The effect of sample area on heterogeneity and
plant species richness in coastal barrens

By
Madeline Clarke

A Thesis Submitted to
Saint Mary's University, Halifax, Nova Scotia
in Partial Fulfillment of the Requirements for
the Degree of Bachelor of Science with Honours

Approved: Dr. Jeremy Lundholm
             Supervisor

Approved: Dr. Zhongmin Dong
             Examiner

Date Submitted: April 25, 2018

Table of Contents

The effect of sample area on heterogeneity and

plant species richness in coastal barrens

by Madeline Clarke

Abstract

Spatially varying environments are expected to provide more niche breadth than homogeneous areas, and should thus support a larger number of plant species. The observed sample area, or spatial scale, can also influence the relationship between this environmental heterogeneity and plant species richness. Few studies have been conducted at a multi-scalar level and none have been conducted in coastal barrens habitats. This study looked at two types of environmental variation: 1) Spatial heterogeneity and 2) Average conditions, at Chebucto Head, NS, at three different scales: subplot (0.5 m x 0.5 m), plot (1 m x 1 m), and transect (25 m x 2 m). Spatial heterogeneity was calculated as the standard deviation of substrate depth, substrate moisture, and topographic elevation as well as the Shannon-Weiner diversity index of six cover type variables. Average conditions were calculated as the mean of substrate depth, substrate moisture, and topographic elevation. Results of a multivariate linear regression analysis indicated that the strongest environmental predictor of plant species richness varied with sample area and also showed a general trend towards an increase in the strength of the relationship between environmental heterogeneity and plant species richness with increasing sample area. This study is one of the first to assess environmental heterogeneity and plant species richness on a multi-scalar level in coastal barrens and underlies the importance of how spatially varying environments can influence the diversity of plant species and how vegetation sampling design can affect the strength of predictor variables.

Date submitted: April 25, 2018

1 Introduction

1.1 Coastal Barrens

Barrens are described as extreme habitats with shallow, acidic, nutrient poor soil, sparse tree cover, predominantly low-growing, shrubby Ericaceous vegetation, and harsh environmental conditions (Oberndorfer, 2006; Balsdon et. al., 2011; Porter, 2013). The harsh nature of barrens drastically reduces the vegetation height and alters the morphology of many residing plant species. Those that have successfully adapted are generally slow growing and take a long time to recover from damaging events. Barrens support a variety of unique plant communities, however they do support plant species that are found in neighbouring forests as well (Balsdon et. al., 2011). Thus, barrens are generally considered to be successional habitats that tend to become forested areas. Coastal barrens of Nova Scotia are located mainly along the Atlantic coast of the province and consist mainly of heathland community types (Porter, 2013) but do often incorporate intermittent bog and grassland areas (Oberndorfer, 2006).

While coastal barrens are less than 3% of the area of Nova Scotia, they have provincially rare plant species and many plant species that may be restricted to this habitat type (Oberndorfer & Lundholm, 2009). These habitat-specific species are important in maintaining community diversity which can lead to increased stability, resistance, and resiliency of the ecosystem. Coastal barrens sites are at risk for habitat loss through a variety of means including tree encroachment from succession and human

disturbances which includes coastal development projects, hiking trails, etc. (Oberndorfer & Lundholm, 2009).

1.2 Species Richness

Species richness is only one part of species diversity and is generally counted as the total number of species living in an area. Species diversity also incorporates species evenness, where the relative abundances are accounted for. Species richness is largely determined by the number of rare species present (Hewitt et al., 2016). It has been well documented that species richness increases with the area of the sample (Arrhenius, 1921; Fahrig, 2013; Evju & Sverdrup-Thygeson, 2016) thus underlying the importance of spatial scale.

1.3 Heterogeneity

Heterogeneity can be considered the variation of some measure through physical space or time. Heterogeneity in the environment is known to have a major role in the persistence of a species' population stability, and the coexistence between organisms (Chesson, 2000; Rayburn & Schupp, 2013). It is thought that heterogeneous environments can support more species than homogeneous ones, however some studies have shown that this is not always the case (Lundholm, 2009). With respect to vegetation, environmental heterogeneity describes variation of environmental factors that affect plant survival and growth such as substrate depth, substrate moisture and nutrient content, wind exposure, elevation etc.

Plant species are constantly interacting with their neighbours, whether it is to gain access to limited resources, space, or fertilizations. Individuals in different habitats are generally not interacting with each other, and so physical distance, or extent, plays a role in which species can be actively competing. These species are all competing together and must consider their environment to ensure proper allocation of resources in the maintenance of essential functions. Understanding spatial heterogeneity is necessary for understanding species interactions (Chesson, 2000) as well as the spatial scale that is being used to assess the relationship.

Plant species can differ widely in their habitat requirements and this helps to ensure their survival when interacting with neighbours. The niche theory states that species utilize resources in different ways, and this distinction allows species to partition their environment accordingly and increases coexistence by experiencing a reduction in competition (Whittaker, 1972; Silvertown, 2004). Species can change physically and/or physiologically to survive in an area with a specific set of resources that may be different than another species', to reduce the amount of niche overlap. This process subsequently reduces the amount of competition between the two species and results in improved coexistence between species, which would then allow more species to thrive an a given area, provided suitable niche types are present for each.

It is assumed that as the environment becomes more heterogeneous, the species diversity will increase accordingly (Lundholm, 2009; Dufour et. al., 2006; Oberndorfer, 2006). A more heterogeneous environment would be subject to more variations and gradations in resource availability, which should increase the diversity of niches

available. More niche types will provide the opportunity for more species to establish in the same area, thus increasing the overall species richness. Once a species is established in a location, its persistence is dictated by the local climactic, biotic, and abiotic dynamics of the area (Dufour et al., 2006, Chesson, 2000). A habitat is characterized by the physical and chemical properties of the environment of the species (Whittaker, 1972). The environment itself plays a huge role in the types of vegetation that will colonize an area. A suitable habitat may be found in an area of high heterogeneity, however if the actual habitat size is too small, it is more likely to experience local extinction because it can only support a small number of individuals.

1.4 Spatial Scale

Spatial scale is an important factor when considering plant species richness and environmental heterogeneity. The spatial competition hypothesis describes that competitive exclusion occurs when species compete for a single limiting resource (Tilman, 1994) and the number of coexisting species should be no greater than the number of limiting resources (Tilman & Pacala, 1993). Niche differences are necessary for species coexistence to occur (Chesson & Huntly, 1997) and understanding the scale at which these interactions are occurring can influence the relationship between species and the physical characteristics of the environment.

Many studies on vegetation sampling are only conducted at a single scale, and as such it is not always clear how spatial scale is affecting the environmental influences on community composition (Siefert et. al., 2012). Understanding the effect of spatial scale is

crucial when sampling an area where ecological processes themselves occur at different scales and measuring at the incorrect scale of the variable in question can greatly impact its relationship (Anderson et. al., 2007; Jackson & Fahrig, 2014). Few studies have been conducted at a multi-scalar level (Dufour et. al., 2006; Anderson et. al., 2007; Bergholz et. al., 2017) and while it is thought that species richness should increase with heterogeneity, this relationship is highly dependent on spatial scale and particularly the size of the area being sampled (Lundholm, 2009; Chase, 2014; Bergholz et. al., 2017).

1.5 Objectives

Our objectives are to 1) assess plant species richness at three different spatial scales, 0.5 m x 0.5 m, 1 m x 1 m, and 2 m x 25 m, 2) determine if there is a correlation between environmental heterogeneity and spatial scale, and 3) through several environment measures such as substrate depth, elevation, etc., to assess the relationship between plant species richness and environmental heterogeneity at these three sample areas. We predict that, as the sample area increases, the strength of the heterogeneity-richness relationship should increase as well. Increasing the area sampled incorporates more room for variation which can lead to an increase in heterogeneity. Oberndorfer and Lundholm (2009) observed no relationship between spatial heterogeneity and richness examining soil moisture and depth in 1 m x 1 m plots in coastal barrens. However, a wider range of environmental factors needs to be considered at multiple scales to gain a more complete understanding of the heterogeneity-richness relationship. There is a gap in knowledge on the effects of spatial scale as it relates to plant species diversity and environmental heterogeneity on coastal barrens habitat types.

