



Vegetation controls vary across space and spatial scale in a historic grassland-forest biome boundary

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Ecological boundaries are critical landscape regions of transition between adjacent ecological systems. While environmental controls of boundaries may operate in a scale-dependent manner, multiple-scale comparisons of vegetation–environment relationships have been characterized for few boundary systems. We used approximately 250 000 point records on the occurrence of woody versus grassland vegetation in conjunction with climatic, topographical, and soils data to evaluate scale effects and spatial heterogeneity in a 650-km section of the historic prairie–forest biome boundary of Minnesota, USA. We chose this as a model system because of the availability of historical vegetation data, a considerable spatial extent, a sharp ecological transition, and the ability to avoid confounding from more recent anthropogenic land use change. We developed modeling techniques using hierarchical variance partitioning in a spatially-structured format that allowed us to simultaneously evaluate vegetation–environment relationships across two-dimensional space (i.e. the prairie–forest boundary) and across spatial scales (i.e. varying extents). Soils variables displayed the least spatial autocorrelation at shortest lag distances and tended to be the least important predictors of woody vegetation at all spatial extents. Topographical variables displayed greater spatial heterogeneity in regions dominated by forest compared with prairie and were more important at fine-intermediate spatial scales, highlighting their likely control on fire regimes. An integrated climatic variable (precipitation minus potential evapotranspiration) displayed a trend of increasing spatial variance across the study region and was unambiguously the strongest biome boundary control, although its joint influence with fire was difficult to characterize. Spatially heterogeneous vegetation–environment relationships were observed at all scales, especially at finer scales. Our results suggest that the importance of environmental controls changes smoothly rather than discretely across scales and demonstrate the need to account for spatial non-stationarity and scale to predict and understand vegetation distribution across ecological boundaries.

Ecological boundaries are regions of transition between adjacent ecological systems and as such play a crucial role in controlling flows of organisms, materials, and energy across the landscape (Cadenasso et al. 2003). Referred to in the literature by various terms such as ecotone, border, and edge, ecological boundaries are not limited to a particular spatial or temporal scale, and they exist between many kinds of systems and organisms (Risser 1995, Bestelmeyer and Wiens 2001, Belnap et al. 2003). At coarse spatial scales, ecological boundary dynamics are the driving forces behind landscape structure and change (Peters et al. 2006). Accordingly, understanding the controls of boundary structure is a primary goal of ecology and biogeography.

At the biome scale, the boundary region between adjacent systems harbors high concentrations of species reaching their distributional limits, due to physiological and ecological constraints operating across the boundary

(Neilson 1993). Temporal changes in climatic constraints are known to be concomitant with changes in biome boundary location and structure in both the long term (e.g. >1000 yr, Williams et al. 2000) and short-term (e.g. <50 yr, Allen and Breshears 1998). Because of strong observed relationships between climate and world vegetation (Holdridge 1947), biome boundaries are presumed to be especially sensitive to anthropogenically-induced climate change. Hence, studies of vegetation boundaries that existed prior to extensive human modification serve as an important source of baseline information for comparison with current and future conditions as predicted under global climate change scenarios.

In central North America, there has existed for several millennia a boundary between grassland and forest named the prairie–forest boundary (PFB) (Transeau 1935). While much less than 5% of original prairie remains today,

explanations for the position and structure of the PFB continue to attract ecologists (Anderson 2006). At a continental scale, climatic conditions related to aridity (e.g. drought, precipitation, evapotranspiration) along with fire (e.g. lightning strikes) have been noted to play a primary role in the position of the boundary (Borchert 1950, Changnon et al. 2002), while at a local scale fire frequency alone can regulate the vegetation mosaic (Peterson and Reich 2001, McIntire and Fortin 2006).

In Minnesota, USA, prior site-specific and broader-scale studies taken together suggest that the apparent controls on the PFB vary across space and spatial scale (McAndrews 1966, Grimm 1984, Almendinger 1992, Wheeler et al. 1992). The challenge for ecologists working along grassland–forest transitions such as the PFB is to identify processes operating at different spatial scales and to differentiate the ultimate versus proximate modifiers of boundary structure (Mills et al. 2006). Some ecologists have proposed that vegetation controls operate at discrete spatial scales (Kotliar and Wiens 1990, Gosz 1993, Gillson 2004), for example Gosz (1993), proposed that boundary controls proceed down a scale hierarchy, with climate considered the major control at biome boundaries, topography and soil characteristics at landscape and patch scales, and biotic interactions at population and plant boundaries. Conversely, other ecologists advocate a continuum based approach (Meisel and Turner 1998, Xu et al. 2004). For example, McNaughton (1983) suggested that vegetation is controlled by a constellation of weak forces acting probabilistically across scales.

A practical difficulty in addressing the scale dependence of vegetation–environment relationships is that as scale becomes finer, the number of potential controls and their interactions increase drastically, making it difficult to tease apart the most important controls. Moreover, high-, or fine-resolution data are often not available across large spatial extents, or these data are difficult to process due to computing limits. Studies of vegetation–environment relationships that take a multi-scale perspective (Schneider 1995) are increasingly being used to disentangle the controls (Sarr and Hibbs 2007), but little attention has been given to exploring scale dependence across ecological boundaries (Cadenasso et al. 2003, Fagan et al. 2003). Relatively little attention has also been given to characterizing boundaries in more than one spatial dimension, partly because of the lack of developed two-dimensional analytical techniques (Hufkens et al. 2009).

In this study, we developed techniques employing variance partitioning in a spatially-structured format that allowed us to simultaneously evaluate vegetation–environment relationships across two-dimensional space (i.e. the prairie–forest boundary) and across spatial scales (i.e. varying extents). We used high-resolution data, ca 250 000 point records of vegetation, across a 650-km portion of the PFB that traverses Minnesota, USA. Our overarching objectives were to understand how vegetation controls varied throughout a grassland–forest boundary and whether these controls operated at a hierarchy of discrete scales or along a scale continuum.

We focused on the pre-European settlement (ca 1850–1900) boundary for several reasons. The PFB spanned a

large spatial extent in Minnesota and historical information on pre-European settlement vegetation enables consideration of biome controls without excessive confounding by settler-to-modern land use and management. Studies of pre-settlement conditions can serve as a model system for addressing fundamental questions and additionally as an important source of baseline data for comparison with current and future conditions, as predicted under global climate change scenarios.

