# Edge Effects on Liverworts and Lichens in Forest Patches in a Mosaic of Boreal Forest and Wetland

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**Abstract:** *In studies of edge effects, it is difficult to separate edge from size effects because size and edge are strongly correlated in most cases. In our study we separated these two effects by examining small forest patches of two different size classes (<1 ha and 4–6 ha), with patches chosen so that area and perimeter were not correlated within each class. We conducted our study in a mosaic of old-growth* Picea abies *forest and wetland, consisting of forested moraine hills ("islands") in a Sphagnum-bog matrix. On each island, we demarcated a 0.1-ha sample plot and measured site and forest characteristics. In each plot, we examined all fallen logs for the occurrence of epixylic hepatics (liverworts), and all standing trees for the occurrence of calicioid lichens. We examined correlations between species and area, shape, and distance to nearest edge. The effect of shape on forest-interior conditions was analyzed with a core-area model. Site and forest characteristics were similar between the island size groups. The majority of hepatics and lichens occurred more frequently on larger islands, and the cover of hepatics tended to be higher on larger islands. A rough estimation of depth-of-edge influence was made at 50 m, but the two species groups did not respond similarly to edge effects. The lichens showed several important correlations with island shape on small islands, suggesting that circular small islands may have a forest structure approaching interior conditions. Hepatics tended to respond to small islands as edge environments. We conclude that the response of species to edges is strongly species-specific and context-dependent. This points to the limitations of extrapolating results from studies on depth-of-edge influence to forest-management situations.*

Efectos de Borde sobre Hepáticas y Musgos en Fragmentos de Bosque en un Mosaico de Bosque Boreal y Humedales

**Resumen:** *En estudios de los efectos de borde es difícil separar los efectos de borde de los efectos de tamaño, porque en la mayoría de los casos el tamaño y el borde están fuertemente correlacionados. En nuestro estudio separamos esos dos efectos al examinar fragmentos de bosque de dos tamaños diferentes (<1 ha y 4-6 ha), con fragmentos elegidos de tal manera que el área y el perímetro no estaban correlacionados en cada clase. Desarrollamos nuestro estudio en un mosaico de bosque maduro de* Picea abies *y humedales, consistentes de colinas de morrena glaciales con bosque ("islas") en una matriz de ciénegas de Sphagnum. En cada isla delimitamos una parcela de muestreo de 0.1 ha y medimos las características del sitio y del bosque. En cada parcela examinamos los troncos caídos para determinar la presencia de hepáticas epixílicas, así como todos los árboles en pie para determinar la presencia de líquenes calicioides. Examinamos las correlaciones entre especies y área, forma y distancia al borde más cercano. El efecto de la forma sobre la cantidad de condiciones de bosque interior fue analizado con un modelo de núcleo-área. Las características del sitio y del bosque fueron similares entre los grupos de tamaños de islas. La mayoría de las hepáticas y líquenes tuvieron frecuencias mayores en las islas más grandes, y la cobertura de hepáticas tendió a ser mayor en las islas grandes. Se estimó que la profundidad aproximada de la influencia del borde es de 50 m. Sin embargo, los dos grupos de especies no respondieron de manera similar a los efectos de borde. Los líquenes mostraron varias correlaciones importantes con la forma de la isla en islas pequeñas, lo que sugiere que los bosques en islas circulares pueden tener una estructura cercana a condiciones interiores. Las hepáticas tendieron a responder a las islas pequeñas como ambientes de borde. Concluimos que las respuestas de las especies a los bordes son marcadamente específicas a la especie y dependen del contexto. Esto señala las limitaciones de extrapolar los resultados de los estudios de la influencia de la profundidad del borde a situaciones de manejo de bosques.*

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## Introduction

Old-growth Fennoscandian boreal forests have been subjected to intensive fragmentation during the last 150 years (Östlund et al. 1997). This has resulted in landscapes composed mainly of managed stands of fairly young forest and a small number of isolated patches of old growth. The associated decline in the abundance of many species is considered a major threat to biodiversity in the region. Conservation measures depend heavily on the ability of remnant old-growth patches to serve as refugia and dispersal centers for declining species.

Although the spatial configuration of available habitat has received considerable theoretical focus (e.g., Hanski 1998; Kareiva & Wennergren 1995), most empirical data suggest that changes in patch quality related to patch size and edge effects are of major concern (Fahrig 1998; Harrison & Bruna 1999). In studies of such effects it is difficult to separate edge effects from size effects, because size and edge influences are strongly correlated in most cases. Another problem associated with many studies of edge effects is variation among patches in patch history and matrix type (Murcia 1995). It has thus been difficult to draw general conclusions from many edge studies despite the growing focus on such landscape issues in conservation ecology.

