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Spatial patterns of vegetation structure and structural diversity across edges between forested wetlands and upland forest in Atlantic Canada

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Abstract

Forested wetlands are an integral but understudied part of heterogeneous landscapes in Atlantic Canada, although they are known to provide habitat for species at risk. Our objectives were to explore patterns of forest structure across edges between forested wetland and upland forest, to locate changes in vegetation structure and to assess multivariate relationships in vegetation structure. Our study sites were in temperate (Acadian) forested wetland landscapes. We sampled trees and recorded canopy cover every 20 m along 120 m long transects. We estimated the cover of trees, saplings, shrubs in three height classes, *Sphagnum*, other bryophytes, lichens, graminoids, ferns and forbs in contiguous 1 x 1 m quadrats. We calculated structural diversity using the Shannon index and used wavelet analysis to assess spatial patterns. We found few clear patterns except for lower tree structural diversity at the edge of forested wetlands. Structural diversity was not a reliable measure for distinguishing forested wetland from upland forest. Forested wetlands are an integral part of many forested landscapes in Atlantic Canada but their detection and differentiation from surrounding ecosystem can be difficult. Policy should err on the side of caution when mapping forested wetlands and include them in wetland protection.

Key words: forested wetland landscapes, plant community transitions, spatial pattern analysis, *Sphagnum*, treed bog, vegetation structural diversity

Introduction

Forested wetlands are an integral but understudied part of many heterogeneous

landscapes. An understanding of the distribution and abundance of forested wetlands on the

landscape has been recognized as a knowledge gap by the Nature Conservancy of Canada

(2015). Forested wetlands can have high plant (Cameron 2009) and bird diversity (Brazner and

MacKinnon 2020), and provide habitat for rare bird species such as the Canada Warbler

(*Cardellina canadensis*, Westwood 2016, Brazner and MacKinnon 2020), epiphytic lichen

species at risk (Padgett and Wiersma 2020) and rare species of odonate and tabanid insects

(Hurlburt, D., pers. comm.). Trees and shrubs provide carbon inputs through litterfall in forested

wetlands, which enables them to serve as a carbon sink even with a doubling of greenhouse gas

emissions (Kendall et al. 2020). Forested wetlands may be susceptible to changes in land use

such as forest harvesting that alter their hydrology and nutrient dynamics. For example, bumble

bees were more abundant in forested wetlands than in harvested sites (Brooks and Nocera 2020).

Forested wetlands may also be sensitive to climate change as their soil moisture would be near

the threshold required for maintaining wetland conditions.

Ecotones, such as the edges of forested wetlands, might be indicators of the initial

impacts of climate change (Risser 1993). Forested wetland boundaries are also important for

wetland conservation as their locations are needed for mapping. It can be difficult or impossible

to detect the boundary between forested wetland and upland forest using aerial photography

(pers. obs.), particularly for coniferous forested wetlands (Lang and McCarty 2009), or

unmanned aerial imagery (Wilson 2019). Boundary delineation based on LiDAR and

topographic metrics has been more successful (Lang et al. 2013, Langlois et al. 2017).

Transitions between plant communities have been related to greater species diversity (Harris

1988). Natural edges can be more complex and exhibit unique landscape features that could provide important habitat for conservation at bog, lake and insect outbreak edges (e.g., Franklin et al. 2015, Dazé Querry and Harper 2017).

The complexity of vegetation at natural edges can be assessed using the diversity of plant structural elements, a useful measure for any ecosystem regardless of species diversity or composition. Structural diversity is a measure of the variability in vegetation structure and has been measured as the diversity, equitability, variance or standard deviation of the number of trees in different tree size classes (Staudhammer and Lemay 2001, McElhinny et al. 2005, McRoberts et al. 2008). Other measures of structural diversity (e.g., the number and abundance of different vegetation structural components such as shrubs, trees and logs) have been explored in the forest-tundra landscape near Churchill Manitoba, in cerrado savanna vegetation in southern Brazil (Dodonov 2015) and at lakeshore edges in Nova Scotia (Dazé Querry and Harper 2017). Greater habitat complexity increases the number of species that coexist (Tilman 1982); for example, vertical foliage distribution and horizontal structural complexity are important for bird habitat (MacArther 1964, Zellweger et al. 2013). Structural diversity has been shown to be an important explanatory factor for the diversity of Atlantic Coastal Plain Flora on lakeshores in southwestern Nova Scotia (Dazé Querry and Harper 2017) and breeding habitat of the Canada Warbler (Hallworth et al. 2008). Structural diversity is considered a useful indicator of ecosystem health (Parrott 2010) and could help identify priority areas for conservation if greater structural diversity is found at forest edges.

At natural edges, edge influence from increased light and wind can be extensive, and variable structure creates more gradual but complex and variable transition zones (Hanson and Stuart 2005, Larivée et al. 2008, Braithwaite and Mallik 2012, Harper et al. 2014). Dazé Querry

& Harper (2017) found greater structural diversity accompanied by high richness of Atlantic Coastal Plain Flora at lakeshore edges but only at a fine scale on the lakeshore itself and not in the adjacent forest due to the low competitive abilities of this group of plant species. There were also unique patterns of shrubs at lakeshore edges in the forest-tundra landscape (Harper et al. 2018). Transitions may have greater structural diversity than adjoining ecosystems because of the overlap of plant communities with different structure.

