FOREST DIVERSITY ACROSS SPACE AND ENVIRONMENTAL GRADIENTS

VARIATION IN TREE AND SHRUB DIVERSITY ACROSS SPACE, ALONG ENVIRONMENTAL GRADIENTS AND THROUGH TIME IN A TEMPERATE FOREST IN EASTERN NORTH AMERICA

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TITLE: Variation in tree and shrub diversity across space, along environmental gradients and through time in a temperate forest in eastern North America

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ABSTRACT

The variation in community composition among sites is often used to gain insight into the processes of plant community assembly. In this study, we looked for evidence of environmentally and spatially mediated community assembly mechanisms in a temperate forest in eastern North America. To test this, we measured, identified and mapped all woody stems >1 cm in diameter at breast height (DBH) in 12 ha of a 20 ha forest plot. We used principal coordinates of neighbor matrices (PCNM) to obtain variables that modelled spatial processes (eg. dispersal, drift) at the community level. Topographic variables (slope, elevation, convexity, aspect) were used to model environmental conditions. Variation partitioning was used to isolate the unique and shared effects of topographic and spatial variables on community composition. We were also interested in studying how associations with the environment change with tree size. For this we assessed the abundance of a subset of focal species in response to topography as well as human disturbance. Species abundance were divided into three stem size classes: small (< 5 cm), medium (\geq 5 cm and < 15), and big (\geq 15 cm). We found that topography and space jointly explained 63% of the variation in community composition. This variation was almost entirely spatially structured with the component of pure topography only contributing 1% to the total explained variation. A redundancy analysis showed that slope and elevation were the most important topographic variables structuring the distribution of trees. The focal species had largely independent distributions across the environmental gradients and three of the five species showed within-species differences associated with

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size class effects on the relationship with topography and human disturbance. The implications of these results are relevant to conservation efforts and suggest that large contiguous areas of heterogeneous environments are essential in maintaining biodiversity.

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INTRODUCTION

Understanding the mechanisms that shape the diversity, abundance, and distribution of species is the major, longstanding aim of community ecology (Schimper 1903; Whittaker 1956). One body of theory posits that community assembly processes determine the coexistence of species as well as their relative abundance in a local community (Weiher et al. 1995). These assembly processes are broadly classed into space and neutral theories, in which all species are assumed alike (Hubbell 2001), vs. niche theories, in which species do differ ecologically (Chase and Leibold 2003). Many studies have looked at measuring the effects of niche and neutral processes in large tropical forest plots and have found varying degrees of evidence for both (Tilman 2004; Latombe et al. 2015). However, relatively few studies have been done on temperate forests. In this study, we looked for evidence of topography and spatially mediated community assembly mechanisms in a temperate, deciduous forest in eastern North America.

The niche and neutral theories of community assembly

The three mechanisms often used to explain community assembly processes are neutrality, competitive exclusion and abiotic filtering (Swenson et al. 2007). Dispersal is described as the movement of individuals through space and it contributes to the presence or absence of species at a given location. In species with restricted movement of individuals (i.e. most plant communities) referred to as dispersal limitation, a negative relationship between the similarity of species assemblages and the geographic distance between sites is expected (Nekola and White 1999). Hubbell's neutral theory of biodiversity (2001) proposes that all species within a community are functionally equivalent. Neutral theory relies primarily on dispersal limitation and stochastic demographic processes (birth and death) to drive patterns of community structure and diversity. Following neutral theory, abundant and rare species are only so because of random fluctuations in population size (ecological drift) and diversity is maintained through a balance of speciation and extinction in the long term. Hubbell's neutral theory was initially developed to explain complex systems of species rich communities with many rare species like the lowland tropical forests (Hubbell 2001). Data from multiple tropical forest plots show some support for Hubbell's neutral theory, but a recent metaanalysis showed that neutral theory alone cannot account for the variation in community structure and that meaningful differences between species must be incorporated (Brown et al. 2013).

Alternatively, classical niche-based theories incorporate species differences among traits which interact with environmental factors (Gause 1934; reviewed in Chu et al. 2007). Niche theory predicts that sites characterized by similar environments would also host similar communities (Tilman 2004). Within niche theory, the environment can lead to contrasting results for either more similar species with converging traits through an ecological filter, or diverging of species through competition of those with the same traits. Through the evolution of different patterns of resource use (ie. resource partitioning), niche differentiation can maintain species diversity by minimizing interspecific competition (reviewed in Punchi-Manage et al. 2013) as evidenced by the

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superior performance of individuals whose neighbours possess differing trait values (Lasky et al. 2014) When there is niche overlap, the species with superior adaptive abilities in a niche may outperform others resulting in competitive exclusion within a habitat causing a negative association between species with similar traits (Hardin 1960).

Habitat filtering predicts niche clustering where environmental conditions only permit the coexistence of species with similar niches (Baraloto et al. 2012; Keddy 1992) and as a result, co-occurring species are more similar in their trait values. Without measuring traits, it can be difficult to test the extent of habitat filtering and competitive exclusion in a community. However, both of these niche processes result in individuals within a species showing a defined habitat association (ie. species sorting) (Leibold et al. 2004) and are evidence for niche theory (Tuomisto et al. 2003). These two perspectives of niche and neutral theory are contrasting but have also been found to be complementary as both, to some degree, jointly explain the assembly of species in every community and the focus of recent community assembly studies aims to disentangle their relative roles across different forest and climate types.

Tropical CTFS forest plots as a tool to study forest communities

The Smithsonian Center for Tropical Forest Science (CTFS) has devised a censusing method for large forest plots that maps and measures all woody stems at least 1 cm DBH. Previously, most studies were limited to small study plots (<1 ha) of larger individuals (>5 cm DBH) (Gilbert et al. 2010). The first plot, Barro Colorado Island (BCI) in Panama, was established in 1980 and 62 more plots have since been completed (http://www.forestgeo.si.edu). This has created a worldwide network of comparable plots across all forest types. The comprehensive and detailed size and spatial data collected in these plots makes them powerful tools to study community assemblage across spatial scales and environmental conditions. Highly diverse tropical forests provoke the question of how such a large number of species can be maintained (eg. Leigh et al. 2004) and as such have been a particular area of interest for community assembly studies. Tree species often play keystone roles providing habitat, food, or mutualisms with many animals, fungi, micro-organisms, and other plants in addition to other ecosystem services (carbon storage, shade, pollution removal and nutrient cycling) and recreation for human use (Nowak et al. 2006; Jim and Chen 2009; Gamfeldt et al. 2013). Forest trees are long-lived and consequently subject to prolonged exposure to consistent environmental stresses before they reach maturity and can reproduce. Because of their long lifespan, this makes trees ideal study organisms to track community changes with changing environmental conditions over time.

While many researchers have used CTFS studies to look for niche and spatial processes in tropical forests, relatively few have done so in temperate forests. Unlike tropical forests, temperate forests tend to have lower species diversity, richness, abundance and rate of speciation, but higher basal area (the cross-sectional area of stems) (Janzen 1970; Mittelbach et al. 2007; Gilbert et al. 2010). Due to these differences, we may expect different processes to drive community assembly. Furthermore, given the vast biogeographical range of the temperate forest in the northern hemisphere, regional effects may cause the assemblage of communities to differ between eastern Asia and eastern North America. This variation may be attributed to the higher rate of speciation in eastern Asia, regional species pools, local ecological mechanisms and as well as glacial and colonization history (Latham and Ricklefs 1993; Ricklefs et al. 2004; Xiang et al. 2004; Chisholm and Pacala 2011; Myers et al. 2013).

As forests across North America continue to be fragmented and influenced by human activities, the importance of maintaining biodiversity is becoming widely recognized as a priority. The Carolinian forest (the Canadian term for the Eastern deciduous woodlands) is a biome that spans eastern North America beginning at southern Ontario in the northern-most region. Prior to European settlement, southern Ontario was blanketed by a dense cover of deciduous forest. By 1920, large tracts of land had been cleared for agriculture and logging and reduced the natural area to about 6% of the original landscape (Larson 1999; Henry and Quinby 2010). Today, this area is one of the most populous in Canada. Due to urbanization and continued agricultural practices, the original intact habitat has been reduced to less than 5% and is highly fragmented (Falk et al. 2008; McLachlan and Bazely 2003) and this reflects the land use trends across eastern North America (Flinn and Vellend 2005). The area of southern Ontario is home to the most biologically diverse forests in all of Canada as well as some of its most threatened species (Tanentzap et al. 2011), many of which are at the northern limit of their range (FAO 2012). Many of the plant populations in this region are locally adapted to harsher conditions (longer winters, colder average temperatures) than their southern counterparts

(Howe et al. 2003; reviewed in Savolainen et al. 2007; Savolainen et al. 2013). These adaptations can result in northern populations having unique genetic characteristics that help them resist disease, parasites and herbivory (Sork et al. 1993; Linhart and Grant 1996), traits that may become increasingly important for species facing the predicted rising temperatures currently modelled in climate change projects (Deser et al. 2012). Hence, understanding processes of community assembly leads to a better understanding of local biodiversity for forest conservation and management as well as climate change.

Environmental heterogeneity in topography explains plant resource availability

Environmental heterogeneity is a major component to the composition and structuring of ecological communities. The relevant underlying mechanisms that contribute to environmental heterogeneity and affect species occurrence and distribution will depend on spatial scale (reviewed in HilleRisLambers 2012). At a continental scale, climate is the predominant determiner of species occurrence and distribution while at the local scale, disturbance, soil and topographic factors are important and at a finer scale, plant-plant interactions are the most relevant factors (Weiher and Keddy 1995; Kubota 2003). Indeed, many studies have found evidence for environmental factors of topographic and soil gradients explaining species composition and functional traits.

Topography is a detailed description of the surface features of a land area often characterized by elevation, slope, aspect and convexity. Topographical information is collected as part of the CTFS forest censusing method and as a result is often used to describe environmental variation. Many studies have found significant associations

between topography and species composition (Murphy and McCarthy 2012; Brown et al. 2013; Liu et al. 2014; Punchi-Manage et al. 2013). Topography acts as predictor of habitat because it is an indirect measure of soil moisture (Qiu et al. 2001), pH and mineral content (McEwan and Muller 2006) as well as exposure to solar radiation (Larsen and Speckman 2004) which are factors that influence growth and survival of plants. Therefore, forest tree species sensitive to topographically defined habitats would be expected to show preferred habitat types and segregate along topographic gradients. For example, ridge top areas are drier and nutrient-scarce due to the gravitational movement of water as well as increased evaporation from exposure to higher solar radiation and provide a more suitable habitat for drought-tolerant species (Frey et al. 2007). Conversely, valleys with low elevation and concave shape have more moist and nutrientrich soils. Deeper depressions (areas of high concavity), tend to be wetter than planar areas where concavity is low. Similarly, steeper slopes are likely to be drier than flat areas due to lower infiltration rates, rapid subsurface drainage, and higher surface runoff especially during heavy rainfall (reviewed in Famiglietti et al. 1998). Slope angle (aspect) determines the amount of solar radiation received and thus is associated with water stress. In the northern hemisphere, north facing slopes receive less direct sun and are more moist and cooler while south facing slopes receive more sun and are drier and warmer. Along the other aspect gradient, east-facing slopes are typically more sheltered from wind and storm disturbance due to the predominantly westerly direction of prevailings winds (Hiemstra et al. 2006). Since topography is a good analogue of habitat through its

association with essential plant resources, if habitat variation does shape community assemblages then topography is an interesting and important variable to study. However, topography alone cannot capture the complete suite of factors that contribute to a community's assemblage and studies are necessary to determine its relative importance and at what scales topography is shaping and operating on the community.