Methods

Study area

The state of Minnesota, USA, sits at the intersection of three main vegetative biomes: tallgrass prairie, broadleaf forest, and mixed boreal forest (Fig. 1). It also sits at the intersection of arctic, Pacific, and maritime tropical air masses (Borchert 1950), which result in a continental climate with warm summers and cold winters. Annual precipitation in the boundary region (100 km on either side of boundary, Fig. 1) follows a spatial gradient from ca 500 mm yr⁻¹ in the west to 750 mm yr⁻¹ in the east, which is a large variation in precipitation for such a distance for a flat, mid-continental region far from mountains (Borchert 1950). Soils in the boundary region are comprised predominantly of acidic alfisols (especially udalfs) in forest environments to the northeast and fertile, calcium-rich mollisols (especially udalfs) that underlie prairie to the southwest (Anderson and Grigal 1984). A wide variety of landforms exist in the boundary region due to the region's glacial history. Elevation range in the boundary is ca 200–600 m (mean 400 m). Southeastern Minnesota was not covered by the most recent glaciation and is characterized by steep ridge and valley topography as a result of erosional processes, while the west-central portion of the state has strongly morainal topography. Northwestern Minnesota has generally low topographic relief and large peatland complexes interspersed with uplands. Two major rivers in Minnesota contribute to the topography in the boundary region. In southwest Minnesota, the Minnesota River valley flows through a wide (i.e. >100 km) flat plain, although there is a steep bluff system adjacent to the river. The Red River in far northwest Minnesota runs north and forms the state border with North Dakota.

Response variable

One way to view the PFB is as a continuum between grassland and forest (Breshears 2006), i.e. a gradient of increasing cover of woody vegetation, from prairie vegetation at one end of the gradient, proceeding up through savanna and forests (Belsky and Canham 1994, Breshears and Barnes 1999). Although percents of woody coverage have been used to define grassland, savanna, and forest types (Anderson et al. 1999), we do not employ such cutoffs here. Instead, we use the term prairie to generally refer to grassland ecosystems with low woody cover and the term forest to mean ecosystems with high levels of woody cover. Because woody plants dramatically modify the environment below their canopies, e.g. by altering soil

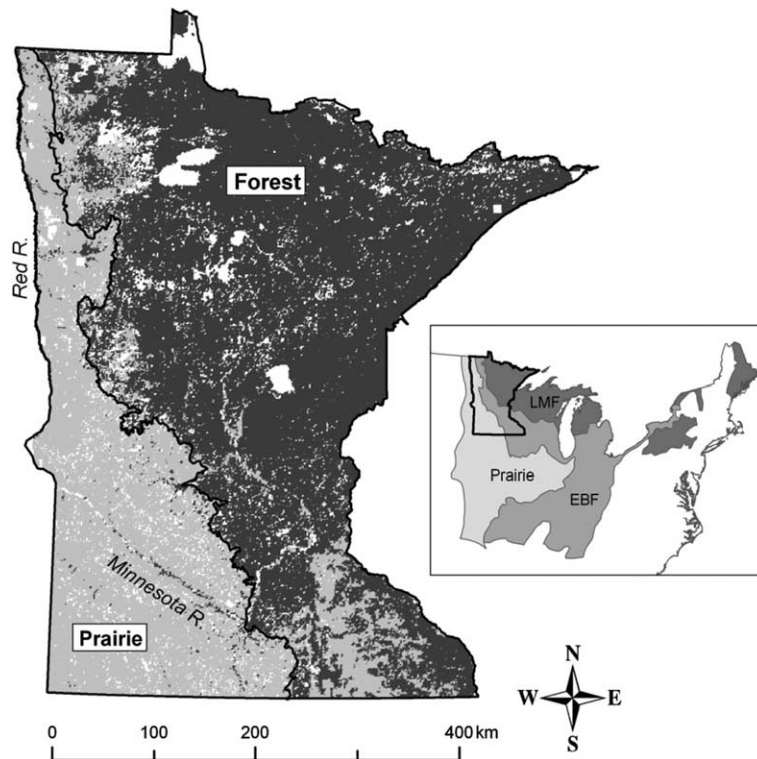


Figure 1. Historic prairie and wooded vegetation in Minnesota, USA, as recorded in the presettlement land survey (PLS; 1847–1908). The line separating prairie and forest regions is from an ecological classification system created by the Minnesota DNR. Unshaded areas include water bodies and vegetated areas classified neither as woody nor prairie vegetation. Inset: LMF = Laurentian Mixed Forest, EBF = Eastern Broadleaf Forest.

nutrients and water (Veetas 1992) and influencing plant community diversity (Peterson and Reich 2008), the amount of woody vegetation at a locality is an important and useful first-order descriptor of many ecosystem properties. The PFB, then, can be considered not only a transition in vegetation physiognomy, but also a transition of critical ecosystem processes, and can be quantified using descriptors related to the occurrence of woody vegetation present on a site.

We summarized the pre-European settlement occurrence of woody and prairie vegetation using records of the presettlement land survey (PLS) undertaken by the General Land Office (GLO) in Minnesota between 1847 and 1908 (Almendinger 1996). While potential biases and data quality issues arise when using PLS data, several authors have provided examples and guidance for proper use that enable robust ecological interpretation (Bourdo 1956, Grimm 1984, Schulte and Mladenoff 2001, Friedman and Reich 2005). The PLS was a highly systematic survey designed as part of the township-range grid system. The state was divided into square townships 9.7 km on a side and further subdivided into 36 square sections 1.6 km on a side. Surveys were undertaken at the intersection of all section lines (section corners) and the midpoint between section corners (quarter corners, 0.8 km apart). Surveyors were not ecologists, but they recorded the nearest tree or up to four trees (i.e. bearing trees) at survey corners in addition to the type of vegetation ($n = 25$ vegetation classes, Table 6 in Almendinger 1996) present at the corner. Geographic coordinates for survey corners were available from the

Minnesota DNR (Almendinger 1996) and subject to post-processing, resulting in 248 226 corners.

We constructed our response variable by combining information from the records of vegetation type with the bearing tree records as follows: a value of zero was assigned to corners recorded as prairie or wet prairie (33% of all corners); a value of 1 was assigned to corners recorded as any wooded type (40%), including oak barrens, forest, timber, grove, pine openings, pine barrens, scattered pine, pine grove, scattering oak, scattering timber, oak openings, thicket, brush, underbrush, windthrow, windfall, or only tree around. Corners recorded as swamp (12%) were assigned a 1 if they were forested (e.g. black ash or tamarack bearing trees present), but excluded if a bearing tree was absent because they could not reliably be classified as wet prairie. Other classes not reliably related to forest or prairie vegetation (15%) were excluded from consideration, including creek, plowed field, dry ridge, bottom, marsh, dry land, river, burned area, valley, ravine, and island.

