Minnesota State University, Mankato

Cornerstone: A Collection of Scholarly and Creative Works for Minnesota State University, Mankato

All Graduate Theses, Dissertations, and Other Capstone Projects

Graduate Theses, Dissertations, and Other Capstone Projects

2023

Environmental Heterogeneity as a Driver of Understory Vegetation Composition in Midwestern Oak Savannas

Jean Pengra
Minnesota State University, Mankato

Follow this and additional works at: https://cornerstone.lib.mnsu.edu/etds

Part of the Biology Commons

Recommended Citation

Pengra, Jean R. (2023). *Environmental Heterogeneity as a Driver of Understory Vegetation Composition in Midwestern Oak Savannas* [Master's thesis, Minnesota State University, Mankato]. Cornerstone: A Collection of Scholarly and Creative Works for Minnesota State University, Mankato. https://cornerstone.lib.mnsu.edu/etds/1392/

This Thesis is brought to you for free and open access by the Graduate Theses, Dissertations, and Other Capstone Projects at Cornerstone: A Collection of Scholarly and Creative Works for Minnesota State University, Mankato. It has been accepted for inclusion in All Graduate Theses, Dissertations, and Other Capstone Projects by an authorized administrator of Cornerstone: A Collection of Scholarly and Creative Works for Minnesota State University, Mankato.

Environmental Heterogeneity as a Driver of Understory Vegetation Composition in Midwestern Oak Savannas

By

Jean R. Pengra

A Thesis Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

In

Biological Science

Minnesota State University, Mankato

Mankato, Minnesota

September 2023

September 22nd, 2023

Environmental Heterogeneity as a Driver of Understory Vegetation Composition in Midwestern Oak Savannas

Jean R. Pengra

This thesis has been examined and approved by the following members of the student's committee.

Advisor

Committee Member

Committee Member

Table of Contents

Acknowledgements

Thank you to the Vonderhaar family, the Darlene and William Radichel Herbarium, and the MNSU Graduate Studies Department for your assistance in funding this project. Thank you to the Nature Conservancy, the US Fish and Wildlife Service, the University of Minnesota, and the City of Burnsville for the generous use of their lands. Thank you to Ryan Wersal, PhD, and Mriganka De, PhD, for your valuable input as committee members. Thank you to Matthew Kaproth, PhD, for leading my committee and providing me with the much-needed support and flexibility to push through a hard two years. Thank you to Jenna Eklund, whose field assistance made this project possible, not to mention much (much) more enjoyable. Thank you to my parents, Ellen and Bruce Pengra, for their encouragement and support. Finally - thank you to Ashley Selee, Maxwell Gebhart, and Hunter Mayhew, for being the kindest cohort I could ask for during our time at MNSU.

Research done on this project was carried out on the traditional homelands of the Dakota and Ojibwe peoples, many of whom were forcibly driven away or killed by violent settler colonialism. We would also like to acknowledge the history the Ottawa Bluffs site as a former burial place for local indigenous peoples and encourage proper respect and reverence for the land.

Abstract

The following thesis is submitted as two chapters. Chapter one contains background information, literature review, and predictions. Chapter two is formatted as a paper submission to *Invasive Plant Science and Management.* Note that this journal requires a combined results and discussion section and a summary of management implications written after the abstract. The appendix contains supplementary materials that are relevant to study hypotheses but do not necessarily align with the scope of the article submission.

Oak (*Quercus spp.*) savannas are one of the most threatened ecological systems within the United States. Like many ecotones, these savannas are considered biodiversity hotspots due to their high environmental heterogeneity (EH). While select studies have assessed how EH in oak savannas relates to the success of individual species, less work has been completed on a community scale. To better inform management targets, quadrat-based understory vegetation surveys were taken alongside measurements of soil moisture, canopy cover, and elevation in a nested plot design. Two definitions of EH, horizontal heterogeneity (total variation over area) and spatial heterogeneity (intensity of clustering), were used to assess EH-vegetation quality relationships using generalized mixed linear models with nested covariates for study sites and plots. Metrics of vegetation diversity and quality included native richness, native cover, potential native vegetation (PNV), woody cover, exotic richness, and exotic cover. Species richness was intentionally omitted due to a strong link with woody cover and higher ratios of exotic to native abundance. Both horizontal and spatial metrics of canopy cover heterogeneity had only positive or neutral associations with vegetation quality and diversity metrics. More specifically, greater variation of canopy cover values was associated with higher percentages of savanna-associated vegetation (PNV) and lower exotic richness. Increases in native richness were observed alongside greater distinctiveness of shade and light patches, suggesting a significant role of niche partitioning in this environment. Soil moisture heterogeneity models had mixed effects on vegetation quality and diversity. Further experimentation is likely necessary to separate the roles of canopy shading and woody encroachment on resulting EH trends. Elevational heterogeneity had a moderate negative association with native species richness – an unexpected finding affirming previous results suggesting that steeper areas decrease native richness within this environment. These EH-vegetation quality trends may be partially explained by differences in how habit generalists and specialists respond to gradients in EH. More specifically, higher EH increased the presence of light specialist species and decreased shade specialist species, whereas high EH increased soil moisture generalists and decreased both moist and dry soil specialists. Model quality was consistently highest at the medium spatial extent (12 by 12 m), suggesting that environmental controls on the microclimatic scale have a strong impact on resulting savanna vegetation.

Chapter 1: Study Justification and Predictions

Introduction

Establishment and maintenance of oak (*Quercus spp.*)-dominated savannas requires a persistent disturbance regime of fire, grazing, and drought. The recommended management regime reduces woody plant encroachment into what would otherwise become a woodland, leaving a prairie-like understory with nearly full coverage of graminoids and forbs and a well-spaced stand of fire-resistant oak trees (Anderson 1998; Campbell et al. 1994; Dey and Kabrick 2015; Grimm 1984; Nuzzo 1986; Peterson and Reich 2001). Predating US settler-colonialism, midwestern oak savanna was maintained through spreading prairie fires and the trampling and grazing of large ungulates such as the American Bison [*Bison bison* (*L.*)] (Campbell et al. 1994; Grimm 1984; Nuzzo 1986). Oak savannas covered wide swaths of the prairie-forest border, spanning an estimated 10-13 million hectares at their peak (Anderson 1998; Brudvig and Asbjornsen 2008). However, due to modern land use, fire suppression, and the near extinction of the American Bison, these savannas have become one of the most threatened ecosystem types in the US (Nuzzo 1986).

Environmental characteristics and vegetation patterns of oak savannas are not well characterized compared to similar ecosystems or other ecotones. It was not until the mid-late 20th century that oak savannas were identified as distinct phenomenon worthy of study (Grimm 1984; Nuzzo 1986). Environmental variables such as canopy cover, soil characteristics, or topography, have been generally described, but there are fewer studies linking these characteristics with elements of savanna structure and function (Aaseng et al. 2011; Leach and Givnish 1999; Schetter et al. 2013; Walsh 2017).

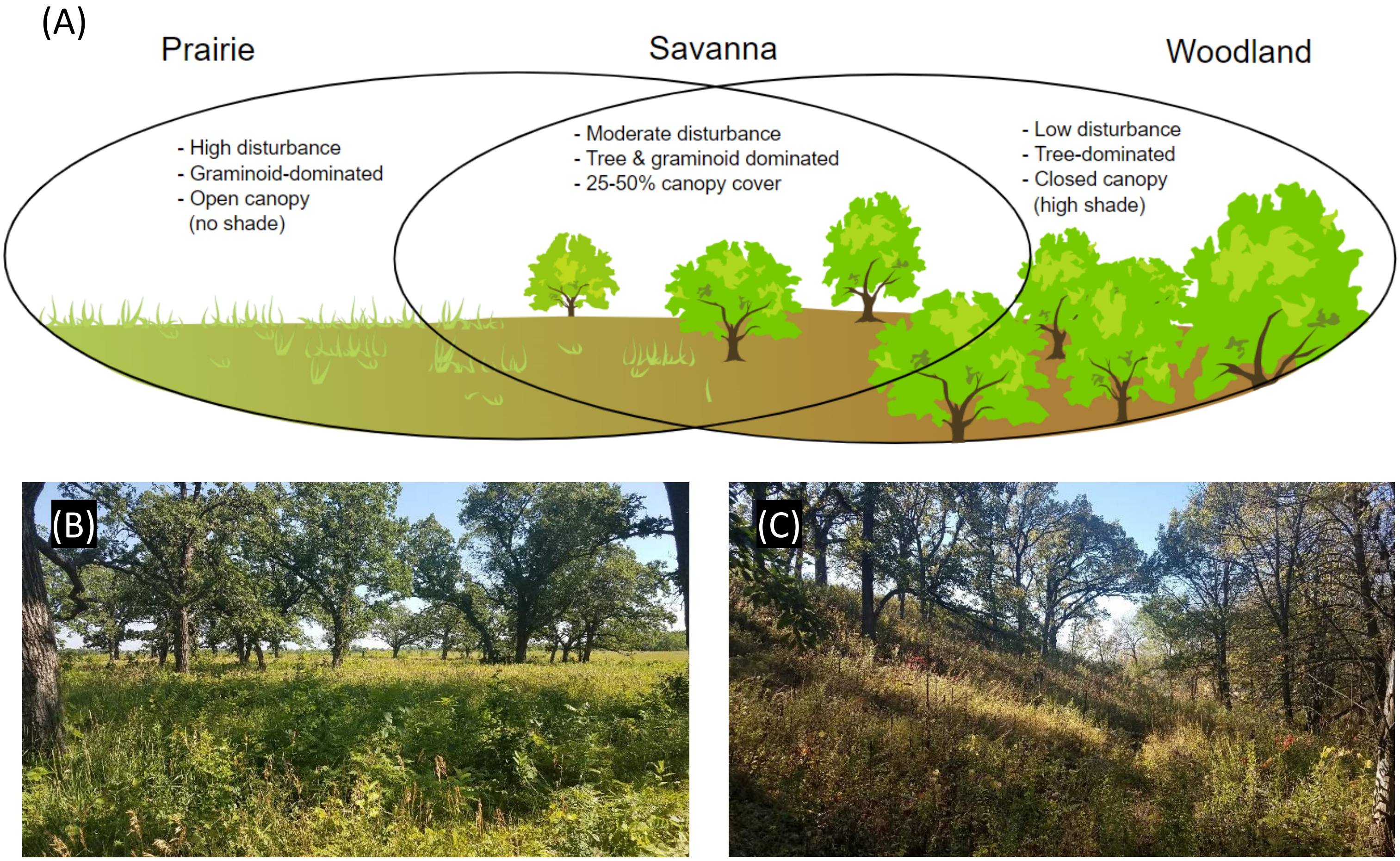


Figure 1. Examples of Oak Savanna systems. *Illustration of the prairie-savanna-woodland continuum (A) and imagery of (B) Rapids Lake Unit, and (C) Ottawa Bluffs study sites depict the highly heterogenous character of savanna systems.*

Like many ecotones, oak savannas have a high degree of environmental heterogeneity (EH). This is most evident in their high-contrast patches of shade and light, but may also manifest as differences in moisture, heat load, soil character, or topographical difference. The habitat heterogeneity hypothesis states that EH at multiple scales (biome, ecosystem, local area, microclimate, etc.) improves species richness in almost all cases (Blonder et al. 2018; Deák et al.

2021; Scheffers et al. 2017; Stein et al. 2014; Suggitt et al. 2018). This is most likely due to increased opportunities for niche partitioning and environmental filtering (Helbach et al. 2022; Willis et al. 2009). In cases where environmental heterogeneity does not increase species richness, there is generally a neutral relationship or non-directional relationship (unimodal distribution); negative relationships are extremely uncommon (Lundholm 2009). Similarly, high EH is thought to be key in characterizing the unique mix of prairie and woodland vegetation present in oak savannas (Haworth and McPherson 1995; Leach and Givnish 1998; Lettow et al. 2014; Schetter et al. 2013; Walsh 2017). The role of EH in oak savannas has been a somewhat active topic of research. However, other work has focused on light availability, heat load, and proximity to anthropogenic disturbance (Lettow et al. 2014; Schetter et al. 2013; Volder et al. 2013; Walsh 2017; Weiher 2003), with lesser study into the impacts of soil character, topography, or coupled environmental effects.

Heterogeneity of canopy cover has been a focus of past research, with results suggesting it to be a critical factor in habitat quality for several native organisms (Davis et al. 2019; Leach and Givnish 1999; Walsh 2017). For example, a co-dependent pair of threatened organisms - the karner blue butterfly [*Plebejus samuelis* (Nabokov)] and wild blue lupine [*Lupinus perennis* (L.)] - may be fully dependent on oak savannas as a refugia. One study directly tied species success to environmental heterogeneity, as savannas with more heterogenous light availability and heat load hosted significantly more of both species (Walsh 2017). Many charismatic bird species may also be reliant on oak savanna such as the red headed woodpecker [*Melanerpes erythrocephalus* (L.)], northern bobwhite [*Colinus virginianus* (L.)], mourning dove [*Zenaida macroura* (L.)], indigo bunting [*Passerina cyanea* (L.)], and Baltimore oriole [*Icterus galbula* (L.)] (Brawn 2006). Critical thresholds of openness of the environment and rates of woody turnover are likely important for these bird’s life history strategies, especially considering nesting behaviors (Brawn 1998, 2006). The full extent of species endemic to or reliant on midwestern oak savanna is likely broader due to the need for additional knowledge on this ecosystem.

The presence of highly heterogenous environments is thought to be a buffer against broader biodiversity loss (Blonder et al. 2018; De Pauw et al. 2022; Munson 2013; Suggitt et al. 2018). This is especially true in times of environmental stress. Spatially heterogenous areas can create local microrefugia for species which may not be able to tolerate quick changes in temperature or drought stress (De Pauw et al. 2022; Lindgren et al. 2018). Similar observations have been made with anthropogenic disturbances - larger, more complex transition zones away from logged or farmed areas into forests significantly increases species diversity (Blonder et al. 2018; Lindgren et al. 2018). Quality management of oak savanna and other ecotone systems may provide a novel tool for preservation of biodiversity on a greater scale than the management of the parent systems alone.

Considering the likely importance of EH on savanna ecosystem dynamics, a greater understanding of these environmental characteristics is necessary in order to improve on current restoration practices (Brudvig and Asbjornsen 2008; Walsh 2017). To address this need, the following study aims to help scientists and land managers better understand the relationship between EH of canopy cover, topography, and soil moisture, and key management outcomes of understory diversity and quality in midwestern oak savanna systems. Results may be used to refine restoration techniques, improve site selection, and answer important scientific questions about how environmental variation relates to habitat quality in complex ecotone environments.

Research Questions:

(1) Does EH drive community composition in midwestern oak savannas (as defined by species richness, native/exotic presence, woody cover, or potential native vegetation (PNV))?

(2) How does composition of understory vegetation change along gradients of canopy cover and soil moisture within midwestern oak savannas?

(3) At what scale (site, plot, around quadrat, single quadrat) are these effects most prominent?

Hypotheses:

(1.A) Horizontal heterogeneity of canopy cover and topography increase species richness and desired management outcomes in oak savannas due to increased opportunities for niche partitioning and environmental filtering. Horizontal soil moisture heterogeneity decreases metrics of diversity and quality due to a strong association with woody encroachment.

(1.B) Spatial heterogeneity, as defined by the intensity of clustering or discreteness of patches, increases metrics of understory diversity and quality as more habitat patches are formed and increase availability distinctive niche partitioning and microrefugia.

(2) Due to the dominance of prairie species in these systems, higher average canopy cover and soil moisture values act to decrease metrics of understory diversity and quality.

(3) Scale of greatest influence will vary dependent on dominant physical controls for each environmental variable. For soil moisture, control will rely both on canopy shade and root system influences, and thus be influential on a smaller scale than canopy cover which is influenced by tree size and clustering.

Literature Review

Oak Savanna Characteristics & Definitions

There are some discrepancies in identifying habitat that constitutes oak savanna. Definitions typically cite tree cover as a dominant factor, but there is disagreement regarding how much cover is required. Averages range from ~20-50%, with some definitions as high as 70%, and others as low as 10% (Aaseng et al. 2011; Bucini et al. 2017). Above a threshold of ~70-80%, light availability may become too low for savanna-associated understory communities to survive (Bucini et al. 2017). Conversely, low canopy coverage (<10%) may cause prairie-pattern communities to develop (Anderson 1998; Bucini et al. 2017). Some argue that % canopy coverage is an inept metric for defining savannas altogether, and that patterns of 'oak spread' or 'oak openness' are more useful as a functional ecosystem trait (Leach and Givinish 1998). Oak spread describes the ability of oak trees, especially bur oak [*Quercus macrocarpa* (Michx.)], to spread out into a well-spaced canopy with many lower branches, creating a pattern of patchy shade and frequent sun flecks. Additional definitions reject a formalized habitat classification, favoring a focus on the relationships between prairies, savannas, and woodlands as an ongoing continuum based on disturbance (Anderson 1998). While useful as a concept, most prairies, savannas, and woodlands conform to structural and community patterns that can be identified through discrete thresholds (Bucini et al. 2017).

In addition to canopy cover, oak savannas are strongly defined by their understory community. Not all species which may survive in a prairie or a woodland will survive in an oak savanna, and small differences within environmental characteristics such as water availability or soil nutrient content can result in vastly different community structures, defined as entirely different sub-classifications of oak savanna by some experts (Aaseng et al. 2011). Understory plant communities are a common choice for delineating habitat types as this category is present in all types of terrestrial environments and is typically more sensitive to environmental difference than mid-story or overstory vegetation (Aaseng et al. 2011; Rollinson et al. 2021). For this same reason, EH is likely to play its greatest role in the understory. The most dominant species in oak savanna understories are prairie grasses such as little bluestem [*Schizachyrium scoparium* (Michx.) Nash], porcupine grass [*Stipa spartea* (Trin.) Barkworth], and big bluestem [*Andropogon gerardii* (Vitman)] (Aaseng et al., 2011). Woodland-pattern vegetation is less dominant within savannas but includes species such as Virginia creeper [*Parthenocissus quinquefolia* (L.) Planch.] and Pennsylvania sedge [*Carex pensylvanica* (Lam.)] (Aaseng et al., 2011). A commonality between many of these species is that they are generalists in terms of their light requirements or otherwise thrive in highly disturbed areas. For the purposes of this proposal, an oak savanna will be defined as an area with an overstory of primarily oak trees, ~10-50% average canopy cover, and a history of an understory dominated by prairie grasses and forbs as specified by Minnesota NPC class UPs14 (Table 1) (Aaseng et al. 2011)

Table 1. Observed frequency & cover of species in Minnesota UPs14 classified savannas. **Erect, Smooth, or Illinois carrion-flower (Smilax ecirrata, S. herbacea, or S. illinoensis) **Tall wormwood or Tarragon (Artemisia dracunculus or A. campestris) (Table from Aasang et al., 2011)*

Forbs, Ferns & Fern Allies	**Freq (%)**	**Cover**
Western ragweed (*Ambrosia psilostachya*)	80	●●
Virginia ground cherry (*Physalis virginiana*)	73	●
Hairy puccoon (*Lithospermum caroliniense*)	70	●
Gray goldenrod (*Solidago nemoralis*)	67	●
Hoary frostweed (*Helianthemum bicknellii*)	67	●
Horseweed (*Conyza canadensis*)	60	●
White sage (*Artemisia ludoviciana*)	53	●
Bearded birdfoot violet (*Viola palmata*)	53	●
Starry false Solomon's seal (*Smilacina stellata*)	47	●
Purple prairie clover (*Dalea purpurea*)	47	●
Common milkweed (*Asclepias syriaca*)	40	●
Long-headed thimbleweed (*Anemone cylindrica*)	40	●
Hoary puccoon (*Lithospermum canescens*)	40	●
Prairie pinweed (*Lechea stricta*)	33	●
Round-headed bush clover (*Lespedeza capitata*)	33	●
Skyblue aster (*Aster oolentangiensis*)	33	●
Rough blazing star (*Liatris aspera*)	33	●
Rock spikemoss (*Selaginella rupestris*)	30	●
Missouri goldenrod (*Solidago missouriensis*)	30	●
Bird's foot coreopsis (*Coreopsis palmata*)	30	●
Harebell (*Campanula rotundifolia*)	30	●
Hairy golden aster (*Chrysopsis villosa*)	30	●
Bastard toad-flax (*Commandra umbellata*)	30	●
Heath aster (*Aster ericoides*)	27	●
Showy goldenrod (*Solidago speciosa*)	27	●
Flowering spurge (*Euphorbia corollata*)	23	●
Mock pennyroyal (*Hedeoma hispida*)	23	●
Large-flowered beard tongue (*Penstemon grandifloras*)	23	●
Erect, Smooth, or Illinois carrion-flower*	23	●
Tall cinquefoil (*Potentilla arguta*)	23	●
Stiff sunflower (*Helianthus pauciflorus*)	20	●●
Horsemint (*Monarda punctata*)	20	●●
Tall wormwood or Tarragon**	20	●
Silky prairie clover (*Dalea villosa*)	17	●

Grasses & sedges	**Freq (%)**	**Cover**
Junegrass (*Koeleria pyramidata*)	80	●
Porcupine grass (*Stipa spartea*)	73	●●●
Little bluestem (*Schizachyrium scoparium*)	70	●●●
Big bluestem (*Andropogon gerardii*)	67	●●
Hay sedge (*Carex foenea*)	53	●●
Purple lovegrass (*Eragrostis spectabilis*)	53	●
Indian grass (*Sorghastrum nutans*)	40	●●●
Muhlenberg's sedge (*Carex muhlenbergia*)	37	●●
Pennsylvania sedge (*Carex pensylvanica* var. *pensylvanica*)	37	●●
Sand reed-grass (*Calamovilfa longifolia*)	37	●
Switchgrass (*Panicum virgatum*)	37	●
Prairie dropseed (*Sporobolus heterolepis*)	37	●●
Long-leaved panic grass (*Panicum perlongum*)	37	●
Scribner's panic grass (*Panicum oligosanthes*)	30	●●
Hairy grama (*Bouteloua hirsuta*)	30	●
Side-oats grama (*Bouteloua curtipendula*)	23	●●●
Fall witch grass (*Leptoloma cognatum*)	23	●
Woody vines		
Virginia creeper (*Parthenocissus vitacea* or *P. quinquefolia*)	47	●
Semi-shrubs		
Leadplant (*Amorpha canescens*)	53	●●
Prairie rose (*Rosa arkansana*)	43	●
Shrubs		
Chokecherry (*Prunus virginiana*)	50	●
American hazelnut (*Corylus americana*)	43	●
Smooth sumac (*Rhus glabra*)	40	●●
Low or Saskatoon juneberry (*Amelanchier humilis or A. alnifolia*)	37	●

Trees	**Canopy**		**Shrub layer**	
	Freq (%)	**Cover**	**Freq (%)**	**Cover**
Bur oak (*Quercus macrocarpa*)	43	●●●	67	●
Northern pin oak (*Quercus ellipsoidalis*)	27	●●●	37	●
Black oak (*Quercus velutina*)	23	●●●	23	●●
Jack pine (*Pinus banksiana*)	17	●●●	17	●

Environmental Heterogeneity

Environmental heterogeneity can be defined as the number of habitat types or the degree of variation in environmental factors within a given area (Pincebourde et al. 2016). The current study, taking place on the habitat scale, will use the latter definition based on environmental variation. EH can be notably difficult to conceptualize within an applied context. The spatial scale studied and resolution of measurements taken within that space can vastly change interpretation. Selections of scale and resolution are often made based on the research questions at hand. When the most biologically relevant scale of analysis is unknown, one may use an experimental design with nested windows of analysis to better understand the influence of scale in that system (De Pauw et al. 2022; Deák et al. 2021; Schetter et al. 2013; Walsh 2017).

