



Human-induced edges alter grassland community composition

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ABSTRACT

Habitat fragmentation alters the edges of remnant habitat patches. We examined changes in the plant community and soil in relation to distance from edge and edge type for shrub-steppe and pine savannah grasslands in southern British Columbia, Canada. Community composition showed significant nonlinear relationships with distance-to-edge more frequently at paved roads and fruit crops than at dirt roads or control sites (i.e., in the interior of grassland patches), with changes typically extending 25–30 m. More exotic species and fewer native species were found near edges, and edges showed decreased cryptogam cover and increased bare ground, especially near paved roads. The soil factors that best predicted compositional changes were soil pH and Cu/Mn at paved roads, soil pH and nitrogen at fruit crops, and soil resistance at dirt roads. Variation partitioning suggested that both direct (e.g., propagule pressure) and indirect (environmental change) factors mediated edge-related community changes, and provided evidence that nonlinear responses at developed edges were not due to natural gradients. Given the range of grassland patch sizes in this region (many patches 1–100 ha), the edge effects we observed represent a considerable loss of “core” habitat, which must be accounted for in conservation planning and site restoration.

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1. Introduction

The detrimental effects of habitat fragmentation involve loss of habitat and isolation of fragments from each other (Piessens et al., 2005; Steffan-Dewenter and Tscharrntke, 1999). However, if community composition or environment are also altered at patch edges, such edge effects could create additional unsuitable habitat, amplifying the effects of habitat fragmentation for certain species. Recent reviews agree that edge effects are a primary influence on biodiversity in habitat fragments (Debinski and Holt, 2000; Fischer and Lindenmayer, 2007; Harrison and Bruna, 1999).

Edge effects are systematic changes in community composition or environment as a function of distance from a patch edge (Harper et al., 2005; Ries et al., 2004). The magnitude of edge effects depend on the type and degree of difference between the conditions on either side of the boundary, and the permeability of the edge to the movement of organisms, materials, or energy (Cadenasso and Pickett, 2001; Cadenasso et al., 2003; Ries et al., 2004). Since most human development contrasts sharply with natural habitat, edge effects adjacent to developed land may be particularly strong.

Edge effects are well studied in forests at clearcuts (Harper et al., 2005; Laurance et al., 2002), and at roadsides (Coffin, 2007; Forman and Alexander, 1998; Spellerberg, 1998), but are not well characterized in grasslands or other types of human-induced edges (Bond and Parr, 2010; Cilliers et al., 2008; Lindenmayer et al., 2008). Changes in plant composition and environment at forest edges often extend 50–100 m from the edge (Broadbent et al., 2008; Laurance et al., 2002; Ries et al., 2004), while changes in community composition at roadsides may extend farther (Angold, 1997; Bernhardt-Romermann et al., 2006). Effects at roadsides have been attributed to physical disturbances, dust deposition, nitrogen, chemical pollutants, altered pH, and invasion of exotic species (Coffin, 2007; Forman and Alexander, 1998; Myers-Smith et al., 2006). Agricultural landscapes can also alter nutrient availability and plant community composition in adjacent grasslands (Wesche et al., 2012).

Community composition is expected to have a nonlinear relationship with distance-from-edge, with the rate of change greatest at the edge, and composition gradually approaching that of the patch interior (Ewers and Didham, 2006b; Ries et al., 2004; Williamson, 1989). However, such nonlinear responses have traditionally been difficult to model in multi-species community datasets due to the lack of suitable multivariate techniques (Millar et al., 2005). Edge effect analyses typically focus on single response variables, such as the abundance of a key taxon, or indices of community structure like species richness (Laurance et al., 2002;

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Marchand and Houle, 2006; Ries et al., 2004). Nonlinear canonical analysis of principal coordinates (NCAP) allows nonlinear models to be fitted to multivariate community dissimilarity matrices along a gradient, such as distance from edge (Millar et al., 2005).

Here we test for the presence and spatial extent of edge effects in grasslands of south-central British Columbia, Canada. This region is a national biodiversity hotspot, but human development such as orchards, vineyards, and roads have replaced and fragmented much of the grassland habitat (Lea, 2009; Wikeem and Wikeem, 2004). Our primary hypothesis is that the frequency and magnitude of edge effects are greatest where development contrasts most strongly with native grassland (paved roads) relative to weaker contrasts (dirt roads, agricultural areas). We also address the secondary hypothesis that plant community changes at habitat edges are due both to indirect effects of altered environmental conditions and to a direct effect of proximity to edge (e.g., direct input of exotic seeds).

2. Methods

2.1. Study region

Study sites were situated within 50 km of each other in the adjacent and connected Okanagan and Similkameen Valleys of southern British Columbia. The grasslands in this region are semi-arid bunchgrass, shrub-steppe, and ponderosa pine (*Pinus ponderosa*) savannah (Appendix A). Mean annual precipitation is 280–500 mm, falling mostly during winter and in June (Environment Canada, 2010).

2.2. Study design

We selected 26 grassland sites: eight were by paved roads, six next to dirt roads, six adjacent to fruit crops (drupe and pomeaceous fruit orchards, and vineyards), and six were “control” sites. Since community structure may vary along natural environmental gradients, we surveyed control sites in areas away from roads or cropland (i.e., these sites did not have edges). The patches ranged from 7 to 100 ha, with slopes from 0° to 30°. Most developed edges were located at the bottom of local topographical features, so transects often ran upslope. Sites were on the east-facing slope or the valley bottom, ranging from 280 m to 1000 m elevation. All but four sites, two dirt roads and two control sites, were below 600 m. Control transects on sloped sites were similarly positioned.