Our study provides a detailed analysis of vegetation structure on forested wetland landscapes in Atlantic Canada. For our first objective, we measured forest structure characteristics and calculated structural diversity in forested wetland landscapes in Atlantic Canada to explore patterns across edges between forested wetland and drier upland forest. For our second objective, we used spatial pattern analysis to determine locations of change in structural diversity, shrub height and individual vegetation structural components. We assessed bivariate relationships between structural diversity and vegetation structural components, and multivariate relationships in vegetation structure across forested wetland landscapes to explore non-spatial patterns as our third objective. We hypothesized that structural diversity would be greatest at edges, which can contain elements of both adjoining plant communities, and that changes in vegetation structure would occur at or near the edge.

Methods

Study area

Our 10 study sites were located in temperate (Acadian) forests with both forested wetland and drier upland forest dominated by *Picea, Abies, Betula* and *Acer* in Nova Scotia, New

Brunswick and Prince Edward Island in Atlantic Canada (Figure 1, Table 1). Climate normals

from major cities in the area indicate that the January and July average temperatures are -6.5°C

and 19°C, respectively; annual precipitation varies from 1200 to 1500 mm (Environment Canada

2019). Sites were selected subjectively mostly from other research projects used in this special

issue (e.g., Brazner and MacKinnon 2020, Kendall et al. 2020) based on ease of access,

geographic representation and absence of obvious recent anthropogenic disturbance.

Data collection

      Six of our study sites (A-F) included a single clear transition between forested wetland

and upland forest (Table 1). At these sites we established a 120 m transect that straddled a clear

edge between forested wetland and upland forest (evident as an edge of a very wet area, which

often coincided with an area dominated by *Sphagnum*). These transects were oriented

perpendicular to the forest edge and crossed it at 0 m with 60 m on either side. Sites G and H

crossed two edges at 60 and 120 m (Site G) and at 30 and 80 m (Site H); the transect at Site G

extended a further 40 m for a total of 160 m. Sites I and J consisted of fine-scale mosaics of

wetland and drier ground underneath a forest canopy, as indicated by patchy cover of *Sphagnum*

moss; the transect at Site I was only 100 m long to avoid being close to a river and a road. Data

collected from transects at these sites were organized into two data sets: an edge data set (Sites

A-F) with transects across a single edge and the entire data set (all sites, Sites A-J) with transects

in forested wetland landscapes that crossed one or more edges (including a mosaic of wetland

and upland).

      For Sites A-F in the edge data set, we used seven 20 x 5 m plots every 20 m along each

transect to record the species, dbh and canopy position (*i.e.*, dominant, codominant, intermediate

or suppressed, Côté 2000) of every live tree with dbh > 5 cm. Tree plots were oriented such that the longer 20 m side was perpendicular to the transect and therefore were spaced such that there was 15 m between plots. At the centre of each plot, we estimated canopy cover using a spherical convex densiometer by taking the average of two measurements facing towards and away from the start of the transect. We also recorded the number of snags (dead trees) in each plot and measured the height of the tallest tree using a laser rangefinder.

At all ten sites, we estimated the cover of eleven structural categories of plants in contiguous 1 x 1 m quadrats along the length of each transect. The categories were: lichens (on the ground, not arboreal), *Sphagnum*, other bryophytes, graminoids, herbs, ferns, <1 m tall shrubs, 1-2 m tall shrubs, >2 m tall shrubs, saplings (< 5 cm dbh) and trees (> 5 cm dbh). Cover was estimated to the nearest 10% except to the nearest 1% for cover less than 5%. In each quadrat, we also measured the maximum height of shrubs.

Data analysis

For our first objective, we examined the trend across the edge from data in the 20 x 5 m plots using eight response variables: canopy cover, maximum height, tree density, snag density and four measures of tree structural diversity. Following Staudhammer and Lemay (2001), we calculated measures of tree structural diversity using the Shannon index with the number of trees in different categories as pseudospecies: 1) tree height diversity – different canopy positions (4 possibilities: dominant, co-dominant, intermediate, suppressed), 2) tree dbh diversity – different 10 cm dbh classes (6 possibilities: 5-10, 10-20, 20-30, 30-40, 40-50, 50-60 cm) and 3) tree height x dbh diversity – different combinations of canopy position and 5 cm dbh classes (17 possibilities with at least one tree). We calculated a fourth measure (tree structure diversity) as the average of tree height diversity and tree dbh diversity (extended Shannon index,

Staudhammer and Lemay 2001). We performed repeated measures ANOVA with post-hoc

Tukey tests and $\alpha = 0.05$ using PAST 3.25 software (Hammer et al. 2001) to determine which

distances along the forested wetland to upland gradient had significantly different values of these

eight response variables compared to other distances.