For example, one study examining species richness and invasive species presence in a mixed-disturbance oak savanna found that there were significant differences in 60 m and 120 m nested diameter windows at predicting both invasive species presence and overall species richness in understory vegetation (Schetter et al. 2013). This window size was intended to investigate broader trends in heterogeneity related to anthropogenic habitat fragmentation. Additionally, these results showed a significant negative relationship between topographic heterogeneity and native species richness, contrary to most investigations on the habitat heterogeneity hypothesis (Schetter et al. 2013). These outcomes were thought to be indicative of the impact of anthropogenic disturbance on study site edges and may not be representative of EH-diversity relationships at all scales. In prairie systems, highly localized topographical differences such as hummocks and hallows have shown to significantly increase species richness (Deák et al. 2021).

Another challenge in testing EH-diversity relationships is that the concept of heterogeneity itself can be defined in multiple ways. One definition quantifies the total range or variation present in a variable over a select unit of area. This concept will henceforth be referred to as horizontal heterogeneity. Simple numeric assessments are often used to represent horizontal heterogeneity such as range and standard deviation. Other metrics such as a Shannon index of land cover types or counts of habitat types are also common, but consistency of terminology and quantitative methods is lacking (Stein and Kreft 2015). Alternatively, EH can consider the structuring of resources over physical space. This will be referred to as spatial heterogeneity. Qualitative descriptions of spatial heterogeneity are frequently utilized, and quantitative indices are even more limited and inconsistent, especially at smaller spatial extents (Stein and Kreft 2015). Using either horizontal or spatial heterogeneity in analyses can provide unique advantages. Indexes of horizontal heterogeneity require fewer measurements and typically use easily understood metrics. However, using spatial analysis to understand resource clustering patterns can be helpful in describing the complex role of environmental limitations on plant dispersal and allows for different hypotheses to be tested (Costanza et al. 2011; Mayora et al. 2020; Rammette and Tiejde 2006). The main drawback of this approach is the high volume of data necessary to effectively describe change through physical space. To simplify spatial analyses, data can be taken using an array of survey points along a grid. This collection method suits the needs of both horizontal and spatial heterogeneity analyses and easily facilitates the use of nested windows to quantify EH differences at various spatial extents.

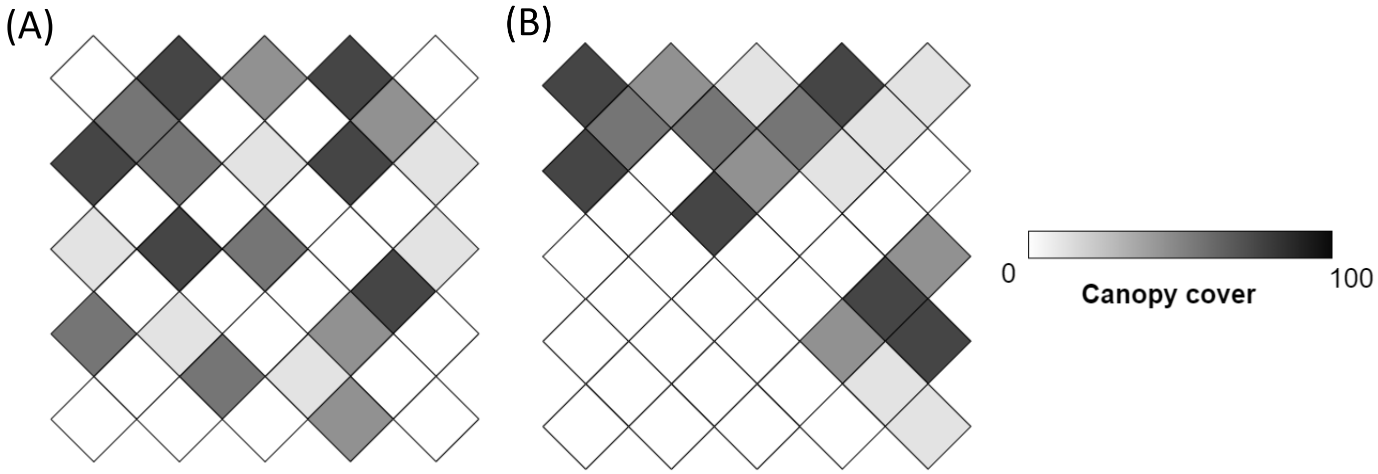


Figure 2. Illustration of canopy cover heterogeneity differences*. Plots A & B have the same number of black, white, and grey squares. This would result in the same horizontal heterogeneity. However, plot A shows a more random pattern while plot B has higher spatial heterogeneity, with distinct 'pockets' of resources which may have different effects on vegetation distribution patterns.*

Microclimate Heterogeneity as a Driver of Oak Savanna Understory Composition

High EH is present in oak savannas compared to similar ecosystems such as woodlands or prairies. Woodland environments have greater average % canopy cover and frequent shrub colonization in areas with upper canopy breaks, making light availability less abundant overall and more patchy in areas where light availability peaks (D'Odorico et al. 2013). For prairies, environmental homogeneity is more evident, with almost all graminoids and forbs receiving similar levels of resource availability, save the influence of topography or infrequent trees (Deák et al. 2021). Conversely, oak savannas feature a stark difference in resource availability between the shade of mature oak trees and fully sun-exposed prairie-like patches – which is thought by some to be their defining feature as a habitat (Haworth and McPherson 1995; Leach and Givnish 1998; Lettow et al. 2014; Schetter et al. 2013; Walsh 2017).

Heterogeneity of soil moisture and topography may also play a role in oak savanna community structure. Soil moisture heterogeneity significantly increases woody encroachment into prairie areas, providing a net negative effect on diversity and habitat quality (Breshears and Barnes 1999; Kleb and Wilson 1997). However, within woodlands, soil moisture heterogeneity has been observed to increase plant diversity away from the influence of habitat edges (Baer et al. 2005). This may be less relevant within the mosaic-like structure of savanna environments where edge space is plentiful. Variation in topography increases biodiversity in prairie areas (Deák et al. 2021) and may indirectly increase biodiversity in woodland areas through impacts on nutrient content and light availability as the angle of the landscape changes (Figure 3) (Fu et al. 2004; Heatherbell 1985; Small and McCarthy 2005).

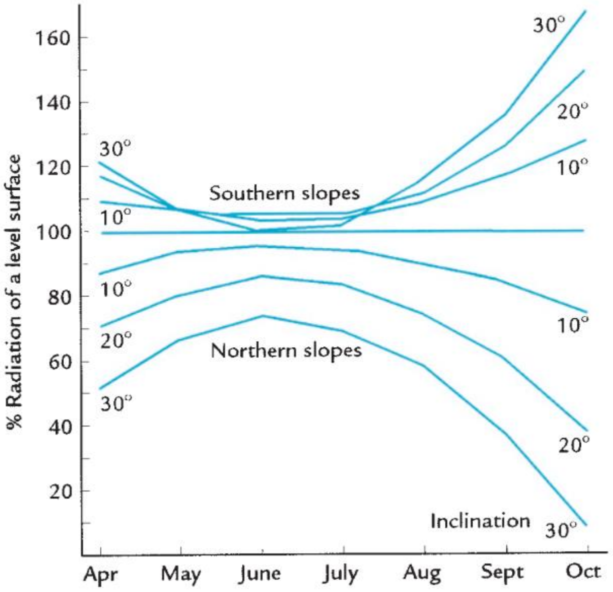


Figure 3. Reception of direct sunlight in relation to position and inclination of slope in the northern hemisphere. *Example is from the upper Rhine Valley, Germany: 48 15'N (from Heatherbell, 1985).*

Topography, soil moisture, and canopy cover may have compounding effects that influence understory composition. The most pertinent example may be their influence of fire regimes. In the case of topography, landforms such as steep hills, cliffs, or waterbodies such as streams and lakes can impact fire's movement across an area. Cliffs and waterbodies can stop fire entirely, while more complex topography can alter its movement as it changes wind patterns and substrate (Fang et al. 2018; Gibson and Hulbert 1987). Canopy cover can impact fire through presence of leaf litter, especially if the canopy has a large proportion of oak trees. Oaks act as an ecosystem engineer, actively facilitating a particular fire regime with their leaf litter (Engber and Varner, 2012; Varner et al., 2015). Leathery oak leaves are slower to decompose due to the presence of highly acidic tannin compounds, allowing them to remain longer, forming a dense layer of flammable tinder for a fire (Engber and Varner, 2012). All these factors come together to facilitate an appropriate regime of fire intensity and frequency within a savanna.

Considering a broad range of ecosystems, there seems to be no universal relationship between the impact of environmental heterogeneity on biodiversity with site size (Lundholm 2009). However, individual ecosystem types tend to have a relevant biological window, or a scale at which where heterogeneity is a stronger driver of biodiversity trends (Costanza et al. 2011; Mayora et al. 2020; Rammette and Tiejde 2006). Smaller scales (<60 m) of analysis are likely necessary to characterize the biologically relevant scale of light heterogeneity in oak savanna understories, as seen in previous examples (Schetter et al. 2013; Walsh 2017).

Predictions

The habitat heterogeneity hypothesis states that high EH increases niche partitioning, allowing for greater overall species diversity (Blonder et al. 2018; Deák et al. 2021; Scheffers et al. 2017; Stein et al. 2014; Suggitt et al. 2018). However, we believe that EH-diversity relationships will differ between heterogeneity of canopy cover, soil moisture, and topography. We predict that metrics of understory diversity and quality will increase with more heterogenous canopy cover as observed in multiple studies in woodland and savanna systems (De Pauw et al. 2022; Helbach et al. 2022; Walsh 2017) (Table 2). This effect may be especially noticeable under high spatial heterogeneity, or where light and shade are well segregated into separate parcels where niche differentiation can effectively occur. Heterogeneous soil moisture, on the other hand, has shown to significantly increase woody encroachment into prairie areas, which will likely act to outcompete prairie vegetation and decrease overall savanna diversity (Breshears and Barnes 1999; Kleb and Wilson 1997). Spatially defined soil moisture heterogeneity, however, may be more beneficial. More concentrated, distinctive wet and dry patches are not likely to be associated with the same meter-to-meter variation often seen alongside woody encroachment. If adequately sized wet and dry patches can be established, niche distinctiveness may function to benefit the system. For topography, we predict that metrics of diversity and quality will improve on steeper, more complex slopes as this is the condition associated with more variation in light and nutrient availability, creating additional micro-niches (Fu et al. 2004; Heatherbell 1985; Small and McCarthy 2005). Note that spatial heterogeneity will not be assessed for this variable and analyses are limited to the largest spatial extent. The impact of canopy cover and soil moisture gradients are predicted to favor drier and sunnier prairie-like conditions due to the high dominance of prairie vegetation within savanna pattern communities (Aaseng et al. 2011).

Table 2. Summary of study predictions. *Positive (+) and negative (-) symbols represent a beneficial or detrimental effect on metrics of understory diversity and quality such as species richness, native or exotic presence, woody cover, and potential native vegetation (PNV). 'Climatic gradient' refers to the direct increase of canopy cover or soil moisture values.*

	Canopy cover	Soil moisture	Topography
Horizontal heterogeneity	+	-	+
Spatial heterogeneity	+	+	n/a
Climatic gradient	-	-	n/a
Scale of greatest influence	Medium (12 by 12 m)	Small (6 by 6 m)	n/a

Predictions for the effects of topographical and soil moisture heterogeneity are more uncertain than effects of canopy cover heterogeneity or climatic gradients. In the case of topography, the only savanna-based study on this relationship observed a negative association between native richness and topographical heterogeneity as measured by greater elevation range over 60 and 120 m windows (Schetter et al. 2013). However, this study notes that results may have stemmed from a strong relationship between high EH and human disturbance at the scale observed. Topographical heterogeneity is the most frequently studied relationship in work on the habitat heterogeneity hypothesis and there is overwhelming evidence in many other systems of a positive relationship between the two variables (Deák et al. 2021; Stein et al. 2014; Stein and Kreft 2015). In the case of soil moisture heterogeneity, most studies have not considered aspects of both spatial and horizontal heterogeneity and fewer have considered impacts across multiple scales. Investigation of this phenomenon under these conditions may provide new perspectives on the relationship between EH and woody encroachment.

It is also possible that the EH present within midwestern oak savannas may not create enough niche differentiation to facilitate an observable effect on metrics of diversity in quality (Helbach et al. 2022). It is possible that dominant oak savanna species, a number of which are light-generalists, have a lesser sensitivity to environmental difference than hypothesized (Aaseng et al. 2011; Chadde 2019). If savanna floral communities are defined more chiefly by their adaptability to a range of resources, rather than a utilization of contrasting niche differentiation, these hypotheses will likely be proven false. Additionally, non-climatic variables such as varying dispersal techniques or overwhelming seed rain from neighboring woodland and prairie systems may be more important in determining overall community composition than those considered in this study (Primack and Miao 1992).

References

Aaseng N, Almendinger J, Robert D, Hanson D, Lee M, Rowe E, Rusterholz K, Wovcha D (2011) Minnesota's native plant community classification: A statewide classification of terrestrial and wetland vegetation based on numerical analysis of plot data. Page 27. 108. St. Paul, MN: Minnesota County Biological Survey, Ecological Land Classification Program, and Natural Heritage and Nongame Research Program. St. Paul: Minnesota Department of Natural Resources

Anderson RC (1998) Overview of Midwestern oak savanna. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:1–18

Baer SG, Collins SL, Blair JM, Knapp AK, Fiedler AK (2005) Soil Heterogeneity Effects on Tallgrass Prairie Community Heterogeneity: An Application of Ecological Theory to Restoration Ecology. Restoration Ecology 13:413–424

Blonder B, Both S, Coomes DA, Elias D, Jucker T, Kvasnica J, Majalap N, Malhi YS, Milodowski D, Riutta T, Svátek M (2018) Extreme and Highly Heterogeneous Microclimates in Selectively Logged Tropical Forests. Frontiers in Forests and Global Change 1:5

Brawn JD (1998) Effects of Oak Savanna Restoration on Avian Populations and Communities in Illinois. Page 53. University of Illinois at Urbana-Champaign: Center for Wildlife Ecology, University of Illinois

Brawn JD (2006) Effects of Restoring Oak Savannas on Bird Communities and Populations. Conservation Biology 20:460–469

Breshears DD, Barnes FJ (1999) Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology 14:465–478

Brudvig LA, Asbjornsen H (2008) Patterns of oak regeneration in a Midwestern savanna restoration experiment. Forest Ecology and Management 255:3019–3025

Bucini G, Beckage B, Gross LJ (2017) Climate seasonality, fire and global patterns of tree cover. Frontiers of Biogeography 9:2

Campbell C, Campbell ID, Blyth CB, McAndrews JH (1994) Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360–362

Chadde S (2019) Minnesota Flora: An Illustrated Guide to the Vascular Plants of Minnesota. 2nd ed. United States: Orchard Innovations. 784 p

Costanza JK, Moody A, Peet RK (2011) Multi-scale environmental heterogeneity as a predictor of plant species richness. Landscape Ecol 26:851–864

Davis FW, Synes NW, Fricker GA, McCullough IM, Serra-Diaz JM, Franklin J, Flint AL (2019) LiDAR-derived topography and forest structure predict fine-scale variation in daily surface temperatures in oak savanna and conifer forest landscapes. Agricultural and Forest Meteorology 269–270:192–202

De Pauw K, Sanczuk P, Meeussen C, Depauw L, De Lombaerde E, Govaert S, Vanneste T, Brunet J, Cousins SAO, Gasperini C, Hedwall P-O, Iacopetti G, Lenoir J, Plue J, Selvi F, Spicher F, Uria-Diez J, Verheyen K, Vangansbeke P, De Frenne P (2022) Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. New Phytologist 233:219–235

Deák B, Kovács B, Rádai Z, Apostolova I, Kelemen A, Kiss R, Lukács K, Palpurina S, Sopotlieva D, Báthori F, Valkó O (2021) Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. Science of The Total Environment 763:144199

Dey DC, Kabrick JM (2015) Restoration of Midwestern Oak Woodlands and Savannas. Pages 401–428 in Restoration of Boreal and Temperate Forests. 2nd ed. Florida: Boca Raton

D'Odorico P, He Y, Collins S, De Wekker SFJ, Engel V, Fuentes JD (2013) Vegetation–microclimate feedbacks in woodland–grassland ecotones. Global Ecology and Biogeography 22:364–379

Fang L, Yang J, White M, Liu Z (2018) Predicting Potential Fire Severity Using Vegetation, Topography and Surface Moisture Availability in a Eurasian Boreal Forest Landscape. Forests 9:130

Fu BJ, Liu SL, Ma KM, Zhu YG (2004) Relationships between soil characteristics, topography and plant diversity in a heterogeneous deciduous broad-leaved forest near Beijing, China. Plant and Soil 261:47–54

Gibson DJ, Hulbert LC (1987) Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175–185

Grimm EC (1984) Fire and Other Factors Controlling the Big Woods Vegetation of Minnesota in the Mid-Nineteenth Century. Ecological Monographs 54:291–311

Haworth K, McPherson GR (1995) Effects of Quercus emoryi trees on precipitation distribution and microclimate in a semi-arid savanna. Journal of Arid Environments 31:153–170

Heatherbell DA, ed. (1985) Proceedings of the International Symposium on Cool Climate Viticulture and Enology. Corvallis, OR: Oregon State University, Depts. of Food Science and Technology, Horticulture, and Extension Service, in cooperation with the Oregon Winegrowers Association and Oregon Wine Advisory Board

Helbach J, Frey J, Messier C, Mörsdorf M, Scherer-Lorenzen M (2022) Light heterogeneity affects understory plant species richness in temperate forests supporting the heterogeneity–diversity hypothesis. Ecology and Evolution 12:e8534

Kleb HR, Wilson SD (1997) Vegetation Effects on Soil Resource Heterogeneity in Prairie and Forest. The American Naturalist 150:283–298

Leach MK, Givnish TJ (1998) Identifying highly restorable savanna remnants. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 86:119–127

Leach MK, Givnish TJ (1999) Gradients in the Composition, Structure, and Diversity of Remnant Oak Savannas in Southern Wisconsin. Ecological Monographs 69:353–374

Lettow MC, Brudvig LA, Bahlai CA, Landis DA (2014) Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. Forest Ecology and Management 329:89–98

Lindgren J, Kimberley A, Cousins SAO (2018) The complexity of forest borders determines the understorey vegetation. Applied Vegetation Science 21:85–93

Lundholm JT (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. Journal of Vegetation Science 20:377–391

Mayora G, Scarabotti P, Schneider B, Alvarenga P, Marchese M (2020) Multiscale environmental heterogeneity in a large river-floodplain system. Journal of South American Earth Sciences 100:102546

Munson SM (2013) Plant responses, climate pivot points, and trade-offs in water-limited ecosystems. Ecosphere 4:art109

Nuzzo VA (1986) Extent and Status of Midwest Oak Savanna: Presettlement and 1985. Natural Areas Journal 6:6–36

Peterson DW, Reich PB (2001) Prescribed Fire in Oak Savanna: Fire Frequency Effects on Stand Structure and Dynamics. Ecological Applications 11:914–927

Pincebourde S, Murdock CC, Vickers M, Sears MW (2016) Fine-Scale Microclimatic Variation Can Shape the Responses of Organisms to Global Change in Both Natural and Urban Environments. Integrative and Comparative Biology 56:45–61

Primack RB, Miao S l. (1992) Dispersal Can Limit Local Plant Distribution. Conservation Biology 6:513–519

Rammette A, Tiejde J (2006) Multiscale responses of microbial life to spatial distance and environmental heterogeneity in a patchy ecosystem. https://www.pnas.org/doi/10.1073/pnas.0610671104. Accessed March 2, 2022

Rollinson CR, Alexander MR, Dye AW, Moore DJP, Pederson N, Trouet V (2021) Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. Ecology 102:e03264

Scheffers BR, Edwards DP, Macdonald SL, Senior RA, Andriamahohatra LR, Roslan N, Rogers AM, Haugaasen T, Wright P, Williams SE (2017) Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica 49:35–44

Schetter TA, Walters TL, Root KV (2013) A Multi-scale Spatial Analysis of Native and Exotic Plant Species Richness Within a Mixed-Disturbance Oak Savanna Landscape. Environmental Management 52:581–594

Small CJ, McCarthy BC (2005) Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217:229–243

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880

Stein A, Kreft H (2015) Terminology and quantification of environmental heterogeneity in species-richness research. Biological Reviews 90:815–836

Suggitt A, Wilson R, Isaac N, Beale C, Auffret A, August T, Bennie J, Crick H, Duffield S, Fox R, Hopkins J, Macgregor N, Morecroft M, Walker K, Maclean I (2018) Extinction risk from climate change is reduced by microclimatic buffering. Nature Climate Change 8:713-717

Volder A, Briske DD, Tjoelker MG (2013) Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Glob Change Biol 19:843–857

Walsh RP (2017) Microclimate and biotic interactions affect Karner blue butterfly occupancy and persistence in managed oak savanna habitats. J Insect Conserv 21:219–230

Weiher E (2003) Species richness along multiple gradients: testing a general multivariate model in oak savannas. Oikos 101:311–316

Willis CG, Halina M, Lehman C, Reich PB, Keen A, McCarthy S, Cavender-Bares J (2009) Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. Ecography 33:565-577

Chapter 2: Influence of multi-scalar environmental heterogeneity on understory vegetation diversity and quality in four Minnesota oak savannas

Abstract

Oak (*Quercus spp.*) savannas are one of the most threatened ecological systems within the United States. Like many ecotones, these savannas are considered biodiversity hotspots due to their high environmental heterogeneity (EH). To better inform management targets, quadrat-based understory vegetation surveys were taken alongside measurements of soil moisture, canopy cover, and elevation variation in a nested plot design. Two definitions of EH, horizontal heterogeneity (total variation over area) and spatial heterogeneity (intensity of clustering), were used to assess EH-vegetation quality relationships using generalized mixed linear models with nested covariates for study site and plot. Models showed that higher horizontal heterogeneity of canopy cover was related to increased potential native vegetation (PNV), along with a decrease in percent exotic cover. Elevation heterogeneity had a negative relationship with native species richness – representing a potential violation of the habitat heterogeneity hypothesis. Spatial heterogeneity of both soil moisture and canopy cover appeared to have universally positive effects on vegetation quality. EH-vegetation quality trends may be best explained by differences in how habit generalists and specialists respond to gradients in EH. More specifically, higher EH increased the presence of light specialist species and decreased shade specialist species, whereas high EH increased soil moisture generalists and decreased both moist and dry soil specialists. Model quality was frequently highest at the medium spatial extent (12 by 12 m), suggesting that environmental effects over this scale have the greatest impact on savanna understory vegetation.