At each site, vegetation, ground cover, and soil characteristics were surveyed along two 100 m transects at least 10 m apart, aligned perpendicularly to the edge. Longer transects would have frequently come in close proximity to other edges. Paved roads were 50–100 years old and typically carried 100–500 vehicles per day (Ministry of Transport and Infrastructure, pers. comm.; Argo Roads, pers. comm.). Roads were maintained with roadside mowing twice per year and application of salts for de-icing (Argo Roads, pers. comm.). Orchards in this region were typically watered, fertilized and sprayed with pesticides using broadcast methods. The dirt roads were used mostly for recreation by hikers and motorized vehicles, and for the passage of cattle.

2.3. Plant community surveys

Line transects were surveyed between May and July, 2008. In 39 1-m sections along each transect (Fig. 1a), we recorded the identity and percent cover of all vascular plant species, as well as the cover of leaf litter, cryptogam and bare soil to the nearest 0.1 m (e.g., if species A covered 0.44 m, we recorded it as 0.4 m). Small plants less than 0.1 m wide were designated as 0.05 or 0.01 m. Nomenclature follows Douglas et al. (1998–2002) and exotic status was determined from E-Flora BC (Klinkenberg, 2009). Unique plants too immature to identify (31 occurrences) were excluded, and nine taxa were identified only to genus, resulting in 126 taxa included in statistical analyses (Appendix B).

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2.4. Characterizing the soil environment

To explore the impact of soils on community change we sampled four randomly selected sites for each edge type, and four control sites, at six locations along each transect (Fig. 1a). The plant community data suggested that the majority of compositional change occurred within 20–30 m of the edges. Therefore, soil samples were taken more frequently within 30 m of the edge to better characterize any corresponding changes in the plant community (Fig. 1a). We measured soil characteristics known to influence growth and success of individual plants in natural settings, including compaction (penetration resistance), water content (time-domain reflectometry soil moisture probe), chemistry (on three pooled soil cores to 15 cm depth at each meter), and soil texture (Brady and Weil, 1999; Nicholson et al., 1982). We also measured air temperature 50 cm above the soil surface. We estimated the following soil properties: sand/silt/clay fractions, percent organic matter, pH, exchangeable cations, and mineralizable nitrogen (Appendix A).

2.5. Data analysis

2.5.1. Overview

We conducted three types of statistical analyses. First, we tested for nonlinear relationships between community composition and distance-to-edge, comparing frequency and strength of significant nonlinear relationships among the three types of edges and control sites. Second, we determined how the plant community was altered at developed edges by testing for differences in species richness, proportion of exotic species, and percent ground cover between the edge (first 10 m) and interior (last 10 m) of transects at each site. Third, we determined which soil variables best predicted variation in species composition along nonlinear compositional gradients, and tested for independent effects of environmental factors, and distance-to-edge per se. All statistical analyses were conducted in R (version 2.9.1, R Development Core Team, 2009).

2.5.2. Relationships between community composition and distance-to-edge

We drew inferences concerning the presence or absence of edge effects as follows. If there was no change in composition with distance from edge, then there was no obvious edge effect (Fig. 1b). A linear relationship in composition with distance-to-edge (Fig. 1c) could indicate either a natural environmental gradient, or an edge effect that extends beyond the length of our transects. We conservatively made the former interpretation. We interpreted a nonlinear, saturating relationship between composition and distance-to-edge (Fig. 1d) as evidence of an edge effect. Although slopes and natural environmental gradients can cause a shift in the vegetation, we accounted for this possibility by including control sites on slopes and we considered significant results to be those greater than observed at the control sites.

Nonlinear canonical analysis of principal coordinates (NCAP) was used to determine how well nonlinear gradients of community change can be predicted by distance from the edge (using square root Bray–Curtis dissimilarities; Appendix A). NCAP first ordinated the community dataset according to dissimilarity between pairs of sample plots, then finds the best direct correlation between the community and the predictor variables (details and R packages

