inhibitory for seedling growth and establishment, showcasing the dynamic role of dominant species in temperate forests.

Introduction

Seedling establishment, which marks the point at which seedlings can survive independently of maternal reserves (Fenner & Thompson, 2005), is a crucial stage in forest ecosystem regeneration and adaptation (Grime & Hiller, 1992). For example, seedling establishment is important for natural forest regeneration of previously logged plantations (Yamagawa & Ito, 2006). Understanding the factors that affect seedling establishment and survival is necessary for predicting the structure of overstory communities and how forests might function. Seedling establishment and survival are influenced by various factors, including environmental conditions (Acácio *et al.* 2024) and herbaceous understory cover (George & Bazzaz, 1999a). Herbaceous understory plants can act as an ecological filter that determines if a tree successfully emerges and establishes in a forest by influencing both biotic and abiotic components of an ecosystem (George & Bazzaz, 1999a). Thus, understory plants play an important role in how forests regenerate, adapt, and change over time.

Forest understories can vary in species composition and abundance, ranging from highly diverse communities to those dominated by a single species. Grime (1998) proposed that these highly ubiquitous species impact ecosystems proportionally to their abundance and termed it the *mass ratio hypothesis*. Dominant species strongly influence ecosystems, by having a large impact on productivity (Livingstone *et al.* 2020; Lisner *et al.* 2023; Smith & Knapp, 2003). Studies show that removing dominant species can reduce productivity (Lisner *et al.* 2023) and stability (Song *et al.* 2019). The role of dominant species in seedling establishment and recruitment is well-documented (Grime, 2002; Royo & Carson, 2008). Herbaceous dominant species cover can affect aboveground factors such as light availability at the soil surface (Eckberg *et al.* 2023; Hernandez *et al.* 2022) and belowground factors such as soil moisture and nutrient availability

(Avolio *et al.* 2019; Hernandez *et al.* 2022), all of which impact the success of seedlings through their effects on plant traits. In addition to their influence on aboveground abiotic conditions, dominant species can also influence their neighbors via belowground processes. Allelopathy–the phenomenon where plants can cultivate a soil environment that inhibits neighboring species–is a type of plant-soil feedback that has been observed, specifically with dominant species (Dolling, 1996; Muller, 1966). Overall, dominant species have the ability to influence above- and belowground abiotic conditions

Dominant species also influence biotic interactions by shaping species interactions (Avolio *et al.* 2019; Eckberg *et al.* 2023). In old fields, for instance, removal of the dominant species alters community trophic structure by decreasing detritivore and herbivore predator abundance (Eckberg *et al.* 2023). In forests, dense understory cover may house more herbivores, leading to increases in seed predation (George & Bazzaz, 1999a; Royo & Carson, 2008). Plants also influence microbial community structure and function (Innes *et al.* 2004; Zak *et al.* 2003). For instance, with higher levels of plant diversity, microbial biomass and activity and fungal abundance increased due to greater detritus production (Zak *et al.* 2003). Indirectly, dominant species can impact the environmental conditions–such as soil temperature and moisture–that mediate microbial activity (Cui *et al.* 2020; Yang *et al.* 2021). Taken together, we expect that dominant species will alter ecosystem functioning.

While the ecological importance of dominant species in grasslands is well-studied, there is limited research on their role in forest ecosystems. We hypothesize that the dominant species, *Pteridium aquilinum* (bracken fern), will affect light availability, microclimate, and understory plant diversity and that higher levels of bracken cover will negatively impact seedling growth and survival. To explore the influence of bracken fern on understory abiotic conditions, light

availability, and plant diversity we used a paired plot experimental design to address two key questions: ***(1) how does natural variation in the density of a dominant species impact understory abiotic conditions and plant diversity? (2) How does the cover and removal of a dominant species affect seedling survival and success?*** Understanding the mechanisms through which dominant species regulate seedling establishment and survival is important to predict and manage future forest structure.

Materials & Methods

Site Description

We conducted this experiment at the University of Michigan Biological Station (UMBS) in Pellston, Michigan. In May 2024, we selected three experimental forest sites (~ 1.7 acres each) similar in age and tree composition (Frelich & Reich, 1995) located approximately 450 m apart. The first site (S1) is at 45.559° N, 84.681° W, the second site (S2) is at 45.562° N, 84.685° W, and the third site (S3) is at 45.562° N, 84.691° W. UMBS forests are located on an outwash plain with sandy, well-drained, acidic soils and characterized as mixed hardwood forests dominated by *Pinus resinosa* (Red Pine), *Quercus rubra* (Northern Red Oak), *Acer rubrum* L. (Red Maple), and *Fagus grandifolia* (American Beech) in the overstory (Pearsall, 1995; Hardiman *et al.* 2011). The understory primarily consists of American Wintergreen (*Gaultheria procumbens*), Bracken Fern (*Pteridium aquilinum* (L.) Khun subsp. *Latiusculum)*, and seedlings of *Acer rubrum*, *Pinus resinosa*, and *Fagus grandifolia* (Pearsell, 1995; Hardiman *et al.* 2011). Bracken fern can be found in both sparse and dense patches across the understory (Moseley-McCloud, unpublished data).

Experimental Establishment

In June 2024, we established ten 4-m^2 plots at each site (total of 30 plots). First, we assessed bracken fern cover across the forest landscape. We selected sites that represented a gradient of bracken fern cover, ranging from 0-100%. Due to the variation in bracken fern size within the plots, we used the following criteria to determine cover: plots that had no stems were assigned 0% cover, plots with 2-4 stems were assigned 25% cover, plots with 5-8 stems were 50% cover, plots with 9-11 stems were 75% cover, and plots with 12-15 stems were 100% cover. At each forest site, I paired two plots of each bracken density. For example, each site had two paired plots with 75% bracken fern cover established near one another. In each of the 30 plots, we collected a 0-10 cm soil sample. Each soil sample was kept cool in the field and then stored at -26.6 °C. Next, we removed all of the bracken biomass from one of the paired plots in each of the forested sites and left one plot with intact cover. For example, in the 75% cover paired plots, one plot would still have 75% bracken cover, while the other would now have 0% bracken fern cover (3 sites × 2 treatments × 5 plots per treatment = 30 plots total) (Figure 1). We removed bracken fern by clipping it to the ground level.

Bracken Fern Measurements

Following harvest, the bracken fern biomass was dried in a forced air oven for 48h at 60 °C and weighed (g). We maintained the removal treatment by re-clipping any aboveground bracken fern biomass that grew back. Prior to drying the removed biomass, five of the bracken fern stems from the removal plots were preserved at 5 °C to measure the following plant traits: height (cm), stem diameter (mm), stipe diameter (mm), frond length (cm), width (cm), and area (cm^2). To calculate plant height we measured length (cm) from the base of the stem to the tip of the longest

frond. We measured stem diameter at the midpoint of the stem using a digital caliper (mm). We measured frond height with a meter tape from the base of the stipe to the apex of the frond (cm). Frond width was measured from apex to apex of the non-central fronds (cm). Frond area was measured using a LI-3100C (LI-COR, Lincoln, Nebraska) scanner. We ran each frond through the LI-3100C, and recorded the area measurement from the instrument. After taking the plant trait measurements, we proceeded to dry and weigh the fronds as described above. The measurements were used to build allometric equations for bracken fern biomass based on equations from Vogel *et al.* 1999 (unpublished data). We fit an allometric equation that explained 75% of the variation in the data ($R^2 = 0.752$).