Key words

Oak savanna, environmental heterogeneity, vegetation quality, biodiversity, native species

Management Implications

All metrics of canopy cover heterogeneity had beneficial or neutral associations with vegetation quality and diversity metrics. More specifically, greater variation of canopy cover values was associated with higher percentages of savanna-associated vegetation and lower exotic richness. Increases in native richness were observed alongside greater distinctiveness of shade and light patches, suggesting a significant role of niche partitioning in this environment.

Soil moisture heterogeneity models had mixed effects on vegetation quality and diversity. Further experimentation is likely necessary to separate the roles of canopy shading and woody encroachment on resulting EH trends.

Elevational heterogeneity had a moderate negative association with native species richness – an unexpected finding affirming previous results suggesting that steeper areas decrease native richness within this environment (Schetter et al. 2013). Savanna management should focus on flat areas of land when feasible for the overall project.

Consistently higher model quality at the medium spatial extent suggests that patch sizes of 12 by 12 m or greater be used to improve habitat quality and vegetation diversity within oak savannas. To improve understory quality and diversity, overstory management should aim to maximize horizontal heterogeneity on a local level (12 by 12 m) while maintaining a level of patch distinctiveness. In other words, patches of high contrast shade and light are more favorable than larger areas of medium canopy cover. Distinctiveness could be achieved by felling or girdling trees where appropriate and leaving select areas of high canopy cover intact.

Introduction

Establishment and maintenance of oak (*Quercus spp.*)-dominated savannas requires a regular disturbance regime of fire, grazing, and drought (Campbell et al. 1994; Grimm 1984). This reduces woody encroachment, leaving a well-spaced stand of fire-resistant oak trees and a lush understory of prairie and woodland vegetation (Anderson 1998; Dey and Kabrick 2015; Nuzzo 1986; Peterson and Reich 2001). High contrasts in understory resource availability between the shade of mature oak trees and more sun-exposed open patches may provide increased niche diversity on a relatively small scale — this environmental heterogeneity (EH) is thought to be key in characterizing the unique mix of prairie and woodland vegetation present in high-quality savanna communities (Haworth and McPherson 1995; Leach and Givnish 1998; Lettow et al. 2014; Schetter et al. 2013; Walsh 2017). The role of EH in oak savannas has been a somewhat active topic of research. However, other work has focused on the roles of light availability, heat load, and proximity to anthropogenic disturbance (Lettow et al. 2014; Schetter et al. 2013; Volder et al. 2013; Walsh 2017; Weiher 2003), with lesser study on the impacts of soil character, topography, or the coupled influence of environmental variables. Additionally, a majority of EH research is done on larger spatial scales or only examines single species or taxa. However, broader assessments of community diversity or measurements over smaller spatial extents may be necessary to fully understand the role of EH-diversity relationships in this structurally complex ecotone (Walsh 2017).

The habitat heterogeneity hypothesis states that EH at multiple scales (biome, ecosystem, locality, microclimate, etc.) improves species richness (Blonder et al. 2018; Deák et al. 2021; Scheffers et al. 2017; Stein et al. 2014; Suggitt et al. 2018). This is likely due to increased opportunities for niche partitioning and environmental filtering, allowing individual species to experience success in cases where dispersal abilities may be biologically or geographically limited (Helbach et al. 2022; Willis et al. 2009). In cases where EH does not increase species richness, there is often a neutral or a non-directional relationship (unimodal distribution); negative relationships are extremely uncommon (Lundholm 2009). Environmental heterogeneity may be defined as either the number of habitat types present with a piece of land or as the amount of variation in environmental factors over a given area (Pincebourde et al. 2016). The current study, (habitat scale), will use the latter definition based on environmental variation. More specifically, heterogeneity of canopy cover, soil moisture, and elevation will be assessed for their relationship to savanna understory floral diversity and quality.

Several technical challenges persist in the testing of EH-diversity relationships. For example, spatial scale and measurement density can change interpretations of EH. Scale and density are frequently chosen based on the research question, but relationships are often unknown. To avoid error, an experimental design featuring nested windows of analysis can be used to better understand the influence of scale (De Pauw et al. 2022; Deák et al. 2021; Schetter et al. 2013; Walsh 2017). For example, a study examining species richness and invasive species presence in a mixed-disturbance oak savanna found consistent differences in how EH measured over 60 m and 120 m diameter windows predicted invasive species presence and overall species richness (Schetter et al. 2013).

Another challenge is that the concept of heterogeneity itself can be defined in multiple ways. One definition quantifies the total range or variation present over a unit of area. This concept will be referred to as ‘horizontal heterogeneity’. Assessments such as range and standard deviation are often used to measure horizontal heterogeneity. Other metrics such as a Shannon index of land cover types are also common, but consistency of terminology and quantitative methods are lacking (Stein and Kreft 2015). Alternatively, EH can consider the structuring of resources over physical space, henceforth ‘spatial heterogeneity’. Qualitative descriptions of spatial heterogeneity are common though quantitative indices are highly limited and inconsistent (Stein and Kreft 2015). Using either definition has its advantages. Horizontal heterogeneity typically requires fewer measurements and is more easily understood. However, using spatial heterogeneity to understand resource clustering can be helpful to describe the complex role of environmental limitations on plant dispersal (Costanza et al. 2011; Mayora et al. 2020; Rammette and Tiejde 2006). The main drawback of this approach is the high volume of data necessary to describe change through physical space. To simplify analyses, data can be taken using a regular array of survey points. This collection method suits the needs of both horizontal and spatial heterogeneity analyses and can easily facilitate the use of nested windows to quantify EH differences at various spatial extents.

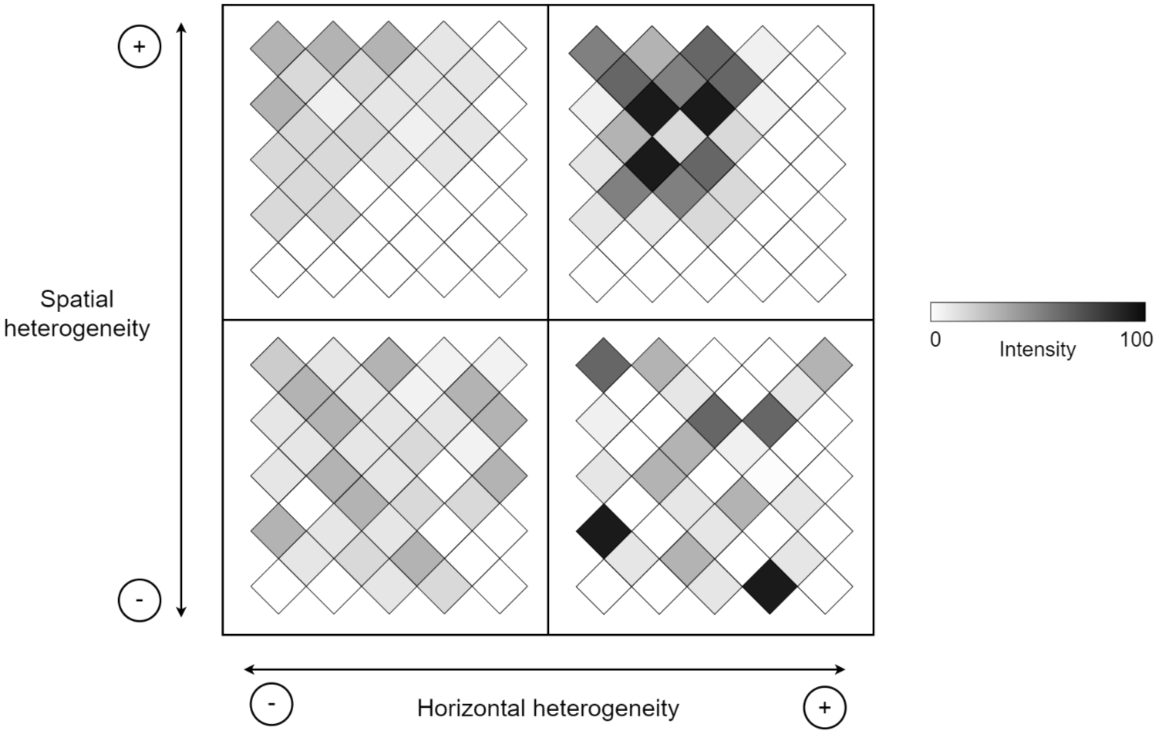


Figure 1. Illustration of horizontal and spatial environmental heterogeneity definitions.

Oak savanna canopy cover heterogeneity has been a topic of past research, with results suggesting it as a critical factor in habitat quality for select native plants, insects, and birds (Brawn 2006; Davis et al. 2019; Leach and Givnish 1999; Walsh 2017). Impacts of EH on community-scale savanna diversity are currently less clear. In a temperate woodland system, both horizontal and spatial heterogeneity of light availability was linked with greater understory biodiversity (Helbach et al. 2022). At time of writing, no comparable studies on light heterogeneity have been completed on a community scale for oak savanna and comparable studies in prairie systems are functionally impossible.

Most works suggest that soil moisture heterogeneity has an overall detrimental effect on savanna diversity and quality. In other grassland-woodland transitional systems, soil moisture heterogeneity was highly correlated with woody encroachment, which tends to decrease overall species richness in systems dominated by prairie pattern grasses and forbs (Baer et al. 2005; Breshears and Barnes 1999; Fu et al. 2004; Kleb and Wilson 1997; Small and McCarthy 2005). However, the exact mechanisms of this relationship are still unclear – other phenomena like differences in woody root system stratification and adaptability (Ansley et al. 2014), and the influence of woody plant presence on evapotranspiration and soil compaction need to be considered (Acharya et al. 2018; Aldworth et al. 2023).

Topographic heterogeneity has shown varying impacts on savanna vegetation quality and diversity. The only other study directly considering topographical heterogeneity in midwestern oak savanna systems showed a negative relationship between greater elevation range and native species richness (Schetter et al. 2013). This is especially notable as it may represent an exception to the habitat heterogeneity hypothesis. Work in prairie and woodland systems, however, has shown that small variations such as localized hummocks and hollows can increase biodiversity

(Deák et al. 2021) or that larger scale variation can increase biodiversity, likely through impacts on nutrient content and light availability as the angle of the landscape varies (Fu et al. 2004; Heatherbell 1985; Small and McCarthy 2005).

While oak savanna formerly spanned up to ~10-13 million hectares at the prairie-forest border of the central United States, due to modern land use practices and fire suppression, < 0.1% of this estimated acreage remains (Nuzzo, 1986; Anderson 1998; Brudvig and Asbjornsen 2008). Considering the likely importance of environmental heterogeneity on savanna ecosystem dynamics, a greater understanding of these environmental characteristics is necessary in order to improve on current restoration practices within this highly threatened environment (Brudvig and Asbjornsen 2008; Walsh 2017). While EH may be difficult to define, understanding its role may lead to insights on how to best manage land selection, patch size, patch arrangement, and canopy density to best foster favorable oak savanna communities.

The presence of highly heterogenous ecotones are theorized to serve as a buffer against wider-scale biodiversity loss (Blonder et al. 2018; De Pauw et al. 2022; Munson 2013; Suggitt et al. 2018). This is especially true in times of environmental stress, as spatially heterogenous areas can create local microrefugia for species which may not be able to tolerate quick changes in temperature or drought stress (Blonder et al. 2018; De Pauw et al. 2022; Lindgren et al. 2018; Walsh 2017). In the face of global climate change and land-use degradation, well-managed ecotone environments could be a novel tool in strengthening biodiversity.

The current study considers the impacts of heterogeneity on several positive (native richness, native cover, and PNV or the % UPs14 listed species present) and negative (exotic richness, exotic cover, and woody cover) management outcomes for oak savanna restoration (Dey and Kabrick 2015; Peterson and Reich 2001)**.** We predict that horizontal heterogeneity of canopy cover and elevation will improve listed management outcomes due to increased niche partitioning. Horizontal heterogeneity of soil moisture, often associated with high woody encroachment rates, will have an overall negative impact on these outcomes. Spatial heterogeneity of canopy cover and soil moisture — defined in this study using the Moran's I spatial autocorrelation index — is predicted to increase favorable management outcomes. Spatial heterogeneity of topographic features will not be considered in the bounds of this study. In addition to the direct effects of EH-diversity and EH-vegetation quality relationships, explanations for observed trends will be further analyzed by assessing the percentage of habitat generalists and specialists present along EH gradients.

Materials and Method

Study sites and plot arrangement

Site selection was guided by characteristics outlined for the southern dry savanna ecosystem subtype, native plant community (NPC) code UPs14, as defined by the Minnesota Department of Natural Resources' NPC classification system (Aaseng et al. 2011). Investigators visited each site for visual assessment before making a final selection. Four study sites with a diversity of management history and length were chosen within central and south-central Minnesota (Table 1). Maps and complete descriptions of each location can be found within the supplementary materials (Supplementary Figures S1-S3)

Based on a visual assessment of understory vegetation and percent canopy cover as described by NPC class UPs14, GPS points were recorded on foot dictating the outer limits of each site using a smartphone-based application (Geo Tracker version 5.2.4, Ilia Bogdanovich). Using GIS (ArcMap v10.8.2, Esri Inc., 380 New York St., Redlands, California, United States, 92373), GPS points were connected to delineate site boundaries for randomized plot placement.

Table 1. Summary of study site characteristics. *Site area describes the total area suitable for study and is not representative of total land cover at each location. Soil texture information provided by United States Department of Agriculture's web soil survey service (USDA, NRCS. 2023. Soil Survey Staff. Web soil survey (websoilsurvey.nrcs.usda.gov). USA.).*

Study site	Coordinates	Managing bodies	Site area	Soil texture	Description
			ha		
Ottawa Bluffs Nature Preserve	(44.366°N, -98.935°W)	The Nature Conservancy	6.34	Loam to sandy loam	Long-term project on partial remnant. Rural setting.
Rapids Lake Unit	(44.734°N, -93.647°W)	US Fish and Wildlife Service	11.42	Sandy loam to sand	~5-year restoration project over remnant. Agricultural setting.
Terrace Oaks Park	(44.760°N, -93.242°W)	City of Burnsville Parks and Recreation	9.36	Sandy loam to sand	~8-year restoration project over partial remnant. Suburban setting
Helen Allison Savanna	(44.770°N, -93.242°W)	The Nature Conservancy, University of Minnesota	20.61	Fine sand	Long-term management project on large savanna remnant. Rural setting.

Five 24 m by 24 m plots were surveyed at each study site. GIS was used to generate 10 random points within site boundaries to act as the northwest corner of each study plot. Each dot was assigned an associated plot number 1 through 10 and five plots were randomly chosen as the first-preference study plots in the field. In cases where a chosen plot was found to have major obstructions (i.e. large trailways, multiple fallen trees, cliffsides), the next plot was sequentially chosen from the remaining numbered plots. Plots were also rejected in cases where non-savanna systems were clearly present within plot bounds (i.e. patches of obligate wetland vegetation).

Plots were sectioned into a square array of 81 measurement points with 3-meter spacing between all rows and columns. In the field, study arrays were outlined using field measurement tapes. Placement of tapes was checked at each end using a hand compass to ensure evenness. Every point in the array was measured for soil moisture, while a regularly spaced subset of 41 points were surveyed for overstory canopy cover. Nine spots in the middle of the array were subject to a quadrat-based vegetation survey (Figure 2A). This study design allowed for the analysis of nested windows within each plot. Canopy cover and soil moisture measurements featured plot level (24 by 24 meter), medium (12 by 12 meter), and small (6 by 6 meter) spatial extents, while analyses of elevation were limited to the plot level extent due to available measurement resolution (Figure 2B).

Canopy Cover

Canopy cover was measured using a high-resolution digital camera (EOS Rebel T7, Canon, 30-2 Shimomaruko 3-chome, Ota City, Tokyo, Japan, 146-8501) with a 180° fisheye lens attachment (Rokinon FE8M-C 8mm F3.5 Fisheye Fixed Lens, Elite Brands Inc., 40 Wall Street, 61st Floor, New York City, New York, United States, 10005). The camera was fastened to a tripod with the lens pointed directly upwards as verified with a multi-directional level. Distance from the camera to the ground directly between the 3 legs of the tripod was adjusted to 1 meter before each photo capture. Photographs were analyzed with ImageJ2 software (Rueden et al. 2017) in order to calculate a precise % canopy cover using a ratio of canopy to open sky (*sensu* Beckschäfer 2015).

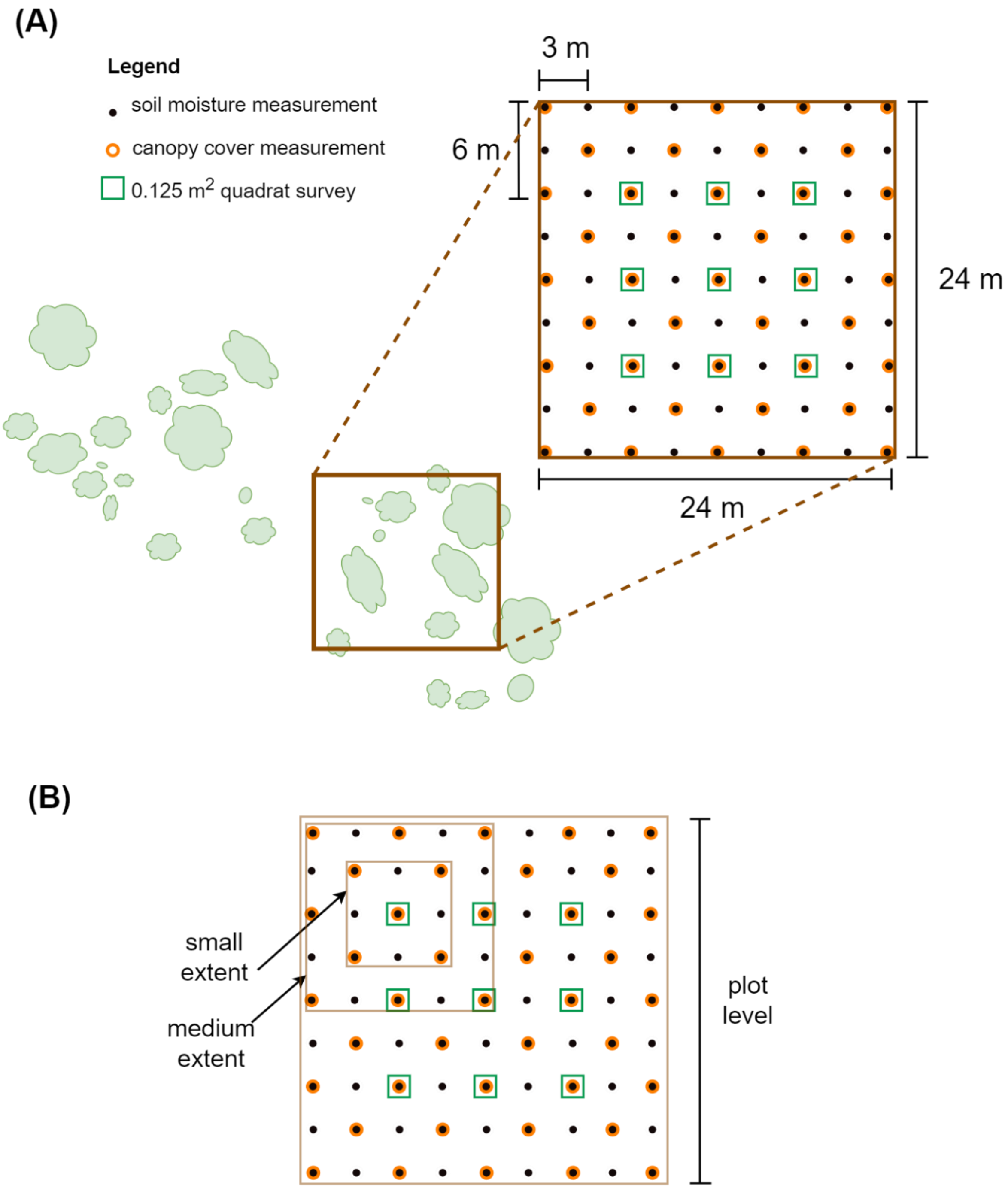


Figure 2. Illustration of plot layout and nested window design. *Plot layout (A) features relevant dimensions of measurements. Nested window design (B) features plot level (24 by 24 meter), medium (12 by 12 meter), and small (6 by 6 meter) spatial extents.*

Soil moisture

Soil moisture was measured as volumetric water content (VWC) using a time-domain reflectometry (TDR) moisture sensor with 20 cm probes (Fieldscout TDR 350, Spectrum Technologies Inc., 3600 Thayer Court, Aurora, Illinois, United States, 60504). Three measurements were taken randomly within ~0.5 meters from the associated measurement point. Measurements were averaged before recording VWC for a given point. All measurements were taken at field capacity (≥ 2 days after precipitation events) to allow for effective comparison of moisture content across the dataset (Burns et al. 2016).

