



# Ecotone characteristics of a southern Appalachian Mountain wetland

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## ABSTRACT

Southern Appalachian Mountain wetlands support important habitat and serve several hydrologic functions. However, they may be threatened by human activities and global climate change. These wetlands are often located in remote, biogeographically isolated locations at high elevations. One of the largest of these wetlands – the peatlands within the Cranberry Glades Botanical Area – was assessed for meadow–forest ecotone characteristics. The Cranberry Glades have been reported to be infilling with trees from the surrounding forest, but little research has been conducted on the patterns of tree growth within the moss-dominated communities. Tree establishment patterns were analyzed in regard to location within the ecotone, hummock/hollow topography, and soil conditions by recording the growing conditions of 1389 trees located within nine, 10×100 m belt transects. The results indicated that tree growth within the ecotone occurred in decreasing density from the forest to the meadow interior, and much of the tree establishment occurred in tree islands (80% of trees were found in tree islands). Significantly more trees (92%) were also found on hummocks than hollows (8%), likely in response to the greater distance from the water table that the hummocks provide. Most soil properties did not vary significantly across the ecotone or in association with topography. The results add to the minimal literature on southern peatlands and may assist in peatland restoration and conservation efforts.

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## 1. Introduction

Global climate change may be contributing to the loss of valuable habitat in areas around the world (e.g. Barry, 1992; Theurillat and Guisan, 2001). Changing temperatures and moisture regimes will result in shifts in vegetation communities as they attempt to adjust to changing climate conditions. Some communities, however, exist as biogeographic islands – distinct ecosystems surrounded by different plant communities (MacArthur and Wilson, 1967) – and may not be able to migrate into other areas. A classic example is the alpine tundra near mountain summits, where alpine plants may not be able to move downslope as warm temperatures force them upwards. A similar situation may exist in a little studied ecosystem – that of the southern Appalachian Mountain peatlands. Several studies have indicated that these peatlands are infilling with trees, potentially from climate changes and human activities, shifting a moss-dominated system to one of trees (Darlington, 1942, 1943; Edens, 1973; Kokesh, 1988; Franci et al., 2004). Understanding the spatial patterns that are characterizing these encroachment processes is important because it will provide insight into the mechanisms that may be occurring within these threatened peatlands. However, literature on the patterns and processes of this infilling is greatly lacking. In this study we aim to address the following

research objectives: 1) to determine the characterization of the ecotone between the forest and the open peatland meadow where the tree infilling is occurring; 2) to assess whether or not a spatial pattern of tree establishment exists within the ecotone; 3) to evaluate the influence of microtopography on tree establishment patterns; 4) to analyze how soil properties and depth to saturation relate to tree establishment and microtopography; and 5) to discuss what potential patterns may indicate about tree infilling processes. Our results will determine the spatial pattern of tree infilling and characterization of the ecotone, which will aid in a better understanding of the processes of tree encroachment into the peatland meadows.

Small (usually <5 ha) often isolated, remote wetlands within the southern Appalachian Mountains harbor distinctive habitat for numerous plant and animal species and perform various hydrological services, including water filtration and flood mitigation (Core, 1974; Smith and Michael, 1982; Murdock, 1994). However, southern peatlands are sensitive to climate conditions (Darlington, 1942, 1943; Edens, 1973), and human activities, such as cattle grazing, are threatening the continued existence of these systems (Franci et al., 2004). The ecological importance of these wetlands is gaining increasing attention in the scientific literature, though, significant gaps still remain in the understanding of these systems (Stewart and Nilsen, 1993; Moorhead and Rossell, 1998; Franci et al., 2004; Rossell et al., 2008; Byers et al., 2007). One such gap is the characterization of the open wetland–forest ecotone, which can serve as a baseline for future studies on ecotone dynamics and assist in understanding the tree encroachment processes occurring in the peatland–forest ecotone. The goal of our research was to

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assess tree patterns within the meadow–forest ecotone of *Sphagnum*-dominated southern Appalachian Mountain wetlands in an aim to increase knowledge of these unique highland ecosystems and provide a better understanding of the patterns of tree infilling, and therefore provide indications to the processes that may be the factors of infilling. Many southern mountain wetlands are actually fens, though they are often given the broad term bog (Moorhead and Rossell, 1998). Fens receive most of their nutrients from groundwater. Bogs, conversely, obtain most of their nutrients from precipitation. The differences between bogs and fens in southern wetlands can sometimes be difficult to distinguish however, since the classification is based primarily on northern wetland characteristics. For the purposes of this paper we will focus on bog and fen peatland wetlands and refer to them collectively as peatlands.

Peatlands are defined as wetlands that are covered with peat, which is partially decayed organic material that has formed *in situ* in anoxic, water saturated conditions (Rydin and Jeglum, 2006). Peatlands contain acidic, nutrient-poor soil, and a very moist ground cover of soils and organic matter (Rydin and Jeglum, 2006). The hydrology of peatlands is a strong determinant on the vegetation communities present within the meadows. Trees are often precluded from peatland meadows because of the saturated conditions and high water levels. However, variations in microelevation can provide areas that are slightly higher above the water table than surrounding topography. Hummocks, mounds of peat that may be over 50 cm in height, can provide habitat more suitable for plant species that prefer slightly drier conditions, such as trees, whereas others prefer the accompanying hollows, which are depressions that surround hummocks and are characteristically moister.

Plants that grow in peatlands are adapted to these harsh conditions. Southern peatlands are often several degrees cooler than the surrounding area and the open meadows are exposed to full sunlight and high winds (Edens, 1973). Southern peatland ecosystems are situated as biogeographic islands within temperate mixed hardwood forests in the highlands (700–1500 m) of West Virginia, Virginia, Kentucky, Tennessee, North Carolina, and Georgia (Moorhead and Rossell, 1998).

