



Factors driving structure of natural and anthropogenic forest edges from temperate to boreal ecosystems

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Keywords

Agricultural edge; Boundary abruptness; Clear-cut edge; Climate; Edge influence; Edge length; Lakeshore edge; Land use; Linear disturbance edge; Patch contrast; Tree species; Wetland edge

Nomenclature

Mossberg et al. (1992)

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Introduction

Transition zones between adjacent ecosystems in forested landscapes constitute ubiquitous landscape elements and have received much attention, particularly in studies of land transformation processes and edge influence (Ries et al. 2004; Harper et al. 2005; Ewers & Didham 2006; Laurance et al. 2011). Numerous studies have shown that

edge influence (edge effects) from land-use changes is one of the most important drivers of species loss in fragmented forests across the globe through processes such as higher nest predation, elevated tree mortality and invasion of alien species (Lindenmayer & Fischer 2006; Broadbent et al. 2008; Haddad et al. 2015). Transitions have important functions in both natural and human-modified landscapes by providing habitat and affecting ecological flows

Abstract

Questions: What factors control broad-scale variation in edge length and three-dimensional boundary structure for a large region extending across two biomes? What is the difference in structure between natural and anthropogenic edges?

Location: Temperate and boreal forests across all of Sweden, spanning latitudes 55–69° N.

Methods: We sampled more than 2000 forest edges using line intersect sampling in a monitoring programme (National Inventory of Landscapes in Sweden). We compared edge length, ecosystem attributes (width of adjacent ecosystem, canopy cover, canopy height, patch contrast in canopy height, forest type) and boundary attributes (profile, abruptness, shape) of natural edges (lakeshore, wetland) with anthropogenic edges (clear-cut, agricultural, linear disturbance) in five regions.

Results: Anthropogenic edges were nearly twice as abundant as natural edges. Length of anthropogenic edges was largest in southern regions, while the abundance of natural edges increased towards the north. Edge types displayed unique spectrums of boundary structures, but abrupt edges dominated, constituting 72% of edge length. Anthropogenic edges were more abrupt than natural edges; wetland edges had the most gradual and sinuous boundaries. Canopy cover, canopy height, patch contrast and forest type depended on region, whereas overall boundary abruptness and shape showed no regional pattern. Patch contrast was related to temperature sum (degree days ≥ 5 °C), suggesting that regional variability can be predicted from climate-controlled forest productivity. Boundary abruptness was coupled with the underlying environmental gradient, land use and forest type, with higher variability in deciduous than in conifer forest.

Conclusions: Edge origin, land use, climate and tree species are main drivers of broad-scale variability in forest edge structure. Our findings have important implications for developing ecological theory that can explain and predict how different factors affect forest edge structure, and help to understand how land use and climate change affect biodiversity at forest edges.

(Forman & Moore 1992). Several terms have been used to describe transition zones (van der Maarel 1990; Yarrow & Marín 2007); we use the term 'edge' to indicate the transition between a forest and non-forested ecosystem, or between two forests differing in composition and structure (Harper et al. 2005). Although progress has been slow, there have been important steps in the development of theory for understanding transitions between various ecosystems (Cadenasso et al. 2003; Ries et al. 2004; Harper et al. 2005), including a hierarchical approach to examine ecological boundaries (e.g. Peters et al. 2006; Yarrow & Salthe 2008).

Forest edges are complex three-dimensional landscape elements with structural attributes such as width, vertical stature and form along the boundary (Forman & Moore 1992). Strayer et al. (2003) incorporated additional attributes into a comprehensive classification system of ecological boundaries based on edge origin and maintenance, spatial structure, function and temporal dynamics. Edge width and structure directly affect the quantity and quality of habitat that edges can provide and therefore impact biodiversity at a landscape level. Edge structure also plays a key role for both the magnitude and distance of edge influence (Didham & Lawton 1999; Ries et al. 2004; Harper et al. 2005). Patch contrast (Cadenasso et al. 2003), the difference in composition, structure, function or microclimate between adjoining ecosystems (Harper et al. 2005), drives edge influence and dynamics by modifying flows of energy, materials and species. The structure of forest edges is shaped by complex interactions among environmental gradients, edge origin, edge maintenance, patch contrast, edge orientation, time since edge creation, and regional flora and fauna (Forman & Moore 1992; Matlack 1994; Strayer et al. 2003). Patch contrast is closely linked to forest productivity through effects of climate, soil and other site conditions on canopy height (Harper et al. 2005).

Most previous research on forest edge structure has been done on created edges, which are often of high contrast and thus have the potential to generate significant edge influence (Didham & Lawton 1999; Lindenmayer & Fischer 2006; Laurance et al. 2011). Natural edges have received much less attention, but are probably more structurally complex than human-induced boundaries (Harper & Macdonald 2001; Harper et al. 2004; McIntire & Fortin 2006). A few studies have compared natural and created edges (e.g. Braithwaite & Mallik 2012; Harper et al. 2015). However, little is known about the variation in forest edge structure among regions differing in land cover, land use and productivity. Such knowledge is needed to formulate general principles of edge influence towards a theory that extends beyond the simple fact that edge influence is site and context specific (Harper et al. 2005; Campbell et al. 2011).