Vegetation Surveys

Between June 26th and August 12th, 2022, vegetation surveys were performed as a census of species richness & species cover within a 0.5 m x 0.25 m quadrat frame. Frames were placed so the upper left-hand corner aligned with the relevant survey point (Figure 2). The 0.5-meter edges faced North and South and while the 0.25-meter edges faced East and West. Flora was identified to the species level as frequently as possible. Individuals unable to be identified were labeled with known functional groups, families, or genera followed by a number. Percent cover for each species was visually estimated with the aid of a transect. Multiple overlapping plants of different heights could each possess the same % cover for the area in which they overlap and total % cover does not necessarily add up to 100 (sensu Damgaard 2014).

Supplemental data

Additional information on plant habits and exotic or native classifications was gathered via literature search to use as additional variables in analyses. Specimen unable to be classified to the species level were omitted from analyses which utilized said classifications. All literature searches began by reading species and habitat descriptions from a peer-reviewed field guide on Minnesota flora (Chadde 2019). If a given trait or classification was unclear from the former reference, assessment was made using a combination of publicly available herbarium records (University of Minnesota Bell Museum 2023. Bell Museum Herbarium. Accessed via bellatlas.umn.edu on 2023-08-17.) and a national database of plant traits (USDA, NRCS. 2023. The PLANTS Database. Accessed via plants.usda.gov, on 2023-08-16. National Plant Data Team, Greensboro, NC USA.). The NPC class UPs14 plant community list was provided by the Minnesota Department of Natural Resources (Aaseng et al. 2011). Non-native and invasive plants were grouped together under ‘exotic’ for relevant analyses. Soil descriptions for each study site were provided by United States Department of Agriculture’s web soil survey service (USDA, NRCS. 2023. Soil Survey Staff. Web soil survey (websoilsurvey.nrcs.usda.gov). USA.).

In select analyses, species were sorted into qualitative specialist and generalist groups based on the words present in habitat descriptions. Light habit was split up into five groupings of sun specialist, sun semi-specialist, generalist, shade semi-specialist, or shade specialist. Exclusively sun-associated words ("full sun", "prairie", "fields", "upland", "open") or shade-associated words ("full shade", "forest", "woodland", "covered", "thickets") categorized a species as a sun or shade specialist. Semi-specialist classification was chosen for sun-leaning descriptions (a majority sun-associated words or description as a "waste area") or shade-leaning descriptions (a majority shade-associated words, with minor references to edge or sun-associated words). Generalists were species described as having a wide-ranging light habit (even mix of sun-associated and shade-associated words) or with a description of exclusively edge-associated words ("forest edge", "edge", "transition area", "open woods"). Soil moisture habit was split into three groups of dry soil specialists, generalists, and moist soil specialists. Descriptors associated with dry habit (sandy", "dry", "low moisture") or moist habit ("moist", "saturated", "damp") were designated dry or moist soil specialists, respectively. Intermediate or highly variable descriptions were considered generalists (*sensu* Kirsch and Kaproth 2022).

Metrics of understory floral diversity and quality

Six descriptors of understory vegetation were chosen to describe management success. Positive management outcomes include percent native species, percent native cover, and potential native vegetation (PNV) — an established metric of vegetation quality which takes the number of species present from a location's native plant class listing (UPs14) over total species richness (Galatowitsch and Bohnen 2020). Negative management outcomes include percent exotic species, percent exotic cover, and percent woody cover (Table 2).

Table 2. Definitions for understory vegetation descriptors. *Classifications for native, non-native, and invasive species, as well as species lists for the southern dry savanna native plant community class (NPC), UPs14, were sourced from the Minnesota Department of Natural Resources* (Aaseng et al. 2011).

Term	Definition
Species richness	Count of unique species within a given area
Percent native richness	Number of native species divided by species richness
Percent native cover	Cover for all native species divided by the total cover observed
Potential native vegetation (PNV)	Number of UPs14 listed species divided by species richness
Percent exotic richness	Number of non-native and invasive species divided by species richness
Percent exotic cover	Cover for all non-native and invasive species divided by the total cover observed for that area
Percent woody cover	Cover for all woody species present divided by the total cover observed within that area

Horizontal Heterogeneity

Horizontal heterogeneity was assessed in two ways: standard deviation and a Horizontal Heterogeneity Index (HHI) based on the Shannon-Weiner diversity index. HHI acts to measure functional thresholds of heterogeneity for soil moisture and canopy cover within a given area of space. Where the Shannon-Weiner index uses individual species as groupings, HHI uses ecologically relevant thresholds to sort each data point into 4 functional classes. Higher HHI values indicate a greater diversity of functional class types, with a greater weight placed on the presence of a functional class and a lesser weight on the number of observations present in each functional class.

$$HHI \ = \ -\sum_{i=1}^{fc} p_{fc} * \ln\left(p_{fc}\right) \ [1]$$

Equation 1. Horizontal Heterogeneity Index

Where:

p_{fc} = *number of observations fitting within each functional class*

fc = *number of functional classes*

Functional class selection for canopy cover was based on the canopy cover limits from UPs14 NPC classification and additional literature on savanna environmental requirements (Aaseng et al. 2011; Anderson 1998; Bucini et al. 2017). The four classes for this metric were < 10% overstory cover, ≥ 10% to < 30% cover, ≥ 30% to < 50% cover, and ≤ 50% cover. These ranges represent upper and lower thresholds for successful savanna community establishment and two intermediate groups within the expected environmental character.

Soil moisture functional class selection was based on the average limits of plant wilting points, available water, and field capacity for the dominant soil material (sand, loam, or clay) at that location. If soil texture was intermediate, an average value of two types was used (Table 3).

Table 3. Dominant soil types and associated soil moisture functional classes for each study site. *Soil texture information was provided by United States Department of Agriculture's web soil survey service (USDA, NRCS. 2023. Soil Survey Staff. Web soil survey (websoilsurvey.nrcs.usda.gov). USA.) Associated soil moisture classifications are based on a normalized scale of water potential for soil texture. AW = available water, FC = Field capacity, C1,2,3, and 4 = functional class 1, 2, 3, and 4.*

Study site	Soil texture	C1: Permanent wilting point	C2: Below average AW	C3: Above average AW	C4: Above FC
		(VWC %)	(VWC %)	(VWC %)	(VWC %)
Ottawa Bluffs Nature Preserve	Loam to sandy loam	< 10	10 - 18.5	18.5 - 27	>27
Rapids Lake Unit	Sandy loam to sand	< 7.5	7.5 - 12.25	12.25 - 17	>17
Terrace Oaks Park	Sandy loam to sand	< 7.5	7.5 - 12.25	12.25 - 17	>17
Helen Allison Savanna	Fine sand	< 2	2 - 4.5	4.5 - 7	>7

Spatial Heterogeneity

A polygon-based spatial autocorrelation index – Moran's I – was used within GIS to assess the clustering of soil moisture and canopy cover values. To reduce errors associated with small Moran's I sample sizes, analysis was limited to two spatial extents – the plot level analysis utilizing the full study array of measurements for each plot's soil moisture (n = 81) and canopy cover values (n = 41), or a smaller 5 by 5 quadrat level analysis used only for soil moisture analysis (n = 25). Moran's I values can range from -1 to +1, with negative values representing dispersion, 0 representing a random or Poisson distribution, and positive values representing autocorrelation of values across space.

Linear Modeling Analyses

To better understand how key management metrics change along environmental gradients of canopy cover, topography, and soil moisture heterogeneity at multiple spatial scales, the datasets were split into two separate model scales: 1) plot level models (n = 20) which summarize the data collected for all of the windows of the study plot and 2) quadrat level models (n = 180) which count each quadrat as an individual. Using covariates, plot level models were adjusted for site differences and quadrat level models were adjusted for site & plot differences through nested generalized linear mixed models (GLMM; JMP v17, JMP Statistical Discovery LLC., 100 SAS Campus Drive, Cary, North Carolina, United States, 27513). Models were assessed using Akaike information criterion (AICc) and L-R Chi square (L-R X^2) values to compare fit and quality. Identical methods were used to assess how the presence of generalist and specialist groups changed along gradients of EH.

A model was declared to have positive or negative directionality if over 75% of significant slopes at the finest organizational level pointed in the same direction. Models were only considered significant if the predictor being tested was individually held significant; site and plot predictors were not considered but were almost always highly significant. AICc is an estimator of prediction error. Lower values represent a higher quality model. AICc values were only comparable amongst plot level models or quadrat level models due to differences in sample size for each model type.

Results and Discussion

Site characteristics

Flora was identified to the species level in 94.8% of observations, and to the genus level in 98.5% of observations. Of the remaining 5.2%, a majority of individuals were *Cypraceae* species – which have been observed to show little change in response to gradients in savanna environmental character (Cavender-Bares and Reich 2012). As such, further analyses were restricted to observations with complete species identification.

Metrics of environmental and floral character varied highly amongst study sites. Average species richness was 88.5 ± 15.5 with a minimum of 61 at the HA site and a maximum of 100 at the RL site. Native richness varied from 46 to 76 species at HA and OB sites, respectively, and exotic richness varied from 29 at RL to 2 at HA. Exotic cover followed similar trends, with a minimum average of 3.1 ± 1.4% at the HA site and maximum of 23.0 ± 8.3% at the RL site. Site PNV averaged 18.6% with the highest value of 33.9% at HA and a minimum of 10.0% at RL. Woody cover ranged from 1.3 ± 1.4% at HA to 6.2 ± 0.4% at RL (Supplementary Table S1). Notably, areas with higher species richness had consistently higher ratios of exotic to native cover and % woody cover (Supplementary Table S2). While species richness is often a suitable generalized indicator for biodiversity, it can be inadequate to describe functional ecosystem value and is highly dependent on site history and context (Fleishman et al. 2006; Hillebrand et al. 2018). In many cases, assessment of species turnover, rarity, identity, and abundance may be more appropriate, especially in environments with high levels of disturbance and community changes, such as savannas (Hillebrand et al. 2018). These results suggest that assessment of savanna floral quality strongly requires such functionally descriptive diversity metrics (Supplementary Note 4).

Average canopy cover for all sites fell within the range of 10-50% typically associated with savanna community establishment (Aaseng et al. 2011; Anderson 1998; Bucini et al. 2017)**.** The sparsest cover was present at the HA site with an average of 20.1 ± 12.2%, and the densest cover was at TO with 41.8 ± 9.7%. Soil moisture ranged from an average of 2.2 ± 1.3**%** at HA to 19.4 ± 10.3% at OB. This range was expected considering the diverse soil textures present at each site. RL and TO, with more intermediate sand to sandy loam textures featured averages of 11.9 ± 0.8% and 10.9 ± 2.2**%**, respectively. Elevation variation ranged from a standard deviation of 1.0 ± 0.3 m at RL to 3.5 ± 2.2 m at HA (Table 4).

Table 4. Study site characteristics. *Environmental character and vegetation quality were examined at four locations (OB – Ottawa Bluffs Nature Preserve; RL – Rapids Lake Unit; TO – Terrace Oaks Park; and HA – Helen Allison Savanna). Elevation variation was measured as the standard deviation of elevation within a plot. Error ranges indicate ± 1 standard deviation.*

Study site	Species richness	Native richness	Exotic richness	Native Cover	Exotic Cover	PNV	Woody Cover	Canopy Cover	Soil Moisture	Elevation variation
				(%)	(%)	(%)	(%)	(%)	(%)	m
OB	94	76	12	84.2 ± 5.4	10.0 ± 8.7	19.1	4.1 ± 1.4	21.5 ± 17.8	19.4 ± 10.3	3.5 ± 2.1
RL	100	60	29	72.6 ± 11.2	23.0 ± 8.3	10.0	6.2 ± 0.4	28.9 ± 11.9	11.9 ± 0.8	1.0 ± 0.3
TO	98	67	20	79.0 ± 5.4	12.4 ± 3.75	11.2	2.0 ± 1.2	41.8 ± 9.7	10.9 ± 2.2	2.4 ± 0.3
HA	62	46	2	84.5 ± 5.6	3.1 ± 1.4	33.9	1.3 ± 1.4	20.1 ± 12.2	2.2 ± 1.3	3.5 ± 2.2

Canopy cover heterogeneity

At the medium spatial extent (12 by 12 m), horizontal canopy cover heterogeneity measured as standard deviation and HHI had a positive relationship with PNV. Measured via standard deviation, canopy cover had a negative relationship with percent exotic richness. There were no significant relationships at the plot (24 by 24 m) or small (6 by 6 m) spatial extents (Table 5).

For spatial heterogeneity, greater autocorrelation of canopy cover values had a positive relationship with the percentage of native species present within a plot (Table 5). Moran's I values ranged from 0.078 to 0.704 with an average of 0.484, indicating a global trend of autocorrelation. (Table 5). No distinct pattern of patch size was evident amongst high or low scoring plots, suggesting an emphasis on patch cohesiveness over patch size.

To enhance floral diversity, overstory management should aim to maximize horizontal heterogeneity on a local level (12 by 12 m) while still maintaining a level of patch distinctiveness. In other words, patches of high contrast shade and light are more favorable than larger areas of medium canopy cover. Distinctiveness could be achieved by felling or girdling trees where appropriate and leaving select areas of high canopy cover intact. If desired, keeping dead trees within savannas has also shown to be useful in improving bird habitat (Brawn 2006; King et al. 2007; Waldstein 2012).

Soil moisture heterogeneity

Horizontal soil moisture heterogeneity had favorable associations with management outcomes over the plot extent (24 by 24 m) and mixed associations over the medium spatial extent (12 by 12 m). No significant associations were present over the small extent (Table 5).

More specifically, moisture heterogeneity was correlated with an increase in native cover and a decrease in exotic cover at the plot extent. At the medium extent, associations with exotic cover changed to positive and associations with woody cover were negative for both HHI and standard deviation measures of moisture heterogeneity. The latter relationship was highly unexpected considering the volume of studies observing a link between moisture heterogeneity and woody cover (Baer et al. 2005; Breshears and Barnes 1999; Fu et al. 2004; Kleb and Wilson 1997; Small and McCarthy 2005) (Table 5).

A possible explanation for these mixed results could be that soil moisture heterogeneity is highly influenced by canopy cover heterogeneity. This conclusion is further supported by visual assessment of study plots, where high and low values of both canopy cover and soil moisture tend to overlap. Most available studies have observed woody encroachment onto prairie where effects are most likely caused by locally higher infiltration rates from woody rooting systems (Kleb and Wilson 1997; Leite et al. 2020; Qiao et al. 2017). However, in savannas, the factors controlling moisture heterogeneity are not only limited to interactions with woody encroachment but also to reduced evaporation rates from overstory shading (He et al. 2014; Pariente 2002). Experimental research with greater control over overstory structure may be necessary to understand the complex role of this phenomenon within oak savannas.

For plot level soil moisture, Moran’s I scores ranged from 0.099 to 0.693, with an average of 0.370. At the medium extent for soil moisture, there was an average score of 0.213 and a range of -0.213 to 0.556. Higher Moran’s I values for soil moisture were associated with higher percent native cover and lower percent exotic cover at the plot level. At the medium spatial extent using the quadrat level dataset, higher values were positively associated with percent native species. All other associations were directionally ambiguous or non-significant

(Table 5). No unfavorable management outcomes were associated with higher Moran's I values for any variable or at any spatial level.

These results again suggest that more distinctive patches of wooded and non-wooded areas will likely lead to greater habitat quality compared to a more spatially homogeneous setting of medium density canopy. Considering the overlap of results and values between soil moisture and canopy cover heterogeneity, we do not recommend any unique management actions addressing soil moisture heterogeneity aside from canopy restructuring.

Topographical heterogeneity

Topographical heterogeneity was recorded as standard deviation of elevation across a plot and only analyzed at the plot scale to avoid misalignment errors possible from the projection of the 3m digital elevation model (DEM) onto the 81-point array study design. Results of these models defied hypotheses – elevation heterogeneity had a strong negative relationship with the percentage of native species present (Table 5). This directly supports results from Schetter et al. (2013), who found a link between native species richness and elevation range in a midwestern savanna of mixed management history. Elevation variation in oak savannas may represent a rare violation of the habitat heterogeneity hypothesis. These results are especially notable considering that elevation variation and elevation gradients are some of the most commonly considered metrics in environmental trait-based investigations of the habitat heterogeneity hypothesi**s** (Stein and Kreft 2015)**.**

Studies in prairie systems have uncovered mixed results between upland, lowland, and more heterogenous slope sites, with some studies observing a slight decrease in native diversity on sloped sites (Collins and Calabrese 2012) and others seeing diversity improvements or no differences (Bartha et al. 1995). Further complicating conclusions are the challenges that sloped areas bring to management efforts. Fire treatments may increase in speed and intensity when travelling upslope (Silvani et al. 2012), but may also have increased difficulty traversing topographically complex areas with irregular firebreaks (Krawchuk et al. 2016; Meigs et al. 2020). An additional factor could be the physical difficulty managers may face when mowing, cutting, and seeding on extreme slopes. Overall, our results combined with the similar findings of Schetter et al. (2013) suggest moderate benefits to native diversity on flatter areas, but the complexities of this relationship are likely to be highly dependent on management history and site context. Emphasis of flat terrain may be most effectively done through the initial planning of a restoration to focus efforts on flatter sections of land where feasible.

Table 5. Environmental heterogeneity-vegetation quality relationships. *Generalized linear mixed models with a nested site covariate (plot model type) or nested site and plot covariates (quadrat model type) were used to assess relationships between environmental heterogeneity and metrics of diversity and quality. Positive (+), negative (-) or ambiguous (+/-) directionality (dir.) was assessed at the finest level of model organization. Positive or negative directionality indicates ≥75% of significant slopes point in the same direction. Directionality was left blank for any non-significant models ($p > 0.05$). Log-ratio Chi square values (L-R X^2)* can only be compared amongst plot level models or quadrat level models. *PNV = potential native vegetation, CC = canopy cover, sd = standard deviation, HHI = Horizontal Heterogeneity Index, DEM = 3m digital elevation model, and SM = soil moisture. 'Small' refers to the 6 by 6 m spatial extent, 'medium' refers to the 12 by 12 m extent, and 'plot' refers to a 24 by 24 m extent.*

Environmental predictor	Spatial extent	Model type	Percent native richness		Percent native cover		PNV		Percent exotic richness		Percent exotic cover		Percent woody cover	
			L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.
CC sd	small	quadrat	31.92	+/-	37.03	+/-	44.18	+/-	39.54	+/-	45.21	+/-	27.27	
CC sd	medium	quadrat	30.08		24.61		57.32	+	48.47	-	32.36	+/-	39.16	+/-
CC sd	plot	plot	4.41		10.33	+/-	6.21		4.02		6.86		8.75	
CC HHI	small	quadrat	15.22		12.78		33.20	+	17.72		13.12		40.32	+/-
CC HHI	medium	quadrat	25.32		23.08		34.75	+	31.28	+/-	26.96		28.71	
CC HHI	plot	plot	3.95		7.76		8.12		1.59		5.71		7.41	
SM sd	small	quadrat	21.29		43.67	+/-	25.46		39.31	+/-	48.99	+/-	36.53	+/-
SM sd	medium	quadrat	58.98	+/-	58.80	+/-	38.41	+/-	72.06	+/-	70.22	+/-	45.77	-
SM sd	plot	plot	1.35		10.67	+	11.33	+/-	2.70		20.82	-	5.30	
SM HHI	small	quadrat	28.73	+/-	26.40		6.37		53.99	+/-	30.49	+/-	36.53	+/-
SM HHI	medium	quadrat	44.40	+/-	59.04	+/-	34.28	+/-	58.18	+/-	82.96	+	54.55	-
SM HHI	plot	plot	3.00		11.85	+/-	9.13		4.14		12.17	+/-	9.49	
DEM sd	plot	plot	11.59	-	1.08		2.07		0.63		11.05	+/-	5.27	
CC Moran's I	plot	plot	10.12	+	2.79		7.02		0.25		2.17		5.91	
SM Moran's I	medium	quadrat	51.23	+	50.48	+/-	47.71	+/-	50.46	+/-	90.10	-	27.01	
SM Moran's I	plot	plot	7.15		11.17	+	13.21	+/-	2.80		9.92	+/-	1.59	

Spatial scale

The medium spatial extent was most effective in predicting management outcomes as designated by higher log-ratio Chi square (L-R X^2) values, lower AICc values (Supplementary Table S4), and a greater overall number of significant models (Table 5). In addition to EH based models, management outcomes were also most effectively predicted by environmental gradients at the medium spatial extent (Supplementary Table S1. This suggests that environmental effects are the most influential if assessed on a scale of 12 by 12 m or greater. Medium scale quadrat level models were more frequently significant than the plot level models, however, the quadrat models had a greater sample size (n = 180 vs. n = 20) making them more likely to provide a significant p-value and providing incomparable AICc and L-R X^2 values to discern model quality. Therefore, a minimum patch size of 12 by 12 meters is suggested, but larger extents may also be successful in facilitating desired outcomes.

