Do vegetation boundaries display smooth or abrupt spatial transitions along environmental gradients? Evidence from the prairie–forest biome boundary of historic Minnesota, USA

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Abstract

Questions: Two alternative mechanisms of abrupt vegetation change across ecological boundaries have been proposed: (1) concomitantly abrupt gradients in physical environmental variables and vegetation across the boundary, and (2) gradual environmental gradients that vegetation responds to in a non-linear or threshold manner. Here, we evaluate spatial patterns of climate and vegetation across a grassland–forest biome boundary to examine evidence in favour of either of these alternatives.

Location: Minnesota, USA.

Methods: Vegetation data represented the presence of prairie vs. forest vegetation in Minnesota from 1847 to 1908, generally prior to European settlement of the region, while the climatic variables represented an index of long-term average moisture availability (precipitation minus potential evapotranspiration (P – PET). Using linear and sigmoidal regression models, we evaluated spatial patterns of change in vegetation, climate and vegetation–climate relationships across 22 transects (170–400 km) oriented perpendicular to the biome boundary. We also evaluated boundary characteristics in light of dominant topographical controls and position along the boundary.

Results: Vegetation followed a sigmoidal pattern of change across the boundary, with mean boundary width of ca. 100 km. The P – PET increased by ca. 100 mm across the boundary following a comparatively smooth pattern of change. Climate–vegetation relationships were clearly non-linear across the boundary, indicating these variables did not change in a common spatial pattern. Regional topographical controls modified relationships between vegetation and climate along the length of the boundary.

Conclusions: Our results document strong non-linear relationships between the presence of forest vegetation and its dominant climate control across a grassland–forest biome boundary. An average change of ca. 100 mm in P – PET moving across the boundary is about 40% of the long-term mean annual range of this variable, suggesting that modest changes to P – PET may potentially cause substantial shifts in the location of the prairie–forest boundary.

Introduction

Ecological boundaries are regions of transition between adjacent ecosystems, and exist at a variety of spatial and temporal scales. Also known as edges, borders, interfaces and ecotones, ecological boundaries are important landscape elements that control the fluxes of organisms, materials and energy between ecosystems (Cadenasso et al. 2003). Because ecological boundaries are usually small or narrow relative to their adjacent systems, they are sometimes drawn as lines on a map indicating a lack of dimensionality; however, boundary regions are best viewed as

two- or three-dimensional regions with a rich diversity of structural attributes that influence their function (Strayer et al. 2003).

One of the universal features of ecological boundaries is that the boundary region displays more internal heterogeneity (compositional and structural) than the adjacent ecosystems (di Castri et al. 1988). Therefore, the rate of spatial change in ecosystem structure or function is higher in the boundary region than outside the boundary. *Abruptness* refers to the rate of change from one ecosystem to another across the boundary (Bowersox & Brown 2001). If the rate of change is abrupt across space, the boundary will appear as a step function, while more gradual changes may approximate a linear model. An important consideration is that boundary abruptness is relative, i.e. it can only be interpreted in comparison to some other boundary or environmental gradient. Additionally, the perception of boundary steepness will depend on the spatial resolution or scale at which the boundary is being measured (Strayer et al. 2003).

While the existence of abrupt boundaries in forest systems is well known from studies at fine–moderate spatial resolution (10–100 m), e.g. forest–field edges (Cadenasso et al. 1997), there is less evidence to suggest forest systems also display abrupt transitions at broader scales. Working at the biome scale, Timoney et al. (1993) showed that the transition between sub-arctic forest and tundra ecosystems followed a sigmoid wave (S-shaped) functional form, where percentage tree cover changed abruptly in regions of intermediate cover, but changed slowly in areas of high or low cover. Timoney et al. (1993) hypothesized that the sigmoid wave pattern of vegetation change was a defining feature of undisturbed biome transition regions in general when there is one dominant environmental control or a set of correlated controls. In a test of Timoney et al.'s hypothesis, Cairns & Waldron (2003) found a similar sigmoid wave pattern for the boundary between alpine tree line and tundra systems. Globally, alpine tree lines are known to be controlled primarily by temperature (Jobbágy & Jackson 2000). A physiognomically similar gradient from grassland to savanna to forest occurs worldwide in lower-elevation ecosystems of warmer climates (Breshears 2006). An open question remains whether grassland–forest transitions would also follow a sigmoidal form, given that these transitions are thought to be controlled primarily by moisture gradients (Sankaran et al. 2005) and that they tend to occur over greater distances than tree lines.

The shape and steepness of a vegetation boundary are presumed to be controlled through environmental gradients, disturbances or biotic interactions operating across the boundary (Mills et al. 2006). Physical environmental gradients such as climate factors are thought to be more important at broader spatial scales and are our focus here. Two alternative mechanisms of abrupt boundaries have been proposed: (i) concomitantly abrupt gradients in physical environmental variables and vegetation across the boundary, and (ii) gradual environmental gradients that vegetation responds to in a non-linear or threshold manner (Gosz 1992; Risser 1995; Fagan et al. 2003). In the first case, steep changes in an environmental gradient bring about equivalent steep changes in vegetation, while in the second case dramatic changes in vegetation can be caused by small changes in the environment.

Although understanding relationships between vegetation and environmental controls is a fundamental goal of ecology and biogeography (Kent et al. 2006), there are few empirical examples of the spatial structuring of these relationships across boundaries. Boundary features such as width and abruptness bear directly upon spatial and temporal dynamics between the adjacent systems. For example, boundaries have often been proposed as regions for focused ecological monitoring due to their presumed sensitivity to climate (Loehle 2000). In two recent examples, anthropogenic climate change has been implicated in the repositioning of montane forest boundaries (Allen & Breshears 1998; Beckage et al. 2008). Moreover, in grassland–forest transitions, studies of vegetation–environment relationships may also provide insights into mechanisms of grass–tree co-existence, a long-debated issue in savanna research (Mills et al. 2006).

