

Interaction of edge influence from multiple edges: examples from narrow corridors

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Abstract The simultaneous influence from multiple edges on remnant forest patches (such as wildlife corridors, protection buffers, small unharvested remnants or corners of larger patches) in harvested forest landscapes could impair, or possibly enhance, their effectiveness. When multiple edges are in close proximity, there may be interactions of edge influence such that the observed response is greater or less than would result from the influence of either edge alone. We examined possible ways in which two nearby forest edges of similar or different types might interact in terms of their influence on forest structure. We present an ‘edge interaction’ model for three possible types of interaction of edge

influence: (1) no interaction, edge influence is limited to the strongest influence from either edge, (2) positive interaction, observed edge influence is greater than from either edge alone; (3) negative interaction or resistance, the influence from both edges is less than from a single edge (e.g., an older edge is resistant to effects from a younger edge). Empirical data for forest structure at the edges of cutblocks (harvested areas) and water bodies were entered into the models to predict edge influence in narrow forest corridors assuming the null hypothesis of no interaction. Randomization tests were used to compare predictions to observed edge influence on recently-fallen logs and *Populus* spp. (*P. tremuloides* Michx. and *P. balsamifera* L.) sapling density in lakeshore buffers in boreal mixedwood forest as well as on canopy cover and log, tree and snag abundance in riparian buffers and forested corridors separating cutblocks in *Picea mariana* (Mill.) BSP. forest. In lakeshore buffers, there was evidence of both positive and negative interaction at different locations within the buffer or at different times since buffer creation for both the abundance of logs and *Populus* sapling density. Trends suggested positive interaction for canopy cover and live tree density in riparian buffers and cutblock separators, and for snag density near the cut edges of riparian buffers. Testing hypotheses arising from our model of interaction of edge influence could

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lead to a clearer understanding of edge influence in fragmented landscapes.

Keywords Fragmentation · Forest corridors · Multiple edge effects · Riparian buffers · *Populus* saplings · Windthrow

Introduction

The influence of the adjacent non-forest environment on forest structure and species composition at forest edges is now widely recognized (Murcia 1995; Matlack and Litvaitis 1999; Harper et al. 2005). Many studies have documented abiotic and biotic responses to edge creation in forest landscapes including changes in microclimate, structural damage to the canopy, accelerated growth and recruitment of woody plants, and changes in plant community composition (e.g., Chen et al. 1995; Laurance et al. 1998; Burton 2002; Harper and Macdonald 2002a). Edge influence typically declines with distance from the non-forest area; the nature of the forest ecosystem itself along with a variety of local and regional factors determine how far edge influence penetrates into the intact forest (Harper et al. 2005). In heterogeneous or fragmented landscapes, where edge density is high, many locations could be close enough to two or more edges such that they may experience simultaneous influences from multiple edges (Euskirchen et al. 2006). The zone of ‘close proximity’ to multiple edges includes any area in which the distance of edge influence from two or more edges could overlap; the specific distance will vary with ecosystem type and response variable. Any attempt to quantify edge effects or the area of edge influence in fragmented landscapes thus requires an understanding of the nature of ecosystem responses to multiple edges (Ries et al. 2004).

When two edges are located in close proximity, their combined influence may be such that the observed response is greater or less than would result from the influence of either edge alone (Ries et al. 2004). A few studies have considered approaches for inclusion of edge influence from multiple edges in close proximity (e.g., Fletcher 2005), but empirical evidence has been lacking

(Ries et al. 2004). Malcolm (1994), and subsequently Fernández et al. (2002), conceptualized an approach which included additive effects in models that considered total edge influence as the sum of edge influence from all nearby edges, while Zheng and Chen (2000) used a similar additive approach to quantify the area of edge influence in fragmented landscapes. Mancke and Gavin (2000) assessed distance to edge using distances to four nearby edges rather than only one edge for plots located within woodlots. These studies have all assumed that influences from multiple edges would be stronger than from a single edge. However, there are some patch configurations in which we might observe weaker edge response close to multiple edges than would be observed an equal distance from a single edge (see Ries et al. 2004). One example is that trees that have grown near an inherent edge such as a wetland-forest boundary could be windfirm and therefore resistant to additional influence from a subsequently created edge. One study demonstrated that trees can become windfirm through increased root growth following exposure to wind, thereby helping to stabilize the trees (Urban et al. 1994).

Possible interaction of influence from multiple edges is particularly important in corridors or small forested remnants in harvested forest landscapes. Narrow forest strips are often left between harvested areas to provide dispersal or movement corridors for wildlife (Debinski and Holt 2000), to serve as a seed source or because of restrictions on the size of harvested areas. Forested buffers around water bodies are maintained following timber harvest or agricultural development to protect aquatic ecosystems (Lowrance et al. 1984; Peterjohn and Correll 1984; Gregory et al. 1991; O’Laughlin and Belt 1995) and riparian habitat (Pearson and Manuwal 2001; Hylander et al. 2002), and they may also provide wildlife habitat and help to maintain connectivity across the landscape (Castelle et al. 1994; Brosnoff et al. 1997; Hannon et al. 2002). Lakeshore buffers are influenced by a natural lakeshore edge and a cut edge, whereas riparian buffers along small streams are influenced by cut edges on two sides. Edge influence from these multiple edges could seriously impair, or possibly enhance, the

effectiveness of these forested buffers adjacent to water bodies.

