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Modelling long-term effects of forest management on epiphytic lichens in northern Sweden

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Abstract

Species-habitat models are important tools in conservation and wildlife management today. Models simulating the long-term ecological consequences of forestry on biodiversity have large potential as guidance for management. In this paper, we evaluated a model, lichen biomass spatially explicit model (LIBSEM) that predicts the temporal and spatial distribution of epiphytic lichens in boreal coniferous forests. We assessed model performance by simulating the standing crop of pendulous lichens (*Bryoria* spp.) over a 50-year period in a managed forest landscape (Brattåker, 4405 ha). We compared the simulated data with independent field data based on sampling of lichen litter in 54 plots stratified by forest age class. Simulated epiphyte standing crop was significantly related to field data but overall model performance was rather poor at the cell level (50 m × 50 m cells) with a modelling efficiency of 12%. Results suggest that the model succeeded better in predicting lichen biomass on the landscape level. We used LIBSEM to assess possible long-term consequences on epiphytes of four management scenarios differing in the length of the rotation cycle. The change in epiphyte biomass was projected over a 200-year period. Results show that an even-aged silvicultural system with a normal rotation (110 years) only can support a low amount of pendulous lichens while short rotation (60 years) is very detrimental to epiphyte communities. Thus, to enhance the abundance of epiphytic lichens it is necessary to use extended rotations, preferably in combination with forest reserves. We conclude that spatially explicit landscape models may act as a guide for managing boreal forests to improve conditions for epiphytes.

Keywords: Epiphytic lichen; Spatially explicit model; Boreal forest; Extended rotation

1. Introduction

Most of the boreal forests in Fennoscandia are used by commercial forestry. This has numerous and mostly negative consequences for biodiversity (Esseen et al., 1997; Niemelä, 1997). However, it is not a trivial task to assess the long-term effects of forest management on biodiversity. This is because of the intrinsically slow development of forest stands and because disturbance plays a major role in shaping the structure and dynamics of forest ecosystems (Oliver and Larson, 1990; Engelmark, 1999). The processes that influence the dynamics of both natural and managed forests operate over a vast range of spatial and temporal scales (Spies and Turner, 1999). This makes it difficult or at least costly to assess the ecological effects of forest management activities on biodiversity through comparative field studies or large-scale landscape experiments.

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Species-habitat models are important tools with large potential in conservation and wildlife management (e.g. Verner et al., 1986; Haefner, 1996; Beutel et al., 1999). Spatially explicit landscape models have much to offer to conservation managers (Meir and Kareiva, 1999; Mladenoff and Baker, 1999). For example, landscape models may help us to better understand the long-term consequences of different forest management scenarios. They can, thus, act as a guide to find the best compromise between multiple management goals.

Forest management practices have important implications for canopy-dwelling organisms such as epiphytes. Epiphytic lichens are particularly sensitive to forestry (Esseen et al., 1996; Sillett et al., 2000). This is because many species are associated with particular conditions only found in old-growth forests, and because epiphytic lichen biomass accumulates slowly over time. For example, it may take 100–400 years to build up high epiphyte biomass in the forest canopy (McCune, 1993; Esseen et al., 1996). Recent studies strongly suggest that dispersal limitation is a key factor behind the low epiphyte abundance in young managed forests (Dettki et al., 2000; Sillett et al., 2000; Hilmo and Såstad, 2001). Epiphytic lichens have several important functional roles in forest ecosystems. They increase structural complexity, modify canopy water regimes, influence nutrient cycling and provide habitat, food and nest material for many animals (Galloway, 1992; Rhoades, 1995). There is, thus, a need to develop forest management methods that permit the accumulation of abundant and diverse epiphyte communities.

In this paper, we applied the spatially explicit landscape model, lichen biomass spatially explicit model (LIBSEM); Dettki, 2000) to a managed forest landscape. LIBSEM predicts the spatial and temporal distribution of epiphytic lichen biomass in boreal forest landscapes by linking lichen population dynamics (growth, dispersal, litterfall) to the pattern of forest harvesting and succession. The paper has two objectives. First, we validated the efficiency of the model by comparing predicted data with field data on abundance of pendulous lichens (*Bryoria* spp.) for a managed boreal forest landscape. Second, we analysed possible long-term consequences of forestry on epiphyte abundance in the landscape by simulating four different management scenarios, differing in the length of the rotation cycle, over a period of 200 years and assessed the overall effect of these scenarios.

2. Study area

Field sampling was performed in the Brattåker area, located in Västerbotten county, northernmost Sweden (Fig. 1). The Brattåker area is located at 63°35′N, 20°15′E (WGS84), 60 km north-west of Umeå, and has a total area of 6400 ha. It belongs to the middle boreal zone as defined by Ahti et al. (1968). The landscape is limited to the east by the Vindel River. From the riverbanks at 150–170 m a.s.l., the landscape comprises to the west of coarse glaciofluvial sediments, followed by hilly terrain with deep moraines and mires in the valleys. The highest hills were just above 400 m a.s.l. Conifers dominate the forests and they are relatively little influenced by air pollution. Most (87%, 4405 ha) of the landscape consists of productive forest land (annual production $> 1\ \mathrm{m}^3$/ha), followed by open mires (9%) and lakes (2%). Remaining landscape elements (2%) are mainly agricultural land and forest impediments. Forest fire was the most important natural disturbance in the area until about 1875, when the extent of fires decreased steeply due to the fire suppression policy (Zackrisson, 1977; Niklasson and Granström, 2000). The mean fire interval was about 100 years prior to fire suppression. Large scale logging, mainly through cutting of large pines, started around 1850 (Bunte et al., 1982; Östlund, 1993). Clear-cutting was introduced into the area in the 1930s and has been the dominant logging method since the 1950s (Fries and Lämås, 2000). Almost all of the area is currently used by commercial forestry. Nearly half (49%) of the forest is comprised of stands younger than 50 years while stands between 50 and 130 years comprise 49%. Only 2% of the forests are older than 130 years. Scots pine (*Pinus sylvestris*) is the most abundant tree species (46% of total basal area) followed by Norway spruce (*Picea abies*; 41%) and deciduous trees (mainly birch, *Betula* spp.; 13%). For a more detailed description of the study area, see Lämås and Fries (1995), Wallerman (1998) and Fries and Lämås (2000).