Southern peatlands differ from their northern counterparts in several respects with regard to their geomorphology (including origin), geochemistry, and vegetation (Wieder et al., 1981; Stewart and Nilsen, 1993; Walbridge, 1994; Moorhead and Rossell, 1998). Northern peatlands – those above 41°N latitude (Wieder and Lang, 1983) – typically form from infilling of glacier-carved lakes. In southern unglaciated regions, cold climates, high precipitation, and little vegetation cover associated with the Wisconsin Glaciation contributed to the formation of peatlands in high elevation basins (Darlington, 1942, 1943; Gates, 1942; Conway, 1949; Walbridge, 1982). Cooler temperatures found in mountain basins from cold air drainage and greater moisture concentrations from the collection of precipitation along mountain ridges continue to facilitate the function of these systems. Southern peatlands receive more ions and nutrients from the soil than do northern peatlands, which typically obtain nutrients from rainwater (Almquist-Jacobson and Foster, 1995; Moorhead and Rossell, 1998). Northern peatlands often have convex topographic profiles because of the greater accumulation of peat on the surface (Heinselman, 1970), whereas southern peatlands are generally bowl-shaped in profile. Southern peatlands also often contain greater species diversity than northern peatlands (Core, 1983; Moorhead and Rossell, 1998).

Though less extensive than northern peatlands, southern peatlands host numerous rare species, including over 100 vascular plants (Murdock, 1994; Byers et al., 2007). These wetlands also define the southern boundary of several plant species (Fortney, 1975; Ingham, 1996). During the last glacial (the Wisconsin Glaciation), the southern Appalachian Mountains experienced a much cooler climate than they do presently, however, the Laurentide ice sheet only reached as far south as Pennsylvania along the Appalachians and therefore did not directly impact southern peatlands (Ingham, 1996). When the ice sheet retreated and temperatures warmed, pockets of vegetation that

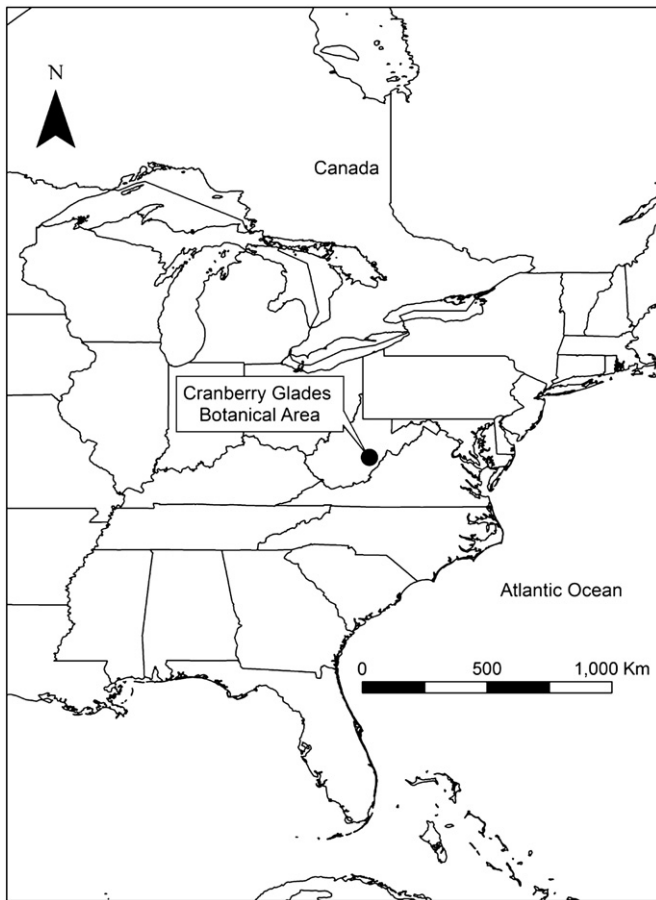
were adapted to cool and moist conditions, found refuge in geomorphically formed basins that retained cool local climates and high moisture (Ingham, 1996; Moorhead and Rossell, 1998; Byers et al., 2007). Rocks that eroded into smooth surfaces and soils that inhibited water drainage were often necessary factors for the formation of southern peatlands (Darlington, 1942, 1943; Diehl, 1981; Walbridge, 1982; Moorhead and Rossell, 1998). Peatlands may serve as flood mitigation by providing broad, low gradient floodplains in the otherwise steep slopes of mountains. The peat also acts as a water filtration system for both stream-water and precipitation (Rydin and Jeglum, 2006).

Changes to peatlands, such as tree encroachment into peatland meadows, may significantly alter the function and processes of the moss-dominated communities. The high acidity and moisture present in peatlands often deter tree establishment (Moorhead and Rossell, 1998; Bedford et al., 1999; Rydin and Jeglum, 2006), however several southern peatlands are reported to be infilling with trees (Darlington, 1942, 1943; Core, 1974; Walbridge, 1982). We were interested in the patterns of tree encroachment across the peatland meadow–forest ecotone, and what factors may be facilitating tree growth within peatlands. Our research was conducted within three peatlands at the Cranberry Glades Botanical Area, located in east-central West Virginia. We chose this location because it has been recorded to be infilling with trees (Darlington, 1942, 1943; Edens, 1973; Kokesh, 1988), has been researched before (Strausbaugh, 1934; Darlington, 1942, 1943; Core, 1949, 1955; Rigg and Strausbaugh, 1949; Edens and Ash, 1969; Edens, 1972, 1973; Kokesh, 1988), and has had limited recent human impacts (Clarkson, 1966, 1993). Very little quantitative research has been performed on tree infilling into the peatland meadows. Our objectives were to quantify patterns of tree growth within the ecotone and how it may relate to microtopography and soil conditions. Our specific research questions were as follows: 1) What is the pattern of tree growth within and across the ecotone? 2) Are specific soil conditions associated with tree growth patterns within the ecotone? 3) Is there a relationship between the depth to saturation and tree density across the ecotone, and 4) Are trees establishing on hummocks more than in hollows?