Variation partitioning of space and environment

The spatial scale of species distributions can give insight into the primary mechanisms shaping communities. Spatial structuring in communities can be generated by plants themselves through mode of dispersal (Seidler and Plotkin 2006), intra- and interspecific competition (Getzin et al. 2006) or through environmental heterogeneity. Dispersal limitation is a neutral process that leads to spatial aggregation (clustering) of species because seeds are constrained to a short dispersal range even in homogeneous environments (Lin et al. 2011; X. Wang et al. 2011). On the other hand, at the fine scale of plant-plant interactions, strong competition between neighbouring plants can lead to a more regular spatial pattern of roughly uniform distance between plants (Laessle 1965). This is the case for negative density-dependence, when mortality rates are higher in localized regions of higher density and cause a decline in population growth due to factors like crowding and competition (Wright 2002). For example, regularly distributed canopy trees may suppress the growth of smaller trees through limiting access to light. These suppressed trees have higher mortality rates than the canopy trees, leading to an increasingly regular spatial pattern of surviving trees (Suzuki et al. 2008). These spatial

processes can cause strong spatial autocorrelation (Dray et al. 2012), where objects closer together show either greater (positive) or less similarity (negative) in their traits than if they were randomly distributed (Legendre 1993). Environmental variables themselves are often spatially autocorrelated (ie. the environmental variables of one site are not independent of neighbouring sites) (Legendre 1993). Therefore, the relationship between environment and species is often confounded by space.

Variation partitioning is a statistical method used to separate the importance of different groups of explanatory variables in explaining a response dataset (Borcard et al. 1992). It can parse out the relative contribution of spatial and environmental factors that determine community composition (Peres-Neto et al. 2006) and has been useful in addressing the roles of niche and neutral theory and exploring different species coexistence mechanisms (Jia et al. 2015; Legendre et al. 2009; Wang et al. 2013). The principal coordinates of neighbour matrices (PCNM) technique creates variables that quantify spatial structure. PCNM eigenfunctions are closely related to Moran's eigenvector maps and represent spatial structuring from broad to fine scales through the relationships between sites in the sampling plot (Borcard and Legendre 2002; Dray et al.2006). Therefore, they can be used to discern the underlying mechanisms that shape the distribution of forest trees from the patterns in their scale-specific distributions (Lin et al. 2010; Velazquez et al. 2015). The variation partitioning method allows partitioning of the variation in community structure as either a) purely from environmental variables b) spatially structured environment c) purely spatial and d) undetermined (Legendre et al.

2009). Variation in the community explained from the environment-related fractions (a) and (b) can be attributed to niche processes (Laliberte et al. 2009). However, evidence for neutral processes is less clear, as the purely spatial portion (c) may be composed of unmeasured spatially structured environmental variables and other unobserved spatially structured processes of community dynamics. Dispersal limitation falls under this purely spatial portion but can only be purely neutral if all species show similar patterns in effective dispersal distances, and other biological processes that can generate spatial structures independent of habitat (Legendre et al. 2009). The remaining unexplained variation (d) can be caused by stochasticity in birth, death and dispersal or by non-spatially structured biological or environmental factors (Legendre et al. 2009)

Spatial distribution and environmental requirements depend on tree size

Resource availability, selective pressures, temperature tolerance (Parish and Bazzaz 1985), and physiological requirements change throughout an individual's life time (Werner and Gilliam 1984). Tree species distributions have been seen to vary among size classes in temperate (Schurman and Baltzer 2012; Spasojevic et al. 2014), subtropical (Lai et al. 2009) and tropical forests (Kanagaraj et al. 2011) in response to environmental heterogeneity. Due to the longevity of trees, long term studies are difficult and expensive to perform, so a snapshot of forest trees at one point in time is often used to infer temporal variation through the comparison of size classes. Since plants cannot actively seek environmental conditions that improve their survivorship they must adapt by adjusting their traits or resource use across life stages in order to meet these requirements. For example, under a dense forest canopy, light is a limiting resource for saplings, however this stress is gradually relieved as they grow larger in the adult stage due to both increase in stem height and leaf area (Valladares and Niinemets 2008; Comita et al. 2007). However, in many cases it remains unclear if responses to the environment in the early life stages would be maintained through later stages even if these traits become disadvantageous (Arieira et al. 2016) or alternatively, if traits expressed in early stages are adapted for the adult stage (eg. Thomas and Bazzaz 1999). Ultimately, where there are trade-offs between advantageous traits that differ between life stages this affect the distribution and proportion of plants that reach reproductive age (Arieria et al. 2016).

Intraspecific changes across size class distribution patterns can be used to infer the dominant mechanism driving community assembly and the stage at which it is strongest (Cheng et al. 2014). The stochasticity involved in the early life stages such as light availability through the death of a canopy tree (ie. gap formation) and dispersal suggests seedlings are likely to show the greatest variation in habitat associations (Kanagaraj et al.2011; Brown et al.2013). In a community predominantly shaped by habitat filtering, the effect of this filter may strengthen with time, causing differential mortality for individuals without the necessary traits to tolerate the environment. Therefore, adults of a species should show narrower habitat associations since their existence is less a result of stochastic events and more representative of the species' environmental niche preferences (Tsujino and Yumoto 2007; Brown et al. 2013). Alternatively, if the filter acts only on the germination or seedling stage, species would show a consistent habitat through their

lifetime where seedlings only succeed where their parents are. Distinguishing the habitat associations of specific stages can be obscured by limited dispersal since seeds fall close to parents causing the bulk of offspring to be in the parents' preferred habitat. Seedlings may even experience high mortality in their parents' habitat but this is masked by their high density causing seedlings' habitat preference to appear the same as their parents. Therefore, the influence on distribution from seed dispersal may confound apparent associations with habitat in smaller individuals (Webb and Peart 2000). The species' method of dispersal may influence the spatial distribution especially at its seedling stage. Even with limited dispersal, seeds can be distributed across a wide range of environmental variables, even beyond that of their parent tree. Species with primarily gravity-dispersed seed will typically stay within a small range of the parent tree and show a clumped distribution while seeds from wind and bird dispersed species are able to travel more widely (Seidler and Plotkin 2006) into various habitats.

Alternatively, interactions between individuals within size classes affect the spatial patterns of species and can be an indirect cause of apparent habitat associations. Typically, there is a shift from clumped towards uniformity as individuals increase in size as a result of higher mortality in higher density areas (Kenkel 1988; Getzin et al. 2006). If negative density dependence from competition or pest pressure is the primary cause of tree mortality, then the degree of habitat structuring would be expected to decrease with size class (Baldeck et al. 2013a). Large trees in the canopy physically require a certain area that allows minimal overlap with other large trees. They compete most with those in

their cohort for access to light leading to a regular pattern where they are nearly equally spaced in the canopy (Perry et al. 2009). This would result in large trees under a variety of habitats since environmental heterogeneity increases with distance (Bell et al. 1993). Ultimately, examining species without separating by size class may obscure the degree of habitat-associated signaling and is essential for understanding the spatial and temporal dynamics of populations (Li et al. 2008).

Outline of this study

In this study we compare the relative contribution of environmental and spatial factors in determining the distribution patterns of forest tree species as well as how species-habitat associations change across size classes in a temperate forest plot. Following the CTFS forest census protocol, we measured, identified, tagged and mapped every living woody stem ≥ 1 cm DBH in 12 ha of a northern Carolinian forest plot. To identify the strength of niche-based processes of community assembly we compared species abundances and distribution across several topographic gradients using redundancy analysis. To quantify the contribution of spatial structuring on the community, a redundancy analysis with PCNMs was performed. Additionally, we performed separate analyses of habitat for six focal tree species and then partitioned these species into size classes for a cross-sectional approach to examine the habitat associations relevant to each size class. We asked 1) To what extent does topography explain the variation in community composition? 2) How much of the variation in community composition? 3) What are the relative

contributions of topography and space in structuring the community? 4) What are the topography and human disturbance-mediated habitat associations of focal species and how do they change with size? This study contributes to understanding the spatial organization of forest trees at multiple scales and the role played by habitat heterogeneity that shapes temperate forest communities in highly urbanized areas and how future changes in forests will affect the diversity and composition of communities.

METHODS AND MATERIALS

Study site characteristics, location and history

The area studied is McMaster Forest (MF), a 48 hectare natural area in Hamilton, Ontario, Canada (43°25'W, -79°95'N). It is located near the northern edge of the Carolinian forest which spans eastern North America. The local climate is humidcontinental with annual temperatures ranging from a daily mean of -4.7°C in January to 22.0°C in July and an annual precipitation of 897 mm equally distributed throughout the year. MF is situated between two large protected natural areas, the Dundas Valley and Cootes Paradise, which are connected by Ancaster Creek. MF has a history of human disturbance with farming (Figure 1) up until the 1960s in parts of the site, which ceased after the land was purchased by McMaster University in 1964. These fields were left abandoned without maintenance or restoration work and have naturally regenerated to their current state. Consequently, areas of many different ecological land classifications and different ages exist across the site. MF is also surrounded by a densely populated urban area that is continuously growing and supports an overabundance of white-tailed deer (.35 deer/hectare; 3x the carrying capacity) in the adjacent Dundas Valley (HCA presentation 2011 (data from 2009)).

A 20 hectare permanent forest plot (500 m x 400 m) within MF was surveyed from 2013-2014. The procedure follows the methodology detailed in Condit (1998) for CTFS plots. Permanent stakes (EcoStakes, Berntsen, Madison WI) were placed at precisely every 20 m along N/S and E/W gridlines and labeled with their grid coordinates. The relative elevation and distance between stakes was calculated using a theolodite (Leica PinPoint r100). All distances were slope corrected. Stakes were mapped relative to a city fire hydrant of known elevation and coordinates 500 m south of the forest plot.

One source of disturbance in the plot was through a history of agricultural use. Using aerial photographs from 1943, 175 censused quadrats were classified as forest, 35 as edge and 93 as farmed land. Most of the farmed quadrats were towards the south side of the plot and had low slope and high elevation. The edge habitat was a narrow buffer of quadrats that had both farmed and unfarmed habitat. Additionally, the creek running through the plot provides a natural form of disturbance in the floodplain. This area was characterised by low elevation and flat topography.

Plant sampling

Plant censusing began May 2014 and continued through to August 2015 by teams of 4-6 people. Quadrats (20 x 20 m) were censused one at a time, sequentially working through adjacent quadrats. First, temporary ropes were set up along the perimeter, connecting each of the 4 corner stakes of the quadrat. Next, the sides of each quadrat were measured and temporarily staked at 5 m intervals. Ropes were attached between these 5 m points to create a grid of 16 square subquadrats (each 5 x 5 m) within the 20 m² quadrat. Poles (1.5 m long) marked with 5 cm increments were used to map tree coordinates relative to the surrounding ropes. Mapping measurements were taken from the centre of the base of the tree and rounded to the nearest 5 cm. All living woody stems greater than 1 cm in diameter at breast height (DBH), defined as 130 cm from the base,

were included in the census. Trees were marked at the point of measurement (POM) 130 cm from the ground at which diameter was measured. For trees growing on slopes, this measurement was taken from the ground on the uphill side. For leaning trees, the measurement was taken from the upward-facing side of the tree. For trees with branches or irregularities that impeded measurement at that location, an alternate POM would be used instead. A nearby height on the stem that would give a regular measurement, typically \pm 5 or 10 cm from the initial POM, was used instead. Stems greater than 4 cm in diameter were measured with diameter tape while stems less than 4 cm were measured with electronic calipers. For oval stems, the largest diameter measurement at POM was recorded. A stripe was painted over the POM so it could be accurately remeasured in future censuses. All individuals received an aluminum main stem tag stamped with a unique ID number that was either nailed above POM (trees > 10cm DBH) or attached with zipties or stretchy plant ties (trees <10 cm) near POM. For trees with multiple stems greater than 1 cm at POM, the largest stem was tagged with a main stem tag as well as a 0 tag. Subsequent stems were marked with metal tags labelled 1, 2, 3... etc. When possible, a 7-character species code containing the first four characters of the genus and three characters of the species name were recorded. For trees that could not be identified to species, the lowest taxonomic level recognized was recorded. For healthy specimens of unknown species, samples were taken of live plant material which were pressed and stored in the lab. Descriptive notes were recorded for trees that were leaning greater than 40 degrees, prostrate, bending or had other irregularities. As of September 2015,

censusing has been completed for 303 of the 500 quadrats (60.6%), covering 12.12 hectares. Censused quadrats were roughly selected to exclude areas of newer growth to maximize undisturbed sampling sites. All field data were entered independently into two separate digital data sheets and compared to minimize errors.

