



# Spatial patterns of structural diversity across the boreal forest-tundra ecotone in Churchill, Canada

Pavel Dodonov<sup>a,\*</sup>, Karen A. Harper<sup>b</sup>

<sup>a</sup> Federal University of Bahia, Federal University of Bahia - Rua Barão de Jeremoabo, 668, Salvador, Bahia, 40170-115, Brazil

<sup>b</sup> Saint Mary's University, Biology Department - 923 Robie St., Halifax, Nova Scotia, B3H 3C3, Canada

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## ABSTRACT

Vegetation structural diversity, also called structural complexity, has great effects on biodiversity and ecological processes, with higher biodiversity often observed in areas with higher structural diversity. As for other ecological variables, structural diversity is spatially heterogeneous. Thus, quantifying its spatial heterogeneity may provide clues to the spatial variation in ecological processes. We studied the spatial patterns of structural diversity in two different environments, tundra and forest-tundra ecotone, near Churchill, MB, Canada. We sampled vegetation and quantified five types of structural diversity (ground cover, herbaceous plants, woody plants, all live plants, and deadwood) along five transects, with lengths of 81–227 m, and used wavelet analysis to assess the scales of spatial pattern. We also assessed the effects of soil pH, microtopography, elevation, and distance from lakes on structural diversity. In general, structural diversity was spatially structured on a variety of scales, from 2 to 55 m, with larger scales being observed in the tundra than in the ecotone transects. In addition, structural diversity in the tundra was generally higher near lakes and in areas with a higher pH, whereas in the ecotone it increased mostly with increasing pH and microtopographic variation. Spatial heterogeneity is an important characteristic of the forest-tundra ecotone and even tundra areas that appear homogeneous are structurally diverse at a variety of scales.

## 1. Introduction

Spatial heterogeneity in vegetation is apparent in the distribution of canopy gaps (Bradshaw and Spies 1992), the size of individual plants (Harper et al., 2018), the distribution of different plant species (Dodonov et al., 2019) and the ecological functions performed by these species (Feagin and Wu 2007). Such heterogeneity may be observed at different spatial scales, with complex patterns often resulting from the combination of different processes occurring at different scales (Brosfokske et al., 1990; Keitt and Urban 2005). Understanding spatial pattern may provide clues to the underlying ecological processes (McIntire and Fajardo 2009). For example, spatial heterogeneity in vegetation may reflect underlying environmental gradients, topographic and microtopographic patterns (Holtmeier and Broll 1992), biotic interactions such as competition and facilitation (Armas and Pugnaire 2005), spatially structured disturbances such as fire (Dodonov et al., 2014), biotic effects such as herbivory and trampling (Koning 2005; Sørensen et al., 2009), or autocorrelation related to dispersal and other processes.

Plant communities are often compared based on their similarity in

species composition, but it has been argued that species composition, without accounting for variation in individual size, is insufficient to assess the similarity of different communities (De Cáceres et al., 2013), as vegetation structure is also of paramount importance. Vegetation structure, in turn, affects ecological patterns and processes. It is one of the factors determining the amount of fuel on the ground (Hoffmann et al., 2012), thus affecting fire occurrence, intensity and extent. Structural complexity also affects the occurrence and movement of flying animals (Jung et al., 2012). Vegetation structure may also determine ecologically important factors such as shelter for different animal species and amount of light reaching the ground. For example, tundra vegetation height and grass cover (a proxy for moisture) were observed to be linked to arthropod assemblage patterns (Hansen et al., 2016). Higher structural complexity may also provide more microhabitats for lichens, resulting in higher species richness (McMullin et al., 2010). In general, higher structural complexity and higher habitat heterogeneity is often associated with greater animal richness (Tews et al., 2004), although the opposite pattern, with more species in less complex vegetation, may also be observed (Lassau and Hochuli 2004). Thus,

\* Corresponding author. Telephones Salvador, BA, Brazil.

E-mail addresses: [pdodonov@gmail.com](mailto:pdodonov@gmail.com), [pdodonov@ufba.br](mailto:pdodonov@ufba.br) (P. Dodonov).

quantifying spatial heterogeneity of structural complexity, or structural diversity, of vegetation may provide clues to ecological processes; there is evidence that structural diversity is a better predictor of ecosystem functions than biodiversity (LaRue et al., 2019). Alternatively, structural diversity may be the link between species diversity and ecosystem characteristics such as above-ground biomass (Godlee et al., 2021). Assessments of structural diversity are also important for management; in species-poor but structurally complex environments structural diversity may be managed to increase biodiversity (Deal 2007).

The forest-tundra ecotone is a spatially heterogeneous environment (Hansen et al., 2016) in which there is important interplay between vegetation structure and composition, microtopography, and soil characteristics (Holtmeier and Broll 1992; Gamon et al., 2012). For example, the effects of different plant groups - lichens, mosses, grasses and prostrate shrubs - on light absorption and heat transfer may aid in maintaining stable topographic features such as high-centered polygonal areas divided by troughs (Gamon et al., 2012). Trees in the forest-tundra ecotone are generally aggregated, which may reflect the effects of wind on tree establishment, but these spatial patterns vary widely among sites (Harper et al., 2011). In alpine tundra, slight variation in microtopography may allow the establishment of tree islands, which afterwards affect wind erosion, snow deposition and soil characteristics (Holtmeier and Broll 1992). Even treeless areas are not spatially homogeneous, as they may have an alteration of different plant groups (lichens, mosses, prostrate shrubs, graminoids), as well as of different species, which are likely related to environmental characteristics such as elevation, microtopography, moisture, and soil characteristics (Harper et al., 2018, Gough et al., 2000). For example, higher shrub richness was observed close to lakes and in areas with more variable microtopography (Harper et al., 2018).

The spatial pattern of vegetation is expected to vary along the gradient from forest to tundra, with larger and more aggregated tree patches in the forest, smaller and more sparsely distributed tree patches in the ecotone, and almost no tree patches in the tundra (Harper et al., 2011). Thus, in terms of tree cover, the tundra ends of forest-tundra ecotones may be considered as relatively homogeneous, with only a limited occurrence of scattered trees; in contrast, ecotonal areas between forest and tundra, in which patchiness is added by the occurrence of scattered trees, tree islands and forest patches, are more heterogeneous. In such areas, two features of structural diversity may be of interest: quantification of scales of spatial pattern, for example by the average size of patches with high and low structural diversity (Harper et al., 2011), and the relationship of structural diversity with environmental factors, such as soil pH and microtopography (Gough et al., 2000; Schmitz et al., 2020; Ferrari et al., 2021).

Here we studied the spatial variation in structural diversity in two contrasting areas of the forest-tundra ecotone: transitional areas between forest and tundra (hereafter referred to as “ecotone”) and mostly treeless tundra (hereafter referred to as “tundra”). Our second objective was to assess whether structural diversity may be explained by environmental factors, namely soil pH, microtopography, and distance from edges. We expected to observe greater structural diversity in areas with more variable microtopography. Our second objective was to assess the spatial scales of structural diversity and compare them between the environments and the structural diversity components. We hypothesized that the scales of spatial pattern would be smaller in the ecotone, as it is more heterogeneous, with alternating patches of woody vegetation and open areas. We also hypothesized that the scales of spatial pattern would differ between the components of structural diversity, with smaller scales being observed for woody vegetation (occurring in patches) than for ground cover (more continuous throughout the areas).

## 2. Methods

### 2.1. Study site

We performed this study in the subarctic forest-tundra ecotone near Churchill, Manitoba, Canada, near the western coast of Hudson Bay (58°31'–58°47' N, 93°58'–93°43' W; Fig. 1), in the summer of 2013. Our study sites included tundra areas (Fig. 1 c-e), mostly lichen heath tundra with prostrate shrubs such as *Vaccinium vitis-idaea* and *Empetrum nigrum*, and ecotone areas (Fig. 1 a-b), including shrubby areas with taller shrubs (*Salix planifolia* and *Betula glandulosa*) and more forested areas with *Picea glauca* and *Picea mariana* (Harper et al., 2018). Due to logistic and time constraints we did not include forest areas. In Churchill, the average temperature is 12 °C in July and –26.7 °C in January, with an average annual precipitation of 430 mm, approximately 40% of which is represented by snowfall (Environment Canada 2009). At our study transects, elevation varied from 13 to 22 m above sea level and soil pH varied from 5.2 to 7.0 (mean of 6.3 ± 0.3 SD).