The forest floor vegetation varied from dry *Vaccinium vitis-idea* and *Cladonia* spp. dominated stands to mesic dwarf shrub type stands dominated by *V. myrtillus* (Arnborg, 1990). Foliose and fruticose lichens with green-algal photobionts dominated the epiphyte vegetation. The most abundant foliose lichens were *Hypogymnia physodes*, *H. tubulosa*,

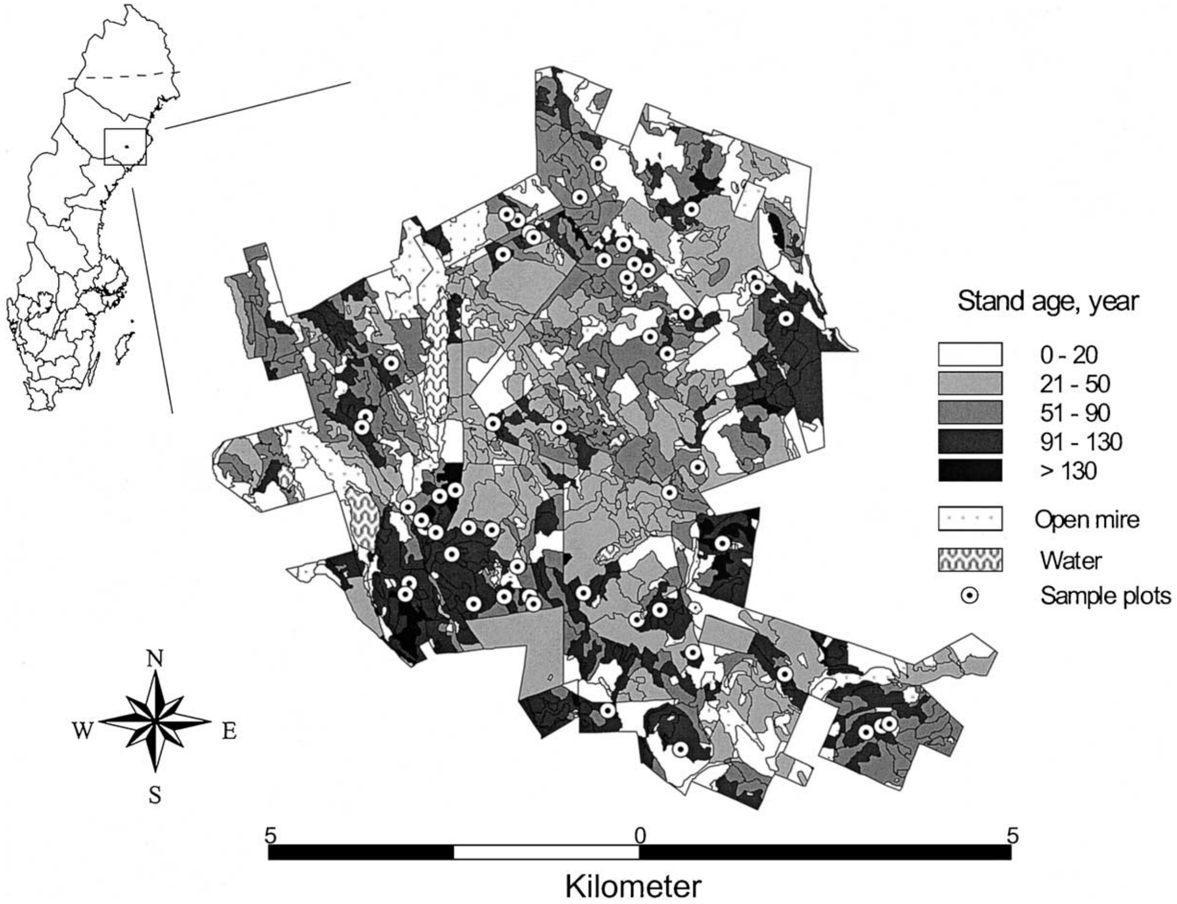

Fig. 1. Map of the study area at Brattåker. Sample plots are indicated with (⊙). The inset map shows the location of the Brattåker landscape in northern Sweden.

and *Platismatia glauca*, while pendulous lichens such as *Bryoria capillaris*, *B. fremontii*, and *B. fuscescens* dominated the fruticose lichens. In young and intermediate-aged stands *Hypogymnia* spp. were most abundant followed by *Bryoria* spp. *Alectoria sarmentosa* was abundant in old spruce stands, while it was absent from most younger stands.