Data analysis

An elevation map of the site was made in ArcGIS using the elevation data of the permanent stakes. Mean elevation and slope for each quadrat were computed with the R package "CTFS" (Condit 2012). Mean elevation was computed as the average of the 4 corner stakes. Slope was calculated as the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners (Harms et al. 2001). Convexity and aspect were derived using the ArcGIS Spatial Analyst Tools "curvature" and "aspect", respectively. Convexity was calculated as a function of the focal quadrat's slope relative to the slopes of all the immediately adjacent quadrats (8 for centre quadrats). Positive values indicate convex surfaces (eg. hill top), whereas negative values indicate concave surfaces (eg. valley). Reasonably expected values for a hilly area (moderate relief) can vary from -0.5 to 0.5; while for steep, rugged mountains (extreme relief), the values can vary between -4 and 4 (http://pro.arcgis.com). Aspect is a circular variable measured clockwise from 0 (due north) to 360 degrees (also due north). The aspect function identifies the downslope direction of the maximum rate of change in value from each quadrat to its neighbors. In the northern hemisphere, slopes that are south-facing theoretically receive the highest solar radiation. However, SSW slopes

experience the highest heat load due to delayed ground heating (Geiger 1966). Therefore, aspect was first adjusted by subtracting 22.5°. Aspect was then linearized by sine and cosine transformations. In the cosine transformation, values close to 1 are NNE and values close to -1 are SSW. The eastness transformation is similar, except that values close to 1 are nearest to ESE (Roberts and Cooper 1989). The computation of specified topographic variables was done in ArcGIS (v10.2, ESRI). All other statistical analyses were conducted with R (v3.2.3, The R Foundation for Statistical Computing).

Forest size structure

Species having a stem (sometimes 1-3) with a usually elongate main stem were classified as trees (Conservation Ontario) and separated into size classes to analyse how predicted abundances from environmental variables (ie. habitat associations) changed with DBH. Size classes were based on the DBH of the tree's largest stem. Small trees were defined as all individuals smaller than 5 cm DBH; medium trees had a DBH \geq 5 cm and <15 cm; and big trees were \geq 15 cm. Most reproductive trees would fall into the largest size category.

Relationship between topographic variables

A Pearson correlation matrix was used to assess the correlation between topographic variables. The matrix of topographic variables consisted of all 5 original topographic variables (elevation, convexity, slope, cosine and sine of aspect) as well as the squared and cubed functions of slope, elevation and convexity for a total of 11 variables (Table 1). The combination of variables first suggested by Legendre et al. (2009) has become the standard for examining the effects of topography in CTFS plots. The polynomial functions allowed us to look at non-linear relationships between species and environment. Only measurements from the 303 censused quadrats were used. In all analyses the environmental variables were centered around 0 and scaled to unit variance.

The original topographic variables were largely uncorrelated or weakly correlated with each other, with the exception of a moderate positive correlation between convexity and elevation (Table 2). The strongest correlations in expanded topographic data set were between first and third order monomials of the same variable: convexity was positively correlated with convexity³, and elevation positively correlated with elevation³, while slope, slope², and slope³ were all positively correlated with each other. Slope was also positively correlated with convexity² and slope², and negatively correlated with elevation². Therefore, as sites approached mid-elevations, slope and curvature increased becoming either more convex or concave. Cosine and sine of aspect were inversely related therefore, as quadrats became more east-facing, they also became more southfacing. Principal component analysis (PCA) was used on the topography and species data as an exploratory analysis to reduce the dimensionality of the datasets by transforming the variables into uncorrelated variables called principal components.

Relationship between species

Another PCA examining the trends among species used a matrix composed of species abundance calculated as the number of individuals of each species per quadrat. In the species PCA and all other community-wide analyses, rare species with a total

abundance of less than 10 individuals were removed (representing <0.5% of individuals). The remaining species matrix contained 33 species (Table S1) each present in at least 8 quadrats.

Species-habitat associations

To test the explanatory power of topographic variables on species distribution within the censused quadrats, we used redundancy analysis (RDA). RDA is a constrained multivariate ordination technique that is essentially the multivariate extension of multiple regression (Rao 1964; Legendre and Legendre 1998). An RDA arranges species and sites along environmental gradients. For the RDA, the species abundance matrix of 33 species was transformed by the Hellinger transformation to reduce the weight of the most abundant species and to make the data appropriate for viewing community-wide trends on the influence of environmental variables (Legendre 2007). Explanatory relationships among variables from both species and environment datasets were explored through a triplot of the full RDA model. Species-environment scores from the RDA were used to assess the importance of the environmental variables. Significance of the overall model and all axes were measured using 999 permutations of the Monte Carlo test (P = 0.05). The variance inflation factor function (vif) in the R package "car" (Fox & Weisberg 2011) was used to quantify the extent of collinearity between the five original topographic variables (convexity, slope, elevation, sine and cosine of aspect) as well as the expanded set of environmental variables. Vif values ranging from at least 5-10 are typically interpreted as collinearity among predictor variables (Craney and Surles 2007).

The RDA with the expanded model of 11 variables reaffirmed the high collinearity for elevation (vif = 10.8), elevation³ (vif = 9.7), and slope³ (vif = 7.4) (RDA not shown). To reduce the collinearity in the model, another RDA was performed with the cubic transformations removed. This RDA gave similar ordination results to the previous RDA including cubic variables, but strong effects of collinearity were removed (vif range from 1.15 to 1.64). The reduced model with 8 environmental variables (five original and slope², elevation² and convexity²) was used as the final RDA model to analyse community composition.

Spatial structuring

To investigate the effect of spatial variation in the community composition, space was described using spatial variables from the multi-step principal coordinates of neighbour matrices (PCNM) technique. In the PCNM procedure, each 20 x 20 m quadrat was used as a site. A principal coordinates analysis (PCoA) was performed on a truncated Euclidean distance matrix and n - 1 eigenfunctions were returned (n = number of sites). In this distance matrix, all directly adjacent and diagonal quadrats were set as neighbouring sites and the distance between these sites was retained. However, the distance between all non-neighbouring sites was replaced with a value of four times the distance between diagonally adjacent quadrats. Eigenfunctions are spatial components that each directly correspond to a spatial pattern and scale. PCNMs were identified as the eigenvectors with positive eigenvalues. Moran's I is a measure of spatial autocorrelation that can be calculated for each PCNM. The null hypothesis of no autocorrelation was

tested for each PCNM (P < 0.05), if the observed value of I is significantly greater than the expected value, then the values of the PCNM eigenvector are positively autocorrelated, whereas if I observed < I expected, this indicates negative autocorrelation. Only PCNMs with positive autocorrelation were kept. A two-step forward selection was run to reduce the amount of PCNMs to only those which significantly captured the spatial pattern of species composition. This was done by a permutation test with 999 randomizations. The forward selection process uses a double stopping criterion and stops adding variables when either $R^2 < R^2$ threshold (0.001) or P > alpha (0.05) are reached (Blanchet et al. 2008). Only the 303 censused guadrats were used in the analysis, the remaining 197 quadrats were removed. This maintained the regular spatial structures that would be modeled by the full plot, but allowed us to remove uncensused quadrats without species information. The PCNMs selected through forward selection were split into two arbitrarily partitioned submodels representing spatial variation at different scales. Broad scale (PCNMs within the range of 1 and 20) and fine scale (PCNMs 21 and greater) spatial variation were the two submodels used in further multivariate regression.

The principal coordinates analysis generated 499 eigenfunctions from the 500 sites. Of these eigenfunctions, 285 were identified as PCNMs by having positive eigenvalues. 156 PCNMs had an observed Moran's I greater than the expected Moran's I representing positive spatial autocorrelations and were kept for further analysis (P=0.05). Forward selection kept the 82 PCNMs (49%) that had significant associations (P=0.05)

with the species matrix (Table S3). Each of these PCNM variables models a spatial pattern that is significantly associated with community composition.

Variation partitioning

Variation partitioning (VP) was used to quantify the unique, shared, and total explanatory power of the environmental and spatial descriptors (Borcard et al. 1992; Peres-Neto et al. 2006). VP uses RDA to determine the variation that can be related simultaneously to multiple sets of explanatory variables. The first VP procedure was used to partition the overall effect of topography and spatial PCNM variables on the community composition. The second VP procedure partitioned the effect of 3 sets of variables: topographic, broad scale and fine scale spatial PCNM variables on community composition. The RDA, PCNM technique and VP were performed with R package "vegan" (Oksanen et al. 2016), forward selection of PCNMs with the "packfor" package (Dray 2011), and Moran's I was calculated with the "ape" package (Paradis et al 2004). Regression coefficient plots were created using the "dotwhisker" package (Solt and Hu 2015).

Habitat associations of focal species and their size classes

To investigate the differences between the focal species and their size classes, a set of linear models were conducted. The six species with the highest basal area were selected as focal to study species-specific habitat associations. Basal area was calculated for each stem as π * (DBH/200)² and summed for all stems per species. This variable indicates the species that have greatest biomass rather than simply greatest abundance and
therefore are likely dominant forest species. Multivariate linear regression was used to examine plot-wide associations of the focal species abundance and distribution with habitat. Count per quadrat was modeled as a generalized linear model (glm) with a negative binomial distribution (link=log). The negative binomial regression was selected because the count data were over-dispersed. It can be considered as a generalization of Poisson regression since it has the same mean structure as Poisson regression but with an extra parameter to model the over-dispersion (Ver Hoef and Boveng 2007). To reduce the redundancy and amount of predictor variables in the model, RDA axes were used rather than the 11 individual topographic variables. Particularly, using the axes from the RDA emphasizes the environmental variables that most separates species. The first four axes from the community and topography RDA explained 91.8% of the total RDA model as well as land use history were used. The historic land use classification was taken from a georeferenced aerial photograph from 1943 (Figure 2). Land use history was categorized as either past farmland, edge, or forest corresponding to the values of 0, 1, and 2 for each censused quadrat and modeled as a continuous variable of human disturbance. Significance was assessed using P=0.01. Georeferencing was completed using the georeference tool in ArcMap.

To analyse how the habitat association changed with size class, a glm was performed similarly to the individual focal species models except count was broken down into species count per quadrat per size class and size was included as an interaction term. The negative binomial glm was performed using the glm.nb function from the "MASS" M.Sc. Thesis - S. L. Muñoz

package in R (Venables and Ripley 2002). Maps of the environmental variables were made using the "spatstat" package (Baddeley et al. 2015).