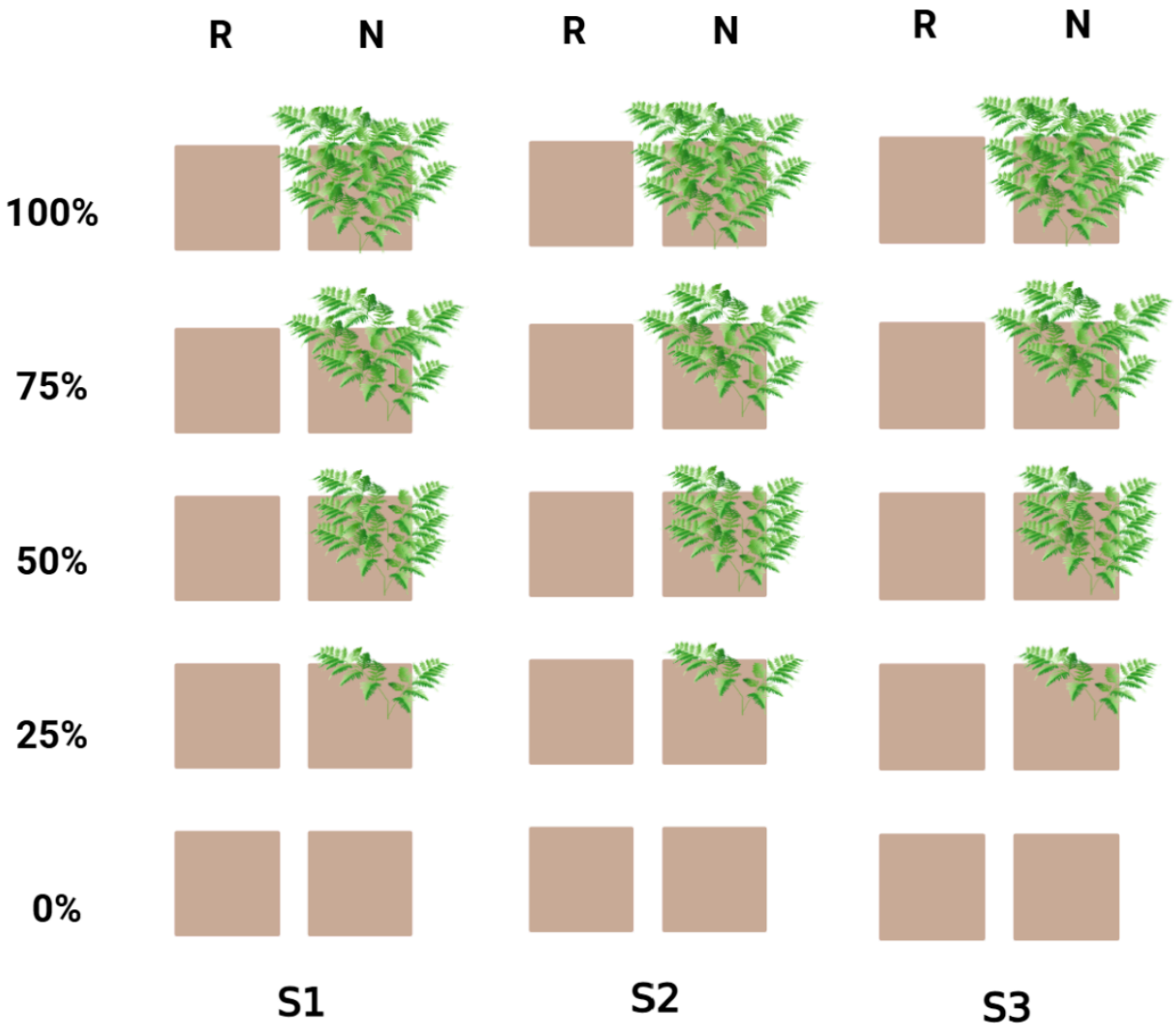

Figure 1. A schematic displaying our experimental design. We established three forest sites (S1-S3; ~1.7 acres) with 10 plots (4 m^2 each) within each forest plot (total of 30 experimental plots). At each site (S), there are paired plots established across a gradient of bracken fern densities (0, 25, 50, 75, 100%). In the removal (R) plots, bracken fern cover was removed, and in the natural plots (N) the bracken fern cover was left intact.

Measuring Environmental Conditions

To examine how bracken fern affects abiotic conditions, we deployed a TMS-4 datalogger (TOMST, Prauge, Czech Republic) in each plot to record air temperature (+15 cm; relative to the soil surface), soil moisture (0-14 cm; relative to the soil surface), and soil surface temperature (0 cm; at the soil surface) every 15 minutes (Wild *et al.* 2019). I retrieved data from June 19, 2024, to August 12, 2024. We calculated the weekly average, maximum, and minimum air temperature, soil moisture, and soil temperature for each plot. For soil temperature and moisture, we calculated variation, or the difference between the maximum and minimum measurements, for each week of the growing season. Additionally, we measured photosynthetic active radiation (PAR) once at peak-season above and below the canopy of bracken fern using a MQ-200X full spectrum quantum PAR sensor (Apogee Instruments, Logan, Utah). Ten measurements were collected in each plot on clear days and averages for each plot were calculated.

Analyzing Seedling Success

Within each plot and one week after establishing the removal plots, we planted six 15-30 cm bare-root Red Maple seedlings (Cold Stream Farms, Free Soil, Michigan). The Red Maple seedlings were planted in a 3 × 2 grid inside a 1 m^2 subplot located in the center of the main plot to account for edge effect. Red Maple is one of the most widely distributed canopy species in northeastern North America, which highlights its importance in deciduous forest ecosystems (Chapman & Bolen, 2015). Additionally, studies indicate that Red Maple will likely positively respond to climate change because they grow well in warmer soils (Wheeler *et al.* 2017) and accelerate spring seedling phenology with warmer temperatures (Kaye & Wagner, 2014). Before transplanting, we measured total biomass (g), stem height (cm), and diameter (mm). Seedlings

that showed no signs of budding within two weeks of transplanting were replaced with new seedlings. Leaf phenology was tracked during the last five weeks of the field season.

In August 2024, seedlings were removed, and survival was recorded based on the presence of green leaves. Seedling height (cm), diameter (mm), and total biomass (g) were measured for each seedling upon removal. We measured seedling height from the base to the apex of the stem using a meter tape and diameter was measured at the midpoint of the stem using a digital caliper. We removed green leaves by clipping them at the base of the petiole and then we measured the area with a LI-3100C scanner (LI-COR, Lincoln, Nebraska). Once scanned, leaves were air dried for 48h at 60 °C in a Grieve 343 oven (Grieve Corporation, Round Lake, Illinois) and ground using the Mini-BeadBeater 96 (Biospec Products Incorporated, Bartlesville, Oklahoma). Subsamples of the ground leaf material were analyzed by combustion for % N and C:N using a LECO CN628 (LECO Corporation, St. Joseph, Michigan).

Measuring Overstory and Sub-dominant Understory Community Composition

We conducted an overstory census at each plot, using the plot as a focal point, and recorded the diameter at breast height (DBH) of all overstory trees with a DBH ≥ 10 cm within the defined radius. The radius varied around each plot to ensure we sampled all the trees that influenced the plot of study. This represents 4-16 individual trees of 2-6 tree species (Table 2).

We identified and calculated the percent cover for all non-bracken understory plants within each plot using the visual inception method (Catchpole *et al.* 1992). We used that data to calculate Hulbert's probability of interspecific encounter (PIE), a diversity index, using the *calc_PIE* function from the mobr package in R. PIE is calculated using the following equation (Hulbert, 1971):

$$PIE = N/(N - 1) * (1 - p_i^2)$$

where N is the total number of individuals and p_i is the relative abundance of species i.

Statistical Analyses

All statistical analyses were performed using R version 4.2.3 (R Core Team, 2025). A one-way analysis of variance (ANOVA) was used to test for differences in light availability and plant traits (LA, SLA, % N, and C:N) across bracken densities. To analyze if time (i.e., week) and bracken coverage affected soil temperature and volumetric moisture, we ran a linear mixed effects model with a temporal autocorrelation. Due to the lack of interaction between bracken coverage and time, we instead calculated the seasonal average of the difference of the maximum and minimum, or variation, in soil temperature and volumetric moisture across bracken fern densities. We then used an ANOVA to test for differences in variation between densities. To understand how removals affect seedling survival and seedling plant traits including leaf area, specific leaf area (SLA), green leaf % nitrogen content (% N), and leaf carbon-to-nitrogen ratio (C:N), we calculated Hedge's g effect size to correct for small sample size bias. We used the *cohen.d* function from the effsize package in R to calculate Hedge's g. We used a linear regression analysis to examine the relationship between understory sub-dominant species diversity, reported as Hulbert's probability of interspecific encounter (PIE), and bracken fern cover (%). We used generalized linear mixed models (GLMM) with site as a random effect to understand how bracken biomass affected seedling survival in natural and removal plots. We used the g*lmer* function from the lme4 package in R to run the GLMMs. For the GLMM of seedling survival in natural plots, we used estimated bracken fern biomass as the predictor variable. We estimated biomass in each natural plot by fitting an allometric equation that explained 38% of the data ($R^2 = 0.387$). For the GLMM of seedling survival in removal plots, we

used the removed biomass as a predictor variable. PAR data was log-transformed to meet the assumption of normality.