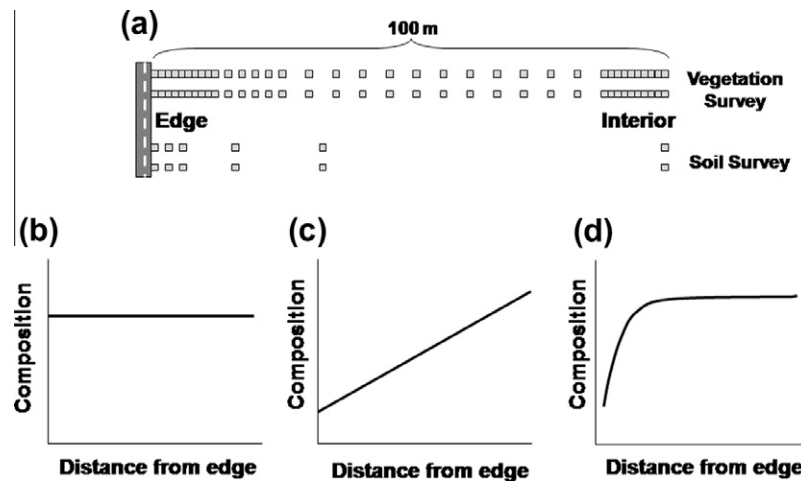


Fig. 1. Sampling design (a) and possible patterns of community response along a distance from edge gradient (b–d). (a) Species composition and percent cover were surveyed in 1-m sections along each line transect at the locations shown (1–10, 12, 14, 16, 18, 20, 25, 30, 35...90–100 m). Soil samples and environmental data were collected in 1-m sections along the same two transects, at 1, 3, 5, 15, 30, and 100 m. No relationship between composition and distance from edge (b) indicates the absence of an edge effect. A linear relationship (c) suggests that either the transects were too short to encompass the entire nonlinear edge effect, or a linear natural environmental gradient is present. A nonlinear change up to an asymptote indicates an edge effect (d).

provided in Millar et al., 2005). Here the nonlinear canonical correlation (NCCorA) determines how well the variation in community composition can be predicted by distance from the edge along a nonlinear gradient, and tests if the nonlinear model is a significantly better fit than a linear model, or a flat (intercept-only) model. The relationship (decelerating change to an asymptote) was modeled using the Von Bertalanffy (1938) gradient, $Y = 1 - e^{-bX}$, where Y is the reduced community matrix from principal coordinate analysis (PCO; Gower, 1966; Torgerson, 1958), X is distance from the edge, and b is the regression coefficient that maximizes the canonical correlation between Y and X (Fig. 1d; Appendix A). This model was fit to the composition data for both transects from each site.

To test if nonlinear responses at edges were more common and stronger than those in the interior of grassland patches, we compared the frequency, extent, and strength of significant nonlinear responses at edge sites to those from control sites. Frequency of significant edge responses between edge types was compared with exact binomial tests of homogeneity due to the small number of nonlinear responses at dirt and control sites (Milton, 1999; Whitlock and Schluter, 2009). The extent of edge influence at each site was calculated as the distance from the edge within which 90% of the change in community occurred (Brand and George, 2001; Ewers and Didham, 2006a; Hylander, 2005). NCAP estimates the canonical correlation between distance-to-edge and species composition, while the magnitude of this correlation coefficient was used to indicate strength of the edge responses. We used Welch Two Sample t-tests with a Bonferroni corrected alpha value ($\alpha = 0.05/3$) to determine if the three edge type means differed significantly from the control group for extent or strength (Milton, 1999; Welch, 1947).

2.5.3. What community attributes distinguish edge from interior habitat?

To determine if any individual species were consistently affected at grassland edges, we calculated the Pearson correlation (r) between NCAP scores and individual species abundance along the transects at each site. We also calculated an index of “edge bias” (Appendix B) for each species as the difference between the percentage of species occurrences falling within 25 m of the edge, and the percentage expected given a random distribution with respect to edge (41%, given that 16/39 survey meters were within

25 m of the edge). Control sites were withheld from this analysis, and we analyzed rare species (observed in <50 sample plots) separately from more common species. One sample t-tests were used to assess the mean edge biases of native and exotic species.

We also examined changes in species richness, proportion of exotic species present, and cover of cryptogamic soil crust, bare ground, and litter in the first 10 m (edge) and last 10 m (interior) of each transect. With significant edge effects, we expect relative differences between the edge and interior for these indices to be greater at edge sites than between two locations at control sites. We calculated the relative difference (d_r) between edge and interior for any given variable Z as $(Z_e - Z_i) / \max(Z_e, Z_i)$, where e and i indicate the edge and the interior respectively (Tornqvist et al., 1985). We compared mean relative differences for the edge types in a one way analysis of variance (ANOVA) using the average relative difference of the two transects for each site. We used Welch Two Sample t-tests to determine which of the edge type means differed significantly from the others.

2.5.4. Relationships between the soil environment and community composition

We reduced the 23 soil environmental variables measured to 10 key soil factors (Table 1a) for subsequent analyses: three individual variables plus seven axes from a factor analysis (factanal function in R with a varimax rotation; Appendix A). For each edge type, we first fit a model predicting NCAP scores using all 10 soil variables, without accounting for edge distance. We then applied all subsets regression to determine which soil variables best predicted the variation in community composition (leaps package; Lumley, 2009). The best fitting model was selected for each edge type using both Mallows C_p and AICc (leaps2AICc; Schluter, 2010), and used in subsequent analyses.

To determine the relative importance of the effects of distance-to-edge per se on the plant community versus the indirect effects of distance via environmental alteration, we conducted a variance partitioning analysis (Legendre, 2008). Only sites that showed a significant nonlinear response in NCAP were included in these analyses. Generalized least squares and linear mixed effects models (using restricted maximum likelihood) were fit to the NCAP composition scores for each edge type using the reduced set of soil variables, plus log distance from edge (full model). Distance and environmental variables were also used separately to predict the

Table 1

Results from a factor analysis of environmental variables and fitting of models between species composition (first axis from NCAP analysis) and environmental factors. (a) Soil variables with a loading of 0.5 or more on a given factor; “–” indicates variables with negative relationships to a given factor (all others were positive). (b–e) AICc values and supporting statistics for the top five models from the all-subsets regression analysis for each edge type, and for the control sites. Only the best model was used in subsequent analyses. Supporting statistics were calculated as per Burnham and Anderson (2002).