To separate size effects from edge effects, it is necessary to study patches where area and perimeter are not correlated. Patches with equal area but different shapes have different areas affected by edge. This diversity of patch sizes and shapes is found in the nature reserve Granlandet (county of Norrbotten in northern Sweden), which is composed of roughly 1000 forest "islands" situated in a wetland matrix. The system represents a situation where the matrix is homogenous and isolation has a long history. Thus, transient patterns caused by recent fragmentation and edge creation are not an issue.

As in situations where forest has been fragmented by harvesting into small, isolated patches of old forest, the species in Granlandet have experienced both small population sizes (area effect) and edge effects that are likely to increase extinction risks. In our study system and with the chosen study design, however, we can separate the long-term effects of patch area and edge effects. This is accomplished by choosing forest stands from two size classes within which there is no correlation between perimeter and size. Specifically, we (1) compared species richness and number of occurrences of individual species in small stands (<1 ha) and medium-sized stands (4–6 ha), (2) analyzed the importance of increasing edge exposure in the two size classes of stands, and (3) measured how far into the fragments the edge influence can be traced for the studied species groups, epiphytic calicioid lichens and epixylic liverworts.

## Study Area

Granlandet is at lat. 66°28–44′N and long. 21°15–50′E in the county of Norrbotten in northern Sweden. The area belongs to the northern boreal zone (Ahti et al. 1968). It is one of the largest areas with natural forests in Sweden, and most of the area is located within a large (20,300-ha) nature reserve. The landscape is a mosaic of forested morain hills situated in a sphagnum wetland. The hills (hereafter called islands) are mostly covered by Norway spruce (*Picea abies* L. [Karst.]) and rise above the mire up to 10 m. Birch (*Betula pubescens*) is subdominant, and scattered individuals of Scots pine (*Pinus sylvestris* L.) and goat willow (*Salix caprea* L.) also occur. The tree layer is 150–200 years old, with individual spruces more than 300 years old. The fire history of the area has not been studied in detail, but fires are likely to have been rare or absent in most islands. Human influence has been limited and is restricted to a few cut stumps on one or two of the studied islands. Thus, the forest can be regarded as an example of virgin boreal spruce forest.

Low shrubs (mainly *Vaccinium* spp.) dominate the field layer, and species richness among vascular plants is low. The flora of cryptogams (mosses, lichens, and fungi) is species-rich, however, and many rare and threatened species are known from the area.

## Methods

Fieldwork was conducted during August and September of 1996. The choice of islands was guided by a geographic information system (GIS) map of the area. A total of 42 islands in two size classes, 0.7–1.0 ha ($n = 22$) and 3.8–5.6 ha ($n = 20$), were chosen so that island size and perimeter were not correlated (small islands: $r = 0.17$, $p = 0.45$; large islands: $r = 0.334$, $p = 0.15$). In the selection procedure, we also considered island shape so as to include as wide a range as possible. We described island shape following Patton (1975) and Laurance and Yensen (1991):

$$S = \frac{P}{200\sqrt{A\pi}}, \tag{1}$$

where $S$ is a shape index, the higher the value the more irregular the shape; 1 means the island is circular, $P$ is the perimeter in meters, and $A$ the area in hectares.

On each island, a circular sample plot of 0.1 ha was located at the island centroid, which was identified in the GIS map and defined as the center of the smallest quadrat that could be placed over the entire island and where the sides followed north-south and east-west directions. This point was identified in the field with a differential global positioning system (dGPS). This sample point was random in relation to the edge and also resulted in a

**Table 1. Habitat variables (mean values) for large (*n* = 20) and small "islands" (*n* = 22) in the nature reserve Granlandet, Sweden.**