## 2. Study area

The Cranberry Glades Botanical Area (also referred to as the Glades), located in Pocahontas County, West Virginia (~38.20° N, -80.27° W) (Fig. 1), is a series of naturally occurring open peatlands that are presently infilling with trees from the surrounding mixed temperate forest (Fig. 2) (Brooks, 1911; Darlington, 1942, 1943; Edens, 1973; Kokesh, 1988). The Glades are situated on Cranberry Mountain within the Cranberry Glades Wilderness Area and Monongahela National Forest at elevations ranging from 1024 to 1037 m. This elevation range is characterized by southern Appalachian high elevation vegetation (Core, 1974; Moorhead and Rossell, 1998). The Cranberry Glades Botanical Area is ranked as G2, S2 (Conservation Ranking, Global and State imperiled) (Byers et al., 2007), and is comprised of 243 ha. Within the Cranberry Glades Botanical Area lie four peatlands: Big Glade (60 ha), Flag Glade (28 ha), Long Glade (20 ha), and Round Glade (8 ha) (Kokesh, 1988) (Fig. 3). The primary soil type for all four Glades is medihemists (Mh) (wet organic material, in the order of histosols). The northeastern edge of Flag Glade also contains udifluvents (Uf) (flood-prone soil with little profile development, also within the order of histosols).

The Cranberry Glades Botanical Area is situated in a bowl-shaped basin with poor drainage, characteristics that likely facilitated its formation and persistence during periods of climate warming at the end of the Pleistocene glacial period and into the early Holocene. The headwaters of the Cranberry River and several other streams flow through or nearby the Glades and were key agents to the formation of the peatlands (Darlington, 1942, 1943). Locally wet and cool climate



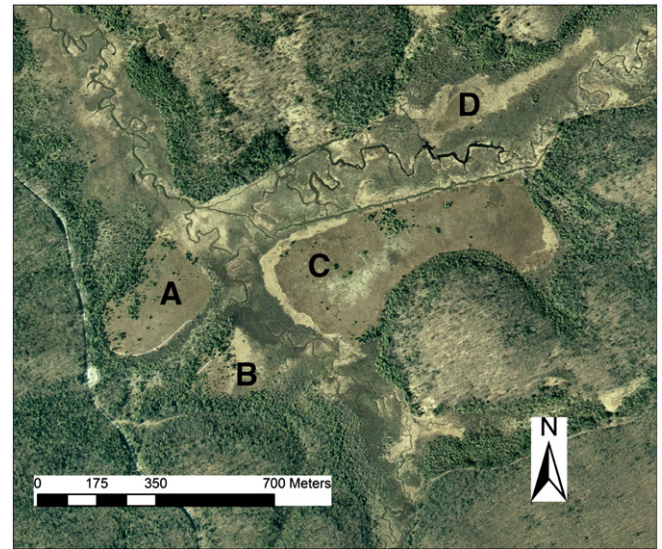
**Fig. 1.** Location of the Cranberry Glades Botanical Area, Pocahontas County, West Virginia, USA.

conditions, exacerbated by lake-effect precipitation from the Great Lakes, and the Glades' location within western slopes of the Appalachians have helped to maintain this wetland (Rigg and Strausbaugh, 1949; Johnson, 1986). Under present climate conditions, the Glades experience on average a 3 °C cooler temperature than surrounding higher elevations due to the settling of cool air from surrounding mountains (Edens, 1973).

The physical isolation characterizing the Glades has created a biogeographic island of refuge for several rare (e.g. *Cornus canadensis*) and unique plant species, as well as forming the southern-most



**Fig. 2.** Trees growing in the peatland meadow-forest ecotone at the Cranberry Glades, WV (photograph taken June 2008).



**Fig. 3.** Spring/summer 2007 aerial photograph of the Cranberry Glades. The following letters correspond to the respective Glade: A – Flag Glade, B – Round Glade, C – Big Glade, D – Long Glade. Study transects were placed on Glades A, B and C. Source: USDA.

distribution of several plants (e.g. *Saxifraga pennsylvanica*, *Menyanthes trifoliata*, *Andromeda polifolia*) found otherwise only in northern boreal environments (Strausbaugh, 1934; Braun, 1947; Core, 1974; Stewart and Nilsen, 1993; Murdock, 1994). Stewart and Nilsen (1993) determined that *Vaccinium oxycoccus* (small cranberry) was the dominant vegetation in the Cranberry Glades. Other plants include *Vaccinium macrocarpan* (large cranberry), *Rhynchospora alba* (white beaksedge), and *Sphagnum* spp. (sphagnum spp.) (Byers et al., 2007).

The three primary vegetation communities found within the Cranberry Glades Botanical Area, as termed by Darlington (1942, 1943), are open bog, shrub, and bog forest communities. The four open peatlands are dominated by *Sphagnum* spp. and contain up to about 3 m of decaying plant material. Shrub communities (dominated by *Alnus* spp.) cover extensive parts of the Cranberry Glades Botanical Area, particularly along the streams. Portions of Big Glade and Flag Glade also contain shrubs, and shrubs border all four of the peatland meadows to some extent. The forest is often accompanied by shrubs and is dominated by trees rather than by mosses as in the ecotone and the open meadow (Kokesh, 1988).