3. Methods

3.1. Sample plots

An extensive data set on stand structure was already available from the Brattåker area. Information on size and form of forest compartments was obtained from the landowner, the forest company Holmen AB, in the form of GIS-data (Arc/Info; ESRI, 1998). Data on stand structure from 1996 was obtained from a detailed stand inventory performed in the area (Christoffersson and Jonsson, 1996; Wallerman, 1998). This inventory was based on measurements made in 2446 circular plots (10 m radius) distributed in a regular grid and stratified by the density of the forest: more sample plots were allocated to mature and well-stocked stands (Wallerman, 1998). We used the following variables from the stand database: tree age, stem density, basal area, volume, and tree species composition. For the purpose of the present study we estimated stand age for all 639 compartments, sized 0.2–111 ha, by calculating the mean age for all sample plots located within each compartment.

We used square sample plots (sized 50 m × 50 m hereafter 'forest cells') for sampling pendulous lichens to enable comparison with model predictions. Fifty-four forest cells were selected by stratified random sampling from a total of 17,620 cells. The strata constituted the three oldest age classes: intermediate age (51–90 years), mature (91–130 years), and old stands (>130 years). Sample plots were allocated in proportion to stratum area: 19 in intermediate aged stands, 30 in mature stands, and 5 in old stands. No sampling was done in stands younger than 50 years as such stands normally have very low epiphyte biomass (Dettki and Esseen, 1998) and it is difficult to obtain accurate estimates. The 54 selected cells fulfilled the following criteria: (1) the midpoint of the cell was within 10 m distance from one of the 2446 plots in the stand inventory, (2) the entire cell was located within one compartment (i.e. no compartment borders were crossing the cell), and (3) any unmapped non-forest vegetation patches within a cell comprised less than 10% of the cell area (checked in the field).

3.2. Data collection

In July 1999 the midpoint of each cell was located with a handheld global positioning system receiver (Garmin GPS 12XL) with differential real time correction (maximum positional error <10 m). The stand structure was briefly checked against the data from the stand inventory (Wallerman, 1998). In a few cases the stand had been cut since the inventory and a new cell had to be chosen. We estimated the abundance of epiphytic lichens in the canopy by sampling lichen litter on the ground based on procedures presented and discussed by McCune (1994), Dettki and Esseen (1998), and Esseen and Renhorn (1998a). Three sub-samples (2 m × 2 m) were placed out on the forest floor in the 50 m × 50 m cells based on a random direction and distance from the midpoint of the cell. We collected all thalli and fragments of pendulous lichens including those on fallen twigs and branches. After air-drying the litter samples to prevent decomposition, all pendulous lichens >1–3 mm were cleaned from non-lichen material like bark, twigs, or needles and separated into three groups: *A. sarmentosa*, *Bryoria* spp., and *Usnea* spp. The samples were dried for 24 h at 80 °C and weighed to the nearest mg. Pendulous lichens were found in most (91%) of the 162 sub-samples. The distribution of litter biomass was strongly skewed towards small values: the mean was nearly five times larger than the median, 1.03 and 0.22 g per 4 m^2, respectively. We pooled the data from the three sub-samples in each forest cell and calculated mean biomass of epiphyte litter in g dry weight (d.w.) per m^2. However, two of the sub-samples had very high lichen biomass (>10 g), clearly deviating from the others. This was probably due to heavy load of epiphytes on large branches. Inclusion of these two sub-samples resulted in unrealistically high lichen biomass in relation to the age of the stands. We, therefore, treated these sub-samples as outliers and excluded them from further analysis. Hence, the biomass estimates in these cells are only based on two sub-samples. For *Bryoria* spp. we converted the lichen litter to epiphyte standing crop in the canopy by multiplying with a factor of 56.7 following the procedure described and discussed by Dettki (2000). This conversion was based on assumptions of annual rate of litterfall, litter decomposition rate, and sampling efficiency.

3.3. Lichen abundance model

We used a cell-based, mechanistic model (LIBSEM) to predict the abundance of epiphytic lichens in the Brattåker landscape. LIBSEM estimates the standing crop (in g/m^2) of pendulous lichens in the genus *Bryoria* in forest cells (50 m × 50 m). It is assumed that all stands in the landscape are even-aged and that they all are managed by clear-cutting. The initial lichen biomass was first estimated for all 17,620 cells in the landscape. The annual change in biomass was then calculated based on lichen growth, litterfall, local dispersal (affected by distance to adjoining cells), regional dispersal (constant), and the carrying capacity, i.e. the maximum possible lichen load in the forest (determined by forest age and proximity to forest edge). LIBSEM has been parameterised and validated with biomass data for *Bryoria* spp. taken from Dettki and Esseen (1998). The key algorithms of LIBSEM and further details are given in Appendix A and in Dettki (2000).

3.4. Model validation

Only very limited quantitative information is available in the literature on population parameters regulating the dynamics of epiphyte populations (Dettki, 2000). For the purpose of this paper we selected one combination of parameter values that we assumed to be biologically relevant. We used an annual lichen growth rate g of 30%. This is higher than reported by Renhorn and Esseen (1995), from a site not far from the present study area, but in the same range as found in other studies (McCune et al., 1996; S.K. Stevenson, personal communication). The growth rate found by Renhorn and Esseen (1995) refers to growth of individual thalli in the lower canopy and is probably lower than the 'mean' growth in the forest canopy as a whole. We used a local dispersal rate d of 10% (i.e. percent of annual litterfall that re-established in the canopy within a 200 m distance). No data on this parameter are available in the literature, but 10% is a reasonable value (Dettki, 2000). A sensitivity analysis showed that the model outcome was not particularly sensitive to changes in the local dispersal rate for the used parameter set. Further, we estimated the annual regional dispersal R to be 0.01 g/m^2, based on the number and size of fragments found at least 200 m distance from a forest edge (Dettki, 1998) and on the dry weight of cm-sized fragments of *B. fuscescens* (Dettki, unpublished data). We arbitrarily used a carrying capacity in the landscape $K_{\max}$ of 50 g/m^2. Model runs started in 1949 with reconstructed landscape structure and epiphyte distribution over the landscape. The estimated initial standing crop of *Bryoria* spp. (in g/m^2) in all cells in the landscape was based on a relationship between epiphyte biomass and forest age as described in Appendix A.2. and Dettki (2000).