Our objective was to identify factors controlling broad-scale variation in the structure of forest edges for a large region extending across two biomes. Using data from the monitoring programme National Inventory of Landscapes in Sweden (NILS; Ståhl et al. 2011), we examined the variability in the three-dimensional boundary structure in a large, representative sample of forest edges distributed throughout Sweden, covering a productivity and land use gradient from temperate to boreal and subalpine ecosystems. We compared natural inherent edges (lake-shore and wetland) with anthropogenically created edges, which were regenerating (clear-cut) or maintained (agriculture and linear corridors such as roads and power lines). Our specific objectives were: (1) to compare the length of these edge types among different regions; (2) to compare ecosystem attributes (width of adjacent ecosystem, canopy cover, canopy height, patch contrast and its link to productivity, forest type) and boundary attributes (profile, abruptness, shape) among different regions and types of edges; and (3) to relate boundary abruptness to forest type.

Methods

Study area

The study area covers all of Sweden, with a land area of 41 million ha and a further 2.6 million ha covered by freshwater. Sweden spans latitudes 55–69° N, has a length of 1500 km and a maximum width of about 400 km (Fig. 1). Biogeographically, the temperate zone forms a narrow belt in the south and southwest. It is dominated by deciduous trees, particularly beech (*Fagus sylvatica*), which forms the northern limit of the zone, but also oak (*Quercus* spp.), lime (*Tilia cordata*), maple (*Acer* spp.) and ash (*Fraxinus excelsior*). Most of southern Sweden is in the hemiboreal zone, where temperate deciduous trees and spruce (*Picea abies*), a conifer, dominate on better soils whereas poorer soils are mostly dominated by conifers. The boreal zone, which covers most of Sweden, is dominated by conifers (*P. abies* and *Pinus sylvestris*), birch (*Betula pendula*, *B. pubescens*) and other deciduous trees.

We divided Sweden into five regions along the south–north gradient (Fig. 1). Forests dominate all regions except the mountain region (Table 1). Open land is mainly found in the south and central regions. The area of wetlands increases from south to north. The dominant land use is industrial forestry, which is practiced throughout the country, followed by agriculture. The climate ranges from humid warm temperate in the south to humid snow climate with a cold summer in most of the country, to polar tundra in the northwestern mountains.

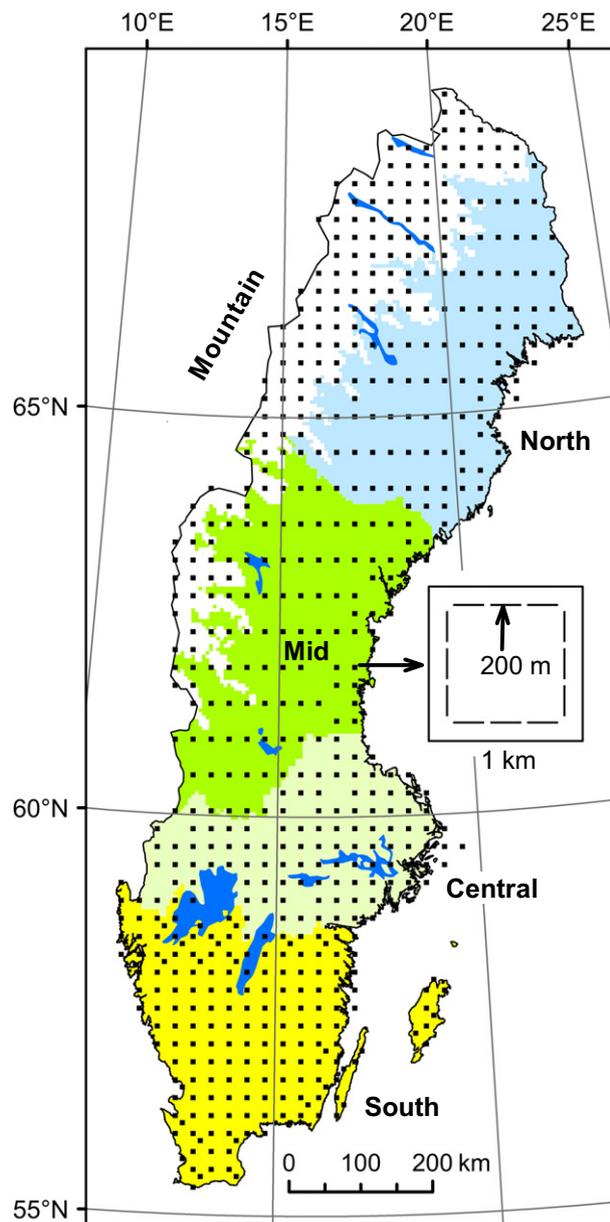


Fig. 1. Map of Sweden with the 631 sample units in the NILS programme and the five regions in the present study, and a 1×1 km square with twelve 200 m sample lines used in the field survey.