Predictor variables

While there are multiple climatic variables related to moisture availability, we calculated one variable that integrated environmental moisture inputs and evaporative loss: precipitation minus potential evapotranspiration (P-PET) (Table 1). Thus, increasing values of P-PET indicated increasing wetness. Input values of potential evapotranspiration and precipitation were obtained from McKenney et al. (2006), who used a thin-plate spline

Table 1. Variables used in this study.

Type	Name	Mean	Range	Description
Response	Vegetation	0.61	0–1	presence (1) or absence (0) of woody vegetation at PLS survey corner
Predictor	Precipitation minus PET	116	–159–494	mean annual precipitation minus mean annual potential evapotranspiration (mm yr ⁻¹) 1961–1990
	Topographic roughness	17.4	0–222	topographic roughness index – standard deviation of 30-m elevation in 2 km square cell
	Distance to water	1402	0–14 391	distance to nearest perennial waterbody (m)
	Soil % sand	38	2–97	percent sand in soil surface layer
	Soil drainage	4.7	1–7	soil drainage class (ordinal 1–7)

technique to model climatic parameters for North America at 1 km spatial resolution. Values represent the sum of the monthly precipitation averages (in mm) minus the sum of the monthly potential evapotranspiration averages for 1961–1990. P-PET data were unavailable at a time period contemporary with vegetation data. However, other climatic variables (e.g. temperature, precipitation) highly correlated with P-PET were available (McKenney et al. 2006) for a time period coincident with the end of the PLS survey (1901–1930). In Danz (2009) and Danz et al. (unpubl.), we carried out extensive statistical analyses to show that these other climatic variables highly correlated with P-PET have changed in a spatially isotropic manner across the PFB from 1901–1930 to 1961–1990. The implication is that P-PET would have changed in a similarly isotropic manner, thereby alleviating concerns of potential bias introduced by the time discrepancy among climate and vegetation data.

We computed two variables related to topography 1) topographic roughness and 2) distance from the nearest perennial water body. Both variables were derived from operations in a geographic information system (GIS) applied to a 30-m digital elevation model (DEM) for Minnesota from the MN Dept of Natural Resources (MN DNR). Topographic roughness was calculated as the standard deviation of elevation within a 2 km square window using the block statistics tool in ArcGIS 9.2 (ESRI 2006). Distance from nearest perennial water body was calculated by merging three hydrological layers from the MN DNR (MN DNR 2008): 1) 1:24 000 scale perennial streams, 2) major river centerline traces, and 3) 1:100 000 scale ponds, lakes, and rivers. The merged layer was converted to a statewide 30-m grid of water bodies and then processed with the proximity tool in ArcGIS to compute the distance (m) of each grid-cell to the nearest body of water.

We used two soils variables related to texture and water availability: percent sand in the surface layer and soil drainage class. Both variables were obtained from the SSURGO database, which contains the most finely resolved, extensive soil data available in digital format for this region (US Dept of Agriculture 2008). SSURGO data are mapped as polygons at the county level for most counties in MN. Median polygon size is 22.5 ha, and the 75th percentile is 44 ha. We used the Soil Data Viewer (US Dept of Agriculture 2007) to obtain soil polygons for all mapped Minnesota counties (Fig. 2) and converted each polygon layer into a 30-m grid. Grids were stitched together

into a statewide coverage for each variable using the mosaic tool in ArcGIS. Sand as a soil separate consists of mineral soil particles that are 0.05–2 mm in diameter. The surface layer generally extends to 25 cm (Soil Survey Division Staff 1993), although deeper layers have percent sand values very highly correlated with the surface layer (i.e. >0.95; unpubl.). Soil drainage class is an ordinal variable 1–7 that refers to the frequency and duration of wet periods under conditions similar to those under which the soil developed (Soil Survey Division Staff 1993). We treated soil drainage as a continuous variable in our analyses (Calef et al. 2005).

Using GIS, each survey corner location was intersected with the five predictor variables described above to develop digital representations of presettlement environmental conditions at corners. To facilitate a multi-scale analysis, we created four nested spatial grids with square cells 10, 20, 40, and 80 km on a side. In a separate study (Danz et al. unpubl.), we found the boundary width to range from 38 to 178 km (mean 99 km). Thus, this range of grid cell sizes allowed us to evaluate vegetation relationships both across and within the prairie–forest transition region; the 10-km cells fit entirely inside the transition zone itself in many cases, while the 80-km grid cells were large enough to span the PFB in many locations. We intersected each grid with the response variable (wooded versus prairie) and predictors. Grid cells were retained for subsequent analysis if they contained at least 50 survey corners, with at least 10 prairie and 10 wooded (at the 10- and 20-km grid size) or at least 20 prairie and 20 wooded (at the 40- and 80-km grid size). There were 403 retained grid cells at 10 km resolution, 206 at 20 km, 72 at 40 km, and 22 at 80 km, for a grand total of 703 retained grid cells across the four grids.

Analysis

We computed experimental semi-variograms (Perry et al. 2002) of response and predictor variables using SAS 9.1 (SAS Inst. 2002) to evaluate spatial structure of the environment in adjacent biomes and the transition zone between them. Semi-variograms describe spatial variability in data as a function of the distance between sites (Meisel and Turner 1998) and can be used to identify the dominant scales of environment–biota relationships (Mayor et al. 2007). We computed individual semivariograms for several 80-km grid cells occurring discretely in forest, transitional (boundary), or prairie regions and then averaged the