Model performance was evaluated at the level of individual forest cells by comparing simulated lichen biomass with field data for the 54 cells that we sampled in 1999. We used the modelling efficiency EF (Loague and Green, 1991) for model validation. The modelling efficiency can be interpreted as the proportion of variation explained by a 'regression line' with slope $= 1$ and intercept $= 0$. By this, an EF value of 100% would mean a 'perfect' fit, i.e. the predicted values equal the field samples, while EF values less than zero, though possible, indicate models that cannot be recommended (Loague and Green, 1991). We also assessed model performance at the landscape level by calculating the quota between the average predicted biomass for all 54 cells and the average biomass for the field data.

3.5. Forest management scenarios

We assessed the possible long-term consequences on abundance of epiphytic lichens by using LIBSEM to simulate four different forest management scenarios. We only considered an even-aged silvicultural system based on clear-cutting of whole compartments. Three different rotation cycles were used: short-rotation forestry (60 years), normal rotation (110 years), and long rotation (160 years). As a reference ('no forestry' scenario) we also simulated the development of epiphyte abundance in the absence of logging or other forest management activities. Natural disturbances, such as forest fire and windthrow, were not considered in the scenarios. Therefore, the 'no forestry' scenario will overestimate epiphyte abundance compared to the natural state. The simulations were performed using the same parameter set as in the model validation. For the first 50 years of model simulation (1949–1999) we used the actual data on forest harvesting taken from historical records for the area. We projected the biomass of *Bryoria* spp. and stand age distribution over a 200-year period (2000–2199) for the different management scenarios.

4. Results

4.1. Lichen abundance

The litter of pendulous lichens on the forest floor was dominated by *Bryoria* spp. (84.5%), followed by *Alectoria sarmentosa* (10.2%) and *Usnea* spp. (5.3%). There was large variation in the amount of lichen litter among forest cells, from 0.001 to 1.99 g/m^2, with an overall mean of 0.303 g/m^2 ± 0.055 g/m^2 (mean ± 1S.E.; $n = 54$; Table 1). The combined biomass of all pendulous lichens increased with forest age ($r = 0.33$, $P = 0.014$). Old stands (>130 years) had four times higher litter biomass than stands of intermediate age (51–90 years), 0.59 g/m^2 ± 0.24 g/m^2 ($n = 5$) and 0.14 ± 0.04 g/m^2 ($n = 19$), respectively (Table 1).

We converted the litter samples of *Bryoria* spp. to epiphyte standing crop. The estimates ranged from 0.06 to 68.5 g/m^2 with an overall mean of 14.5 g/m^2 ± 2.4 g/m^2 (mean ± 1S.E. $n = 54$). The standing crop of *Bryoria* increased strongly with forest age class:

Table 1
Mass (g d.w./m^2) of lichen litterfall by forest age class for three groups of epiphytic lichens

Age class	*n*	*Alectoria*	*Bryoria*	*Usnea*	Total
Intermediate (51–90 years)	19	0.005 ± 0.005	0.134 ± 0.040	0.004 ± 0.002	0.142 ± 0.044
Mature (91–130 years)	30	0.038 ± 0.036	0.299 ± 0.062	0.021 ± 0.008	0.357 ± 0.083
Old (>130 years)	5	0.089 ± 0.079	0.465 ± 0.184	0.033 ± 0.018	0.587 ± 0.236
Total	54	0.031 ± 0.014	0.256 ± 0.042	0.016 ± 0.005	0.303 ± 0.055

Mean ± 1S.E. Sample plots were stratified by forest age class.

7.6 ± 2.3, 17.0 ± 3.5 and $26.3\,\mathrm{g/m^2} \pm 10.4\,\mathrm{g/m^2}$, in intermediate, mature, and old stands, respectively. The relationship between standing crop and stand age was significant ($r = 0.36$, $P = 0.007$) but there was a large scatter among the points (Fig. 2). Overall, however, the abundance of *Bryoria* was best explained by the amount of spruce in the forest cells. The strongest relationships were found for density ($r = 0.64$, $P = 0.000$; Fig. 3), basal area ($r = 0.45$, $P = 0.001$) and volume of spruce ($r = 0.38$, $P = 0.004$). In contrast, the abundance of *Bryoria* showed no significant relationships with the amount (basal area and volume) of pine or deciduous trees.

4.2. Model performance

The estimated lichen biomass values showed less variation than the field data, with coefficients of variation (CVs) of 51 and 121%, respectively. Simulated biomass showed a significant positive relationship with the field observations ($r = 0.38$, $P = 0.005$; Fig. 4). Modelling efficiency was rather low (12%) but the performance was strongly dependent on tree species composition. The model succeeded better in spruce-dominated (by volume) forest cells: the relationship between predicted and observed biomass was highly significant ($r = 0.51$, $P = 0.000$, $n = 27$; Fig. 4). However, the model underestimated epiphyte biomass by a factor of about 2 in the spruce stands. In contrast, the relationship was not significant for pine-dominated cells ($r = 0.33$, $P = 0.092$; $n = 27$).