Notably, soil moisture heterogeneity models predicted opposite impacts on exotic cover between medium and plot level extents, suggesting a possible spatial threshold how moisture-vegetation interactions present in this environment. This is further supported by the fact that assessment of soil moisture gradients featured an identical difference in results (Supplementary Table S1). We highly recommend further study to effectively separate the impacts of overstory canopy shading and woody rooting structures on savanna soil moisture.

Influence of environmental heterogeneity on generalist and specialist presence

Specialist and generalist categorizations were more evenly distributed across observed species compared to a subset of UPs14 species. For both observed species and UPs14 species, a greater share of sun specialists and semi-specialists compared to shade specialists and semi-specialists was evident (Figure 3). Note that the UPs14 list only provides a selection of common native savanna species. The presence of unlisted species is expected and different functional group trends of may not necessarily indicate poor community quality (Aaseng et al. 2011; Galatowitsch and Bohnen 2020).

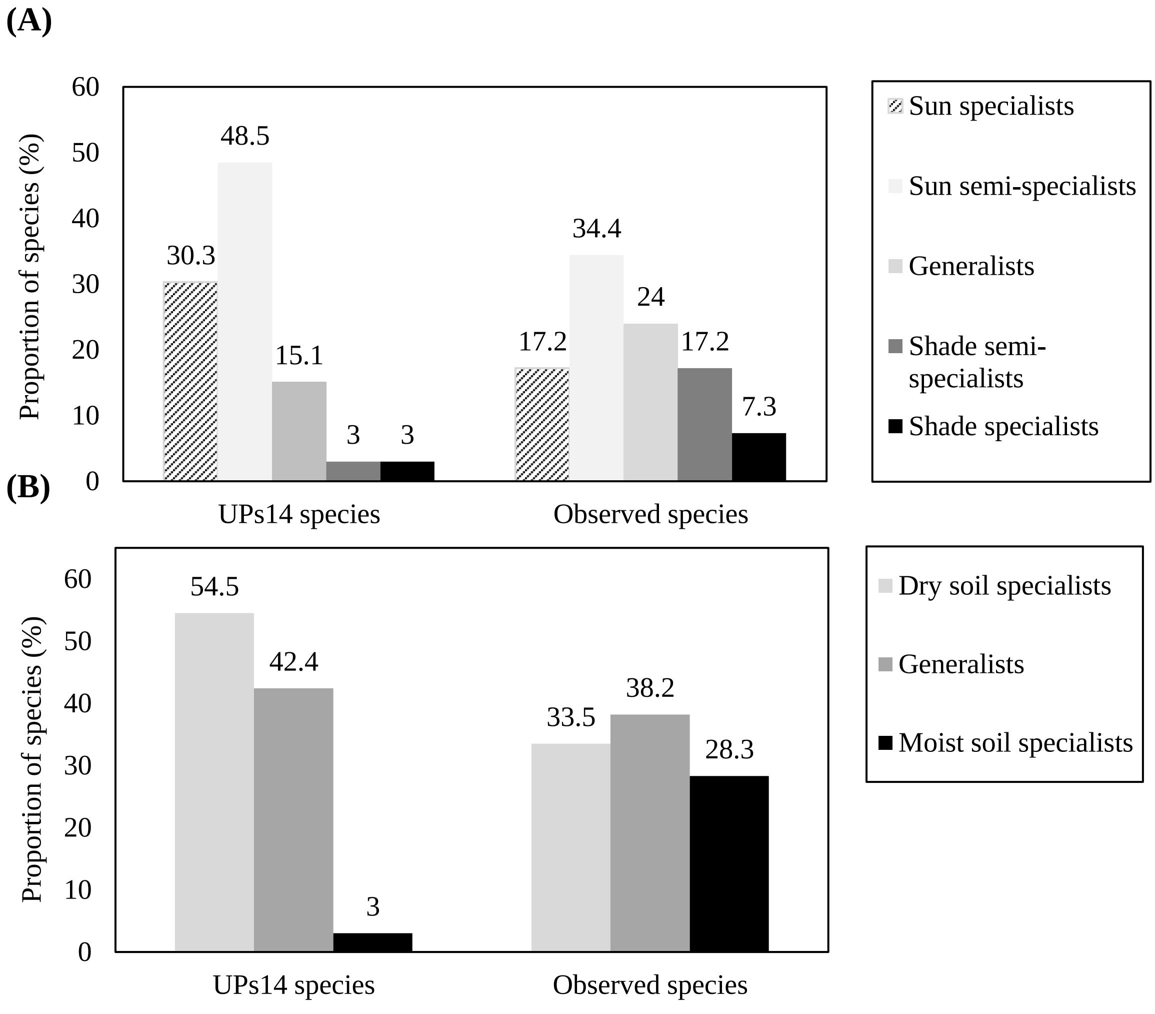


Figure 3. Distribution of light specialization (A) and soil moisture specialization categories (B) across UPs14 species and observed species.

While plot scale analyses of light and moisture specialization had no significant and directionally consistent relationships with EH metrics, analyses using the medium spatial extent showed several robust relationships with stark differences in how moisture specialists and light specialists interacted with EH (Table 6). More specifically, canopy cover heterogeneity broadly increased the presence of light specialists and semi-specialists and decreased the presence of shade specialists and semi-specialists. No significant associations were observed for light generalists (Table 6A). Conversely, soil moisture heterogeneity universally increased generalist presence. Dry and moist soil specialists decreased or had a neutral relationship with EH. (Table 6B).

Plants falling into the shade specialist and semi-specialist categories appear to be less competitive under high canopy heterogeneity – this provides a possible explanation for observed increases in PNV (Table 5). A potential hypothesis for this phenomenon may lie in the difference in adaptive strategies to light and shade present in common savanna plants. Shade specialist plants can be grouped into shade tolerant species, which are able to thrive under low light conditions, and shade avoidant species which respond to low light with shade avoidance responses (SARs) (Keuskamp et al. 2010; Ruberti et al. 2012). SARs are recognized as a series of responses to low light, including shoot elongation, rapid spreading, and selective petiole and foliar investment to the upper shoots (Ruberti et al. 2012; Xu et al. 2021). Our study and broader-scale demographic analyses have observed that most abundant UPs14 species consist of disproportionately tall grasses such as big bluestem [*Andropogon gerardii* (Vitman)] or Indian grass [*Sorghastrum nutans* (L. (Nash))]. As such, it is possible that in medium light environments, especially those in such as present in savanna, shading effects from highly dominant tallgrass species may reduce the competitiveness of SARs for shade avoidant species in areas of medium-to-low shade where they may have otherwise been able to survive.

Table 6. Relationships between heterogeneity and specialist or generalist presence using quadrat level models. *Generalized linear mixed models with nested site and plot covariates were used to assess relationship significance between specialist or generalist presence and heterogeneity of canopy cover (A) or soil moisture (B). Log-ratio Chi square values (L-R X^2) and positive (+), negative (-) or ambiguous (+/-) directionality (dir.) were assessed at the finest level of model organization. Positive or negative directionality indicates that ≥75% of significant slopes point in the same direction. No listed directionality indicates non-significant relationships ($p > 0.05$). HHI = Horizontal heterogeneity index.*

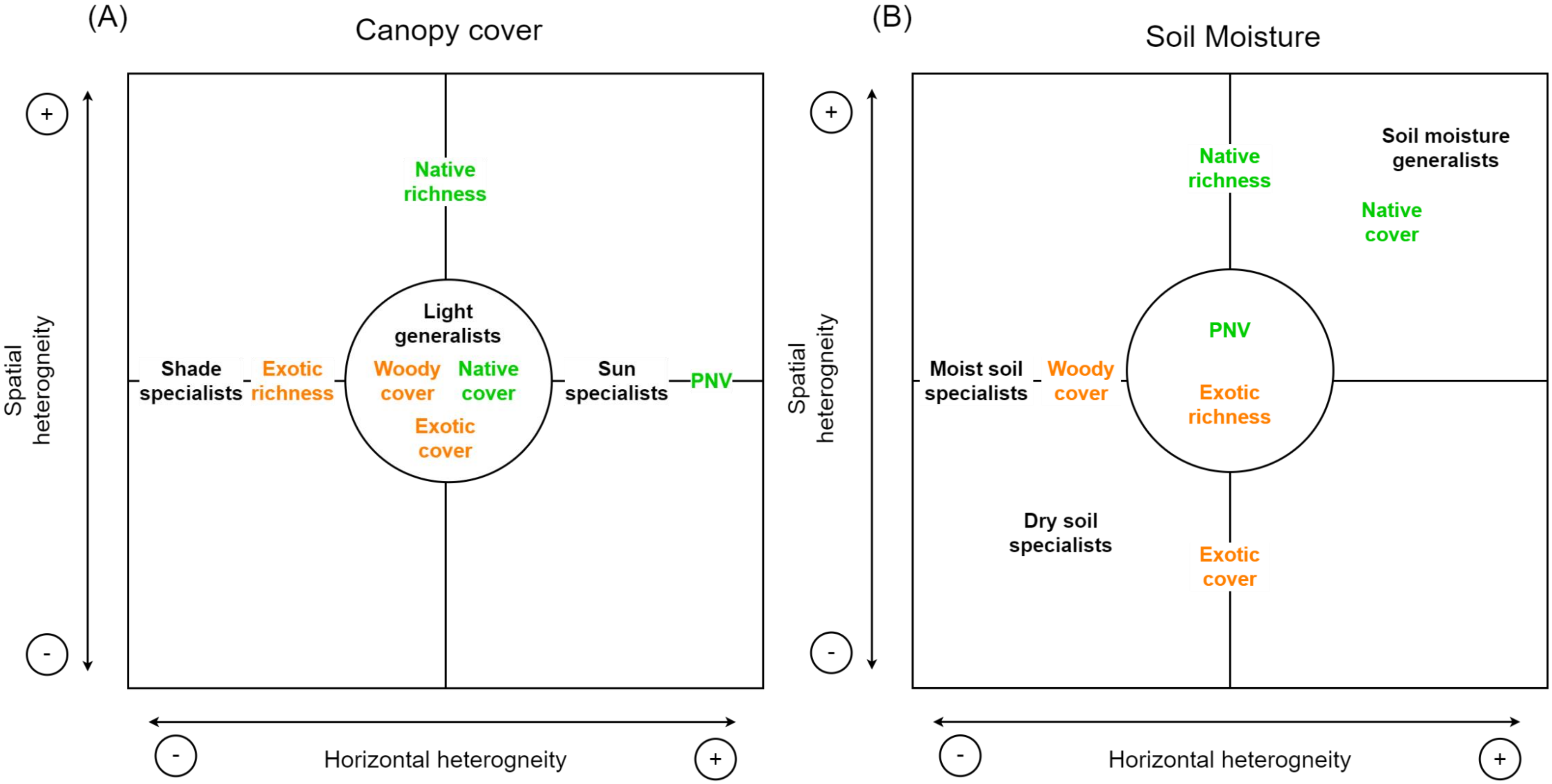
(A)

	Canopy cover standard deviation		Canopy cover HHI	
Group	L-R X^2	Dir.	L-R X^2	Dir.
Sun specialists	63.39	+	23.38	
Sun semi-specialists	35.12	+/-	20.07	
Generalists	21.37		16.79	
Shade semi-specialists	41.69	-	19.67	
Shade specialists	55.16	-	41.90	-

(B)

	Soil moisture standard deviation		Soil moisture HHI		Soil moisture Moran's I	
Group	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.
Dry soil specialists	39.28	-	32.90	+/-	33.09	-
Generalists	54.95	+	35.80	+	35.98	+
Moist soil specialists	41.47	-	32.78	+/-	12.15	

Figure 4. Generalist-specialist presence and select diversity and quality metrics across gradients of heterogeneity. *Canopy cover (A) and soil moisture (B) heterogeneity differ in their relationship with generalists and specialists (black), and positive (green) and negative (orange) metrics of savanna understory diversity. Placement was decided based on significance and direction of generalized linear model results at all spatial scales. Variables within the circle had exclusively ambiguous relationships with EH metrics.*



Summary

Canopy cover heterogeneity metrics had only beneficial or neutral associations with desired management outcomes. Horizontal soil moisture heterogeneity persistently decreased woody cover at smaller spatial scales but had positive associations at the plot scale. This is hypothesized to be due to the difference in scale of canopy shading and woody plant encroachment effects on soil moisture. Spatial heterogeneity of canopy cover and soil moisture had consistently beneficial associations with metrics of diversity and habitat quality. Highly discrete patches of shade and light, as opposed to larger areas of thin, homogeneous canopy cover is recommended.

Elevational heterogeneity had a negative relationship to native species richness, confirming the results of Schetter et al. (2013) who used larger spatial extents (60 and 120 m windows) to observe the same connection in a mixed management savanna. Models suggest moderate benefits to focusing management efforts on flatter areas, but the complexities of this relationship are likely to be highly dependent on management history and site context.

Select trends may be explained by how generalists and specialists interact with EH. More specifically, species specialized in high-light environments saw greater success under high canopy heterogeneity compared to shade specialists. On the other hand, soil moisture heterogeneity promoted greater soil moisture generalist presence and decreased both moist soil and dry soil specialists.

Consistently higher model quality at the medium spatial extent suggests a spatial extent of 12 by 12 m is most relevant in assessing environmental-vegetation feedbacks in this system, especially in regards to light environment.

Acknowledgements

We would like to acknowledge that the research done on this project was done on the traditional homelands of the Dakota and Ojibwe peoples. We would also like to acknowledge the history the Ottawa Bluffs site as a former burial place for local indigenous peoples and encourage proper respect and reverence for the land.

Thank you to Jim and Katheryn Vonderhaar, the Darlene and William Radichel Herbarium, and the MNSU Graduate Studies Department for your assistance in funding this project. Thank you to the Nature Conservancy, the US Fish and Wildlife Service, the University of Minnesota, and the City of Burnsville for the generous use of their lands.

Competing interests: The authors declare none

References

Aaseng N, Almendinger J, Robert D, Hanson D, Lee M, Rowe E, Rusterholz K, Wovcha D (2011) Minnesota's native plant community classification: A statewide classification of terrestrial and wetland vegetation based on numerical analysis of plot data. Page 27. 108. St. Paul, MN: Minnesota County Biological Survey, Ecological Land Classification Program, and Natural Heritage and Nongame Research Program. St. Paul: Minnesota Department of Natural Resources

Acharya BS, Kharel G, Zou CB, Wilcox BP, Halihan T (2018) Woody Plant Encroachment Impacts on Groundwater Recharge: A Review. Water 10:1466

Aldworth TA, Toucher MLW, Clulow AD, Swemmer AM (2023) The Effect of Woody Encroachment on Evapotranspiration in a Semi-Arid Savanna. Hydrology 10:9

Anderson RC (1998) Overview of Midwestern oak savanna. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:1–18

Ansley RJ, Boutton TW, Jacoby PW (2014) Root Biomass and Distribution Patterns in a Semi-Arid Mesquite Savanna: Responses to Long-Term Rainfall Manipulation. Rangeland Ecology & Management 67:206–218

Baer SG, Collins SL, Blair JM, Knapp AK, Fiedler AK (2005) Soil Heterogeneity Effects on Tallgrass Prairie Community Heterogeneity: An Application of Ecological Theory to Restoration Ecology. Restoration Ecology 13:413–424

Bartha S, Collins SL, Glenn SM, Kertész M (1995) Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. Folia Geobot 30:169–184

Beckschäfer P (2015) Hemispherical_2.0 – Batch processing hemispherical and canopy photographs with ImageJ – User Manual.

Blonder B, Both S, Coomes DA, Elias D, Jucker T, Kvasnica J, Majalap N, Malhi YS, Milodowski D, Riutta T, Svátek M (2018) Extreme and Highly Heterogeneous Microclimates in Selectively Logged Tropical Forests. Frontiers in Forests and Global Change 1:5

Brawn JD (2006) Effects of Restoring Oak Savannas on Bird Communities and Populations. Conservation Biology 20:460–469

Breshears DD, Barnes FJ (1999) Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology 14:465–478

Brudvig LA, Asbjornsen H (2008) Patterns of oak regeneration in a Midwestern savanna restoration experiment. Forest Ecology and Management 255:3019–3025

Bucini G, Beckage B, Gross LJ (2017) Climate seasonality, fire and global patterns of tree cover. Frontiers of Biogeography 9:2

Burns TT, Berg AA, Cockburn J, Tetlock E (2016) Regional scale spatial and temporal variability of soil moisture in a prairie region. Hydrological Processes 30:3639–3649

Campbell C, Campbell ID, Blyth CB, McAndrews JH (1994) Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360–362

Cavender-Bares J, Reich PB (2012) Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. Ecology 93

Chadde S (2019) Minnesota Flora: An Illustrated Guide to the Vascular Plants of Minnesota. 2nd ed. United States: Orchard Innovations. 784 p

Collins SL, Calabrese LB (2012) Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. J Vegetation Science 23:563–575

Costanza JK, Moody A, Peet RK (2011) Multi-scale environmental heterogeneity as a predictor of plant species richness. Landscape Ecol 26:851–864

Damgaard C (2014) Estimating mean plant cover from different types of cover data: a coherent statistical framework. Ecosphere 5:20

Davis FW, Synes NW, Fricker GA, McCullough IM, Serra-Diaz JM, Franklin J, Flint AL (2019) LiDAR-derived topography and forest structure predict fine-scale variation in daily surface temperatures in oak savanna and conifer forest landscapes. Agricultural and Forest Meteorology 269–270:192–202

De Pauw K, Sanczuk P, Meeussen C, Depauw L, De Lombaerde E, Govaert S, Vanneste T, Brunet J, Cousins SAO, Gasperini C, Hedwall P-O, Iacopetti G, Lenoir J, Plue J, Selvi F, Spicher F, Uria-Diez J, Verheyen K, Vangansbeke P, De Frenne P (2022) Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. New Phytologist 233:219–235

Deák B, Kovács B, Rádai Z, Apostolova I, Kelemen A, Kiss R, Lukács K, Palpurina S, Sopotlieva D, Báthori F, Valkó O (2021) Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. Science of The Total Environment 763:144199

Dey DC, Kabrick JM (2015) Restoration of Midwestern Oak Woodlands and Savannas. Pages 401–428 in Restoration of Boreal and Temperate Forests. 2nd ed. Florida: Boca Raton

Fleishman E, Noss RF, Noon BR (2006) Utility and limitations of species richness metrics for conservation planning. Ecological Indicators 6:543–553

Fu BJ, Liu SL, Ma KM, Zhu YG (2004) Relationships between soil characteristics, topography and plant diversity in a heterogeneous deciduous broad-leaved forest near Beijing, China. Plant and Soil 261:47–54

Galatowitsch S, Bohnen J (2020) Predicting restoration outcomes based on organizational and ecological factors. Restoration Ecology 28:1201–1212

Grimm EC (1984) Fire and Other Factors Controlling the Big Woods Vegetation of Minnesota in the Mid-Nineteenth Century. Ecological Monographs 54:291–311

Haworth K, McPherson GR (1995) Effects of Quercus emoryi trees on precipitation distribution and microclimate in a semi-arid savanna. Journal of Arid Environments 31:153–170

He L, Ivanov VY, Bohrer G, Maurer KD, Vogel CS, Moghaddam M (2014) Effects of fine-scale soil moisture and canopy heterogeneity on energy and water fluxes in a northern temperate mixed forest. Agricultural and Forest Meteorology 184:243–256

Heatherbell DA, ed. (1985) Proceedings of the International Symposium on Cool Climate Viticulture and Enology. Corvallis, OR: Oregon State University, Depts. of Food Science and Technology, Horticulture, and Extension Service, in cooperation with the Oregon Winegrowers Association and Oregon Wine Advisory Board

Helbach J, Frey J, Messier C, Mörsdorf M, Scherer-Lorenzen M (2022) Light heterogeneity affects understory plant species richness in temperate forests supporting the heterogeneity–diversity hypothesis. Ecology and Evolution 12:e8534

Hillebrand H, Blasius B, Borer ET, Chase JM, Downing JA, Eriksson BK, Filstrup CT, Harpole WS, Hodapp D, Larsen S, Lewandowska AM, Seabloom EW, Van de Waal DB, Ryabov AB (2018) Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. Journal of Applied Ecology 55:169–184