We calculated vegetation structural diversity using the Shannon index with the cover of

the eleven plant structural types as pseudo-species for the 1 x 1 m plots. For our second

objective, we used wavelet analysis to evaluate spatial patterns and determine locations of

change along each transect for vegetation structural diversity, maximum shrub height and each of

nine plant structural types excluding saplings and trees (objective 2). Wavelet analysis quantifies

spatial patterns at different scales and positions by moving a template along the transect that

assesses the similarity between the template and the data at each distance, and at several scales

by increasing the size of the template. We used two different wavelet templates, Haar and Sine,

that represent abrupt and gradual transitions, respectively. The Haar wavelet has been used in

plant ecology studies (e.g., Battlori et al. 2009) but we have found no examples of using the Sine

wavelet. High wavelet transform indicates a match between the template and the data, revealing

the presence of the spatial structure defined by the template (Dale and Mah 1998; Kembel and

Dale 2006; James and Fleming 2010). We used wavelet position variance (with 10% maximum

scale), which sums wavelet variance across all scales for each position, to identify transitions in

vegetation structure along transects (Dale and Mah 1998); peaks of position variance indicate

locations of the spatial structure (Kembel and Dale 2006). To determine the locations of

significant spatial structures (abrupt and gradual transitions), we used the randomization test of

position variance with 999 permutations and a 95% confidence interval, which compares wavelet

position variance with a null model of complete spatial randomness. Null models represent

spatial processes deprived of pattern and involve the same analysis but with a random resampling of the data along transects (James and Fleming 2010). Positions for which the wavelet variance is higher than the value provided by null models (i.e., above the 95% confidence interval) are considered significant. All wavelet analyses were conducted in PASSAGE 2.0 (Rosenberg and Anderson 2011).

We used the set of all ten transects for the remaining analyses to investigate bivariate and multivariate relationships across all types of forested wetlands landscapes. We used bivariate wavelet covariance analysis with the Mexican Hat wavelet with 25% maximum scale to assess the relationship between vegetation structural diversity vs. different plant structural groups at different scales along each transect. Wavelet covariance multiplies the wavelet transforms of two variables to assess spatial relationships between two variables at different scales (Kembel and Dale 2006). Positive wavelet covariance implies that the two variables vary in the same direction, whereas negative values indicates that the variables vary in opposite directions. Scales for which wavelet covariance value is higher or lower than the value provided by null models (i.e., above the 95% confidence interval determined by a randomization test with 999 permutations) are considered significant.

We explored patterns in the composition of vegetation structural groups across forested wetland landscapes using detrended correspondence analysis (a matrix of 11 structural groups and 1497 quadrats) using the *decorana* function in the *vegan* package (Okansen et al., 2019) and plotted findings using *ggplot2* (Wickham, 2016) in R (R Core Team, 2020). To prevent quadrats from being excluded if they contained all zeroes, we included 1% for tree cover to nine quadrats, which ensured that all quadrats were present on the ordination.

Results

Forest structure generally differed between the forested wetland and upland forest with intermediate values at the edge, but not always (Figure 2). Canopy cover and maximum tree height were significantly lower in the wetland compared to upland forest; intermediate values found at the edge were only significantly different than some of the wetland distances for canopy cover (Figure 2A, B). There were fewer trees in the wetland compared to upland with the lowest density 20 m on the wetland side of the edge, which was only significantly lower when compared to 40 m into upland forest (Figure 2C). Although not significant, there were more snags at the edge and 20 m into the wetland compared to other distances (Figure 2D). All four measures of tree structural diversity exhibited the same trend of lower values in the wetland reaching a trough at 20 m into the wetland and consistently higher values both at the edge and in upland forest (Figure 2E-H). Results of specific pairwise comparisons differed among the four types of diversity but all had some distances in upland forest with greater diversity than some distances in wetland. Dbh and height diversity were very similar to each other and the other two measures, which differed only in their magnitude with tree structural diversity having lower values than dbh x height diversity.

Trends in vegetation structural diversity along transects were not clear or consistent (Figure A1). Although some sites had higher diversity in the forested wetland (sites A, D, F), patterns of greater diversity at the edge were not distinct. Abrupt and gradual changes in diversity along the transects indicated by significant Haar and Sine wavelet position variance, respectively, were infrequent and spread throughout the wetland – upland gradient and not only close to forest edges (Figure 3).

Patterns in shrub height were more pronounced at some sites (A, C, D), where shrubs were taller in forested wetland with a transition to shorter shrubs at the forest edge (Figure A1). This finding for a distinct pattern in shrub height was also evident by more transects with significant gradual transitions (Sine wavelet) at or near the edge (Figure 3). However, significant transitions were found at other locations along the transects. Almost all significant transitions in shrub height were gradual as detected by the Sine wavelet.

The cover of certain plant structural groups displayed clearer patterns across forested wetland landscapes (Figure A1). The cover of *Sphagnum,* graminoids and shrubs of all sizes was greater in forested wetlands than uplands, whereas the opposite was found for bryophytes other than *Sphagnum*. Abundance of different structural groups was variable along the transects except for *Sphagnum*, which often exhibited an abrupt transition from up to 100% cover in forested wetland to being virtually absent from uplands. Significant transitions were evident at edges primarily for *Sphagnum* and low shrubs (Figure 3). Transitions only rarely coincided for different structural groups indicating that patterns varied for different types of plants. Results using the Haar and Sine wavelets were similar for low shrubs, *Sphagnum* and graminoids, but were quite different (abrupt and gradual transitions occurring at different positions along the transects) for medium tall shrubs, other bryophytes and herbs.

Wavelet covariance can be thought of as similar to correlation at different scales (plot sizes). Significant wavelet covariance indicates that vegetation structural diversity had similar (positive covariance) or different spatial structure (negative covariance) with different plant groups at different scales (Figure 4). Vegetation structural diversity was negatively correlated with most plant structural groups (especially shrubs and to a lesser extent *Sphagnum*, herbs and graminoids), on several transects at small scales. This indicates that vegetation structural

diversity is low in areas close to patches dominated by these plant structural groups. Positive correlations were found with shrubs, *Sphagnum* and herbs at greater distances. Overall, local pockets of low diversity were found in areas with dense cover of a particular plant group in an overall diverse forested wetland landscape with heterogeneous cover of shrubs, *Sphagnum* and herbs.