Field survey

Forest edge data were collected within the NILS programme, an on-going multiscale survey (Ståhl et al. 2011). The sampling design includes stratification, various sampling intensities and clustered sampling. A total of 631 permanent sampling units are distributed across Sweden using systematic sampling with a random start (Fig. 1). Each unit consists of a 5×5 km square with an inner 1×1 km square, where field data are collected. Twenty

per cent of the units are surveyed each year. Here we report results from 2005 to 2009, covering an entire national sample.

Full details of the methods are given in Esseen et al. (2007) and Appendix S1. Data on edge length, ecosystem and boundary attributes were collected by applying line intersect sampling along twelve 200-m sample lines in each unit (Fig. 1). A forest edge was sampled when the line intersected a transition between a forest ecosystem and an 'adjacent ecosystem' (non-forested or forested). Edges had to fulfil a set of edge detection criteria: (1) total boundary width (perpendicular to edge) ≤ 40 m, including any shrub zone; (2) trees and shrubs with DBH ≥ 10 cm, mean height of dominant woody vegetation ≥ 5 m and canopy cover $\geq 30\%$ in the forest ecosystem; (3) mean height of dominant woody vegetation ≤ 5 m and $\leq 10\%$ cover of emergent taller trees in the adjacent ecosystem; and (4) both the forest and the adjacent ecosystem ≥ 20 m wide and area ≥ 1000 m². The following variables were recorded: edge type, width of the adjacent ecosystem, canopy cover, canopy height, forest type, boundary profile (after Stierlin et al. 1994) and boundary shape. Patch contrast was calculated as the difference in canopy height between the forest and the adjacent ecosystem.

Analyses

Edges were categorized into six broad classes of 'edge types': lakeshore, wetland, clear-cut, agricultural, linear disturbance and 'other' edges (Appendices S1 and S2). For 'other' edges we only present data on edge length. Taking the sampling design of NILS into account, we statistically analysed relationships between edge length, ecosystem attributes and proportion of edge length with certain characteristics (mean values in Appendix S3, 95% confidence intervals in Appendix S4) using IBM SPSS Statistics Complex Samples (SPSS, Chicago, IL, US). Edge length was estimated from the number of recorded forest edge intersections and the length of inventoried sample lines following Esseen et al. (2006). The edge length estimates represent a spatial resolution of ca. 1–10 m.

We used a design-based General Linear Model (GLM; Heeringa et al. 2010; Appendix S4) to test for differences in width of the adjacent ecosystem, canopy cover, canopy height and patch contrast among regions and edge types. Differences among regions and edge types were evaluated based on comparison of the confidence intervals. We applied a standard GLM to examine the relationship between patch contrast (data pooled within each NILS unit), temperature sum (number of day degrees above $+5$ °C) and edge type, and the interaction between temperature sum and edge type. Temperature sum was used as a proxy for forest productivity based on a linear

Table 1. Land area, cover of different land uses, elevation and temperature sum for five regions in Sweden.

	Region				
	South	Central	Mid	North	Mountain
Land area (1 000 ha)	8162	6280	9418	9060	8064
Land use (% of land area)					
Forest	60.2	71.1	80.1	75.4	25.6
Open land	30.9	20.1	4.2	3.0	0.3
Urban land	2.2	2.3	0.3	0.3	0.0
Wetland	6.8	6.5	15.2	21.1	13.7
Alpine	—	—	0.2	0.3	60.4
Mean elevation (m a.s.l.)	115	101	315	241	584
Mean temperature sum (degree days)	1363	1238	898	765	467

Land area and cover of land uses were extracted from a map with scale 1:100 000. Elevation was extracted from a digital elevation model with 50 × 50 m horizontal resolution. Elevation and temperature sum only include units with edges.

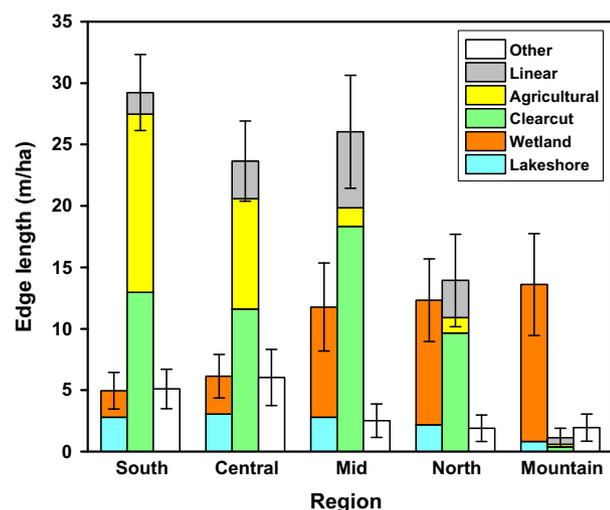


Fig. 2. Mean edge length for natural, anthropogenic and other forest edges in five regions in Sweden. Error bars represent 95% confidence intervals for total natural (lakeshore + wetland), anthropogenic (clear-cut + agricultural + linear) and other (riparian, fire, urban, treeline, gap, unspecified) edges.