The modelling efficiency cannot be calculated at the landscape level due to lack of replication. However, the mean simulated biomass for the 54 cells was rather close to the field data, with a ratio of 0.83 between simulated and actual biomass. This suggests that LIBSEM is capable of delivering reasonable biomass estimates for the landscape as a whole.

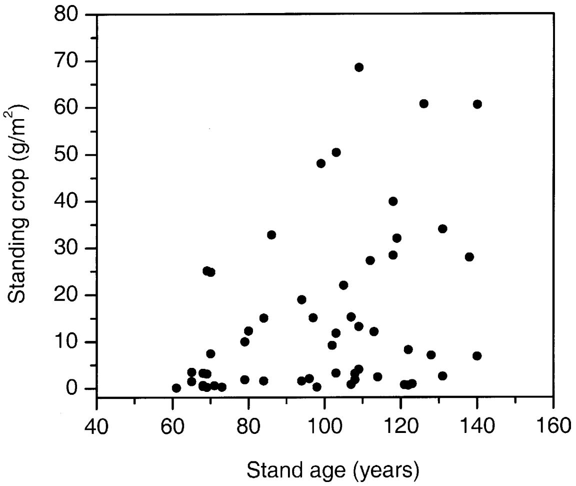

Fig. 2. Relationship between standing crop of *Bryoria* spp. and stand age. $n = 54$.

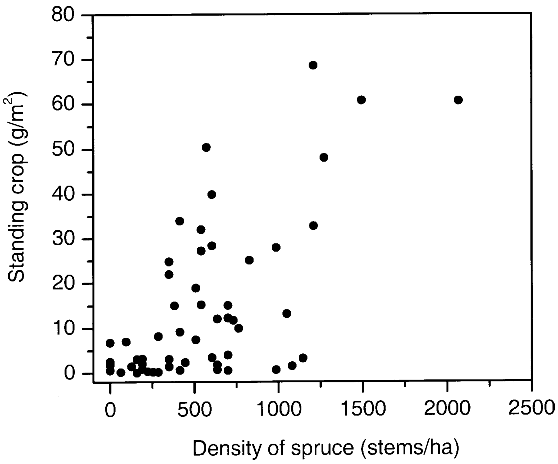

Fig. 3. Relationship between standing crop of *Bryoria* spp. and stem density of spruce. $n = 54$.

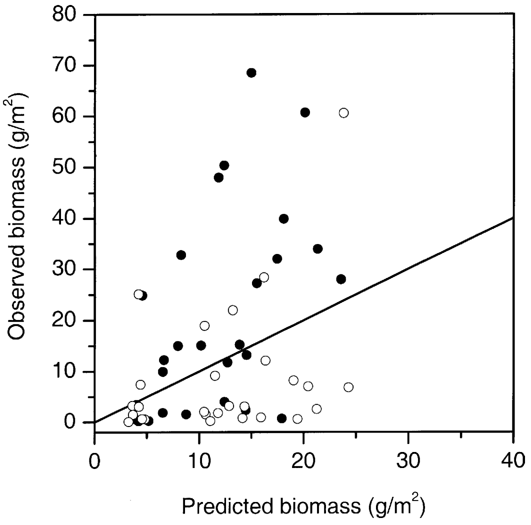

Fig. 4. Relationship between observed and predicted standing crop (g/m^2) of *Bryoria* spp. Closed symbols denote spruce-dominated (by volume) forest cells ($n = 27$) and open symbols denote pine-dominated cells by ($n = 27$). The solid line indicates a 1:1 relationship.

4.3. Forest management scenarios

The simulated management scenarios showed that the abundance of pendulous lichens in the landscape was strongly influenced by the length of the rotation cycle. The abundance of *Bryoria* spp. decreased rapidly when shortening the rotation cycle. We evaluated the four management alternatives by calculating the average lichen biomass over the simulated 200-year period. Average biomass constituted 1.7% in short rotations, 14.5% in normal rotations, and 37.8% in long rotations compared to the 'no forestry' scenario (Fig. 5). Continued use of clear-cutting with a 110-year cycle will lead to 19% lower lichen abundance after 100 years (2099) and 15% lower after 200 years (2199) compared to the present (1999) situation (Fig. 5). The short-rotation scenario could only support a very small amount of pendulous lichens: the biomass was 13.5 times lower than in the normal-rotation scenario after 200 years (Table 2). In contrast, the simulations suggest that a forestry with long rotations (160 years) can support nearly three times higher standing crop of lichens compared to normal rotations (Table 2), approaching the levels found 50 years ago (Fig. 5).