Herein, we present a simple model that describes possible interactions of edge influence that might be observed at locations in a forest landscape that are in close proximity to two edges. Based on this model, randomization tests can be used to test a null hypothesis of no interaction of edge influence. We used empirical data from lakeshore buffers in boreal mixedwood forest and from riparian buffers and cutblock separators (narrow corridors of unharvested forest between harvested areas) in *Picea mariana* (Mill.) BSP. forest in order to explore which type of edge interaction is operating.

Methods

A general model of edge interaction

We present a general conceptual ‘edge interaction’ model which includes three alternatives for the interaction of influences from two edges. This model is for a given location close to two edges and can be applied to any response variable for which we know there to be significant edge influence at a similar distance from a single edge. The three possibilities for interaction of edge influence are as follows:

- (1) No interaction: edge influence is from one edge only, whichever has the strongest influence (i.e., this is the null hypothesis).
- (2) Positive interaction: observed edge influence is greater than from either edge alone.
- (3) Negative interaction or resistance: observed edge influence is less than from either edge alone.

The first two alternatives apply to any situation where two edges are in close proximity, for example, in a narrow corridor or near two sides of a forest remnant. We consider no interaction as the null hypothesis because the response variable will have the same values at equivalent distances from single edges as from multiple edges. The ‘no interaction’ alternative is likely if the influence of one edge is so strong that it preempts additional

response from the second edge. For example, an understory species that is completely eliminated or increases to a cover of close to 100% due to the effects of one edge would be unlikely to be affected further by a second edge.

Positive interaction might be observed as a result of increased light, wind and other microclimatic changes owing to effects from edges on two sides. In this situation, there might be greater potential for damage to canopy trees and snags; and there might also be greater shrub and understory development than would be observed due to the influence of a single edge. For example, the growth of regenerating saplings might increase in response to greater light received as a result of two nearby openings more than it would in response to light from a single edge. Positive interaction may be considered a simple additive effect of influences from the two edges or as something more than additive (perhaps multiplicative). However, quantitative prediction of these different possibilities for positive interaction will depend on the metric used to quantify the magnitude of edge influence. In this paper, we focus on our general model with three alternatives that can be used for any metric for the magnitude of edge influence.

Negative interaction or resistance could occur in situations where one edge is older. If the forest has already responded to the effect of one edge, it could be resistant to additional influence when a new edge is created nearby. We would expect to see such resistance, for example, when trees surviving under exposed conditions at an older edge have become windfirm and are therefore resistant to blowdown following creation of another edge nearby. Also, an understory community that has adjusted to edge conditions might be resistant to the influence from another edge created nearby because competition precludes further changes in response to additional light or microclimatic changes. We might also see negative interaction at two edges of similar age if a response variable has a non-linear relationship with a driving factor. For example, a species might show increased growth with moderate increases in light but reduced growth with more extreme increases in light; the net effect of increased light from two edges could therefore lead to reduced

growth as compared to what would be seen near a single edge.

We can assess which type of interaction (none, positive or negative) is operating by comparing observed edge influence on a variable at a location near two edges ($e_{1,2}$) with that observed at equivalent distances from comparable single edges (e_1 and e_2):

$$\text{if } \text{abs}[EI_{1,2}] \begin{cases} = \max(\text{abs}[EI_1], \text{abs}[EI_2]) & H_0 \text{ (no interaction) cannot be rejected} \\ > \max(\text{abs}[EI_1], \text{abs}[EI_2]) & H_0 \text{ is rejected, combination is supported} \\ < \max(\text{abs}[EI_1], \text{abs}[EI_2]) & H_0 \text{ is rejected, resistance is supported} \end{cases}$$

where EI_1 = the edge influence on a variable at distance d_1 from e_1 ; EI_2 = the edge influence on a variable at distance d_2 from e_2 ; $EI_{1,2}$ = the edge influence on a variable at distance d_1 from e_1 and distance d_2 from e_2 ; $\max(\text{abs}[EI_1], \text{abs}[EI_2])$ refers to the edge influence at distance d_1 from e_1 or at distance d_2 from e_2 , whichever is stronger. We use absolute values for edge influence because it can be either negative or positive. Our model can accommodate any metric quantifying edge influence such as the average value at a given distance from the edge, the difference between edge and interior values (significance of edge effects, Chen et al. 1995), the edge to interior ratio (Burton 2002) or the standardized difference (e.g., magnitude of edge influence, Harper et al. 2005).