In the detrended correspondence analysis (eigenvalues of 0.625 and 0.438 for axes 1 and 2, respectively), there was a clear separation along the first axis between quadrats on the forested wetland and upland forest sides of the single edge transects (Figure 5). Interestingly, the quadrats close to the edge were found amongst other quadrats on either side of the edge and not close to the middle of the ordination diagram, and therefore did not appear to be intermediate in structural composition between the forested wetland and upland forest. Quadrats from the multi-edge and mosaic transects were scattered throughout the ordination diagram. Upland forest quadrats were associated with greater abundance of lichens and other bryophytes, whereas forested wetland quadrats were subdivided into those more closely associated with greater cover of *Sphagnum* vs. high cover of shrubs of all sizes and graminoids.

Discussion

Patterns of vegetation structure in forested wetland landscapes

Contrary to our hypothesis, tree structural diversity was not greater at the edge but instead was lower in the forested wetland compared to upland forest, particularly 20 m from the edge. This is a similar location to the rand-forest on the bog side of the edge of the lagg zone, which is composed of a band of dense *Picea* and shorter vegetation height (Langlois et al. 2015,

Paradis et al. 2015). We found fewer trees at this distance, likely because *Picea* and other tree species stems were too small to be considered trees. Tree structure was not as diverse because there were fewer trees of similar short stature.

The forested wetland edge was also characterized by a marked decrease in canopy cover and tree height from upland forest. Overall, we found that forested wetlands in the Canadian Maritime provinces were short forests with low tree density and tree structural diversity. Padgett and Wiersma (2020) also found shorter forests with smaller trees compared to upland forests of similar age in nearby Newfoundland due to stunted growth in wetlands. Dimitrov et al. (2014) found a decrease in tree productivity from upland forest to fen as measured by tree gross primary production, tree carbon stock and leaf area index.

Despite clear patterns of tree structural diversity, we found no general patterns for vegetation structural diversity and no evidence of greater diversity at the edge. However, some transects had greater diversity in forested wetland than in the adjacent upland. Other groups of organisms have higher diversity in forested wetlands compared to upland such as epiphytic lichens (Padgett and Wiersma 2020) and birds (Brazner and MackKinnon 2020). Padgett and Wiersma (2020) found intermediate levels of lichen diversity at the ecotone between wetland and upland. Brazner and MacKinnon (2020) found greater habitat complexity in forested wetlands compared to uplands, but they used a different measure of the total cover of different vegetation strata, which may be higher for a uniform shrub cover compared to the measure of vegetation structural diversity that we used. Our lack of evidence for greater plant diversity at natural edges contributes to the inconclusive literature on this theory. Brownstein et al. (2013) suggest there is not enough empirical evidence for either lower or greater plant species richness in ecotones.

Although there were no general trends in patterns of vegetation structural diversity, other aspects of forest structure had clearer patterns with taller shrubs, and greater cover of shrubs, graminoids and *Sphagnum* in forested wetlands compared to upland forests. Tall shrub dominance is a common feature of the lagg zone in the transition between bog and forest at bog edges (Paradis et al. 2015). *Sphagnum* cover also exhibited a clear trend replacing other bryophytes along the transition from upland forest to forested wetlands. Andersen et al. (2011) found that *Sphagnum* played a dominant role in determining the spatial pattern of wetlands.

Change in vegetation structure as revealed by wavelet analysis

The results of the univariate wavelet analysis showed few consistent trends in the locations of gradual or abrupt changes across the edge between forested wetland and upland forest. Contrary to our prediction, significant change in vegetation structural diversity rarely occurred at the edge. Brownstein et al. (2013) also found no obvious changes at ecotones for functional trait diversity or species richness across a bog-forest transition. The abundance of significant transitions across the entire gradient from forested wetland to upland forest rather than just at the edge indicates the presence of fine scale heterogeneity in vegetation structure. Multiple scales have been found for the spatial structure of the hummocky nature of bogs of less than 50 cm and 130-140 cm (Bennie et al. 2011).

Wavelet analysis detected change in some vegetation structural components at the edge between forested wetland and upland forest along some transects. Significant changes included a gradual transition from tall to short shrubs, and decreases in the cover of *Sphagnum* and low shrubs from wetland to upland. However, change was not unique to the edge as significant wavelet position variance was often found elsewhere along the transects. We also noticed that

significant changes for different plant structural groups did not necessarily coincide at the same distances along the transects. Edge detection methods have found that edges delineated by steep gradients of trees are different than those identified by changes in shrubs (Fortin 1997), suggesting that different vegetation structural groups exhibit incongruous patterns even across forest edges.

Factors affecting structural diversity in forested wetlands

The bivariate wavelet analysis results provide evidence that at fine scales structural diversity is greatest away from patches of high abundance of any one plant structural group, which makes sense as diversity is greater with a more even distribution of structural groups. Vegetation structural diversity was positively associated with *Sphagnum*, shrubs and herbs at greater scales, suggesting that greater structural diversity can be found within 20-30 m of areas with high cover of *Sphagnum*, shrubs and herbs. As *Sphagnum* and shrubs are characteristic of forested wetlands, these results suggest that structural diversity can be high in and near the edges of forested wetlands. Our mosaic sites provide anecdotal evidence that at least some forested wetland landscapes have interspersed wetland and upland patches. In placing the transects, we observed that moving the transect a few metres in either direction would have yielded different results (pers. obs.).