2 Methods

2.1 Study site

Chebucto Head is a part of the Duncan's Cove Nature Reserve and is located along the Atlantic coast approximately 40 km southeast of Halifax, Nova Scotia (Oberndorfer, 2006). It is mainly composed of Ericaceous vegetation, which is generally slow-growing and shrubby, and contains many granite outcroppings where the terrain is highly variable. Many plant communities are found at the site such as bog, heathland, and tall shrubs. Chebucto Head is recognized as a hiking area and has cultural significance with numerous berry-producing species including low-bush blueberry (*Vaccinium angustifolium*) and black huckleberry (*Gaylussacia baccata*). A 500 m x 500 m area of the site was used for study as drone imagery data had already been collected for that particular region (Buckland-Nicks, 2017) (Figure 1).
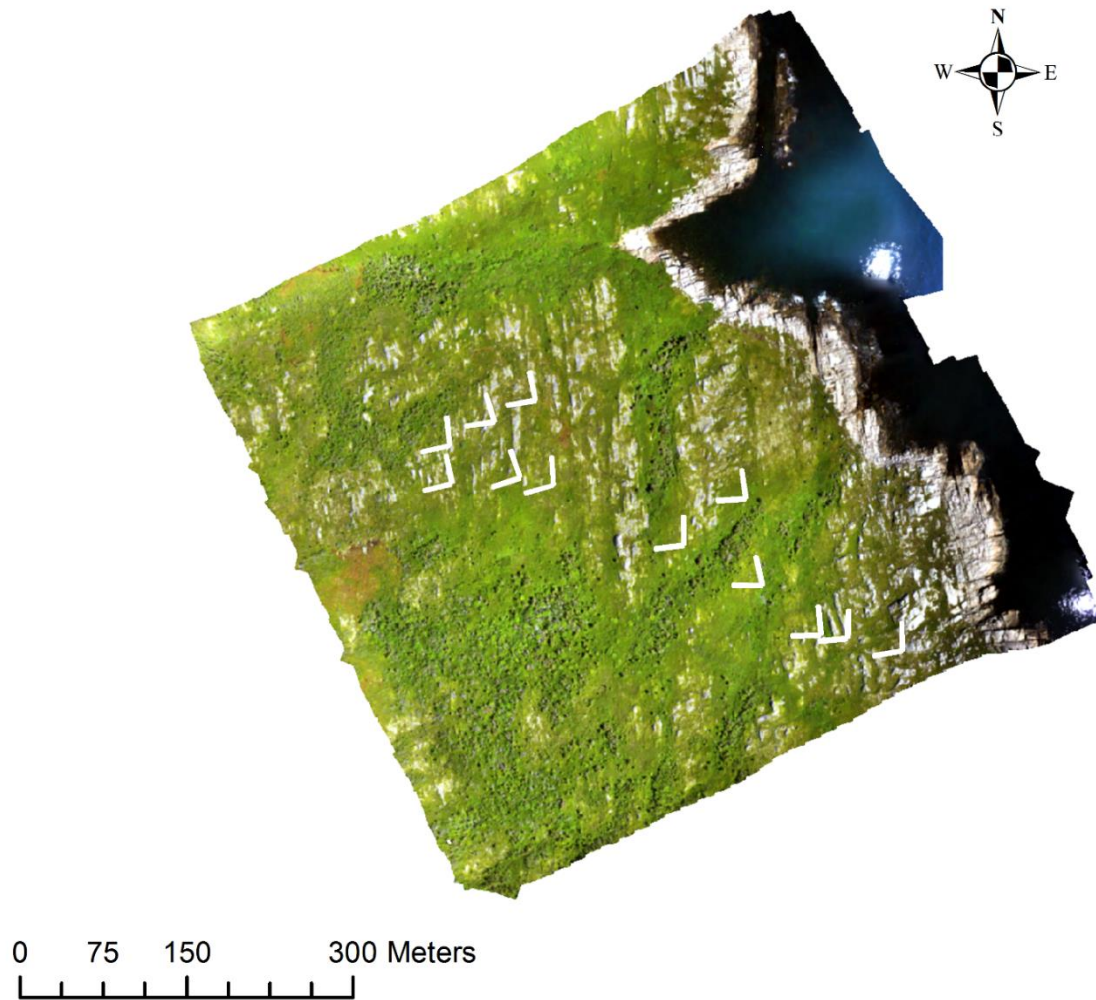
Figure 1. Drone imagery colour mosaic of 500 m x 500 m study site at Chebucto Head. Imagery was captured by Michael Buckland-Nicks on July 5, 2017. Transects (25 m x 2 m) are represented by white rectangles. This image shows ridgetops that appear to follow a linear direction from North to South.

2.2 Sampling design

The sampling design consisted of a three-tiered system of nested plots. Drone imagery was captured in a 500 m x 500 m area (Figure 1) in July 2017 by Michael Buckland-Nicks displaying natural rock outcroppings oriented from North to South. To capture the variability of the environment, 24 locations were originally selected as possible study sites where half of the sites were located North-West of a forested depression and the other half, South-East. Six sites from each side of the depression were randomly selected, using a table of randomized digits, for a total of twelve sites. At each site, two 25 m x 2 m 'transects' were placed: one oriented North to South and the other, East to West, for a total of 24 transects at 12 sites. Perpendicular transects were used because it was expected that the North-South transects (following the ridges) would have relatively homogeneous environmental conditions while East-West transects would include ridgetop, side and troughs, resulting in a high level of environmental heterogeneity, with the overall goal of capturing a large range of within-transect spatial heterogeneity. Within each of the 24 transects, 10 1 m x 1 m 'plots' were evenly spread throughout. Each 1 m x 1 m plot was subsequently divided into four equal 0.5 m x 0.5 m 'subplots' (Figure 2). All environmental factors (independent variables) were measured at the subplot scale.
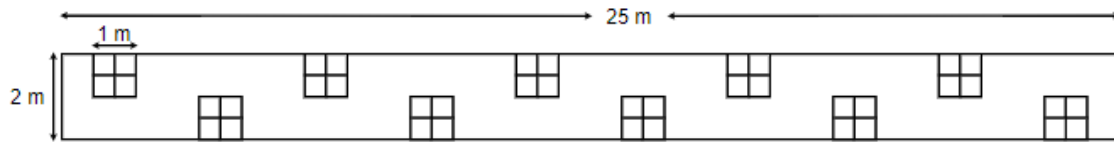
Figure 2. Sampling design of a single transect (25 m x 2 m). One transect contains 10 plots (1 m x 1 m) and each plot is subdivided into 4 equal subplots (0.5 m x 0.5 m). Environmental factors were measured in each subplot.

2.3 Independent variables

The environmental factors that were measured include substrate depth, substrate moisture, rock and soil exposure, fruticose lichen and moss cover, and topographic elevation. Substrate depth was measured three times randomly in each subplot using a 40 cm long thin, metal rod. Measurements that were greater than 40 cm in depth were simply recorded as 40 cm. Soil depth is known to vary widely at the study site and so multiple measurements were taken for each subplot to capture the most variability.

Substrate moisture was measured in one day, August 30th, 2017, three days after a rainfall event. Thus, all transects received relatively similar amounts of water from rainfall, but was neither too inundated nor too dry, ensuring the maximum variability among subplots. If samples were taken immediately following a rainfall event, then all samples would likely be equally saturated with water and if samples were taken too long after a rainfall event, then all samples would likely be equally dry. Thus, sampling on a day in between these extremes ensured there was enough time for some areas to dry out, but not all for all areas. This created a range of substrate moisture that could be analyzed.

Substrate moisture was collected using the 10HS Soil Moisture Sensor and the Decagon Inc. Procheck. When soils were too shallow to use the moisture sensor, moisture was recorded as 0. This included all mineral type soils. To calibrate the soil moisture sensor for the organic soils at the study site, two representative substrate samples were collected from the site (to a depth of 10 cm of the uppermost layer of soil) and allowed to dry completely in a drying oven, then added to plastic pots of known volume. Samples were weighed then saturated with water and allowed to air dry. Measurements with the soil moisture probe as well as pot weights were taken once a day until the samples were completely dry to plot a calibration curve using volumetric water content against sensor output. The relationship between sensor output and volumetric water content was linear with a high degree of fit ($R^2 = 0.98$). As the relationship was linear, millivoltage output was used as an equivalent to percent water content in terms of comparing means and standard deviations (SD) in further analyses.

Rock and soil exposure, as well as moss and fruticose lichen cover were estimated visually as percent cover at the subplot level. Rock can greatly affect species composition as it is impenetrable to root networks and thus limits the space available for plant growth. Crustose lichen and foliose lichen grow almost exclusively on rock substrate and were incorporated as part of rock exposure. Soil exposure can be indicative of repeated disturbances that can also impact plant communities. Fruticose lichens can be found on a variety of substrates and thus was recorded separately from the rock exposure. Mosses were divided into two categories: sphagnum and other. Sphagnum is distinctive from other mosses and generally prefers very wet environments and thus was given its own

category. Due to time constraints, it was not possible to identify mosses and lichens down to the species level. These variables were chosen as they were expected to most impact the number of vascular plant species found. They were then compiled into one heterogeneity measure using a Shannon-Weiner diversity index (H'), which accounts for the number of cover types present (cover richness) as well as their relative distributions compared to one another (cover evenness).

Topographical elevation was determined using georeferenced drone imagery by Michael Buckland-Nicks from July 2017 in ArcMap 10.5.1. Subplots were located visually on a colour mosaic model (Figure 1) using flagged corners and when flags could not be identified from the aerial photo, ground photographs were used to pinpoint their locations as accurately as possible. A 3D point cloud was used to create a 10 cm elevation model. This was georeferenced to the colour mosaic model and subsequently used to determine total elevation, in meters, within each subplot as an average of 25 data points. Vegetation height, measured to the nearest centimeter as the average height of the dominant vegetation in each subplot, was subtracted from the elevation to determine topographical elevation.

Overall, substrate depth, substrate moisture, and topographic elevation were described in terms of average conditions, or mean, and spatial heterogeneity, or standard deviation (SD) and the six cover variables were described as a Shannon-Weiner diversity index (Table 1). Comparing average conditions will help to identify the variability between different subplots, plots, and transects. Comparing spatial heterogeneity will help to identify the variability within each subplot, plot, and transect and how each differs

from others at the same sample area. Ideally, the sampling design was created to capture some subplots, plots, and transects that are very heterogeneous (e.g. some very dry plots and some very wet plots in one transect) and others that are very homogeneous (e.g. all very dry plots in one transect). While some could be very homogeneous, they may differ greatly in their average conditions (e.g. all very dry plots in one transect versus all very wet plots in another transect).

Five independent environmental factors were described at the subplot scale: mean and standard deviation (SD) of substrate depth (three subsamples per subplot), topographic elevation (25 points per subplot) and the Shannon-Weiner diversity index of cover variables. All independent environmental factors were described for both plot and transect scales (Table 1). Variables for substrate moisture could not be described at the subplot scale as it was only sampled once per subplot and thus no mean or SD could be derived. Substrate depth varies widely at the site and, therefore it was consciously determined to sample three times per subplot in attempts to capture that variability. Topographic elevation was extrapolated using at 10cm elevation model in ArcMap 10.5.1, and thus a data point existed for every 10 cm^2 for a total of 25 data points for each subplot. At the plot scale, mean and SD were derived from the 4 subplots of each plot for substrate moisture, 4 x 3 = 12 subplot samples for substrate depth and 4 x 25 = 100 data points for topographic elevation. At the transect scale, mean and SD were derived from the 40 subplots of each transect for substrate moisture, 40 x 3 = 120 subplots samples for substrate moisture and 40 x 25 = 1000 data points for topographic elevation. A summary can be viewed in Table 1.