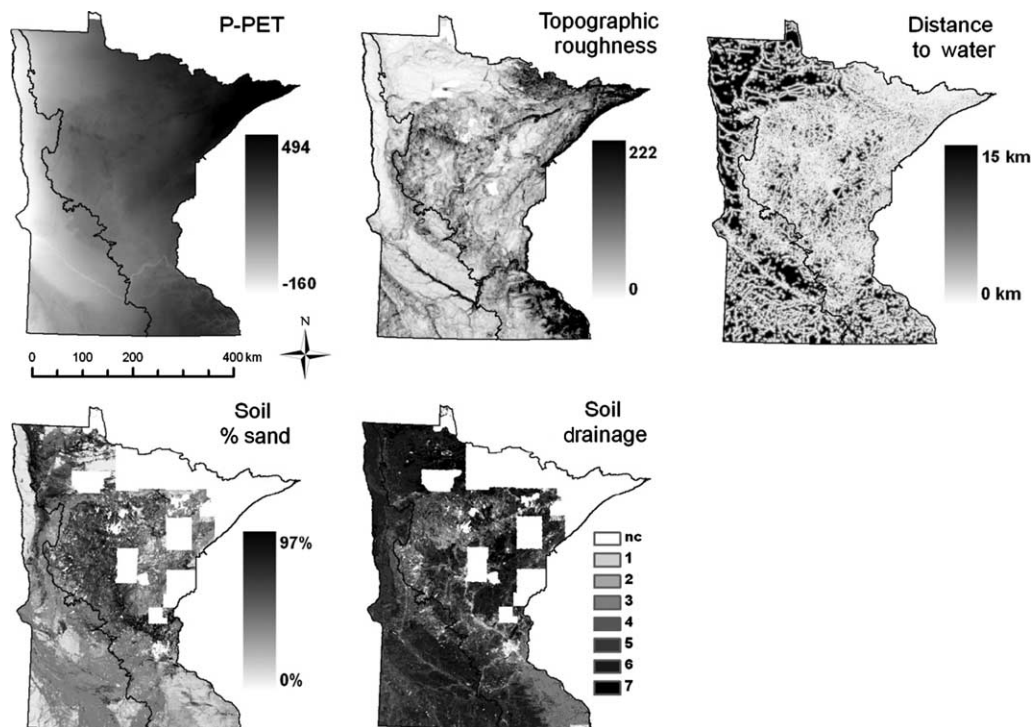


Figure 2. Environmental predictor variables used in this study. Precipitation minus potential evapotranspiration (P-PET) was summarized for a statewide 1-km grid, while topographic roughness was summarized for a 2-km grid. Other variables were summarized in 30-m grids. Unshaded areas for the two soils variables indicate unclassified (nc) and unavailable data.

variograms for each ecosystem type. Grid cells for prairie and forest were selected from the full statewide grid so that cell boundaries occurred entirely within their intended regions, while for transitional cells there was a fair representation (>25%) of prairie corners. Input data were values of response and predictor variables present at survey corners, totaling approximately 7500 corners per grid cell.

We developed a statewide global logistic regression model using the wooded vegetation binomial as the response variable and the five environmental factors described above as the predictor variables. Further, we used hierarchical partitioning (HP) of the log-likelihood to evaluate the independent contribution to explained variance of each predictor (Chevan and Sutherland 1991). In HP the goal is to compare the influence of each predictor variable on a response over a hierarchy of all possible 2^N models for N predictors instead of identifying a single best model (MacNally 2000, 2002). The importance of each predictor is estimated by averaging the increase in model fit over all models in which a predictor occurs; this is reported as the independent contribution to explained variance (I) for each predictor variable. Conceptually, HP can be used in a variety of multiple regression settings (e.g. normal linear regression, logistic, Poisson) with any goodness of fit measure (e.g. R^2 , log-likelihood). Because we used five main effects, the HP utilized $2^5 = 32$ models. To keep track of the proliferation of models, each HP output includes only one summary measure (mean I) for each predictor. Hence, each set of 32 component models is referred to as one HP analysis and we did not evaluate the component hierarchical models themselves. We used area under the receiving operator characteristic curve (AUC) and maximum rescaled R^2 to evaluate model fit in the fully-parameterized

(5-predictor) models (Fielding and Bell 1997). AUC can range from 0.5, when no model discrimination exists, to 1.0 for perfect discrimination; values above 0.90 are considered indicative of high model accuracy (Swets 1988).

In the same manner as for the statewide global model, we calculated local logistic regression models followed by HP for grid cells individually at each spatial extent. For example, at the 10-km grid cell size, we ran one HP analysis for each of 403 cells and reported one summary of the HP model for each grid cell, for a total of 403 HP summaries. The spatial heterogeneity of relationships between vegetation and environmental predictors was evaluated using maps and summary statistics of the parameter estimates (slopes) and independent proportion of variance explained (I) for each predictor.

Results

The two soils variables had the greatest spatial dependence at shortest lag distances (Fig. 3). Nugget values (y-intercept) for percent sand and soil drainage were substantially greater than zero, indicating a high degree of variability in soil features in adjacent PLS corners (Fig. 3). Range values (lag distance at which semivariance reaches a plateau, or sill) were generally <5 km for the soils variables. Distance to water and topographic roughness had lower nugget values and larger range values (~8 km) compared with soils, indicating a greater degree of similarity of topographical values for adjacent points and longer distance of spatial correlation. The lone climate variable, P-PET, had low variability among

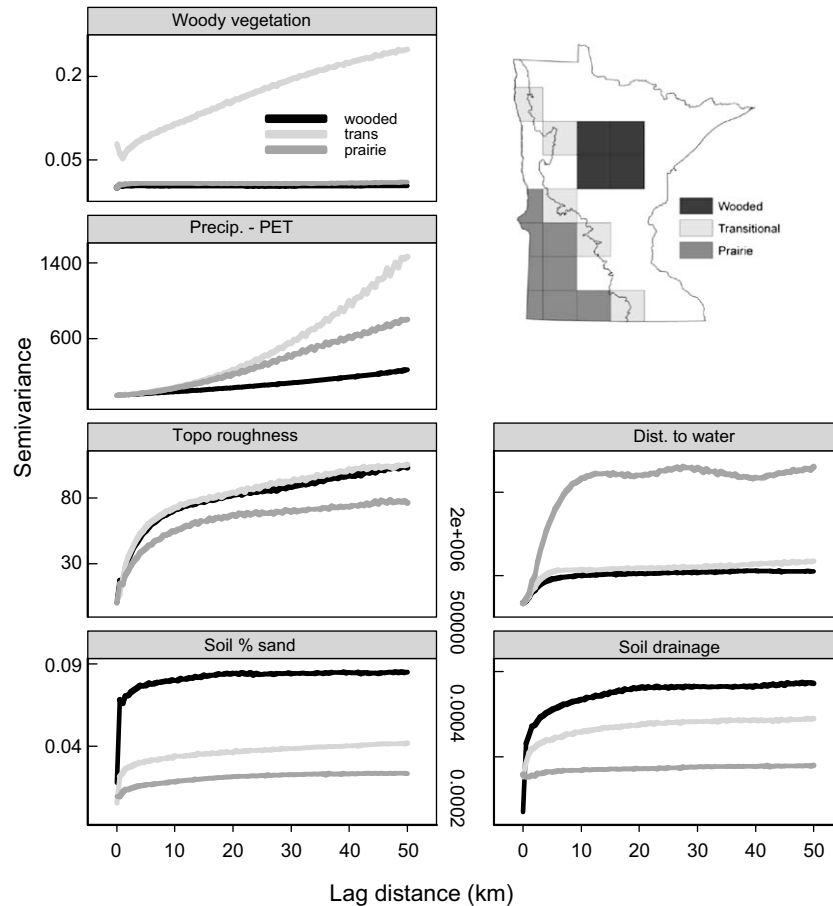


Figure 3. Experimental semivariograms for response and predictor variables in wooded, prairie, or transitional (boundary) regions. Variograms were computed separately for 80-km grid cells and then averaged for each vegetation region indicated by different shading patterns (inset). Approximately 7500 historic vegetation records were used for each 80-km grid cell.

adjacent sites and displayed increasing semi-variance and no sill with increasing distance. The woody vegetation response variable was essentially homogeneous in both prairie- and forest-dominated grid cells, and displayed increasing semivariance (i.e. decreased autocorrelation) with increasing distance in the transition zone (Fig. 3). Grid cells in the predominantly forested region had soils variables and topographic roughness that were more spatially variable at all lag distances compared with prairie areas, while transitional regions were intermediate for soils and about equivalent for topographic roughness. Transitional areas displayed the greatest amount of spatial variability in P-PET, while prairie regions had intermediate variability of this variable. Prairie regions had the most spatial variability in distance to water, presumably because forest and transitional areas were more uniformly near water.