RESULTS

Environment characteristics: topography and land-use history

The elevation of the 12 ha censused area ranged from 88 to 132 m above sea level. The slope ranged from 0 to 32 degrees and the degree of convexity ranged from -3.0 to 2.5 (Table 1; Figure 3a-f). Aspect values from 0-360 degrees in all 8 cardinal directions and were represented by values of -1 to 1 in both sine (eastness) and cosine (northness) transformations of aspect (Figure 4). The plot was strongly represented by northwestfacing quadrats but poorly represented by south-southwest-facing quadrats.

The first four principal components of the PCA on the first, second, and third order monomials of slope, elevation and convexity as well as the sine and cosine of aspect had eigenvalues greater than 1 and cumulatively explained 73.0% of the variance in the dataset (Table 3). The first axis (PC1) accounted for 27.0% of the variance and showed positive associations with slope and negative associations with elevation², thus describing mid-elevation areas of high slope (Figure 5, Table 4). PC2 accounted for 22.5% of the variance and was positively associated with slope and negatively associated with elevation and convexity. PC2 represented a gradient from concave basins to convex peaks. PC3 accounted for 12.7% of the variation and was positively correlated with convexity and negatively correlated with elevation. PC3 thus described convex low elevation areas. PC4 explained 10.8% of the variation and was positively associated with cosine of aspect and negatively associated with sine of aspect. PC4 described north and west-facing aspects.

Community structural characteristics

Of the 16 000 trees, shrubs, and woody vines that were censused from the 303 quadrats. 15 978 individuals were at least partially identified. Species that were only identified to genus include Fraxinus americana, F. pennsylvanica, Elaeagnus angustifolia, E. umbellata, Amelanchier spp., Viburnum spp., Salix spp., and Crataegus spp. Another 45 taxa were identified to species to give 52 morphospecies (henceforth referred to as "species") from 36 genera and 22 families. The maximum DBH of all stems was 113.9 cm and mean DBH was 8.7 cm (median of 4.1 cm). Of the 52 species, 31 species were trees, 22 species were shrubs, and 1 species was a woody vine. Non-native species (n = 12) represented 8% of the individuals in the plot. Multiple stems greater than 1 cm in diameter were found on 2348 individuals (14.7%) giving an additional 4412 stems. The overall density was 52.8 individuals/quadrat ranging widely from 438 individuals/quadrat in the dogwood shrub thicket to 4 individuals/quadrat in the black walnut woodland. The total basal area (BA) of all stems was 277.6 m^2 (23.1 m^2 per ha) with 92.8% composed of individuals with stems larger than 10 cm DBH. The 5 most numerous species Fraxinus spp., A. saccharum, C. foemina ssp. racemosa, F. grandifolia, J. nigra accounted for 10498 (65.7%) of all individuals. Fraxinus spp (americana and pennsylvanica) and A. saccharum were the most prevalent species with 3268 individuals (20.4% of total count) across 242 quadrats (80.1% of censused quadrats) and 2553 individuals (15.9%) across 189 quadrats (62.6%), respectively.

The six focal species selected for having the greatest basal area were *A*. saccharum, *J. nigra*, *Fraxinus spp.*, *Q. rubra*, *T. canadensis*, *F. grandifolia* (in descending order). Together they represent 206.26 ha (78.8%) of the total BA (Table 5). These native canopy trees had individuals in all 3 size classes and accounted for slightly over half (52.1%) of all individuals in the plot.

Relationship between species

To compare the relationship among species, a PCA was performed on the count per quadrat (abundance) for all species with at least 10 individuals (n = 33) (Figure S3). The first axis (PC1) explained 13.3% of the species variance while the second explained 7.6% (Table 6). The first 12 components had eigenvalues greater than 1. Most species were weakly correlated with the principal components. Because the PCA demonstrated many components each explaining a small amount of variance, the results indicate strong independent distributions of species. Species did not appear to form marked subgroups within the community from their similarity or dissimilarity in abundance across quadrats.

Relationship between topography and species using redundancy analysis

The RDA of 8 topographic variables (slope, elevation, convexity, slope², elevation², convexity² as well as the sine and cosine of aspect) and counts per quadrat for the 33 species in all 303 censused quadrats explained 25.6% of the total constrained inertia (adjusted $R^2 = 23.6\%$) (Figure 6 and Table 7). The Monte Carlo test with 999 permutations indicated that the RDA ordination gave significant results (P<0.01) for the full model and first four axes. The first axis (RDA1) explained 17.1% of the total inertia

and had a positive correlation with elevation and sine and cosine of aspect (north- and east-facing slopes), and strong negative correlations with slope as well as convexity² (Table 8). RDA1 was positively associated with abundances of J. nigra, L. tatarica, Crataegus spp., and O. virginiana and negatively associated with A. saccharum and F. grandifolia. It could be summarized as a gradient of flat, high and low elevations areas to high slope, mid-elevations. The second axis (RDA2) added a further 3.6% of explained variance and correlated positively with elevation and sine of aspect (east-facing slopes), thus describing east-facing, high elevation areas. It was positively associated with the abundance of C. foemina ssp. racemosa and negatively associated with Fraxinus spp. The third axis (RDA3) only explained 2.2% of the variance and was positively correlated with elevation and cosine of aspect and negatively correlated with elevation² and sine of aspect, thus describing mid-high elevations of low curvature and west and north-facing slopes. C. foemina ssp. racemosa and Fraxinus spp. were positively associated with RDA3 while F. grandifolia, A. negundo, C. caroliniana, and T. canadensis had negative correlations. RDA4 explained 1.3% of the variation and was positively associated with sine of aspect and negatively associated with slope and elevation thus describing eastfacing, flat, low elevation areas. It was positively associated with C. caroliniana and R. *cathartica* and negatively associated with A. saccharum and L. tatarica. The first 4 axes explained 24.3% of the inertia and were used as explanatory variables in later analyses. The separation among the focal species is highlighted in the plot. A. saccharum, F. grandifolia, and J. nigra in particular were the species best explained by topography but

all focal species had >15% cumulative variance explained from the RDA model (Table 9). These three species separated along RDA1 with *J. nigra* in the flat, high and low elevation areas and *A. saccharum* and *F. grandifolia* in the high slope, mid-elevation areas.

Spatial structure of community composition

To model spatial structuring in the community composition, the multi-step principal coordinates of neighbor matrices (PCNM) technique was used. The RDA with the forward selected PCNMs showed a highly spatially structured community composition (adjusted $R^2 = 62.6\%$, P=0.05). Within the spatial variation, the 17 significant PCNMs representing broad spatial structuring (within PCNMs 1-20) accounted for 36% of the species variation while the 65 significant PCNMS within the PCNMs range 21-156 representing fine scale space accounted for 30% of the variation (see Figure S5 for examples of modeled spatial variables). The 13 PCNMs that explained the greatest amount of variation (using adjusted R^2) were all broad scale (Table S3). Thus, spatial structuring was largely associated with PCNMs at broad scales.

Variation partitioning

Using both topographic and spatial variables, we used variation partitioning to separate the amount of variation in the community composition each set could explain (Figure 7). The combination of spatial PCNM eigenfunctions and topographic variables explained 63.4% of the variation in the community composition. The proportion of variation in the community composition uniquely explained by spatial variables was

39.7%, while only 0.8% was purely explained by topographic variables. Topography accounted for 23.6% of the variation and was highly spatialized (96.8%). The remaining 36.7% of the variation in the community was unexplained residual variation unaccounted for by the model. The second variation partitioning separating space into two submodels (Figure 8) showed that 36.4% of the total variation was modeled by broad scaled PCNMs and 29.8% was from fine scaled PCNMs. The variation explained by fine scale space was largely unique, while most of the broad scale variation was shared with topography. Most (73.8%) of the variation explained by spatially-scaled topography was also explained by broad scale PCNMs.

These results indicated that the majority of the variation in the community can be explained by the measured spatial and environmental variables. The community structure was largely explained by space and this was maintained across a range of spatial scales. The variation explained by topography was almost entirely co-explained by spatially structured PCNM variables and was largely associated PCNMs at broad scales.

Prediction of focal tree species abundances

An analysis of covariance (ANCOVA) demonstrated significant differences between species in the relationship between abundance and the topography and land-use variables. Predictive models for the individual focal species showed differences in response to the environment between species. Most species abundance correlations with the RDA axes were significant (24/30; P<0.01) and the direction of correlation varied by species (Table 10). No two species followed the same profile of habitat associations.

The abundance of *Fraxinus spp.* was negatively associated with RDA1 (low slope and high and low elevations), RDA2 (elevation and easterly aspect) and human disturbance, and positively associated with RDA3 (mid-elevation and low curvature), RDA4 (low elevation and low slope) (Figure 9). The abundance of A. saccharum was negatively associated with RDA1 (low slope and high and low elevations) and RDA2 (elevation and easterly aspect) and positively associated with RDA3 (mid-elevation and low curvature) and human disturbance. F. grandifolia was negatively associated with RDA1 (low slope and high and low elevations), RDA3 (mid-elevation and low curvature). T. canadensis was negatively associated with RDA1 (low slope and high and low elevations), RDA3 (mid-elevation and low curvature), and human disturbance. J. nigra's habitat patterns contrast those of F. grandifolia and T. canadensis as it was positively correlated with RDA1 (low slope and high and low elevations) and human disturbance and negatively correlated with RDA2 (elevation and easterly aspect). O. rubra was negatively associated with RDA1 (low slope and high and low elevations) and human disturbance and positively associated with RDA2 (elevation and easterly aspect), RDA3 (mid-elevation and low curvature), RDA4 (low elevation and low slope).

The greatest separation of focal species was seen along RDA1 (low slope and high and low elevations) which is negatively associated with all species except *J. nigra*. *A. saccharum*, *F. grandifolia* and *T. canadensis* had higher abundance in the high slope, mid-elevation areas relative to the other species. *F. grandifolia* and *Q. rubra* were the only species positively associated with RDA2 (elevation and easterly aspect). RDA3 (mid-elevation and low curvature) separated *F. grandifolia* and *T. canadensis* from the other focal species as they were the only species negatively associated. No species were negatively associated with RDA4 (low elevation and low slope). Only *T. canadensis* was negatively associated with historical farmland.

Variation among size classes of focal tree species

Summing over the focal species, small trees were the most common (n=3447, 41.4%), then medium (n=2736, 32.9%), then big (n=2141, 25.7%) (Figure 10). However, the size distribution varied among the focal species. The counts of the three most prevalent focal species, *A. saccharum, Fraxinus spp.* and *F. grandifolia*, decreased with increasing size class. In contrast, most *J. nigra*, *Q. rubra*, and *T. canadensis* trees were in the largest size class (Figure 10), with few small and medium sized individuals. The separation of size into 5 cm DBH ranges showed 73% of *F. grandifolia* censused were <5 cm (Figure 11c). *T. canadensis* had very few (1.5%) small trees (Figure 11f). Consequently, *T. canadensis* was not included in further size class analyses.

For three of the five species, the regression coefficients for topography and land use on the abundances of the focal species differed between size classes for at least one predictor (Table 11). Only 6 of the 25 interactions between size class and an environmental variable were significant at P<0.01. Three species (*Fraxinus spp., J. nigra* and *Q. rubra*) demonstrated size class effects on the relationship between abundance and RDA1, RDA3, and RDA4. *A. saccharum* and *F. grandifolia* did not show any differences in habitat association between size classes. For *Fraxinus spp.*, the relationship between abundance and three of the five environmental (regression coefficient) variables differed between size classes. Therefore, *Fraxinus spp.* showed greatest effect of size of any species (Tables 11 and 12a). The abundance of *Fraxinus spp.* increased with RDA3 and RDA4 across all size classes. Small and medium *Fraxinus spp.* trees were more positively associated with RDA3 (midelevation and low curvature) than were big trees, but the small and medium size classes did not differ. The abundance of small *Fraxinus spp.* trees increased along RDA4 (low elevation and low slope) more than the other size classes. *Q. rubra* also showed an effect of size class on the association between abundance and RDA4 (low elevation and low slope) (Table 12e). For *Q. rubra*, small trees were the most positively correlated with RDA4 (low elevation and low slope). The medium size class of *Q. rubra* showed an intermediate response to RDA4 compared to big and small trees. In the three cases where there was an effect of size class on the association of abundance with RDA3 and RDA4, smaller trees were more strongly positively associated than big trees.