| | *Small islands (SD)* | *Large islands (SD)* | p[a] |
|---|---|---|---|
| Islands variables | | | |
| Area (ha) | 0.87 (0.06) | 4.55 (0.59) | <0.001[b] |
| Perimeter (m) | 421 (47) | 1039 (173) | <0.001[b] |
| Shape index[c] | 1.27 (0.14) | 1.38 (0.21) | 0.06 |
| Nearest edge (m) | 24.9 (6.7) | 57.3 (21) | <0.001[b] |
| Site variables[d] | | | |
| Basal area, living spruce | 10.7 (4.0) | 10.9 (3.7) | 0.84 |
| Basal area, dead spruce | 0.7 (0.8) | 1.0 (1.1) | 0.36 |
| Basal area, living deciduous trees | 3.5 (2.1) | 3.2 (3.4) | 0.74 |
| Basal area, dead deciduous trees | 0.5 (0.8) | 0.5 (0.8) | 0.99 |
| Canopy height (m) | 16.3 (2.9) | 16.6 (3.1) | 0.72 |
| Canopy cover (%) | 58.4 (31.6) | 60.0 (35.8) | 0.88 |
| Log variables | | | |
| Total number of logs across plots | 184 | 179 | |
| Number of logs per plot | 8.4 (3.9) | 8.9 (3.7) | 0.62 |
| Diameter (cm) | 26.7 (2.6) | 29.2 (3.5) | 0.011[b] |
| Surface area (m$^2$) | 6.93 (1.9) | 8.93 (2.8) | 0.010[b] |
| Decay stage (mean) | 3.7 (1.0) | 4.0 (1.6) | 0.64* |
| Bark cover (%) | 36.4 (15) | 32.9 (18) | 0.50 |
| Ground contact (%) | 70.7 (16) | 75.3 (15) | 0.35 |
| Tree variables | | | |
| Total number of trees across plots | 320 | 347 | |
| Number of trees per plot | 14.6 (6.9) | 17.4 (6.2) | 0.18 |
| Diameter at breast height (cm) | 27.8 (6.5) | 29.2 (16.1) | 0.12 |
| Vitality | 1.6 (1.0) | 1.6 (1.0) | 0.36* |
| Bark texture | 2.6 (0.6) | 2.7 (0.6) | 0.062* |

[a] *Those with an asterisk represent a chi-square test; those without an asterisk represent a Mann-Whitney* U *test.*

[b] *Significant* p *value (<0.05).*

[c] *Increasing shape index relates to an increasing perimeter-to-area ratio scaled so that an index of 1 corresponds to a circular shape.*

[d] *Basal area is in square meters per hectare.*

range of distances to the nearest edge. Edge effects may vary with aspect, and, in our system, wind and sun are likely to be strongest at the southern and western exposed edges. However, because we had no objective information about which edge-related factor was most important for the studied species groups, we chose to include only distance to the nearest edge in the analyses.

In the sample plot, basal area (m$^2$/ha) was measured for all tree species separately and divided into dead and living trees. Tree canopy height and tree canopy cover (with a "moose-horn"; sensu Robinson 1947) was also estimated.

We studied two groups of species: epiphytic calicioid lichens and epixylic hepatics. These groups were chosen for their known sensitivity to microclimate variations, because of the attention they have received as threatened species, and for their potential as indicators of old-growth conditions (Hallingbäck 1995, 1998; Norén et al. 1995; Gärdenfors 2000). Calicioid lichens are species with stalked apothecia in which the spore layer is exposed in a maezedium. Taxonomically they all used to belong to the order Caliciales, but recent systematic studies have put this placement in question (Tibell 1999). Also included in the study are some nonlichenized fungi closely related to the calicioid lichens, namely *Chaenotecopsis* spp. and *Microcalicium* spp.

Within the sample plots, we studied all fallen logs with a maximum diameter of >15 cm and a length of >3 m. On these we noted the occurrence of all hepatics and estimated the total cover of hepatics (excluding *Ptilidium pulcherrimum*) in square centimeters. *P. pulcherrimum* was excluded because of its strong dominance and its known wide range of habitat tolerance. Although dominant in relative terms, the total cover of hepatics was usually low, and it is unlikely that variation in cover of *P. pulcherrimum* influenced the occurrence of other species. For each log, we noted minimum and maximum diameter, length, stage of decay, bark cover (in percent), and ground contact. Stage of decay was noted on a seven-grade scale (modified after McCoullugh 1948; Söderström 1988*b*): (1) wood hard, all bark remaining; (2) wood hard, some bark loss but more than 50% remaining; (3) wood hard, <50% bark remaining; (4) wood starting to soften; (5) wood soft, with small pieces lost; (6) wood soft, with large pieces lost and trunk starting to deform; and (7) outer surface hard to define but with a core of hard wood.

All living and dead standing Norway spruce trees >20 cm diameter at breast height (dbh) in the sample plots were inventoried for calicioid lichens. For each tree, we noted dbh, vitality, and bark texture. Vitality was classified in five classes (Kruys & Jonsson 1997): 2, living healthy tree; 1, sick and dying tree; 0, newly dead tree with $>50\%$ bark remaining; −1, dead tree with $<50\%$ bark but with hard wood; −2, dead standing tree with soft wood. Bark texture was classified in four classes: 1 smooth; 2, bark flaky but without cracks; 3, bark with cracks; and 4, bark with cracks within deep cracks.