relationship between temperature sum and forest growth ($\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) at the county level in Sweden (Morén & Perttu 1994). The temperature sum for each NILS unit was calculated from latitude and elevation.

We tested for independence among forest type, boundary profile, boundary abruptness, boundary shape and region using a design-based Chi-square test (Appendix S4). Separate tests were used to examine the independence between these five attributes and edge type, and to determine if boundary profile depended on forest type.

Results

A total of 2512 forest edges were recorded in 463 sample units. Most observations were from clear-cut (781) and

least from lakeshore edges (161). 'Other' edges (294) were dominated by 'unspecified', followed by riparian edges, urban edges and forest gaps. Fire edges and alpine tree lines were rare.

Edge length

Total estimated edge length was $32 \text{ m} \cdot \text{ha}^{-1}$ and length varied from 16.7 to $40.2 \text{ m} \cdot \text{ha}^{-1}$ among regions. Edge length was highest in the mid, south and central regions, but the confidence intervals overlapped among these regions (Fig. 2, Appendix S5). Total length of anthropogenic edges was nearly twice that of natural edges. Anthropogenic edges dominated south to mid regions, whereas natural edges increased towards northern regions. The proportion of natural edges increased from the south to mountain regions. Agricultural edges were mainly confined to the southern regions.

Ecosystem attributes

Width of the adjacent 'open' ecosystems differed by edge type but not region (Table 2). Lakeshore edges were most exposed, followed by agricultural, clear-cut, wetland and linear edges (mean across regions = 299, 199, 172, 133 and 67 m, respectively; Appendix S6). Canopy cover differed by region and edge type, but the interaction was significant so the pattern for edge type was not consistent across regions. Cover was lowest at wetland edges (62%) and highest at agricultural edges (80%). Canopy height and patch contrast also differed by region and edge type, but patterns were consistent across regions. Wetland edges had the lowest patch contrast (10.3 m) and agricultural edges had the highest (16.9 m). Patch contrast did not differ among lakeshore, clear-cut and linear disturbance edges (means between 14.1 and 14.4 m). Patch contrast pooled over all edges of the same type increased with tem-

perature sum but showed wide scatter (Fig. 3). Regression slopes for different edge types did not differ so the final model was fitted without the interaction term. Temperature sum explained between 17 and 22% of the variation in patch contrast, but only 5% at agricultural edges as these mainly occurred in warmer climates.

Edges were dominated by conifer forest (55% of edge length), followed by mixed (34%) and deciduous (11%)

forests. Forest type varied by region and edge type (Appendix S6). Deciduous forest contributed more to edge length in the south (temperate deciduous trees) and mountain regions (birch forest) than in central–north regions. Lakeshore and wetland edges had lower proportions of conifer and higher proportions of mixed forest than clear-cut edges, which were strongly conifer-dominated.

Table 2. Summary of GLMs testing the effect of region and edge type on width of the adjacent ecosystem, canopy cover and canopy height in the forest ecosystem, as well as patch contrast.

Variable	Region		Edge Type		Region × Edge Type		Model Summary R^2
	$F_{4, 436}$	P	$F_{4, 436}$	P	$F_{16, 424}$	P	
Width	0.2	0.943	105.0	<0.001	5.3	<0.001	0.22
Canopy Cover	20.1	<0.001	5.0	0.001	1.9	0.023	0.23
Canopy Height	37.6	<0.001	14.8	<0.001	0.9	0.572	0.28
Patch Contrast	39.6	<0.001	17.9	<0.001	1.0	0.482	0.28

Width was log-transformed and canopy cover was arc-sine square root-transformed before analysis.