### 2.2. Sampling

We sampled three transects in tundra (transect lengths of 227, 81, and 198 m) and two in ecotone (transect lengths of 225 and 117 m) vegetation; the transects of the same vegetation type were placed along a single line, with water bodies dividing the transects, so that they could be analyzed as either single long transects or as separate transects (Fig. 1). All transects were bordered by lakes, except for one ecotone transect located between a lake and a smaller water body. Transect location was determined based on satellite imagery and field visits, according to several criteria: transects were bordered by water bodies as described above; transects spanned the desired environments along the entire transect length (tundra and ecotone); and locations were accessible. We placed contiguous 1x1-m quadrats along each transect to sample the structural elements therein. Within each quadrat, we noted the presence of different structural elements. The structural elements were defined to fully characterize the vegetation structure of each quadrat and correspond to the following broad categories: open ground (bare soil, gravel, rocks); litter and fine woody debris (broadleaf leaves, conifer needles, dead graminoids, dead herbaceous plants, dead lichens, twigs); deadwood (logs, snags, dead shrubs); lichens (crustose lichens, i. e. those forming a crust on a surface; foliose lichens, with a flat shape; fruticose lichens, usually taller and with three-dimensional shapes; and the reindeer lichen *Cladonia rangiferina*, an ecologically important fruticose lichen); moss (*Sphagnum*, non-*Sphagnum*); herbaceous plants (forbs, graminoids, horsetails, and other herbaceous plants such as lycopods); shrubs (prostrate, standing); and trees (layering, standing, and trees with skirt characteristic of windswept areas).

We classified each structural element according to the following height classes: < 0.1 m, 0.1–0.4 m, 0.4–1.0 m, 1.0–1.6 m, 1.6–3.0 m, 3–5 m, and >5 m. We also classified the woody elements (twigs, deadwood, shrubs and trees) by their diameter (at the base of trees, shrubs and snags, and at the midpoint of twigs and logs), using the following classes: < 0.6 cm, 0.6–2.5 cm, 2.5–5.0 cm, 5–15 cm, 15–30 cm, and >30 cm. The first of these classes correspond to 1- and 10-h fuels (Schimmel and Granström 1997); these classes represent how long deadwood takes to respond to weather conditions and we used this classification because deadwood structural diversity may be related to fire spread. When there were two elements of the same type but different classification (e.g., two shrubs in different height classes) we recorded them as different elements.

We also collected data on elevation, pH and microtopography; because of time constraints we did not collect these data for the third tundra transect. To calculate elevation, we placed Trimble Juno ST GPS devices along the transects every 20 m or where there were perceivable changes in topography, and recorded at least 1000 waypoints with the TerraSync™ software, calculating altitude as the average of these

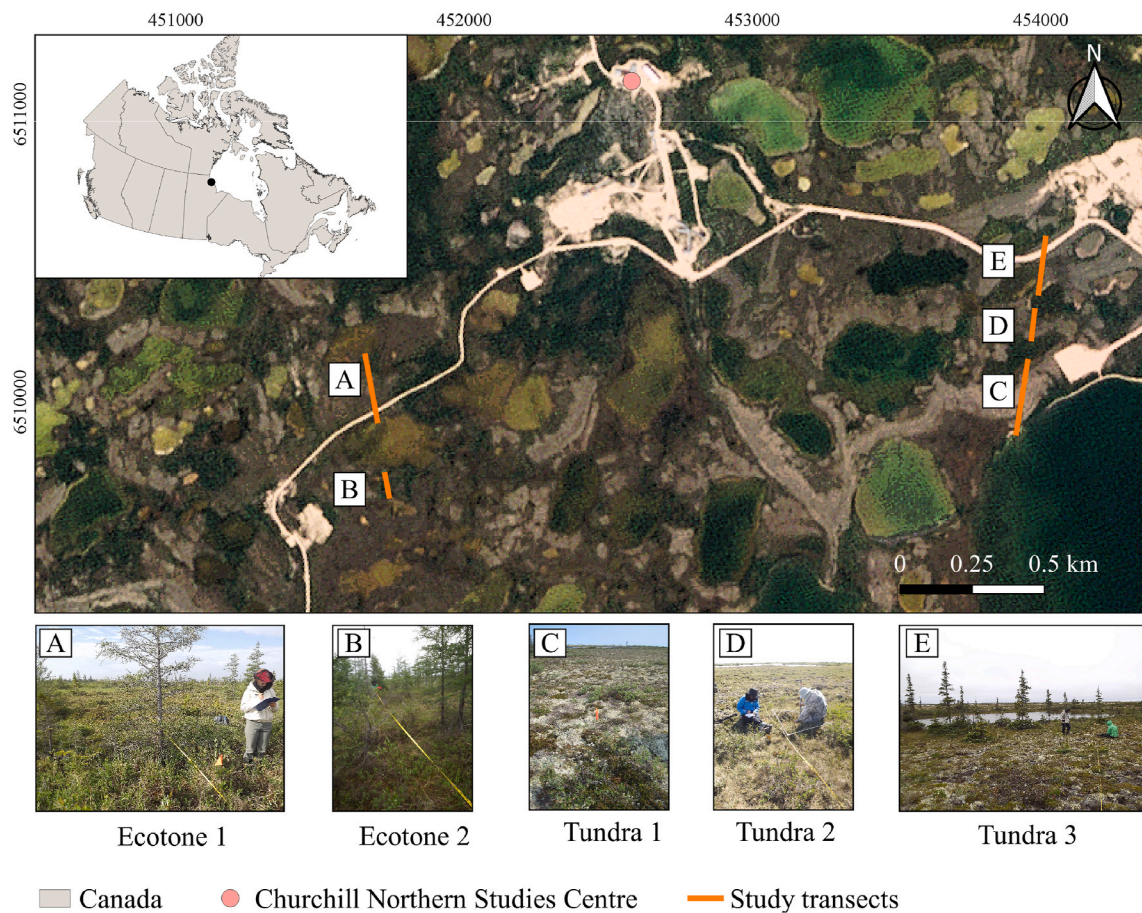


Fig. 1. Map showing the location of the study site in Canada and the location of the transects in the study site, as well as photos of each transect. Satellite image: Rapid Eye from 2013 to 08–14. Photos by Pavel Dodonov (A, C) and Danielle St. Louis (B, D, E).

Table 1

Structural elements included in this study, the variables according to which they were characterized, and whether they were considered in the calculation of structural diversity of each layer.

Category	Element	Measures	Ground	Herbaceous	Woody	Deadwood	Live plants
Deadwood	Log (fallen tree)	Diameter, height	no	no	yes	yes	no
	Dead shrub	Diameter, height	no	no	yes	yes	no
	Snag (standing dead tree)	Diameter, height	no	no	yes	yes	no
Bare ground	Gravel		yes	no	no	no	no
	Rock		yes	no	no	no	no
	Soil		yes	no	no	no	no
	Forb	Height	no	yes	no	no	yes
Herbaceous plants	Graminoid	Height	no	yes	no	no	yes
	Horsetail	Height	no	yes	no	no	yes
	Other	Height	no	yes	no	no	yes
	Lichens	Crustose lichens		yes	no	no	no
Folioous lichens			yes	no	no	no	no
Fruticose lichens			yes	no	no	no	no
Reindeer lichens			yes	no	no	no	no
Plant litter	Broadleaf leaves		yes	no	no	no	no
	Conifer needles		yes	no	no	no	no
	Dead graminoids	Height	yes	yes	no	no	no
	Dead herbaceous	Height	yes	yes	no	no	no
	Dead lichens		yes	no	no	no	no
	Twigs	Diameter	yes	no	no	yes	no
Moss	Non-Sphagnum moss		yes	no	no	no	no
	Sphagnum moss		yes	no	no	no	no
Woody	Prostrate shrub	Height	yes	no	no	no	yes
	Standing shrub	Diameter, height	no	no	yes	no	yes
	Tree (layering)	Diameter, height	no	no	yes	no	yes
	Tree (with wind-skirt)	Diameter, height	no	no	yes	no	yes
	Tree (standing)	Diameter, height	no	no	yes	no	yes

waypoints. We used a pH meter (model pH-707 from Tecpel) to measure pH to a depth of 5 cm in every other quadrat, taking either one measure per quadrat or two measures and calculating their average. To quantify microtopographic variation within each quadrat, we visually divided each quadrat into two or three parts, corresponding to higher ground, lower ground, and middle ground (in quadrats where the topography was more complex). We measured the height difference between these sections and visually estimated the proportion of the quadrat occupied by each, and quantified microtopography as a measure of variance in height weighted by the proportion of higher and lower ground (see Harper et al., 2018 for details).