Results

First, we examined how natural variation in bracken fern density (0-100% cover) influenced abiotic microsite factors, light availability, and understory species diversity. In general, soil abiotic factors varied with changes in bracken fern density (Figure 2; Supplemental Figure 1). The difference between maximum and minimum soil temperature fluctuates across the growing season with the highest difference occurring in week 25 and the lowest with the treatments converging in week 33 (Supplemental Figure 1). At the peak of the growing season (July, week 29), the largest difference between maximum and minimum soil temperature occurred in plots with 50% cover (Supplemental Figure 1A). Average soil temperatures ranged from 14 ℃ to 20 ℃ across all bracken fern densities (Supplemental Figure 2B), with a peak of ~20 ℃ in week 25 and a minimum of ~14 ℃ in week 33. Air temperatures generally ranged from 15 ℃ to 18 ℃ (Supplemental Figure 2B), with a peak of ~18 ℃ in week 25 and a minimum of ~15 ℃ in week 33 (Supplemental Figure 2B).

Variation in volumetric soil moisture across bracken fern densities fluctuated throughout the growing season. Both the 0% and 100% bracken fern cover plots exhibited the highest soil moisture variation (Supplementary Figure 1B). On average, volumetric soil moisture ranged from ~7% to17 %, with the highest moisture observed in week 26 and the lowest in week 33. The 0% bracken fern cover plots generally had the lowest average volumetric soil moisture, followed by the 25%, 75% and 50% natural plots, respectively (Supplementary figure 2A).

A linear mixed effect model showed that time significantly affected seasonal soil moisture variation ($P < 0.01$), but the interaction between bracken fern cover and time did not (P

= 0.914). Similarly, time significantly affected soil temperature variation ($P < 0.01$), but the interaction between time and bracken cover did not ($P = 0.902$). Given this, we compared seasonal averages in both soil temperature and volumetric soil moisture variation (max - min). There were no significant differences in seasonal soil temperature variation across bracken fern densities ($P = 0.416$; Figure 2A), but seasonal soil moisture variation did differ significantly ($P = 0.003$; Figure 2B). Notably, the 25% bracken fern cover plots exhibited the highest soil moisture variation (Figure 2B).

Photosynthetic active radiation (PAR), a measure of light availability, ranged from 12 to 536 μ mol^{-1} m^{-2} across plots with natural bracken fern densities, but we were unable to detect statistically significant differences among cover classes ($P = 0.389$; Figure 2C). Plant diversity, represented as PIE, varied among the natural bracken fern density plots, but we detected no significant differnecs across across natural plots ($P = 0.161$; Figure 3A).

Next, we examined how removal of different bracken fern densities (0-100% cover) influenced abiotic microsite factors, light availability, and understory species diversity. In general, soil abiotic factors varied with the removal of different bracken fern densities (Supplemental Figure S4; Supplemental Figure S5). With the removal of bracken cover, the difference between maximum and minimum soil temperature fluctuates across the growing season with the highest difference occurring in weeks 27 and 29 and the lowest with the treatments converging in week 33 (Supplemental Figure 4). The highest fluctuations in soil temperature variation occurred in 100% bracken removal plots, of which there was 29 ℃ of variation, followed by 75%, 50%, 25%, and 0% removal plots (Supplementary figure 4A). Average soil temperatures ranged from 13 ℃ to 22 ℃ across all plots (Supplemental Figure 4A), with a peak of ~22 ℃ in week 31 and a minimum of ~13 ℃ in week 33. Average air

temperatures ranged from 16 ℃ to 21 ℃ (Supplemental Figure 2B), with a peak of ~21 ℃ in week 31 and a minimum of ~16 ℃ in week 33 (Supplemental Figure 2B).

Seasonal soil temperature did differ significantly across plots ($P < 0.05$; Supplemental Figure 4A), but seasonal soil moisture variation did not differ significantly ($P = 0.416$; Supplemental Figure 4B). At peak season, variation in volumetric soil moisture was highest in 50% removal plots (Supplementary Figure 4B).

PAR ranged from 19 to 215 μ mol^{-1} m^{-2} across plots where bracken fern was removed, but we were unable to detect statistically significant differences among cover classes ($P = 0.356$; Supplementary Figure 4C). There was not a relationship between PIE and removed biomass ($R^2 = -0.063$; $P = 0.688$; Figure 3B).

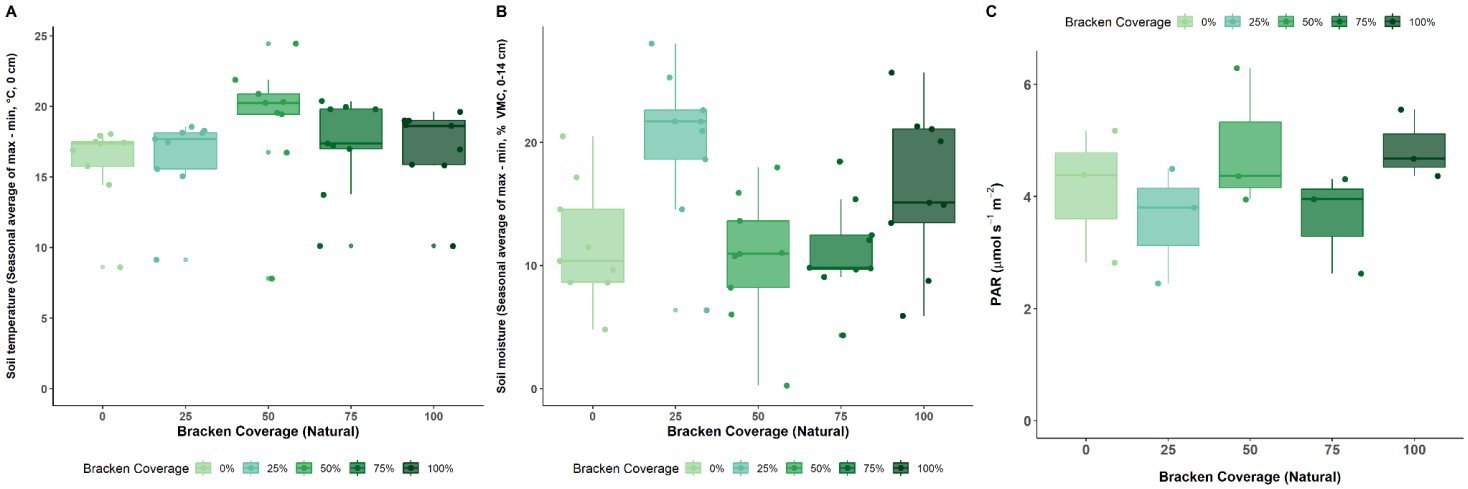

Figure 2. Variation in soil temperature (A) and moisture (B), and average PAR (C) across all bracken fern densities in natural bracken fern density plots for each week of the growing season (from June 19, 2024 to August 12, 2024).

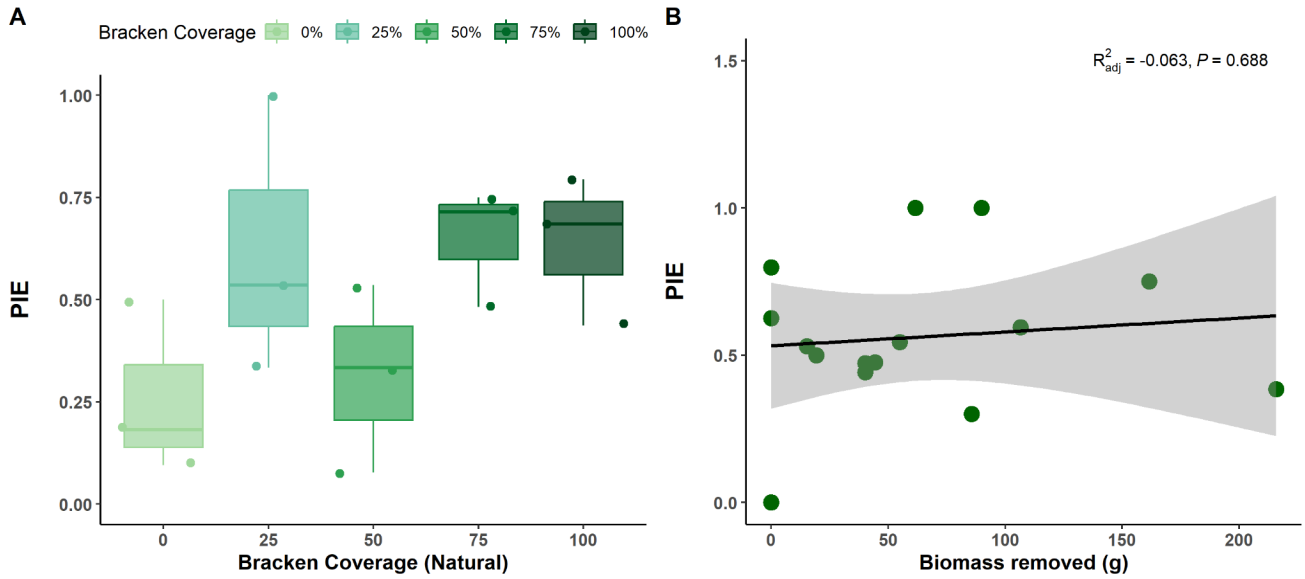

Figure 3. PIE, a measure of subdominant plant diversity, across all bracken densities in natural bracken density plots (A) and a correlation between PIE in each removal plot and the actual biomass removed from that plot (B). There was no significant correlation between PIE and removed biomass (P = 0.688). Each dot in the linear regression represents a removal plot.