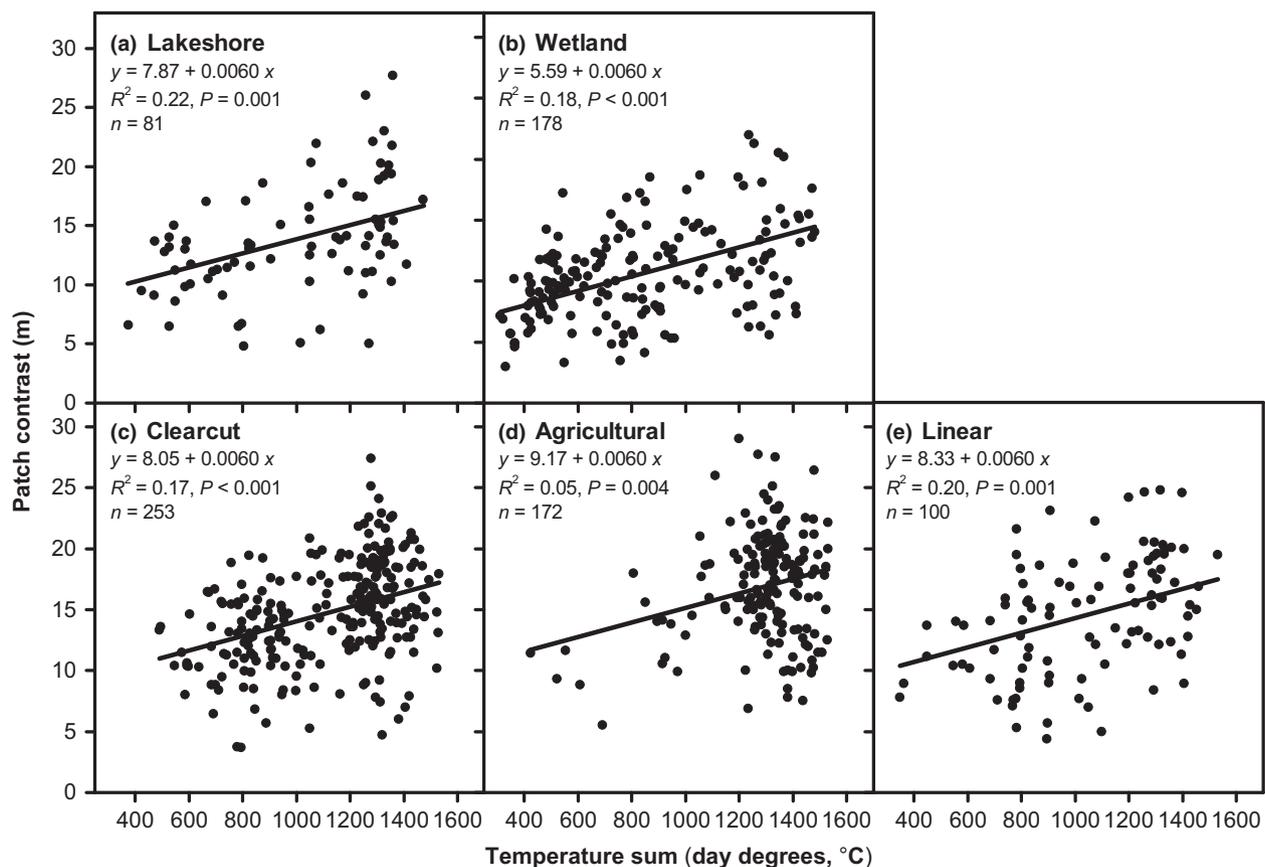


Fig. 3. Relationship between patch contrast and temperature sum for five edge types. Each point represents the pooled patch contrast over all edges of the same type within each NILS unit. Lines represent linear functions from a GLM without the interaction term (not significant). Both temperature sum ($F_{1,778} = 134.9, P < 0.001$) and edge type ($F_{4,778} = 15.7, P < 0.001$) were significant. All four edge types were different from wetland edges, which were used as a reference ($t = 4.3-7.5, P < 0.001$).

Table 3. Distribution (percentage of edge length) of boundary profile by edge type and forest type. Bold face indicates the profile with highest proportion for each edge type and forest type. For confidence intervals and test results, see Appendix S7.

Variable	Unmodified	Shrubs/Low Trees	Abrupt Mantel	Extended Mantel	Shrubs Under Mantel	Shrubs Before Mantel	Step-Formed	Mosaic	Continuous
Edge Type									
Lakeshore	18.5	7.4	33.2	2.8	21.2	9.8	1.5	1.9	3.7
Wetland	21.6	10.8	13.1	2.0	1.7	8.9	1.9	6.3	33.6
Clear-cut	69.0	3.2	16.3	0.6	2.0	3.0	0.2	1.7	4.1
Agricultural	14.8	4.9	39.5	12.3	13.8	10.0	1.5	2.3	0.9
Linear	46.4	5.8	30.1	2.6	5.4	6.1	—	0.7	2.8
Forest Type									
<i>Picea</i>	52.2	6.8	19.2	1.7	3.4	5.8	1.3	3.1	6.5
<i>Pinus</i>	47.4	4.7	19.9	1.6	3.6	5.1	—	1.5	16.2
Mixed Conifer	49.7	3.8	20.8	1.4	6.2	4.5	0.6	1.7	11.3
Mixed	30.9	7.3	25.2	2.7	6.3	8.2	1.4	4.5	13.4
Mixed Deciduous	12.8	4.9	26.8	19.3	24.5	9.1	0.8	1.9	—
Deci w/o Temp	33.6	9.4	23.8	8.4	6.5	9.6	1.8	2.1	4.7
Deci w Temp	3.1	3.1	23.0	41.4	10.5	11.7	—	7.1	—
Total	40.5	6.1	22.3	3.4	5.9	6.7	1.0	3.0	11.2