### 2.3. Data analysis

#### 2.3.1. Structural diversity measurements

We calculated two measures of structural diversity. The first, which we call structural richness (StrS), is simply the number of different structural elements for each layer in a quadrat (Table 1). Thus, it does not take into account how different the structural elements are from one another. Our second measure of structural diversity takes into account the dissimilarity among structural elements. We call this index StrD, as it is calculated in a way similar to the FD index of functional diversity (Petchey and Gaston 2006), on which StrD was inspired, and on the PD index of phylogenetic diversity (Faith 1992).

To calculate this index, each structural element is first classified according to some characteristics: whether it corresponds to plant material or to bare soil; its general class (ground cover; plant litter; lichens and mosses; herbaceous plants; and woody plants); the structural element *per se* (e.g. tree, shrub, prostrate shrub, graminoid); whether it is standing; whether it is alive or not; and whether it is woody or not. We also considered the diameter and height classes, which we treated as an ordinal variable. We chose these variables because we believe that they describe the characteristics of the structural elements in sufficient detail to permit assessing which of them are more similar or less similar to one another.

Thus, each structural element present in each plot is described by the variables or structural traits listed above, which may be binary, categorical, or ordinal, in a way similar to the functional traits used in functional diversity measures (e.g. Petchey and Gaston 2002). This permitted us to quantitatively measure the dissimilarity between two structural elements. The next step is to calculate, within each quadrat, the dissimilarity between all pairs of structural elements present; as there were both categorical and ordinal variables, we used the Gower index. For categorical variables, this index takes the value of 1 when the two values are different and 0 when they are the same, and for ordinal variables it is the difference between the two values standardized by the variable's range of variation (Legendre and Legendre, 1994, p. 258–259). This resulted in a dissimilarity matrix for each quadrat. Afterwards, unweighted pair group method with arithmetic mean (UPGMA) cluster analysis was performed on this dissimilarity matrix resulting in a dendrogram. The final step was to sum the lengths of the connecting segments in this dendrogram. In summary, this is done by expressing the dendrogram as a vector of branch lengths and a matrix showing whether the pathway from the dendrogram's base to the tip for a given structural element includes a given branch; technical details can be found in Petchey and Gaston (2002). The sum of the branch lengths is the StrD index of structural diversity. When there were none or a single structural element in a quadrat we defined StrD as equal to zero.

We calculated these two measures of structural diversity for five aspects of vegetation: ground cover (including bare ground, moss, lichen, litter, herbaceous plants, and prostrate shrubs); herbaceous plants (live and dead); woody plants (live and dead); deadwood (snags, logs, fine woody debris, and litter); and live plants (excluding moss and lichen) (Table 1). We acknowledge that the selection of structural elements is subjective but we believe that these five aspects and the elements included in each one provide a detailed assessment of vegetation

structure.

To assess whether the different indices of structural diversity are redundant or complementary, we calculated Pearson's correlation coefficients between the different indices for each layer and transect; we excluded quadrats in which no structural elements were found.

#### 2.3.2. Spatial scales of structural diversity

We used wavelet analysis, specifically continuous wavelet transforms (Percival and Walden 2000; Dong et al., 2008; Rouyer et al., 2008), to assess the spatial scales of variation in structural diversity (StrS and StrD) for each layer. Continuous wavelet transforms work by multiplying the data by a wavelet template of a given shape; large positive values are obtained if the spatial pattern is similar to the wavelet template and large negative values if the pattern is opposite (Percival and Walden 2000; Dong et al., 2008; Rouyer et al., 2008). For example, the Mexican Hat wavelet has the shape of a patch (positive values) with gaps (negative values) on both sides (Dale and Mah 1998; Percival and Walden 2000). Thus, applying this wavelet template on the data will result in high values when there is a patch of higher structural diversity at a given location.

This operation is repeated along the transects by moving the wavelet template and at different scales by increasing the size of the wavelet template. Thus, locations along the transect corresponding to patch centers will have large positive values at the scale corresponding to patch size, and locations at gap centers will have large negative values. It is then possible to calculate the scale of spatial pattern by calculating wavelet variance across all positions for each scale (Dale and Mah 1998; Rosenberg and Anderson 2011). For this, the wavelet transform values are squared and summed for all positions along the transect, separately for each scale, resulting in the measure called wavelet scale variance (Dale and Mah 1998; Rosenberg and Anderson 2011). Peaks in scale variance may be interpreted as the main scales of spatial pattern.

We calculated wavelet scale variance for our data using the Mexican Hat wavelet and a maximum scale equal to one-fourth of the length of each transect (rounded downwards). Thus, the maximum scales for the two ecotone transects were 55 and 29 m and for the three tundra transects were 55, 20, and 49 m. We then assessed whether the observed patterns deviate from randomness by comparing the observed scale variance with 95% confidence intervals obtained from 9999 random reorderings of the data (the real data was included as the 10,000th reordering as it is one of the possibilities that can be observed randomly, Manly 2007). Scales at which the observed scale variance is greater than these confidence interval represent statistically significant scales of spatial pattern. Within the statistically significant scales, we calculated the main scale of spatial pattern by looking at peaks in scale variance, i. e., scales at which scale variance was larger than at smaller and larger scales. We did not detrend the data prior to analyses because we did not expect any linear trend in structural diversity along our transects.

#### 2.3.3. Relations between structural diversity and the environment

To examine the relationship between structural diversity and the environment, we used only the quadrats for which we had measured pH, thus using every second quadrat of the ecotone and of two tundra transects. We did not have pH data for the third tundra transect and so did not include it in these analyses. We also removed quadrats located on a road along the first ecotone transect and outliers with very high microtopographic variation, which were located on an embankment near the edge of one tundra transect.

For this analysis, we combined the transects within each vegetation type, thus performing one analysis for the tundra and one for the ecotone. We used the StrS and StrD values obtained for the different layers as response variables and pH, microtopography, distance from lakes, and elevation as explanatory variables. As the data were spatially structured, we used generalized estimation equations, with Gaussian distribution for StrD and Poisson distribution for StrS, which is a count variable, and accounted for spatial structure by means of a first-order

autoregressive (AR1) model with data grouped by transect (Zuur et al., 2009). For StrD, residuals were not always normal (Supplementary Material), so these results should be interpreted with caution. The explanatory variables were not correlated with one another either in the ecotone or in the tundra (all variance inflation factors <2.7).

We used the quaslikelihood under the independence model information criterion (QIC), an information criterion which can be used instead of Akaike’s information criterion for generalized estimation equations (Zuur et al., 2009) to compare between different models. Thus, we fitted models with all possible combinations of the explanatory variables without interactions resulting in a total of 16 models. We calculated QIC for each of these models and the difference in QIC between each model and the model with the lowest QIC ( $\Delta$ QIC). Afterwards, for the most plausible model we selected the simplest model (i.e. the model with the fewest variables) among those with a  $\Delta$ QIC  $\leq$ 2.0 following the criterion often used for  $\Delta$ AIC, for which two models with a  $\Delta$ AIC of 2.0 or lower are essentially indistinguishable (Burnham and Anderson, 2002). When two or more equally simple models had a  $\Delta$ QIC  $\leq$ 2.0, we selected them all as plausible.

2.4. Software used

We performed all analyses in R 4.1.0 (R Core Team 2021), with the packages vegan (Oksanen et al., 2019) and cluster (Maechler et al., 2019) to calculate StrD; wmtsa (Constantine and Percival 2017) for the wavelet analyses; car (Fox and Weisberg 2019) to calculate the variance inflation factors; geepack (Højsgaard et al., 2006) for adjusting the generalized estimation equations; MuMin (Bartoń, 2020) for model comparison; and rsq (Zhang 2021) to calculate the pseudo- $R^2$  of the

generalized estimation equations. The data and codes used are available at <https://github.com/pdodonov/publications>.

3. Results

The number of structural elements per quadrat varied from 0 to 11, depending on the layer being analyzed, and varied widely along the transects; larger variation was observed for the structural diversity of the ground layer (one to twelve structural elements per quadrat) whereas the smallest was observed for deadwood (zero to four structural elements) (Fig. 2), but this likely reflects at least in part our choice of which structural elements to include in each category. Patterns for StrS and StrD were visually similar (Figs. 2 and 3). For all groups of structural elements (ground cover, herbaceous, woody, deadwood, and live plants), we observed large within-transect variation, but no obvious differences between tundra and ecotone transects. In general, there was a high correlation between the two measures of structural diversity ( $R^2$  ranging from 0.53 to 0.95; Fig. 4) and most of the other results were qualitatively similar for these two variables.