The relation between on abundance and RDA1 (low slope and high and low elevations) depended on size class for three species (*Fraxinus spp., J. nigra* and *Q. rubra*). In all cases, the abundance of medium trees was more positively associated than small trees (Table 12a, d, and e). Small and big *Fraxinus spp.* trees were more negatively associated with RDA1 (low slope and high and low elevations) than were medium *Fraxinus spp.* trees, but the small and big size classes did not differ from each other and medium trees were not associated with this axis. *Q. rubra* showed a difference in

abundance associated with RDA1 between only small and medium trees. Small and big trees were negatively associated with RDA1 while medium trees showed no association. The abundance of big and medium *J. nigra* trees increased equally with RDA1 but there was no effect of RDA1 on small trees (Table 12d).

McMaster University (Biology)

DISCUSSION

We examined the roles of niche and neutral processes in determining community structure in a temperate forest in eastern North America. The large contribution of topography from our results on an analysis on nearly 16 000 spatially mapped woody individuals suggests that niche processes shape species abundances in this temperate forest. The high predictability of spatial variables on the variation in the community composition indicates strong effects of neutral processes. Results from the variation partitioning used to determine the relative contributions of topography and space in this community were comparable to results from other CTFS plots. The distribution of focal tree species was found to be strongly affected by topography and human disturbance. The relative contributions of niche processes changed with the size class of some but not all of the focal species. Surprisingly, habitat associations were often weaker with increased, implying that species filtering may not be occurring over the lifetime.

Role of environmental variables

Environmental variables associated with topography explained about one quarter of the community composition. Evidence for niche processes was shown by the dispersion of species in the RDA indicating habitat specialization of individual species. Slope and elevation were the two key topographic gradients with the greatest explanatory power (ie. associated with RDA1) on the community composition. This does not suggest that they are directly responsible for species' differential success, but that they are likely correlated with important environmental variables like soil nutrients, light and water

availability and disturbance at the local scale (Brown et al. 2013). This is not surprising given the prominent high slope/mid-elevation and low slope/high and low elevation forest structure which is closely associated with mature growth and new growth areas, respectively. Low-lying areas are often characterized by recurring floods due to intense rainfall events that disperse soil cover (Girdler and Barrie 2008) and would be expected as a cause of disturbance in the creek and floodplain area of McMaster Forest. In contrast, disturbance associated with the land use history of the site is associated with flat, high elevation quadrats. Even after more than 50 years without human disturbance, the area of historic farmland shows a marked difference in community from the adjacent natural area. Old farmland was the preferred habitat of early successional J. nigra, shrubs like Crataegus spp. and C. foemina ssp. racemosa and non-natives L. tatarica and A. *negundo*. C. foemina ssp. racemosa is a small shrub that grows in dense clusters by producing extensive networks of horizontal roots making it difficult to distinguish nongenetically identical individuals from ramets (Boeken and Canham 1995). While its range is limited to east-facing high elevation areas, C. foemina ssp. racemosa was the second most common species in the plot due to its means of reproduction allow it to locally dominate in abundance. Meanwhile, the areas adjacent to the historic farmland described by high slopes and mid-elevations have unsuitable conditions for farming and are occupied by mature forest. Late successional species like A. saccharum, F. grandifolia, T. canadensis and the accompanying understory of O. virginiana and H. virginiana primarily inhabit the mature growth area.

The second most explanatory RDA axis influencing community composition was strongly associated with aspect and elevation. Interestingly, eastness rather than northness appeared to be a more important environmental variable in modelling community composition. This suggests solar radiation was only weakly influential or that the variation in exposure to direct sunlight in this community was insufficient to influence species distributions possibly associated with the mild variation in slope and elevation and that a microclimate sheltered from wind may be more important. These associations with the environment show environmental heterogeneity influenced community composition and is evidence for niche theory.

Role of spatial variables

Spatial structure as measured by PCNM variables explained nearly 2/3rds (63%) of the community composition. This indicates a strong degree of spatial autocorrelation and hence aggregation in species distributions. Almost all of the variation explained topographic variables was also explained by the spatial variables, indicating that topography is highly spatially structured and also that the spatial variables are approximating real gradients. Most of the variation in community composition unique to spatial variables was fine scale. Biotic interactions typically occur at this fine scale and suggest dominance of biotic processes (Laliberte et al. 2009) indicating effects of limited dispersal (Chang et al. 2013) since it is a spatial process associated with a spatial signature. Pure spatial variables also explained a moderate fraction (38%) of the community data, however, with more measured environmental variables, the variation

attributed to purely spatial processes may be revealed as spatially structured environment (Peres-Neto and Legendre 2010). For example, the inclusion of soil data has been shown to considerably lower the amount of variation explained by space, thus reducing the strength of community assembly processes attributed to neutral theory (Baldeck et al. 2013b; Chang et al. 2013). The largest fraction of variation is attributed to spatial variables which suggests this is the focal factor affecting species however, habitat preferences of species are still clear indicating the both processes are responsible in shaping the community. A moderate proportion (37%) of community composition was not explained by the environmental variables, by the spatial position, or by their shared effects. The unaccounted for variation may be a result of unmeasured non-spatially structured environmental factors or random sources such as ecological drift (Legendre et al. 2009).

Comparison of the McMaster Forest community among CTFS plots and climate types

The results from this study can be compared to other studies using the same methodology. The use of variation partitioning to assess community composition has been applied in many other studies on CTFS forest plots that followed the same methodology to census trees. A cross-continental meta-analysis of eight tropical plots compared the effects of PCNMs, topography, and soil variables (Baldeck et al. 2013b). The total proportion of variation explained by the individual topography and spatial components as well as the combination of all spatial and environmental variables (topography and soil) was on average 10% less than that of McMaster Forest (Baldeck et al. 2013b). Studies based in temperate to subtropical climates were from forest plots located in southeast Asia. Compared to the subtropical plots, the variation explained in the McMaster Forest community matched closely to Dinghushan (Lin et al. 2013), Lienhuachih (Chang et al. 2013), and Gutianshan (Legendre et al. 2009) but less so with Baotianman (Jia et al 2015). For all plots except Baotianman, topography and space explained most of the variation in community composition. The other plots had a similar variation explained by topography (20-31%) and PCNM spatial variables (54-62%) to McMaster Forest. Conversely, in a Chinese temperate plot in Changbaishan (Yuan et al. 2011) with a fairly homogeneous environment (elevation range of 16 m) less than half of the variation (39%) of the variation was explained by soil, topography, and space and the contribution of topography was minimal.

The results from the McMaster Forest community show similar trends to other forest plots, where spatial variables account for the bulk of the variation, and environmental variables contribute minimally to explaining additional variation. Flatter plots (Changbaishan, Baotianman, BCI) tended to have lower variation explained by topographic variables than more mountainous, topographic varied plots (Gutianshan, Dinghushan) (de Caceres et al. 2012; Jia et al. 2015). While the only other temperate plot (Changbaishan) had a similarly low species richness, the variation explained due to both topography and space were greatly reduced compare to McMaster Forest. Thus, the invariant environment of Changbaishan diminishes the similarity between the two

analysed temperate plots. Interestingly, compared with McMaster Forest, the subtropical plots had more heterogeneous topography with elevation range of approximately 200 m and four times greater species richness, yet topography did not play an appreciably greater role than it did in McMaster Forest. The strong effects of topography in structuring the McMaster Forest community is likely attributed to the strong association between topography with land use history in this forest plot. The other plots were often on undisturbed, nature reserves and thus had sources of habitat heterogeneity. The results from previous studies also suggest adding soil data as variables to explain community composition only helps to explain existing spatial variation rather than adding to the amount of variation explained (ie. environmental data is nested within the spatial variation). In comparison to McMaster Forest, the fraction of variation explained by topography was more similar to the subtropical than tropical plots, as topography tends to play less of a factor on community composition in the tropics. However, the variation among these studies also depends on plot size, sampling design, species transformations, number of eigenvectors used in the model (threshold distance), resolution, quality of environmental variables (Murphy et al. 2015). However, unlike the plots in these published studies, this community has not yet been fully censused, and analysis on the completed plot may differ from the current results due to the change in sample size, inclusion of new species, and remove any complications from PCNM spatial scales (Borcard and Legendre 2002).

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Habitat association of focal species

All environmental variables were significant predictors of abundance for the individual focal tree species. Abundance of most focal species was highest in steep, westfacing slopes and low to mid-elevations. These two most common and widespread species, *Fraxinus spp.* and *A. saccharum*, showed similar habitat patterns and only differed along one environmental gradient that described low elevation and low slope areas is explained by *Fraxinus spp*.'s ability to dominate the floodplain more than A. saccharum. F. grandifolia and T. canadensis also showed similar patterns, but with F. grandifolia being more successful with vastly more small trees and an expanding range into the edge habitats. The six focal forest tree species can be grouped into five different overall habitat associations suggesting that each dominates a different area. T. canadensis and F. grandifolia associated together and shared similar patterns. The success of all focal species in attaining the relatively largest large basal area of species in the plot may be attributed to their individual strategies that caused their differential occupation of habitats. A. saccharum and Fraxinus spp. were successful at colonizing across the edge habitats and into the old farmland. O. rubra preferred the edge and T. canadensis was limited to undisturbed forested area. J. nigra showed the greatest difference from other focal species, preferring disturbed areas including human disturbance in the old farm and natural disturbance in the creek and floodplain. F. grandifolia and T. canadensis preferred the same elevation, curvature and slope areas, while J. nigra is found in the opposite areas. J. nigra had the greatest abundance in high elevation old farmland and low

elevation floodplain. However, most trees were positively associated with farmland use even though they prevailed in more densely wooded areas. This shows their ability to spread into the less colonized, sunny areas even for *A. saccharum*, a very shade tolerant species adapted for forest growth. Meanwhile, *T. canadensis* was the only species to never be found in the farmland or edge, perhaps associated with its poor regeneration abilities. The focal species appeared to separate across the environment, but other trees often group with them, defining the different forest types. *F. grandifolia* and *T. canadensis* appeared to be co-dominant in high slope, mid-elevation, east-facing sites. **Size distribution of focal trees**

Overall, the abundance of focal trees decreased with increasing tree size. The three most prevalent species, *A. saccharum*, *Fraxinus spp.* and *F. grandifolia*, decrease with size class indicating a growing population. *F. grandifolia* had the highest proportion of individuals in the small size class perhaps because it is capable of reproducing through root suckers (Jones and Raynal 1986). In censusing, difficulty separating true individuals likely lead to an inflation of their recorded abundance relative to the fewer non-clonal individuals that exist. However, *J. nigra*, *T. canadensis* and *Q. rubra* are all focal trees with a severely reduced small size class and were mostly comprised of individuals in the largest size class (>15 cm) suggesting a population following negative growth that will struggle to replace itself in the future. The similarity of these three species' size structures is likely attributed to different factors. Low abundance of small *J. nigra* could be due to a shift away from this early-successional tree to more tolerant climax species such as *A*.

saccharum. Q. rubra is a fire adapted species with low shade tolerance and is favored over competing vegetation in fires due to its sprouting ability (Crow 1988). The few small *Q. rubra* in the plot are constrained to the forest edge on the tops of slopes, an intermediate between the deep shade of the forest and exposed open areas. T. canadensis is a highly shade tolerant species and would be expected to show a size distribution with many small individuals and long tail of large individuals ("reverse J") suggesting the species is failing to regenerate (Coomes and Allen 2006; Wright et al. 2003). T. *canadensis* is also the only focal species that has not been able to spread into the old farmland or edge habitats. T. canadensis litter is known to be allelopathic to its own regeneration (Ward and McCormick 1982) and requires a moist organic substrate and sustained favorable weather for establishment (Mladenoff and Stearns 1993). A Michigan study showed white-tailed deer as the primary factor inhibiting sapling growth (Witt and Webster 2010). However, T. canadensis often shares the forest overstory with A. saccharum which is preferred by deer but also more tolerant of browsing (Anderson and Loucks 1979). Few T. canadensis seedlings were seen at McMaster Forest (pers. observ.) and the stage limiting T. canadensis success may be germination, even before deer become a threat. Furthermore, A. saccharum may become favored by the seedbed conditions that reduce germination substrate availability for T. canadensis created by a mixed overstory (Witt and Webster 2010).