In a separate study (Danz et al. 2011), we showed that precipitation minus potential evapotranspiration (hereinafter P – PET) was the predominant control on tree occurrence at a spatial resolution above 40 km in the historic prairie–forest boundary of Minnesota, USA. Topographic and soil variables were influential within the boundary, but were less important across the boundary. Our objectives here are to evaluate the spatial structure of vegetation–environment relationships across the prairie–forest boundary in Minnesota prior to European settlement. This area has been suggested to have a sharper vegetation and climatic transition for a flat interior continental location than would commonly be expected (Changnon et al. 2002). Moreover, this region has been the focus of many studies of vegetation dynamics in paleoecological and contemporary times (e.g. McAndrews 1966; Grimm 1984; Peterson & Reich 2001) and has high-quality historical vegetation and environmental data, thereby making it an excellent model system of a grassland–forest transition. We test the hypothesis that the spatial pattern of change across the boundary is the same for both climate and vegetation compared to the alternative that vegetation does not follow the climatic pattern directly, i.e. that vegetation changes abruptly along a smooth change in the environment.

Methods

Study area

The grassland–forest boundary in Minnesota spans 650 km along a northwest–southeast axis and separates tallgrass prairie vegetation to the south and west from forest vegetation to the north and east (Fig. 1). At the time of European settlement, the boundary region consisted of a mosaic of prairie, savanna, woodland and forest ecosystems (Grimm 1984). Forest vegetation in this region is commonly divided into two types: mixed boreal forest that reaches its southern limit in central Minnesota and broad-leaf deciduous forest that reaches its western limit. Bailey (1995) referred to these regions as Laurentian Mixed Forest and Eastern Broadleaf Forest, respectively. Quaking aspen (*Populus tremuloides*) and bur oak (*Quercus macrocarpa*) were the two dominant tree species along the boundary, with quaking aspen being more abundant to the northwest and bur oak to the southeast (Wheeler et al. 1992).

The region has a continental climate with warm summers and cold winters due to the intersection of Arctic, Pacific and maritime tropical air masses (Borchert 1950). The spatial zone of interaction among these three climatic air masses roughly coincides with the position of the boundary. Annual precipitation in the boundary region (100 km buffer on either side of the boundary) 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 in a flat, mid-continental region far from mountains (Borchert 1950). A wide variety of land forms exists along the boundary in Minnesota due to the region's glacial history, highlighted by three main topographic regimes: (1) fairly level terrain and poorly drained soils in the northwestern portion of the state, (2) strongly morainal topography in the west-central region, and (3) highly dissected topography in the unglaciated southeastern region (Fig. 2). Elevation range in the boundary is ca. 200–600 m (mean 400 m).

We developed a curvilinear baseline representation of the boundary in a geographic information system (GIS) by smoothing the prairie ecoregion border available from the Minnesota Department of Natural Resources (MN DNR; Fig. 1). Further, we defined 22 rectangular 15 × 400-km transects perpendicular to the smoothed PFB at 30-km intervals along the curve (Fig. 2, top panel). All transects spanned a gradient in tree occurrence from prairie in the west to forest in the east. Transects were truncated to the east or west by Minnesota state borders, resulting in a range of final transect lengths from 170 to 400 km (mean 228 km). Due to the curved nature of the boundary, some transects had endpoints that were spatially clustered, e.g. transects 7–13 had eastern endpoints within 50 km of each other (Fig. 2).

Data

Vegetation from a time period prior to widespread European settlement of the region is represented by the occurrence of prairie and forest vegetation taken from records of the pre-settlement land survey (PLS) in Minnesota between 1847 and 1908 (Almendinger 1996). The PLS was a highly systematic survey designed as part of the township–range grid system, with survey locations (corners) occurring on a square grid 0.5 miles (0.8 km) apart, resulting in ca. 250 000 survey locations in Minnesota. Land surveyors recorded the nearest tree or up to four trees (i.e. bearing trees) at survey corners in addition to the type of vegetation present at the corner in 25 vegetation classes. We constructed a binomial 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 forest (31%) and several minor wooded types totalling 9% (e.g. timber, grove, pine grove, windthrow, windfall, etc.). 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
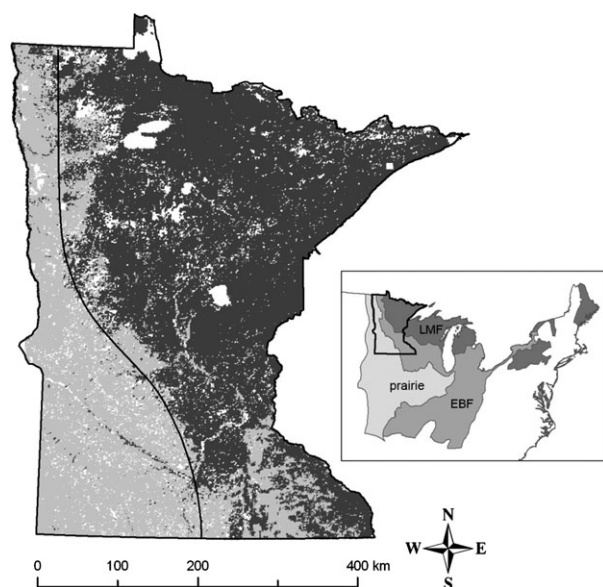

Fig. 1. Pre-settlement prairie (light) and forest (dark) vegetation in Minnesota, USA. Unshaded areas indicate locations not attributed to prairie or forest vegetation, e.g. water bodies (see Methods). The smooth curve indicates the reference prairie–forest boundary for this study. Inset: Minnesota ecoregions from Bailey (1995). LMF = Laurentian Mixed Forest, EBF = Eastern Broad-leaf Forest, Prairie = Tallgrass Prairie.
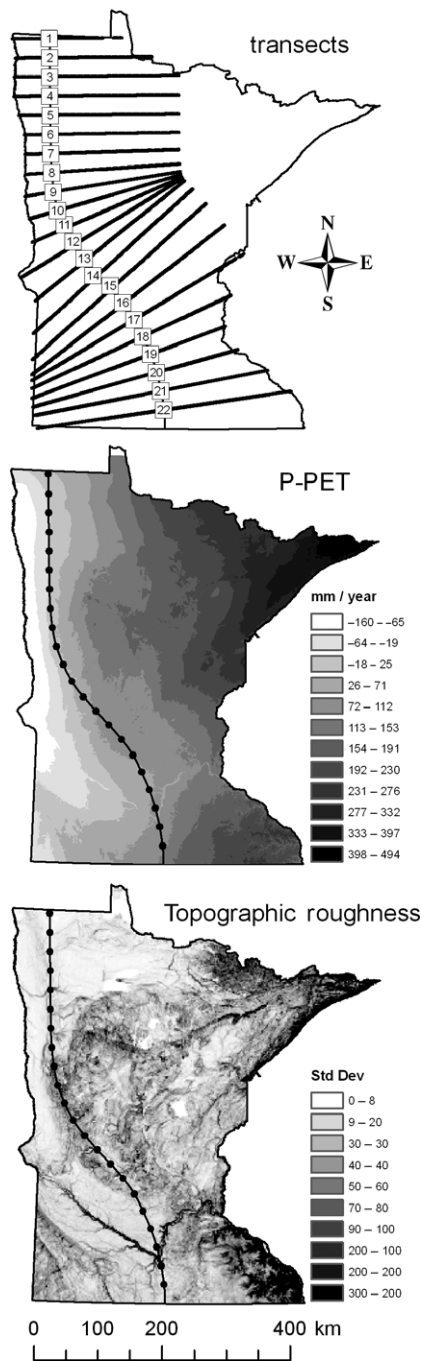
Fig. 2. Sample transects, P − PET (mm·yr^{-1}) and topographic roughness (SD of 30-m elevation in 2-km grid cells) in Minnesota. In the lower panel, the Minnesota River valley is the dominant darkly-shaded linear element running in a NW–SE direction in the southwestern portion of the state.