The statewide global logistic regression model for all included data points was highly statistically significant ($p < 0.0001$), with all five predictors contributing significantly the probability of a PLS survey corner being wooded (Table 2). With a max-rescaled R^2 of 0.56 and an AUC of 0.90, this model was considered to have good fit. Increasing values of P-PET, topographic roughness, soil percent sand, and soil drainage all resulted in increased probability of a wooded PLS corner, while increasing distance from water

decreased the probability of a wooded corner. P-PET explained 75% of the independent explained variance in the global model (Table 2), with the other variables all explaining $<10\%$.

Across all grid cells at all spatial extents, 89% of the 703 full models were significant and they had mean AUC of 0.85 (Table 3). As judged by hierarchical partitioning, the two soils variables were generally the least explanatory at all spatial extents, with median explained variance $<10\%$ (Fig. 4). At the 10 km extent these variables explained the greatest amount of variance in 74 (33 soil drainage, 41 soil percent sand) of 403 models (18%) and accounted for $>50\%$ of the variance in 30/403 (15 for each variable).

Table 2. Results from statewide global logistic regression and hierarchical partitioning. Sample size was 80 551 for prairie and 83 868 for wooded survey corners. Overall model $p < 0.0001$, AUC = 0.90, maximum re-scaled $R^2 = 0.59$.

Predictor	Parameter estimate	p-value	Percent I*
Precipitation minus PET	0.02	<0.0001	75
Topographic roughness	0.01	<0.0001	4.8
Distance to water	-0.0003	<0.0001	9.4
Soil% sand	0.03	<0.0001	9.1
Soil drainage	0.3	<0.0001	1.8

*percent of independent explained variance.

Table 3. Summary statistics for fully parameterized models (5 predictors) at each spatial extent.

Extent	n grid cells	n significant* models	AUC full model**		Max re-scaled R ² full model**	
			mean	std dev	mean	std dev
10 km	403	339	0.85	0.10	0.45	0.19
20 km	206	193	0.85	0.08	0.39	0.19
40 km	72	72	0.84	0.08	0.36	0.17
80 km	22	22	0.84	0.07	0.34	0.11

*Likelihood ratio p-value <0.05.

**Significant models only.

The two topographical variables, distance to water and topographic roughness, had their greatest explanatory power at the 10 km extent, each independently accounting for roughly 20% of the explained variance, on average. These variables also had fairly constant proportions of explained variance at all spatial extents. Topographic roughness was the predictor with the highest explanatory power in 105/403 (26%) models at the 10 km extent and 6/22 (27%) 80-km models. Similarly, distance to water was the best predictor in 103/403 (25%) 10-km models and 4/22 (18%) of 80-km models. On average, P-PET accounted for 19% (median) of the explained variance at the 10 km extent and nearly 40% of the explained variance at the 80 km extent. This variable accounted for >50% of the explained variance in 17, 23, 21, and 36% of the models at the 10-, 20-, 40-, and 80-km extents, respectively, showing that the importance of this variance increased with cell extent compared to the other predictors. Predictor importance (as measured by average I values) generally followed a smooth rather than peaked pattern across the four spatial extents for all five variables (Fig. 4), suggesting a continuum rather than discrete model of environmental controls of vegetation across scales.

Parameter estimates for the individual predictors from logistic regressions at the four spatial extents showed considerable spatial variability, with highest variability at the 10-km spatial resolution and lowest at 80-km resolution. We briefly discuss spatial patterns of parameter estimates for all predictors below, but for illustrative purposes include a map for the distance to water predictor only (Fig. 5). Maps for other predictors are included as online appendices (Supplementary material Appendix 1–4).

The two soils variables had the greatest parameter variability across all extents (Supplementary material Appendix 1–2). On average, soil percent sand was positively related to the probability of a wooded PLS survey corner, especially at 10- and 20-km extents in southeast MN, where soil percent sand is typically low and in northwest MN, where it is typically high. However, soil percent sand tended to have a negative relationship with wooded vegetation in the central portion of the prairie–forest boundary and near the Anoka Sand Plain, a region of glacial outwash containing high amounts of sand in east-central Minnesota. The clearest spatial pattern of response to soil drainage was a generally positive relationship, i.e. forest on less well-drained (wetter) soils, in the central portion of the state

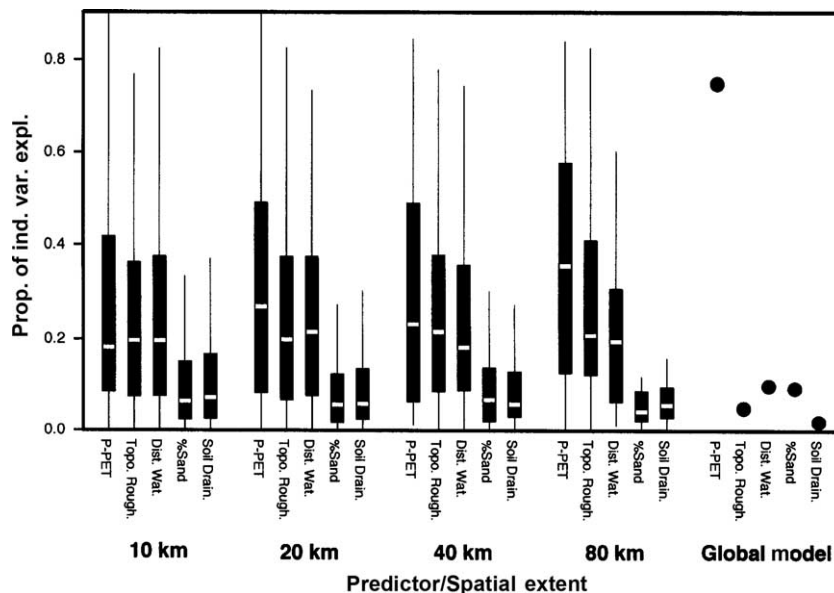


Figure 4. Boxplots of proportion of independent explained variance (I) from hierarchical partitioning of logistic regression for each grid cell at each spatial extent. Effects of predictors apparently follow a continuum model across spatial scales rather than predictors operating at a hierarchy of discrete scales. Boxplots represent the median (white), interquartile range (upper and lower box values), and outliers of I values. The number of models at each spatial extent is listed in Table 3. Values for the global model are included for comparison.