Table 1. Summary of environmental factors used in analysis at each sample area for average conditions (Avg cond) and spatial heterogeneity (Spat het). At the subplot scale, substrate depth was the mean and standard deviation (SD) of three subsamples, and topographic elevation was the mean and SD of 25 points extrapolated from ArcMap 10.5.1 using a 10cm elevation model. The mean and SD at the subplot scale does not take the average dominant canopy height into consideration; however it is considered at the plot and transect scales. Substrate moisture was not described at the subplot scale as only one sample was taken for each. At the plot scale, mean and SD were derived from the 4 subplot samples for substrate moisture (3 x 4 = 12 subplot samples for substrate depth and 25 x 4 = 100 points for topographic elevation). At the transect scale, mean and SD were derived from the 40 subplot samples for substrate moisture (3 x 40 = 120 subplots samples for substrate depth and 25 x 40 = 1000 points for topographic elevation). A Shannon-Wiener diversity index was calculated from six percent cover variables (leaf litter, rock, exposed soil, fruticose lichen, sphagnum moss, and other moss) and thus could be identified at all three scales. Average conditions were not calculated for percent cover variables.

Environmental Factors	Subplot (n=960)		Plot (n= 240)		Transect (n= 24)	
	Avg cond	Spat het	Avg cond	Spat het	Avg cond	Spat het
Substrate depth	Mean (n= 3 subsamples)	SD (n= 3 subsamples)	Mean (n= 12 subplot samples)	SD (n= 12 subplot samples)	Mean (n= 120 subplot samples)	SD (n= 120 subplot samples
Substrate moisture	N/A (n= 1 sample)	N/A (n= 1 sample)	Mean (n= 4 subplots)	SD (n= 4 subplots)	Mean (n= 40 subplots)	SD (n= 40 subplots)
Topographic elevation	Mean (n = 25 points)	SD (n= 25 points)	Mean (n= 100 subplot samples)	SD (n= 100 subplots)	Mean (n= 1000 subplots)	SD (n= 40 subplots)
Percent cover variables	N/A	Shannon-Wiener index (n= 1)	N/A	Shannon-Wiener index (n= 4)	N/A	Shannon-Wiener index (n= 40)

2.4 Dependent variable

Species richness was directly sampled at the transect and subplot scales. A full species list was created at the transect scale by identifying any vascular plant species present until no more new species could be identified. At the subplot scale, vascular plant species were marked for either presence or absence to determine the number of species. Richness in plots was determined by combining the number of species within its four subplots, accounting for redundancies in species composition.

2.5 Statistical analysis

All statistical analyses were completed using R (RStudio 1.1.383).

2.5.1 Normality:

Where necessary, normality of each predictor variable was tested using the Shapiro-Wilks test. For values of $p < 0.05$, the variables were transformed using Tukey's ladder of powers of transformation to determine the lambda which maximizes the W statistic of the Shapiro-Wilks test. Variables that were unable to be transformed to normality used the Tukey transformation as the closest to normality as possible.

2.5.2 Species-area relationship

To determine the relationship between plant species richness and sample area, a three-way ANOVA was used to determine if there were any significant differences in richness at the three sample areas: subplot, plot, and transect. The Shapiro-Wilks test was used to check for normality and the Bartlett test was used to check the homogeneity of variances. In the case of non-normally distributed data and heterogeneous variances, Kruskal-Wallis analysis was used instead.

2.5.3 Heterogeneity-sample area relationship

To determine the relationship between environmental variables and spatial scale for average conditions and spatial heterogeneity, a three-way ANOVA was used to determine if there were any significant differences at the three scales for each variable. The Shapiro-Wilks test was used to check for normality and the Bartlett test was used to check the homogeneity of variances. In the case of non-normally distributed data and heterogeneous variances, Kruskal-Wallis analysis was used instead.

2.5.4 North-South vs East-West transects

At each sampling location, one transect was oriented North-South and the other East-West either with or against the natural landscape gradient observed from drone imagery, respectively. This was to attempt to capture a greater range of variability within transects. A paired t-test was performed to determine whether there was any significant difference in the orientation of transects at each site for each environmental factor and species richness.

2.5.5 Univariate regression

To determine the correlation between species richness with each variable (see Table 1), univariate linear regressions were used on non-transformed data for each scale. They were also used on transformed data to compare whether it was able to better explain the variances. Curvilinear regressions were used when a quadratic was better able to explain the variances than a standard line, i.e. a larger R^2-adjusted value.

2.5.6 Multiple linear regression

Multiple linear regressions were conducted to select the best set of environmental predictor variables for species richness at a given scale. Predictor variables included estimates of mean and standard deviation of environmental variables at the relevant scale (Table 1). Procedures followed guidelines set out in Zuur et al. (2009). First, all predictor variables were transformed to normality or as close to normal as possible where appropriate. Next, mixed models were constructed to account for the nested nature of the sampling design: transect nested within site; plot nested within transect within site; subplot nested within plot within transect within site (Table 2), with nested factors as random effects. The full model for each scale was assessed in its mixed form and within the nested factors. When nested factors explained substantial variance, they were retained. Transect and plot scale species richness were modeled with fixed effects only, but subplot scale models fit best with the full nested structure, so we used mixed models for that scale only. As species richness is a count variable, three variance structures were examined and compared: Gaussian, Poisson or Negative-Binomial using the lmer or glmer functions in R (lme4 package: Bates et al. 2015). These were also compared with a linear model using the transformation that brought richness closest to normality and the best fitting model was used for the next step. Fit was assessed by examination of the residuals and a Chi-square test where possible (not implemented for mixed models). For the transect scale, richness was transformed ($y = richness ^ -3.425$) and we used Gaussian error structure; plot scale richness: Gaussian error structure; subplot scale richness was modeled using (transformed) $richness ^ 1.5$ and a Poisson error structure.

Next, the full model was subject to all subsets selection and models with delta

weights less than 7 (Burnham et. al., 2011) were subjected to model averaging using the

MuMIn package (Bartoń, 2018); predictor beta coefficients whose confidence intervals

did not overlap zero were considered "significant".

Table 2. Tested multiple linear regression models for random effects for nested design. Checkmarks represent which random effects were tested for each scale. The multiple linear regression at the subplot scale tested random effects of site location, transect number, and plot number. At the plot scale, site location and transect number was considered as a random effect. At the transect scale, site location was considered as a random effect.

	Subplot	Plot	Transect
Site location	✓	✓	✓
Transect number	✓	✓	x
Plot number	✓	x	x

3 Results

3.1 Species richness and spatial scale

I found 63 species overall, within the 24 transects. The most plant species found

in one transect was 43 and the fewest was 24 with an average of 30.3 species per transect.

The average number of species found at the plot scale was 12.8, where the maximum was

25 and the minimum was zero. The average number of species found at the subplot scale

was 8.6, where the maximum was 21 and the minimum was also zero. The Shapiro-Wilks

normality test and Bartlett test for homogeneity of variances were used and both had p-

values less than 0.05, indicating that the data were not normally distributed, and variances

were not homogenous. I therefore used Kruskal-Wallis tests with all three scales which

produced a significant result such that the number of plant species varied significantly between sample areas (Figure 3). The number of species found increased with sample area.
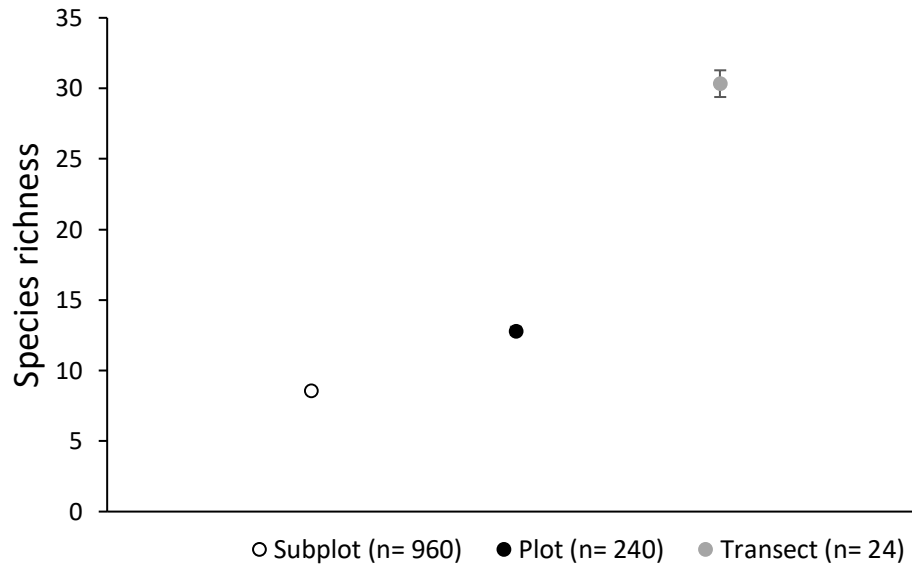

Figure 3. Species richness for each scale: subplot (n= 960), plot (n= 240), and transect (n=24) (means ± standard error). Data were non-normally distributed (Shapiro-Wilks test: p-value < 0.05). Bartlett homogeneity of variances was significant with p-values <0.05. Kruskal-Wallis analysis showed significant difference between all three scales, p-value < 0.05.

3.2 Environmental factors and spatial scale

Spatial heterogeneity factors were also significantly different between sample areas. From Shapiro-Wilks tests, all data were non-normally distributed and only substrate moisture had homogeneous variances from the Bartlett test. Kruskal-Wallis tests were therefore performed for substrate depth, topographic elevation, and the percent cover variables. ANOVA and Kruskal-Wallis tests were performed for substrate moisture and both tests produced significant results.

In all four cases, the mean spatial heterogeneity of substrate depth, topographic elevation, and substrate moisture as well as the mean Shannon-Wiener diversity index of percent cover variables increased with sample area (Figure 4). Mean spatial heterogeneity of substrate moisture could not be calculated at the subplot scale because only one measurement was taken per subplot. Standard error did generally increase with sample area.