classes not reliably related to wooded or prairie vegetation (15%) were excluded from consideration, including creek, ploughed field, dry ridge, bottom, marsh, dry land, river, burned area, valley, ravine and island.

State-wide, surveyors recorded about 5% of corners as savanna or woodland vegetation types including oak barrens, oak openings, pine openings, scattered pine, scattering oak and scattering timber (Almendinger 1996). Savanna systems have lower tree density than forests, and in some locations along the PFB they served as a transition between prairie and forest over tens of kilometers; in other cases, prairie and forest were essentially adjacent ecosystems (Marschner 1974). Although we do not know the criteria used by PLS surveyors to distinguish among prairie, savanna and forest vegetation at survey corners, we found in exploratory analysis that tree spacing was higher in savanna types (mean distance from corner 13 m) compared to forest types (mean distance from corner 7 m). If we were to treat savanna as forest, it would likely result in the praire–forest transition appearing more spatially abrupt than it really was. Therefore, we omitted all savanna corners from our binomial vegetation variable to avoid the potentially confounding effects of tree density. Omitting these savanna corners from our response variable did not preclude our characterization of spatial changes across the PFB, however; values for these corners were interpolated in a smoothing step later in our analysis (see below).

Geographic coordinates for survey corners were available from the Minnesota Department of Natural Resources (MN DNR; Almendinger 1996) and subject to post-processing in a GIS (ESRI Inc., Redlands, CA, USA), resulting in 248 226 corners. For analytical purposes, we projected PLS survey locations onto the long axis of our 22 rectangular transects perpendicular to the boundary, effectively transforming the two-dimensional transects into one dimension (Timoney et al. 1993).

To facilitate comparisons of spatial models of vegetation and climate (described below), we transformed the binomial vegetation variable into a continuous probability of forest vegetation using LOESS regression (SAS PROC LOESS; SAS Institute, Cary, NC, USA). LOESS is a locally-weighted, non-parametric smoothing technique that imparts no functional shape on the data. We modelled the relationship between the binomial vegetation variable and distance along each transect for each survey corner, specifying automatically generated smoothing parameters, which were quite low (range 0.01–0.05, mean 0.02), indicating a low degree of smoothing. The predicted values on the LOESS curve were used to represent the probability of forest vegetation (range 0–1) in all subsequent vegetation analyses. Survey corners originally excluded from the binomial variable due to the occurrence of savanna vegetation (see above) were also used to generate predicted values.

Our climate variable, precipitation minus potential evapotranspiration (P − PET), integrates environmental moisture inputs and evaporative loss and has been used as an index of climatic moisture availability (Bonan 1989).

The zero isoline of this variable was closely correlated with the southern limit of the boreal forest in the prairie provinces of western Canada (Hogg 1994), which share a political border with Minnesota to their southeast. Additionally, P – PET accounted for 75% of the explained variance in statewide occurrence of prairie vs. woody vegetation in a separate study in Minnesota (Danz et al. 2011). Given commonly high statistical correlations among climate factors (Changnon et al. 2002), P – PET may to some degree serve as a surrogate for other climate variables and for interactions with non-climate factors at other spatial scales, e.g. fire or biotic interactions. Input values of potential evapotranspiration and precipitation were obtained from McKenney et al. (2006), who used historical climate station data in combination with elevation to model climate parameters for North America at 1 km spatial resolution. Values represent the sum (in mm) of the monthly precipitation averages minus the sum of the monthly PET averages for 1961–1990.

Input variables for P – PET were not available for a time period contemporary with the PLS. This temporal mismatch in our vegetation and climate data could result in biases, especially if P – PET has changed non-constantly through space since pre-settlement. While the degree of climate change since pre-settlement (ca. 1850) remains poorly quantified in this region, we used additional climate variables (summer mean daily maximum temperature and summer total precipitation) from time periods 1901–1930 and 1931–1960, in conjunction with the P – PET data from 1961 to 1990 to evaluate regional climate change through the 1900s (see Appendix S1). Although the prairie–forest boundary region has warmed and experienced increased precipitation over the past 100 yr, these changes have been fairly spatially stationary throughout the boundary region, thereby alleviating concerns of potential bias introduced by the time discrepancy of vegetation and climate data (see also Danz 2009; Danz et al. 2011).

Boundary analysis

The main objective of our boundary analysis was to evaluate whether the transition from prairie to forest across the boundary resulted from a smooth or abrupt climatic gradient, i.e. whether the transition followed pattern '(a)' or pattern '(b)' in Fig. 3. We used three analytical tactics to address this objective: (1) description of the spatial pattern of vegetation transition across the boundary, (2) evaluation of whether the climate gradient P – PET followed a steeper or shallower pattern of change across the boundary, and (3) direct modelling of the vegetation–climate relationship across the boundary. In (1) and (2), we constructed linear and sigmoidal models of vegetation or P – PET vs. distance along transects, while in (3) we

constructed linear and sigmoidal models of vegetation vs. P – PET.