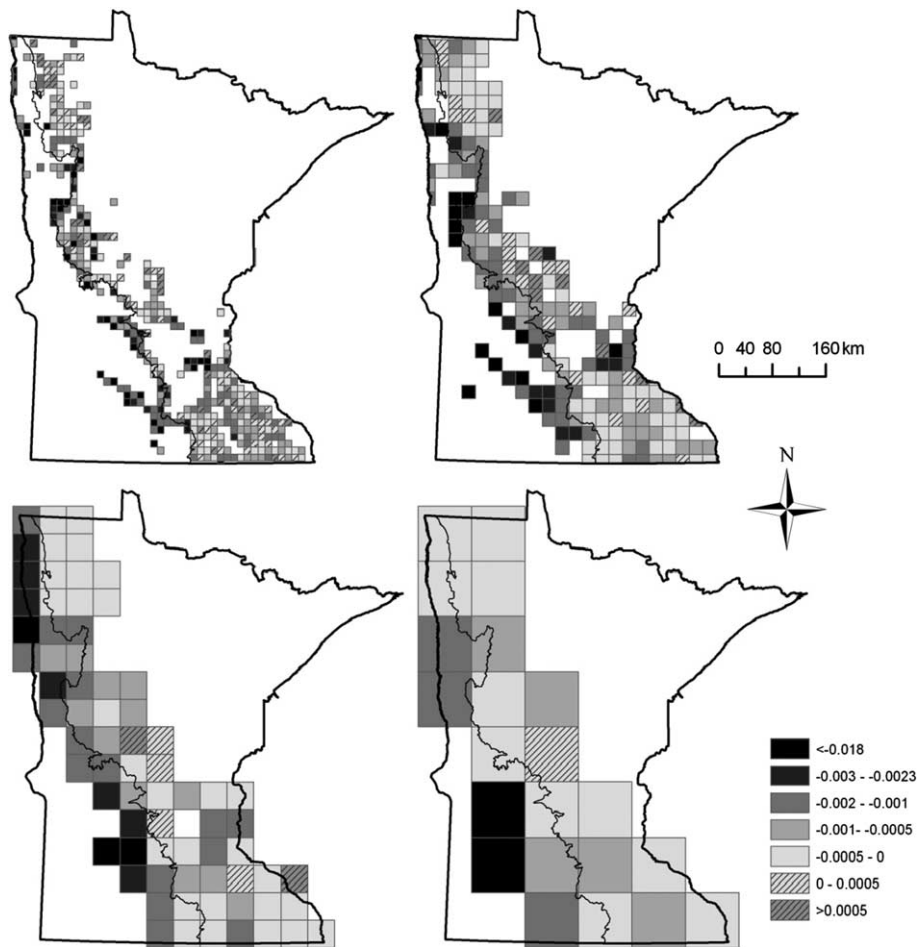


Figure 5. Parameter estimates (slope coefficients) for the distance to water predictor from logistic regressions that model the relationship between woody vegetation and five environmental predictors. Distance to water was especially important as a predictor west of the boundary in the prairie region along major riverways. Regressions were carried out individually for grid cells at 10-, 20-, 40-, and 80-km spatial resolution.

on the eastern edge of the boundary at all spatial extents. Conversely, woody vegetation preferentially occurred on well-drained soils (steep slopes) in southeast Minnesota, where topography is highly dissected.

Distance to water and topographic roughness displayed less variable parameter estimates than soils variables both across spatial extents and spatially across the state. Topographic roughness increased the probability of woody vegetation all along the transition, especially in the northwestern and southeastern portions of the state (Supplementary material Appendix 3). The spatial pattern of the influence of distance to water was particularly interesting because this predictor clearly was more strongly related to the presence of woody vegetation along the western compared to the eastern edge of the boundary (Fig. 5). At the 20-km resolution, this variable was especially prominent along the Minnesota River in the southwest portion of the state, while at 40-km it was especially prominent along the Red River that defines over 250 km of the state's western border.

P-PET had parameter estimates with intermediate variability compared with soils and topographic variables at all spatial extents (Supplementary material Appendix 4).

At the 80-km extent, this variable was positively related to the probability of woody vegetation at all grid cells except for one grid cell in southeast MN, where there was a strong pattern of woody vegetation to the west (the Big Woods region, Grimm 1984) and prairie to the east, the opposite of the pattern found elsewhere.

Interpretations of spatial patterns of independent amounts of variance (I) attributed to individual predictors were similar to those from parameter estimates. Compared with other predictors, P-PET was most responsible for variance explained along the entire length of the boundary (Fig. 6), although it explained an increasing fraction moving further north. Further west toward the state boundary, where trees were more widely scattered, distance to water was the most explanatory predictor, especially along major riverways. Topographic roughness was especially important as a predictor in southeast MN, where landforms are driven by highly dissected river-valley systems in the unglaciated region. Notably, the only soil variable that explained the greatest amount of variation in woody vegetation occurrence at the 80-km extent was soil percent sand, in the Anoka sand plain (see above).