3.1. Scales of spatial pattern

Patterns for StrS and StrD were similar; plots for scale variance for StrS and StrD are shown in the Supplementary Material. With one exception, there were some significant scales of variation for all kinds of structural diversity at all transects, indicating that its variation is not random (Table 2; Supplementary Material). As above, there were differences between transects in the same vegetation type. Larger scales were more common in the tundra, but apart from this there were no

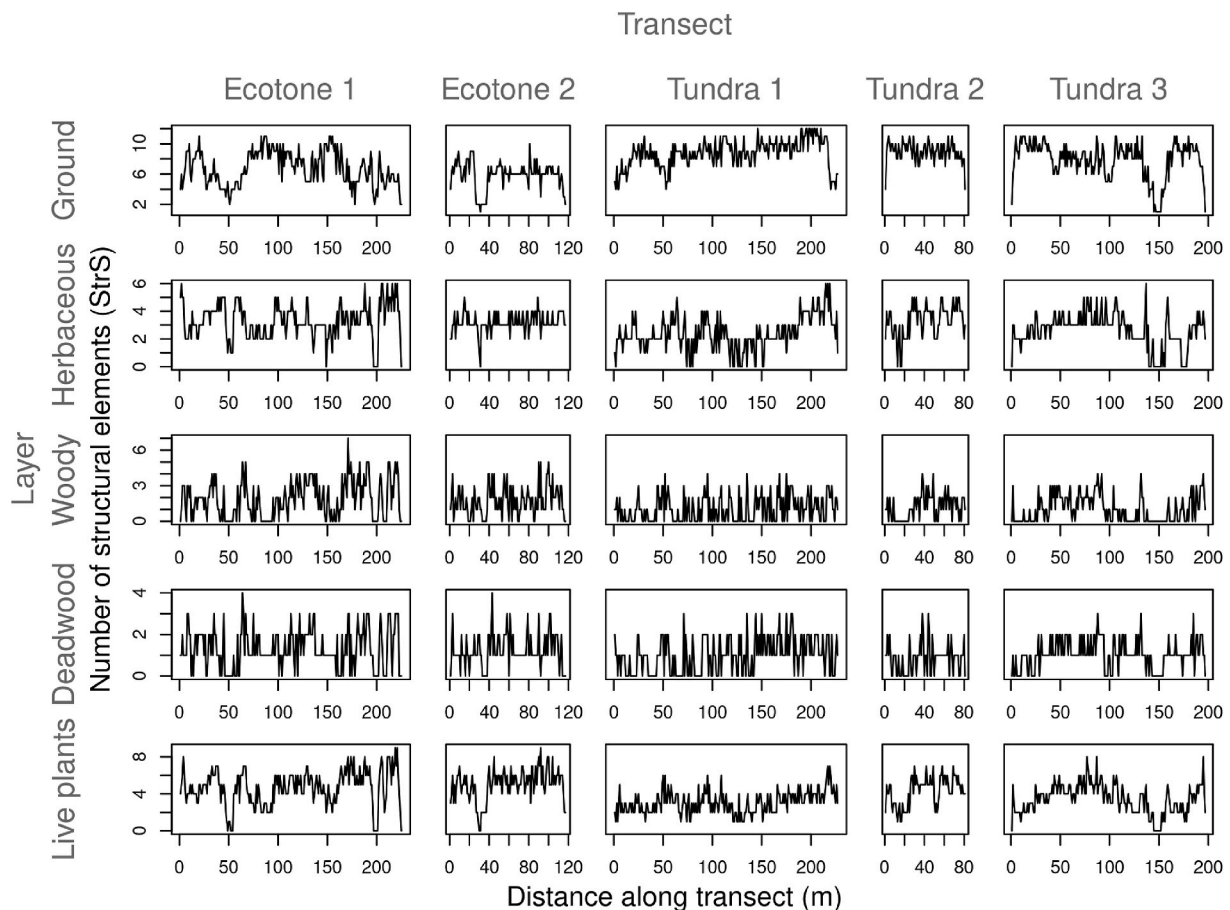


Fig. 2. Variation in structural diversity (StrS, number of structural elements) for ground layer, herbaceous plants, woody plants, deadwood and live vascular plants along the three tundra and the two ecotone transects.

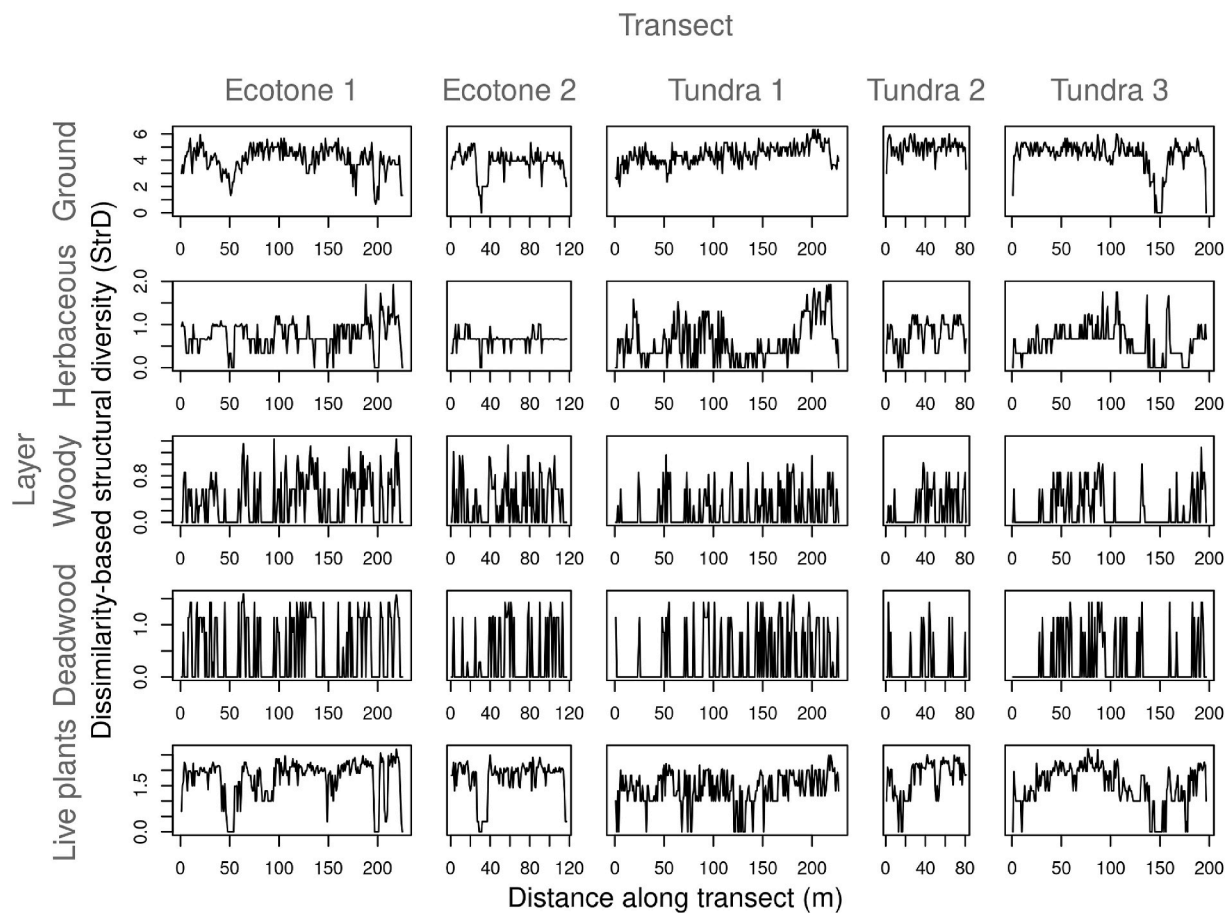


Fig. 3. Variation in structural diversity (StrD, a dissimilarity-based measure of structural diversity) for ground layer, herbaceous plants, woody plants, deadwood and live vascular plants along the three tundra and the two ecotone transects.

clear differences between tundra and ecotone. The main scales of spatial pattern (corresponding to peaks in scale variance) were often between 4 and 10 m, with the scale of 7 m being the most common; larger scales, between 10 and 20 m and between 32 and 55 m were also observed, but interestingly there were no peaks in scale variance for scales between 21 and 31 m for StrS (Table 2). In some cases, especially in the tundra, scale variance peaked at the maximum scale analyzed, which may indicate that the scale of spatial pattern may be greater than the maximum scale examined, as a peak was not yet reached. Two peaks in scale variance for the same variable in the same transect were common, indicating that there may be two overlapping patterns. In such cases, one of the scales was usually (but not always) under 10 m whereas the second scale ranged from 18 to 55 m. Three peak scales were never observed (Table 2; Table S1; Figures S1 and S2).