The spatial distribution of lichen abundance in the landscape (Fig. 6) largely reflected differences in stand age distribution between the four management scenarios. In the short-rotation scenario, there was a four-fold increase in the area of clear-cuts and young

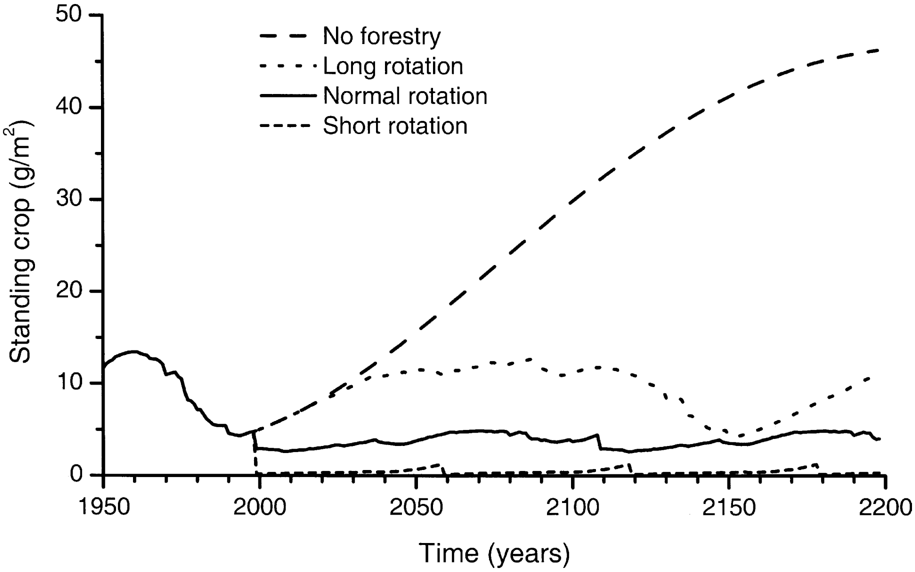

Fig. 5. Long-term change in predicted standing crop of *Bryoria* spp. and forest area following four different management scenarios: (1) short rotation (60 years), (2) normal rotation (110 years), (3) long rotation (160 years), and (4) no forestry. Standing crop is expressed as average biomass (g/m^2) for all forest cells in the Brattåker landscape.

Table 2
Predicted long-term consequences on standing crop of *Bryoria* spp. following four different management scenarios

Scenario	100 years	200 years
Short rotation (60 years)	16865	13172
Normal rotation (110 years)	169490	177343
Long rotation (160 years)	484926	480066
No forestry	1288748	2037181

Standing crop is expressed as total epiphyte biomass (kg d.w.) in the Brattåker landscape (4405 ha forest land) after 100 years (2099) and 200 years (2199).

forests (0–20 years) after 200 years compared to the present situation (1999; Table 3). In contrast, prolonging the rotation cycle to 160 years will result in a tenfold increase in the area of old forest (>130 years). However, even with this increase, old forest will only represent 19.5% of the Brattåker landscape in this scenario.

5. Discussion

5.1. Lichen abundance

The composition of the epiphyte community in the Brattåker landscape showed large similarity with that of other managed forests in northern Sweden (Dettki and Esseen, 1998; Dettki et al., 2000). Green-algal foliose lichens as *Hypogymnia* spp. were common and the abundance of pendulous lichens was low due to the large proportion of young stands. This is because