Data collected at different distances from single edges (along with data from appropriate ‘interior’ forest which may be required for some metrics of edge influence) can be used to quantify edge influence at different distances from single edges and subsequently predict the observed edge influence at different locations within a remnant patch or narrow corridor under the null hypothesis of no interaction. If sampling is not contiguous, data will need to be fit to a curve in order to estimate edge influence at distances that were not sampled. It is preferable to avoid curve fitting, if possible, since edge-to-interior trends may be

non-monotonic (Murcia 1995; Kapos et al. 1997; Harper and Macdonald 2001).

Observed edge influence for a given response variable at different distances from two edges in close proximity can be compared to predicted edge influence under the null hypothesis by using randomization tests (see below). It is also possible to test for interaction of edge influence by

sampling at the edges of corridors of different width. If edge influence right at the edge is similar among corridors of different width, the null hypothesis of no interaction cannot be rejected. When edge influence at the edge is stronger in narrower than in wider corridors, positive interaction is supported. Weaker edge influence right at the edge of narrower (versus wider) corridors provides evidence for negative interaction. These effects arise because there is a greater probability of overlap of edge influence from two edges at locations right near the edge of a narrower corridor than near the edge of a wider corridor.

Testing for interaction of edge influence in lakeshore buffers in *Populus* mixedwood

We tested for interaction of edge influence using empirical data from lakeshore buffers in *Populus*-dominated (*P. tremuloides* Michx. and *P. balsamifera* L.) boreal mixedwood forest in northern Alberta. We used previously-published data from 12 transects at lakeshore edges (Harper and Macdonald 2001) and 10 transects at 1- and 2-year-old cut edges (Harper and Macdonald 2002a) to quantify edge influence from single edges of the two types (lakeshore and cut edges). We chose two variables: the abundance of newly-fallen logs (>8 cm diameter and decay classes 1–3 out of 7, Lee et al. 1995) and *Populus* sapling

density (data from only 10 of the 12 lakeshore edge transects). Previous studies showed that edge influence was strong for both variables in this forest type at one or both edge types and that the distance of edge influence was such that edge influence from the two edges would likely overlap in 25 m buffers (Harper and Macdonald 2001, 2002a). We defined the edge at 0 m as the limit of the continuous forest canopy. We used previously-collected data from these single edges to predict edge influence at various locations within lakeshore forest buffers, which are bounded by a lakeshore edge on one side and a cut edge on the other, based on the null hypothesis of no interaction. Edge influence was positive for both variables (higher values near an edge than in the interior forest) and was quantified using data collected from adjacent interior forest (see Harper and Macdonald 2001, 2002a). Because we used the same interior forest data to quantify edge influence in the lakeshore buffers we were able to simply use actual values for the variables in our testing, rather than another metric of edge influence. Thus, the predicted value within the lakeshore buffer, at distance 1 from the lakeshore edge and distance 2 from the cut edge, was equal to the average value of the variable at distance 1 from the sampled lakeshore edges or at distance 2 from the sampled cut edges, whichever was larger. We did not have data for locations 15 or 25 m from the single cut or lakeshore edges (see Harper and Macdonald 2001, 2002a) so we used the values at 20 m to create the predicted values for 15 and 25 m from the two edge types in the lakeshore buffers.

Complementary empirical data on edge influence in narrow corridors were obtained from 1- and 3-year-old lakeshore forest buffers of 25 m width. These sampled lakeshore buffers surrounded one lake in northern Alberta in *Populus*-dominated forest in the same area where the lakeshore and cut edges were sampled (Harper and Macdonald 2001, 2002a). Sampling was conducted in 1997 and 1999, 1 and 3 years, respectively, after creation of the lakeshore buffers by harvesting of the adjacent forest. Most trees were removed in the cutblocks (harvested areas) with some residual patches and individual trees. We sampled along transects

which spanned the width of the forested buffers and were perpendicular to both the lakeshore and cut forest edges. Samples were collected along one transect each in three buffers (adjacent to three different cutblocks) at 0, 5, 10, 15, 20, and 25 m from the lakeshore edge (corresponding to 25, 20, 15, 10, 5, and 0 m from the cut edge) using the same methods that were used to collect the lakeshore and cut edge data (Harper and Macdonald 2001, 2002a). At each sampling distance, we tallied the number of pieces of recently-fallen logs intersecting a 20 m line parallel to the edge (size and decay class as described above). Within two 2 × 2 m subplots at either end of the 20 m line, we counted the number of *Populus* saplings <5 cm dbh. Data for *Populus* sapling density at the cut edge were not available for one 25 m buffer transect because harvesting did not always follow the prescribed edge exactly and data were collected post-harvest to match pre-harvest data.