The average conditions for substrate depth, topographic elevation, and substrate moisture were the same at each scale. There were no significant differences. Standard error did increase with sample area.
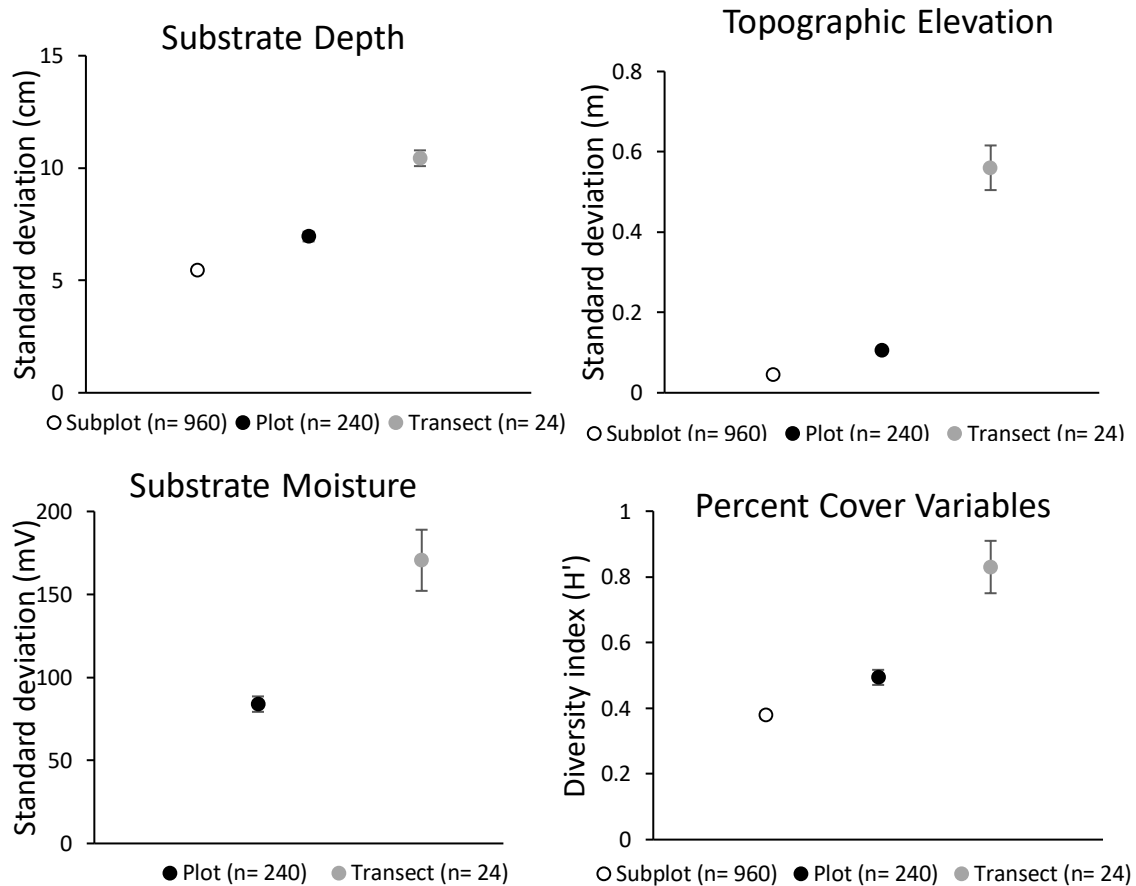
Figure 4. Standard deviation (SD) to represent spatial heterogeneity of subplot (n= 960), plot (n= 240), and transect (n= 24) scales for substrate depth, topographic elevation, and substrate moisture (means ± standard error) and Shannon-Weiner diversity index (H^1) of percent cover variables. Substrate moisture SD values could only be compiled for plot and transect scales because there was only a sample size of one at the subplot scale. Data were non-normally distributed (Shapiro-Wilks test: p-value < 0.05). Bartlett homogeneity of variances was significant with p-values <0.05 for all but substrate moisture. Kruskal-Wallis analysis showed significant difference between all three scales for substrate depth, topographic elevation, and the cover diversity index, p-value < 0.05. Both ANOVA and Kruskal-Wallis analysis were significant for substrate moisture.

3.3 North-South versus East-West transects

There were no differences between transects oriented North-South and those oriented East-West for either average conditions (Figure 5) or spatial heterogeneity (Figure 6). Paired t-tests were performed for each environmental factor at the transect scale (Table 1) and, while there were often slightly larger values for average conditions and spatial heterogeneity in transects oriented East-West, there were no significant differences (all p-values > 0.05).
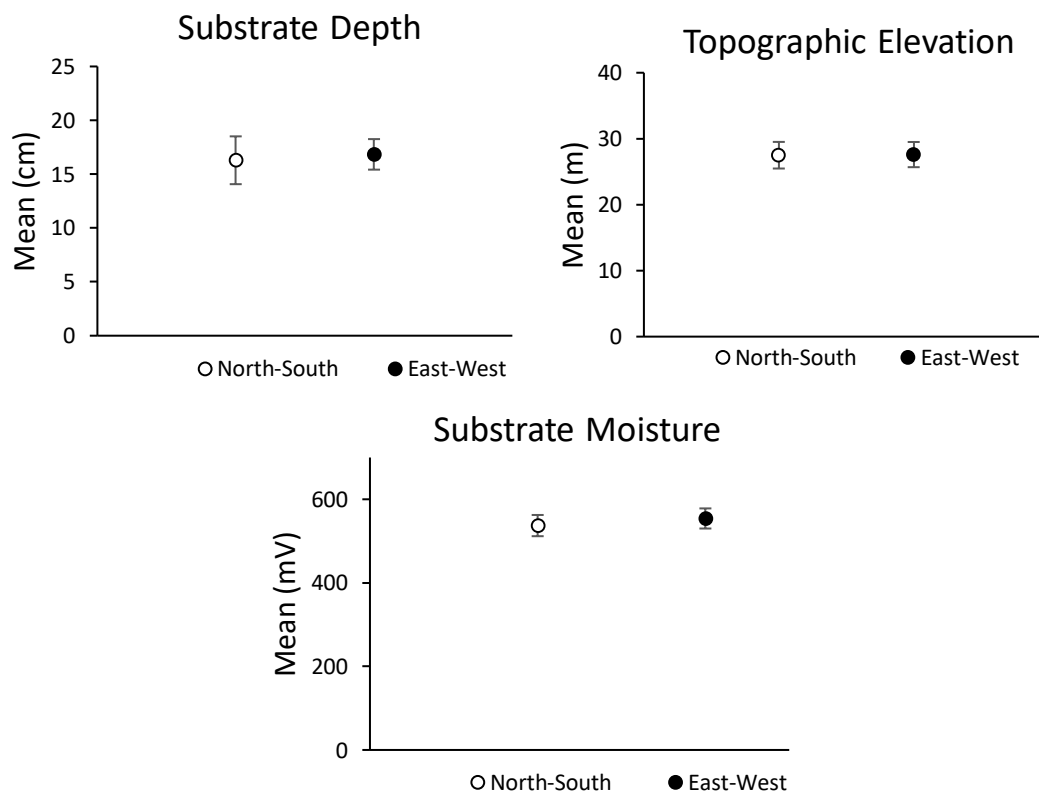

Figure 5. Average conditions of North-South versus East-West transects for substrate depth, topographic elevation, and substrate moisture (means ± standard error). No significant differences were found for any environmental factor between the two orientations of each transect site using paired t-tests: p > 0.05.
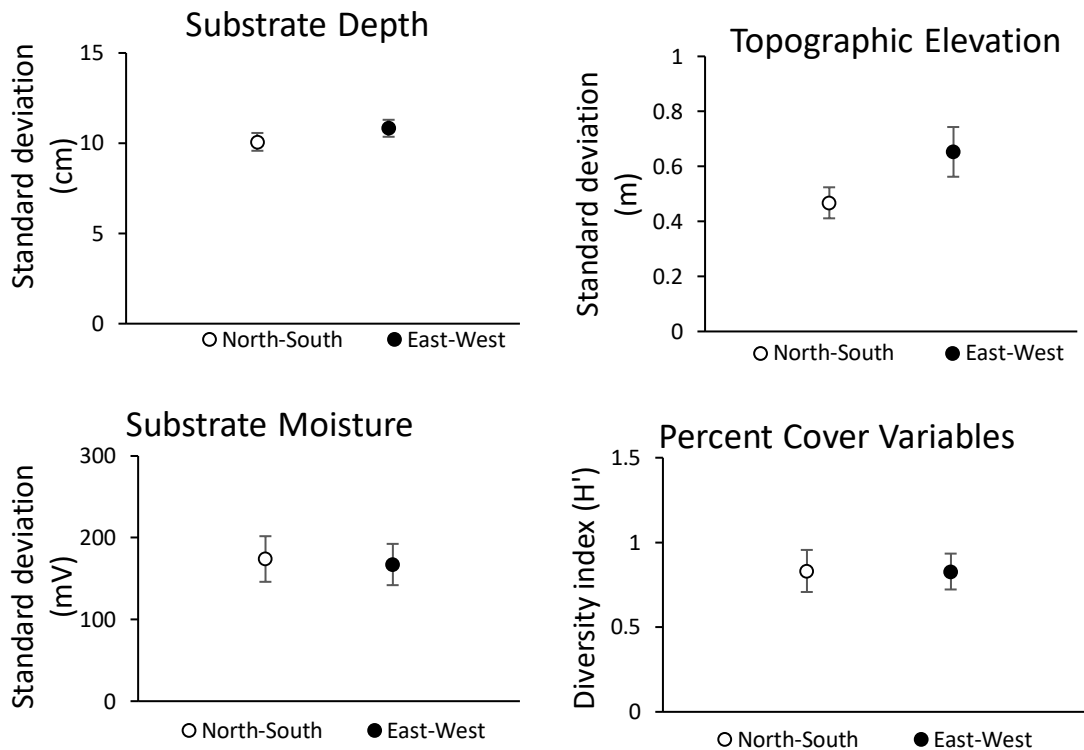
Figure 6. Spatial heterogeneity of North-South versus East-West transects for substrate depth, topographic elevation, substrate moisture, and percent cover variables (means ± standard error). No significant differences were found for any environmental factor between the two orientations of each transect site using paired t-tests: $p > 0.05$.