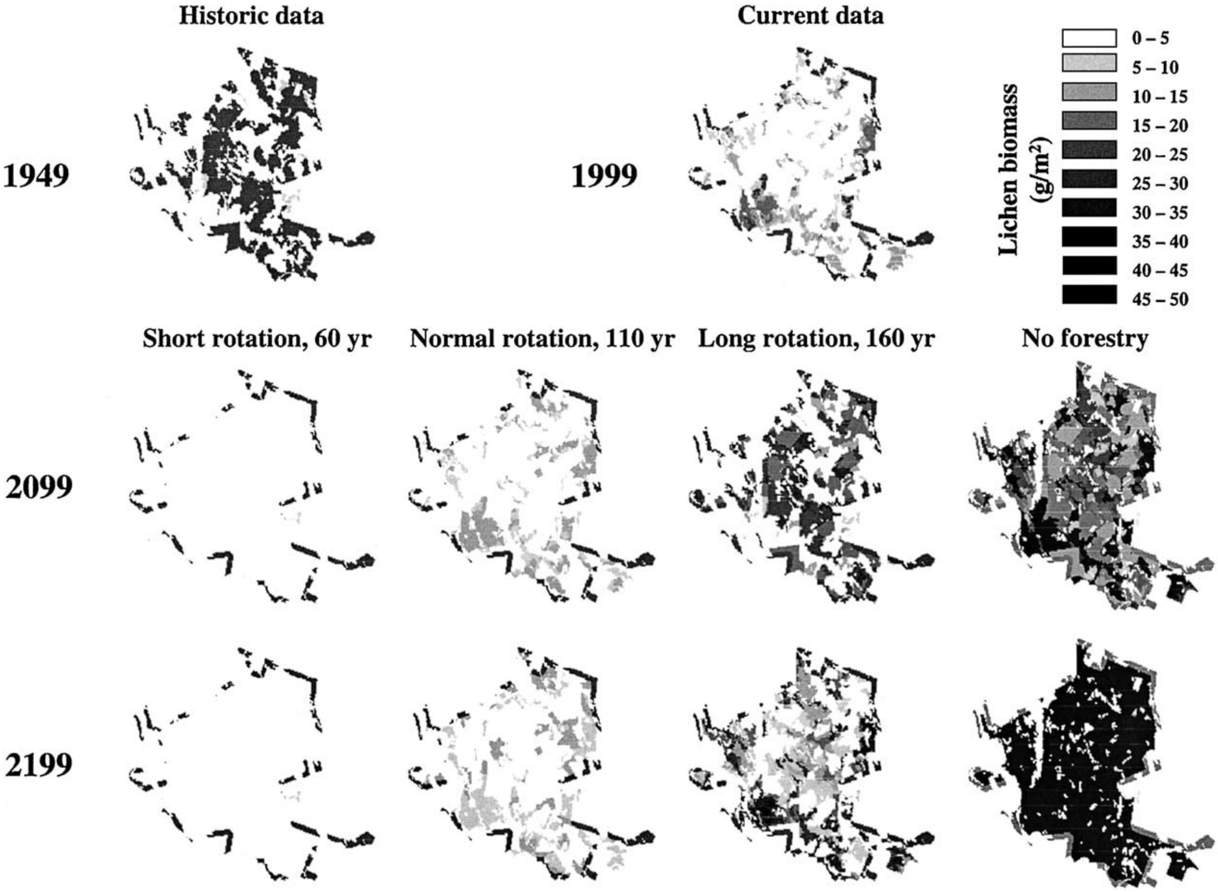

Fig. 6. Maps showing the spatial distribution of standing crop of *Bryoria* spp. in 1949 and 1999 and predictions after 100 and 200 years in four different management scenarios differing in the length of the rotation cycle. The lichen biomass was kept constant in a 250-m wide artificial buffer zone along the map border.

Table 3
The area (ha) of forest land in five different age classes for the present situation (1999) and estimated after 200 years (2199) in four different management scenarios differing in the length of the rotation cycle

	Forest age (years)				
	0–20	21–50	51–90	91–130	>130
Present situation (1999)	652	1516	1175	977	85
After 200 years (2199)					
Short rotation (60 years)	2652	1333	420	0	0
Normal rotation (110 years)	1174	1068	1547	616	0
Long rotation (160 years)	195	222	1955	1175	858
No forestry	0	0	0	0	4405

of the generally slow accumulation of epiphyte mass in boreal forests (Esseen et al., 1996). The dominant pendulous lichens were *Bryoria* spp., while *A. sarmentosa* was rare except in a few old spruce stands. We found strong relationships between lichen biomass and several stand structural parameters paralleling the findings of Dettki and Esseen (1998). Thus, Brattåker has an epiphyte community representative for managed boreal forests in northern Fennoscandia and is well suited for validation of the simulation model, LIBSEM.

5.2. Model validation

LIBSEM was able to predict the current (1999) biomass of *Bryoria* spp. based on reconstructed biomass data 50 years back in time. The relationship between predicted and observed values was significant but modelling efficiency was low at the cell level. The low efficiency is not surprising considering the numerous factors that can influence model performance. In the following we discuss three of these factors: (1) the data set used for validation, (2) the assumptions and functions in LIBSEM, and (3) variables not considered in the model.

First, the low modelling efficiency (12%) may be partly explained by the field data set used for validation. There was a rather small range in stand age (61–140 years) among the sample plots implying a reduced variation in epiphyte biomass. Inclusion of clear-cuts and young stands, with no or only tiny amounts of lichens, and old-growth stands (however absent in the area), often with high standing crop, would probably have increased the modelling performance. Further, we evaluated the model after 50 years. This is a rather short time in relation to the slow accumulation of epiphyte biomass (McCune, 1993; Esseen et al., 1996). Finally, there was a large variation in the standing crop between the sampled forest cells. This is partly due to the characteristic patchy distribution of epiphyte litter on the forest floor (McCune, 1994) and partly due to the sampling procedure. Much of this variation is caused by higher litter deposition beneath source trees (Esseen, 1985; Sillett and Goslin, 1999). This was probably the main reason for the large variation in lichen litter among the three sub-samples in some plots. Thus, we have probably underestimated the modelling efficiency of LIBSEM because of variation in the field data. A dramatic increase in the litterfall sampling is clearly required to accurately characterise the distribution of epiphytic lichens at the landscape level. Although such sampling is costly and time-consuming it should nevertheless be considered in future studies.

Second, several assumptions and simplifications are made in LIBSEM (Dettki, 2000). For example, the form of the dispersal curve is of crucial importance for the pattern of epiphyte colonisation in young forests (Dettki et al., 2000). The dispersal curve for *Bryoria* spp. implemented in LIBSEM is based only on data for dispersal by thallus fragments, ignoring that dispersal by soredia is also important in this genus. Soredia are much smaller than thallus fragments and are therefore expected to be more efficient in long-distance dispersal, thus showing a different dispersal curve. We may have also chosen the wrong parameter values or functions due to the scarcity of available data (Dettki, 2000). For example, the available data on lichen growth is very sparse and the literature data refer to growth of individual thalli rather than the gross growth rate used in the model. Further, the carrying capacity may be different in pine- and spruce-dominated stands and the chosen 50 g/m^2 was probably too low for spruce stands and too high for pine stands (cf. Fig. 4).

Third, several variables are currently not included in LIBSEM, for example topography, wind direction, and stand structural attributes. Our results show that the biomass of *Bryoria* spp. is strongly linked to the amount of spruce. The stem density of spruce, reflecting substrate availability, was clearly an important variable (Fig. 3), explaining 41% of the variation in biomass. The performance of LIBSEM was strongly dependent on tree species composition: only spruce-dominated stands showed a significant relationship between predicted and observed lichen biomass (Fig. 4). This suggests that model performance could be improved by including information on stand structure, especially tree species composition.