Boundary attributes

The dominant boundary profile was abrupt unmodified, followed by abrupt forest mantel and continuous (Table 3). Overall, abrupt boundaries constituted almost three-quarters of edge length (72%). The proportion of abrupt boundaries did not depend on region (Appendix S7). However, edges with extended forest mantel and with shrubs under the forest mantel were most abundant in the south region. Continuous boundaries were about equally common in the mid to mountain region but rare in the south.

Natural edges were less abrupt than created edges (51% and 84% of edge length, respectively). However, lakeshore edges had a higher proportion of abrupt boundaries (62%) than wetland edges (48%; Appendix S7). The edge types displayed unique spectra of boundary profiles. Over half of the lakeshore abrupt boundaries had a forest mantel and most of the gradual ones had a shrub zone. In contrast, one-third of the wetland edges had continuous boundaries. The anthropogenic edges were less variable. Clear-cut and linear disturbance edges were strongly dominated by abrupt boundaries (89% and 85%, respectively), but linear edges had twice as much boundary with a forest mantel than clear-cut edges. Although abrupt boundaries also dominated agricultural edges (71%), they were more diverse. About 76% had a forest mantel, with (24%) or without (52%) a shrub zone indicating boundary maturation.

Abruptness varied by forest type (Table 3; Appendix S7). Abrupt boundaries had a higher proportion of conifer forest (58% of edge length) than gradual boundaries (47%) and a lower proportion of mixed forest (31% and 42%, respectively). The three dominant profiles were also the most conifer-dominated. Only one profile, extended forest mantel, was dominated by deciduous forest and had a significant proportion of temperate trees. Overall, mixed and deciduous forest had the highest proportions of gradual edges.

Boundary shape did not depend on region but differed by edge type (Appendix S7). Linear edges were straightest followed by agricultural edges, which overlapped with lakeshore and clear-cut edges. Wetland edges had the most sinuous boundaries, but overlapped with clear-cut edges in all regions.

Discussion

We found that edge length, ecosystem attributes and boundary attributes varied among regions and edge types. Our identification of factors controlling this broad-scale variation is unique as previous studies have only provided information on forest edge structure in one, two or, rarely,

three or more edge types within a single landscape or region. A strict edge detection protocol combined with a sample-based design in a national monitoring programme allowed us to obtain a large, statistically representative data set rarely seen in studies of edges (Kleinn et al. 2011; Pellissier et al. 2013) for an area of large spatial extent with land use and climate-controlled productivity gradients. This increases the generality of our findings.

We developed a simple framework to better understand the factors driving variability in forest edge structure (Fig. 4). Region and land use are the main drivers of broad-scale variability in forest edge structure. Regional drivers include land forms, climate and natural disturbance regimes, whereas key land-use drivers are forestry, agriculture and construction of linear infrastructure.

Regional variation in edge length

Knowledge of edge length is fundamental for understanding factors affecting edge structure as the regional distribution of boundary characteristics depends on the abundance of different edge types. Our estimate of edge length of 17–40 m·ha⁻¹ is conservative as we did not sample edges adjoining narrow linear features. Total edge length in boreal forests may exceed 100 m·ha⁻¹ (Wulder et al. 2008; Jansson et al. 2011). Our finding of larger edge length in southern regions represents a snapshot of the

present distribution of edge types and results from more fragmentation by land use, denser road network and smaller patch size. The abundance of natural edges is more stable as most are influenced by land forms and therefore older. However, in southern regions, wetlands have been subjected to extensive draining and logging operations with large areas converted for agriculture and forestry, which suggests that the length of natural edges was higher in the past.

Of the anthropogenic edges, the large extent of clear-cut edges highlights industrial forestry as the main driver of edge creation (Jansson et al. 2011). Clear-cutting, with about 60–120-yr rotations, has dominated throughout Sweden since the 1950s, resulting in a highly fragmented landscape. Although agriculture with permanent cultivated arable land dates back to the Iron Age (ca. 2000 BP), most agricultural edges probably resulted from agricultural expansion peaking in the 1920s. Agriculture has undergone major changes during the last 100–150 yr, focusing on intensified management, larger fields and afforestation of farmland, resulting in a rapid loss of species-rich, semi-natural grasslands and field margins (Cousins 2009).