Keuskamp DH, Sasidharan R, Pierik R (2010) Physiological regulation and functional significance of shade avoidance responses to neighbors. Plant Signaling & Behavior 5:655–662

King RS, Brashear KE, Reiman M (2007) Red-Headed Woodpecker Nest-Habitat Thresholds in Restored Savannas. The Journal of Wildlife Management 71:30–35

Kirsch A, Kaproth MA (2022) Defining plant ecological specialists and generalists: Building a framework for identification and classification. Ecology and Evolution 12:e9527

Kleb HR, Wilson SD (1997) Vegetation Effects on Soil Resource Heterogeneity in Prairie and Forest. The American Naturalist 150:283–298

Krawchuk MA, Haire SL, Coop J, Parisien M-A, Whitman E, Chong G, Miller C (2016) Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7:e01632

Leach MK, Givnish TJ (1998) Identifying highly restorable savanna remnants. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 86:119–127

Leite PAM, Wilcox BP, McInnes KJ (2020) Woody plant encroachment enhances soil infiltrability of a semiarid karst savanna. Environ Res Commun 2:115005

Lettow MC, Brudvig LA, Bahlai CA, Landis DA (2014) Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. Forest Ecology and Management 329:89–98

Lindgren J, Kimberley A, Cousins SAO (2018) The complexity of forest borders determines the understorey vegetation. Applied Vegetation Science 21:85–93

Lundholm JT (2009) Plant species diversity and environmental heterogeneity: spatial scale and competing hypotheses. Journal of Vegetation Science 20:377–391

Mayora G, Scarabotti P, Schneider B, Alvarenga P, Marchese M (2020) Multiscale environmental heterogeneity in a large river-floodplain system. Journal of South American Earth Sciences 100:102546

Meigs GW, Dunn CJ, Parks SA, Krawchuk MA (2020) Influence of topography and fuels on fire refugia probability under varying fire weather conditions in forests of the Pacific Northwest, USA. Can J For Res 50:636–647

Munson SM (2013) Plant responses, climate pivot points, and trade-offs in water-limited ecosystems. Ecosphere 4:109

Nuzzo VA (1986) Extent and Status of Midwest Oak Savanna: Presettlement and 1985. Natural Areas Journal 6:6–36

Pariente S (2002) Spatial Patterns of Soil Moisture as Affected by Shrubs, in Different Climatic Conditions. Environ Monit Assess 73:237–251

Peterson DW, Reich PB (2001) Prescribed Fire in Oak Savanna: Fire Frequency Effects on Stand Structure and Dynamics. Ecological Applications 11:914–927

Pincebourde S, Murdock CC, Vickers M, Sears MW (2016) Fine-Scale Microclimatic Variation Can Shape the Responses of Organisms to Global Change in Both Natural and Urban Environments. Integrative and Comparative Biology 56:45–61

Qiao L, Zou CB, Stebler E, Will RE (2017) Woody plant encroachment reduces annual runoff and shifts runoff mechanisms in the tallgrass prairie, USA. Water Resources Research 53:4838–4849

Rammette A, Tiejde J (2006) Multiscale responses of microbial life to spatial distance and environmental heterogeneity in a patchy ecosystem. PNAS 104:8

Ruberti I, Sessa G, Ciolfi A, Possenti M, Carabelli M, Morelli G (2012) Plant adaptation to dynamically changing environment: The shade avoidance response. Biotechnology Advances 30:1047–1058

Rueden CT, Schindelin J, Hiner MC, DeZonia BE, Walter AE, Arena ET, Eliceiri KW (2017) ImageJ2: ImageJ for the next generation of scientific image data. BMC Bioinformatics 18:529

Scheffers BR, Edwards DP, Macdonald SL, Senior RA, Andriamahohatra LR, Roslan N, Rogers AM, Haugaasen T, Wright P, Williams SE (2017) Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica 49:35–44

Schetter TA, Walters TL, Root KV (2013) A Multi-scale Spatial Analysis of Native and Exotic Plant Species Richness Within a Mixed-Disturbance Oak Savanna Landscape. Environmental Management 52:581–594

Silvani X, Morandini F, Dupuy J-L (2012) Effects of slope on fire spread observed through video images and multiple-point thermal measurements. Experimental Thermal and Fluid Science 41:99–111

Small CJ, McCarthy BC (2005) Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217:229–243

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880

Stein A, Kreft H (2015) Terminology and quantification of environmental heterogeneity in species-richness research. Biological Reviews 90:815–836

Suggitt A, Wilson R, Isaac N, Beale C, Auffret A, August T, Bennie J, Crick H, Duffield S, Fox R, Hopkins J, Macgregor N, Morecroft M, Walker K, Maclean I (2018) Extinction risk from climate change is reduced by microclimatic buffering. Nature Climate Change 8:713-717

Volder A, Briske DD, Tjoelker MG (2013) Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Glob Change Biol 19:843–857

Waldstein AL (2012) Nest-site selection and nesting ecology of red-headed woodpeckers. Master's thesis. St Paul, MN: University of Minnesota. 43p

Walsh RP (2017) Microclimate and biotic interactions affect Karner blue butterfly occupancy and persistence in managed oak savanna habitats. J Insect Conserv 21:219–230

Weiher E (2003) Species richness along multiple gradients: testing a general multivariate model in oak savannas. Oikos 101:311–316

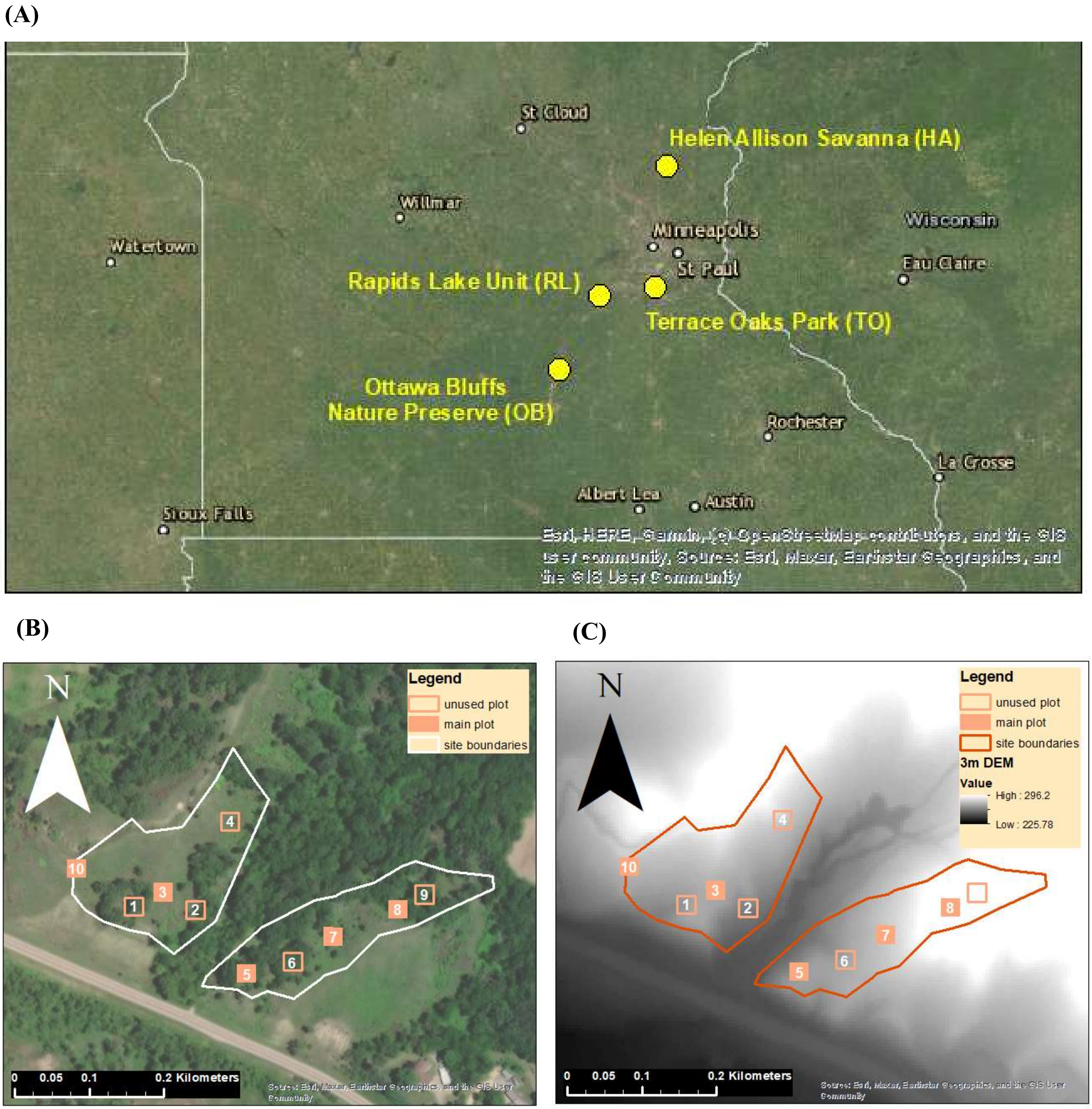
Willis CG, Halina M, Lehman C, Reich PB, Keen A, McCarthy S, Cavender-Bares J (2009) Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. Ecography 33:565-577

Xu H, Chen P, Tao Y (2021) Understanding the Shade Tolerance Responses Through Hints From Phytochrome A-Mediated Negative Feedback Regulation in Shade Avoiding Plants. Front Plant Sci 12:813092

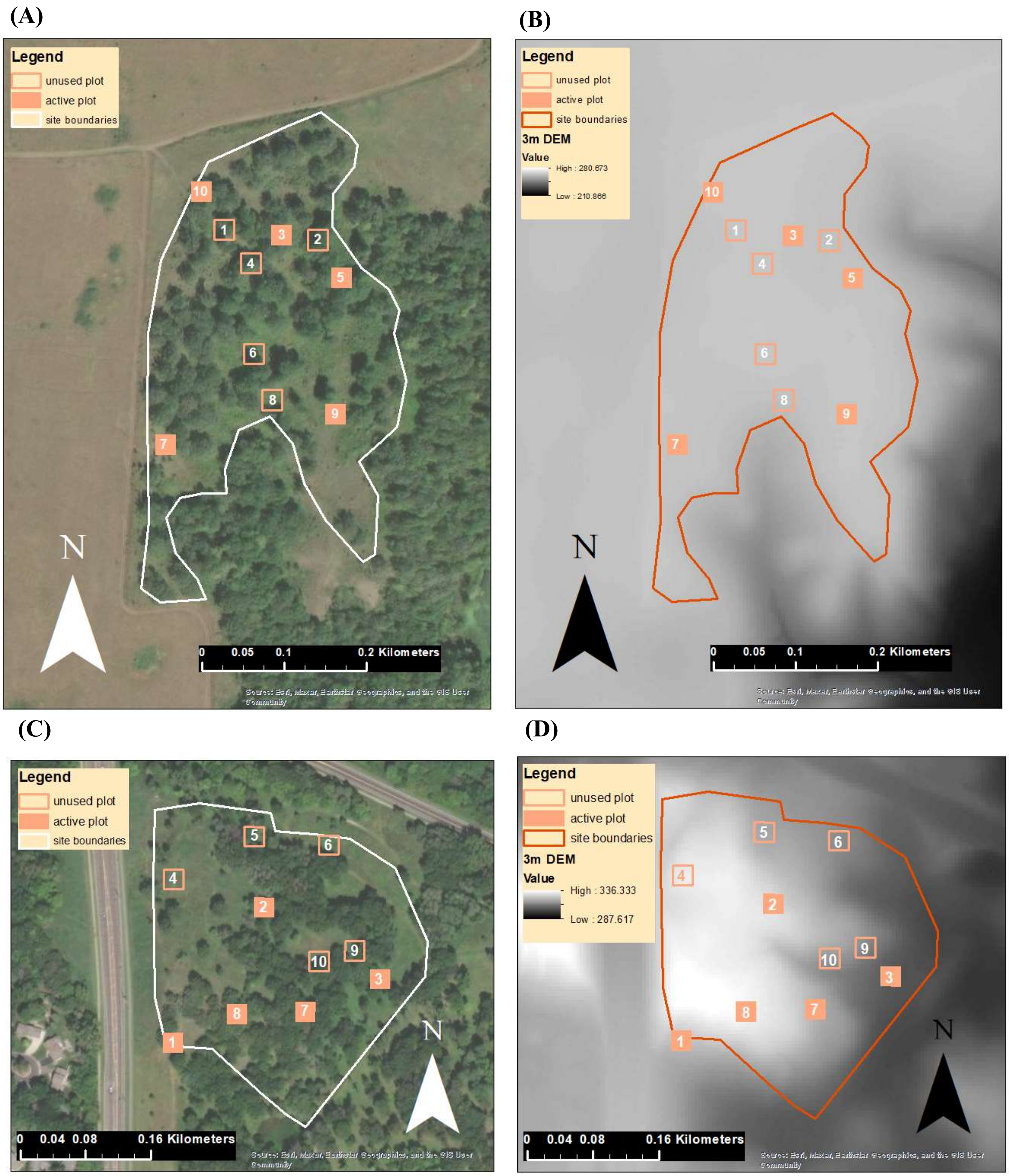
Supplemental materials

Supplemental note 1: Study site description and maps

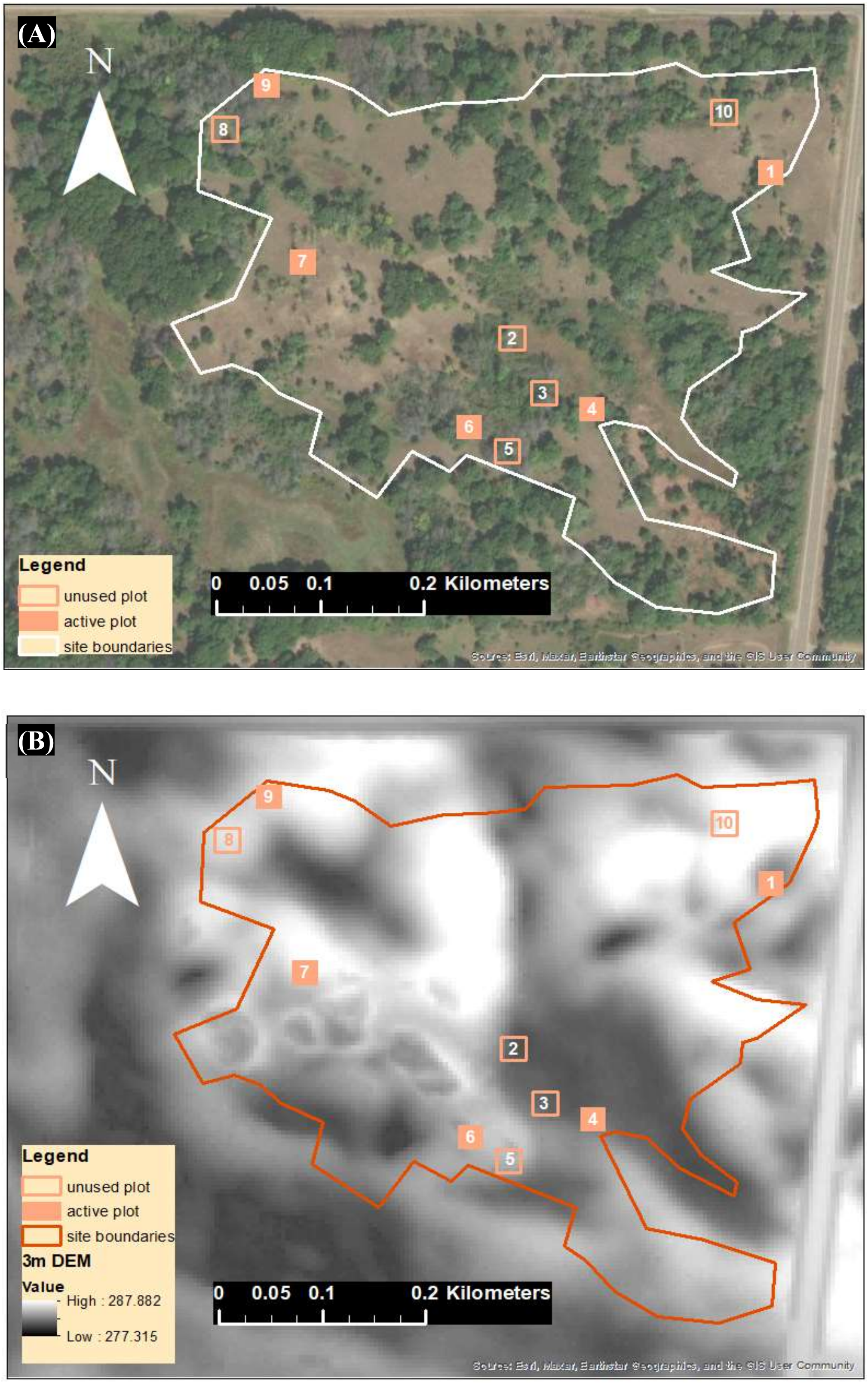
Four study sites with a diversity of management histories were chosen within central and south-central Minnesota (Supplementary Figure S1 – S3). Ottawa Bluffs Nature preserve (44.3665°N, -98.9354°W), managed by the Nature Conservancy, is a long-term restoration project on fragmented savanna and prairie remnants. This site features notably high topographical variance and loam to loamy sand soils. Hand cutting, burns, and spreading of local seed mixes have dominated management at this location. Within the Minnesota Valley National Wildlife Refuge, Rapids Lake Unit (44.7348°N, -93.6476°W), is a smaller restoration project started over remnant savanna in 2017 managed by the US Fish and Wildlife Service. Management tactics include burns, mowing, and oak girdling. Managers have largely utilized the existing seed banks at this site. Terrace Oaks Park (44.7699°N, -93.2421°W), managed by the City of Burnsville, MN, is a restored site with small areas of remnant savanna. Burns, oak thinning, mowing, and native seed mixes have been used at this site. Helen Allison Savanna (45.3826°N, -93.1681°W), managed collaboratively by the Nature Conservancy and the University of Minnesota, is a long-term management project on a large savanna remnant. Soils at this site are extremely sandy and well drained, with infrequent patches of moist soil with clear wetland-pattern vegetation.



Supplementary Figure S1. Study site locations and Ottawa Bluffs site layout. *Maps feature study site locations within central and southern central Minnesota (A) as well as aerial imagery (B) and 3m DEM projection (C) of the Ottawa Bluffs study site.*



Supplementary Figure S2. Rapids Lake and Terrace Oaks Park site layouts. *Maps feature study site layouts over aerial imagery and 3m DEM projections of the Rapids Lake (A, B) and Terrace Oaks Park (C, D) study sites.*



Supplementary Figure S3. Hellen Allison Savanna site layout. *Maps feature study site layouts with aerial imagery (A) and 3m DEM projection (B) for the Helen Allison site.*

Supplemental note 2: Effects of climatic gradients on understory diversity and quality

Generalized linear mixed models with a nested site covariate ('plot level') or nested site and plot covariates ('quadrat level') were used to assess relationships between environmental gradients and metrics of diversity and quality.

As hypothesized, higher canopy cover values have either unfavorable or neutral effects on metrics of understory diversity and quality. More specifically, higher cover was associated with greater woody presence in all quadrat level models, and was associated with lower PNV at the small, medium, and plot, extents (Supplementary Table S1). All other associations were directionally ambiguous or non-significant.

Within the quadrat level models, soil moisture largely behaved as expected, with positive to neutral associations with exotic richness, exotic cover, and woody cover (Supplementary Table S1). At the plot scale, however, higher soil moisture values appeared to decrease exotic cover. This trend was also observed between higher soil moisture heterogeneity at medium and plot scales (Chapter 2, Table 5), suggesting a possible spatial threshold in how soil moisture interacts with exotic presence in this environment.