Finally, we explored how bracken density, and its removal, would impact maple seedling survival and traits. Seedling survival did not significantly differ across bracken fern densities in natural (Figure 4A; $P = 0.749$) or removal plots (Figure 4B; $P = 0.997$). Effect size analysis confirmed no significant effect of bracken fern removal across densities on seedling survival (Figure 4C). Similarly, bracken fern biomass did not significantly affect seedling survival in either the natural ($P = 0.183$; Table 1) or the removal plots ($P = 0.375$; Table 1).

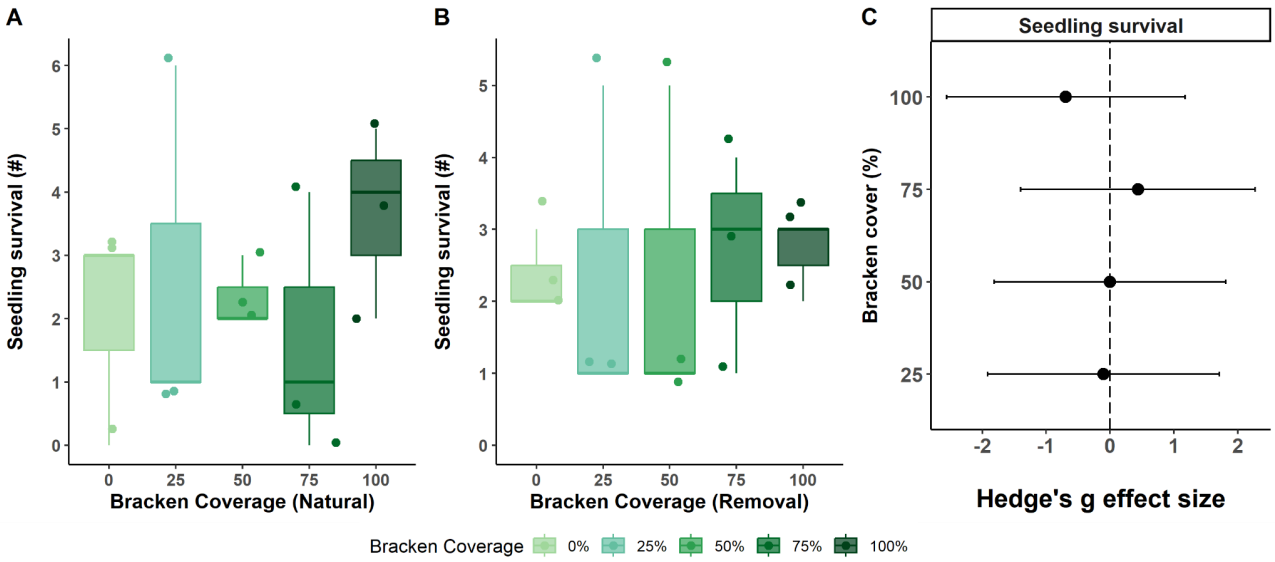

Figure 4. Seedling survival across bracken fern densities in natural bracken density (0-100%) plots (A) and in plots where the natural density of bracken (25-100%) was removed (B). Effect sizes of each treatment on seedling survival (C) across the bracken fern densities. The effect sizes were calculated using Hedge's g where each natural bracken density plot was compared to its paired removal plot. Values on the right side of the zero indicate greater seedling survival in removal plots compared to natural bracken density plots. (C) The removal treatment had no significant effect on seedling survival across bracken fern densities.

Table 1. Results from the generalized linear mixed effects regression used to predict the effect of estimated or removed bracken fern biomass on seedling survival in the natural and removal plots, respectively.

	Response variable		
Predictor variable	Seedling Survival (#)		
Estimated bracken biomass (g)	***P*** = 0.183	**SE** = 0.557	**Estimate** = 0.006
Removed bracken biomass (g)	***P*** = 0.375	**SE** = 0.003	**Estimate** = 0.003

Seedling specific leaf area (SLA) did not differ significantly across bracken fern densities in natural ($P = 0.780$; Figure 5A) or removal ($P = 0.215$; Figure 5B) plots. Effect sizes also indicated no significant effect of the removal treatment on seedling SLA across bracken densities (Figure 5C).

Seedling green leaf nitrogen content (% N) showed no significant differences in natural plots ($P = 0.218$; Figure 5D). However there was a marginally significant difference across removal plots ($P = 0.089$; Figure 5E). Removal treatments significantly decreased green leaf % N, specifically in the 75% removal plots (Figure 5F). Overall, seedling SLA was consistent across natural bracken fern cover plots (Figure 5A), but a decreasing trend in seedling leaf area was observed in removal plots (Figure 3B).

Seedling leaf area did not differ significantly across bracken fern densities in either natural ($P = 0.229$; Supplementary figure 3A) or removal ($P = 0.441$; Supplementary figure 3B) plots. In general, seedling leaf area remained consistent across both natural and removal treatments.

Finally, seedling green leaf carbon-to-nitrogen ratios (C:N) did not vary significantly across bracken fern densities in natural ($P = 0.362$; Supplementary figure 3D) or removal plots ($P = 0.103$; Supplementary figure 3E). However, removal treatments did have a significant positive effect on green leaf C:N (Supplementary figure 3F).