We tested for a significant difference between predicted and observed values at each distance using randomization tests as follows. (1) We calculated the difference between the mean observed value in the buffer and the value predicted under the null hypothesis (mean value at the given distance from either the lakeshore or cut edge, whichever edge had the stronger edge influence), (2) We took the actual values at the given location in the buffer and those used to calculate the mean value under the null hypothesis (at the given distances from the lakeshore and cut edges) and randomized them between the three ‘treatments’ (buffer, lakeshore edge or cut edge), (3) We calculated the randomized difference as in step 1 but using the randomized values, (4) Steps 2 and 3 were repeated 5,000 times to create a distribution of 5,000 randomized differences, (5) When the observed difference (observed–predicted) lay at or above the 95th percentile within the distribution of randomized differences, we rejected the null hypothesis and concluded that positive interaction of edge influence was operating. When the observed difference lay at or below the 5th percentile within the distribution of randomized differences we rejected the null hypothesis and concluded that negative interaction was operating. Otherwise the null hypothesis could not be rejected

and we concluded there was no interaction. This procedure was followed for each of the sample years separately (1- and 3-year-old lakeshore buffers). Randomization tests were conducted using our own program written using the Visual Basic Editor in Excel (Microsoft Excel 2002; similar to the Critical Values Program, Harper and Macdonald 2002b).

We also tested for interaction of edge influence by comparing edge influence right at the lakeshore and cut edges separately (0 m) among lakeshore buffers of different widths (25, 100, 200 m; 1- and 3-years-old separately) using ANOVA with buffer width as a fixed factor followed by post-hoc Tukey tests when the results of the ANOVA were significant. These tests were conducted using SPSS version 13.0 for Windows (SPSS Inc. 2004). We used $\alpha = 0.10$ since we were more concerned about Type II error due to our small sample sizes. In addition to the 3 transects from 25 m buffers, we also had data from 5 and 4 transects from buffers of 100 and 200 m width, respectively, surrounding five additional lakes in northern Alberta (55° N, 112–114° W; for details see Harper and Macdonald 2001). Data for *Populus* sapling density were not available for one 25 m and one 100 m buffer transects because harvesting did not always follow the prescribed edge exactly. It was not possible to sample additional transects for the 25 and 200 m buffers because of a lack of lakes with these buffer widths. Data were collected in 1997 and 1999, 1 and 3 years, respectively, after creation of the buffers. Transects were approximately north–south oriented (+/–60°), and situated at least 100 m from each other and from other edges.

Testing for interaction of edge influence in stream buffers and cutblock separators in *Picea mariana* forest

We also tested for interaction of edge influence by examining forest riparian buffers and cutblock separators in boreal *Picea mariana* (Mill.) BSP. forest in northwestern Quebec (49° N, 76–77° W). For the initial quantification of edge influence, we used data on canopy cover, densities of live trees and snags (≥ 5 cm dbh), and the abundance of newly-fallen logs (≥ 5 cm diameter, decay classes 1

and 2, Maser et al. 1979) collected at different distances along 10 transects perpendicular to edges of 7–9 year old cutblocks (Mascarúa-López et al. 2005). Sampling was conducted in summer 2003 in contiguous 5 × 20 m plots (long axis parallel to the forest edge). Edge influence was positive for abundance of newly-fallen logs and thus, the predicted value within a narrow corridor was calculated as described above. Edge influence was negative for canopy cover and density of live trees and snags (i.e., lower values at the edge than in interior forest). Thus, the predicted value within a narrow corridor, at distance 1 from one edge and distance 2 from the other edge, for these variables was equal to the average value of the variable at distance 1 or distance 2 from a cut edge, whichever was smaller.

Complementary empirical data on edge influence in narrow corridors were obtained from 5–8 year old linear forest corridors separating cutblocks and 7–11 year old riparian buffers surrounding small streams (Mascarúa-López et al. 2006). The empirical data were collected in 2003 along transects that spanned the width of ten 60 m wide cutblock separators and ten 45–75 m wide riparian buffers in the same study area where the cut edges were sampled. Transects in cutblock separators were mostly oriented southeast–northwest, while transects in riparian buffers had a variety of orientations (Mascarúa-López et al. 2006). The response variables and sampling protocol were the same as above. Two plots were sampled at every distance from the edge in the linear corridors, data from these two plots were averaged for each distance. Observed and predicted values were compared using the randomization tests as described above. For canopy cover and density of live trees and snags, for which there was negative edge influence, positive interaction was supported when the observed difference (observed–predicted) lay at or below the 5th percentile within the distribution of randomized differences (i.e., observed value was lower than predicted); negative interaction was supported when the observed value lay at or above the 95th percentile within the distribution of randomized differences (i.e., observed value was higher than predicted).