Although forested wetlands in the region have been classified by tree and shrub height and cover (Brazner and Achenbach 2019), we found evidence of different types according to the relative abundance of different plant groups. However, different categories of forested wetlands may not be distinct but instead might represent ends of a gradient of forested wetlands with different plant structural composition. The ordination also showed that the forest edge did not

form a distinct community and was not intermediate in terms of structural composition but instead resembled either wetland or upland vegetation structure.

Conclusions and implications for conservation

We sought to determine if structural diversity was higher at edges in forested wetlands or if there was an abrupt change in vegetation structure at edges. However, we found no clear patterns in vegetation structural diversity and tree structural diversity across the edges of forested wetlands. We did find shrubs of all sizes, particularly tall shrubs, associated with some forested wetland sites. Shrubs of various heights produce structural complexity in forested wetlands that may be particularly important habitat for bird species (Brazner and MacKinnon 2020). However, it does not seem prudent to use structural diversity as an indicator of the conservation value of forested wetlands and it may be difficult to detect changes in vegetation structure for identifying forested wetlands. Remote sensing methods have been used to delineate forested wetlands on broader scales (e.g., Lang et al. 2013).

We originally included heterogeneous sites with smaller patches of forested wetland and upland forest to see if we could predict the occurrence of forested wetlands based on an indicator of structural diversity. The existence of these mosaic sites with numerous edges between interspersed patches of wetland and upland suggests that it might be best to consider all forested wetland landscapes for conservation including ones with only patches rather than continuous wetland. Further fine-scale sampling in landscapes with abundant forested wetlands will help assess the abundance of small wetlands, which may be difficult to detect otherwise. Mosaic areas may cover much of the landscape yet would be difficult to identify and sample. The lack of pattern in vegetation structure across forested wetland mosaics with interpsersed patches of

wetland and upland suggests that landscapes should be considered for conservation rather than individual wetlands as small patches of forested wetlands within forested wetlands might be overlooked.

Patterns in tree structural diversity showed a distinction between upland forest and forested wetland. The zone of lower tree structural diversity at the edge of forested wetlands provides a clear demarcation of the boundary of forested wetland that was not detected by patterns of vegetation structural diversity. It appears that lower tree structural diversity and an abrupt edge of *Sphagnum* cover can be used to delimit some, but not all, forested wetlands. Personal experience by the authors and others show that this is reliable only on the ground and not through classification from aerial photograph interpretation or unmanned aerial vehicle imagery (Wilson 2019). Paradis et al. (2015) and Langlois et al. (2015) emphasize that conservation of peatland complexes must include the transitional lagg area at the boundary, which provides important habitat for biodiversity. Forested wetland, including the full extent of the transition to upland forest, is an integral part of many forested landscapes in Atlantic Canada and should be included in conservation plans to protect wetlands. Since detecting forested wetlands can be difficult and their diversity relative to bordering habitats is still an open question, forestry policy should err on the side of caution when mapping forested wetlands.

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Table 1. Locations and characteristics of the ten study sites.

Site	Year sampled	Province	Coordinates (Lat N / long W)	Dominant trees*	Edge†
A	2017	Prince Edward Island	46.663 / -64.038	*Picea, Acer, Thuja*	Wetland / upland
B	2017	Prince Edward Island	46.230 / -62.476	*Picea, Abies, Acer*	Wetland / upland
C	2017	Nova Scotia	45.766 / -62.015	*Picea, Abies, Acer*	Wetland / upland
D	2017	Nova Scotia	44.659 /- 63.533	*Picea, Betula, Acer*	Wetland / upland
E	2016	Nova Scotia	44.388 / -65.207	*Picea, Abies, Acer*	Wetland / upland
F	2016	Nova Scotia	44.281 / -65.127	*Abies, Acer, Picea*	Wetland / upland
G	2017	Prince Edward Island	46.663 / -64.045	*Picea, Acer, Betula*	Upland / wetland / upland
H	2016	Nova Scotia	44.435 / -65.080	*Picea, Betula, Acer*	Upland / wetland / upland
I	2018	Nova Scotia	43.830 / -65.190	*Acer, Abies, Picea*	Mosaic, multiple edges
J	2018	Nova Scotia	43.837 / -65.101	*Acer, Picea, Abies*	Mosaic, multiple edges

* Dominant tree genera are listed in order of highest to lowest density.
† Wetland indicates forested wetland.

Figure captions

Figure 1. Map of the study sites in Atlantic Canada. Letters refer to sites in Table 1. The map was made using *tmap* version 3.2 (Tennekes, 2018) in R (R Core Team, 2020) with a source base map from Natural Earth (2020).

Figure 2. Trends from forested wetland (negative values) across the forest edge (0 m) to upland forest (positive values) for forest structure and tree structural diversity measures: canopy cover (A), maximum tree height (B), tree density (C), snag density (D) and four different measures of tree structural diversity using the Shannon index (H) with categories of dbh (E) and relative canopy height (F) as pseudospecies, combinations of dbh and relative height as pseudospecies (G), and tree structure diversity defined as the average of dbh and height diversity (H). Average values are shown with standard error bars. Averages with the same letter are not significantly different (p < 0.05, Tukey pairwise tests following a repeated measures ANOVA, p-values for the ANOVA were all less than 0.01 except for p = 0.03 for tree density and p = 0.15 for snag density). Differences in snag density among distances were not significantly different. Sample size = six transects.