F

Supplementary Table S1. Effects of climatic gradients on understory diversity and quality. *Generalized linear mixed models with a nested site covariate (plot model type) or nested site and plot covariates (quadrat model type) were used to assess relationships between environmental gradients and metrics of diversity and quality. Positive (+), negative (-) or ambiguous (+/-) directionality (dir.) was assessed at the finest level of model organization and indicates ≥75% of significant slopes pointing in the same direction. Directionality of non-significant models was left blank (p > 0.05). PNV = potential native vegetation, CC = canopy cover, sd = standard deviation, HHI = Horizontal Heterogeneity Index, DEM = 3m digital elevation model, and SM = soil moisture. 'Small extent' refers to the 6 by 6 m spatial extent and 'medium extent' the 12 by 12 m extent. 'Point measurement' refers to the single measurement taken at the related quadrat.*

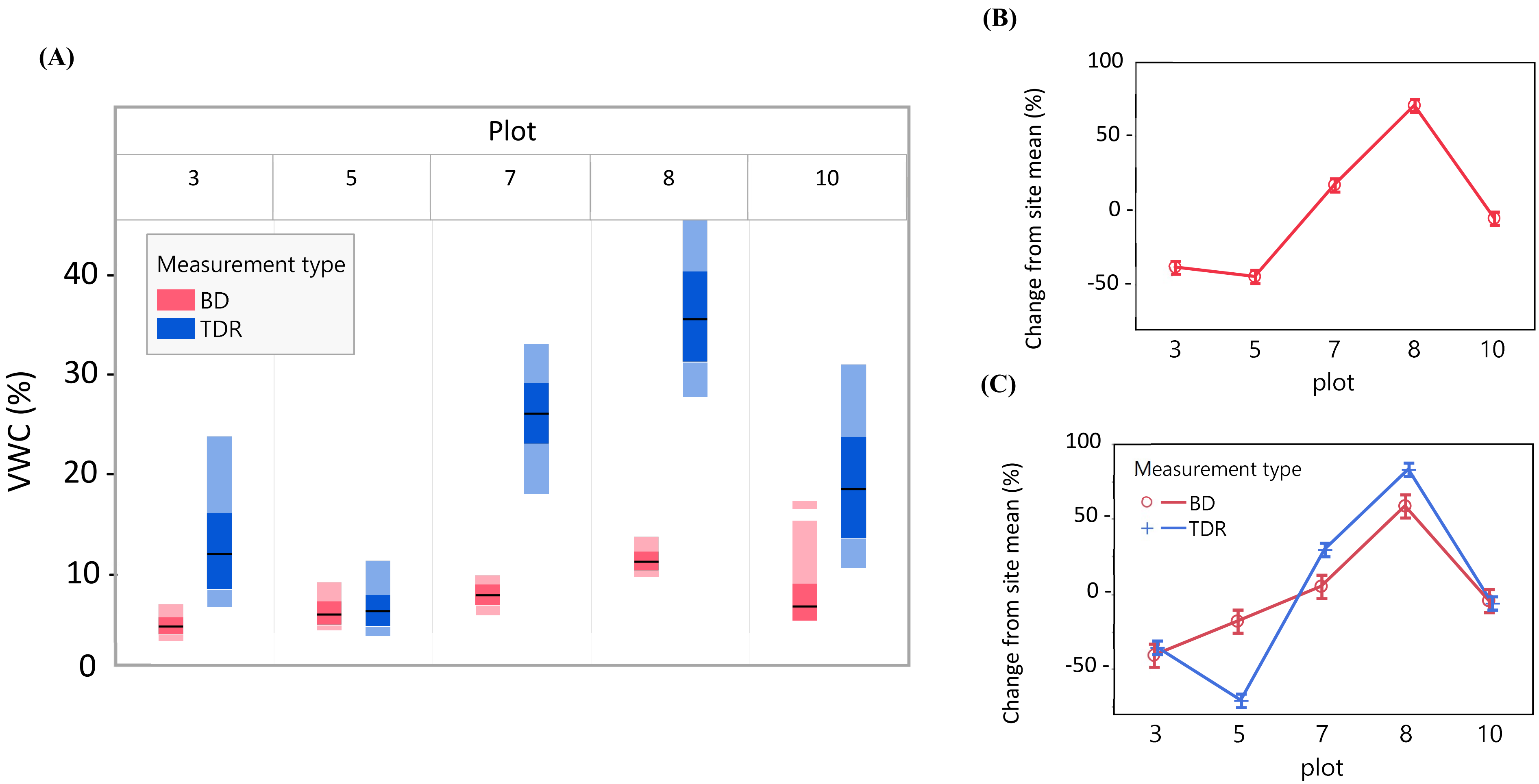
Environmental predictor	Spatial Extent	Model type	Percent Native Species		Percent Native Cover		PNV		Percent exotic species		Percent exotic cover		Percent woody cover	
			L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.	L-R X^2	Dir.
CC point	point	quadrat	22.13		32.11	+/-	39.52	+/-	23.98		40.08	+/-	35.35	+
CC average	small	quadrat	24.46		29.19		45.20	-	39.54	+/-	34.24	+/-	40.12	+
CC average	medium	quadrat	46.49	+/-	57.35	+/-	51.84	-	61.22	+/-	70.97	+/-	61.93	+
CC average	plot	plot	8.26		7.12		19.35	-	10.39	+/-	12.96	+/-	5.14	
SM point	point	quadrat	22.89		34.32	+/-	13.99		44.02	+	57.89	+/-	46.10	+
SM average	small	quadrat	31.04		40.52	+/-	21.66		62.56	+	53.36	+/-	40.12	+/-
SM average	medium	quadrat	41.16	+/-	64.23	+/-	23.78		69.10	+	96.05	+	49.45	+/-
SM average	plot	plot	2.99		10.91	+/-	6.29		8.68		15.04	-	8.40	

Supplemental Note 3: Soil bulk density

To investigate the validity of VWC values found at the OB study site, VWC was additionally derived from soil bulk density. Note that collection took place October 22-23, 2022, after the conclusion of the main study period. Cores were collected using a 97.196 cm^3 metal cylinder pounded into the ground using a wooden board and rubber mallet. Cylinders were extracted with a hand trowel and soil was transferred into plastic bags for later analysis. To retain moisture, bags were kept sealed in a dark, refrigerated area until processing. Soil mass in grams was taken before and after 24-48 hours of drying in a 105 °C oven. Resulting values were used to calculate Gravimetric Water Content (GWC) for each sample. GWC was converted to VWC by multiplying a sample's GWC by its bulk density over the density of water.

Three bulk density cores were taken within 1 meter of each location where a vegetation survey occurred, for a total of 27 cores per plot. VWC for the three cores at each survey point were averaged before analysis to mimic TDR collection procedures. Group differences between bulk density-derived VWC and TDR-derived VWC were tested with a two-way ANCOVA (analysis of covariance) nested by plot and coordinate (JMP version 17, JMP Statistical Discovery LLC., 100 SAS Campus Drive, Cary, North Carolina, United States, 27513).

TDR-derived soil moisture ranged from a VWC of 2.9 to 45.9 % with an average value of 19.4 %. BD-derived soil moisture ranged from 2.4 to 16.4% with an average of 6.6%. While the overall ranges differed in magnitude, the relative change from plot-to-plot was not significantly different as confirmed by a two-way ANOVA ($p = 0.99999$, Supplementary Figure S4), affirming relative accuracy of the TDR methodology.



Supplementary Figure S4. Comparison of volumetric water content (VWC) collection methods at Ottawa Bluffs (OB) study site. *VWC collected via time-domain reflectometry (TDR) (n = 81) and VWC derived from soil bulk density (BD) (n = 27) was completed at the OB site for quality assurance purposes. Color shading represents IQR (A). Data was transformed as the percent difference from site means for each measurement type (B). A two-way ANOVA test revealed no significant difference between the two transformed datasets (p = 0.99999) (C). Error bars represent ± 1 SE.*

Supplemental Note 4: Evaluation of species richness as an indicator for management success

While initial hypotheses for this study were grounded in the wide body of literature linking species richness and environmental heterogeneity, species richness may be an unsuitable metric for defining savanna habitat quality. Plot level models showed that species richness had a highly significant positive association with % woody cover and no relationship to PNV, ratios of exotic to native richness or exotic to native cover. At the quadrat level, corrected for site and plot differences, species richness had significant positive relationships with woody cover and higher ratios of exotic to native cover (Supplementary Table 2).

Supplementary Table 2. Relationships between species richness and management metrics. *Generalized linear modeling with nested site and plot covariates was used to assess associations with species richness. Positive (+), negative (-) or ambiguous (+/-) directionality (Dir.) was determined from the significant slopes at the lowest level of model organization. Directionality was left blank for non-significant models (p > 0.05). PNV = potential native vegetation.*

	Plot level		Quadrat level	
Variable	L-R X^2	Dir.	L-R X^2	Dir.
Exotic : native richness	4.02		30.90	
Exotic : native cover	4.15		47.13	+
Percent woody cover	14.73	+	32.69	+
PNV	6.41		17.88	

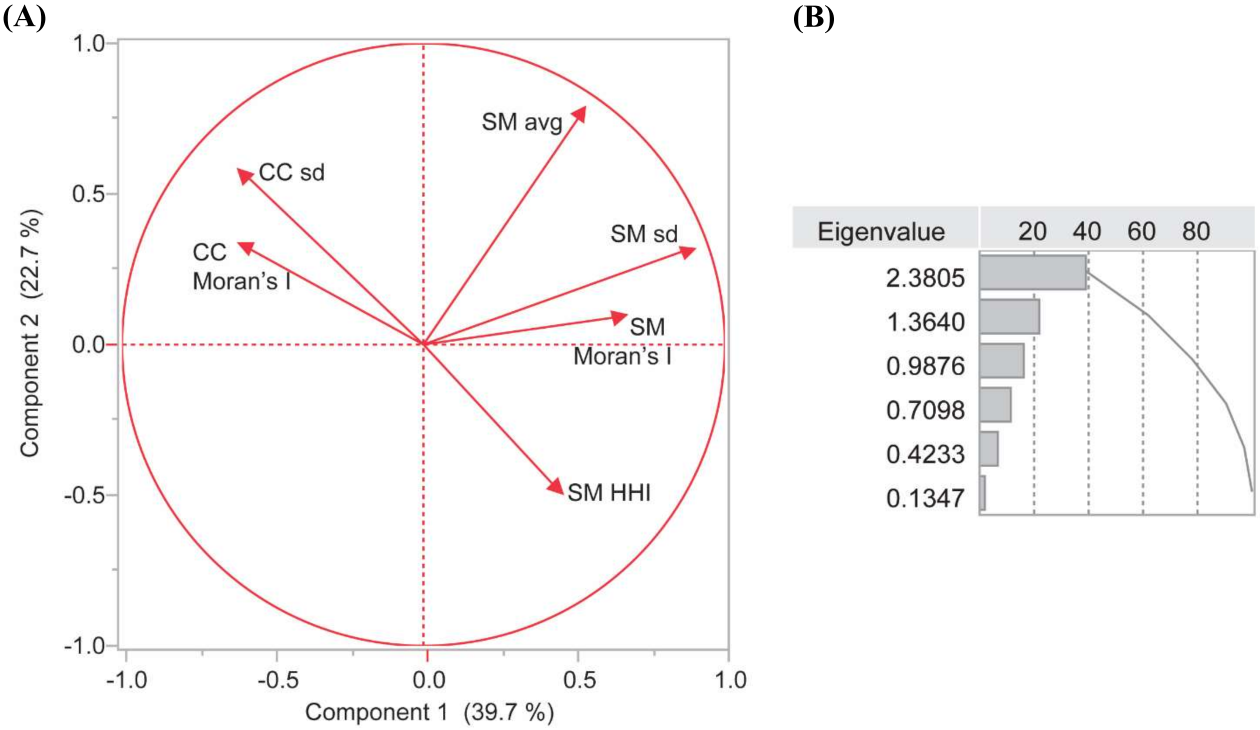
This strong association with negative outcomes leads us to believe that species richness is a poor indicator of habitat quality in savanna environments. We strongly advise against using it in assessments of savanna habitat quality and recommend additional research into the relationship between diversity metrics and habitat quality in ecotone environments which may behave differently than more homogenous systems.

Supplemental Note 5: Aspect

While aspect, or slope direction, was assessed for all plots, randomized plot placement methods biased the dataset disproportionately towards southern and western facing slopes (n = 10) compared to northern or eastern facing slopes (n = 3). Additionally, many plots were classified as flat (n = 7). These flat plots were disproportionately from the RL site (71%). Further analysis of the impact of aspect on savanna vegetation was omitted for these reasons.

Supplemental Note 6: Principal Component Analysis

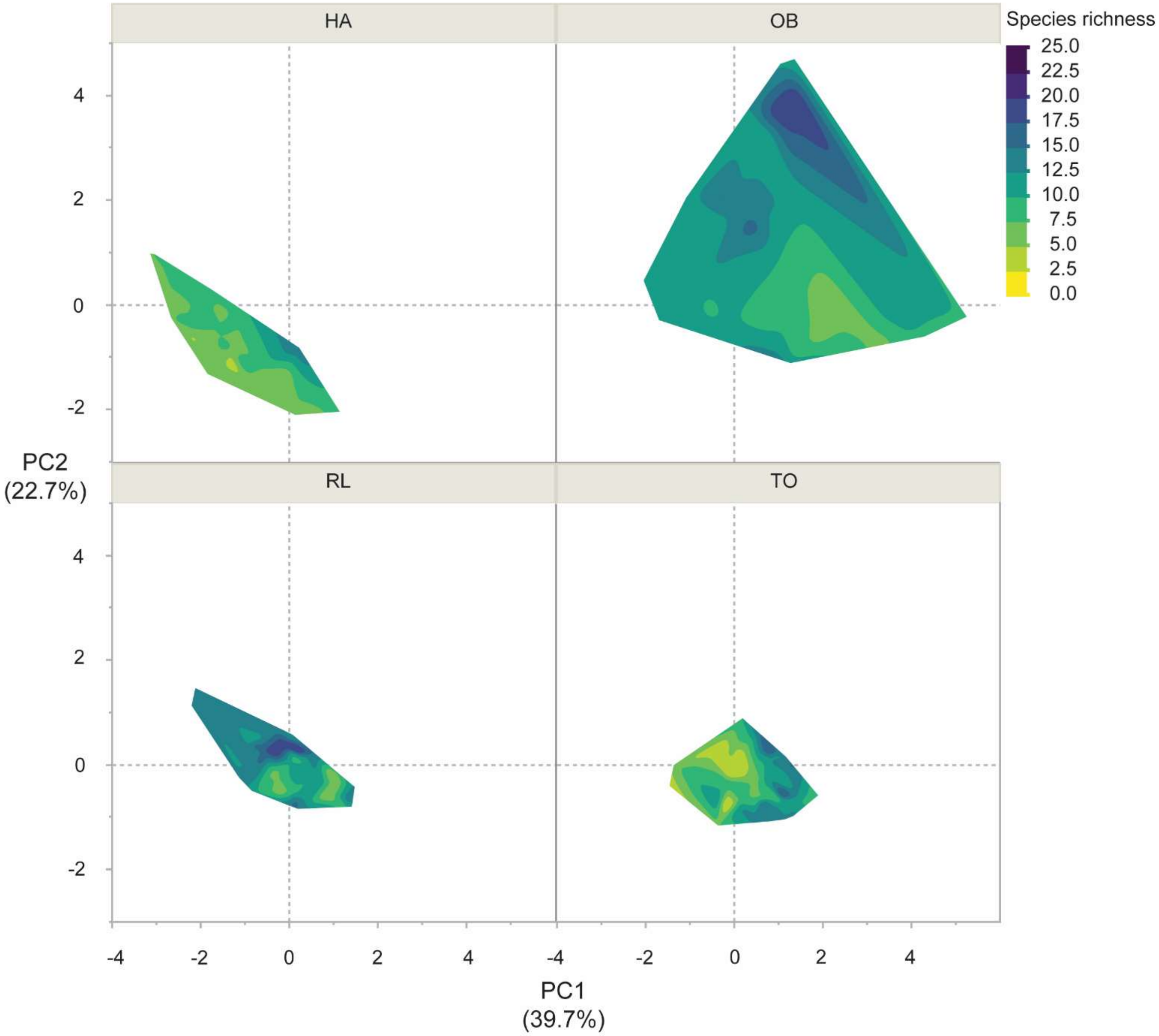
A principal component analysis (PCA) was used to analyze the linked effects of environmental variables on vegetative composition. While axes contained a moderate amount of explanatory power (39.7 and 22.7%) (Supplementary Figure S5, Supplementary Table S3), they were not useful in visualizing the compound effects of soil moisture and canopy cover on key positive and negative management outcomes. They are, however, valuable to assess the environmental character present at each site (Supplementary Figures S6-S12).



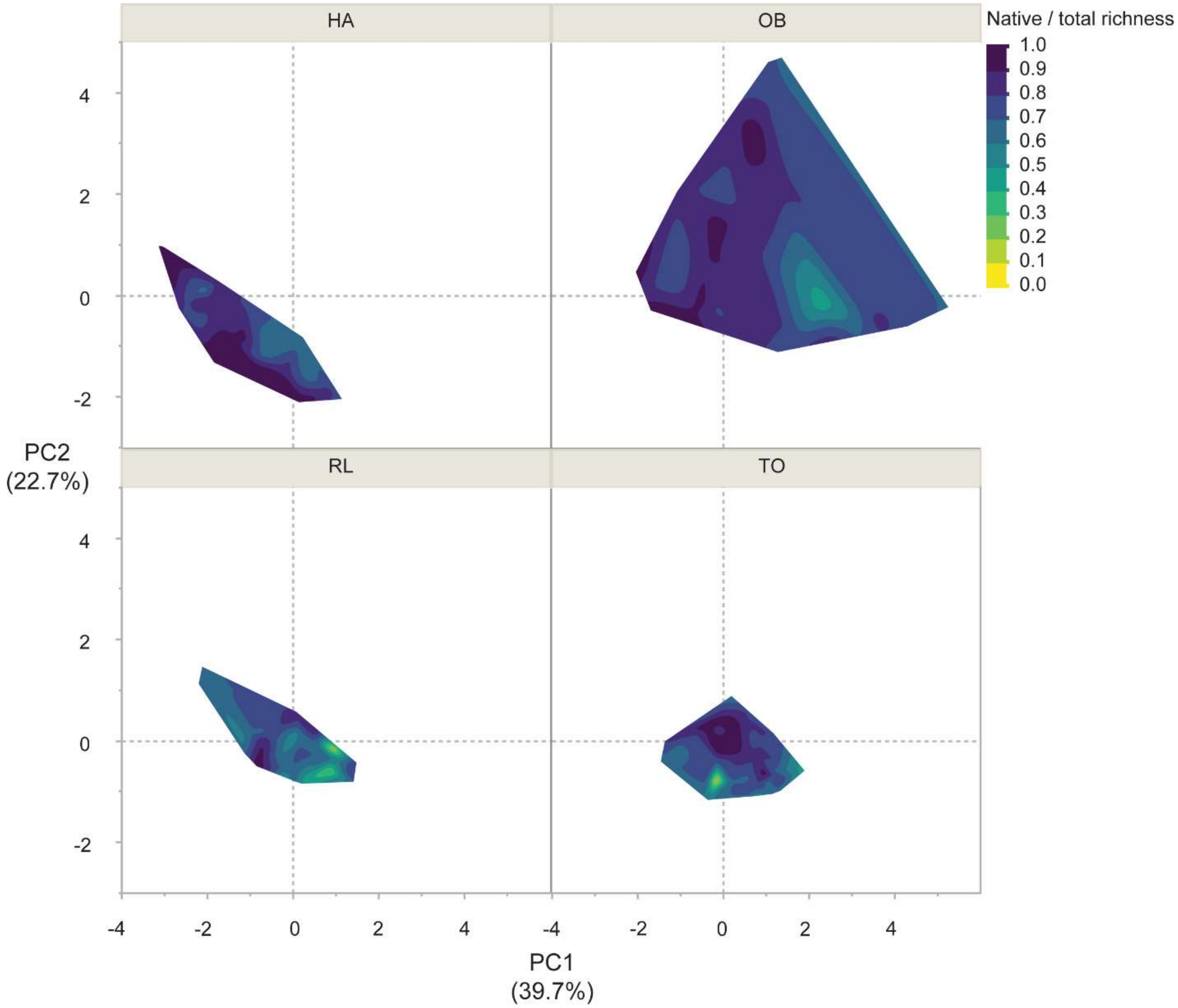
Supplementary Figure S5. Vectors and Eigenvalues for Principal Component Analyses. *Vectors for the Principal Component Analysis show clear aggregation of canopy cover (CC) and soil moisture (SM) heterogeneity metrics (A). Based on an eigenvalue cutoff of 1, Principle Components 1 and 2 were eligible for further analyses (B). All variables consider the medium spatial extent aside from canopy cover Moran's index scores due to limitations on sample sizes at small spatial extents. sd = standard deviation, HHI = Horizontal heterogeneity index.*

Supplementary Table S3. Principal Component Loadings*. All variables consider the medium spatial extent aside from canopy cover Moran's I index scores due to sample size limitations.*

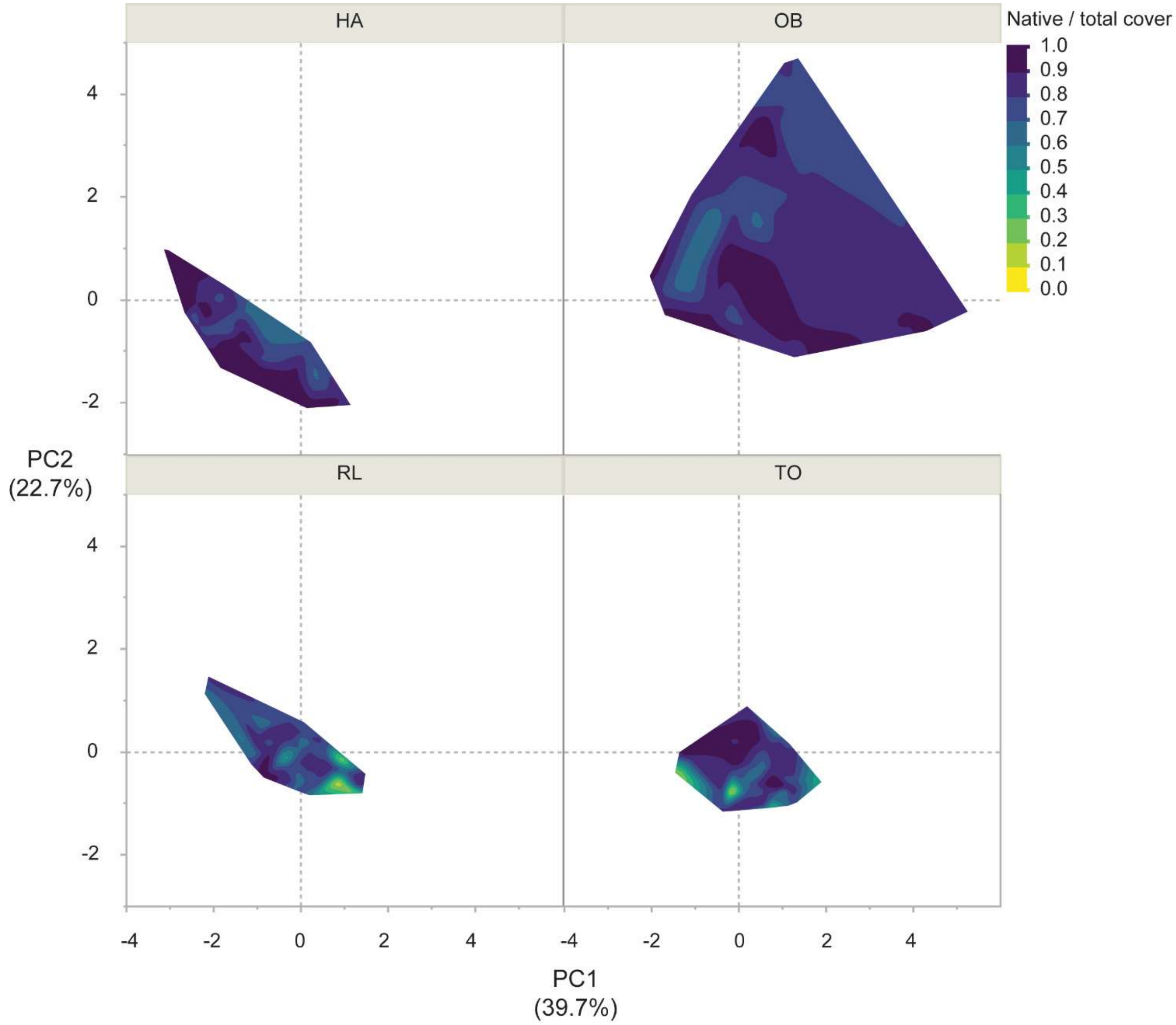
Heterogeneity/environmental variable	Principal Component 1	Principal Component 2
	Weight	
Canopy cover standard deviation	-0.5973	0.5694
Canopy cover Moran's I index	-0.5922	0.3257
Soil moisture standard deviation	0.8781	0.3158
Soil moisture Moran's I index	0.6535	0.0927
Soil moisture Horizontal Heterogeneity Index	0.4434	-0.4789
Soil moisture average	0.5277	0.7721