| (a) Factor | Related soil characteristics | Factor | Related soil characteristics | | | |
|------------------------------------|----------------------------------|----------|--|------------|-------------|----------------|
| 1 | % Sand (–), % clay, Al, K, Mg, B | 5 | Average water content (–), air temperature | | | |
| 2 | P, Fe, % organic matter | 6 | pH | | | |
| 3 | Cu, Mn | 7 | Coarse content (–) | | | |
| 4 | Ca, S | | | | | |
| | | AICc | ΔAICc | Likelihood | AIC weights | Evidence ratio |
| <i>(b) Paved road models</i> | | | | | | |
| Factor3 + Factor6 | | 0.0000 | 0.0000 | 1.0000 | 0.1792 | 1.0000 |
| Factor3 + Factor5 + Factor6 | | 0.5062 | 0.5062 | 0.7764 | 0.1392 | 1.2880 |
| Factor6 + Na | | 1.0471 | 1.0471 | 0.5924 | 0.1062 | 1.6880 |
| Factor1 + Factor6 | | 1.5576 | 1.5576 | 0.4590 | 0.0823 | 2.1788 |
| Factor5 + Factor6 + Na | | 1.8758 | 1.8758 | 0.3914 | 0.0702 | 2.5547 |
| <i>(c) Fruit crop models</i> | | | | | | |
| Factor6 + N | | 0.0000 | 0.0000 | 1.0000 | 0.1793 | 1.0000 |
| Factor6 + Factor7 + N | | 1.0434 | 1.0434 | 0.5935 | 0.1064 | 1.6849 |
| Factor6 + Factor7 | | 1.2479 | 1.2479 | 0.5358 | 0.0961 | 1.8663 |
| Factor1 + Factor6 | | 1.3836 | 1.3836 | 0.5007 | 0.0898 | 1.9973 |
| Factor1 + Factor6 + Factor7 | | 1.3852 | 1.3852 | 0.5003 | 0.0897 | 1.9989 |
| <i>(d) Dirt road models</i> | | | | | | |
| Soil Resistance | | 0.0000 | 0.0000 | 1.0000 | 0.2050 | 1.0000 |
| Factor5 + Soil resistance | | 1.4549 | 1.4549 | 0.4831 | 0.0990 | 2.0698 |
| Factor3 + Soil resistance | | 1.5591 | 1.5591 | 0.4586 | 0.0940 | 2.1805 |
| Factor2 + Soil resistance | | 1.7004 | 1.7004 | 0.4273 | 0.0876 | 2.3401 |
| Factor7 + Soil resistance | | 1.7484 | 1.7484 | 0.4172 | 0.0855 | 2.3969 |
| <i>(e) Control site models</i> | | | | | | |
| All 10 soil variables ^a | | 0.0000 | | | | |
| Factor1 | | 313.7527 | 0.0000 | 1.0000 | 0.4954 | 1.0000 |
| Factor1 + Na | | 315.3060 | 1.5533 | 0.4599 | 0.2279 | 2.1742 |
| Factor1 + Factor3 | | 315.8400 | 2.0873 | 0.3522 | 0.1745 | 2.8396 |
| Factor2 + Na | | 316.9091 | 3.1564 | 0.2063 | 0.1022 | 4.8462 |

^a This model was disregarded because the number of variables in the model was too many for the number of data points available in the dataset.

NCAP scores (reduced models). The best and most parsimonious model structure for each edge type was selected using AICc.

3. Results

3.1. Relationships between community composition and distance-to-edge

Significant nonlinear relationships ($P < 0.05$) were observed between community composition and distance-to-edge at 75% of paved road sites, 83% of sites adjacent to fruit crops, 33% of dirt road sites, and 33% of control sites (Fig. 2). Paved road and fruit crop sites that did not have significant nonlinear responses to the edge had linear responses ($P < 0.05$), while the remaining dirt road and control sites had either linear responses or no relationship with distance from edge. Binomial exact tests of homogeneity indicated that nonlinear edge responses at paved roads (six of eight sites) and fruit crops (five of six sites) were significantly more frequent than nonlinear gradients observed within control sites (two of six sites; $P = 0.019$ and 0.017 respectively).

The spatial extent and strength of the edge effects at sites with significant nonlinear composition–distance relationships were not significantly different between any of the edge types and the natural gradients at control sites (Appendix C). However, comparisons among edge types had relatively low power due to few significant nonlinear responses at dirt road and control sites. The edge influence (distance within which 90% of the community change occurred) extended on average 34.4 ± 8.4 m (mean \pm SE) from the edge at paved roads, 22.4 ± 9.2 m at fruit crops, and 21.0 ± 0.9 m at dirt roads (average extent for all edges was 27.7 ± 5.3 m), while nonlinear gradients at control sites extended 27.5 ± 10.4 m. Aver-

age canonical correlation of nonlinear NCAP models was 0.76 ± 0.06 for paved road sites, 0.46 ± 0.08 for fruit crop sites, and 0.67 ± 0.10 for dirt road sites, while control sites had values of 0.45 ± 0.13 .