3.4 Environmental factors, plant species richness, and spatial scale

To determine whether the relationship between environmental heterogeneity and species richness was stronger at larger sample areas, univariate regressions were performed for each environmental factor, at each scale, for both average conditions and spatial heterogeneity. A summary table of univariate regressions can be seen in Table 3.

Table 3. R^2-adjusted values of univariate regression of all four environmental factors (substrate depth, substrate moisture, topographic elevation, and percent cover variables) for average conditions (mean) and for spatial heterogeneity (standard deviation for substrate depth, substrate moisture, and topographic elevation and Shannon-Wiener diversity index for percent cover variables). Values in **bold** represent factors where transformations improved the fit of the model. Values with an asterisk* represent factors that were significant (p-values < 0.05).

Environmental Factors	Average Conditions			Spatial Heterogeneity		
	Subplot	Plot	Transect	Subplot	Plot	Transect
Substrate depth	0.43*	0.48*	-0.04	0.25*	0.36*	0.04
Substrate moisture	N/A	0.58*	**0.01**	N/A	**0.26***	0.055
Topographic elevation	**0.23***	**0.24***	0.18*	0.016*	-0.0032	**0.19***
Percent cover variables	N/A	N/A	N/A	0.024*	0.011	-0.01

Variances of both subplot and plot species richness for both average conditions and spatial heterogeneity in substrate depth could be explained better using a quadratic model as opposed to a linear model (Figure 7). Transforming the data for both dependent and independent variables did not improve the fit. Heterogeneity-richness relationships were strongest at the plot scale with 48 % of the variance explained for average conditions and 36 % for spatial heterogeneity. These relationships were lowest at the transect scale for both average conditions and spatial heterogeneity where the regressions were not significant (p-value > 0.05).

Figure 7. Average conditions and spatial heterogeneity of substrate depth (cm) compared to species richness at three scales. Average conditions for subplot, plot, and transect scales are A, C, and E, respectively. Spatial heterogeneity for subplot, plot, and transect scales are B, D, and F, respectively. Lines of best fit are represented by linear or quadratic univariate regressions of untransformed variables to maximize R^2-adjusted.

For substrate moisture, only plot and transects scales were measured because there was no data for the subplot scale. Variances were only explained better using a quadratic model at the plot scale for spatial heterogeneity in substrate moisture (Figure 8). Transforming the data only improved the fit for the plot scale of spatial heterogeneity (substrate moisture ^ 0.45 and richness ^ 1.525; 0.16 → 0.26) and the transect scale of average conditions (substrate moisture ^ 5.975 and richness ^ -3.425; 0.004 → 0.01). Heterogeneity-richness relationships were strongest at the plot scale with 58 % of the variance explained for average conditions and 26 % for spatial heterogeneity. The regressions at the transect scales were not significant (p-value > 0.05).
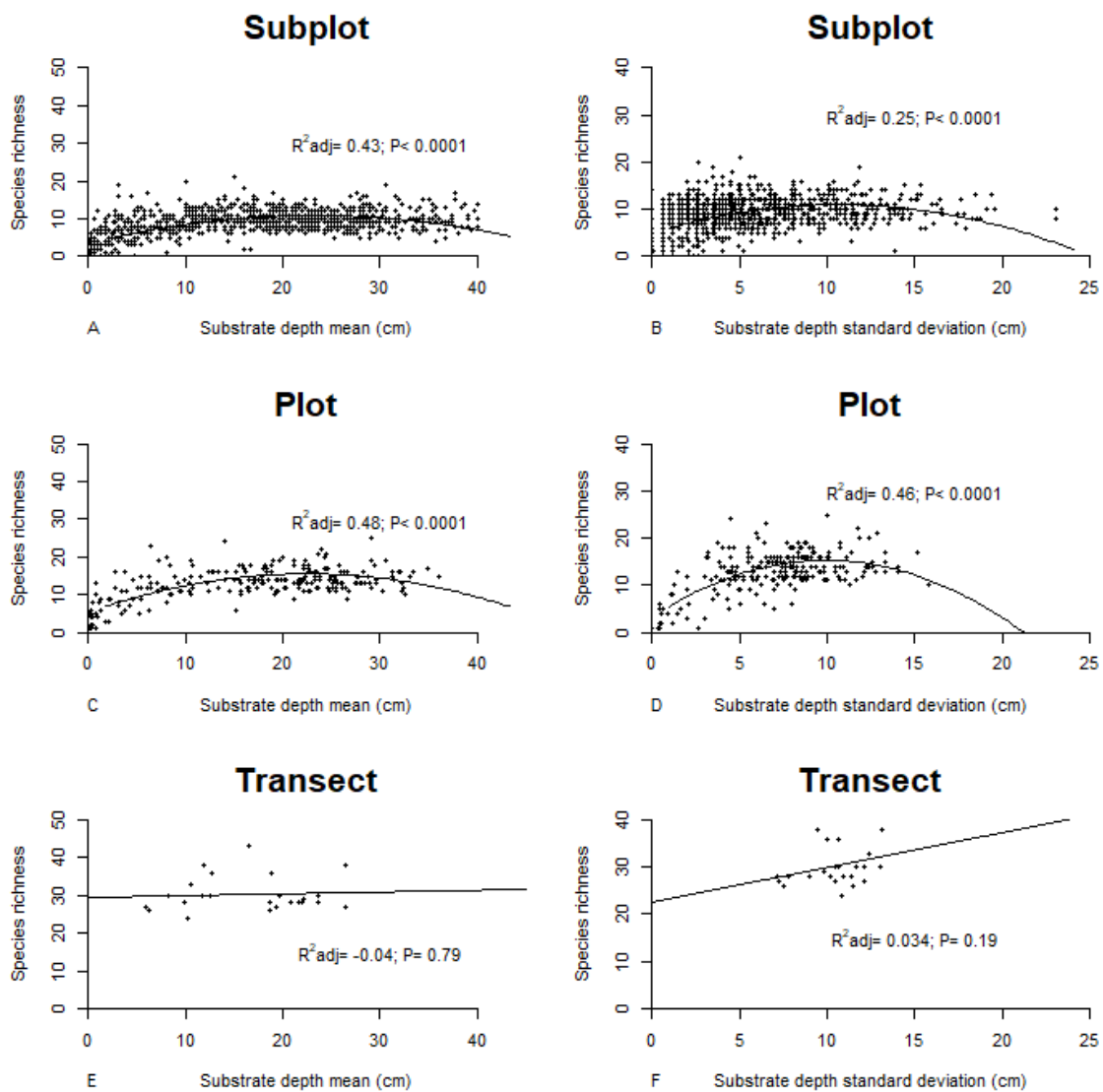

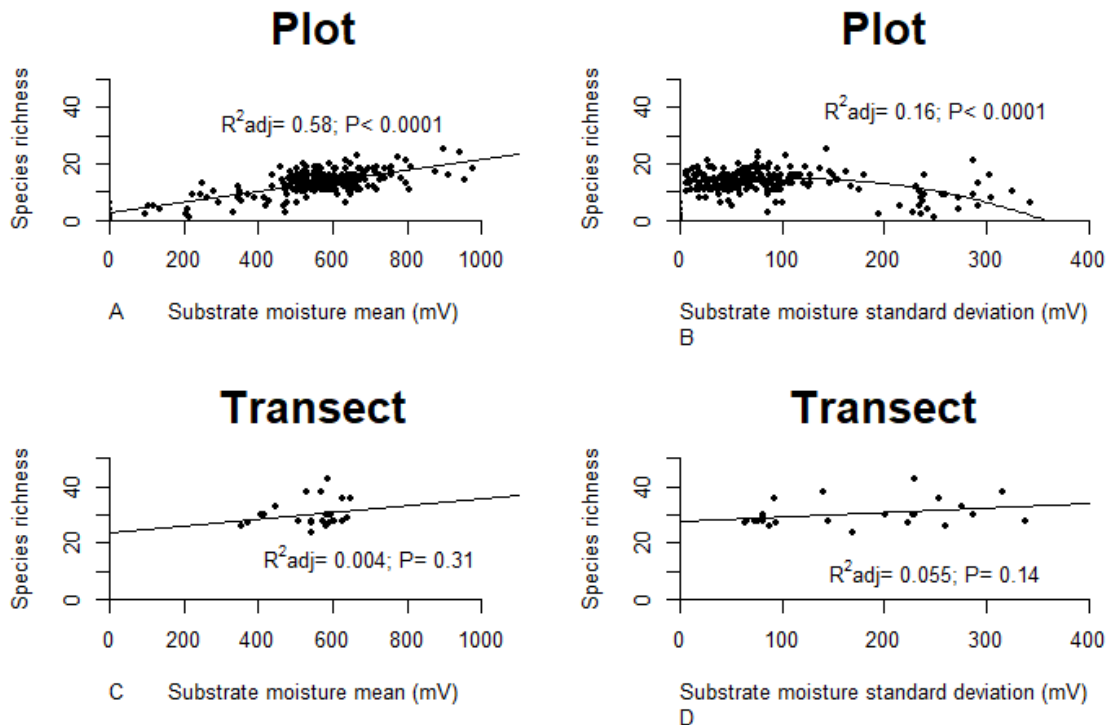**Figure 8.** Average conditions and spatial heterogeneity of substrate moisture (mV) compared to species richness at two scales. Average conditions for plot, and transect scales are A and C, respectively. Spatial heterogeneity for plot, and transect scales are B and D, respectively. Lines of best fit are represented by linear or quadratic univariate regressions of untransformed variables to maximize R^2-adjusted.