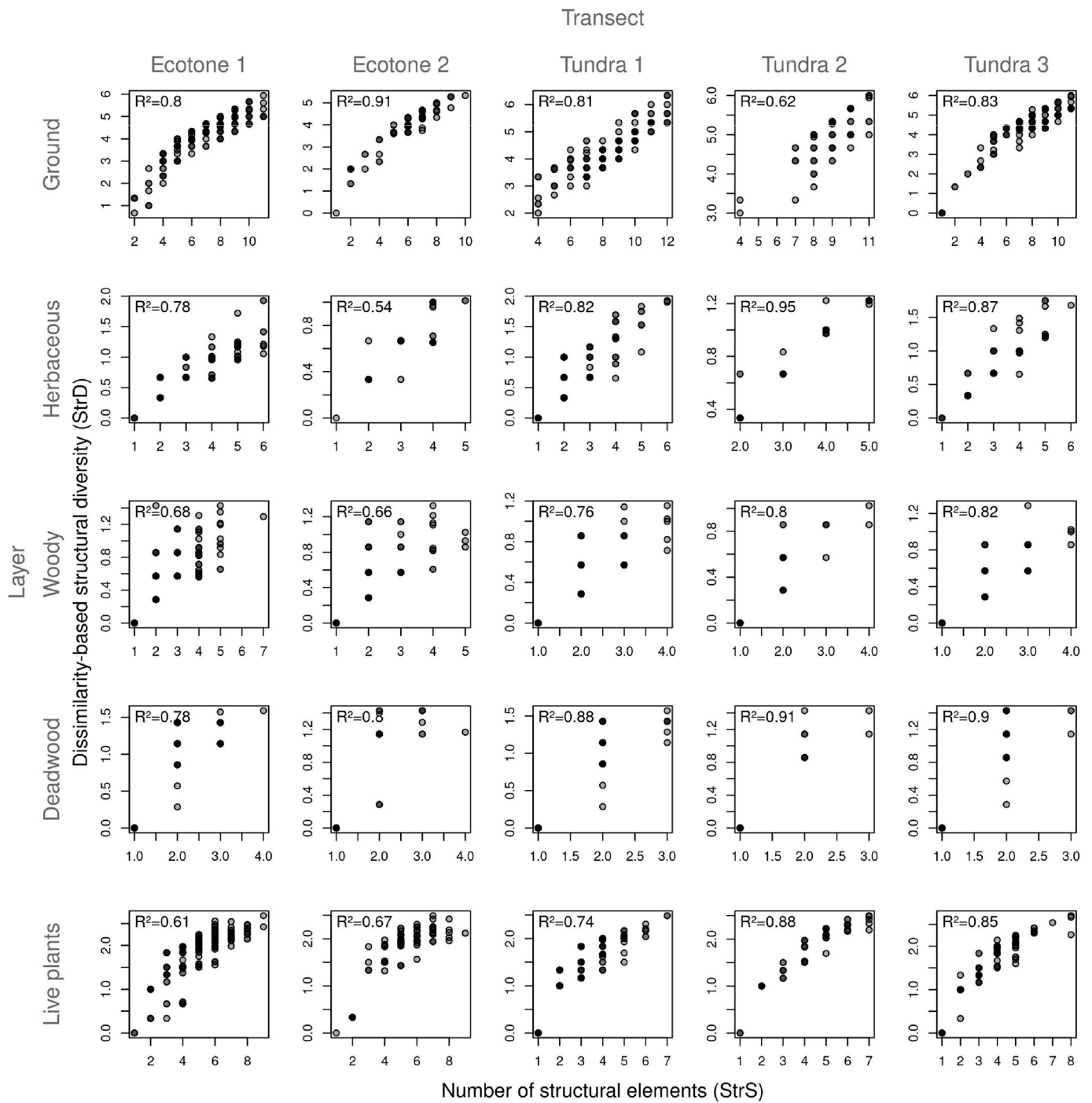
In the ecotone, the maximum scale analyzed was only significant for the structural diversity of ground cover at one transect, where all scales from 5 to 55 m were significant. Apart from this exception, significant scales varied from 3 to 37 m, with the smallest significant scale being of 2–5 m and the largest significant scale ranging from 6 to 37–55 m. Except for one peak scale of 55 m for ground cover, the peak scales in the ecotone ranged from 4 to 19 m for StrS and from 7 to 55 for StrD. Conversely, for the tundra, the maximum scales analyzed were significant in eight out of fifteen analyses for StrS and in five analyses for StrD (there were no significant scales for ground cover in one tundra transect). In two cases along one tundra transect, scale variance was significant at small and large scales but not at intermediate scales: for ground cover (significant scales of 6–20 and 50–55 m) and for deadwood (significant scales of 4–8 and 30–34 m). The smallest significant scales in the tundra were always of 6–7 m whereas the largest scales varied from

12 to 55 m. Peak scales ranged from 6 to 55 m (Table 2).

Along the two ecotone transects, the structural diversity of ground cover had significant spatial patterns at a broader range of scales and up to larger scales than the other groups of structural elements, for all of which relatively similar scales were observed. This, however, was not observed for the tundra transects, in which all groups of structural elements varied on similar scales; interestingly, in one tundra transects, all groups had significant scales of 4 or 5–49 m (the maximum scale analyzed), except for ground cover, which varied on scales of 2–23 m. The structural diversity of herbaceous plants varied on larger scales in the tundra (from 3 to 49 m) than in the ecotone (from 3 to 23 m). Similar, although less conspicuous, differences were observed for deadwood (up to 24 m in the ecotone and up to 49 m in the tundra) and for StrS of live plants (up to 24 m in the ecotone and up to 49 m in the tundra). Conversely, the scales of variation in the structural diversity of ground cover and of woody plants were similar in tundra and ecotone.

### 3.2. Relations between structural diversity and environment

The effects of environmental variables on the number of structural elements differed between tundra and ecotone and between the measures of structural diversity, but the models' explanatory power was always low with pseudo- $R^2$  values ranging from 0.02 (except for one negative pseudo- $R^2$ ) to 0.21 (Tables 3 and 4; full model selection results can be found in the Supplementary Material). In the tundra, distance from lakes was the variable most present in the selected models (Table 3). Ground (only for StrD), herbaceous, and live plant structural diversity were greater closer to lakes, whereas the opposite was observed for deadwood structural diversity (Table 3, Fig. 5). Herbaceous and



**Fig. 4.** Correlation between the two measures of structural diversity - a dissimilarity-based measure (StrD) and the number of structural elements (StrS) - for the five transects and the five groups of structural elements for which we measured structural diversity.

deadwood structural diversity increased with increasing pH, and ground and herbaceous structural diversity were positively related to microtopography (only for StrD; Table 3).

In the ecotone, the variables most observed in the selected models were microtopography and pH, and relationships were much more common for StrS than for StrD (Table 4). Greater microtopography was related to higher ground, woody (only for StrS), and deadwood (only for StrS) structural diversity (Table 4, Fig. 6). Similarly woody, live plant, and deadwood structural diversity increased with increasing pH (only for StrS) (Table 4). Although live plant StrD had a negative relationship with pH, the pseudo- $R^2$  for this model was negative, thus this observed relation may have been a statistical artifact.

#### 4. Discussion

The results of this study show that: 1) a simpler measure of structural diversity, consisting in the count of different structural elements, is strongly correlated with a more complex measure which accounts for the dissimilarity among the structural elements; 2) the spatial patterns of structural diversity deviate from complete spatial randomness; 3) the scales of spatial pattern are largely idiosyncratic, but appear to be greater in the tundra than in the ecotone; and 4) structural diversity appears to be affected by distance from lakes, soil pH, and microtopography, although these relationships are weak and differ between the tundra and the ecotone.

**Table 2**

Scales at which there were significant spatial patterns for the number of structural elements (structural richness, or StrS) and a dissimilarity-based measure of structural diversity (StrD) for each transect. Due to different transect lengths the maximum scale analyzed differs between the transects and is shown in the table. Peaks in scale variance (i.e. scales at which scale variance was greater than at immediately lower and immediately higher scales) are shown in parentheses.