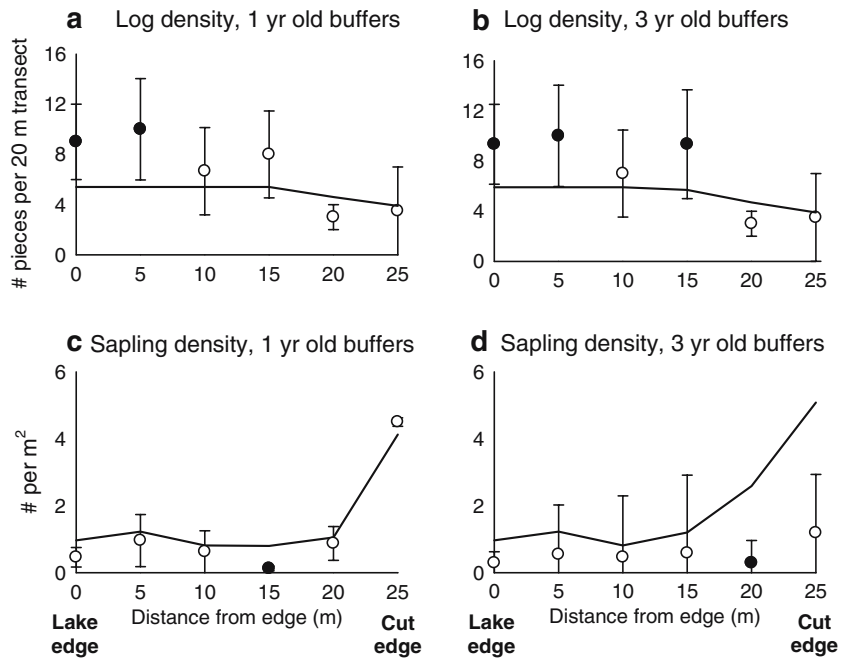


Fig. 1 Predicted values based on the null hypothesis of no interaction (solid line) and mean observed values (circles with standard error bars) in lakeshore buffers of 25 m width for: log density in (a) 1- and (b) 3-year-old buffers, and *Populus* sapling density in (c) 1- and (d) 3-year-old buffers.

Predicted values were the values at the comparable distance(s) from lakeshore or cut edges, whichever had a stronger edge influence in the absence of other edges. Observed values that were significantly different from predicted values are filled circles. $n = 2$ or 3 for empirical data

Results

Lakeshore buffers in the boreal mixedwood forest

Log abundance was greater at the lakeshore edge as compared to elsewhere in the buffer in both

years post-harvest (Fig. 1a, b). At the two closest distances to the lakeshore edge, log abundance was significantly greater than predicted by the null hypothesis in both years; it was also significantly greater than predicted at a distance of 20 m from the lakeshore edge in the 3-year-old buffers. Thus, in these cases the null hypothesis

Table 1 Results of analysis of variance comparing log density and *Populus* sapling density right at lakeshore and cut edges (0 m) among buffers of different widths (25, 100 and 200 m) 1 and 3 years following harvesting

Edge	Variable	Time since harvest (year)	Sample size	F	P
Lakeshore	Log density	1	14	2.947	0.094
Lakeshore	Log density	3	14	3.144	0.083
Lakeshore	<i>Populus</i> sapling density	1	11	0.489	0.630
Lakeshore	<i>Populus</i> sapling density	3	11	0.736	0.509
Cut	Log density	1	12	2.449	0.142
Cut	Log density	3	12	2.552	0.132
Cut	<i>Populus</i> sapling density	1	10	2.229	0.172
Cut	<i>Populus</i> sapling density	3	10	0.400	0.685

Given are the F value and significance (P-value) for the test of differences between buffer widths

Fig. 2 Mean values right at the lake edge (0 m) of forested lakeshore buffers of different widths for: log abundance in (a) 1- and (b) 3-year-old buffers, and *Populus* sapling density in (c) 1- and (d) 3-year-old buffers. $n = 2, 5$ and 4 plots for 25, 100 and 200 m buffers, respectively, in (a) and (b); and $n = 2, 4$ and 4 plots for 25, 100 and 200 m buffers, respectively, in (c) and (d). In (a) and (b) means with the same superscripted letter are not significantly different at $P = 0.10$