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Habitat association changes with size class

Though the species differed in their response to topography and human disturbance, for three of the five focal species there were also within species differences associated with size class effects on the relationship with topography and human disturbance. The primary environmental gradients where abundances differed across size classes were RDA1 and RDA4, the two axes most associated with elevation and slope. The exceptions were A. saccharum and F. grandifolia which demonstrated similar habitat associations across the size classes. F. grandifolia's similarity in distribution across size classes is likely due to its highly limited dispersal through root sprouts which limited small individuals from occupying different habitats than their parents. However, within species, few size classes separated along environmental gradients. Strong habitat associations of species, but weak differences between size classes of a species suggest that the environmental filter acts on seedlings and saplings <1 cm DBH (Feeley et al. 2011). In this case, seedling establishment and early growth will be the determinant of success while effects of sorting are less clear after this crucial stage (see Brown et al. 2013). Stochastic birth and death rates across tree size would also result in consistency of habitat associations between size classes. Although there are size class differences along environmental gradients, their structuring effects are much weaker than the species-levels effects. This may be influenced by limited dispersal restricting the expansion of tree species habitat (Webb & Peart 2000), since it causes a higher density of small trees in the preferred habitat of the adults (Comita et al. 2007).

In most of the cases that showed significant differences between habitat associations of small and big trees, the habitat associations were diminished for trees belonging to the larger size classes. This finding is in contrast to other studies that found neutral processes more important in regulating the distribution of smaller trees but niche processes more dominant in shaping the distribution of larger trees (Swenson et al. 2007; Hu et al. 2012), and a meta-analysis that found no habitat differences (Baldeck et al. 2013a) but in agreement with others who found niche expansion with increasing tree size (Kanagaraj et al. 2011; Ariera et al. 2016). Others found that while abundance changed with size, there was no trend as to whether habitat associations were narrower or wider depended on species (Yamada et al. 2006; Lai et al. 2009).

A species undergoing habitat filtering would show increasingly narrow habitat association as trees age and grow in size (Wang et al. 2014). Our results do not show evidence of this process. It may be that the big trees in their preferred habitat range are the most fecund causing a large cohort in this short range causing young trees to be most abundant there and appearing as strong habitat associations. As these trees grow in size, competition between them reduces clustering. This is consistent with negative density dependence (Baldeck et al. 2013a). Furthermore, these differences are likely due to the differing pressures experienced at each size class where small trees are clustered and under strong competition. Their weaker topographic associations of big trees may be a result of increasing uniformity in the spatial distribution of trees with size and age (Getzin et al. 2006), forcing them to spread across a range of habitats. These habitat associations appeared to be a gradual change across size classes where the abundance of small and big trees differed but medium trees showed an intermediate response compared to small and big trees. Only along one axis (RDA1) were the abundance of big and small trees the same while medium trees differed from both big and small trees.

The size class of big trees is an accumulation of individuals that have been recruited over a long period and have experienced many different environmental conditions, whereas small trees are typically younger and have only been subjected to more recent environmental conditions. Thus, the existence of many older, larger trees may be a consequence of past favourable periods. However, if in recent years have not experienced these favourable conditions then no small trees would be found there. causing big trees to appear to have wider habitat associations (Kanagaraj et al. 2011). Having temporal information can disentangle these differences. Interestingly, small trees were not more associated with the edge or old farmland than big (or medium) trees. However, the different sample sizes across size classes may influence the most abundant size class (typically small trees) to show the greatest amount of habitat and spatial structuring (Baldeck et al. 2013a). In this study, the two species to show size differences along environmental gradients were Fraxinus spp., J. nigra and O. rubra, and two of these (J. nigra and Q. rubra) actually had the fewest small trees but still showed a significantly higher association with the environment than big trees.

Habitat associations typically followed a directional change, being more strongly associated with an increase or decrease in size class. Significant differences between non-

sequential size classes may be associated with a past historic event that upset the usual flow of size class abundance and distribution by differentially affecting a size class. In most cases it was small and big trees that differ, however along RDA1 both *Q. rubra* and *Fraxinus spp.* had differences between the small and medium size classes. *Fraxinus spp.* and *Q. rubra* showed the same effect of size class on the association between abundance and RDA4 which described the floodplain and east facing areas. The abundance of small trees was higher than that of medium and big trees in this area perhaps because of the difficulty in growing in the disturbed area causing mortality in individuals beyond the small size class.

Conclusion

The strong relationships between species distributions, topographic and spatial variables provide evidence that this woody plant community in McMaster Forest is largely structured by species habitat preferences and spatial processes. Further, these habitat associations are not static, within a species the preferences for environmental conditions change with the size of the tree and this is reflected through dynamic habitat associations. These results indicate that mechanisms from niche and neutral theory as well as negative density dependence all contribute to community assembly in a temperate forest. This study adds to the global network of analysis on species coexistence mechanisms and shows similarity between topographically diverse subtropical plots and an urban temperate plot diverse land-use history. Further studies in temperate, eastern North America forests are needed to clarify these biogeographical trends. Given the

impending climate crisis and profound effects it may have on forest biodiversity (Botkin et al. 2007) findings from studies on the processes structuring forest communities are essential for monitoring and maintenance efforts.

TABLES

Table 1: Eleven variables used to describe topography and their ranges in the censused area of McMaster Forest.

Abbreviation	Variable	Range
con1	convexity	-2.9 - 2.5
slo1	slope	0.3 – 32.2 °
ele1	elevation	88.7 – 131.2 m
cosasp	cosine of aspect (north-facing)	-1.0 - 1.0
sinasp	sine of aspect (east-facing)	-1.0 - 1.0
con2	convexity ²	
slo2	slope ²	
ele2	elevation ²	
con3	convexity ³	
slo3	slope ³	
ele3	elevation ³	

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	conl	slo1	ele1	cosasp	sinasp	con2	slo2	ele2	con3	slo3	ele3
conl	1.000										
slo1	0.031	1.000									
elel	0.431	-0.053	1.000								
cosasp	-0.030	-0.114	0.045	1.000							
sinasp	-0.044	-0.145	0.184	-0.204	1.000						
con2	0.070	0.298	-0.067	-0.160	-0.107	1.000					
slo2	0.140	0.506	-0.055	-0.135	-0.184	0.122	1.000				
ele2	-0.139	-0.516	-0.271	0.144	0.110	-0.203	-0.184	1.000			
con3	0.789	-0.026	0.215	0.020	-0.007	0.026	0.082	-0.078	1.000		
slo3	0.107	0.847	-0.055	-0.141	-0.178	0.212	0.755	-0.416	0.041	1.000	
ele3	0.388	0.069	0.935	0.048	0.103	0.026	0.017	-0.306	0.166	0.036	1.000

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Table 3: All principal components of the PCA based on the correlation matrix between all 11
topographic variables. The first row is the square root of the eigenvalues, the second is the proportion
of variance explained by the individual axis, and the third row describes the cumulative variance
explained by the sequential addition of the axes.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
	724	1.573	1.182	1.089	0.990	0.835	0.814	0.575	0.408	0.294	0.220
	270	0.225	0.127	0.108	0.089	0.063	0.060	0.030	0.015	0.008	0.004
C.	270	0.495	0.622	0.730	0.819	0.882	0.942	0.972	0.988	0.996	1.000
				_							

	PC1	PC2	PC3	PC4
con1	0.2566	-0.4028	0.4511	-0.1459
slo1	0.4597	0.2544	-0.1172	0.0555
ele1	0.1813	-0.5269	-0.3148	0.1325
cosasp	-0.1134	-0.0792	0.1737	0.7354
sinasp	-0.1122	-0.1639	-0.3306	-0.5414
con2	0.2087	0.1146	-0.0111	-0.2114
slo2	0.3926	0.2130	0.1367	0.0111
ele2	-0.3810	0.0258	0.2660	-0.0674
con3	0.1795	-0.3312	0.5818	-0.2008
slo3	0.4850	0.2616	0.0058	0.0377
ele3	0.2330	-0.4744	-0.3409	0.1819

Table 4: Matrix of variable loadings for all 11 topographic variables on the first four principal components.

				Total BA	
Species code	Species	Common name	Total count	(m ²)	% BA
ACERSAS	Acer saccharum	Sugar maple	2553	67.5	24.3
JUGLNIG	Juglans nigra	Black walnut	749	58.2	21.0
FRAX	Fraxinus spp	Ash	3318	33.0	11.9
QUERRUB	Quercus rubra	Red oak	280	31.7	11.4
TSUGCAN	Tsuga canadensis	Eastern hemlock	272	15.9	5.7
FAGUGRA	Fagus grandifolia	American beech	1153	12.4	4.5
	Other		7653	58.8	21.2
	Total		15978	277.6	100.0

Table 5: Count and basal area (BA) of the six focal species and all other censused individuals combined.

Table 6: The first 12 principal components of the PCA based on the correlation matrix between 33 species. The first column is the square root of the eigenvalues, the second is the proportion of variance explained by the individual axis, and the third row describes the cumulative variance explained by the sequential addition of the axes. Species correlated with the axes are listed in the last two columns; species with loadings > .35 on a component are positively correlated, while species with loadings < -.35 are negatively correlated with that component.

			Cum.		
	Eigenvalue	Proportion	variance	Positive	Negative
PC1	2.0952	0.1330	0.1330	Amelanchier spp.	
101				C. caroliniana	
				C. foemina ssp.	
PC2	1.5816	0.0758	0.2088	racemosa	
				V. riparia	
	1.4246	0.0615	0.2703		A. nigrum
PC3					A. saccharum
					C. alternifolia
PC4	1.3060	0.0517	0.3220	B. papyrifera	
DC5	1.2287	0.0458	0.3678		P. virginiana
103					Q. rubra
PC6	1.1957	0.0433	0.4111	J. nigra	
100				T. americana	
PC7	1.1550	0.0404	0.4515		A. negundo
107					L. tatarica
PC8	1.1049	0.0370	0.4885	P. serotina	A. freemanii
PC0	1.0910	0.0361	0.5246	R. typhina	J. cinerea
109					Salix spp.
PC10	1.0752	0.0350	0.5596		P. strobus
1010					R. typhina
PC11	1.0392	0.0327	0.5923		L. benzoin
PC12	1.0341	0.0324	0.6247	L. benzoin	A. glutinosa

Table 7: Values of all canonical axes of the RDA based on the explanatory matrix of 8 topographic variables and response matrix of species abundances for 303 sites. The first row is the square root of the eigenvalues, the second is the proportion of variance explained by the individual axis, and the third row describes the cumulative variance explained by the sequential addition of the axes.