Spatial change in vegetation across the boundary

We used a sigmoid wave approach to characterize spatial change in vegetation (Timoney et al. 1993). Specifically, we fit non-linear least squares regression models that estimated parameters b and c in the following sigmoidal function (Hufkens et al. 2008) using SAS PROC NLMIXED (SAS Institute):

$$y = 1/(e^{-b(x-c)} + 1)$$

where y is the fitted value of the continuous probability of forest vegetation, x is distance along the transect, b is the slope parameter and a measure of boundary abrupt-
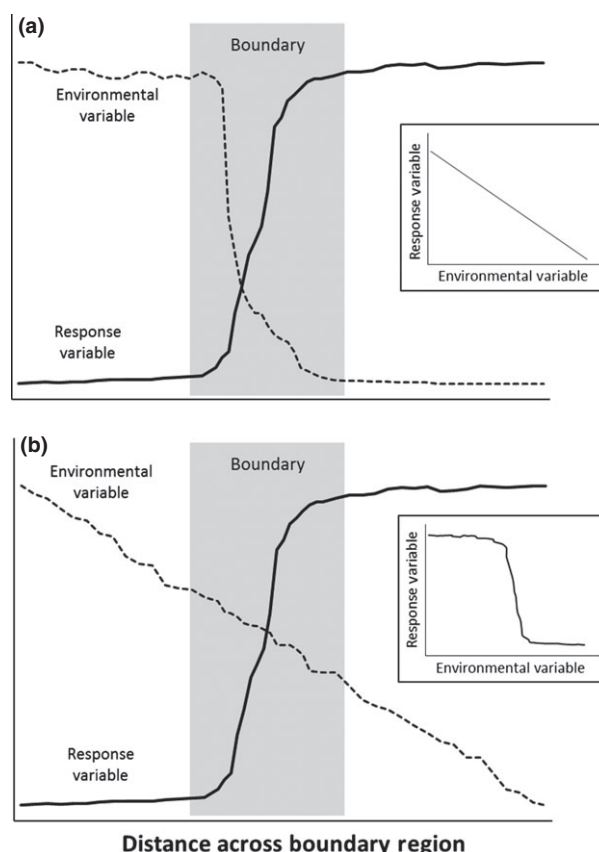

Fig. 3. Two proposed spatial patterns of environmental variables creating ecological boundaries: (**a**) steep gradient in environmental variable, and (**b**) gradual environmental gradient leading to non-linear or threshold response (modified from Fagan et al. 2003; Fig. 1). In (**a**), concomitantly steep gradients in the environment and response are evidenced by a direct relationship between the variables that is approximately linear, while in (**b**), the direct relationship between the environment and response are non-linear.

ness (Bowersox & Brown 2001), and c is the estimated centre of the transition. Good fit to a sigmoid wave model would indicate an abrupt, non-linear pattern of vegetation change. Conversely, less abrupt or smooth changes in vegetation may be better approximated by a linear model. Thus, for the purpose of comparison, we also modelled vegetation as a linear function of distance across the boundary using ordinary least-squares regression (OLS). Model fit of sigmoid wave and OLS models was assessed with Akaike's Information Criterion (AIC) (Radford et al. 2005). We used ΔAIC (Burnham & Anderson 2002) to compare model likelihood between sigmoidal and linear models for each transect ($\Delta AIC = AIC_s - AIC_l$).

We quantified vegetation boundary width as the on-the-ground distance between the points having predicted probability of forest vegetation from 0.05 to 0.95. Further, we investigated spatial patterns in the width of the vegetation boundary by plotting abruptness vs. transect position along the boundary and evaluated transects according to their dominant regional topography (see Study area).

Spatial change in climate across the boundary

We used the same modelling strategy for P – PET as we did for vegetation by calculating both sigmoidal and linear models to describe spatial change. Prior to modelling, we linearly rescaled P – PET to a continuous variable 0–1, with each data point representing the proportion of the maximum P – PET value along each transect. Thus, both vegetation models and climate models use response variables scaled 0–1 and the exact same independent variable (i.e. distance along transect), thereby enabling comparability of model parameter estimates. We used the steepness parameter, b, of sigmoidal models to evaluate how climatic spatial abruptness was related to vegetation spatial abruptness across the boundary.

Spatial vegetation/climate relationships across the boundary

The climate–vegetation relationship in Fig. 3a would be evidenced by a good fit to a linear model, while the relationship in Fig. 3b would be evidenced by a good fit to a non-linear model. Thus, we fitted OLS and sigmoidal regression models using the continuous probability of forest vegetation as a response and P – PET as a predictor for each transect and compared models with AIC. Sigmoidal models were fitted using the function described above. We used the inflection point and the estimate of P – PET at the levels of 0.05 and 0.95 predicted probability of forest vegetation to evaluate where on the climate gradient forest vegetation changed the most abruptly.

Spatial autocorrelation

We noted strong patterns of spatial autocorrelation among the residuals in exploratory logistic models of our vegetation binomial prior to smoothing with LOESS, as well as in the other models of vegetation and P – PET vs. distance along transects described above. This is a likely consequence of including only distance along transect as a predictor variable when other spatially structured covariates are known to be important predictors in this system (Danz et al. 2011). Spatial autocorrelation in regression models can have two negative consequences: (1) increasing the Type I statistical error rate, thereby creating artificially small P-values, and (2) lowering the precision and biasing parameter estimates of covariates in the models (Dormann et al. 2007). In our case, although all models had P-values < 0.0001, we did not use P-values in model comparisons, choosing to use AIC values instead (Hawkins 2012). To investigate whether parameter estimates may be biased, we compared OLS models of forest vegetation and P – PET vs. distance that did not account for spatial autocorrelation with linear generalized least-squares models that included an autoregressive error structure (GLS-AR models; Beale et al. 2010) using SAS PROC AUTOREG (SAS Institute). We compared the steepness parameter, b, from these models to evaluate whether accounting for spatial autocorrelation resulted in bias. We used linear rather than sigmoidal models in these comparisons because existing methods to account for spatial autocorrelation are much better developed for linear models (Beale et al. 2010).

Results

The probability of forest vegetation was well modelled by a sigmoidal function across the prairie–forest boundary, with sigmoidal models having lower AIC (greater likelihood) values than linear models in 21 of 22 transects (Table 1, Appendix S2). Transect 1 was the only one for which a linear model had better fit, although the difference between the linear model and sigmoidal model was comparatively small (Appendix S2). Based on the distance between points having 5% and 95% predicted probability of forest vegetation, boundary width ranged from 38 to 178 km (mean = 99 km) (Table 1, Fig. 4).