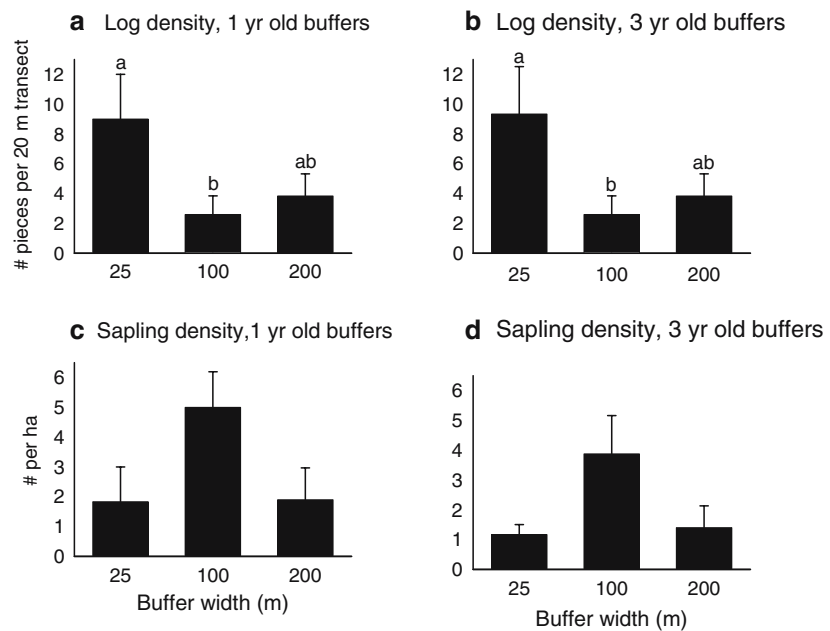
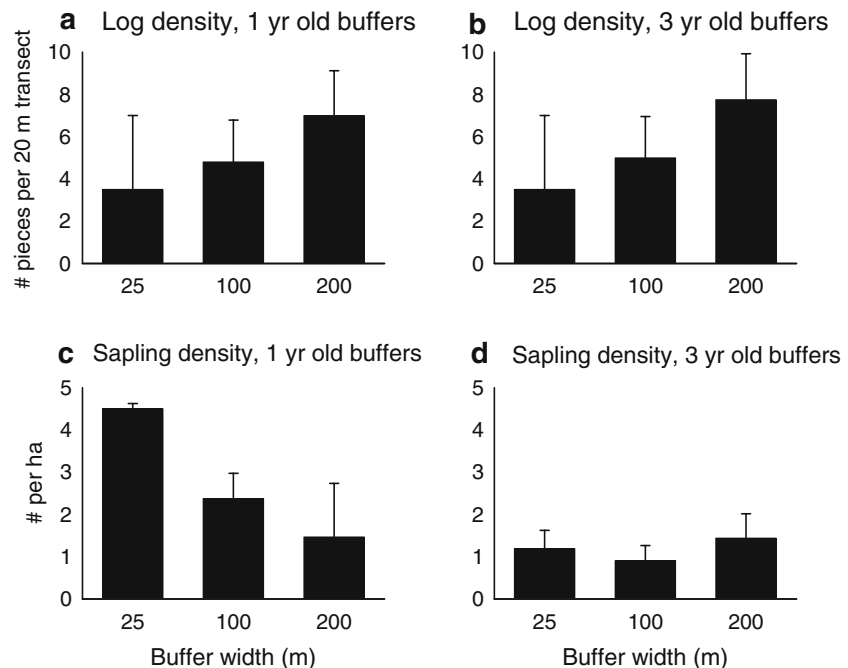


Fig. 3 Mean values right at the cut edge (0 m) of forested lakeshore buffers of different widths for: log abundance in (a) 1- and (b) 3-year-old buffers, and *Populus* sapling density in (c) 1- and (d) 3-year-old buffers. $n = 2, 5$ and 4 plots for 25, 100 and 200 m buffers, respectively, in (a) and (b); and $n = 2, 4$ and 4 plots for 25, 100 and 200 m buffers, respectively, in (c) and (d)



was rejected and the results support the idea that positive interaction of edge influence was operating. Positive interaction was also supported by the fact that log density was significantly greater right at the lake edge of 25 m lakeshore buffers than in 100 m buffers in both years (Table 1, Fig. 2a, b).

Although not significant, the lower number of logs near the cut edge of the lakeshore buffers (Fig. 1a, b) and at the cut edge of narrower (versus wider) buffers (Table 1, Fig. 3a, b) suggests that negative interaction could be operating.

Populus sapling density was significantly lower than predicted at 10 m from the cut edge in 1-year-old buffers and at 5 m from the cut edge in 3-year-old buffers; thus in these cases there was evidence of negative interaction (Fig. 1c, d). Otherwise observed values for sapling density within the lakeshore buffers were similar to those predicted under the null hypothesis of no interaction. There were no significant differences in sapling density right at the lakeshore edge among buffers of different width (Table 1, Fig. 2c, d). Sapling density right at the cut edge was greater in narrower (versus wider) buffers suggesting positive interaction of edge influence, but this difference was not significant and was evident only for 1-year-old buffers (Table 1, Fig. 3c, d).

Cutblock separators and riparian buffers in *Picea mariana* forest

There were no significant differences between observed values and those predicted under the null hypothesis of no interaction for the four response variables in riparian buffers or cutblock separators (Fig. 4). Thus, we cannot reject the null hypothesis of no interaction. We did note,

however, a few trends that suggest some possible interactions of edge influence. Canopy cover in both types of corridor was always lower than predicted; as canopy cover had negative edge influence this suggests possible positive interaction of edge influence, although it was not significant (Fig. 4a). In addition, there was some suggestion of positive interaction of edge influence for snag density in riparian buffers as snag densities at most locations were substantially lower than predicted by the null hypothesis (Fig. 4c). There were also notable differences between the two types of corridors, such as greater live tree density in riparian buffers compared to cutblock separators at 10 and 15 m from the cut edge (Fig. 4b).