	Scales (m) of significant patterns				
	Ecotone 1	Ecotone 2	Tundra 1	Tundra 2	Tundra 3
<b>StrS</b>					
Maximum scale analyzed	55	29	55	20	49
Ground	5-55 (19, 55)	3-18 (8, 18)	6-20, 50-55 (12, 55)	ns	4-23 (13)
Herbaceous	3-23 (6, 19)	5-8 (7)	5-41 (34)	3-20 (7, 20)	4-49 (7, 49)
Woody	3-37 (13, 36)	3-4 (4)	3-12 (7)	6-20 (20)	4-49 (32, 49)
Deadwood	2-20 (13)	3-6 (5)	4-8, 30-34 (6, 34)	7-9, 12-19 (19)	4-49 (12, 49)
Live plants	3-24 (10)	4-14 (10)	7-36 (33)	3-20 (8, 20)	5-49 (7, 49)
<b>StrD</b>					
Ground	4-55 (19, 55)	3-14 (8)	6-16 (12)	ns	4-43 (14, 43)
Herbaceous	3-22 (7, 19)	5-9 (7)	6-43 (33)	3-19 (8, 19)	4-49 (7, 49)
Woody	4-26 (14)	3-5 (4)	5-7 (6)	6-20 (9, 20)	4-45 (31, 45)
Deadwood	2-24 (15)	4-23 (6, 15, 23)	2-5 (3)	ns	4-49 (8, 49)
Live plants	3-52 (11, 52)	4-21 (9, 21)	6-36 (31)	4-20 (8, 20)	5-49 (8, 49)

**4.1. Scales of spatial pattern**

As expected, the variation in structural diversity was not random; at least some statistically significant scales of spatial pattern were observed for all analyses but one. Thus, both in the tundra and in the ecotone the structural diversity of vegetation was spatially structured at different scales. The significant scales varied greatly among the transects as well as among the structural diversity measures. Spatial patterns have been previously observed to be largely idiosyncratic, with difficulties of finding general patterns; this has been observed, for example, for tree spatial pattern as well as for the spatial pattern of shrubs and other plants in the Canadian forest-tundra ecotone (Harper et al., 2014, 2018)

**Table 3**

Model selection results for the relationship between two structural diversity indices (number of structural elements or StrS and the dissimilarity-based structural diversity index StrD) and environmental variables (elevation, in meters above sea level; distance from lakes, in meters; soil pH; and microtopography) along the tundra transect, showing the coefficients (slopes), QIC, ΔQIC and Akaike weights values for the models considered as plausible, i.e. the simplest models among those with a ΔQIC ≤2.0. In some cases, two equally simple models had ΔAIC ≤2.0 and were selected as equally plausible. Full results are in the Supplementary Material.

Layer	Elevation	Distance from lakes	Microtopography	pH	ΔQIC	Akaike weights	Pseudo-R <sup>2</sup>
<b>StrS</b>							
Ground	–	–	–	–	0.79	0.18	N/A
Herbaceous	–	–0.0053	–	–	0.50	0.14	0.16
Woody	–	–	–	0.51	0.06	0.21	0.042
Deadwood	–	0.0034	–	0.37	0.38	0.22	0.044
Live plants	–	–0.0034	–	–	0.66	0.23	0.082
<b>StrD</b>							
Ground	–	–0.0032	–	–	0.32	0.12	0.034
Herbaceous	–	–	0.043	–	0.69	0.098	0.020
Woody	–	–0.0021	0.039	0.16	0.00	0.30	0.15
Deadwood	–	–	–	–	0.00	0.28	N/A
Live plants	0.14	0.0033	–	–	0.26	0.11	0.051
	–	–	–	–	1.40	0.063	0.023
	–	–	–	0.21	1.60	0.057	0.030
	–	–0.0045	–	–	0.00	0.33	0.077

and for graminoids in the Brazilian savanna (Dodonov et al., 2019).

Such variation may be due in part to methodological limitations: a detailed assessment of spatial pattern requires intensive sampling, which, depending on the number of variables studied and on how detailed are the measurements, may demand too much time to permit a larger sample size. In addition, long transects are required to permit the detection of patterns at larger scales, as the maximum scale that can be analyzed depends on the transect length (Dale, 1999). This, however, limits the number of transects than can be sampled in a given study, thus also limiting the possibilities of finding general patterns. Thus, we suggest that future studies in spatial pattern may attempt to increase both transect length and transect number by focusing on a smaller number of variables, in order to decrease the time required for sampling. In addition, information derived from remote sensing data, such as vegetation indices or texture images (Wegmann et al., 2016), may enable the study of spatial pattern for larger areas without the need for extensive fieldwork. Indeed, remote sensing has been used for spatial pattern analysis at regional scales (James et al., 2010). In addition, more heterogeneous landscapes (landscapes with a variety of land uses, vegetation types and variation in physical attributes such as topography, soil and microclimate) have a greater spectral heterogeneity on the same spatial scale, and thus remote sensing data may be used to measure the spatial and temporal heterogeneity of landscapes and ecosystems (Dronova et al., 2021; Rocchini et al., 2021). However, these methods require that the choice of data is capable of describing the spatial patterns on an adequate spatial scale, which will depend on the process being studied (Santos et al., 2021; Dronova et al., 2021); structural diversity, which may vary on a scale of meters, will likely require a fine spatial resolution (e.g. of 5 m or less). Satellite imagery with fine spatial and spectral resolution are often not freely available and satellite imagery with coarse resolution may not permit the differentiation between some categories that may be important for a given study (for example, between different lichen types); in addition, these data would not allow the detection of patterns below tree canopies. Methods such as LiDAR have been used to assess structural diversity (Kane et al., 2010a,b), but the deployment cost of this technology may be prohibitive in some areas. Thus, we believe that a combination of remote sensing technology to assess larger-scale patterns with field sampling for finer-scale assessments may be the best option for more detailed studies on spatial pattern.

Even with the large within-study variation, one common pattern to such studies is that in general a variety of spatial scales are shown to be statistically significant, and patterns in which there is a statistically significant spatial structure at small and large scales, but not at intermediate scales, are not uncommon (Dodonov et al., 2019, as well as the



**Table 4**

Model selection results for the relationship between two structural diversity indices (number of structural elements - structural richness, or StrS - and the dissimilarity-based structural diversity index StrD) and environmental variables (elevation, in meters above sea level; distance from lakes, in meters; soil pH; and microtopography) in the ecotone transects, showing the coefficients (slopes), QIC,  $\Delta$ QIC and Akaike weights values for the models considered as plausible, i.e. the simplest models among those with a  $\Delta$ QIC  $\leq 2.0$ . Full results are in Supplementary Material.

Layer	Elevation	Distance from lakes	Microtopography	pH	$\Delta$ QIC	Akaike weight	Pseudo-R <sup>2</sup>
<b>StrS</b>							
Ground	–	0.0031	0.012	–	0.00	0.55	0.21
Herbaceous	–	–	–	–	0.58	0.12	N/A
Woody	–	–	0.033	0.59	0.00	0.29	0.13
Deadwood	–	–	0.036	0.59	0.47	0.20	0.12
Live plants	0.08	–	–	0.03	1.79	0.12	0.11
<b>StrD</b>							
Ground	–	–	0.043	–	0.00	0.34	0.11
Herbaceous	–	–	–	–	1.85	0.086	N/A
Woody	–	–	–	–	0.00	0.23	N/A
Deadwood	–	–	–	–	1.25	0.13	N/A
Live plants	–	–	–	–0.010	0.00	0.24	–0.0025

current study). This is likely caused by the action of different ecological mechanisms at different scales. For instance, clonal growth, for example by tree layering, may result in smaller-scale patterns, whereas patterns at larger scales may be related to dispersal or to variation in environmental characteristics. Such causes of spatial variation may be explored in future studies.

Another pattern that emerged from our study is that larger scales were observed in the tundra than in the ecotone. Indeed, although in the tundra the maximum scale analyzed was often significant, this was not the case in the ecotone. This may indicate that patches of higher and lower structural diversity are smaller in the ecotone than in the tundra, probably reflecting the alternation of areas occupied by trees or shrubs with more open areas. In the tundra, conversely, although there is spatial structure at a variety of scales, the patches seem to be larger. In addition, larger scales of variation were observed generally (but not always) for the structural diversity of ground cover than for the other measures. This likely reflects the fact that, regardless of the presence of trees, shrubs, and other plants, the ground is usually covered by plant material, which can be composed mostly of lichens and prostrate shrubs in open tundra and by plant litter in areas with trees. The structural diversity of the ground cover thus appears more homogeneous, whereas the structural diversity of different plant forms, both live and dead, varies of finer scales, with an alternation of open and closed areas.