Figure 3. The proportion of transects across forested wetland-upland forest boundaries with significant wavelet variance using the Haar (solid lines) and Sine wavelets (dashed lines) at different distances from the edge (negative in the forested wetland, positive in upland forest) for vegetation structural diversity, maximum shrub height and the cover of nine plant structural types: low <1 m height shrubs, medium 1-2 m height shrubs, tall >2 m height shrubs, *Sphagnum*, other bryophytes, ground lichens, herbs, graminoids and ferns. Transects without any of a plant structural group were excluded such that sample sizes were n = 6 for all plant structural groups except n = 1 for tall shrubs, n = 4 for medium shrubs and n = 5 for lichens.

Figure 4. The proportion of transects across forested wetland-upland forest boundaries with significant positive (solid lines) and negative (dashed lines) wavelet covariance at different scales for vegetation structural diversity vs. the cover of nine plant structural types: low <1 m height shrubs, medium 1-2 m height shrubs, tall >2 m height shrubs, *Sphagnum*, other bryophytes, ground lichens, herbs, graminoids and ferns. Transects without any of a plant structural group were excluded such that sample sizes were n = 10 for all plant structural groups except n = 1 for lichens, n = 2 for tall shrubs, n = 6 for medium shrubs and n = 7 for *Sphagnum*.