For topographic elevation, the variance in species richness at all sample areas could be better explained using a quadratic model rather than a linear model (Figure 9). Transforming the data only improved the fit for the subplot and plot scales of average conditions (topographic elevation $^{4.025}$ and richness $^{1.35}$; $0.18 \rightarrow 0.23$, and topographic elevation $^{4.15}$ and richness $^{1.525}$; $0.18 \rightarrow 0.24$, respectively) and for the transect scale of spatial heterogeneity (log (topographic elevation) and richness $^{-3.425}$; $0.16 \rightarrow 0.19$). Heterogeneity-richness relationships were strongest at the plot scale for average conditions where 24 % of the variance was explained and they were strongest at the transect scale for spatial heterogeneity where 19 % of the variance was explained. Only the regression at the plot scale for spatial heterogeneity was not significant (p-value > 0.05).
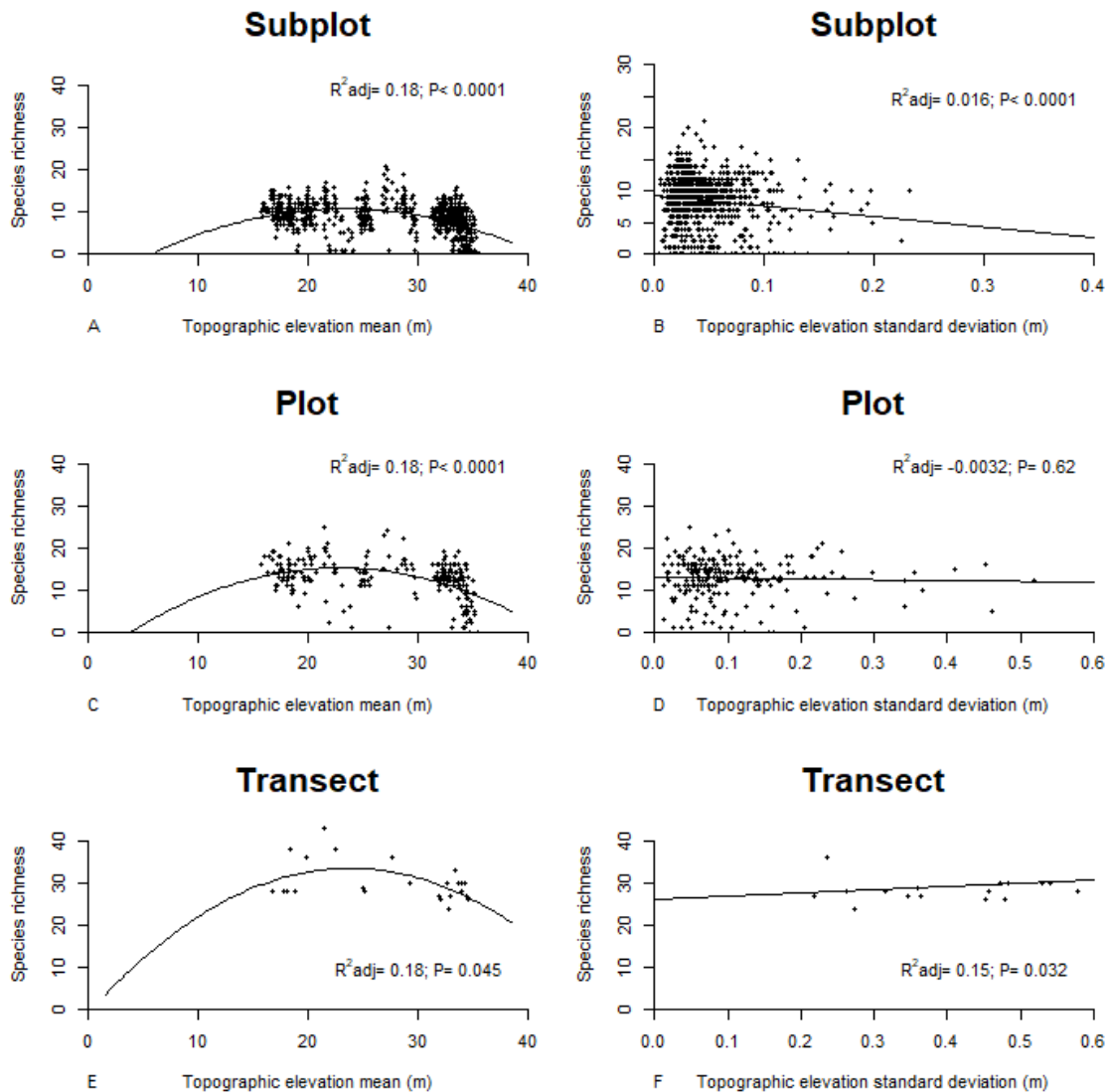
Figure 9. Average conditions and spatial heterogeneity of topographic elevation (m) compared to species richness at three scales. Average conditions for subplot, plot, and transect scales are A, C, and E, respectively. Spatial heterogeneity for subplot, plot, and transect scales are B, D, and F, respectively. Lines of best fit are represented by linear or quadratic univariate regressions of untransformed variables to maximize R^2-adjusted.

For the diversity index of the percent cover variables, all variances were better explained using a linear model as opposed to a quadratic model (Figure 10). Transforming the data did not improve the fit for any scale. Heterogeneity-richness relationships were all weak but the strongest was at the subplot scale where 2 % of the variance could be explained. The regressions at the plot and transect scales were not significant (p-value > 0.05).

Subplot

A

Plot

B

Transect
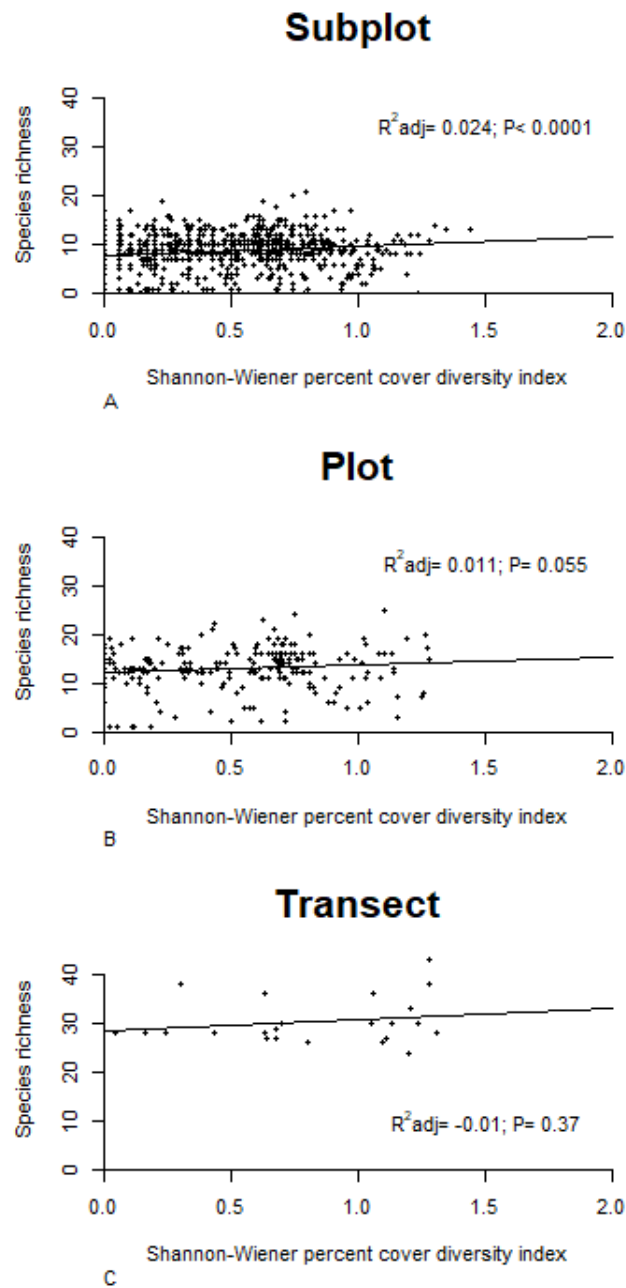

C

Figure 10. Shannon-Wiener diversity index of 6 percent cover variables compared to species richness at subplot (A), plot (B), and transect (C) scales. Cover variables include leaf litter, rock, exposed soil, fruticose, sphagnum moss, and other moss. Lines of best fit are represented by linear or quadratic univariate regressions of untransformed variables to maximize R^2-adjusted.

Multivariate regressions were performed at each scale to assess the effect of each environmental factor while taking the other variables into consideration. A summary of the results can be seen in Table 4 for average conditions, and in Table 5 for spatial heterogeneity. Environmental factors were transformed at the subplot and transect scales, but not for the plot scale. Both transect and plot scales used gaussian models and subplot used a Poisson model. Transect and plot models were linear models with fixed effects only; subplot models were mixed models, taking into consideration the nested effects of location, transect number, and plot number.

The main predictors at the subplot scale were average substrate depth (0.36 and -0.25), average topographic elevation (-0.04), and spatial heterogeneity of percent cover variables (0.02) as these variables had 95 % confidence intervals that did not overlap zero. Average substrate depth had the largest coefficient of these variables. A quadratic model fit average substrate depth better, and thus two coefficients were derived. Not enough data were collected for substrate moisture; therefore, it was not possible to assess its relationship with species richness at the subplot scale.

The main predictors at the plot scale were average substrate depth (0.18), average substrate moisture (0.56), average topographic elevation (-0.20), spatial heterogeneity of topographic elevation (0.10) and spatial heterogeneity of percent cover variables (0.16) as these variables had 95 % confidence intervals that did not overlap zero.

The main predictors at the transect scale were average substrate depth (0.32), average topographic elevation (-0.41), and spatial heterogeneity of substrate moisture (0.63). Spatial heterogeneity of substrate moisture had the largest coefficient.

Table 4. Summary table of multivariate regressions of the average conditions of substrate depth, substrate moisture, and topographic elevation. Data was transformed for subplot and transect scales. Multivariate analyses display the coefficients (Coef.) of the regression output, as well as the 95% confidence intervals shown as the lower (Conf int lower) and upper (Conf int upper) bounds for each scale. Coefficients in **bold** represent values where their 95% confidence intervals do not overlap zero. Substrate depth at the subplot scale fit the model better as a quadratic and both values are shown.