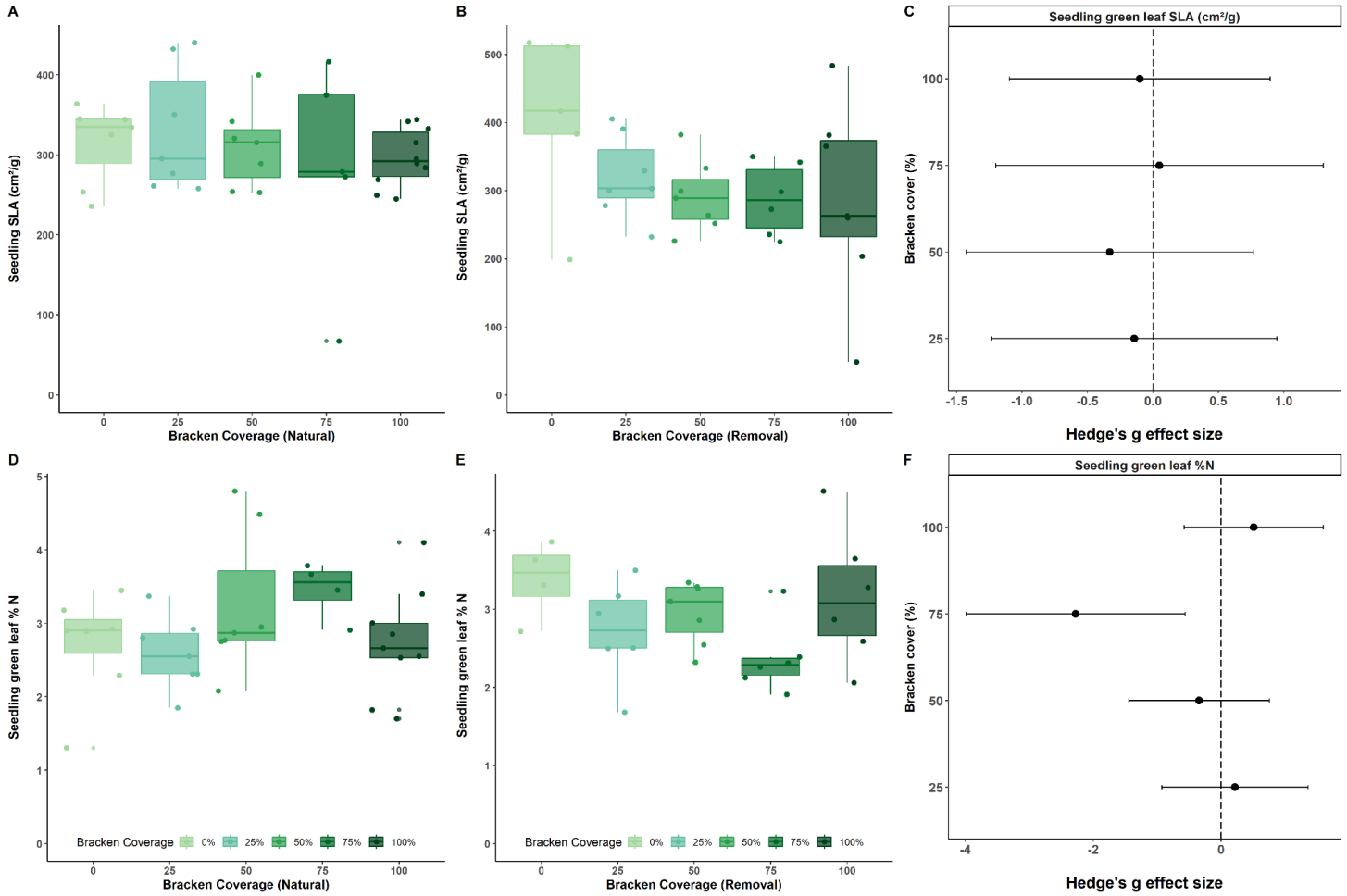

Figure 5. Seedling specific leaf area (SLA) and green leaf nitrogen content (% N) in natural bracken density plots (A and D) and in the density removal plots (B and E). Effect sizes for SLA (C) and % N (F) across bracken fern densities. The effect sizes were calculated using Hedge's g where each natural bracken density plot was compared to its paired removal plot. Values on the right side of the zero indicate greater seedling SLA or % N in removal plots compared to natural plots. (C) The removal treatment had no significant effect on seedling SLA across bracken fern densities. (F) The removal treatment had a significant negative effect on green leaf % N in 75% removal plots.

Table 2. Site, plot, treatment, bracken cover (%), Overstory species (number), trees near each plot (number), total tree basal area (m^2/ha), the amount of bracken fern biomass removed from the biomass removal plots (g).

Site	Plot ID	Treatment	Bracken cover (%)	Overstory species (#)	Trees relative to plot (#)	Total basal area (m^2/ha)	*P. aquilinum* biomass removed (g)
A	1	natural	0	4	10	67.8	N/A
A	2	removal	0	4	12	102.7	N/A
A	3	removal	25	2	10	21.3	15.2
A	4	natural	25	3	9	20.7	N/A
A	5	removal	50	3	11	27.9	85.76
A	6	natural	50	4	11	73.0	N/A
A	7	removal	75	2	4	9.9	161.6
A	8	natural	75	5	7	30.5	N/A
A	9	removal	100	3	6	14.1	215.9
A	10	natural	100	3	9	38.7	N/A
B	11	natural	0	5	10	37.9	N/A
B	12	removal	0	6	10	74.9	N/A
B	13	removal	25	3	6	8.3	40.12
B	14	natural	25	5	9	30.7	N/A
B	15	removal	50	4	10	29.9	40.2
B	16	natural	50	4	9	44.6	N/A
B	17	removal	75	5	12	50.6	61.5
B	18	natural	75	4	10	29.6	N/A
B	19	removal	100	3	7	29.8	89.9
B	20	natural	100	3	6	34.6	N/A
C	21	natural	0	6	10	35.3	N/A

C	22	removal	0	5	16	53.7	N/A
C	23	removal	25	6	15	103.2	19.21
C	24	natural	25	4	5	31.1	N/A
C	25	removal	50	2	4	24.8	44.3
C	26	natural	50	3	9	80.6	N/A
C	27	removal	75	4	9	41.7	106.55
C	28	natural	75	3	12	39.9	N/A
C	29	removal	100	3	9	28.4	54.9
C	30	natural	100	3	8	53.4	N/A

Discussion

In this study, we examined the impact of bracken fern density on both abiotic (such as soil temperature, soil moisture, and light availability) and biotic (such as understory plant species diversity) factors. Our findings suggest that bracken fern density has variable effects on soil temperature, soil moisture, and light availability, but not on sub-dominant plant diversity. We also explored how bracken fern density, as well as its removal, affects seedling survival and traits and what mechanisms might underlie how seedling success responds to understory bracken fern density. Overall, bracken fern did not affect seedling survival. While most seedling traits were unaffected by the removal of bracken fern, we observed a reduction of seedling green leaf nitrogen content in plots where 75% of bracken fern cover was removed.

Impacts of Bracken fern on microclimate and understory plant diversity

Bracken fern is a common understory plant species in forests worldwide (Vetter, 2009) and is particularly common in Northern Michigan forests. We hypothesized that its dominance would have a strong impact on the microclimate of and plant diversity in the forest understory. While our results confirm that bracken fern can modify microclimate in the understory, the effects were not always as expected. For instance, we initially thought that soil moisture would decrease with increasing bracken fern cover, due to higher evapotranspiration. However, we did not find a clear relationship between bracken fern cover and soil moisture, and the removal of bracken fern surprisingly did not lead to an increase in soil moisture. Overall natural bracken fern cover had variable effects on soil moisture, with no statistically significant differences across bracken fern densities. This finding contrasts with a study by Smith & Lockwood (1990). They reported significant differences in soil moisture between areas with bracken fern and other surfaces, and

found that soil moisture initially increases upon the removal of bracken fern, but decreases as subdominant plants begin to establish.

Similarly, we expected photosynthetically active radiation (PAR) and soil temperature to decrease with bracken fern cover because of greater exposure to sunlight. However, the effects of bracken fern cover on soil temperature were variable, and there were no significant differences across densities. Our results differ from those of Griffiths & Filan (2007), who found that bracken fern shades soils, which lowered soil temperature by 27% in plots with bracken fern cover versus plots with conifer and shrub cover, especially in the spring and summer. The lack of significant differences in soil temperature during summer in our study may be due to the overstory canopy, which has a more substantial role in controlling light availability once it is fully leafed out (Moreno *et al.* 2013). Since we measured soil temperature after canopy closure, this could explain why we did not observe significant differences in soil temperature across bracken fern densities.

Although we observed differences in PAR, sub-dominant species diversity remained relatively similar across all natural plots, and we observed no significant increase in species diversity upon bracken fern removal. This finding is inconsistent with other studies, which typically find that removing bracken fern increases the success of neighboring species, whether woody or herbaceous (George & Bazzaz, 1999b, Gliseman & Muller, 1978). The forests we worked at in northern Michigan typically have a low understory species diversity (McFarland, 1916). We measured a maximum of five and a minimum of two species across all of our plots. Perhaps the subdominant species in our study area are resistant to removal of bracken fern because they are likely well-adapted nutrient-poor soils of UMBS and the potentially stressful environment cultivated by bracken fern.

What effects do the presence or absence of dominant species have on seedling survival and success?

As climate change continues, understanding how plant communities may help buffer changing environmental conditions for forest seedlings is important. In fact, prior research indicates that plant community composition in temperate forests is more strongly influenced by microclimate than macroclimate (Zellweger *et al.* 2020). Bracken fern vegetation and litter can promote seedling growth by creating favorable microclimate conditions acting as "nurse plants" (Ssali *et al.* 2019; Gallegos *et al.* 2015). For instance, in plots where we removed 100% of the bracken cover, we saw 33℃ of variation in soil temperature within a single week, compared to natural plots where variation in soil temperature never exceeded ~20℃. Our results demonstrate that bracken fern plays a role in regulating soil temperature and moisture, which can affect forest seedling survival under increasingly variable climate change conditions.

Bracken fern cover can inhibit the growth of neighboring species, particularly seedlings, by affecting both the abiotic and biotic conditions of the understory (Long & Fenton, 1938; George & Bazzaz, 1999a). We hypothesized that seedling survival would decrease as bracken fern cover increased, and that removal of bracken fern would improve seedling success. While seedling survival varied across bracken fern densities in both natural and removal plots, we found no significant differences in survival across densities. This suggests that bracken cover does not have the expected negative impact on seedling survival. Bracken fern can grow up to 2 meters in height, and because of this they typically hinder seedling survival by blocking sunlight. However, we did not observe this anticipated pattern. Our results suggest that aboveground competition for light, often considered the main mechanism of seedling inhibition (Beckage *et al.* 2000; Grime, 2002), is not the primary factor determining seedling success in our study area.