Due to the large non-normal variation in most variables, we used nonparametric statistics throughout the analysis. That is, correlations are Spearman rank correlations, mean values are compared with Mann-Whitney *U* tests, and frequency distributions are compared with chi-square tests. All analyses of individual species were done on number of observations per substrate unit (i.e., tree or log) and island. We used absolute rather than percentage-based data because we assumed that size- and edge-related effects might occur through changes in the abiotic environment (e.g., changed temperature or moisture conditions) as well as through changes in the available substrates (i.e., trees and decaying logs). Thus, relating species occurrences to the percentage of suitable substrate units colonized may hide important size- and edge-related factors. Although analyses in some cases invoke multiple comparisons, the main purpose is exploratory. Thus, no posterior correction of *p* values was applied.

## Results

### Island Characteristics

Small and large islands were generally similar with respect to site, log, and tree variables (Table 1). Only log diameter, and consequently log surface area, was larger on large islands with a difference of 2.5 cm in average maximum log diameter.

Within each island size group, some variables correlated with island shape and distance to edge (Table 2). Log diameter increased with island size on large islands and also increased with distance to nearest edge on large islands. Logs on small islands had less bark cover when islands were more irregular in shape and when plots were situated close to the edge. Tree diameter increased with distance from edge on both small and large islands (Table 2). These differences should be viewed as edge effects on the tree layer and log quality that indirectly may influence species occurrences.

### Epixylic Hepatics

Twenty-six epixylic hepatic species (Table 3) were found on the 363 studied logs. Most of these were rare, and only eight were on average found on more than one log per sample plot. The majority of the species (18 species) had higher numbers of occurrences on large islands (sign test, $p = 0.031$), and *p* values associated with four of those differences were $<0.05$ (Mann-Whitney *U* test; Table 3). Of these four species, two are currently red-listed in Sweden. In contrast, only six species were more common on small islands, and for these the differences were small and in no case significant. The total cover of hepatics was highly variable among islands. On large islands, the cover was 2.5 times as high as on small islands (1720 cm$^2$ compared with 680 cm$^2$, respectively), but the difference was not statistically significant ($p = 0.082$) because of large variation within groups.

The relationships between hepatic species richness and island parameters within the two types of islands were weak. Only total species richness per island ($r = 0.46$, $p = 0.043$) and total cover of hepatics ($r = 0.47$, $p = 0.038$) were positively correlated with island size among large islands. There was a positive relationship between hepatic cover and distance to nearest edge for large islands ($r = 0.42$, $p = 0.069$), probably related to the increased log diameter in plots farther from the edge. A scatterplot of the relationship between cover

**Table 2. Spearman correlation coefficients (*p*) for the relationships between island and substrate variables.**

| | *Island size* | | *Island shape index* | | *Distance to edge* | |
|---|---|---|---|---|---|---|
| | *small* | *large* | *small* | *large* | *small* | *large* |
| Logs | | | | | | |
| no. of logs | −0.21 (0.35) | 0.29 (0.21) | 0.37 (0.09) | −0.36 (0.12) | 0.01 (0.95) | 0.178 (0.46) |
| diameter | 0.008 (0.97) | 0.54 (0.015)* | 0.40 (0.07) | −0.21 (0.38) | −0.07 (0.76) | 0.58 (0.007)* |
| surface area | 0.002 (0.99) | 0.25 (0.29) | 0.15 (0.50) | −0.24 (0.30) | 0.22 (0.33) | 0.28 (0.24) |
| bark cover | 0.16 (0.48) | −0.12 (0.60) | −0.56 (0.01)* | 0.19 (0.43) | 0.64 (0.001)* | −0.13 (0.58) |
| ground contact | 0.18 (0.43) | −0.09 (0.72) | 0.10 (0.66) | −0.26 (0.27) | −0.15 (0.49) | 0.04 (0.85) |
| Trees | | | | | | |
| no. of trees | −0.06 (0.81) | −0.02 (0.92) | 0.04 (0.86) | 0.04 (0.86) | 0.31 (0.16) | 0.001 (0.99) |
| diameter at breast height | −0.10 (0.66) | 0.38 (0.09) | −0.35 (0.11) | −0.07 (0.76) | 0.48 (0.02)* | 0.56 (0.01)* |