Importance of ecosystem attributes for edge structure

The large variability in the type and width of adjacent ecosystems implies that edges were exposed to a diverse

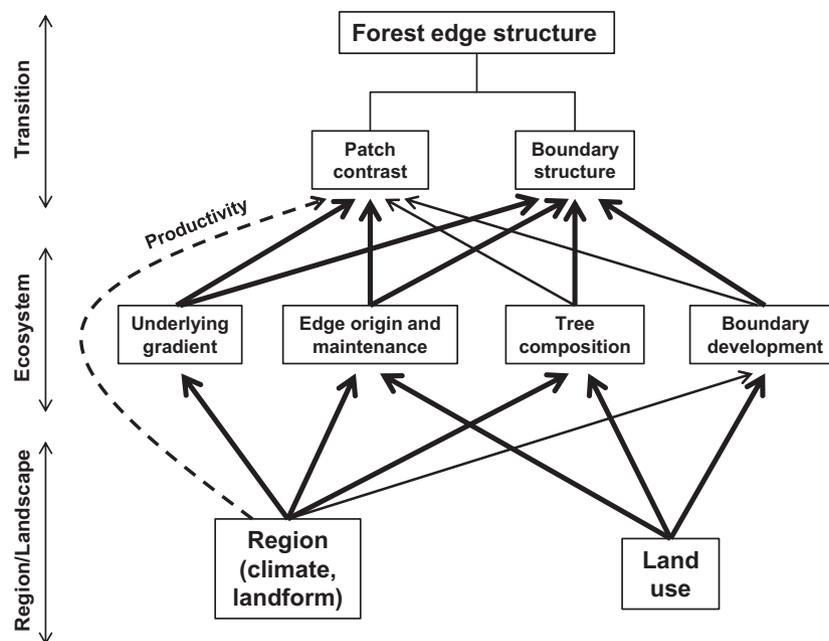


Fig. 4. Framework for understanding variability in forest edge structure. The framework identifies components of a local transition (following Cadenasso et al. 2003): patch contrast (difference in architecture and composition between adjoining ecosystems) and boundary structure (architecture, i.e. abruptness and shape), as well as key drivers at ecosystem and regional/landscape scales. Bold lines indicate strong links. The dashed line indicates that patch contrast in canopy height is linked to climate through forest productivity.

range of microclimates, further modified by topography and edge orientation. The most exposed edges were lakeshore and agricultural edges. Water and agricultural crops are both 'open' ecosystems that have lower surface roughness than forests, thus affecting wind speed, turbulence and energy exchange across the boundary (Oke 2005).

Both cover and height of forest edge ecosystems decreased from south to north following the general decrease in forest productivity from temperate to boreal and sub-alpine ecosystems. Geographical patterns in forest structure and productivity are especially pronounced in Sweden as the relatively narrow country spans 55–69° N latitudes. Likewise, the relationship between patch contrast and temperature sum (Figs 3 and 4) is based on the decrease in forest productivity, and hence tree height, with latitude and elevation in Sweden (Morén & Perttu 1994; Lagergren et al. 2006). This highlights that patch contrast in canopy height, a key factor for edge influence, can be predicted at a landscape scale from readily available standard climate data. This is an important step towards a theory on forest edge structure that has significant predictive power, a basic requirement for being useful to support decision-making in research and conservation (Driscoll & Lindenmayer 2012). The variation in patch contrast of different edge types was linked to the productivity of local ecosystems, which was highest at agricultural edges and lowest at wetland edges where production is limited by a high groundwater table. Our findings support the hypothesis that the magnitude of edge influence on forest structure and composition is more pronounced in productive ecosystems (Harper et al. 2005), and the biomass accumulation hypothesis (McWethy et al. 2009) that predicts that the magnitude of edge influence increases with ecosystem productivity and plant biomass. At the biome scale, this implies that patch contrast and its role in driving edge influence on forest edge structure and composition should be more pronounced in temperate and tropical forests than in boreal forests (Harper et al. 2005, 2015).

Factors affecting boundary abruptness

The lack of regional variation in overall boundary abruptness is hardly surprising with such a high proportion of abrupt edges. Instead, we suggest that abruptness is linked to the underlying environmental gradient, edge origin and maintenance, tree species composition and boundary development over time (Fig. 4). An important conclusion is that natural inherent lakeshore and wetland edges are structurally more complex than anthropogenic edges, which was also found in previous comparisons of fire and clear-cut edges (Harper et al. 2004; Larrivé et al. 2008; Braithwaite & Mallik 2012). Although it is obvious that anthropogenic edges are abrupt, we show that agricultural

edges are less abrupt than clear-cut and linear edges. Natural inherent edges are unique with respect to the character and steepness of the underlying environmental gradient, which results from the interaction of topography, hydrology and soil along the gradient. For example, boundaries with a continuous increase in tree height were mainly found at wetland edges as a result of gradual change in the groundwater table. Lakeshore edges are more abrupt than wetland edges due to the nature of the aquatic–terrestrial interface with the highest proportion of zoned edges of all types and show many similarities with riparian edges (Rydin et al. 1999; Ward et al. 2002).