Despite bracken ferns' well-documented ability to inhibit plant growth, we also expected stronger negative effects of bracken cover on seedling traits. However, we did not observe significant differences in leaf area, SLA, or C:N between natural and removal plots. In our study system, competition for light does not appear to be determining seedling success. The lack of differences among seedling traits or survival may indicate that a soil-mediated inhibitory process is at play. Previous work in bracken fern-dominated landscapes, suggests that allelopathy could hinder the growth of neighboring herbs, with phytochemicals leaching from bracken fern fronds into the soil (Gliessman & Muller, 1978; Muller, 1966). In temperate forests, seedlings generally thrive on exposed mineral soils rather than on soils composed of bracken fern litter, likely due to toxins released from the fronds (Dolling, 1996).

Most studies focus on the effects of dominant species on young seedling emergence and survival, often showing drastic differences between seedlings grown with and without the cover of dominant species. However our study used older seedlings that were past the stage of seedling establishment. Trees can vary in their ability to adapt to environmental changes dependending on their developmental stage (Grubb, 1977), suggesting that younger trees may be more susceptible to microclimate changes caused by bracken fern. Long & Fenton (1938) found that dense bracken fern stands hindered the establishment of younger trees, likely due to changes in abiotic conditions. Species specific adaptations also play a role in how seedlings respond to microclimate changes. For example, red maples, known as “super-generalist”, tolerate a wide range of physical conditions (Abrams, 1998), which may explain the lack of significant differences in seedling survival or between the treatments in our study.

Conclusion

This study provides evidence that bracken fern can alter the understory microclimate of forests and have varying effects on seedling survival and traits. Bracken fern can exert both facilitative and inhibitory effects on seedling success, by regulating microclimate and suppressing neighboring species via soil-mediated processes. Understanding the dynamic role of bracken fern in the forest understory is critical for predicting forest structure and capacity for ecosystems to adapt to variable climate conditions.

Figures

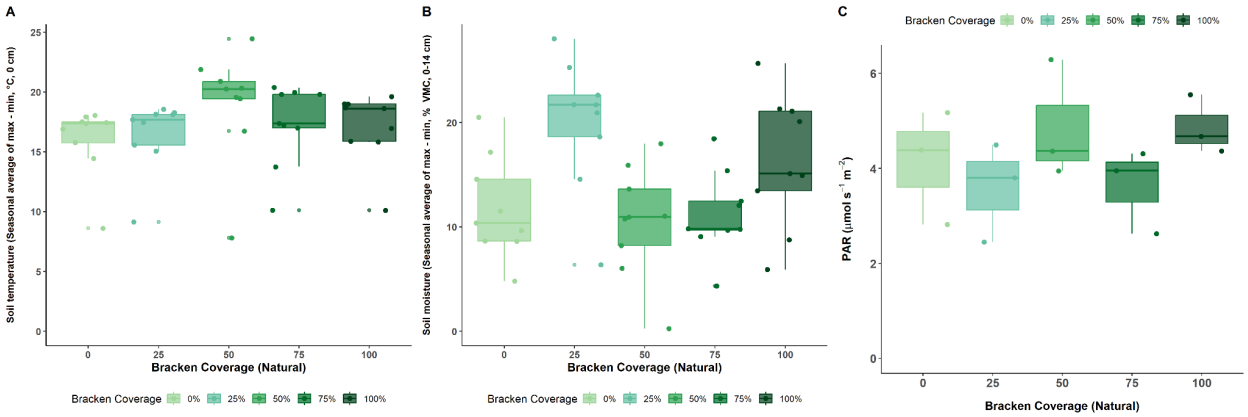

Figure 2. Variation (max-min) in soil temperature (A) and moisture (B), and (C) average photosynthetic active radiation (PAR) at ground level across all bracken fern densities in natural bracken fern density plots for each week of the growing season (from June 19, 2024 to August 12, 2024).

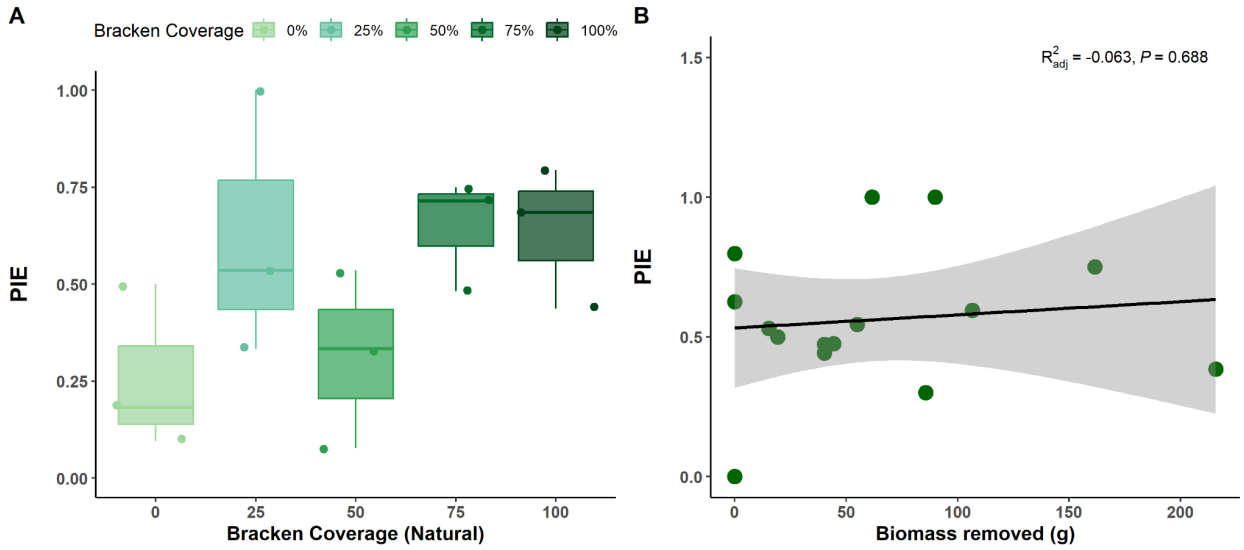

Figure 3. PIE, a measure of subdominant plant diversity, across all bracken densities in natural bracken density plots (A) and a correlation between PIE in each removal plot and the actual biomass removed from that plot (B). There was no significant correlation between PIE and removed biomass (P = 0.688). Each dot in the linear regression represents a removal plot.

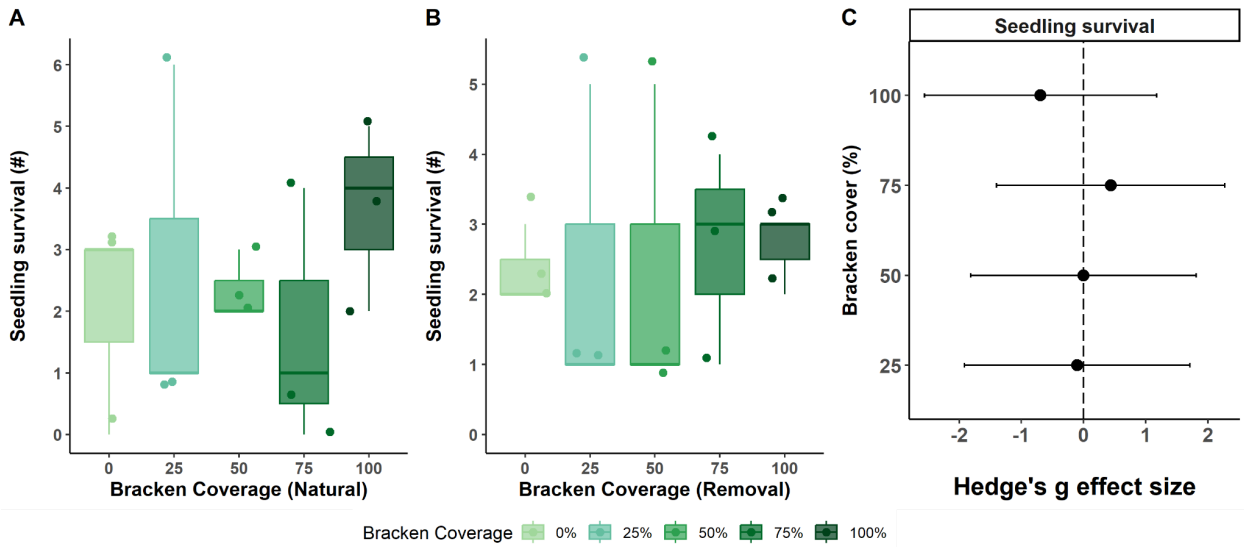

Figure 4. Seedling survival across bracken fern densities in natural bracken density (0-100%) plots (A) and in plots where the natural density of bracken (25-100%) was removed (B). Effect sizes of each treatment on seedling survival (C) across the bracken fern densities. The effect sizes were calculated using Hedge's g where each natural bracken density plot was compared to its paired removal plot. Values on the right side of the zero indicate greater seedling survival in removal plots compared to natural bracken density plots. (C) The removal treatment had no significant effect on seedling survival across bracken fern densities.