Model abruptness parameters b for sigmoidal models of vegetation vs. distance along transects were on average 24 times higher than b values from sigmoidal models of P – PET (Fig. 5), indicating that climate has a much shallower rate of spatial change across the boundary.

Vegetation–climate relationships were clearly non-linear across the boundary (Fig. 6). For 21 of 22 transects,

Table 1. Results from sigmoidal regressions of the probability of forest vegetation vs. distance along transect for 22 transects spanning the prairie–forest boundary. Transects are numbered in order moving southeast along the boundary (Fig. 2). Boundary width values are on-the-ground distances between sites having predicted probability of forest vegetation between 5% and 95%; empty cells indicate the predicted probability did not reach an endpoint.

Transect	Number of corners				Boundary width (km)
	Wooded	Prairie	b	r^2*	5–95%
1	596	554	0.034	0.84	–
2	1615	768	0.051	0.97	104
3	3009	729	0.102	0.99	86
4	1977	1408	0.171	0.97	99
5	2018	1100	0.032	0.93	163
6	2519	725	0.536	0.98	80
7	2104	1069	0.368	0.98	91
8	2018	1169	0.902	0.99	38
9	2289	927	0.078	0.98	91
10	2045	824	0.242	0.96	86
11	1987	1080	0.055	0.96	88
12	1952	1620	0.133	0.99	83
13	2240	1362	0.133	0.99	58
14	2340	2360	0.780	0.99	69
15	2187	2983	0.312	0.99	105
16	2930	2901	0.347	0.97	116
17	2125	2719	0.151	0.97	138
18	1838	2878	0.561	0.98	117
19	1390	3417	0.477	0.93	178
20	1372	3594	0.147	0.70	–
21	1343	4325	0.015	0.78	–
22	1313	4467	0.019	0.81	–
				Average	99

*$r^2 = 1-(SS_{Error}/SS_{Total})$ from non-linear least squares regression.

a sigmoidal model of vegetation–climate relationships displayed a lower AIC than a linear model (Table 2), indicating that vegetation changed comparatively abruptly rather than gradually along the climate gradient. Although the linear model for Transect 1 had a better fit than the sigmoidal model, the difference in fit between models was smaller than in any other transect (Appendix S2).

Structural features of the PFB were influenced by transect location along the boundary. First, vegetation boundary abruptness was unimodally related to transect location along the boundary, with low abruptness values in the topographically flat northwestern Minnesota and the highly-dissected region in southeast Minnesota (Fig. 7). Conversely, vegetation boundary abruptness was highest in west-central Minnesota, where there is strongly morainal topography roughly parallel to the boundary (Fig. 2). Second, the vegetation inflection point on the P – PET gradient (centre of the boundary; 0.50 probability of forest vegetation) increased monotonically from about −30 to 200 mm·yr^{-1} moving along the boundary from transect 1

to 22 (Fig. 7); 18 of 22 transects had inflection points between 0 and 100 mm·yr^{-1} (Fig. 6). The four transects with P-PET outside this range occurred at the northwest and southeast ends along the length of the boundary. The 0.05 predicted probability of forest vegetation (western border) increased similarly from about −50 to 50 mm·yr^{-1}.

Accounting for spatial autocorrelation in linear models resulted in a decline in the abruptness parameter estimate of about 30% for vegetation and about 1% for P – PET (Appendix S3). OLS models of vegetation along transects that did not account for spatial autocorrelation resulted in abruptness parameter estimates on average two times higher than P – PET abruptness. GLS-AR models of vegetation that accounted for autocorrelation resulted in lower parameter estimates for both responses and an average 1.5 times higher vegetation abruptness than P – PET abruptness. Thus, linear models incorporating autocorrelation yielded similar conclusions to those that did not: vegetation changes more abruptly across the boundary than across climate.

Discussion

Ecological boundaries are regions of relatively abrupt spatial change between adjacent ecosystems. While it has been often repeated in the boundary literature that abrupt vegetation boundaries are due to either steep gradients in the physical environment or to non-linear changes along a gradual environmental gradient (e.g. Gosz 1992; Risser 1995; Fagan et al. 2003), there are few studies that directly evaluate these alternatives. We tested the hypothesis that vegetation and climate followed similarly abrupt transitions across the prairie–forest boundary in pre-settlement Minnesota. Our results show that forest vegetation changed abruptly along a comparatively smooth gradient in climate water availability (P – PET).