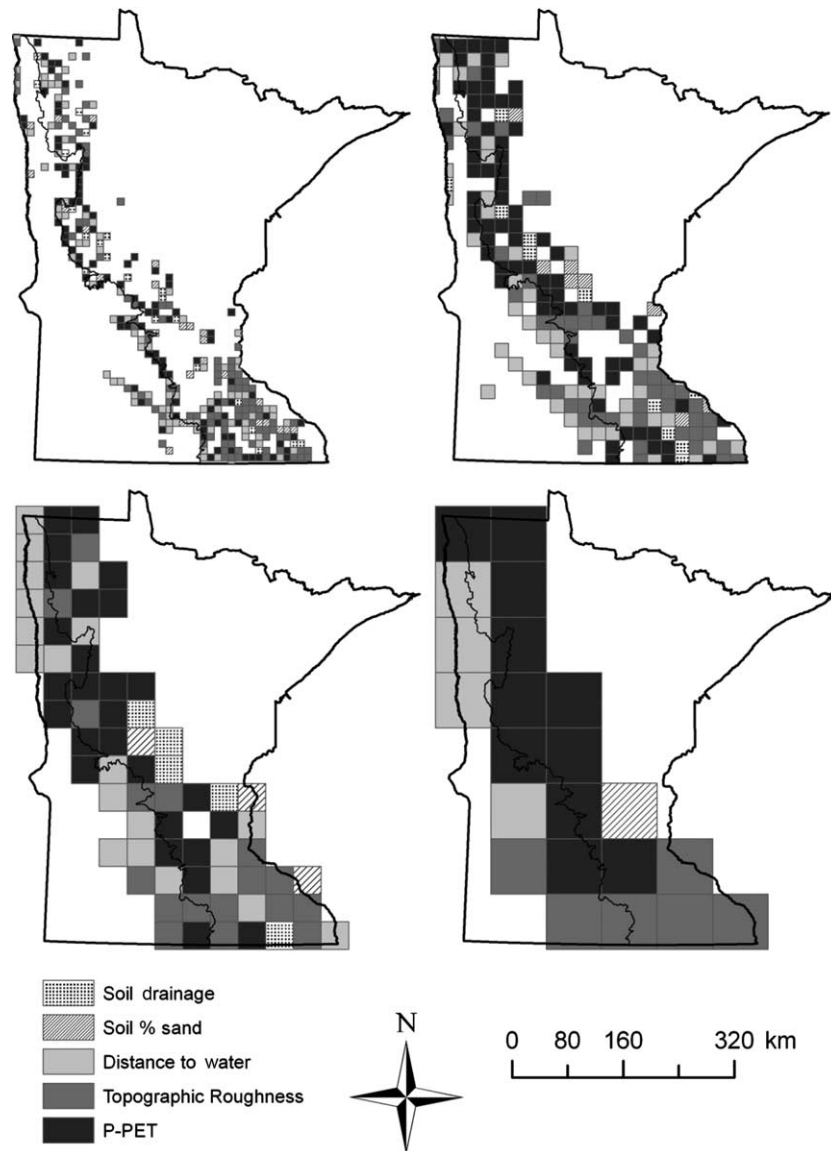


Figure 6. Predictor with maximum proportion of independent variance (I_{\max}) in grid cells at 10-, 20-, 40-, and 80-km spatial resolution. I_{\max} was determined through hierarchical partitioning of logistic regression for each grid cell individually. Notably, P-PET was the dominant vegetation control all along the border at the 80-km spatial resolution, while results were more variable at finer resolutions.

Discussion

Meisel and Turner (1998) posited that coincidence in patterns of variation between environmental controls and vegetation could be used to identify potential linkages. Because ecological boundaries are regions of spatial trend in an ecosystem property, for an environmental variable to be responsible for a boundary, it must display similar spatial patterning. Our results demonstrate a truism regarding boundary analysis that deserves repeating: the spatial structure of an environmental control determines the scale at which the control can explain the distribution of vegetation across a boundary. If a putative environmental control is homogeneous at a particular scale, it cannot be used to explain the position of a boundary at that scale (Urban et al. 2000). Conversely, variables that display

spatial trend at a particular scale can (but do not necessarily) explain a boundary within that scale.

Climate as the ultimate boundary control

In our study, an index of climatic moisture availability (P-PET) displayed a clear pattern of increasing variance with increasing distance across the PFB, the same pattern seen in semivariograms for woody vegetation. In combination with the hierarchical partitioning analysis that showed P-PET was the greatest contributor to explained variance in the global model (i.e. $I = 75\%$), we conclude that this variable was unambiguously the greatest control on the PFB among the variables we tested. Additionally, P-PET was the most important predictor along the entire length of the boundary, except in far southern Minnesota where the

transition region was much broader and apparently influenced most by topographical features. The observed importance of P-PET in controlling the location of the PFB is perhaps not surprising given the long history of considering climate the primary control on biome boundary location (Holdridge 1947) that is further strengthened by more recent findings from grassland–forest boundaries around the world (Hogg 1994, Liu et al. 2000, Sankaran et al. 2005). This climatic control is likely mediated by water balance (Stephenson 1990, Hogg 1994, Sankaran et al. 2005).

It has been recently debated whether fire rather than climate is the ultimate factor in determining boundary location between grassland and forest biomes throughout the world (Bond et al. 2005, Sankaran et al. 2005). Several paleoecological studies from Minnesota have highlighted strong regional differences and feedbacks between climate, vegetation, and fire in the Holocene (~9000 yr bp-present) that make the fire vs climate question difficult to answer. Some studies have concluded that climate-driven changes in fire regimes are likely responsible for the establishment and maintenance of grassland–forest boundaries (Grimm 1983, Nelson et al. 2006). On the other hand, there is growing evidence that changes in fire regimes can also occur due to climatically induced vegetation shifts (Clark et al. 2001, Camill et al. 2003, Nelson et al. 2008), for example, fire frequency and severity are positively related to wetter climatic conditions that caused higher fuel availability. In our study, regional differences and interdependencies in these relationships make unclear the degree to which P-PET acted as a surrogate for or acted jointly with fire as the ultimate boundary control.

A further question with regard to the role of fire and climate in the ultimate position of the PFB is whether fires were predominantly due to climatic lightning strikes or whether they were predominantly the result of purposeful ignition by Native American peoples. It is well known from anecdotal accounts from early Euro-Americans that Native Americans used fire to assist in hunting, to deter pursuing enemies, and to keep the land open (Pyne 1982, Grimm 1985). While Native American-set fires certainly occurred in the PFB, three lines of evidence suggest that climate and climatically-caused fire was a predominant cause of the boundary location: 1) grassland–forest boundaries in other regions have similarly strong relationships between vegetation and climatic moisture availability (Hogg 1994), 2) paired climatic moisture patterns, the frequency of climatic lightning strikes in the region was great enough to result in fire intervals matching early Euro-American accounts (i.e. 1–5 yr) (Changnon et al. 2002), and 3) there is growing scientific evidence suggesting intentional burning by Native Americans was much less extensive than previously thought and that anecdotal accounts of purposeful fires are biased (Kaye and Swetnam 1999, Barrett et al. 2005).

Proximate controls within the boundary

In broad transitions such as the PFB, it has been argued that the boundary is best thought of as 2- or 3-dimensional

feature (Strayer et al. 2003), where finer boundaries, e.g. between patches of prairie and forest, can occur within the transition. Gosz (1993) identified this pattern as a hierarchy of ecotones within a biome transition region. Within a boundary, there may be several important environmental controls on vegetation that are not spatially aligned across the overall boundary itself, but nevertheless influence vegetation. In our study, all of the environmental predictors displayed significant influences on vegetation at finer spatial scales (<80 km) within the boundary.