### 3. Methods

#### 3.1. Field sampling

We collected data in three peatlands with three transects placed in each. Data were gathered on trees, soils, and microtopography from across the meadow-forest ecotone of Big, Round, and Flag Glades (*sensu* Collins et al., 1982; Copenheaver et al., 2004). We excluded the fourth peatland in the complex, Long Glade, from the study because it was surrounded by alder thickets rather than forest, and dominated by grasses that appear to preclude tree establishment. Field data were collected during the summer of 2008.

Transect locations were randomly selected within areas of interest, which we determined on aerial photographs as ecotones that contained trees without extensive shrub cover. Transects extended across the forest-meadow ecotone, and ran perpendicular to the ecotone following a constant compass bearing. We placed the transects where the forest was distinct from the ecotone, which was characterized by a discontinuous tree cover, the presence of moss/peat, and/or moist soils compared to the densely vegetated forest with often drier soils. The Glades contain little difference in elevation across the Cranberry Glades



Botanical Area (slope of 0–3%) and no noticeable differences in elevation were observed across any of the transects.

For the purpose of understanding vegetation composition within the ecotone, we recorded diameter at breast height (DBH) (for trees >1.37 m in height) or diameter at ground level (DGL) (for trees ≤1.37 m and ≥10 cm in height), height class, and species composition for all trees that had at least 25% of their crown cover within the belt transects. Trees were placed in the following size classes: seedlings, ≤30 cm tall; saplings, >30 cm tall and ≤10.2 cm dbh; trees, >10.2 cm dbh. We also recorded whether the tree was growing as an individual or in a tree island — defined here as an aggregation of at least three trees. In islands that measured less than 4 m<sup>2</sup> in size, we recorded all trees. We applied a line-intercept method to measure the composition and dimensions of all tree islands greater than 4 m<sup>2</sup> (e.g. Resler and Fonstad, 2009). A lengthwise transect tape was placed down the center of the tree island, and a transect tape was placed perpendicular to the lengthwise transect tape in order to acquire the maximum width (two width lines were placed for tree islands equal to or in excess of 15 m in length). Diameter at breast height, height class, and species composition were recorded for each tree that was in contact or underneath or above the transect tape. Tree cores would have provided useful data on tree ages, but we did not have permission to extract cores because of the strict policies regarding the protection of the Cranberry Glades Botanical Area.

Microtopographic features have been associated with tree establishment in stressful environments (e.g. Titus, 1990; Resler, 2006), and Collins et al. (1982) found a correlation between woody vegetation growth and hummocks in their study on a northern bog. Hummocks are mounds of peat and moss ranging in size from 10 to over 50 cm in height and up to several meters wide. Hummock and hollow features are common in northern peatlands and influence the spatial patterns of vegetation growth (Lewis and Dowding, 1926; Collins et al., 1982; Rossell et al., 2008). Therefore, we were interested in whether tree growth corresponded to microtopographic features. For each tree measured, we recorded whether it was growing on a hummock or hollow.

We collected 10 soil samples at a 20 cm depth from each transect, for a total of 90 samples. Half of the samples were collected from hummocks and the other half from a corresponding hollow. We collected soil samples at regular intervals across the ecotone for subsequent lab analysis. Specifically, we were interested in soil properties important for vegetation growth and establishment and analyzed the soil samples for moisture, pH, N, C, P, K, B, Al, Fe, Ca, Mg, Mn, Zn, and Cu (Brady and Weil, 2008), and the pattern of these soil characteristics in relation to the ecotone. We also noted water table depth at each point where soil was collected by determining where the soil was saturated and measuring the distance between the ground surface and the depth to saturation.

When comparing soil samples collected from different locations within the ecotone, we analyzed samples from hummocks and hollows separately. We also collected soil from 120 cm below the ground surface in order to analyze mineral soil properties, however, all but two of the samples were peat matter and similar in structure and properties to the 20 cm samples, and we therefore did not include them in this analysis. However, we reached mineral soil in two of the samples and they contained high clay content.

### 3.2. Laboratory analysis

Soil samples were air dried, crushed, and passed through a 10-mesh (2 mm opening) stainless steel sieve. Percent soil moisture and pH were determined using SSSA (Soil Science Society of America-SSSA Book Series: 5, 1996) standard methods. Soil moisture was obtained by acquiring the difference between the wet weight and the dry weight of the soil samples and calculating the percentage of the moisture lost. The samples were air-dried at room temperature for two weeks. We determined soil pH from a buffer pH at a 1:3 ratio due

to the small sizes of some of the samples and the nature of the peat samples to soak up the water. A calibrated Thermo Electron Orion PerPhecT 370 LogR pH/ISO meter was used to record pH values for the samples. Carbon and nitrogen were analyzed in the Virginia Tech Department of Crop and Soils Environmental Sciences' lab using an Elementar Analysensysteme GmbH. Select macronutrients, micronutrients, and metals (P, K, Ca, Mg, Mn, Zn, Fe, Cu, B, Al) were analyzed by the Virginia Tech Extension Soil Testing Laboratory (Mullins and Heckendorn, 2005). Potassium, K, Ca, Mg, Mn, Zn, Fe, Cu, B, and Al were determined using an extraction solution of Mehlich 1, 0.05 N HCl in 0.025 N H<sub>2</sub>SO<sub>4</sub> and analyzed by an ICP (inductively coupled plasma atomic emission spectrometer).