The observed pattern of vegetation transition across the prairie–forest boundary supports work from Timoney et al. (1993) and Cairns & Waldron (2003), who found similar sigmoidal spatial patterns of vegetation change across tree line systems in boreal and alpine regions. Timoney et al. (1993) hypothesized that sigmoidal vegetation transitions across space were a fundamental property of undisturbed biome boundary regions. Sigmoidal transitions *per se* are not necessarily indicative of an abrupt transition because a well-fitting sigmoidal function can have a shallow slope, thereby approximating a linear model. Thus, the abruptness of a sigmoidal transition can only be considered relative to a distance criterion across space, or to some other environmental gradient or transition. Mills et al. (2006) suggested the focus on boundary shape and position should be considered primarily in light of the controlling environmental variables and not simply distance. Hence,
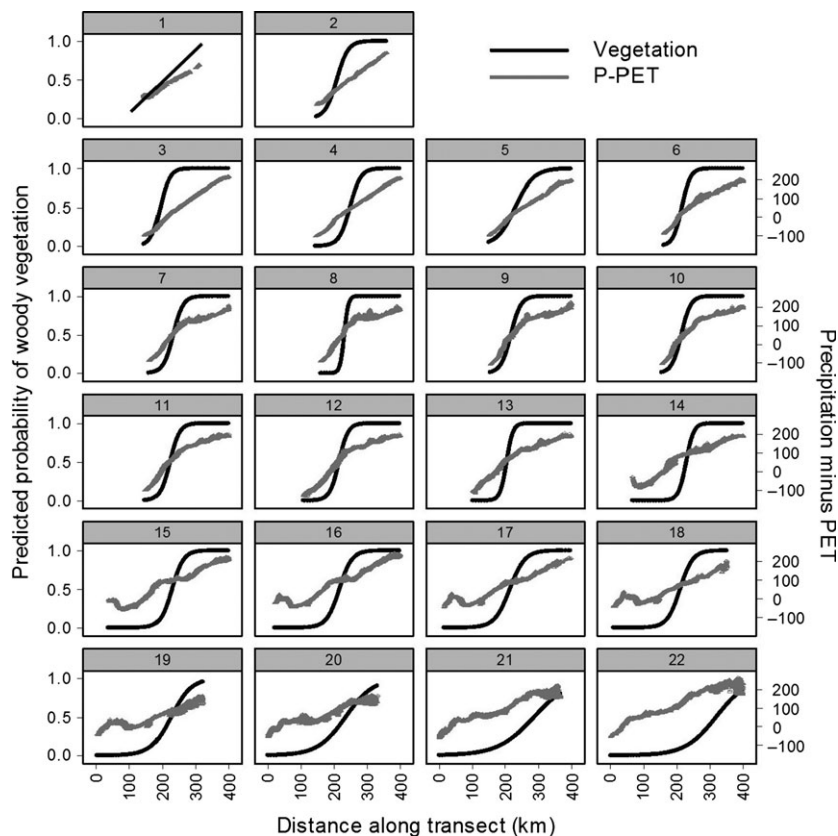
Fig. 4. Modelled probability of forest vegetation from best-fit models and empirical P − PET vs. distance along 22 transects spanning the pre-settlement Minnesota prairie–forest boundary. The best-fit vegetation curve for transect 1 is linear, while sigmoidal curves were best for all other transects.
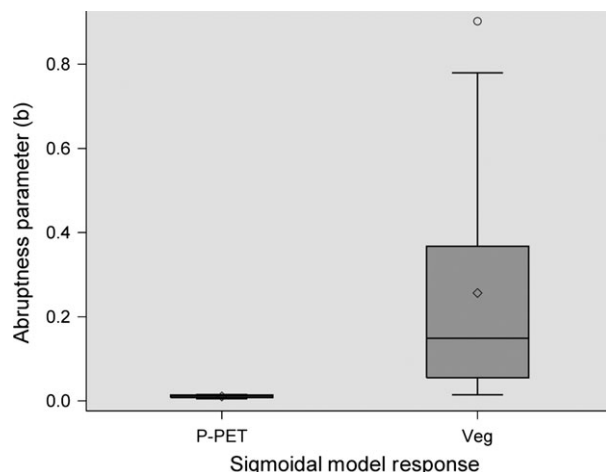

Fig. 5. Box plots of slope parameter estimates (*b*) from sigmoidal regressions of a climatic variable (precipitation minus potential evaporation, P − PET) and vegetation variable (probability of forest vegetation) vs. distance for 22 transects crossing the prairie–forest boundary. Median *b* is indicated by a horizontal line, while mean *b* is indicated by a diamond symbol. On average, the spatial change in woody vegetation across the prairie–forest boundary is 24 times more abrupt than the change in P − PET.

the prairie–forest boundary can be considered an abrupt boundary relative to its climatic control, even though the transition is >100 km in some locations. This abrupt change occurs across a larger spatial scale than traditionally considered in existing grassland–forest boundary studies, which usually span tens to hundreds of meters (e.g. Cadenasso et al. 1997; Camarero et al. 2000).

Although our study documents non-linear vegetation– climate relationships across a biome boundary, there is a lack of consensus regarding the nature of such relationships in other boundaries. Alpine tree lines, which are controlled primarily by temperature, generally experience smooth rather than abrupt declines in temperature with increasing elevation (Jobbágy & Jackson 2000) – a pattern in general agreement with our findings. Conversely, in the Arctic tree line of northern Canada where the Timoney et al. (1993) study was carried out, annual net radiation, absorbed solar radiation and duration of thaw season all displayed a sigmoidal decrease from south to north across the Canadian forest and tundra (Hare & Ritchie 1972). Additionally, working across several sharp biome transitions in South Africa, Van Rensburg et al. (2004) showed that precipitation and temperature were more var-

Table 2. Results from OLS and sigmoidal models of vegetation vs. P − PET across 22 transects spanning the prairie–forest boundary. Sample sizes are listed in Table 1. Values of P − PET at predicted probability levels of forest vegetation indicate the centre of the boundary (inflection point) and estimated western and eastern limits based on 0.05 and 0.95 levels, respectively; empty cells indicate the predicted probability of forest vegetation did not reach an endpoint.

Transect	AIC			P − PET at predicted probability of forest vegetation		
	OLS	Sigmoid	ΔAIC	0.5*	0.05	0.95
1	−3062	−3036	−26	10	−	119
2	−8472	−9868	1396	−6	−80	85
3	−12 384	−18 188	5804	−34	−93	28
4	−10 413	−13 980	3567	52	31	73
5	−9394	−9749	355	26	−84	159
6	−10 646	−13 124	2478	10	−45	64
7	−10 614	−13 301	2687	79	61	97
8	−10 439	−19 999	9560	81	69	94
9	−12 844	−14 821	1977	35	−53	131
10	−10 097	−10 921	824	27	−67	123
11	−11 273	−11 780	507	57	−41	153
12	−13 588	−18 124	4536	50	−14	119
13	−12 580	−22 657	10 077	59	29	86
14	−12 668	−23 137	10 469	90	85	95
15	−14 388	−19 933	5545	97	87	106
16	−18 965	−25 939	6974	92	68	116
17	−14 491	−18 818	4327	79	58	100
18	−13 923	−21 179	7256	70	63	76
19	−14 604	−17 247	2643	71	53	87
20	−13 429	−13 859	430	97	21	163
21	−17 977	−17 978	1	167	12	−
22	−18 544	−19 407	863	207	74	−
			Average	64	11	104

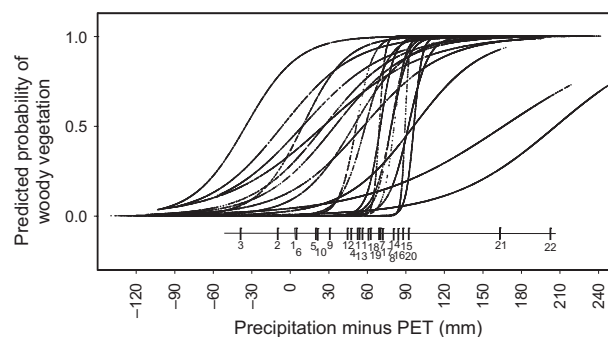*Inflection point of forest vegetation on P − PET.