Our results suggest that the high overall boundary abruptness across Sweden is partly explained by the high proportion of conifers and the low tree species richness in boreal forests (Gamfeldt et al. 2013), further accentuated by industrial forestry that focuses on conifer monocultures. Abrupt boundary profiles, but also gradual wetland–forest transitions, were associated with conifer dominance. Conifers are less flexible than broad-leaved deciduous trees in adjusting their branching and growth to the sudden increase in light availability following edge creation. In contrast, shade-intolerant pioneer deciduous trees such as birch and aspen (*Populus tremula*) have a higher capacity to respond to edge formation and often form a forest mantel. Moreover, the extended forest mantel was associated with temperate deciduous trees, such as oaks, that have high variability in tree architecture. This indicates that regional variation in boundary profile is linked to the distribution of tree species. Hence, we expect larger variability in boundary profiles in temperate and tropical forests because of their higher diversity of woody species.

Boundary abruptness may also change over time. Our analysis suggests that high abruptness of clear-cut edges is caused by rapid re-vegetation, which often prevents the development of boundary structures such as a forest mantel. In contrast, the majority of agricultural edges showed some evidence of boundary maturation by having a forest mantel and shrub zone, but complex boundaries such as step-formed and mosaic profiles were rare. The high proportion of abrupt maintained agricultural edges is clearly caused by the constraints placed on boundary development by land use, such as cultivation, grazing, browsing, clearing, logging, digging and other anthropogenic disturbance (Matlack 1994; Chabrierie et al. 2013) that prevent edges from reaching mature stages.

Implications

The three-dimensional structure of forest edges may affect species and ecological processes in several ways. Low-contrast ('soft') edges are wider than high-contrast

(‘hard’) edges and provide an extension of the habitat for both open-habitat specialists and native forest species (Campbell et al. 2011). Patch contrast in canopy height drives ecological flows across edges. It is well known that the risk for wind-throw rapidly increases with the contrast in tree height (Zeng et al. 2009). The architecture of the boundary, as characterized by abruptness, boundary profile, composition of woody species, stem density and ‘edge openness’, modifies microclimate and vegetation (Didham & Lawton 1999). Abruptness and stand density strongly influence wind loading on forest edges (Ruck et al. 2012), and developed edge structures have been linked to animal-dispersed woody species in a positive feedback loop (Sarlöv Herlin & Fry 2000). Finally, gradual edges can also reduce the deposition of nutrients and pollutants (Wuyts et al. 2009). Consequently, structurally complex edges are probably better for biodiversity than abrupt edges, but this hypothesis needs further examination.

Structurally complex edges are critical as refuges for biodiversity in agricultural landscapes (Marshall & Moonen 2002; Cousins 2009). However, the large extent of abrupt anthropogenic edges in both agricultural and forest-dominated landscapes is alarming and imposes severe threats to biodiversity and ecosystem function. Knowledge of the variability in the amount and structure of natural ecosystem transitions may help to conserve biodiversity in man-dominated landscapes.

Conclusions

Our findings fill a knowledge gap with respect to landscape and regional variability in patch contrast and boundary structure, some of the steps needed to construct a comprehensive theory on forest edges and edge influence (Harper et al. 2005). Our key findings are: (1) the length of anthropogenic edges was nearly twice that of natural inherent edges; (2) anthropogenic edges dominated southern regions whereas natural edges increased towards the north; (3) abrupt edges dominated (72%) because of intense land use and conifer dominance; (4) anthropogenic edges were more abrupt than natural inherent edges; (5) edge types displayed different spectra of boundary profiles; (6) wetland edges had unique structural characteristics with the lowest patch contrast and the most gradual and sinuous boundaries; (7) ecosystem attributes (cover, height, patch contrast, forest type) but not boundary attributes (abruptness, shape) varied regionally across the temperate–boreal gradient; (8) boundary abruptness was coupled with the underlying environmental gradient, edge origin, land use and forest type; (9) deciduous forest, particularly with temperate trees, had higher variability in boundary structure than conifer forest; and (10) patch

contrast had a linear relationship with temperature sum and was highest in the most productive ecosystems. Our finding that patch contrast can be predicted from standard climate data is an important step towards a theory on edges and edge influence. We conclude that edge origin, land use, climate and tree species are the main drivers of broad-scale variability in forest edge structure. Similar studies on variability in forest edge structure are needed from other boreal forests, as well as temperate and tropical forests, to test our hypotheses at a global scale.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Field sampling protocols in the NILS programme.

Appendix S2. Examples of the five studied edge types.

Appendix S3. Estimation of edge length, ecosystem and boundary attributes.

Appendix S4. Estimation of confidence intervals and hypothesis tests.

Appendix S5. Means and confidence intervals for edge length.

Appendix S6. Means and confidence intervals for ecosystem attributes.

Appendix S7. Means and confidence intervals for boundary attributes.