#### 4.2. Relations with the environment

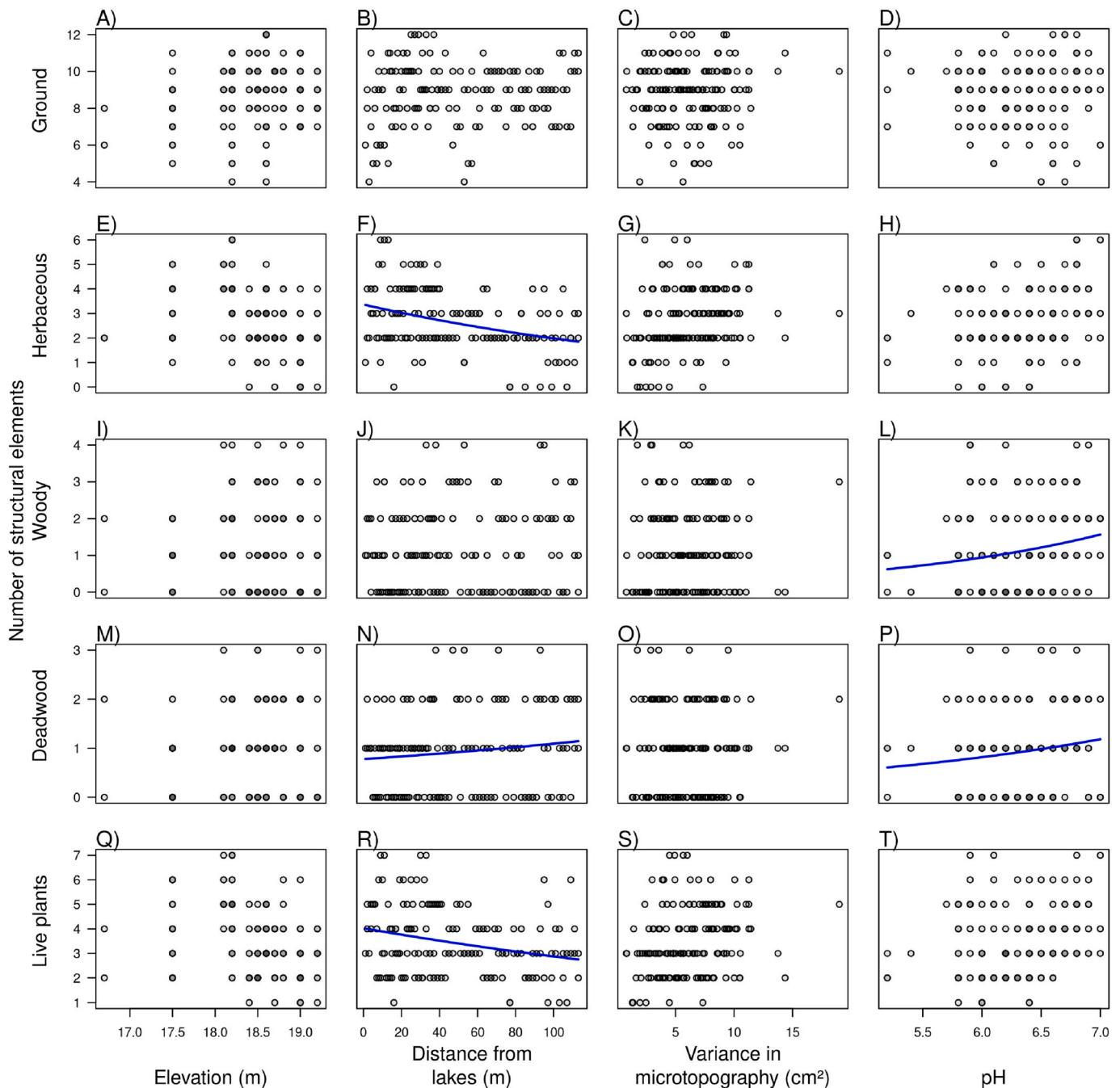
In our study, structural diversity was related mostly to distance from lakes and soil pH in the tundra and to soil pH and microtopography in the ecotone; elevation appeared to be less important. In general, the observed relationships were weak, indicating that the effects of the environmental variables used in our study may be marginal even when significant. It is possible that stronger relationships were not observed due to scale-dependency in the effects and to the small amount of variation in some of the explanatory variables. The importance of the different explanatory variables differed between the ecotone and the tundra. This indicates that the effects of these environmental variables differ between environments and are not universal; this observation is also in agreement with other studies that detected different and sometimes inconsistent effects of soil variables on tundra vegetation (Schmitz et al., 2020; Ferrari et al., 2021).

The near lack of statistically significant relationships with elevation may be due to the fact that our transects were on relatively flat ground, with a variation of only 6 m in the tundra and 5 m in the ecotone. This slight variation in elevation was probably insufficient to affect structural diversity in this environment. It is likely that if a stronger topographic gradient were present, such as is the case for example in alpine tundra, elevation would have stronger effects. It is worth noting that, notwithstanding the small variation in elevation, topographic and

microtopographic gradients have been shown to affect the structure and composition of the tundra on a peat plateau at the study site (Gamon et al., 2012). In addition, the relationship between structural diversity and elevation may not be a simple one as vegetation structure may be strongly determined by the presence of tree islands, the formation of which may depend on a variety of factors such as wind exposure, the existence of wind-protected depressions for the establishment of the original trees and patterns of snow cover (Hotmeier and Broll 1992).

Distance from lakes was an important variable in the tundra, but not in the ecotone. Water body margins are known to affect vegetation structure in the boreal forest (Harper and Macdonald 2001), and so the lack of a relationship with distance from lakes in the ecotone was surprising. Still, edge effects are known to be highly variable even for the same vegetation and edge type (Harper et al., 2005, 2015), and the intrinsic spatial variation in the ecotone may be too large for water bodies to have a detectable effect on structural diversity. However, we did observe a relationship between distance from lakes and structural diversity in the tundra, with higher herbaceous, ground, and live plants structural diversity closer to lakes, similarly to what has been observed for shrub cover at the same site (Harper et al., 2018). Conversely, the structural diversity of deadwood was lower closer to the lakes. It is possible that soil conditions, such as moisture, near lakes are more favourable to increased structural diversity; however, this would need to be tested directly and the relationships were weak. Still, our results provide some evidence of edge influence caused by natural lake edges on the structural diversity in the tundra, somewhat similar to what has been observed for vegetation structure and composition in boreal forests (Harper and Macdonald 2001; Harper et al., 2015). A possible explanation for the weak effect of distance from lakes is that it may affect structural diversity only at short distances, losing explanatory power for longer transects; for example, short distances of edge influence are common in boreal forests (Harper et al., 2015).

Microtopography was somewhat related to structural diversity in the tundra but these relationships were more prominent in the ecotone; when relationships were observed, structural diversity was higher in quadrats with more variable microtopography. This is in agreement with other studies. For example, microtopography is known to affect tundra vegetation (Holtmeier and Broll 1992; Gamon et al., 2012; Harper et al., 2018). It is worth noting, however, that the definition of microtopography differs between these studies and has been assessed on slightly different spatial scales: in our study and in Harper et al. (2018), microtopography was measured within 1-m<sup>2</sup> quadrats, conversely, Gamon et al. (2012) assessed microtopography along a 100 m-long transect with sampling points located every meter. Thus, effects of microtopography are likely to be scale-dependent. Notwithstanding these differences, these studies consistently show that microtopography is an important driver of different features of the vegetation in the tundra and the forest-tundra ecotone, affecting vegetation structure and



**Fig. 5.** Relation between the number of structural elements (StrS) and the environmental variables (elevation, distance from lakes, microtopography and pH) along the tundra transects. The lines represent the relationships present in the models considered as most plausible; the absence of a line means that the given environmental variables was not selected in the model selection procedure. When a model contained two or more environmental variable, the lines show the predicted values for one variable when the other is fixed at its mean value.