P-PET contributed to 20% of the explained variance, on average, across the models at the 10-km extent and increased in explanatory power with increasing spatial scale to ca 40% at the 80-km scale and eventually to 75% in the global model. While climate is often considered fairly homogeneous over fine spatial extents, it is well known that microclimatic variability influences vegetation at fine spatial scales due to both topographical features (Xu et al. 2004) and interactions with vegetation itself (Vetaas 1992, Hennenberg et al. 2008). We were not able to investigate climate relationships below 1-km spatial resolution (i.e. at a microsite scale) due to the nature of our climate data; however, variation in our climate data apparently explains vegetation pattern at even the 10-km scale. Using a similar dataset from Canada, McKenney et al. (2006), found spatial variation related to real, on-the-ground observed climatic differences over a 13-km scale. For example, winter precipitation values varied by –7 to +10% across a series of 13-km distances in Ontario, which borders Minnesota to the north. Moreover, Minnesota has a more spatially abrupt climate transition for a flat interior continental location than would commonly be expected (Changnon et al. 2002), therefore adding to the likelihood of climate having an influence at relatively finer spatial scales.

Topographical variables displayed variation at finer spatial resolution than climate and were more strongly related to vegetation pattern within rather than across the PFB. In our study, topographical roughness and distance to water displayed minimal spatial autocorrelation above ca 10–20 km depending on location along the boundary, thus these variables were unable to explain vegetation boundaries above this scale. Conversely, these variables were the best predictors of woody vegetation within the 10-km scale, on average ca 20% each, with their contribution to explained variance remaining relatively constant across scales.

While topography indirectly influences vegetation in the PFB by mediating soil moisture and solar insolation (McAndrews 1966), several results from our study point to the predominant topographical influences on the boundary being related to its control on the spatial pattern of fire. First, within the transition region itself, prairie corners were less topographically variable (i.e. flatter) than wooded corners (Fig. 4), a pattern that was exacerbated for the biomes separately (Fig. 3). On sites with high topographic variability, slower winds and more highly variable fuel continuity and moisture can mitigate fire spread and behavior, while flatter regions have lower frictional drag of wind, promoting rapid fire spread and more homogeneous coverage (Geldenhuys 1994, Stambaugh and Guyette 2008). Not only were prairie

regions flatter, but they were also less punctuated by firebreaks in the form of perennial water bodies, a pattern evidenced by dramatically greater spatial variability in this variable among prairie corners compared to wooded and transition corners (Fig. 3). The transition region has physical topographical features more similar to forested regions to the east than prairie regions to the west, suggesting that fires began west of the boundary and spread eastward. Thus in the transition region it is likely that fewer fires continued to burn as they spread eastward compared with fires in the prairie biome, resulting in less frequent fire in any given location in the forested region, which would have allowed increased survival of woody vegetation (Peterson and Reich 2001).

Soil texture and drainage are known to influence prairie plant community composition (Corbett and Anderson 2006) and forest vegetation (Grimm 1984, Almendinger 1992) in this region, yet they contributed little to the explanation of vegetation both across and within the PFB relative to climate and topography. The lack of explanatory power of soil properties across the boundary can be explained by fine scale variability in soils features (Lin et al. 2005) relative to the width of the transition region. The lack of explanatory power at finer spatial resolution (within the boundary) may be due to the influence of soils on vegetation being overridden by fire. In south-central Minnesota, Grimm (1984) noted the presence of prairie and woodland at adjacent sites on opposite sides of a sharp firebreak with essentially identical physical soil characteristics. In northwest Minnesota, Almendinger (1992) found that prairie sites on coarsely-textured outwash soils experienced replacement by aspen-oak *Populus-Quercus* and eventually jack pine *Pinus banksiana* due to changes in fire frequency. Two additional possible reasons for the apparent weak effect of soils at fine spatial resolution are specific to our analysis. One, the PLS sampling design may have been too coarse to detect all the effects of soils. Spacing between PLS survey locations (0.3 km) was perhaps large relative to the size of forest patches and known patterns of soil variability in SSURGO map units (Lin et al. 2005). Two, effects of soil texture for some tree species in some localities may have been obscured by our decision to lump all tree species into the 'wooded' category, given that different tree species have different soil preferences.

Spatial heterogeneity in vegetation–environment relationships

Interactions between environmental controls on vegetation are manifested as changing relationships along an ecological gradient or through space. The presence of such interactions in the PFB over gradients of both spatial scale (Grimm 1984, Wheeler et al. 1992, Keitt et al. 2002) and temporal scale (Umbanhowar et al. 2006) can complicate conclusions about the relative importance of controls.

Several clear examples of spatial non-stationarity, or interactions, were apparent, for example, the increased importance of distance to water moving west from the boundary or the changing importance of regional

topography along the boundary (Fig. 5, Supplementary material Appendix 3). With regards to distance to water serving as protection from fire due to leeward position, the observed occurrence of woody vegetation was further complicated by relationships with soil drainage and topography. In many cases, trees occurred in windward locations due to steeper topography (e.g. steep river valleys) or to poorly-drained soils surrounding a water body. Such interactions between disturbances such as fire and other environmental controls undoubtedly provided mechanisms for tree–grass coexistence throughout the boundary (Grimm 1984, Sankaran et al. 2004).

Conclusions

Taken together, the observed effects of scale and spatial heterogeneity in the controls of the PFB in our study lead to a number of implications for ecological boundaries. First, proximate causal variables such as topography and soils are likely to display more spatially heterogeneous relationships than ultimate variables such as climate (Mills et al. 2006). Moreover, these variables are likely to have greater effects at finer spatial scales within the transition, possibly even across finer-scale boundaries (e.g. patch or plant level) within the broader biome transition (Gosz 1993). Second, the effects of scale across biome boundaries may be more likely to follow a continuum model rather than a set of discretely dominant scale domains across a hierarchy (Wiens 1989, Kotliar and Wiens 1990, Gosz 1993, Gillson 2004). Our results provided evidence of a continuous pattern of variable influence across scales, supporting the view of McNaughton (1983) and Meisel and Turner (1998), who posited that vegetation is determined by a continuum of proximate and ultimate factors acting concurrently. Finally, an implication of spatial non-stationarity in environment–vegetation relationships across a boundary is that a global model may not be sufficient to explain or predict vegetation structure throughout the transition; local models across the spatial extent may be necessary. Boundary regions are thought to be especially sensitive to changing climatic conditions (Allen and Breshears 1998), thus they are often the focus of global change modeling (Neilson 1993) and monitoring. Our study demonstrates the need to account for spatial non-stationarity and factors across a range of scales in order to predict and understand vegetation distribution in a biome transition.

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