Fig. 6. Fitted values from sigmoidal regressions of forest vegetation vs. climate for 22 transects spanning the presettlement prairie–forest boundary. The horizontal line below the curves indicates inflection point of vegetation on the P − PET gradient for each transect.

iable in boundary regions than in adjacent biomes, indicating spatial climatic changes in the boundary were steeper.

Our study is based on a snapshot of regional vegetation conditions from the mid- to late 1800s and on the presumption that long-term mean climate water availability was the major control of the location of the PFB at the biome scale. Other grassland–forest boundaries are known to be correlated with similar climatic variables (Sankaran et al. 2005), and in earlier work on this system, P − PET accounted for 75% of explained variance in the statewide occurrence of prairie vs. woody vegetation (Danz et al. 2011). Our results suggest that the 0.50 probability of forest vegetation (centre of boundary) hovered around a long-term annual mean P − PET value between 0 and 100 mm, with the western boundary (0.05 probability of forest vegetation) ca. 0 mm·yr^{-1}. Working in western interior Canada, Hogg (1994) found the southern boundary of boreal forest was closely aligned with 0 mm P − PET. Although we did not directly evaluate other climate variables or non-climate factors at large spatial scales (e.g. fire), such factors were likely correlated with P − PET across the boundary.

Within the limits imposed by climatic water availability, interactions of other environmental controls such as topography, soils and fire undoubtedly operated in conjunction with climate to determine the ultimate within-boundary structure, likely increasing the non-linearity of the relation with climate (Grimm 1984; Peterson & Reich
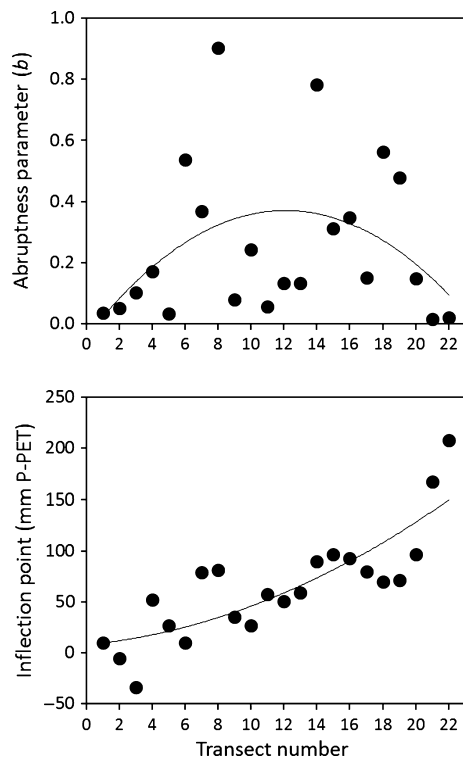
Fig. 7. Vegetation boundary abruptness in relation to transect position along the boundary (top panel), and inflection point for prairie–forest vegetation vs. climate along the boundary (bottom panel). Curves were fit with second-order polynomial trend lines for illustrative purposes.

2001; Danz et al. 2011). In some locations topography was apparently a strong modifier of boundary width through its influence on fire regimes (Grimm 1984; Wheeler et al. 1992). For example, the central boundary (i.e. transects 7–18) is an area suggested by McAndrews (1966) where the prairie–forest transition occurring for climatic reasons was steepened by the spatial shift from relatively flat terrain to morainal topography that impeded fire spread (Fig. 2).

Moving northwest along the prairie–forest boundary in Minnesota, the inflection point (centre of boundary) decreased by about 100 mm $P - PET\ yr^{-1}$, which might suggest compositional change toward increased drought tolerance moving in this direction. The supporting evidence for this pattern is weak in this region. Quaking aspen, a relatively drought-intolerant species (Burns & Honkala 1990) was a dominant species in the northwest where $P - PET$ values were lowest, while bur oak is more drought-tolerant than aspen and was increasingly dominant in the southeast boundary region where $P - PET$ was higher (Wheeler et al. 1992). However, quaking aspen was often limited to wet depressions in northwest Minnesota (Buell & Buell 1959) and bur oak was abundant on well-drained, south-facing slopes in southeast Minnesota (Grimm 1984).

Conclusions

Understanding the nature of vegetation–environment relationships is a primary goal of ecology and biogeography, yet there are few empirical examples describing spatial patterns of such relationships across boundaries (Kent et al. 2006). Our results show a non-linear, sigmoidal relationship between vegetation and climatic moisture availability across a grassland–forest biome boundary from pre-settlement Minnesota, USA. This abrupt vegetation boundary traverses a greater distance than traditionally considered in ecological boundary studies. Further, boundary structural features changed along the 650 km length of the boundary due to dominant topographic controls and presumed interactions with fire, creating conditions for tree–grass co-existence within the boundary (Grimm 1984; Peterson & Reich 2001).

Studies of pre-settlement conditions serve as an important source of baseline data for comparison with current and future conditions. Because of their sensitivity to climate conditions, biome boundaries have often been promoted as areas for focused ecological monitoring in the face of global change (Loehle 2000), with two recent notable examples of montane tree lines experiencing dramatic positional shifts with concomitant climate change (Allen & Breshears 1998; Beckage et al. 2008). On average, the transition between prairie and forest vegetation occurred at a rate of ca. 1% probability of forest per 1 km and per 1 mm $P - PET$. The observed range in the inflection point of $P - PET$ of ca. 100 mm throughout the majority of the length of the boundary (i.e. transects 4–18) is about 40% of the long-term mean annual range of this variable in this region (Fig. 2). Hence, moderately small changes to $P - PET$ may have potential to cause substantial shifts in the boundary location in Minnesota, particularly where the transition was the sharpest. The ultimate utility of the boundary region as a location for environmental monitoring is tempered by the fact that currently <5% of original prairie remains due to land-use conversion, and that the natural fire regime has been almost completely suppressed. Relationships between forest and climate moisture availability uncovered in this study may nevertheless provide a baseline physiological constraint on the westward position of forest and insight into the universality of mechanisms leading to ecological boundary structure.

Acknowledgements

References

Allen, C.D. & Breshears, D.D. 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America* 95: 14839–14842.