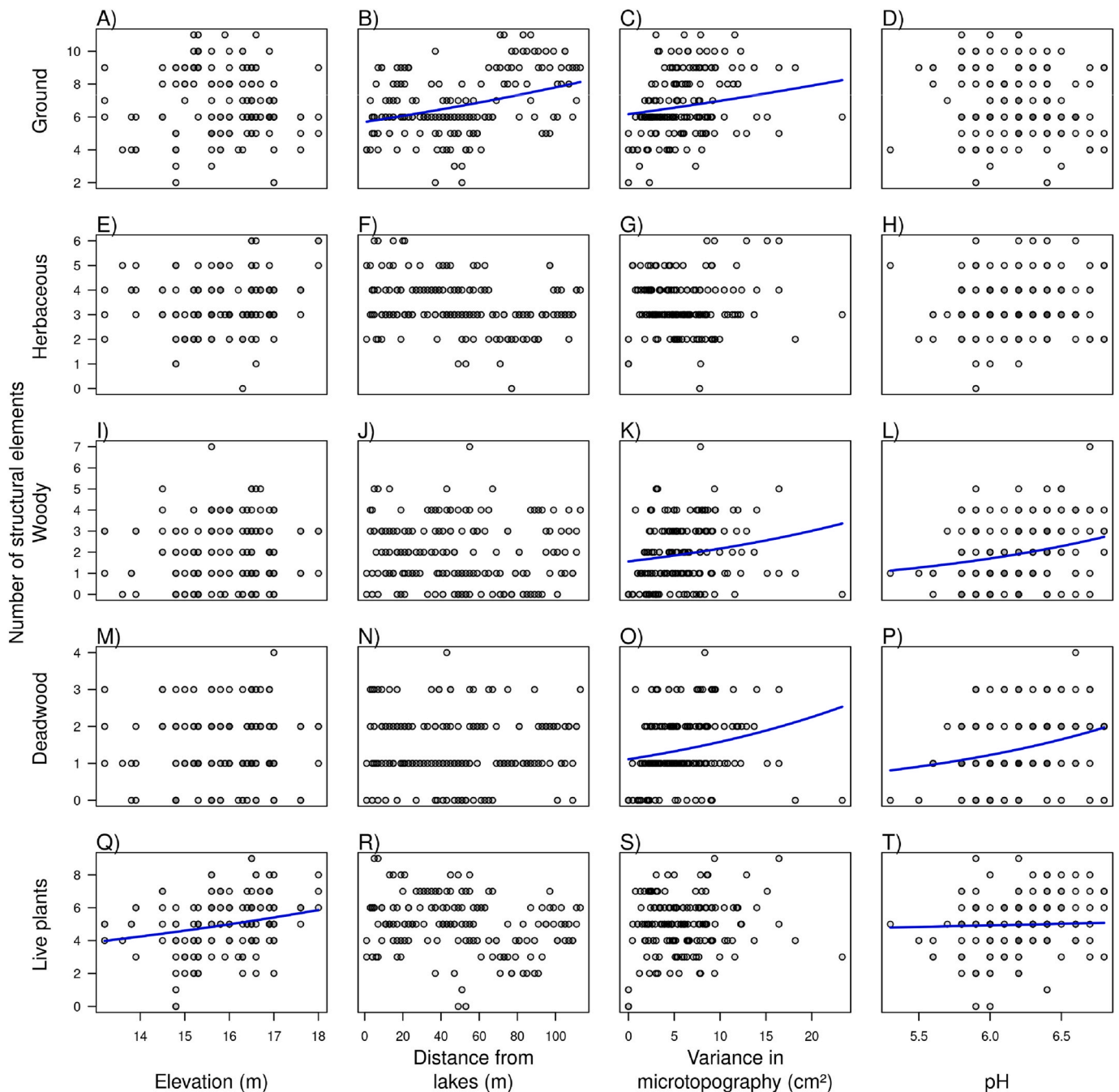
composition, as well as structural and compositional diversity. The importance of microtopography may be due to the shelter offered by microtopographic features against wind (Holtmeier and Broll 1992; Ferrari et al., 2021) and to microtopography-related variation in variables such as heat transfer and albedo (Gamon et al., 2012).

Another important variable, pH, which in our study was related to structural diversity in both environments, has been previously shown to be important for plant communities in the tundra (Gough et al., 2000; Schmitz et al., 2020; Ferrari et al., 2021). In our study, soils were generally acidic, and it is possible that the positive relationship between pH and structural diversity was because higher values of structural diversity were observed where pH was closer to neutral. Soil pH has also

been observed to be positively correlated with species richness in an Alaskan tundra (Gough et al., 2000). Conversely, pH had little correlation with shrubs in our study site (Harper et al., 2018).

#### 4.3. On the use of the different structural diversity indices

Our dissimilarity-based index of structural, StrD, follows the same logic as the functional diversity index FD (Petchey and Gaston 2002) and the phylogenetic diversity index PD (Faith 1992). All these indices are based on making a dendrogram of the different species (in the case of FD and PD) or structural elements (in the case of StrD) present in a given sampling unit and summing the lengths of the dendrogram branches.



**Fig. 6.** Relation between the number of structural elements (StrS) and the environmental variables (elevation, distance from lakes, microtopography and pH) along the ecotone transects. The lines represent the relationships present in the models considered as most plausible; the absence of a line means that the given environmental variables was not selected in the model selection procedure. When a model contained two or more environmental variable, the lines show the predicted values for one variable when the other is fixed at its mean value.

Thus, the more dissimilar the species or structural elements from one another, the greater will be the sum of the dendrogram’s branches. One advantage of such measures is that they cannot decrease by the addition of a new species or structural element, as the sum of branch lengths may either increase if the element added is different from the ones already present or remain constant if it the characteristics of the new element are equal to those of an element already present. However, the functional diversity index FD has been shown to be strongly correlated with species richness for a variety of datasets (Petchey and Gaston 2002, 2006; Schleuter et al., 2010). It is therefore not surprising that StrD was also strongly correlated with the number of structural elements.

Still, having considered this, we believe that other structural

diversity measures can be developed, in a way similar to the developments in indices of functional diversity (Villéger et al., 2008; Schleuter et al., 2010). It has already been argued that similarity between plant communities should take into account both species composition and the size of the individuals (De Cáceres et al., 2013). We agree with this suggestion; however, we also suggest that, depending on the objectives, species identity is less important than their structural characteristics. Focusing on structural characteristics may be especially important when both live and dead individuals are of interest, for example in disturbed areas where standing (snags) and fallen (logs) dead trees are important structural elements (Harper et al., 2014; Menezes et al., 2019), as the species identity of a dead tree is probably of less

importance than aspects such as its size and degree of decay. As such, a structural diversity measure that accounts for dissimilarity in these characteristics may provide additional information.

Finally, as with functional diversity, in which the functional traits considered must be related to the ecological process in question (Petchey and Gaston 2002), the characteristics of the structural elements to be considered should also be related to the ecological process considered. Thus, for example, a structural characteristic such as height may be relevant for fire dynamics, but not so much for the use of deadwood and litter by the soil fauna. This is a limitation of our study, in which we attempted to make a general characterization of the structural diversity without focusing on a specific ecological process. In addition, a general characterization of structural diversity required that we had an exhaustive list of structural elements, which may not be necessary when focusing on a single ecological process. Thus, we recommend that, when assessing variation in structural diversity specifically related to a given ecological process, only the structural elements related to such process are considered and classified according to characteristics relevant to this process.

## 5. Conclusions

Our results corroborate previous observations that the vegetation in the tundra and the forest-tundra ecotone is spatially heterogeneous, showing that the structural diversity of vegetation varies on different scales. These spatial patterns have been observed for different aspects of structural diversity, including the structural diversity of the ground layer, of live plants, and of dead plants. In addition, although many patterns were idiosyncratic, the scales of spatial pattern differed between tundra and ecotone, with smaller scales being observed in the ecotone. Finally, structural diversity increased with increasing pH and microtopographic variation (mostly in the ecotone) and had varying relations with distance from lakes, similar to what has been observed for other vegetation characteristics in previous studies.

Thus, by exploring the spatial variation in a little-explored feature - structural diversity - we believe that this study helps to advance our knowledge of the ecology of the tundra and the forest-tundra ecotone. Spatial heterogeneity is an important characteristic of this system, and even areas that may appear homogeneous, such as open tundra, may harbour a variety of different plant communities (Gamon et al., 2012; Ferrari et al., 2021), with varying structural diversity.

## Author contributions

Pavel Dodonov: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Visualization; Writing - original draft; Writing - review & editing. Karen A. Harper: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision; Writing - original draft; Writing - review & editing.

## Declaration of competing interest

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

## Data availability

The data and codes used are available at <https://github.com/pdodonov/publications> and this is stated in the manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2022.103862>.

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