Discussion

Evidence of interaction of edge influence

Overall we found little evidence of interaction of edge influence, particularly for the riparian buffers in *Picea mariana* forest. There are several reasons why we may have failed to detect

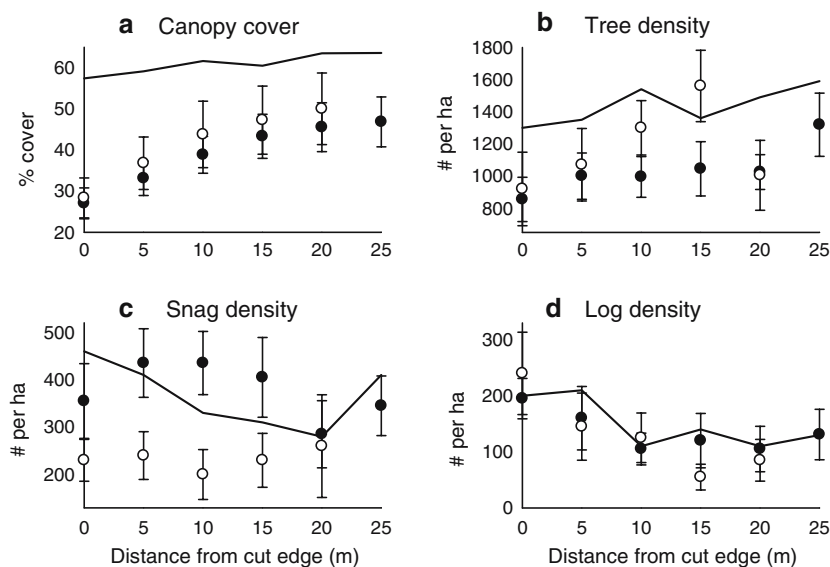


Fig. 4 Predicted values based on the null hypothesis of no interaction (solid line) and mean observed values in 60 m wide cutblock separators (filled circles with standard error bars) and 45–75 m wide riparian buffer strips (open circles with standard error bars) for: **(a)** canopy cover, **(b)** live

tree density, **(c)** snag density and **(d)** log density. Predicted values were the values at comparable distance(s) from a cut edge in the absence of other edges. No observed values were significantly different from predicted values. $n = 10$ for empirical data

interaction of edge influence: (1) too small a sample size for the data sets for the single edges, (2) too small a sample size for the data sets for the corridors, (3) variation in edge influence due to edge aspect, or (4) there is no interaction of edge influence. We think that our sample sizes were adequate for riparian buffers but not for lakeshore buffers; unfortunately it was impossible to obtain more samples of the narrow lakeshore buffers in our study area. Still, we did obtain significant results for lakeshore buffers and we feel that other apparent trends that suggest possible interactions of edge influence warrant further testing with larger sample sizes. We did not take edge aspect into account when testing our models because previous attempts to quantify the influence of aspect on edge influence showed little effect in the boreal mixedwood forest (Harper 1999) and we did not have sufficient data from cut edges of different orientations in *Picea mariana* forest (Mascarúa-López 2005). Mascarúa-López (unpublished data) did find an effect of aspect on edge influence for riparian buffer strips in our study area; edge influence on live tree density and log abundance was stronger and more extensive at wind-exposed edges than wind-protected edges. Since our cut edges were mostly wind-exposed (Mascarúa-López et al. 2006), our predicted values for edge influence were likely stronger than may have been expected in the sampled corridors, which included a variety of edge orientations. This would have made it less likely to reject the null hypothesis and support positive interaction.

For lakeshore buffers in the boreal mixedwood forest we found evidence for both types of interaction of edge influence. Randomization tests supported positive interaction of edge influence for the density of newly-fallen logs near the lakeshore edge in buffers. For narrow buffers, however, weaker edge influence for the creation of newly-fallen deadwood near the cut edge (especially compared to wider buffers) suggests that lakeshore forest may be resistant to the effects of the creation of a cut edge. Natural lakeshore edges are characterized by low densities of canopy trees and snags and high amounts of downed wood (Harper and Macdonald 2001). Resistance could, therefore, arise because

canopy trees near the lakeshore edge have either already fallen or have become windfirm and are therefore resistant to blowdown from increased wind associated with the creation of the nearby cut edge. However, blowdown can also be extensive following increased wind penetration in narrow buffers, especially if trees closer to the lakeshore are more shallowly-rooted. Indeed, we observed almost complete canopy blowdown in some (unsampled) narrow lakeshore buffers in our study area. There may be some threshold edge influence in these narrow buffers such that they are resistant to cut edge influence up to a point; however, if wind effects exceed a certain threshold resistance will be overcome and positive interaction of edge influence will be observed.

Our results provided some suggestion that positive interaction of edge influence could be operating for saplings right near the cut edge of the lakeshore buffers for the first year after buffer creation. The increased light and temperature and removal of mature stems of this clonal species which follow creation of the cut edge could result in increased vegetative reproduction of *Populus*. There was little evidence for positive interaction of edge influence by the third year following buffer creation, perhaps due to shading from regeneration in the adjacent harvested area (Harper and Macdonald 2002a). Indeed, there was even some evidence of negative interaction (resistance) at the cut edge in the third year (Fig. 1d). Since lakeshore edges already have high sapling density (Harper and Macdonald 2001), there may be a limit to the amount of further suckering of *Populus* that would result from the creation of the cut edge. Also, suckering could be limited by higher soil water content, colder soil temperatures and/or competition from the well-developed tall shrub layer near the lakeshore edge. The change in the nature of interaction of edge influence from positive in the first year to negative in the third year may be due to growth and self-thinning which, after a few years, may result in similar sapling density and height as before the creation of the cut edge.