3.2. What community attributes distinguish edge from interior habitat?

Edge-related changes in community composition were not due to responses of one or a few species. Instead, different combinations of species changed in abundance with distance from the edge at each site (Gieselman, 2010). Common native grassland species were less frequent, on average, at the edges (negative edge bias), while exotic species were positively edge-biased (Fig. 3a). Mean bias values were significantly different from zero for common native species (mean = -6.7 , 95% CI [-10.1 , -3.3], $P < 0.001$) but not for common exotic species (10.0 , [-1.3 , 21.3], $P = 0.075$). Rare exotic species (Fig. 3b) were positively edge-biased (30.4 , [16.3 , 44.4], $P < 0.001$), but rare native species were not significantly edge-biased (-2.4 , [-11.0 , 6.1], $P = 0.57$).

The relative difference in the proportion of exotic species at the edge versus interior was not greater for developed sites than was observed between plots at control sites (Fig. 4a). Mean relative differences for proportion of exotic species present varied among edge types ($F_{3,22} = 3.623$, $P = 0.029$), but none of the edge types were significantly different from the control sites (paved edges differed most; 0.614 ± 0.334 (mean \pm SD), $t = 1.95$, $P = 0.091$). However, the exotic cover at paved edges was always greater than the interior of the same site ($t = 5.20$, $P = 0.001$).

The relative difference in cover of cryptogamic crust (Fig. 4b) was significantly lower at the edges of paved roads (-0.77 ± 0.24)

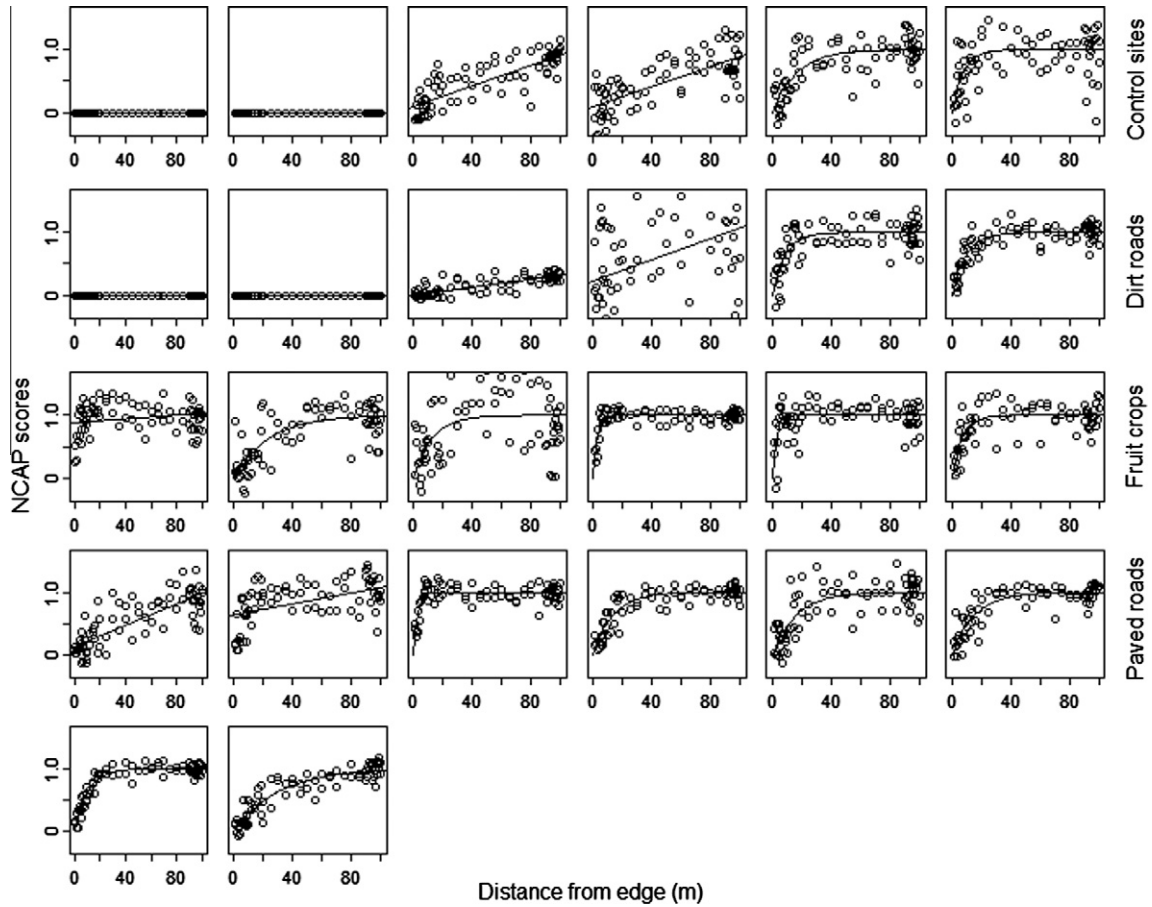


Fig. 2. NCAP models for each site, within each of the four edge types. NCAP scores represent the primary axis of variation in community composition that varies as a nonlinear function of distance-to-edge. Models are constrained between zero and one, with the asymptote approaching an average interior community composition at a value of 1.0. Sites with plots showing average composition at zero (four top-left panels) had no relationship with distance from edge, so the ordination failed.