**Correlations with associated* p *values of <0.05.*

**Table 3. Average number of logs on which the hepatic species was found and species richness estimates (SD).**

| | *Small islands* | *Large islands* | p[a] |
|---|---|---|---|
| *Anastrophyllum hellerianum*[b] | 1.0 (0.9) | 2.6 (2.6) | 0.025[c] |
| *A. minutum* | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *Barbilophozia attenuata* | 0.3 (0.6) | 0.8 (1.1) | 0.19 |
| *Blepharostoma trichophylla* | 0.1 (0.5) | 0.1 (0.3) | 0.96 |
| *Calypogiea integristipula* | 0.4 (0.7) | 0.4 (0.9) | 0.43 |
| *C. neesiana* | 0.3 (1.1) | 0.7 (1.0) | 0.032[c] |
| *C. suecica*[b] | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *Cephalozia bicuspidata* | 1.6 (1.3) | 1.4 (1.3) | 0.63 |
| *C. leucantha* | 0.05 (0.2) | 0.2 (0.6) | 0.46 |
| *C. loitlesbergii* | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *C. lunulifolia* | 0.9 (1.3) | 1.0 (1.2) | 0.52 |
| *C. pleniceps* | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *Geocalyx graveolens* | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *Harpanthus flotovianus* | 0.05 (0.2) | 0.0 (0.0) | 0.34 |
| *Jungermannia leiantha* | 0.0 (0.0) | 0.05 (0.2) | 0.29 |
| *Lepidozia reptans* | 0.2 (0.7) | 0.1 (0.4) | 0.61 |
| *Lophozia ciliata*[b, d] | 3.0 (2.1) | 3.8 (3.0) | 0.48 |
| *L. incisa* | 0.05 (0.2) | 0.4 (1.1) | 0.12 |
| *L. longidens* | 1.6 (1.5) | 2.6 (2.8) | 0.32 |
| *L. longiflora*[b] | 1.6 (1.7) | 2.5 (1.6) | 0.037[c] |
| *L. silvicola* | 1.7 (1.7) | 2.8 (1.8) | 0.043[c] |
| *L. ventricosa* | 0.4 (0.6) | 0.6 (0.9) | 0.94 |
| *Ptilidium pulcherrimum* | 6.9 (3.7) | 7.2 (3.5) | 0.85 |
| *Riccardia latifrons* | 0.3 (0.5) | 0.2 (0.4) | 0.87 |
| *R. palmata* | 0.1 (0.4) | 0.1 (0.3) | 0.72 |
| *Tritomaria exsectiformis* | 0.05 (0.2) | 0.05 (0.2) | 0.95 |
| No. of species per log | 2.77 (1.14) | 3.21 (0.99) | 0.23 |
| No. of species per islands | 8.09 (2.88) | 9.05 (3.33) | 0.07 |

[a] *Differences between small and large islands were tested with a Mann-Whitney* U *test.*

[b] *Species included in the Swedish Red List of threatened species, according to Gärdenfôrs (2000).*

[c] *Significant* p *value (*$p < 0.05$*).*

[d] *Posterior interpretation because the specimens were recorded as* Lophozia ascendens. L. ciliata *is recently described. It is a common species, and the presence of* L. ascendens *is not confirmed from the study area.*

and distance to edge indicates a boundary correlation: the cover of hepatics tended to be quite variable closer to edges but more consistently high at greater distances from the edge) (Fig. 1).

The number of occurrences for several species showed a positive correlation to island shape index (i.e., irregular islands) on small islands (*Blepharostoma trichophylla*, *Cephalozia bicuspidata*, *Lepidozia reptans*, *Lophozia silvicola*, and *Riccardia palmata*). In most cases, correlations varied between 0.43 and 0.51 (Spearman $r$; $p$ values between 0.02 and 0.04). Only *Riccardia latifrons* showed a stronger correlation ($r = 0.65, p = 0.002$). These species thus tended, among small islands, to be more frequent on irregularly shaped islands. On large islands, *Riccardia latifrons* also showed a positive correlation with island shape index, whereas *Lophozia longidens* was negatively correlated with it ($r = 0.64$, $p = 0.002$, and $r = -0.50, p = 0.026$, respectively).

Correlations of number of observations for individual species with distance to nearest edge were generally weak within both island size classes, and only *Anastrophyllum hellerianum* and *Lophozia longiflora* tended to occur more frequently in plots farther from the edge across all islands ($r = 0.33$ and $0.31$, $p = 0.033$ and $p = 0.045$, respectively). In addition, *Barbilophozia attenuata* was positively correlated with distance to edge on large islands ($r = 0.48, p = 0.032$).

## Calicioid Epiphytes

Twenty-one calicioid lichen species (Table 4) were recorded on the 667 studied trees. Several of the species were common, and 11 species occurred on average on more than one tree per sample plot. Similar to the hepatics, most species had higher frequencies on large islands (sign test, $p = 0.043$), and $p$ values for three of these were $<0.05$ (Table 4). Of these three species, one is currently classified as red-listed in Sweden.

The mean number of species per tree was negatively correlated with island shape index on small islands: the more irregularly shaped the island was, the fewer species were found. No other relationships between species occurrences and island parameters were apparent for the lichens, even though tree diameter increased with distance to edge in both island size classes.