Environmental Factors	Subplot			Plot			Transect		
	Conf int lower	Coef	Conf int upper	Conf int lower	Coef	Conf int upper	Conf int lower	Coef	Conf int upper
Substrate depth (Mean)	0.33 0.28	**0.36x** **-0.25x²**	0.39 0.22	0.08	**0.18**	0.29	-1.11	**0.32**	-0.08
Substrate moisture (Mean)	N/A	N/A	N/A	0.45	**0.56**	0.66	-0.72	0.079	0.11
Topographic elevation (Mean)	0.04	**-0.02**	0.01	-0.28	**-0.20**	-0.13	0.14	**-0.41**	0.90

Table 5. Summary table of multivariate linear regressions of the spatial heterogeneity of substrate depth, substrate moisture, topographic elevation, and percent cover variables. Data was transformed for subplot and transect scales. Multivariate analyses display the coefficients (Coef.) of the regression output, as well as the 95% confidence intervals shown as the lower (Conf int lower) and upper (Conf int upper) bounds for each scale. Coefficients in **bold** represent values where their confidence intervals do not overlap zero.

Environmental Factors	Subplot			Plot			Transect		
	Conf int lower	Coef.	Conf int upper	Conf int lower	Coef	Conf int upper	Conf int lower	Coef.	Conf int upper
Substrate depth (SD)	-0.01	-0.002	0.002	-0.01	0.05	0.18	-0.58	0.07	0.09
Substrate moisture (SD)	N/A	N/A	N/A	-0.10	-0.01	0.04	-1.33	**0.63**	-0.19
Topographic elevation (SD)	-0.01	-0.001	0.003	0.04	**0.10**	0.17	-0.68	0.09	0.10
Percent cover variables (H')	0.02	**0.02**	0.03	0.07	**0.16**	0.24	-1.07	0.04	0.63

4 Discussion

4.1 Species richness and scale

A large range of variability in species richness was captured at the transect scale. As some transects had more species than others, it offered the opportunity to study the effects of variation in environmental factors across more homogeneous transects and more heterogeneous ones. At the plot scale, some areas were completely covered by rock and no plants were present and so, species richness was zero in these plots and nested subplots. The average number of species at each scale were significantly different from each other (Kruskal-Wallis analysis) such that the number of species found increased with sample area (Figure 3). This trend was congruent with the species-area relationship (Arrhenius, 1921): the number of species found increases with the size of the area being sampled.

4.2 Environmental factors and scale

Spatial heterogeneity of all 4 variables: substrate depth, topographic elevation, substrate moisture, and percent cover variables showed a significance increase in variability (SD and H') with increasing sample area. Transects displayed the most variability and subplots displayed the least (Figure 4). As the sample area increased, there is more room available for variation within the environment to occur.

When comparing the difference in average conditions at different sample areas, all conditions were about identical for each environmental factor for every scale. As all data was sampled at the subplot scale and then compiled from those values, average

conditions at the plot and transect were directly derived from the subplot dataset, thus all values would be the same. Slight differences were the product of significant digits and rounding. Differences in average conditions among the different sampling scales were not expected, however, these were reported to contrast with the heterogeneity results which clearly show that larger sampled areas contain greater amounts of environmental heterogeneity in all variables measured.

Therefore, as the average conditions do not change with larger sample areas, it can be said that larger sample areas can include more spatial heterogeneity, or a wider range of environmental conditions, which can lead to an increase in species richness. Smaller scales only have room for a narrow range of environmental conditions and thus can only support a limited number of species on the smaller sample area.

4.3 North-South versus East-West transects

No significant differences were found between transects oriented North-South and those oriented East-West for average conditions (Figure 5) and for spatial heterogeneity (Figure 6). While rocky ridgetops appear to be oriented North to South from our drone imagery (Figure 1), the surrounding side and troughs also contain some environmental variation. Some transects that were initially set up following compass-North did not exactly align with ridgetops or troughs. The result was some transects that sloped from a ridgetop to a trough, thus capturing a range of variability akin to transects oriented East-West that cut across these features. Nonetheless, we were able to produce a dataset of plant species variability where the maximum richness was 43 and the minimum was 24.

Therefore, despite no differences in transect orientation, a wide enough range of variability was obtained to be able to compare more homogeneous transects with more heterogeneous ones.

4.4 Environmental factors, plant species richness, and spatial scale

Across the three scales, we can observe an increase in spatial heterogeneity with increasing sample area (Figure 4) as well as a general trend towards an increase in the strength of the relationship between the environmental factors and species richness with increasing sample area. Average substrate depth, average topographic elevation and spatial heterogeneity of substrate moisture all showed increases in their predictive ability of species richness with increasing sample area. As the area increases, there is more room for environmental variation as well as more room to hold more plant species. In such a way, environmental heterogeneity can be considered part of the underlying mechanism for the species-area relationship.

While average conditions do not change with increasing spatial scale, spatial heterogeneity significantly increased. Spatial heterogeneity can help to reduce the amount of niche overlap and thus promote species coexistence which would allow for increased species richness (Adler et. al., 2013). Thus, environmental heterogeneity increases the range of environmental conditions which, in turn, increases with sample area. This range of conditions allows for a range of species with different environmental specializations to inhabit a given area and increase the diversity of that region.

4.4.1 Strongest environmental predictors of species richness vary with scale

Both univariate and multivariate regressions show that average substrate depth is a strong predictor of subplot species richness while average topographic elevation and spatial heterogeneity of percent cover variables were quite weak. Substrate is an important factor when considering the types of plant species that can survive in a given area. Larger volumes of soil have been shown to have a positive effect on plant diversity (Von Felton & Schmid, 2008) where there is more room for larger root networks that can intake more nutrients.

Additionally, average substrate depth fit better using a quadratic function at the subplot scale such that the relationship between depth and richness was unimodal. This suggests that the highest species richness was found at intermediate substrate depths, when the other factors were included in the model. Other research has shown this same relationship, known as the humpback species richness-curve (Graham & Duda, 2011), with numerous ecological processes including, but not limited to: elevation (Rahbek, 1995; Bruun et. al., 2006), disturbance (Roxburgh et. al., 2004), and biomass (Belcher et. al., 1992; Mathur & Sundaramoorthy, 2016). While biomass been observed to have a curvilinear relationship with plant species richness, soil depth is often strongly linearly related to biomass (Belcher et. al., 1992). As biomass was not considered in this study, it is possible that this unimodal distribution is reflected in average substrate depth. Further studies would be needed to determine if there is a relationship between biomass and substrate depth and plant species richness on coastal barrens.

Average substrate moisture was the strongest predictor of species richness at the plot scale in both univariate and multiple regression analyses and is an important determining factor of species richness (D'Odorico et. al. 2007). Wetter areas can facilitate seedling establishment (D'Odorico et. al., 2007), increase ecosystem productivity (Lu et. al., 2014), and can affect transpiration rates (Tromp-van Meerveld & McDonnell, 2006). Wetter areas also tend to encompass more bog species such as the pitcher plant, *Sarracenia purpurea*, and the bog aster, *Oclemena nemoralis*. Bogs contain a very different community assemblage of species with a large species pool when compared to barrens habitats (Porter, 2013). Thus, this might also contribute to a large species abundance in areas with increased substrate moisture.

Spatial heterogeneity of substrate moisture was the strongest predictor of species richness at the transect scale. While Oberndorfer and Lundholm (2009) found no strong correlation between mean substrate moisture and substrate moisture variability with species richness at a 1 m x 1 m sample area on coastal barrens in Nova Scotia, which is consistent with our findings at that size, spatial heterogeneity of substrate moisture was very significant as a predictor of plant species richness at the 25 m x 2 m transect scale. Substrate moisture is largely affected by substrate depth (Tromp-van Meerveld & McDonnell, 2006) and topographic elevation (Roland & Schmidt, 2015) which are also important drivers at larger sample areas.

4.4.2 Scale of substrate depth: average conditions and spatial heterogeneity

Average substrate depth had significant results at each scale, but spatial heterogeneity of substrate depth was not significant (Tables 5 & 6). More substrate depth can likely support a wider range of species. Some plant species can partition the substrate such that some species utilize the upper regions of the substrate while others can penetrate deeper into the substrate when needed to reduce competition and increase species coexistence (Kulmatiski & Beard, 2013). In this way, species that are found in shallower substrate can also be found in areas where there is more soil. A study by Dornbush & Wisley (2010) found that, in tallgrass prairies, species in shallower soils were strongly nested in deeper soils. Further analysis can be conducted to see whether the species that are found in shallower substrates are also found in deeper substrates on coastal barrens. This would be one possibility that explains why average substrate depth was significant whereas spatial heterogeneity of substrate depth was not.

4.4.3 Scale strengthens average topographic elevation-richness relationship

Topographic features generally require larger sample areas before the relationship with species becomes important and this is apparent as the multivariate regression coefficient of average topographic elevation increases from -0.02 at the subplot scale to -0.20 at the plot scale to -0.41 at the transect scale. Average topographic elevation was inversely correlated (ie. had a negative coefficient value) to species richness such that, as the altitude becomes higher, less species were present. This relationship has been noted across many studies (Rahbek, 1995) although others have also reported unimodal, or humpback, relationships (Bruun et. al., 2006; Roland & Schmidt, 2015) as seen in

average substrate depth at the subplot scale of this study. At the subplot scale, the minimum elevation found was 15.7 m and the maximum was 35.7 m, capturing only a 20 m range in elevation overall, which may account for the absence of any unimodal relationship as the range of data is not large enough. Generally, higher elevations at the study site tended to be rocky ridgetops where there would likely have had more exposed rock making it difficult for plants roots to grow on limited substrate.

Very little variation in topographic elevation was found within subplots (0.5 m x 0.5 m; Figure 4). More space is likely required to produce a larger effect on species richness as the terrain is more likely to vary at larger distances. It is unusual for topography to change drastically in a such a small area. The range of the variation in elevation at the subplot scale was from 0.04 m in the flattest subplot to a maximum 0.23 m in one subplot. To compare, at the transect scale the range of variation in elevation was from 0.22 m to 1.16 m.