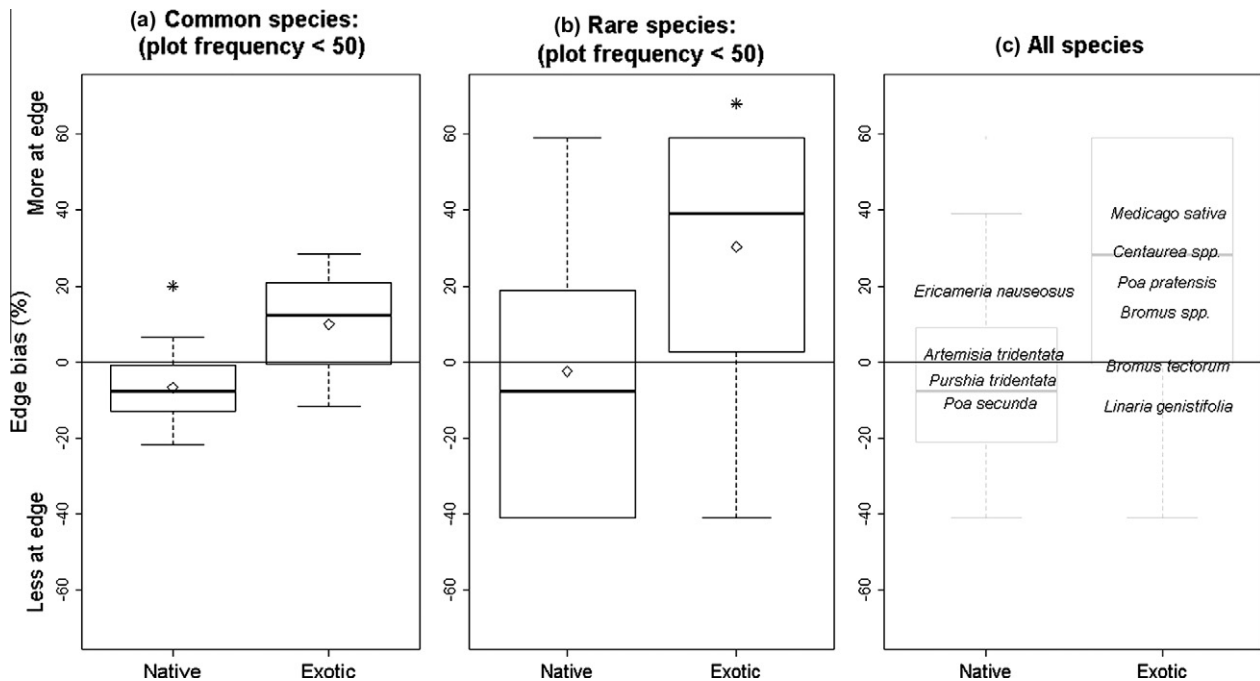


Fig. 3. Edge bias of presence/absence patterns for (a) common, (b) rare, and (c) all native and exotic species. Edge bias indicates the percent difference between observed frequency within 25 m of the edge and the expected frequency in the absence of edge effects (details in Section 2.5.3). Diamonds indicate the mean for each edge type, while the boxplots show the median, quantiles and maxima/minima of the data for each edge treatment. Asterisks indicate means that are significantly different than zero.

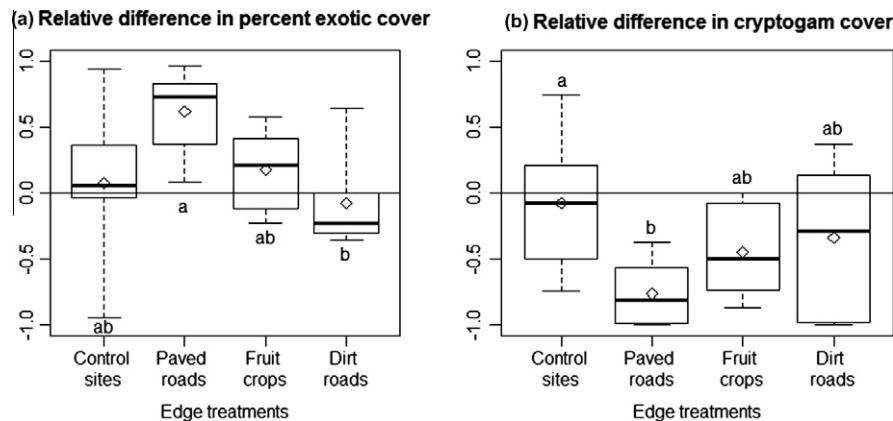


Fig. 4. Relative differences between the edge and interior of each site for (a) percent exotic cover and (b) cryptogam cover. The relative difference is the difference between values at the edge versus interior, divided by the maximum of the two values, with a value of ± 1.0 indicating that either the edge or the interior had no cover for that variable. Diamonds indicate the mean for each edge type, while the boxplots show the median, quantiles and maxima/minima of the data for each edge treatment. Letters indicate significant differences in the mean ($\alpha = 0.05$).