Figure 5. Detrended correspondence analysis biplot of quadrats along transects across forested wetland landscapes and plant structural types including low <1 m height shrubs, medium 1-2 m height shrubs, tall >2 m height shrubs, *Sphagnum*, other bryophytes, herbs, graminoids, ground lichens and ferns. Colours represent distance from the edge (m) from forested wetland (negative values) across the forest edge (0 m) to upland forest (positive values). Quadrats along transects with more than one edge or in forested wetland landscape mosaics are labelled with ×. Eigenvalues = 0.625 for axis 1 and 0.438 for axis 2.
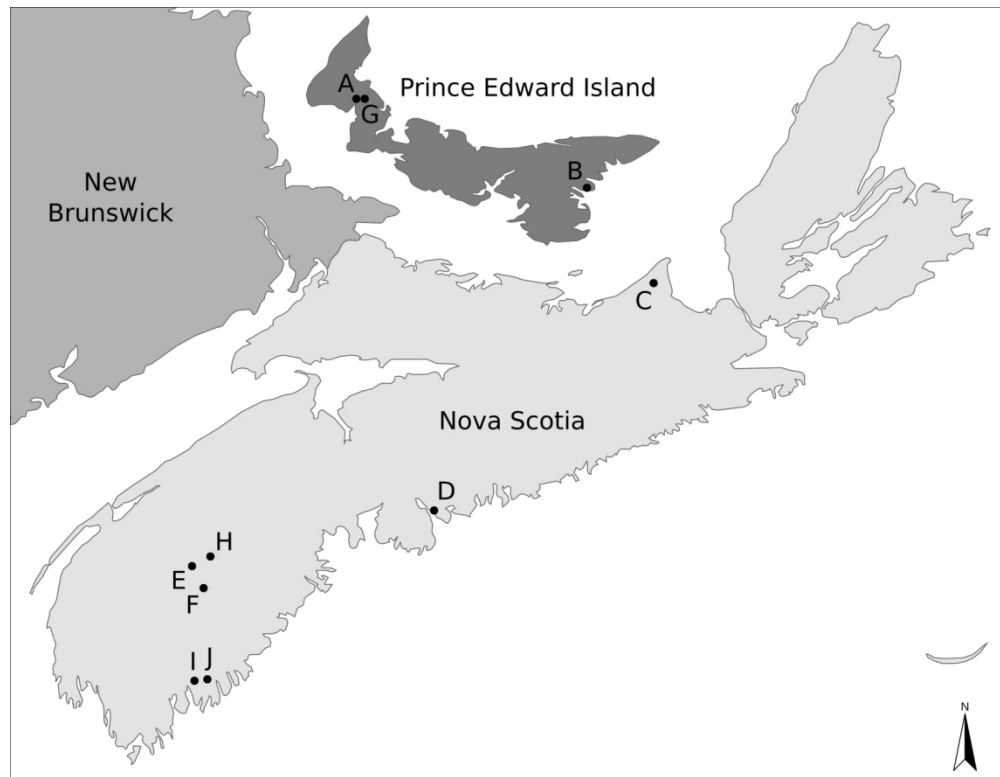
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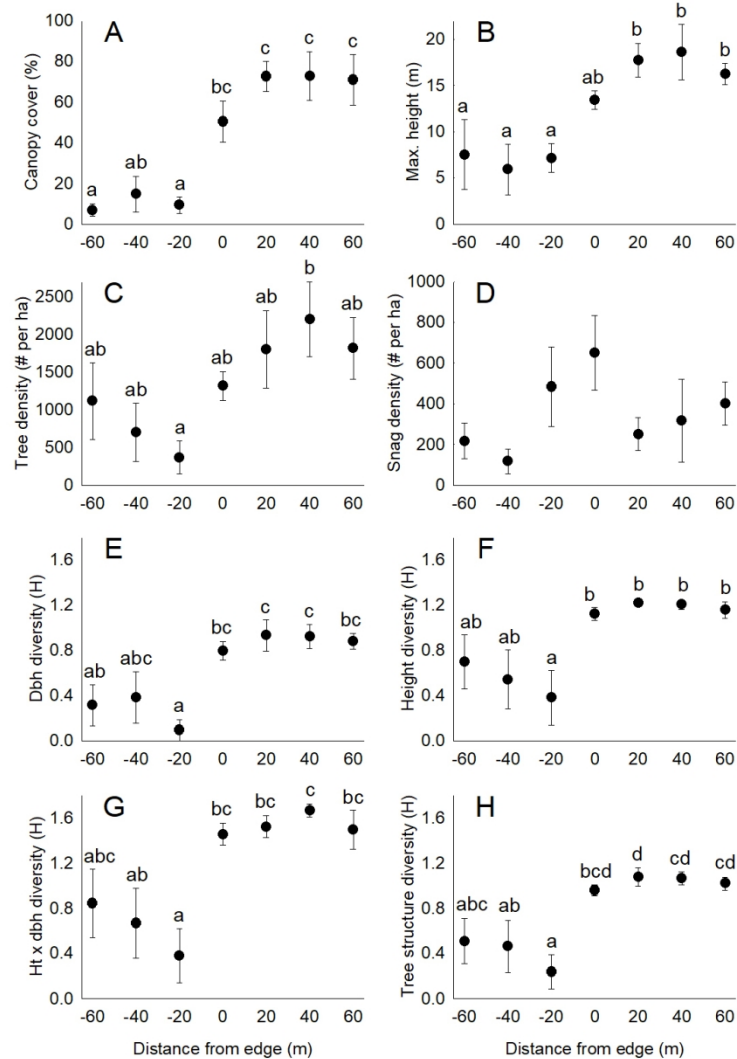
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Figure 2. Trends from forested wetland (negative values) across the forest edge (0 m) to upland forest (positive values) for forest structure and tree structural diversity measures: canopy cover (A), maximum tree height (B), tree density (C), snag density (D) and four different measures of tree structural diversity using the Shannon index (H) with categories of dbh (E) and relative canopy height (F) as pseudospecies, combinations of dbh and relative height as pseudospecies (G), and tree structure diversity defined as the average of dbh and height diversity (H). Average values are shown with standard error bars. Averages with the same letter are not significantly different (p < 0.05, Tukey pairwise tests following a repeated measures ANOVA, p-values for the ANOVA were all less than 0.01 except for p = 0.03 for tree density and p = 0.15 for snag density). Differences in snag density among distances were not significantly different. Sample size = six transects.
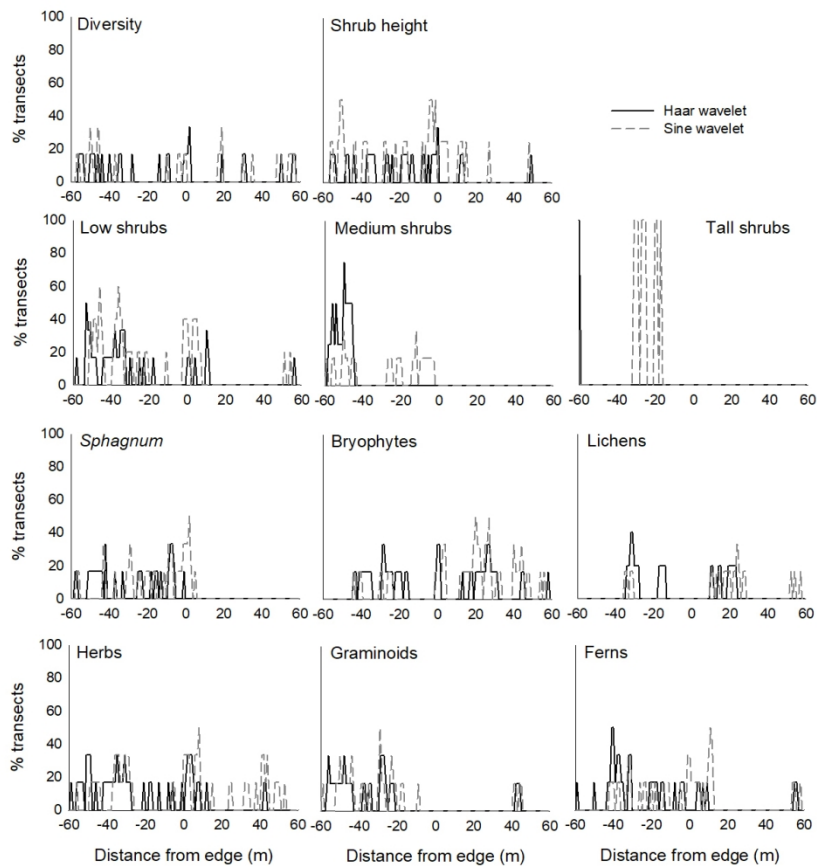
209x296mm (150 x 150 DPI)