### 3.3. Statistical analysis

Data were entered into a spreadsheet and analyzed using JMP® (JMP) version 7.0. We analyzed all appropriate data for normality and equality of variance, and applied log transformations where appropriate. One-way ANOVA and *t* tests were performed on normally distributed data. We used a G-test on the nominal data of the number of trees on hummocks compared to hollows and trees growing in islands compared to those growing as individuals (Sokal and Rohlf, 1981). The Tukey–Kramer *post hoc* was performed on tree density averages that were significantly different across the ecotone. All tests were run and analyzed at the 0.05 significance level. We analyzed tree density across the ecotone by dividing each belt transect into four intervals (0–25 m, 25–50 m, 50–75 m, and 75–95 m) from the forest edge (0 m) out towards the open meadow (95 m). The last interval (75–95 m) only contains 20 linear meters rather than 25 as with the other intervals, and this discrepancy was taken into account when calculating tree density. The soil data were analyzed with the Student's *t* test and ANOVA to determine if significant differences existed in soil properties between hummocks and hollows and at different positions along the ecotone. Standard deviations are reported with means where appropriate.

## 4. Results

### 4.1. Tree patterns

A total of 1389 trees were sampled within the belt transects. These trees represented five species: *Picea rubens* (red spruce), *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch), *Tsuga canadensis* (Eastern hemlock), and *Sorbus americana* (mountain ash). *P. rubens* (red spruce) was by far the most abundant tree recorded (82.8% of total, 1151/1389), followed in abundance by *Acer rubrum* (red maple, 14.5%, 201/1389), *B. alleghaniensis* (yellow birch, 1.2%, 19/1389), *T. canadensis* (Eastern hemlock, 1.0%, 17/1389), and *S. americana* (mountain ash, 0.06%, 1/1389). Diameter at breast height (DBH) for trees >1.37 m ranged from 0.2 to 60.4 cm (mean = 8.87 ± 7.86, *n* = 569), and diameter at ground level (DGL), recorded for smaller trees ranged from 0.1 to 9.4 cm (mean = 1.28 ± 1.14, *n* = 820). Trees ranged in age from seedlings to cone producing trees. Fig. 4 shows size distributions across the ecotone.

Using one-way ANOVA and Tukey–Kramer tests, we found that mean density of trees varied significantly ( $F < 0.0001$ ,  $F$  ratio = 14.30,  $df = 3114$ ,  $P < 0.05$ , one-way ANOVA, Tukey–Kramer,  $P < 0.05$ ) across the ecotone, as recorded in intervals of distance from the forest (0–25 m, 25–50 m, 50–75 m, and 75–95 m). Average tree density (0.32 trees m<sup>-2</sup> ± 0.30) at 0–20 m from the forest was significantly higher compared to the areas in the ecotone closer to the peatland interior (Fig. 5). Average tree density at the meadow interior (75–95 m from the forest, 0.01 trees ± 0.04 m<sup>-2</sup>) was statistically less dense than the 50 m closest to the forest.

In order to gain a better understanding of the spatial pattern of tree establishment, we examined whether trees tended to be found as individuals or growing as part of tree islands. We found that a significant

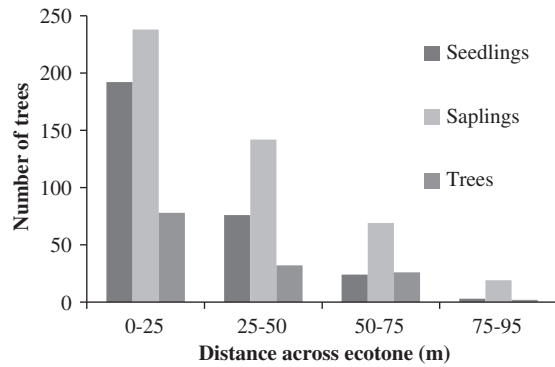


Fig. 4. Distribution of the number of seedlings, saplings, and trees across the ecotone.

proportion of trees are located within tree islands as determined with G-test goodness of fit ( $G = 16.094$ ,  $df = 1$ ,  $1140$ ,  $P < 0.0001$ ,  $n = 1141$ ) with expected proportions of island:individual set at 3:1 since islands, by definition, contained at least three trees. Eighty percent of trees measured across the ecotone were found to be associated with tree islands (913/1141), and 20% were growing as individuals (228/1141). These values were calculated from the total number of trees within the ecotone ( $n = 1141$ ), and did not include trees recorded in the forest ( $n = 248$ ).

#### 4.2. Microtopography

We found 92% of trees located on hummock features. The G-test goodness of fit values ( $G = 931$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n = 1112$ , 1:1) showed a strong association between tree establishment and hummocks. A 1:1 ratio was used since the null hypothesis is that trees would be spatially random with regard to microtopographic features. Hummocks covered approximately 50% of the ground surface and hollows about 50%, providing a ratio of about 1:1 chance of a tree growing on a hummock or hollow. Sample size was 1112 since trees from the forest quadrats were not included, and 29 trees were on level surfaces that could not be categorized as hummock or hollow. The average hummock height for all three Glades was  $21 \pm 8.5$  cm, with a range from 10 to 56 cm ( $n = 189$ ). Hummocks varied in diameter from 15 cm to greater than several meters.

#### 4.3. Soil conditions

Soil moisture, N, P, and Cu were statistically lower close to the forest compared to the soil collected in the quadrats closest to the open peatlands (90–95 m from forest edge) (one-way ANOVA, Tukey–Kramer *post hoc* ( $P < 0.05$ ) comparison among the four sample locations) (Fig. 6). Lower moisture content within the forest is

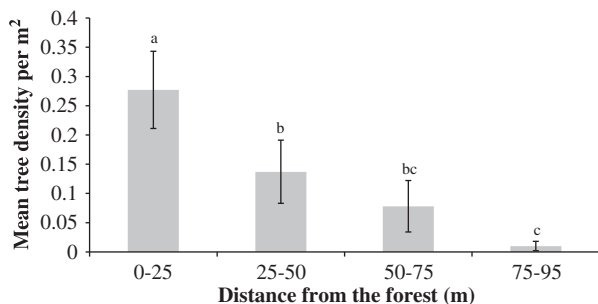


Fig. 5. Mean tree density per square meter across the ecotone. Error bars show  $\pm 1$ SE. Lower-case letters show Tukey–Kramer significant differences in means ( $P < 0.05$ ).