Table 2

The results of variation partitioning for sites where soil was sampled (four sites per edge type), and where NCAV showed significant nonlinear community change with distance from edge. Soil environmental factors used in variation partitioning were those from the best model selected in all subsets regression (Table 1).

| Edge type | Total variance explained by distance and environment (%) | Variance explained by distance alone (%) | Variance shared by distance and environment (%) | Variance explained by environment alone (%) |
|--------------------------|--|--|---|---|
| Paved road ($n = 3$) | 86 | 11 | 70 | 5 |
| Fruit crop ($n = 4$) | 50 | 11 | 24 | 15 |
| Dirt road ($n = 2$) | 42 | 20 | 22 | 0 |
| Control site ($n = 1$) | 63 | 0 | 47 | 16 |

than at control sites (-0.07 ± 0.53 , $t = -2.99$, $P = 0.022$). Cryptogam cover at the edges of fruit crops (-0.45 ± 0.35) and dirt roads (-0.34 ± 0.58) appeared to be lower than in the interior, but was not significantly different than the natural variation at control sites (fruit crops: $t = -1.44$, $P = 0.184$; dirt roads: $t = -0.83$, $P = 0.425$). However, cryptogam cover at the edges of fruit crops was consistently less than in the interior of the same sites ($t = -3.12$, $P = 0.026$).

Most other measures of community structure did not change from edge to interior any more at the edge sites than between plots at opposite ends of control transects (Appendix D). The mean relative difference in species richness ($F_{3,22} = 0.994$, $P = 0.414$), percent bare ground ($F_{3,22} = 1.577$, $P = 0.223$), and percent litter cover ($F_{3,22} = 0.627$, $P = 0.605$) were not significantly different between edge sites and control sites. However, the cover of bare ground was greater at the edge than the interior at all paved roads ($t = -3.71$, $P = 0.008$), and all but one of the dirt roads ($t = -1.53$, $P = 0.187$).

3.3. Relationships between the soil environment and community composition

Three of four paved road sites, four of four fruit crop sites and two of four dirt road sites where the soil environment was analyzed showed significant nonlinear relationships between community composition and distance from edge in NCAV (see Section 3.1). One of the four control sites where the soil environment was analyzed also had a significant nonlinear composition–distance relationship. For these sites, all-subsets regression suggested that the soil factors that best explained the variation in plant community

composition were the soil pH and Cu/Mn factors at paved roads, soil pH and mineralizable nitrogen at agricultural sites, and soil resistance (compaction) at dirt roads, while the nonlinear gradient seen at the control site was most related to changes in soil texture and some mobile cations (Table 1b–e). All factors related to compositional change were increased at edges, except Cu and Mn, which showed variable responses to edge, and were especially high at one control site (data not shown).

For developed edges, a small but significant proportion of the edge-related change in community composition was related to distance from edge independently of the best fit soil factors (Table 2). Conversely, community change at the control site was not directly related to distance independently of the soil environment. The largest portion of variation was shared between distance and environment. A small proportion of community variation was also related to the soil environmental factors independently of distance from edge, except at the dirt road sites. For dirt roads, the community variation explained by the soil factor with the best fit, soil resistance, was completely related to distance from the edge. However, only 42% of the total variation in plant community composition at dirt roads was explained by this one factor and distance from edge together.

4. Discussion

We addressed two important questions concerning edge effects: what is the relative effect of different types of human-induced edges, and how strong are these effects compared to natural variability? Our examination of grassland edges revealed that clear edge effects are present, and although there is considerable variability from site to site of a given type, the frequency and strength of edge effects are related to the type of adjacent development. Furthermore, both soil environmental drivers and direct propagule pressure from the edge likely affect plant community changes at developed edges.

4.1. Documenting edge effects in grasslands

Grassland communities were impacted in multiple ways at developed edges. These changes included shifts in species composition, decreased cryptogam cover, increased bare ground, and changes in the underlying soil chemistry. Common native species were significantly less frequent at edges than expected. Rare natives did not show a significant bias, but patterns may be masked by the higher frequency of extreme bias values for rare species.

However, rare exotic species were significantly more frequent at the edge than expected, possibly because these rare species were newly established, while common exotic species had longer establishment time and further invasion into the interior so were not significantly edge biased.

The majority of edge-related changes in the grassland plant community occurred within 25–30 m of developed edges. In 1–3 ha patches of remnant grassland, the reduction in effective patch size for edge-sensitive species is substantial. Edge effects of this extent would influence the vegetation in at least half of small patches. While protected areas in the south Okanagan are currently much larger, mostly 100 ha (Wikeem and Wikeem, 2004), affected grassland within 28 m of the edges would still equate to at least 10% of the total area. If these edge-affected areas are degraded by pollution or replacement of native flora by weedy exotic species, then the changes in plant community could have cascading effects in other groups of organisms.

4.2. Variability and edge effects

The extent of an edge effect can be altered by many factors, including slope, wind direction, and aspect (e.g., Bernhardt-Romermann et al., 2006; Cadenasso et al., 1997; Gelbard and Belnap, 2003). Some edge effects are expected to increase over time (Gascon et al., 2000), and permeability of the edge also influences how far edge effects can penetrate into the surrounding areas (Cadenasso and Pickett, 2001). In our system edge effects were common, but the effects at different edge types, and at each site, were highly variable. For example, although invasive species were commonly more frequent at edges, the identity of the species differed from site to site. Our results support the recommendations of Harper et al. (2005) that edge effect studies should compare different edge types and also observed edge effects versus natural variation in the interior of study communities.