However, some individual species showed correlations with island parameters. These responses were most evident on small islands and concerned distance to edge

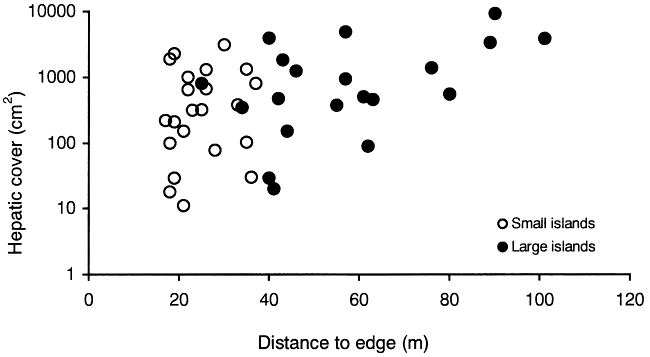

*Figure 1. Total cover (cm$^2$) of hepatics on fallen logs in relation to distance to nearest edge (m) for the entire data set.*

and island shape. Thus, on small islands, *Chaenotheca subroscida*, *Chaenothecopsis* spp., and *Microcalicium disseminatum* occurred more frequently in plots at increasing distance from the edge ($r = 0.51$, 0.44, and 0.43, respectively, with associated $p$ values of 0.016, 0.043, and 0.043), whereas *Chaenotheca phaeocephala* and *Ch. subroscida* were more common on islands with a low shape index ($r = -0.52, p = 0.013$, and $r = -0.57$, $p = 0.006$, respectively). In contrast, *Calicium glaucellum* tended to be more common on small islands with a high shape index ($r = 0.47$, $p = 0.029$). Island size was correlated with the number of occurrences only of *Chaenotheca furfuracea* on large islands ($r = 0.52, p = 0.018$).

The number of lichen species per island was positively correlated with distance to nearest edge across all islands ($r = 0.33$, $p = 0.033$), probably because of to the greater tree size in plots farther from the edge, whereas plots closer to the edge had higher variability in species richness. *Microcalicium disseminatum*, *Chaenothecopsis* spp., *Chaenotheca trichialis*, *Ch. subroscida*, *Ch. Furfuracea*, and *Calicium lichenoides* were all more common on plots farther from the edge when all islands were examined ($r$ values between 0.32 and 0.44, $p < 0.05$).

## Discussion

Our results suggest that both the size and shape of the studied forest islands influenced the occurrences of the studied species groups. Thus, fragmentation may influence species occurrences both by area effects and through influences from the surrounding landscape (i.e., edge effects) (e.g., Andrén et al. 1997; Dettki et al. 1998). Some of the observed edge effects are likely related to the changed forest structure (i.e., tree and log sizes) at the forest edges. It is also evident that the two species groups vary in the way they respond to their fragmented environment. On a species level, three red-listed species (corresponding to one-third of all occurring red-listed

**Table 4. Average number of trees on which the lichen species was found and species richness estimates (SD).**

| *Species* | *Small islands* | *Large islands* | p[a] |
|---|---|---|---|
| *Calicium glaucellum* | 6.6 (4.8) | 9.0 (4.8) | 0.09 |
| *C. lichenoides* | 0.8 (1.1) | 1.2 (1.0) | 0.28 |
| *C. trabinellum* | 1.0 (1.3) | 0.7 (0.8) | 0.76 |
| *C. viride* | 10.6 (4.9) | 13.2 (6.6) | 0.14 |
| *Chaenotheca brunneola* | 0.05 (0.2) | 0.05 (0.2) | 0.95 |
| *Ch. chrysocephala* | 9.6 (6.5) | 9.0 (5.3) | 0.77 |
| *Ch. furfuracea* | 0.7 (1.6) | 0.8 (1.2) | 0.26 |
| *Ch. gracillima*[b] | 0.05 (0.2) | 0.1 (0.3) | 0.50 |
| *Ch. laevigata*[b] | 0.09 (0.3) | 0 | 0.17 |
| *Ch. phaeocephala* | 2.1 (1.9) | 3.8 (4.0) | 0.40 |
| *Ch. stemonea* | 1.5 (2.1) | 1.7 (2.0) | 0.64 |
| *Ch. subroscida* | 6.5 (4.8) | 8.7 (5.4) | 0.18 |
| *Ch. trichialis* | 7.2 (5.4) | 10.0 (5.1) | 0.06 |
| *Ch. xyloxena* | 0.3 (0.5) | 0.3 (0.6) | 0.95 |
| *Chaenotecopsis* spp. | 9.5 (5.4) | 13.4 (5.8) | 0.04[c] |
| *Ch. viridialba*[b] | 0.5 (0.8) | 1.0 (1.5) | 0.16 |
| *Cyphelium inquinans* | 0.1 (0.5) | 0.1 (0.4) | 0.63 |
| *C. karelicum*[b] | 0.7 (1.2) | 1.4 (1.4) | 0.05[c] |
| *Microcalicium ahlneri* | 0.05 (0.2) | 0 | 0.34 |
| *M. disseminatum* | 6.1 (5.0) | 11.2 (6.2) | 0.007[c] |
| *Sclerophora coniophaea*[b] | 0 | 0.05 (0.2) | 0.29 |
| No. of species per tree | 4.5 (2.2) | 5.0 (2.1) | 0.13 |
| No. of species per island | 10.8 (1.7) | 11.6 (1.6) | 0.15 |