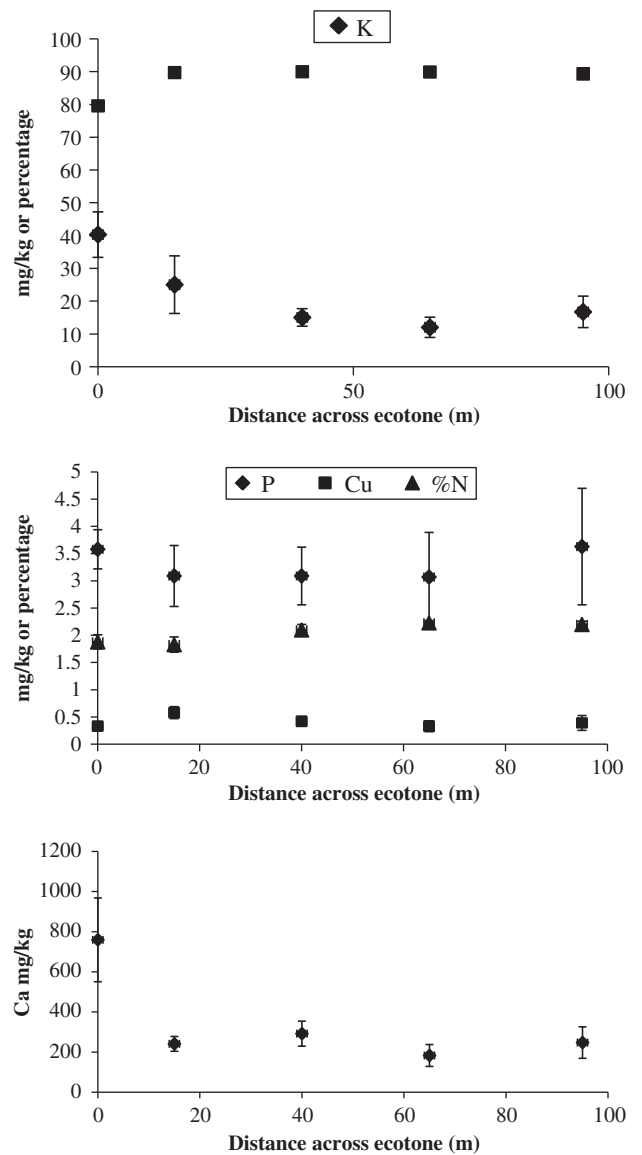


Fig. 6. Mean values for soil properties collected at a depth of 20 cm; these were statistically different between soil collected closest to the forest and those collected closest to the interior of the open peatland ( $P < 0.05$ , as determined by one-way ANOVA). Error bars show  $\pm 1$ SE.

expected due to the characteristically saturated conditions within the open peatlands. Potassium and Ca were found to be higher in the forest quadrats than towards the open peatland area. Depth to saturation on hummocks ranged from an average of 18 cm at 20 m from the forest to 21 cm at 45 m across the transect, and 12 cm at 20 m across the transect to 16 cm at 45 m in the hollows (Fig. 7). Soil properties did not vary significantly relative to location within the ecotone (not including those closest to the forest).

Tree growth was associated with hummocks, so we analyzed soil samples from both hummocks and hollows in order to determine if soil characteristics varied between the two microtopographic features. The depth to saturation was the most notable difference between the two features and averaged 21 cm for hummocks ( $n = 34$ , ranged from 8 to 40 cm) and 13 cm for hollows ( $n = 34$ , ranged from 5 to 33 cm). Our results showed that P and K were in greater concentration on the hummocks, and percent C and Fe was higher in the hollows (Table 1).

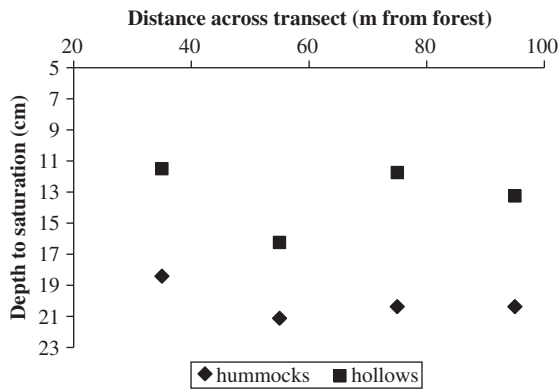


Fig. 7. Mean depth to saturation from the ground surface across the transect for hummocks and hollows.

## 5. Discussion

The purpose of this study was to characterize the tree spatial pattern across the peatland meadow–forest ecotone in relation to microtopography, location within the ecotone, and soil conditions. Overall, we found that tree densities followed a general trend of decreasing towards the open peatland, though trees were still found 90–95 m from the forest; most soil conditions did not change significantly among our variables; and trees were most likely growing in tree islands and located on hummocks. These results provide information on the characteristics of the ecotone and tree establishment patterns within the moss-dominated communities, how these patterns compare to northern peatlands, and may assist in southern peatland restoration efforts.