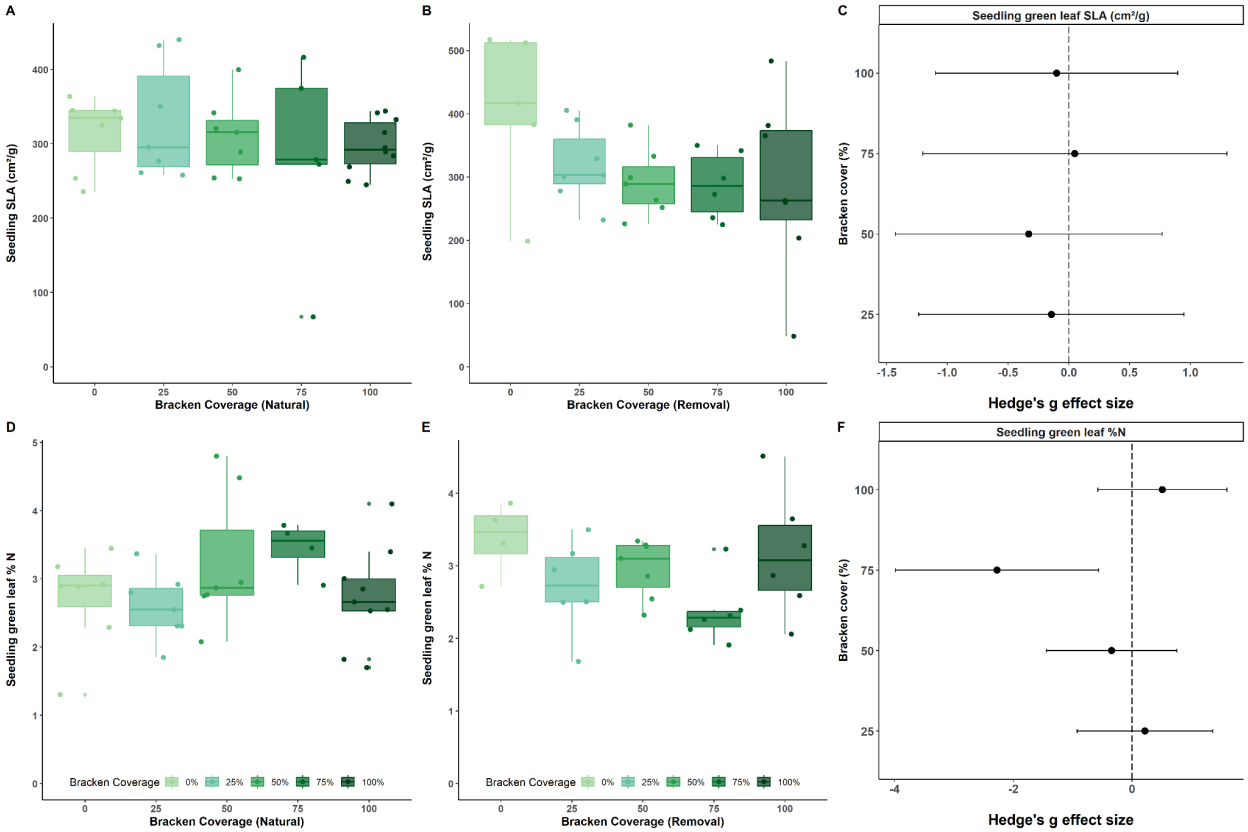

Figure 5. Seedling specific leaf area (SLA) and green leaf nitrogen content (% N) in natural bracken density plots (A and D) and in the density removal plots (B and E). Effect sizes for SLA (C) and % N (F) across bracken fern densities. The effect sizes were calculated using Hedge's g where each natural bracken density plot was compared to its paired removal plot. Values on the right side of the zero indicate greater seedling SLA or % N in removal plots compared to natural plots. (C) The removal treatment had no significant effect on seedling SLA across bracken fern densities. (F) The removal treatment had a significant negative effect on green leaf % N in 75% removal plots.

Supplementary Material

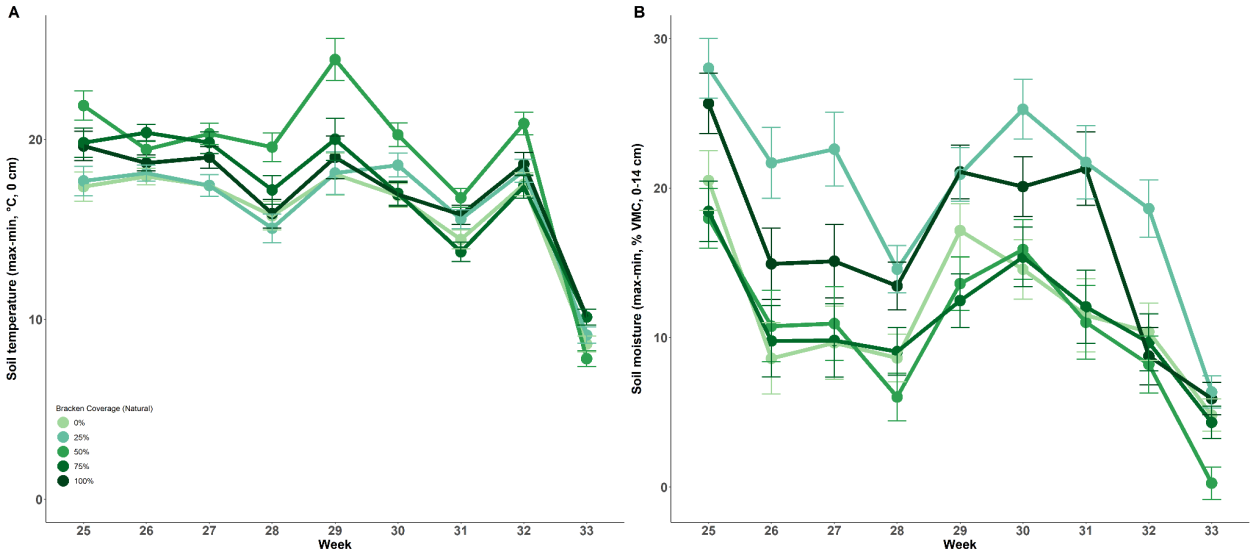

Figure S1. (A) Weekly variation (max-min) of soil temperature (0 cm) and (B) soil moisture (0-14 cm) across natural bracken fern density plots. Weeks represent weeks of the year.

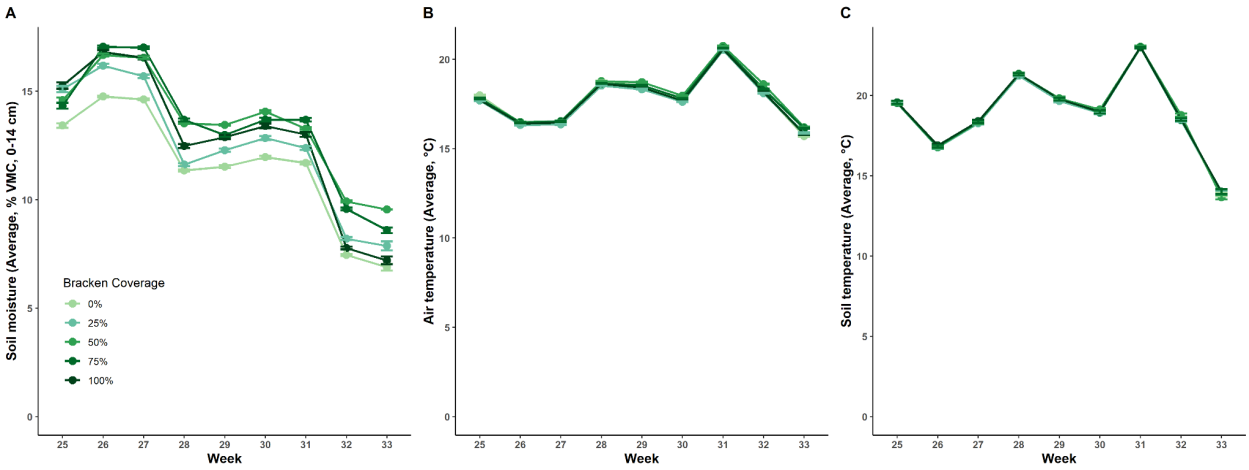

Figure S2. Average soil moisture (0-14 cm) (A), air temperature (B), and soil temperature (0 cm) (C) of natural plots across all bracken fern densities for each week of the growing season.