[a] *Differences between small and large islands were tested with a Mann-Whitney* U *test.*
[b] *Species included in the Swedish Red List of threatened species, according to Gärdenfors (2000).*
[c] *Significant* p *value (<0.05).*

species) (Tables 3 & 4) were among the most strongly affected by island size and/or shape. This finding suggests that these species are indeed sensitive to changes in their environment and is further supported by the very strong relationship between red-listed species and island size in the study area (Berglund & Jonsson 2001).

### Size Effects

For both the epixylic hepatics and the calicioid epiphytic lichens, the number of occurrences was almost always lower on small than on large islands. Although only a limited number of species (7 out of 47) showed a significantly lower frequency on small islands, the overall pattern was clear. Three possible explanations for this pattern are that the environment on the small islands differs from that of the large islands, that smaller populations pose a higher risk of extinction, or that immigration potential is lower on small islands.

In general, the habitat on small and large islands was similar, and the only parameter that significantly differed was log size. Logs were on average 2.5 cm thicker on large islands. Several epixylic hepatics do show a preference for large logs (Söderström 1988*a*, 1988*b*), and this pattern seems to be most evident for red-listed species such as *Anastrophyllum hellerianum* and *Lophozia ciliata* (Kruys et al. 1999). However, the extent to which the observed difference in log size is the only cause for higher numbers of occurrences of these species and other hepatics on large islands is difficult to evaluate.

No differences in biotic stand variables important to the lichens were observed between small and large islands, even though there was a tendency for trees on large islands to have a coarser bark texture ($p = 0.062$). It is thus most likely that the lack of forest-interior conditions on small islands translates into fewer occurrences of many species. This view is supported by another study in the same area, in which the number of species per tree was found to be strongly correlated with increasing island size (Kruys & Jonsson 1997). Among the species showing strong affinity to large islands, one red-listed species was included—in this case, *Cyphelium karelicum*. Its tendency toward smaller population sizes on small islands was similarly observed by Kruys and Jonsson (1997), and they also showed that red-listed species in general occurred less frequently on islands of $<1$ ha.

In addition to offering a small habitat, small islands are also smaller "targets" for dispersing species. If dispersal is a limiting factor in the studied system, small islands may harbor fewer species. However, there are no relevant data for judging to what extent the studied species are dispersal-limited at scales of a few hundred meters. Parallel studies in Granlandet have failed to show any effect of isolation on species richness or composition (Berglund & Jonsson 2001, unpublished data). The distance between the islands was at most 200–300 m, and for many of the studied species this range may fall within their efficient dispersal distance (e.g., Nordén & Appelqvist 2001).

### Shape Effects

Contrary to fairly straightforward size effects, the effects of island shape within the two size classes were more complex. The increase in the frequency of occurrence of some bryophytes on irregularly shaped small islands contrasts with the overall decrease in number of species per tree on such islands among the lichens. In addition, species both increasing and decreasing with increasing shape index were present among the lichens, and two hepatics showed varying responses to the shape of large islands. This supports the notion that edge effects are complex and that species respond to these conditions in a species-specific manner (Saunders et al. 1991; Murcia 1995). Some likely explanations for the observed patterns are suggested below.

Many epixylic hepatics favor moist conditions (Söderström 1988*a*; Hallingbäck 1998). The probability that the logs in the sample plot would be in contact with the mire at the edge of small, irregularly shaped islands was likely high because sample plots on these islands were often close to the forest edge. Such logs would thus be moister and possibly more suitable for several of the studied species. Consequently, this positive edge effect could be an artifact of the study system and not a general feature of isolated forest patches.

Negative edge effects on lichens have been shown for other species, such as pendent epiphytes (Esseen & Renhorn 1998). Such effects have been interpreted as a resulting primarily from changed microclimate at patch edges (Renhorn et al. 1997). Because none of the measured tree variables were correlated with the shape of small islands, it is likely that the shape effects we observed were related to abiotic factors affecting the forest patch. Species showing significant changes in frequency related to island shape on small islands support this notion of direct edge effects. For instance, *Chaenotheca subroscida* (negatively correlated to the shape index) is regarded as a species of moderately shaded conditions (Tibell 1999) occurring in wet forests (Hallingbäck 1995), whereas *Calicium glaucellum* (positively correlated to the shape index) occurs in rather exposed situations (Tibell 1999).