4.3. Edge types determine edge effects

Paved roads had the strongest influence on grassland composition, and fruit crop sites showed more edge effects than were seen at dirt roads. At paved roads, significant shifts in community structure were evidenced by the high frequency of nonlinear edge responses in plant composition, reduced cryptogam cover, the increased proportion of exotic plant species, and increased bare ground. Species composition adjacent to fruit crops also frequently showed nonlinear change, as well as significant decreases in cryptogam cover. While the relative difference in cover of exotic species at fruit crops did not exceed differences at control sites, effects at fruit crops were intermediate to the effects seen at paved roads and dirt roads. Dirt roads showed relatively few effects on community composition, but did show a significant increase in bare ground. These results support the idea that the magnitude and frequency of effects at different edge types are predictable by the patch contrast between the developed area and the natural habitat (Cadenasso et al., 2003; Franklin, 1993; Harper et al., 2005).

In addition to the strength of edge effects, the particular composition of plant communities may be partially predicted based on the type of edge (Aavik et al., 2008; Godefroid and Koedam, 2004). For example, the native grasses *Hesperostipa comata* and *Poa secunda*, and exotic species *Sisymbrium altissimum* and *Poa bulbosa* were each strongly correlated with nonlinear change at 3 out of 6 paved road sites. Generally, disturbance-tolerant exotic species were strongly correlated with changes at both types of roadsides, and some fruit crops. Although the identity of species involved in the edge effects varied among sites (Gieselman, 2010), knowing which species are primarily related to compositional

change is important for management strategies at individual sites, or general edge types within a region.

4.4. Drivers of edge-related change

Ries et al. (2004) proposed that sessile organisms like plants are primarily influenced by edges through movement of energy, materials, or organisms across the edge. Our variance partitioning showed that for all developed edges, a significant proportion of community variation was related to distance from the edge independently of the soil environment, which suggests that direct effects such as invasion of exotic species were important. However, we also found that much of the compositional change was explained by a few key soil factors, demonstrating that the abiotic environment contributed to edge effects.

The factors most related to plant community change at each edge type were generally expected to be altered at those edges (e.g., pH and heavy metals at paved roads are influenced by particulates from automobile exhaust and wear, as well as road construction and maintenance practices). However, the variable nature of the Cu/Mn levels observed at paved roads and control sites suggests that these metals were also influenced by something other than roads. Soil pH and N content were expected to change in areas influenced by agricultural sites using fertilizers and pesticides, and soil compaction can increase along dirt roads due to increased traffic. These exogenous inputs are likely to affect plant germination and survival, which can in turn alter community composition.

Interestingly, we observed changes in composition in nonlinear models, but no significant change in species richness with distance to edge, which suggests that interior species were replaced at the edge, often by exotic species. Dutoit et al. (2007) also reported compositional change without differences in species richness at field boundaries, while others observed variable responses in species richness along transition zones (Kiviniemi and Eriksson, 2002; Lawes et al., 2005; Marchand and Houle, 2006). The fact that some control sites had exotic species concentrated at one end of the transect suggests a patchy distribution of exotics. Previous studies have found similar patterns, with increased exotic cover in grasslands at the edges of roads, but also some interior invasion (Cilliers et al., 2008; Tyser and Worley, 1992).

It was expected and shown that control sites do not show as many nonlinear effects as sites at edges, which quickly reduced the data available for use in the variance partitioning analysis. However, we were able to see that when nonlinear patterns were present at control sites, they appear to be related to different factors than the changes at edges. Some of the community change near edges was related to the distance from edge independent of the soil environment at edge sites, while none of the change at the control site could be attributed to distance alone. The latter result suggests that the nonlinear response at this site was due to a natural soil gradient, while the nonlinear responses at developed edges were due in part to some direct influence from the edge. In addition, the soil factors most related to community change at edges were different than those observed at the control site.

5. Conclusions

Edge-related shifts in grassland community structure were detected at developed edges, particularly at paved roads. The effects were larger and more frequent at edge types with higher contrast to the grassland, and some edges had greater effects than natural gradients. Shifts in community composition at developed edges generally manifested through replacement of native species with exotic species. However, the soil environment and the cover of

cryptogamic crust were also significantly altered at developed edges. Our study demonstrates that by comparing different edge types to control sites one can estimate the magnitude of the changes. NCAP may be an especially useful tool for modeling edge effects given multivariate and nonlinear patterns.

With increasing habitat loss and fragmentation in this region, the extent (25–30 m) and nature (e.g., increasing exotics) of edge effects is clearly cause for concern to managers, in that core habitat may be effectively reduced by more than 50% in small fragments (a few hectares) and 10% or more even in large fragments. At a regional level, habitat maps used to prioritize conservation efforts (e.g., designation of protected areas, restoration efforts) will need to discount the value of areas close to edges, especially paved roads. For highly localized decision making (e.g., where to situate trails within an existing park) the high variability of edge effects and natural heterogeneity in species composition point to the need for site-specific studies to evaluate the most suitable location for different activities. Long-term studies will be needed to determine if the edge effects we observed are stable, or whether their extent and magnitude increase over time.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.08.019>.

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Glossary

- Cryptogamic soil crust*: biological crust of fungi, algae, moss, lichen, and microbes that covers the surface of the soil
- Edge-effect*: a systematic change in the community composition or environment as a function of distance from the edge of a habitat patch
- Extent of edge influence*: the distance from the edge within which 90% of the change in community occurred
- Particle size distribution (PSD)*: the relative amount of soil particles in three size classes: sand (2–0.05 mm), silt (0.05–0.002 mm) clay (<0.002 mm)