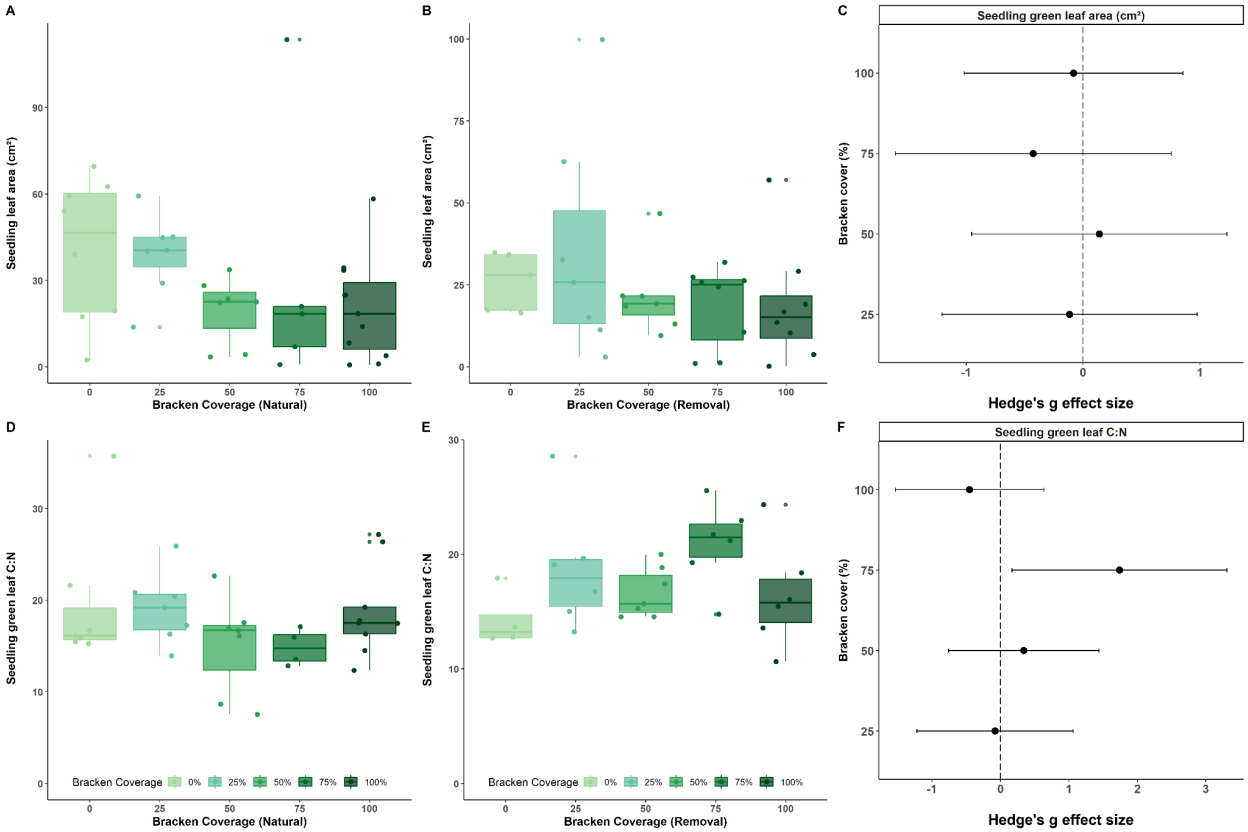

Figure S3. Seedling leaf area and carbon to nitrogen ratios (C:N) of green leaves across bracken fern densities in natural plots (A and D) and removal plots (B and E). Effect sizes for SLA (C) and C:N (F) across bracken fern densities. The effect sizes were calculated using Hedge's g where each natural bracken density plot was compared to its paired removal plot. Values on the right side of the zero indicate greater seedling leaf area or C:N in removal plots compared to natural plots. (C) The removal treatment had no significant effect on seedling leaf area across bracken fern densities. (F) The removal treatment had a significant positive effect on green leaf C:N in 75% natural plots.

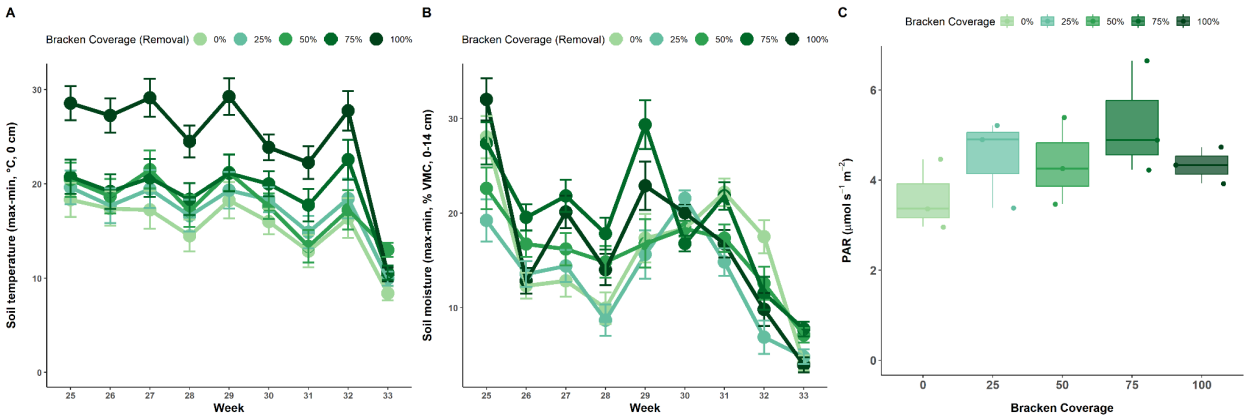

Figure S4. (A) Weekly variation (max-min) of soil temperature (0 cm) and (B) soil moisture (0-14 cm) across removal bracken fern density plots for each week of the growing season. Average photosynthetic active radiation (PAR) at ground level in removal plots.

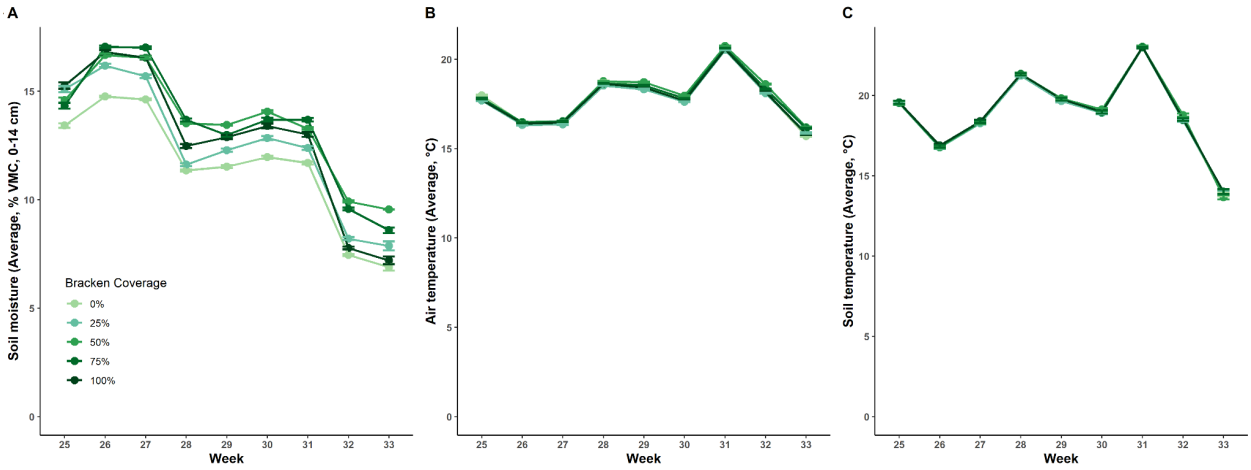

Figure S5. Average soil moisture (A), air temperature (B), and soil temperature (C) of natural plots across all bracken fern densities for each week of the growing season.

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