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6	RDA7	RDA8
Eigenvalue	0.1079	0.0229	0.0141	0.0085	0.0033	0.0026	0.0016	0.0010
Proportion	0.1712	0.0364	0.0223	0.0135	0.0052	0.0041	0.0025	0.0016
Cum.								
variance	0.1712	0.2076	0.2299	0.2434	0.2486	0.2526	0.2551	0.2567
P value	< 0.001	< 0.001	< 0.001	< 0.001	0.020	0.080	0.445	0.857

Table 8: Matrix of variable loadings for all topographic variables on the first four canonical axes of the RDA based on the explanatory matrix of 8 topographic variables and response matrix of species abundances for 303 sites.

	RDA1	RDA2	RDA3	RDA4
con1	0.0441	0.1772	0.0324	-0.1908
slo1	-0.8446	0.0440	-0.1771	-0.4825
ele1	0.3418	0.6282	0.2452	-0.5371
cosasp	0.1794	-0.1011	0.3184	-0.1376
sinasp	0.2023	0.6979	-0.4383	0.2926
con2	-0.4244	0.0658	-0.3833	0.1466
slo2	-0.3721	0.0764	-0.2983	-0.4435
ele2	0.6832	-0.4707	-0.5146	0.0605

Table 9: Goodness of fit for individual focal species showing proportion explained
by first 4 RDA axes as well as the cumulative proportion of variance accounted for
in the full RDA model.

					Cum.
	RDA1	RDA2	RDA3	RDA4	variance
A. saccharum	0.4266	0.4406	0.4505	0.4690	0.4709
F. grandifolia	0.2130	0.2282	0.2661	0.2701	0.2782
Fraxinus spp.	0.0046	0.1295	0.1450	0.1543	0.1569
J. nigra	0.3743	0.3820	0.3916	0.3960	0.3995
Q. rubra	0.0148	0.0984	0.0989	0.1044	0.1562
T. canadensis	0.2040	0.2056	0.2578	0.2581	0.2670

Table 10: Results from predictive models of the counts per quadrat of focal species in response to environmental variables. The (+) indicates a positive association between the species and axis while (-) indicates a negative association. Significance was assessed using minimum alpha=0.01. Significance codes for P values: *** < 0.001; ** < 0.01; ns (not significant) > 0.01.

					Human
	RDA1	RDA2	RDA3	RDA4	disturbance
Fraxinus spp.	** (-)	*** (-)	*** (+)	*** (+)	*** (+)
A. saccharum	*** (-)	*** (-)	*** (+)	ns	** (+)
F. grandifolia	*** (-)	*** (+)	*** (-)	*** (+)	ns
J. nigra	*** (+)	*** (-)	ns	ns	** (+)
Q. rubra	*** (-)	** (+)	** (+)	** (+)	** (+)
T. canadensis	*** (-)	ns	*** (-)	ns	** (-)
Table 11: Analyses of covariance by species for abundances per quadrat as the dependent variable, and RDA1, RDA2, RDA3, RDA4 and human disturbance as independent predictors, testing for whether the effect of the predictor on abundance depended on size class. Significance was assessed using minimum alpha=0.01. Significance codes for P values: *** < 0.001; ** < 0.01; ns (not significant) > 0.01.

					size*human
	size*RDA1	size*RDA2	size*RDA3	size*RDA4	disturbance
Fraxinus spp.	***	ns	**	***	ns
A. saccharum	ns	ns	ns	ns	ns
F. grandifolia	ns	ns	ns	ns	ns
J. nigra	**	ns	ns	ns	ns
Q. rubra	**	ns	ns	***	ns

Table 12: Analyses of covariance results for individual species using abundances per quadrat as the dependent variable, and RDA1, RDA2, RDA3, RDA4 and human disturbance as independent predictors, testing for whether the effect of predictor on abundance depended on size class. The analysis were performed on focal species a) *Fraxinus* spp., b) *A. saccharum*, c) *F. grandifolia*, d) *J. nigra* and e) *Q. rubra*. The coefficients, standard error and p value refer to the deviation of the slope from 0. Bolded environmental axes and significance codes indicate a significant effect of size class on the relationship between abundance and the corresponding environmental variable. Significance was assessed using minimum alpha=0.01. Significance codes for P values: *** < 0.001; ** < 0.01; ns (not significant) > 0.01.

a) Fraxinus spp.

Environmental	Size				
variable	class	Coefficient	Std. error	P value	Signif. code
	small	-0.64	0.10	***	a
RDA1	medium	0.10	0.09		b
	big	-0.40	0.11	***	a
	small	-0.99	0.07	***	a
RDA2	medium	-0.95	0.07	***	a
	big	-0.78	0.09	***	a
	small	0.79	0.07	***	a
RDA3	medium	0.73	0.07	***	a
	big	0.39	0.09	***	b
	small	1.11	0.07	***	a
RDA4	medium	0.80	0.07	***	b
	big	0.51	0.08	***	b
Human	small	0.36	0.09	***	a
disturbance	medium	0.17	0.09		a
	big	0.46	0.11	***	а

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b) Acer saccharum

Environmental	Size	Std.			Signif.
variable	class	Coefficient	error	P value	code
	small	-2.05	0.18	***	a
RDA1	medium	-2.02	0.19	***	а
	big	-1.95	0.19	***	а
	small	-0.67	0.12	***	а
RDA2	medium	-0.40	0.12	**	а
	big	-0.34	0.14		а
	small	0.57	0.11	***	а
RDA3	medium	0.66	0.11	***	а
	big	0.25	0.12		а
	small	-0.02	0.10		a
RDA4	medium	0.05	0.10		а
	big	-0.11	0.10		а
Human	small	0.38	0.15		a
disturbance	medium	0.31	0.16		а
	big	0.09	0.18		а

c) Fagus grandifolia

Environmental	Size	Std.			Signif.
variable	class	Coefficient	error	P value	code
	small	-2.32	0.37	***	а
RDA1	medium	-2.32	0.45	***	а
	big	-2.74	0.52	***	а
	small	1.15	0.22	***	а
RDA2	medium	0.79	0.26	**	а
	big	0.67	0.29		а
	small	-0.75	0.19	***	а
RDA3	medium	-0.64	0.23	**	а
	big	-0.51	0.25		а
	small	1.04	0.16	***	а
RDA4	medium	0.88	0.19	***	а
	big	0.67	0.21	**	а
	small	-0.07	0.34		а
Human disturbance	medium	0.61	0.38		а
	big	0.92	0.39		а

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d) Juglans nigra

Environmental	Size	Std.			Signif.
variable	class	Coefficient	error	P value	code
	small	0.09	0.27		a
RDA1	medium	0.91	0.16	***	b
	big	1.00	0.11	***	b
	small	-0.05	0.18		а
RDA2	medium	-0.16	0.11		а
	big	-0.33	0.09	***	а
	small	-0.01	0.21		а
RDA3	medium	0.26	0.13		а
	big	0.18	0.09		а
	small	0.30	0.21		а
RDA4	medium	-0.07	0.13		а
	big	-0.27	0.08	**	а
Human	small	0.90	0.30	**	а
disturbance	medium	0.51	0.15	***	а
	big	0.11	0.11		а

e) Quercus rubra

Environmental	Size	Std.			Signif.
variable	class	Coefficient	error	P value	code
	small	-3.59	1.19	**	a
RDA1	medium	-0.27	0.31		b
	big	-0.79	0.20	***	ab
	small	-0.14	0.46		а
RDA2	medium	0.40	0.21		а
	big	0.36	0.15		а
	small	1.24	0.53		а
RDA3	medium	0.48	0.21		а
	big	0.26	0.13		а
	small	3.14	0.68	***	a
RDA4	medium	1.04	0.24	***	b
	big	0.11	0.12		c
Human	small	0.37	0.68		а
disturbance	medium	0.77	0.33		а
	big	0.59	0.23		а

FIGURES



Figure 1: The approximate location of the 20 hectare McMaster Forest in Hamilton, Ontario plot is outlined by the white box. Natural areas Cootes Paradise and Dundas Valley Conservation Area lie to the northeast and west of the forest plot, respectively. The grey areas to the east are urban areas.



Figure 2: Plot of McMaster Forest overlayed with grid of 500 quadrats and an aerial photograph from 1943. The purple line signifies the current trail and blue line is the creek. The dark, textured areas are forest cover while the white and light gray areas are agricultural land.













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Figure 5: Biplots of the first four PCA axes composed of all 11 topographic

variables. The left and bottom axes are component scores scaled to unit sum-of-squares. The top and right axes are values of the variable loadings scaled by the standard deviation of the principal components times the square root of the number of observations. The blue arrows depict the topographic variables and the gray numbers are the quadrats. The center of the text represents the value of the variable, rather than the end of the arrow. The direction of environmental arrow relative to the origin is the direction in which it increases in abundance. The correlation between two variables is equal to the cosine of the angle between the vectors. (a) plots the first two components and (b) plots the 3rd and 4th components.







Figure 6: RDA ordination diagrams showing the distribution of 33 species (red text) and 8 topographic variables (blue arrows). The axes show the site and species scores using type II scaling. The blue vectors represent the 8 environmental variables and their lengths are proportional to their correlation with the axes. The placement of the species centroid and environmental arrow relative to the origin is the direction in which it increases in abundance. Each axis is a linear combination of the environmental variables. (a) plots the first two components and (b) plots the 3rd and 4th components.



Figure 7: Variation partitioning results of species abundance matrix against topography and spatial PCNM variables. The box represents 100% of the variation in the species data. The Venn diagram indicates the fraction of variation explained by the sets of variables: (a) = pure topographic ("topo"), (b) = pure space, (c) = shared by topography and space. The shared partition (c) is the variation in the species data that could be explained by both spatial matrices. The remaining residual variation cannot be explained by the modelled variables. The reported fractions are adjusted R² statistics.



Values <0 not shown

Figure 8: Variation partitioning results of species abundance matrix against topography and fine and broad scale spatial PCNM variables. The box represents 100% of the variation in the species data. The Venn diagram indicates the fraction of variation explained by the sets of variables: (a) = pure topographic, (b) = pure broadscale, (c) = pure fine scale, (b + e + c) = pure space, (d) = shared by topography and broad scale, (f) = shared by topography and fine scale. The shared partitions (d,e,f) is the variation in the species data that could be explained by both spatial matrices. The remaining residual variation cannot be explained by the modelled variables. The total variation does not add exactly to 1 because g is negative explained variation produced as an artifact of the variation partioning procedure. The reported fractions are adjusted R^2 statistics.

a) Fraxinus spp.



b) Acer saccharum



c) Fagus grandifolia



d) Juglans nigra



e) Quercus rubra



Figure 9: Plots of regression coefficients from model of abundance of three size classes (small, medium, big) of five focal tree species (*Fraxinus spp., A. saccharum, F. grandifolia, J. nigra*, and *Q. rubra*) in response to five environmental variables (**RDA1, RDA2, RDA3, RDA4, human disturbance ("land43")).** The first three variables are the size class means per species. The relationship between abundance of *Fraxinus spp., J. nigra* and *Q. rubra* and the environmental variable was dependent on size class for at least one axis. Confidence intervals (alpha=0.01) are shown as horizontal lines.



Figure 10: Total count in McMaster Forest of each size class for the six focal tree species. The counts are partitioned by size classes: big trees (\geq 15 cm; dark gray), medium trees (\geq 5 cm and <15 cm; light gray) and small trees (<5 cm; white).