Figure 3. The proportion of transects across forested wetland-upland forest boundaries with significant wavelet variance using the Haar (solid lines) and Sine wavelets (dashed lines) at different distances from the edge (negative in the forested wetland, positive in upland forest) for vegetation structural diversity, maximum shrub height and the cover of nine plant structural types: low <1 m height shrubs, medium 1-2 m height shrubs, tall >2 m height shrubs, Sphagnum, other bryophytes, ground lichens, herbs, graminoids and ferns. Transects without any of a plant structural group were excluded such that sample sizes were n = 6 for all plant structural groups except n = 1 for tall shrubs, n = 4 for medium shrubs and n = 5 for lichens.
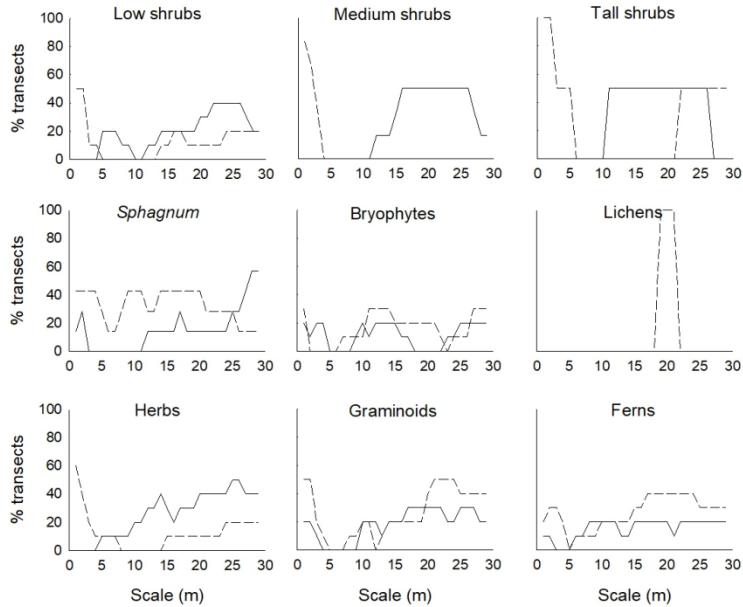
209x296mm (150 x 150 DPI)

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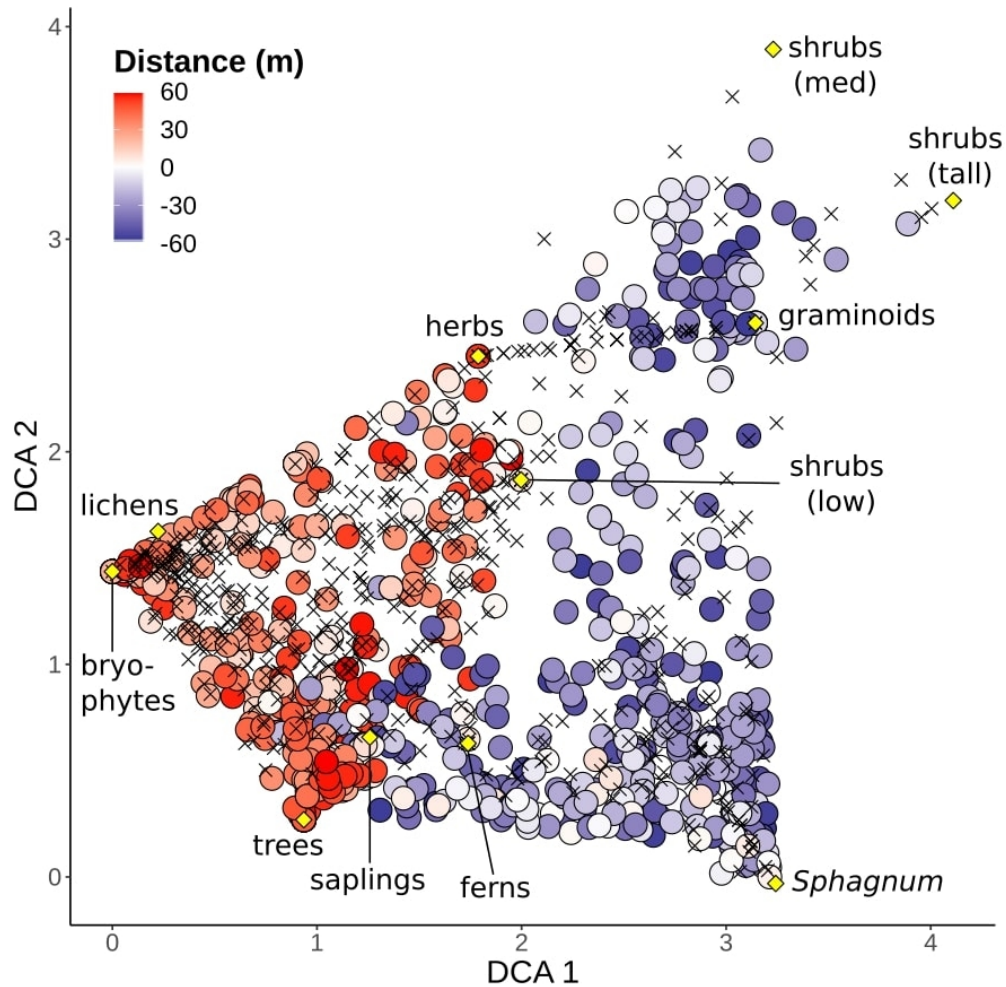
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312x312mm (72 x 72 DPI)

1

Appendix

Figure A1. Trends across all single edge transects from forested wetland to upland forest (negative to positive) for vegetation structural diversity, maximum shrub height and cover of low <1 m height shrubs (shr), medium 1-2 m height shrubs, tall >2 m height shrubs, *Sphagnum*, other bryophytes (bryo), lichens, herbs, graminoids and ferns. Vegetational structural diversity uses the Shannon index with the eleven plant structural types as pseudospecies. See Table 1 for site labels and details of sites. The distance of 0 m indicated the approximate location of the edge between the two communities.

2

Distance from edge (-60 to 60 m)