We expected to see evidence of positive interaction of edge influence on canopy cover and live tree and snag density in cutblock

separators in the *Picea mariana* forest due to increased wind exposure in these narrow corridors. The trends in the data supported this but the differences were not statistically significant. We saw less evidence of positive interaction of edge influence in riparian buffers than in corridors. Although riparian buffers are also exposed to two cut edges, the presence of a stream running through the middle of the buffer likely influences forest structure and the response of that forest to edge creation. Indeed, riparian forest near streams may be more resistant to effects of edge creation for this reason. Unfortunately, we did not have data for continuous forest surrounding streams; however, we know that riparian forest near streams had similar densities of live trees to adjacent ‘interior’ forest (Mascarúa-López 2005). Thus, the slightly higher tree densities in riparian buffers, as compared to cutblock separators, cannot be considered an inherent characteristic of riparian forest. Instead, it could be that trees growing near the inherent edges of the stream have developed resistance to influence from cut edges as a result of their adaptation to an edge environment associated with a small break in the canopy along the stream course. As a result, these narrow riparian buffers around small streams may be more effective as reserves of mature forest than are cutblock separators (Mascarúa-López et al. 2006). Pre-post harvest comparisons are required to clarify the factors leading to the observed higher densities of live trees in riparian buffers.

Model application and further development

The main contributions of our model are the introduction of the concept of negative interaction of edge influences (or resistance) and a null hypothesis against which we can test for evidence of either positive or negative interaction. Both positive and negative interactions may be operating simultaneously for a given response variable at different distances within a patch or corridor. Such an effect might be seen for a variable that has a non-linear response to some driving factor that is associated with the edge (as described above for resistance) in a corridor with north-facing and south-facing edges. Growth of

an understory plant, for example, might respond differently at north-facing edges compared to south-facing edges because of differences in light or moisture or because of competition from other species. For example, greater reduction in bryophyte growth was found at south-facing compared to north-facing edges (Hylander 2005). Further, we suggest that both positive and negative interaction could be operating simultaneously for a given response variable at a given distance within a patch or corridor. For example, in a forest near an older edge and a nearby newly created edge, resistance observed near the older edge may decline with distance from that older edge because it is tempered by positive interaction operating near the newly-created edge. In effect, these opposing interactions of edge influence may occur in varying degrees such that they sometimes cancel each other out. In such situations negative or positive interaction may only be detectable when it is much stronger than the other.

Positive interaction of edge influence is an assumption of Malcolm’s (1994) theory, in which edge influence at any given point would be the sum of edge influence from both edges. Other studies have reported edge effects which might be due to positive interaction. For example, Everson and Boucher (1998) found a negative correlation between tree species richness and the width of the riparian zone. The greater windthrow observed by Ruel et al. (2001) and lower total bird abundance found by Shirley and Smith (2005) in narrower (versus wider) buffers and the observation of greater edge influence on colonization at concave boundaries (Hardt and Forman 1989) could be other examples. Fletcher (2005) provides one of the few studies that specifically tested and found empirical evidence of positive interaction, specifically for the Bobolink (*Dolichonyx oryzivorus*), a bird species associated with open habitats. In another example of positive interaction, Benítez-Malvido and Martínez-Ramos (2003) found that proximity to a greater number of edges resulted in lower tree recruitment. Hibbs and Bower (2001) found little effect on plant community composition or dynamics following buffer formation, suggesting resistance to edge creation.

Differences in edge influence with edge aspect (e.g., Palik and Murphy 1990; Fraver 1994; Zheng and Chen 2000; Hylander 2005) could be incorporated into the application of our model by adjusting predicted values for aspect. Thus, predicted edge influence (with no interaction) would differ for a corridor with east- and west-facing edges as compared to one with north- and south-facing edges.

Our model could be used to determine which type of interaction is operating for different response variables and this could be helpful in further testing the underlying mechanisms of edge influence. The model could also be used to determine under what conditions (e.g., aspect, slope) edge influences interact. As our results show, using the model at different ages of edge allows an assessment of changes in edge interaction along a temporal gradient. Testing the null hypothesis of no interaction right at the edge in corridors of different widths may be an easier way to determine the type of interaction of edge influence, especially since it would allow larger sample sizes for similar effort.

An important consideration for the conservation of biodiversity within fragmented landscapes is the determination of the area influenced by the edge environment. Indeed, interaction of edge influence primarily occurs in highly fragmented landscapes (Malcolm 2001; Fletcher 2005). Positive or negative interaction could result in an expansion or reduction in the area of edge influence, respectively. For example, Fletcher (2005) found evidence of an increase in the distance of edge influence with multiple edge effects, which would result in a greater area of edge influence. The interaction model could be applied in buffers, other narrow corridors, or stepping stones of small patches in fragmented forested landscapes (Bennett 1998) in order to determine the area of edge influence. At the landscape level, interactive edge effects within narrow corridors and small patches could significantly affect forest structure, thus impacting their role in the landscape.

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