### 5.1. Tree establishment patterns

The decreasing tree density from the forest toward the open peatland is a common pattern found in wetland environments (Fig. 8) (Dansereau and Segadas-Vianna, 1952; Walbridge, 1982; van der Valk, 2006). The open peatland is further from seed sources and more exposed to wind and sunlight. Hydrology is often a controlling factor in wetland environments (Schwintzer, 1978; Rydin and Jeglum, 2006), and we initially expected tree growth to correspond to a soil moisture or water level gradient, however, our results did not support this hypothesis. Soil moisture did not vary significantly across the ecotone and the average water table level was actually highest closer

to the forest. Though we did not take tree cores to determine tree age because of strict sampling rules established in the Cranberry Glades Botanical Area, mature trees (seed producing) were found towards the open meadow, indicating that trees are not advancing in a progressive manner with younger trees establishing towards the meadow and a linear age gradient extending with the oldest trees closest to the forest. This result may indicate that the ecotone is rather stable or tree infilling is progressing at a very slow rate in a non-linear manner. However, previous studies postulate that the Glades are infilling, and one small Glade had completely filled in by the time of Darlington's study in the 1930s and 1940s (Darlington, 1942, 1943; Edens, 1973).

In order to gain a better understanding of the history of tree establishment in the ecotone, we examined aerial photographs of the Cranberry Glades Botanical Area from 1957, 1969, 1975, 1986, and 2007 (Source: USDA). The aerial photographs indicated that trees were established towards the interior of the open peatland at least as far back as 1957. However, compared to the 2007 image, the tree or tree islands have increased in size (noticeably more than just individual tree growth) with visible tree establishment occurring in 2007 around the trees that were present in 1957 and 1969. This observation is in accordance with our finding that most of the trees were located within tree islands (Fig. 8). Our data support the conception that trees have established within islands within the ecotone rather than in a linear advancement from the forest out towards the open meadow.

Tree islands are found in several harsh environments, including alpine treeline and large wetland systems such as the Florida Everglades (Wetzel et al., 2005; van der Valk and Warner, 2008; Resler and Stine, 2009). In the low nutrient, high moisture, acidic, and exposed conditions of peatlands, facilitation processes may override competition among the trees. Facilitation is defined as the process in which vegetation or objects (i.e. rocks) assist in the growth of plants and increase the probability of other vegetation establishing nearby (Callaway, 1994; Greenlee and Callaway, 1996; Nunez et al., 1999). Environmental stress is noted to be a determining factor in the relative function of competition and facilitation in vegetation on a landscape (e.g. Greenlee and Callaway, 1996; Pugnaire et al., 1996; Callaway and Walker, 1997). Salt marshes, alpine, arctic, and desert systems are classic examples of how vegetation, limited by stressful conditions, can facilitate the growth of more plants through modification of its local environment (e.g. Parker, 1989; Kikvidze and Nakhutsrishvili, 1998; Bekker, 2005; Resler et al., 2005). Similar to these environments, peatlands are harsh systems in which facilitation may be the dominating process in the competition/facilitation dynamic. An established tree can provide nutrients and a seed source; protection from wind, herbivory, and sunlight; and decrease soil moisture content (Chapin, 1980; Greenlee and Callaway, 1996; Nunez et al., 1999; Resler et al., 2005; Callaway, 2007) within the peatlands at the Cranberry Glades. We observed that many of the tree islands contained a larger tree (a "leader tree" that likely established first) with several smaller trees located within close proximity (Fig. 8). Leader trees may establish during years of optimal growing conditions (plentiful seed source, ideal weather) and evade fatal factors such as herbivory and flooding, creating improved growing conditions for subsequent tree establishment.

### 5.2. Microtopography

Eighty percent of recorded trees were located on hummocks (Fig. 8). Lewis and Dowding (1926) and Collins et al. (1982) observed that woody vegetation was most commonly found on hummocks on their studies in northern bogs. They attributed this relationship to the increased distance between the ground surface and the water table and the corresponding lower acidity and soil moisture on the hummocks. Distance to the water table was greatest on the hummocks compared to

Table 1

Soil conditions in mg/kg (unless noted as a percentage and for pH) in relation to topography. Soil collected at 20 cm across the ecotone on hummocks and hollows. (Samples do not add up to 72 – the total number of soil samples collected from within the ecotone – due to the elimination of some as outliers and not being able to test all samples for all variables due to small samples sizes.)

Soil property	Hummock (n) (mg/kg or %)	Hollow (n) (mg/kg or %)	t ratio	P
pH	3.98 ± 0.23 (36)	3.97 ± 0.24 (32)	−0.21	0.58
% moisture	89.74 ± 1.00 (34)	89.75 ± 1.16 (34)	−0.04	0.52
%N	2.11 ± 0.35 (31)	2.14 ± 0.24 (29)	−0.06	0.72
%C*	51.06 ± 1.02 (31)	51.71 ± 1.25 (28)	−2.18	0.02
P*	5.53 ± 2.68 (18)	4.57 ± 2.65 (24)	2.16	0.02
K*	35.41 ± 33.67 (18)	21.37 ± 12.49 (24)	2.28	0.01
Ca	370.67 ± 206.21 (18)	403.82 ± 238.19 (24)	−0.16	0.56
Mg	50.87 ± 25.25 (18)	46.94 ± 23.51 (24)	0.88	0.19
Zn	2.83 ± 1.07 (18)	2.96 ± 0.97 (24)	−0.35	0.64
Mn	4.16 ± 4.93 (18)	2.87 ± 1.21 (24)	1.13	0.14
Cu	0.64 ± 0.34 (18)	0.69 ± 0.45 (24)	−0.57	0.71
Fe	19.99 ± 5.42 (18)	25.18 ± 10.38 (24)	−2	0.27
B	0.06 ± 0.04 (4)	0.05 ± 0.01 (3)	0.58	0.3
Al	52.49 ± 26.18 (18)	60.49 ± 17.78 (24)	−1.16	0.87

\* Indicates significant difference,  $\alpha = 0.05$ , as determined by *t* test.