Almendinger, J.C. 1996. *Minnesota's bearing tree database. Biological report No. 56*, pp. 23. Minnesota Department of Natural Resources. St. Paul, MN, US.

Bailey, R.G. 1995. *Description of the ecoregions of the United States*, 2nd edn. Miscellaneous Publication No 1391. USDA Forest Service, Washington, DC, US.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D.A. 2010. Regression analysis of spatial data. *Ecology Letters* 13: 246–264.

Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T. & Perkins, T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America* 105: 4197–4202.

Bonan, G.B. 1989. A computer model of the solar radiation, soil moisture, and thermal regimes in boreal forests. *Ecological Modeling* 45: 275–306.

Borchert, J.R. 1950. The climate of the central North American grassland. *Annals of the Association of American Geographers* 40: 1–39.

Bowersox, M.A. & Brown, D.G. 2001. Measuring the abruptness of patchy ecotones. *Plant Ecology* 156: 89–103.

Breshears, D.D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics. *Frontiers in Ecology and the Environment* 4: 96–104.

Buell, M.F. & Buell, H.F. 1959. Aspen invasion of the prairie. *Torreya* 86: 264–269.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York, NY, US.

Burns, R.M. & Honkala, B.H., Technical coordinators. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, US.

Cadenasso, M.L., Traynor, M.M. & Pickett, S.T.A. 1997. Functional location of forest edges: gradients of multiple physical factors. *Canadian Journal of Forest Research* 27: 774–782.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Bell, S.S., Benning, T.L., Carreiro, M.M. & Dawson, T.E. 2003. An interdisciplinary and synthetic approach to ecological boundaries. *BioScience* 53: 717–722.

Cairns, D.M. & Waldron, J.D. 2003. Sigmoid wave transitions at alpine treeline. *Geografiska Annaler. Series A. Physical Geography* 85: 115–126.

Camarero, J.J., Gutiérrez, E. & Fortin, M.-J. 2000. Spatial pattern of subalpine forest–alpine grassland ecotones in the Spanish Central Pyrenees. *Forest Ecology and Management* 134: 1–16.

Changnon, S.A., Kunkel, K.E. & Wistanley, D. 2002. Climate factors that caused the unique tall grass prairie in the central United States. *Physical Geography* 23: 259–280.

Danz, N.P. 2009. *Spatial vegetation–environment relationships and distributional changes in the presettlement Minnesota prairie–forest boundary*. PhD Thesis, University of Minnesota, St. Paul, MN, US.

Danz, N.P., Reich, P.B., Frelich, L.E. & Niemi, G.J. 2011. Vegetation controls vary across space and spatial scale in a historic grassland–forest biome boundary. *Ecography* 34: 402–414.

di Castri, F., Hansen, A.J. & Holland, M.M. 1988. A new look at ecotones: emerging international projects on landscape boundaries. *Biology International* 17: 1–163.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröeder, B., Schurr, F.M. & Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30: 609–628.

Fagan, W.F., Fortin, M.-J. & Soykan, C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience* 53: 730–738.

Gosz, J.R. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hansen, A.J. & di Castri, F. (eds.) *Landscape boundaries: consequences for biotic diversity and ecological flows*, pp. 55–75. Ecological Studies, Volume 92. Springer, New York, NY, US.

Grimm, E.C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54: 291–311.

Hare, F.K. & Ritchie, J.C. 1972. The boreal bioclimates. *Geographical Review* 62: 333–365.

Hawkins, B.A. 2012. Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography* 39: 1–9.

Hogg, E.H. 1994. Climate and the western limit of the southern Canadian boreal forest. *Canadian Journal of Forest Research* 24: 1838–1845.

Hufkens, K., Ceulemans, R. & Scheunders, P. 2008. Estimating the ecotone width in patchy ecotones using a sigmoid wave approach. *Ecological Informatics* 3: 97–104.

Jobbágy, E.G. & Jackson, R.B. 2000. Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecology and Biogeography* 9: 253–268.

Kent, M., Moyeed, R.A., Reid, C.L., Pakeman, R. & Weaver, R. 2006. Geostatistics, spatial rate of change analysis, and boundary detection in plant ecology and biogeography. *Progress in Physical Geography* 30: 201–231.

Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. *Canadian Journal of Forest Research* 30: 1632–1645.

Marschner, F.J. 1974. *The original vegetation of Minnesota*. Map published by US Forest Service, North Central Forest Experiment Station, St. Paul, MN, US.

McAndrews, J.H. 1966. Postglacial history of prairie, savanna, and forest in northwestern Minnesota. *Memoirs of the Torrey Botanical Club* 22: 1–72.

McKenney, D.W., Pedlar, J.H., Papadopol, P. & Hutchinson, M.F. 2006. The development of 1901–2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology* 138: 69–81.

Mills, A.J., Rogers, K.H., Stalmans, M. & Witkowski, E.T.F. 2006. A framework for exploring the determinants of savanna and grassland distribution. *BioScience* 56: 579–589.

Peterson, D.W. & Reich, P.B. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11: 914–927.

Radford, J.Q. Bennett, A.F. & Cheers, G.J. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124: 317–337.

Risser, P.G. 1995. The science and status of examining ecotones. *BioScience* 45: 318–325.

Sankaran, M., Hanan, N.P., Scholes, R.J., Rantnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., LeRoux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Twes, J.,

Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* 438: 846–849.

Strayer, D.L., Power, M.E., Fagan, W.F., Pickett, S.T.A. & Belknap, J. 2003. A classification of ecological boundaries. *BioScience* 53: 723–729.

Timoney, K.P., La Roi, G.H. & Dale, M.R.T. 1993. Subarctic forest–tundra vegetation gradients: the sigmoid-wave hypothesis. *Journal of Vegetation Science* 4: 387–394.

Van Rensburg, B.J., Koleff, P., Gaston, K.J. & Chown, S.L. 2004. Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* 31: 843–854.

Wheeler, G.A., Cushing, E.J., Gorham, E., Morley, T. & Ownbey, G.B. 1992. A major floristic boundary in Minnesota: an analysis of 280 taxa occurring in the western and southern portions of the state. *Canadian Journal of Botany* 70: 319–333.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Climate change in the prairie–forest boundary region 1901–1990.

Appendix S2. AIC values and model abruptness parameters from linear and sigmoidal models.

Appendix S3. Comparison of slope parameter estimates from OLS and GLS-AR models.