### Depth-of-Edge Influence

Our results suggest that the depth of edge influence was different for the two studied species groups. The lichens were affected—in terms of species per tree and the occurrence of three species—by island shape on small islands. This finding suggests that the interior of circular small islands may approach forest-interior conditions, whereas irregularly shaped small islands are more strongly influenced by the edge. The distance to the center of a circular island with an area of 1 ha was 56 m. Thus, we believe that the depth of edge influence was probably <56 m for the lichens.

In contrast, our results suggest that epixylic hepatics respond to all small islands as they would to edge habitat. The total cover of hepatics was larger on large islands. Moreover, most hepatic species (23 of 26 species) were equally or more abundant on large islands. This suggests that conditions were more favorable for hepatic growth on large islands either as a result of abiotic conditions or as a result of increased substrate availability, because log size was also higher on large islands. There was also an almost significant positive correlation of hepatic cover with distance from patch edge among large islands. No such relationship was found on small islands, suggesting that hepatics respond to small islands of any shape in the same way. We interpret this to mean that forest-interior conditions are more common on large islands than on small islands and that the lack of hepatic response to island shape on small islands indicates that small islands represent all edge environment to these species. Our results support this interpretation: hepatic cover on small islands was highly variable and often low at a distance of <50 m, whereas there was a fairly steady increase in cover on large islands when plots were located >50 m from patch edge (Fig. 1). Thus, edge effects probably extended farther than 50 m into the forest patches for epixylic hepatics. It is possible that the large variation in hepatic cover on small islands was due to the positive correlations with island shape for some species that may be favored by the moister conditions discussed above.

To illustrate the effects of shape on the amount of forest-interior conditions, we applied the model of Laurance and Yensen (1991) to an edge effect of 50 m, based on the results of our two species groups. We determined the proportion of core area—the area not affected by edge effects—and the total area for four different shapes: round fragments ($S$ = 1.0) and rectangles with a 2:1, 4:1, or 10:1 relationship between sides ($S$ = 1.2, 1.41, and 1.96, respectively) (Fig. 2). The round shape had the least perimeter-to-area ratio, whereas a 10:1 rectangle can be seen as a linear fragment (e.g., along a creek). As evident in Fig. 2, these variations in shape had a strong effect on the amount of forest interior present. For instance, a patch with a 2:1 relationship between sides had to be >3 ha in size to have any forest interior at all, whereas a round patch of 3 ha contained 25%, or 0.75 ha, forest interior.

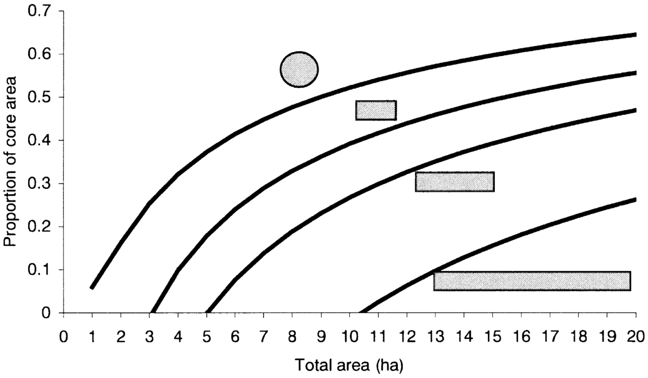

*Figure 2. Proportion of core area in relation to size and shape of habitat fragments. The functions are based on the model of Laurance and Yensen (1991). A round fragment has a shape index of 1.0, and the rectangular fragments with 2:1, 4:1, and 10:1 relationships between sides have shape indices of 1.2, 1.41, and 1.96, respectively.*

## Conclusions

Our study system may be regarded as ideal for studying size- and edge-related factors in boreal forests. It utilizes a unique system of natural stands where transient patterns caused by recent fragmentation do not play a role; thus, it allows for analysis of the long-term effects of fragmentation. In general the study confirms the existence of edge effects on epixylic hepatics and epiphytic lichens in boreal forests. However, they also exemplify the complexity of edge effects. Although some general patterns emerge, several responses may appear contradictory, emphasizing that responses to edges are strongly species-specific and context-dependent. Thus, care must thus be taken in interpreting results from edge-effect studies. The present case has clear implications for forest management—the suggested depth-of-edge influence—but the limitations should be acknowledged. A particular limitation is that the current forest stands are surrounded by a permanent matrix of wetlands and are thus not transient phases after clearcutting or other forestry operations.

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