80

60

40

20

0

Count



DBH range

e) Q. rubura



f) T. canadensis



(1000) (1000)

DBH range

32

Figure 11: DBH distribution for all focal species. Size groups cover a DBH range of 5 cm (except smallest which does not include individuals <1 cm). (a) *Fraxinus spp.* (b)

A. saccharum (c) *F. grandifolia* (d) *J. nigra* (e) *Q. rubra* (f) *T. canadensis. Fraxinus spp., A. saccharum* and *F. grandifolia* size structure shows many small individuals, with count quickly falling as DBH size increases. *T. canadensis* has severe declines in individuals <10 cm.

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M.Sc. Thesis - S. L. Muñoz

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APPENDIX

Supplementary Tables

Table S1: The 33 most abundant (n > 10) species of woody stem plants in the plot represented by 26 genera and 17 families.

Species				
code	Genus	Species	Family	Common name
ACERFRE	Acer	X freemanii	ACERACEAE	Freeman's maple
ACERNEG	Acer	negundo	ACERACEAE	Manitoba maple
ACERSAN	Acer	saccharum	ACERACEAE	Black maple
ACERSAS	Acer	saccharum	ACERACEAE	Sugar maple
ALNUGLU	Alnus	glutinosa	BETULACEAE	European alder
AMEL	Amelanchier	spp	ROSACEAE	Serviceberry
BETUALL	Betula	alleghaniensis	BETULACEAE	Yellow birch
BETUPAP	Betula	papyrifera	BETULACEAE	Paper birch
CARPCAR	Carpinus	caroliniana	BETULACEAE	Musclewood
CARYCOR	Carya	cordiformis	JUGLANDACEAE	Bitternut hickory
				Alternate-leaved
CORNALT	Cornus	alternifolia	CORNACEAE	dogwood
		foemina ssp		
CORNFOR	Cornus	racemosa	CORNACEAE	Gray dogwood
CRAT	Crataegus	spp	ROSACEAE	Hawthorn
FAGUGRA	Fagus	grandifolia	FAGACEAE	American beech
FRAX	Fraxinus	spp	OLEACEAE	Ash
HAMAVIR	Hamamelis	virginiana	HAMAMELIDACEAE	Witchhazel
JUGLCIN	Juglans	cinerea	JUGLANDACEAE	Butternut
JUGLNIG	Juglans	nigra	JUGLANDACEAE	Black walnut
LINDBEN	Lindera	benzoin	LAURACEAE	Spicebush

				Tartarian
LONITAT	Lonicera	tatarica	CAPRIFOLIACEAE	honeysuckle
OSTRVIR	Ostrya	virginiana	BETULACEAE	Ironwood
PINUSTR	Pinus	strobus	PINACEAE	White pine
POPUGRA	Populus	grandidentata	SALICACEAE	Big-tooth aspen
PRUNSER	Prunus	serotina	ROSACEAE	Black cherry
PRUNVIV	Prunus	virginiana	ROSACEAE	Chokecherry
QUERRUB	Quercus	rubra	FAGACEAE	Red oak
RHAMCAT	Rhamnus	cathartica	RHAMNACEAE	Staghorn sumac
				European
RHUSTYP	Rhus	typhina	ANACARDIACEAE	buckthorn
SALI	Salix	spp	SALICACEAE	Willow
				American
TILIAME	Tilia	americana	TILIACEAE	basswood
TSUGCAN	Tsuga	canadensis	PINACEAE	Eastern hemlock
ULMUAME	Ulmus	americana	ULMACEAE	American elm
VITIRIP	Vitis	riparia	VITACEAE	Riverbank grape

	RDA1	RDA2	RDA3	RDA4
A. saccharum	-0.9117	-0.1649	0.1390	-0.1901
F. grandifolia	-0.5019	0.1344	-0.2116	0.0683
Fraxinus spp.	0.0920	-0.4800	0.1688	0.1314
J. nigra	0.7048	-0.1011	-0.1134	-0.0759
Q. rubra	-0.0713	0.1692	0.0129	-0.0433
T. canadensis	-0.2917	0.0259	-0.1476	-0.0108

Table S2: Species scores on significant RDA axes from the RDA of 8 topographic
variables and 33 most abundant species.

Table S3: Significant PCNMs chosen by forward selection using community composition data. Broad scale PCNMs are coloured green and fine scale are coloured pink. PCNMs are sorted by descending adjusted R² value.

			Cum.		
	Variable	Adjusted R ²	adjusted R ²	Cum. R^2	P value
1	PCNM 10	0.0503	0.0503	0.0534	0.0010
2	PCNM 7	0.0445	0.0948	0.1008	0.0010
3	PCNM 1	0.0336	0.1284	0.1370	0.0010
4	PCNM 2	0.0293	0.1577	0.1689	0.0010
5	PCNM 9	0.0262	0.1839	0.1974	0.0010
6	PCNM 19	0.0236	0.2075	0.2232	0.0010
7	PCNM 12	0.0215	0.2290	0.2469	0.0010
8	PCNM 6	0.0207	0.3188	0.3459	0.0010
9	PCNM 18	0.0180	0.2470	0.2670	0.0010
10	PCNM 4	0.0178	0.2648	0.2867	0.0010
11	PCNM 16	0.0170	0.2817	0.3055	0.0010
12	PCNM 15	0.0164	0.2981	0.3237	0.0010
13	PCNM 14	0.0145	0.3334	0.3621	0.0010
14	PCNM 38	0.0130	0.3695	0.4029	0.0010
15	PCNM 36	0.0117	0.3450	0.3754	0.0010
16	PCNM 39	0.0115	0.3565	0.3884	0.0010
17	PCNM 37	0.0114	0.3809	0.4157	0.0010
18	PCNM 23	0.0106	0.3915	0.4278	0.0010
19	PCNM 31	0.0089	0.4090	0.4482	0.0010
20	PCNM 42	0.0086	0.4001	0.4378	0.0010
21	PCNM 44	0.0085	0.4175	0.4580	0.0010
22	PCNM 3	0.0082	0.4257	0.4675	0.0010
23	PCNM 17	0.0080	0.4337	0.4768	0.0010
24	PCNM 33	0.0080	0.4562	0.5030	0.0010
25	PCNM 13	0.0078	0.4415	0.4859	0.0010
26	PCNM 78	0.0072	0.4883	0.5408	0.0010
27	PCNM 24	0.0067	0.4482	0.4939	0.0010
28	PCNM 30	0.0066	0.4628	0.5108	0.0010
29	PCNM 54	0.0064	0.4692	0.5184	0.0010
30	PCNM 63	0.0062	0.4754	0.5258	0.0010

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31	PCNM 25	0.0057	0.4811	0.5327	0.0010
32	PCNM 75	0.0053	0.5125	0.5706	0.0010
33	PCNM 26	0.0048	0.5026	0.5586	0.0010
34	PCNM 67	0.0048	0.4931	0.5468	0.0010
35	PCNM 35	0.0046	0.4977	0.5526	0.0010
36	PCNM 29	0.0046	0.5072	0.5643	0.0010
37	PCNM 73	0.0044	0.5169	0.5761	0.0010
38	PCNM 85	0.0043	0.5332	0.5965	0.0010
39	PCNM 70	0.0042	0.5288	0.5912	0.0010
40	PCNM 50	0.0039	0.5208	0.5811	0.0010
41	PCNM 88	0.0039	0.5370	0.6014	0.0010
42	PCNM 59	0.0038	0.5246	0.5860	0.0010
43	PCNM 79	0.0036	0.5406	0.6060	0.0020
44	PCNM 81	0.0033	0.5439	0.6104	0.0010
45	PCNM 93	0.0030	0.5587	0.6303	0.0030
46	PCNM 68	0.0030	0.5528	0.6224	0.0010
47	PCNM 97	0.0030	0.5469	0.6144	0.0010
48	PCNM 82	0.0029	0.5498	0.6184	0.0030
49	PCNM 117	0.0029	0.5921	0.6758	0.0020
50	PCNM 74	0.0029	0.5557	0.6263	0.0030
51	PCNM 89	0.0029	0.5616	0.6342	0.0020
52	PCNM 136	0.0029	0.5644	0.6380	0.0030
53	PCNM 41	0.0028	0.5673	0.6418	0.0020
54	PCNM 147	0.0026	0.5699	0.6454	0.0020
55	PCNM 95	0.0025	0.5724	0.6489	0.0020
56	PCNM 77	0.0025	0.5845	0.6657	0.0020
57	PCNM 55	0.0025	0.5820	0.6623	0.0030
58	PCNM 138	0.0025	0.5749	0.6523	0.0040
59	PCNM 145	0.0024	0.5869	0.6690	0.0020
60	PCNM 113	0.0024	0.5772	0.6556	0.0030
61	PCNM 92	0.0023	0.5795	0.6589	0.0040
62	PCNM 112	0.0023	0.5892	0.6721	0.0050
63	PCNM 116	0.0022	0.6139	0.7085	0.0090
64	PCNM 71	0.0020	0.5961	0.6817	0.0060
65	PCNM 107	0.0020	0.5941	0.6787	0.0050
66	PCNM 60	0.0019	0.5980	0.6845	0.0110

67	PCNM 101	0.0018	0.6033	0.6926	0.0120
68	PCNM 22	0.0018	0.6051	0.6953	0.0130
69	PCNM 156	0.0018	0.6247	0.7253	0.0110
70	PCNM 72	0.0018	0.6015	0.6899	0.0090
71	PCNM 45	0.0018	0.5998	0.6872	0.0140
72	PCNM 129	0.0017	0.6068	0.6980	0.0060
73	PCNM 127	0.0017	0.6085	0.7005	0.0150
74	PCNM 155	0.0016	0.6101	0.7031	0.0190
75	PCNM 109	0.0016	0.6117	0.7056	0.0110
76	PCNM 124	0.0016	0.6155	0.7110	0.0190
77	PCNM 131	0.0016	0.6170	0.7134	0.0130
78	PCNM 52	0.0015	0.6229	0.7228	0.0180
79	PCNM 69	0.0015	0.6185	0.7158	0.0250
80	PCNM 11	0.0014	0.6214	0.7204	0.0170
81	PCNM 58	0.0014	0.6200	0.7181	0.0210
82	PCNM 154	0.0012	0.6259	0.7274	0.0450

Supplementary figures



Figure S1: Map of McMaster Forest plot (500 x 400 m) with contour lines of elevation. The 500 quadrats (each measuring 20 x 20 m) are represented by the smallest squares. The blue line is the creek. Contour lines are shown for every 5 m change in elevation.



Figure S2: Bar graph of the count of individuals per species for the 23 species with >40 individuals. The graph shows the dominance of three species (*A. saccharum*, *Fraxinus spp.*, and *C. foemina ssp. racemosa*) as well as the count of three growth forms (tree, shrub, and woody vine).



Figure S3: Biplot of the first two principal components from the PCA of all 33 species with at least 10 individuals. Grey numbers are sites and blue arrows are species. More similar points are plotted closer together while dissimilar sites and species are placed further apart. The relationship between points depends on the axes on which the points are plotted.



Figure S4: Map of big trees (\geq 15 cm DBH) belonging to the focal species. Shows the non-random pattern of species distributions. Even though habitat associations appear to weaken through size, the differences between species are still pronounced even for big trees. There is a separation in habitat between *J. nigra* and *A. saccharum*, and *Fraxinus spp.* has an intermediate distribution between them.



Figure S5: Maps of the fitted scores of two significant canonical axes modelling spatial structure from the PCNM analysis on the McMaster Forest community. The size of the circles are proportional to its associated value; black and red colors indicate positive and negative signs of the value associated to the circle, respectively. (a) PCNM10 representing broad scale, (b) PCNM36 representing fine scale.