**Fig. 8.** Tree establishment characteristics within the ecotone (from left to right, top row, then bottom row). (Top, left) Tree density decreased across the transects from the forest out towards the open peatland meadow. This photograph is a view of the ecotone looking towards the forest (indicated by the taller trees in the background) from the open peatland (photograph taken July 2008). (Top, right) A tree island located within the meadow-forest ecotone (photograph taken July 2008). Most of the trees we recorded were located in tree islands rather than growing as individuals. (Bottom, left) A tree island with a leader tree surrounded by smaller trees (photograph taken October 2008). Many of the tree islands contained what appeared to be a more mature tree surrounded by younger trees. (Bottom, right) Most trees within the ecotone were located on hummocks. The photograph shows a hummock colonized by ferns and a *Picea rubens* (only the trunk is visible in this photograph) (photograph taken June 2008).

the hollows at the Cranberry Glades, however we did not find significant differences in pH or soil moisture between the hummocks and hollows. However, soil moisture varies among different times within the year and in response to weather patterns. Darlington (1942, 1943) found that the water table level ranged from 2.5 cm above the surface in April to

30.5 cm below the surface in October. Animal paths may also decrease the occurrence of tree establishment in hollows. We saw numerous animal trails and evidence of animals (scat and herbivory) that followed along the hollows through the peatlands. Consistent trampling may inhibit tree growth.

We determined that C, K, and P varied significantly between hummocks and hollows. Carbon concentrations were possibly greater in the hollows from accumulating within the depressions and in water that may collect in the hollows. In acidic soils, P may bind with Fe, forming iron phosphate. The higher concentration of Fe in the hollows may immobilize P, resulting in higher amounts on the hummocks compared to the hollows. Potassium does not bind with other elements or wash from soils as other nutrients do, making it more likely to remain in place on the hummocks.

### 5.3. Implications for peatland restoration and peatland maintenance

Southern peatlands are rare and important ecosystems and many have been impacted by human activities (Clarkson, 1993). For this reason, efforts have been made to restore some of these peatlands (Rossell et al., 2008). Since they are small, isolated areas that are often difficult to reach, management of these peatlands for conservation purposes is often lacking, and many may have been degraded or lost (Francl et al., 2004). Rossell et al. (2008) found that greater numbers of species would re-establish when ridges and micro-elevation heterogeneity were created in peatland restoration because of the different micro-habits formed by variations in topography. However,



**Fig. 9.** Beaver activity may be an important factor of peatland formation and the maintenance of peatland conditions. This image, taken at the Cranberry Glades, shows the ponding of a stream behind a beaver dam (photograph taken July 2008).



consideration needs to be given to the height of created ridges/hummocks and water table levels if the peatland is to be maintained as an open, moss-dominated system and tree encroachment is a threat to the open meadow.

Wildlife management is also a factor in peatland restoration. Beaver activity has been noted to be important to wetland maintenance (Fig. 9) (e.g. Edens, 1973; Fortney, 1993; Walbridge, 1994). Beaver dams pond water and can raise the water table and possibly flood the surrounding area (Edens, 1973; Butler, 1995; Butler and Malanson, 2005). This action may be important in deterring tree establishment and in maintaining the saturated conditions found in peatlands. Beavers can also form wetlands and may have been vital to the creation of the Cranberry Glades (Edens, 1973) as well as other southern peatlands. Herbivory by deer and rabbits and animal trails may also help prevent tree growth, though too large a population may also damage herbaceous vegetation.

Conversely, many southern wetlands are dominated by trees (Messina and Conner, 1998). Within such wetlands that need to be restored, planting trees in groups or planting fewer, older trees which may then become leader trees, may facilitate tree survival. Staggered planting may also benefit tree growth. Planting several trees and then planting seedlings once the first set has become well established may enhance tree survival within the wetland. Land managers should consider whether facilitation or competition would be the overriding mechanism. If conditions are more favorable to trees, competition may be the dominating process, in which cases, group plantings may result in more harm than good. In harsher wetland environments however, restoration may benefit from the formation of tree islands.

## 6. Conclusion

This study provides data on the spatial pattern of trees and soil conditions within the forest–meadow ecotone, information that can contribute to an improved understanding of the processes occurring. Human activities and global climate change pose a threat to the continued function of these ecosystems and knowledge of southern peatlands is lacking, which can impede management and conservation of these wetlands. *Sphagnum*-dominated peatlands are important and rare ecosystems in the southern Appalachian Mountains. Tree growth within the meadows leads to changes in the hydrology, vegetation structure, and functions of the open peatlands. Our result that most trees were found in tree islands indicated that facilitation processes are likely responsible to tree growth within the harsh conditions of the peatlands. A mosaic of topographic microelevations assists in tree growth within the ecotone by providing a greater distance from the ground surface to the water table. Hummocks offer greater distance between the ground surface and water table which may be more optimal for tree growth than the hollows. The results of this study add to the scant literature available on southern peatlands and the patterns present within the meadow–forest ecotones. Our findings provide characterization of the forest–meadow ecotone, which may aid in understanding tree infilling processes. Further studies need to be conducted on southern peatland to further assess infilling processes. Our results were primarily spatial, however, more information on the temporal components of this system need to be acquired to address the stability of the ecotone and the rate of infilling. Southern peatlands may be sensitive to climate changes, which could threaten the existence of these unique ecosystems.

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