4.4.3 The combined effect of substrate moisture and substrate depth

Substrate moisture was not accounted for at the subplot scale as only one sample was taken, which is not enough to produce a mean or standard deviation. It is possible that the unaccounted effects of substrate moisture might alter the other values obtained in the multivariate regression. For example, soil dries at different rates at different depths (Kurc & Small, 2007) which can lead to a faster depletion of water in shallower soils (Tromp-van Meerveld & McDonnell, 2006). Therefore, substrate moisture would be inherently linked with substrate depth.

The effect of average substrate depth was not as strong at the plot scale when compared to the subplot scale within the multivariate regression. This may have been a product of a relationship between average substrate depth and average substrate moisture. As substrate depth becomes larger (i.e. deeper), the volume of substrate would increase accordingly, thus increasing the substrate's capacity to retain water within the pore spaces. Substrate volume can be an important indices of species diversity (Von Felton & Schmid, 2008). Average substrate depth might appear to have a stronger relationship with richness in the subplot scale because there is no measure of soil moisture in the model. Further data collection would be needed to assess whether average substrate moisture would influence the subplot analyses.

4.4.4 Percent cover variables only significant at smaller scales

By using the Shannon-Weiner diversity index as a measure of spatial heterogeneity of percent cover variables, the average conditions were not derived. Spatial heterogeneity of percent cover variables was significant as a predictor of richness at the subplot and plot scales where multivariate regression coefficient increased from 0.02 at the subplot scale to 0.16 at the plot scale, but not for transect richness. The lack of significance at the transect scale may be the result of most cover types being present for each transect (19 out of 25 transects had 5 or more cover types present of 6 cover types in total). With all or most of the 6 cover types being present, each transect would become more or less equally variable in cover types. Any subsequent increase in species richness would be attributed to another environmental factor, such as substrate moisture.

5 Conclusion

This study is one of the first to assess environmental heterogeneity and plant species richness on a multi-scalar level in coastal barrens. Overall, while some studies do not predict strong relationships of species diversity and spatial heterogeneity with increasing spatial scale (Lundholm, 2009), this study suggests that there are some heterogeneity drivers of species richness in coastal barrens habitats, namely substrate depth, topographic elevation, and substrate moisture. There is a general trend towards an increase in the strength of the relationship between environmental heterogeneity and plant species richness with increasing sample area. Spatial heterogeneity can influence species coexistence and increase the number of niche types in a given area (Chesson, 2000; Adler et. al., 2013) thus promoting species richness. The visibly varied terrain of the study site, Chebucto Head, Nova Scotia, made it an ideal location to study the effects of heterogeneity on plant species richness at a manageable scale.

Understanding how environmental factors help to organize plant communities is important and even more so that these interactions may not always be detectable at a single scale of study. For example, while Oberndorfer and Lundholm (2009) found no correlation of substrate moisture variability and species richness at a 1 m^2 sample area, which is consistent with our findings, spatial heterogeneity of substrate moisture was strongly correlated with species richness at the 25 m x 2 m transect scale. This highlights the need to consider spatial scale in future studies in coastal barrens and other habitat types as well. The scale of observation needs to be taken into consideration when undergoing any ecological survey.

Literature Cited

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*(10), 1294–1306. https://doi.org/10.1111/ele.12157

Anderson, T. M., Metzger, K. L., & Mcnaughton, S. J. (2007). Multi-scale analysis of plant species richness in Serengeti grasslands. *Journal of Biogeography*, *34*, 313–323. https://doi.org/10.1111/j.1365-2699.2006.01598.x

Arrhenius, O. (1921). Species and area. *Journal of Ecology*. 9, 95–99.

Balsdon, J. L., Smith, T. W., & Lundholm, J. T. (2011). Phenotypic and genotypic differentiation of *Vaccinium vitis-idaea* between coastal barrens and forests in Nova Scotia, Canada. *Botany*, *89*(3), 147–155. https://doi.org/10.1139/b11-003

Bartoń, K. (2018). MuMIn: Multi-Model Inference [PDF file]. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bergholz, K., May, F., Giladi, I., Ristow, M., Ziv, Y., & Jeltsch, F. (2017). Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics*, *24*, 138–146. https://doi.org/10.1016/j.ppees.2017.01.001

Belcher, J. W., Keddy, P. A., & Catling, P. M. (1992). Alvar vegetation in Canada: a multivariate description at two scales. *Canadian Journal of Botany*, *70*(6), 1279–1291.

Bruun, H. H., Moen, J., Virtanen, R., Grytnes, J.-A., Oksanen, L., & Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, *17*(1), 37–46. https://doi.org/10.1111/j.1654-1103.2006.tb02421.x

Buckland-Nicks, M. (2017). Mapping landscape structure and plant communities of the coastal barrens using unmanned aerial vehicles. (Master's thesis). Saint Mary's University. Halifax, Nova Scotia.

Burnham, K. P.; Anderson, D. R.; Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and

comparisons. *Behav. Ecol. Sociobiol., 65,* 23-35.

Chase, J. M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science*, *25*(2), 319–322. https://doi.org/10.1111/jvs.12159

Chesson, P. (2000). General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theoretical Population Biology*, *58*, 211–237.

Chesson, P., & Huntly, N. (1997). The Roles of Harsh and Fluctuating Conditions in the Dynamics of Ecological Communities. *Source: The American Naturalist*, *150*(5), 519–553. https://doi.org/10.1086/286080

D'Odorico, P., Caylor, K., Okin, G. S., & Scanlon, T. M. (2007). On soil moisture-vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *Journal of Geophysical Research*, *112*(4), 1–10. https://doi.org/10.1029/2006JG000379

Dufour, A., Gadallah, F., Wagner, H. H., Guisan, A., & Buttler, A. (2006). Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. *Ecography*, *29*, 573–584.

Evju., A. & Sverdrup-Thygeson, M. (2016). Spatial configuration matters: a test of the habitat amount hypothesis for plants in calcareous grasslands. *Landscape Ecology*, *31*, 1891–1902. https://doi.org/10.1007/s10980-016-0405-7

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, *40*, 1649–1663. https://doi.org/10.1111/jbi.12130

Graham, J. H., & Duda, J. J. (2011). The humpbacked species richness-curve: A contingent rule for community ecology. *International Journal of Ecology*, *2011*, 1–15. https://doi.org/10.1155/2011/868426

Hewitt, J. E., Thrush, S. F., & Ellingsen, K. E. (2016). The role of time and species identities in spatial patterns of species richness and conservation. *Conservation Biology*, *30*(5), 1080–1088. https://doi.org/10.1111/cobi.12716

Jackson, H. B., & Fahrig, L. (2014). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, *24*, 52–63. https://doi.org/10.1111/geb.12233

Kulmatiski, A., & Beard, K. H. (2013). Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Source: Oecologia*, *171*(1), 25–37.

Kurc, S. A., & Small, E. E. (2007). Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*, *43*(6), 1–13. https://doi.org/10.1029/2006WR005011

Lu, N., Fu, B., Jin, T., & Chang, R. (2014). Trade-off analyses of multiple ecosystem services by plantations along a precipitation gradient across Loess Plateau landscapes. *Landscape Ecology*, *29*, 1697–1708. https://doi.org/10.1007/s10980-014-0101-4

Lundholm, J. T. (2009). Plant Species Diversity and Environmental Heterogeneity: Spatial Scale and Competing Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. *Journal of Vegetation Science Journal of Vegetation Science*, *20*(20), 377–391.

Mathur, M., & Sundaramoorthy, S. (2016). Patterns of herbaceous species richness and productivity along gradients of soil moisture and nutrients in the Indian Thar Desert. *Journal of Arid Environments*, *125*, 80–87. https://doi.org/10.1016/j.jaridenv.2015.10.011

Oberndorfer, E. C. (2006). *Plant, macrolichen and moss community structure and species richness in the coastal barrens of Nova Scotia* (Master's thesis). Saint Mary's University, Halifax, Nova Scotia.

Oberndorfer, E. C., & Lundholm, J. T. (2009). Species richness, abundance, rarity and environmental gradients in coastal barren vegetation. *Biodiversity and Conservation*, *18*, 1523–1553. https://doi.org/10.1007/s10531-008-9539-5

Porter, C. (2013). *Classification of Dwarf Heath Plant Communities on the Coastal Barrens of Nova Scotia* (Master's thesis). Saint Mary's University, Halifax, Nova Scotia.

Rahbek, C. (1995). The Elevational Gradient of Species Richness: A Uniform Pattern? *Ecography*, *18*(2), 200–205.

Rayburn, A. P., & Schupp, E. W. (2013). Effects of community-and neighborhood-scale spatial patterns on semi-arid perennial grassland community dynamics. *Oecologia*, *172*, 1137–1145. https://doi.org/10.1007/s00442-012-2567-6

Roland, C. A., & Schmidt, J. H. (2015). A diverse alpine species pool drives a "reversed" plant species richness-elevation relationship in interior Alaska. *Journal of Biogeography*, *42*(4), 738–750. https://doi.org/10.1111/jbi.12446

Roxburgh, S. H., Shea, K., & Wilson, J. B. (2004). The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence. *Ecology*, *85*(2), 359–371. https://doi.org/10.1890/03-0266

Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yé, J. C., Carter, B. E., Glennon, K. L., … Fridley, J. D. (2012). Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data. *Journal of Vegetation Science*, *23*, 942–951. https://doi.org/10.1111/j.1654-1103.2012.01401.x

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology and Evolution*, *19*(11), 605–611. https://doi.org/10.1016/j.tree.2004.09.003

Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats. *Ecology*, *75*(1), 2–16.

Tilman, David & Pacala, S. (1993). The Maintenance of Species Richness in Plant Communities in *Species Diversity in Ecological Communities*. In D. Ricklefs, R. E. & Schluter (Ed.) (pp. 13–25). Chicago: University of Chicago Press.

Von Felten, S., & Schmid, B. (2008). Complementarity among species in horizontal versus vertical rooting space. *Journal of Plant Ecology*, *1*(1), 33–41. https://doi.org/10.1093/jpe/rtm006

Whittaker, R. H. (1972). Evolution and Measurement of Species Diversity. *Taxon*, *213*(2), 213–251.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, NY.