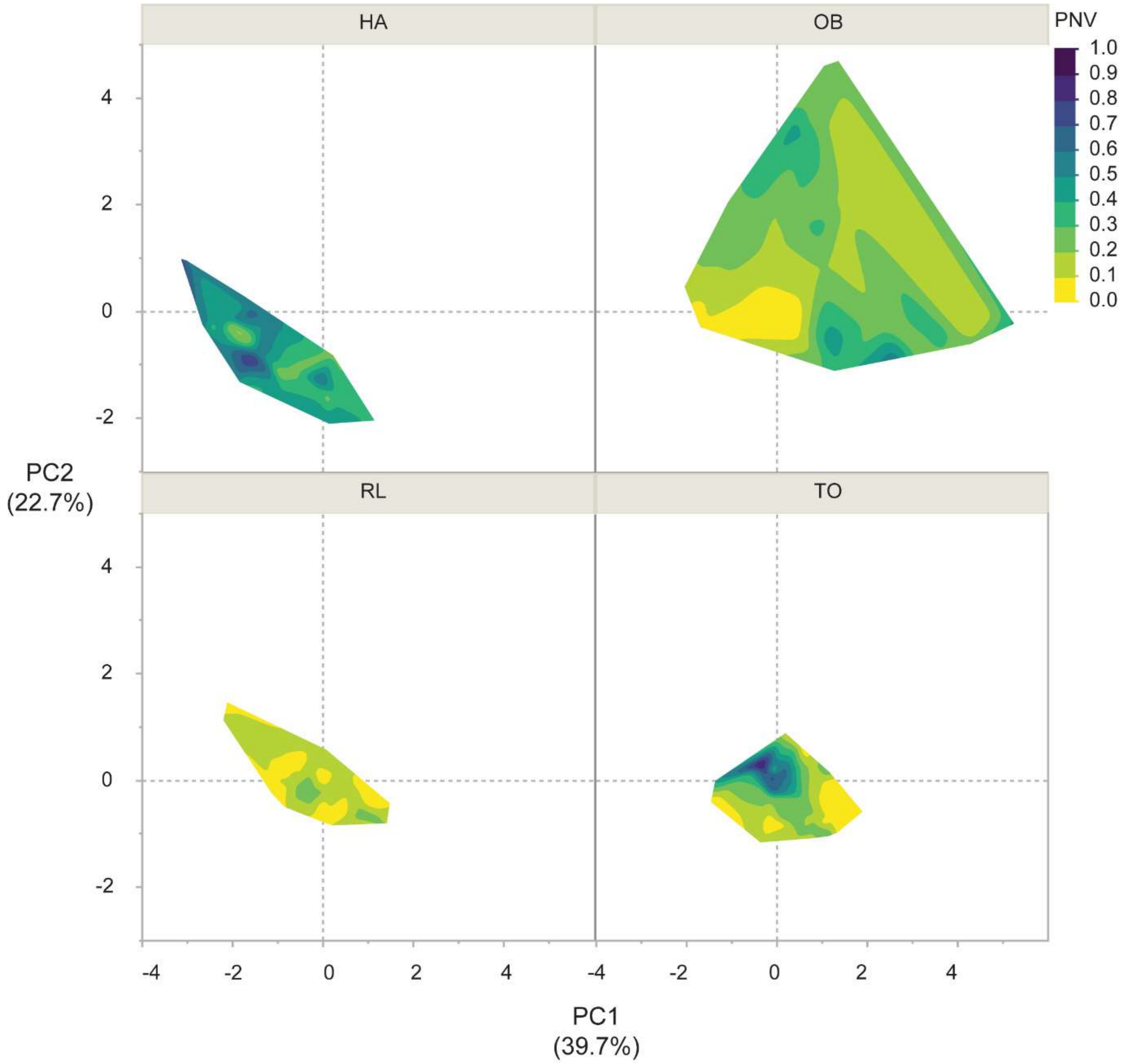
Supplementary Figure S6. Quadrat level Principal Component Analysis color mapped to species richness values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



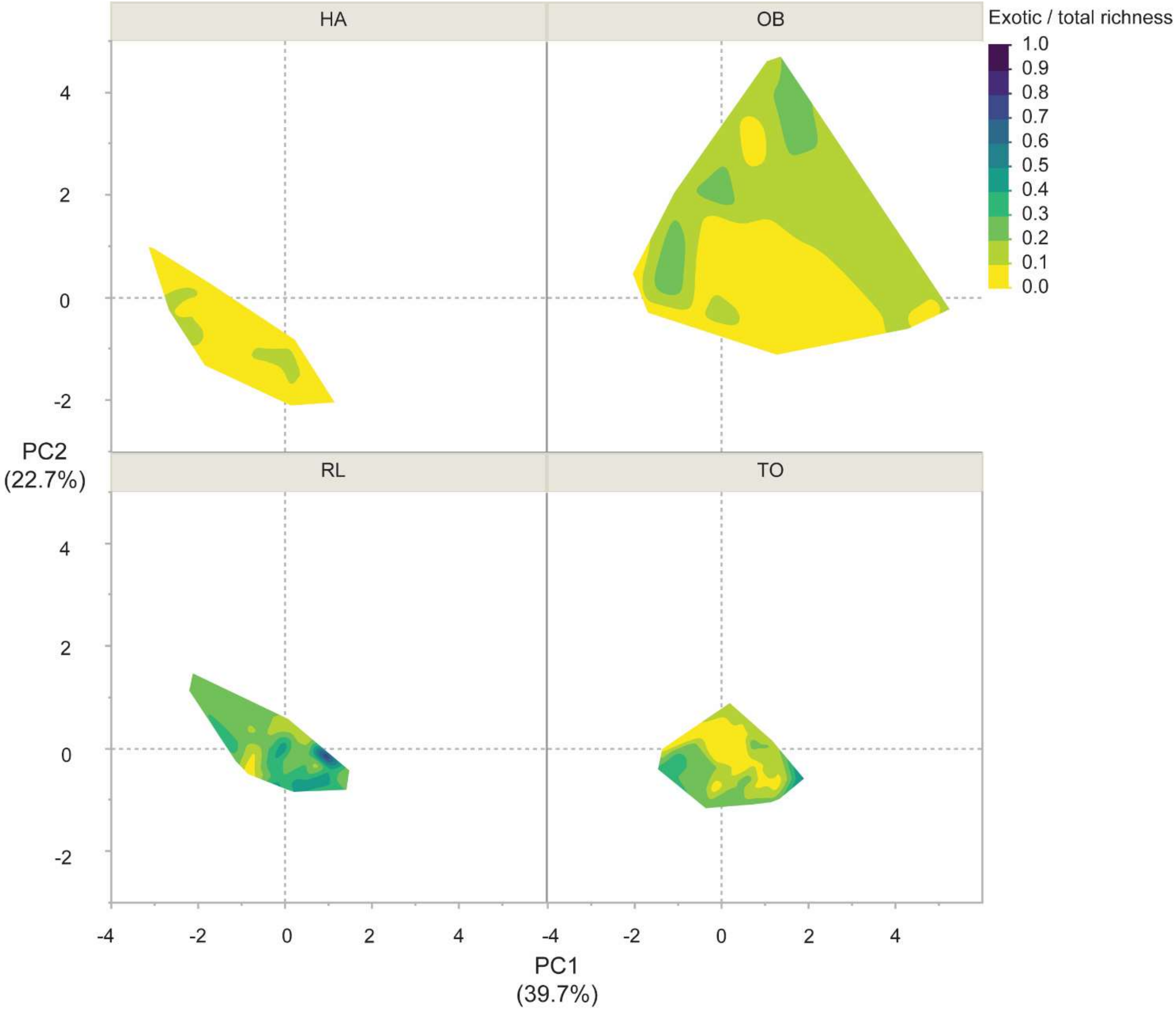
Supplementary Figure S7. Quadrat level Principal Component Analysis color mapped to percent native richness values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



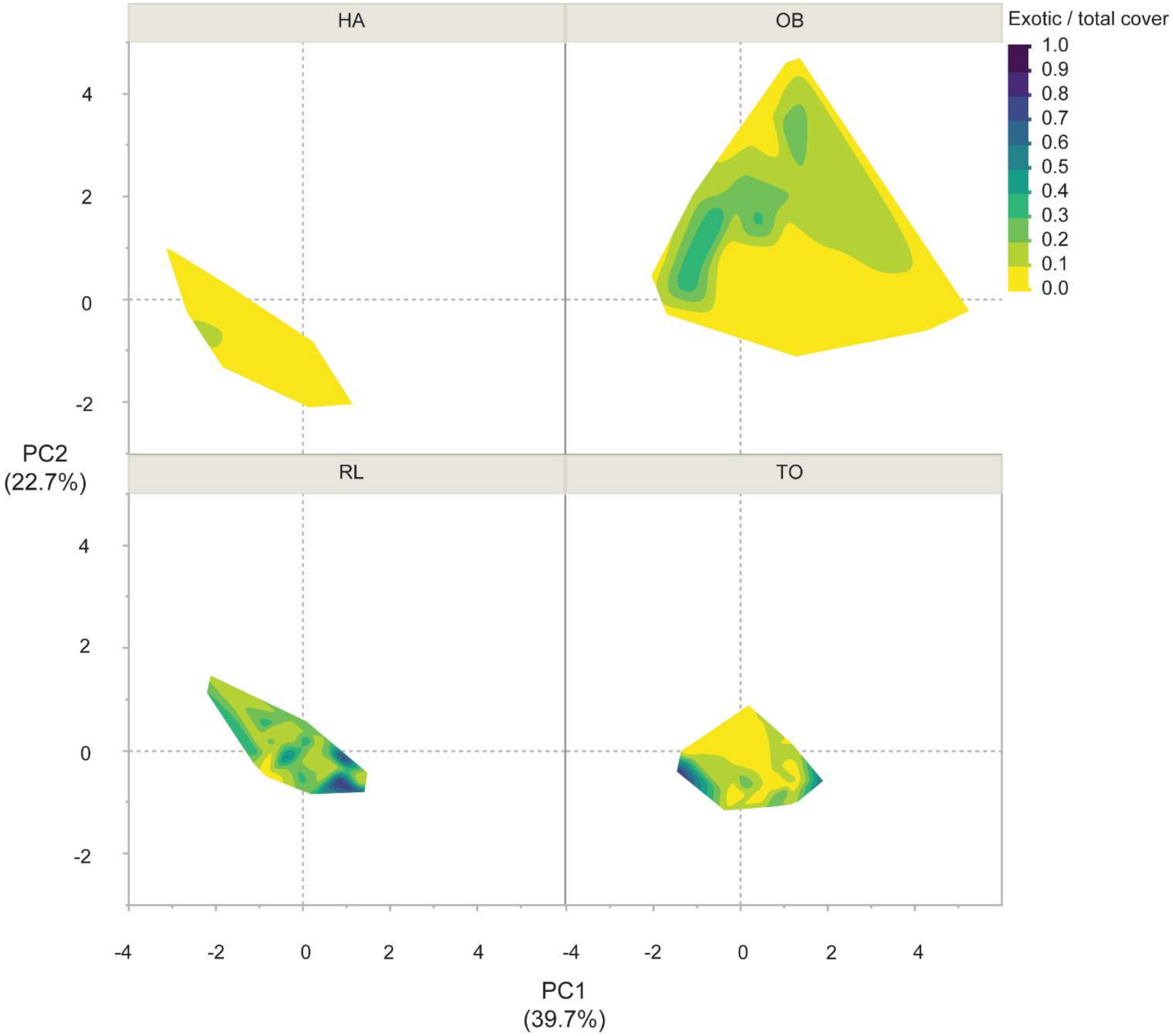
Supplementary Figure S8. Quadrat level Principal Component Analysis color mapped to percent native cover values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



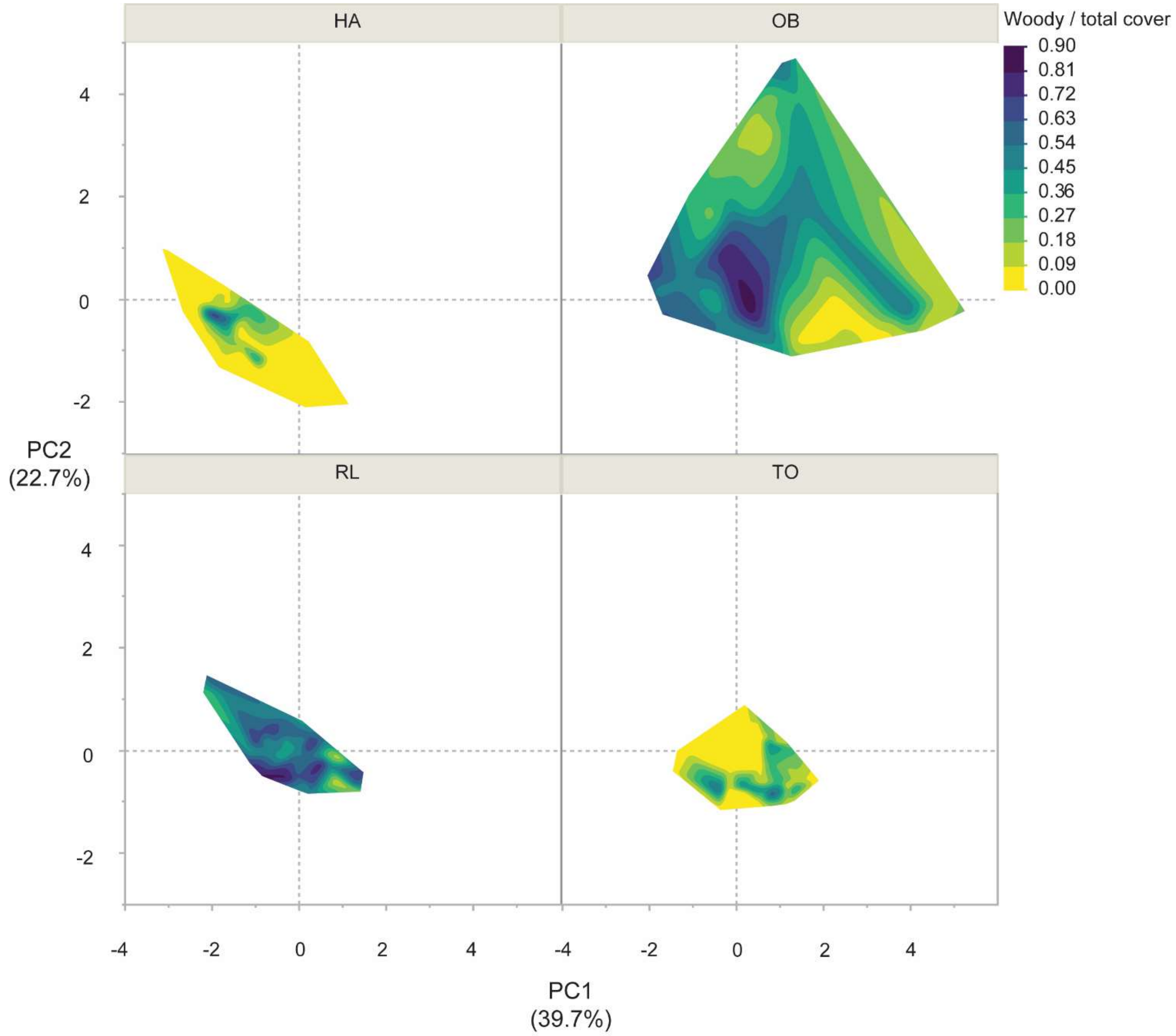
Supplementary Figure S9. Quadrat level Principal Component Analysis color mapped to potential native vegetation (PNV). *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



Supplementary Figure S10. Quadrat level Principal Component Analysis color mapped to percent exotic richness values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



Supplementary Figure S11. Quadrat level Principal Component Analysis color mapped to percent exotic cover values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5).*



Supplementary Figure S12. Quadrat level Principal Component Analysis color mapped to percent woody cover values. *Upper left quadrant values loosely correspond to high canopy cover heterogeneity while positive principal component 1 (PC1) values approximately represent higher canopy cover heterogeneity. Higher principal component 2 (PC2) values represent higher overall soil moisture (Supplementary Figure S5)*

Supplemental Note 7: AICc scores

U

Supplementary Table S4. AICc scores. *Generalized linear mixed models with a nested site covariate (plot model type) or nested site and plot covariates (quadrat model type) were used to assess relationships between environmental gradients or environmental heterogeneity and metrics of diversity and quality. Positive (green), negative (orange) or ambiguous (white) directionality (dir.) was assessed at the finest level of model organization. Positive or negative directionality indicates ≥75% of significant slopes point in the same direction. Non-significant models are written in grey text to allow for effective Akaike information criterion (AICc) comparison (p > 0.05). Scores can be effectively compared within the same column and model type, with lower scores designating a better fit. PNV = potential native vegetation, CC = canopy cover, sd = standard deviation, HHI = Horizontal Heterogeneity Index, DEM = 3m digital elevation model, and SM = soil moisture. 'Small extent' refers to the 6 by 6 m spatial extent and 'medium extent' the 12 by 12 m extent. 'Point measurement' refers to the single measurement taken at the related quadrat.*

Environmental predictor	Model type	Species richness	Percent native richness	Percent native cover	PNV	Percent exotic species	Percent exotic cover	Percent woody cover
					AICc			
CC average	plot	173.09	-27.54	-106.85	-40.40	- 33.93	-118.29	-89.41
CC sd	plot	171.75	-23.68	-110.07	-27.26	-27.56	-112.20	-93.01
CC HHI	plot	172.31	-23.23	-107.49	-29.17	-25.13	-111.04	-91.67
CC Moran's I	plot	172.82	-29.39	-102.52	-28.07	-23.80	-107.50	-90.17
SM average	plot	172.64	-22.26	-110.64	-27.34	-32.22	-120.37	-92.67
SM sd	plot	164.24	-20.62	-110.91	-32.39	-26.24	-126. 15	-89.57
SM HHI	plot	167.70	-22.28	-111.58	-30.18	-27.68	-118.04	-93.76
SM Moran's I	plot	173.86	-26.43	-110.91	-34.27	-26.34	-115.26	-85.86
DEM sd	plot	169.12	-30.87	-107.96	-23.12	-24.17	-116.37	-89.53
CC point measurement	quadrat	958.16	-126.59	-67.18	-151.52	-231.64	-141.81	-29.13
CC average – small extent	quadrat	959.48	-128.92	-64.25	-157.20	-241.89	-135.98	-33.90
CC average – medium extent	quadrat	950.74	-150.95	- 92.42	-163.84	-268.88	-172.70	-55.72
CC sd – small extent	quadrat	957.33	-136.38	-72.10	-156.19	-247.19	-146.94	-21.05
CC sd – medium extent	quadrat	975.04	-134.53	-59.67	-169.32	-256.13	-134.09	-32.94
CC HHI – small extent	quadrat	973.10	-123.04	-51.20	-148.57	-228.73	-118.21	-37.46
CC HHI – medium extent	quadrat	971.07	-133.14	-61.50	- 150.11	-242.30	-132.05	-25.85
SM point measurement	quadrat	959.25	-130.71	-72.75	-129.35	-255.03	-162.98	-43.24
SM average – small extent	quadrat	962.05	-135.50	-75.58	-133.67	-270.22	-155.10	-33.90
SM average – medium extent	quadrat	953.41	-145.62	-99.23	-135.78	-276.75	-197.78	-43.23
SM sd – small extent	quadrat	982.59	-125.75	-78.74	-137.46	-246.96	-150.73	-30.31
SM sd – medium extent	quadrat	968.66	-163.44	-93.86	-150.41	-276.75	-171.95	-39.55
SM HHI – small extent	quadrat	958.25	-143.12	-71.40	-128.31	-271.58	-142.17	-30.31
SM HHI – medium extent	quadrat	969.24	-148.86	-94.12	-146.28	-265.84	-184.69	-48.33
SM moran's I – medium extent	quadrat	960.88	-149.26	-108.79	-163.99	-251.23	-188.27	-16.21