The model thus helped us to identify the gaps in the knowledge regarding the population dynamics of epiphytic lichens. It must be stressed that there is an urgent need for more detailed data on growth and dispersal, both local and regionally, of epiphytic lichens under different environmental conditions. Landscape topography, main wind direction, and tree species composition should be included into the model. Edge effects on lichen abundance, especially between old and young stands, should be investigated further. Thus, by having more information on lichen population dynamics and stand and landscape structure we could probably improve the performance of the model at the cell level (0.25 ha). However, as a mechanistic model, LIBSEM should not primarily judged on predicted precision in terms of absolute values of biomass, but rather on the theoretical correctness of the predicted response (Pickett et al., 1994; Guisan and Zimmermann, 2000). Hence, for deciding the best management strategy very exact estimates of epiphyte abundance for individual forest cells are probably not necessary. We conclude that LIBSEM is well suited to predict lichen abundance on broader spatial and temporal scales and for evaluating the relative performance of different management scenarios.

5.3. Management scenarios

The simulated management scenarios strongly suggested that the current even-aged silvicultural system, based on clear-cutting, is very detrimental to epiphytic lichens. Both normal (110 years) and short-rotation (60 years) scenarios could only support a small amount of pendulous lichens compared to both the historic level and to the amount estimated without forestry. However, it should be kept in mind that our 'no forestry' scenario overestimates the abundance of pendulous lichens that would be found in a landscape regulated by a natural disturbance regime. Instead, the high lichen biomass in this scenario may possibly reflect the future situation in many boreal forest reserves in Sweden. This is based on the increased amount of spruce in reserves following the current fire suppression policy (Linder et al., 1997). We can only speculate about the natural level of pendulous lichens in the Brattåker landscape. An estimation based on the data of Dettki and Esseen (1998) suggests a natural level in the range of 15–30 g/m^2. This is close to the situation in the 'no forestry' scenario after 100 years (Fig. 5).

Rotation cycles have decreased significantly during the past 100 years (Linder and Östlund, 1998). If they continue to shrink, for example, due to the use of faster growing provenances or tree species, this will pose an even more severe threat to epiphyte communities. Our results are in line with another study in the Brattåker area (Fries and Lämås, 2000), where five different management regimes were simulated to assess the effect on biodiversity. Fries and Lämås (2000) predicted a high probability that 17 red-listed species would go extinct within the next 100 years in two of the regimes: one with highest timber production (HTP; resembling the normal-rotation scenario in the present study) and one with modified timber production (MTP). No forest was protected in both regimes. Shifley et al. (2000) simulated five different management regimes in the Mark Twain National Forest, Oregon, with the spatially explicit forest model LANDIS (Mladenoff et al., 1996) to assess timber production and the quantity of edge and interior area as measures of possible biodiversity. While both the 'no forestry' scenario and the intensive rotation regime (50-year rotation) produced the highest amount of timber, total edge length was 13.8 times higher and core area 4.9-fold smaller in the intensive rotation regime, suggesting a lower biodiversity.

Our simulations clearly show that extending the rotation cycle is an efficient method for enhancing the abundance of pendulous lichens. This supports previous studies that advocate the use of extended rotations to enhance abundance and diversity of old-growth associated lichens in managed forests (Esseen et al., 1996; Dettki and Esseen, 1998; Kuusinen and Siitonen, 1998; Sillett and Goslin, 1999). Using extended rotation is probably the most efficient way to restore stands with old-growth attributes. In the Brattåker area, using long rotations (>160 years) on some portion of the landscape is required to enhance the abundance of *A. sarmentosa*, a species strongly associated with late-successional spruce stands (Esseen et al., 1996). The best approach, however, would be to use long rotations in combination with forest reserves.

Our findings are supported by several other studies (e.g. Busing et al., 1995; Halpern and Spies, 1995; Burton et al., 1999; Marshall, 2000), which advocated prolonged rotation cycles to conserve biodiversity. In general, extended rotations have several possible advantages, for example for long-term site productivity, wood quality, hydrology, and biodiversity (Curtis, 1997). Old forests are not only beneficial to epiphytic lichens but also to a large number of other boreal organisms, including many fungi, bryophytes, and invertebrates (Esseen et al., 1997). However, there are both economical and ecological limitations to the extended rotation approach. Even a small increase in rotation age can be quite costly (Hansen et al., 1995; Lämås et al., 1996). Especially for spruce, Lämås et al. (1996) predicted a high economical loss for prolonging the rotation cycle by 50 years. A recent study (Martikainen et al., 2000) showed that some groups of beetles were not favoured by extending the rotation cycle.

We do not argue for extending the rotation age in all stands in the landscape but rather to use a wider range of rotation ages than today. For example, the negative exponential age structure, often used as a model for a natural disturbance regime with stand-replacing fires, could be emulated by varying the rotation age for different portions of the forest (Seymour and Hunter, 1999). Such an approach will create habitat for both early- and late-successional species. Extended rotation may be used with or without partial cutting and thinning to achieve specific management goals (Curtis, 1997). Another approach that may be used in combination with extended rotations is retention of trees on cutting units. Recent studies strongly suggest that retention of live trees, both individually and in groups, can promote abundance of epiphytic lichens in young forests by functioning as source of propagules (Peck and McCune, 1997; Sillett and Goslin, 1999; Dettki et al., 2000). However, currently there are limitations to use retention of lichen-rich trees in the Brattåker area because of the low amount of old forest. Hence, extended rotations are required prior to extensive use of retention in this landscape.

6. Conclusions

We conclude that spatially explicit landscape models may act as a guide for managing boreal forests to improve conditions for epiphytic lichens. This will be important in fulfilling multiple management goals like sustainable forestry, reindeer husbandry, and conservation of biodiversity. Models like LIBSEM may help us to determine the harvest levels and the distribution of rotation ages required for a long-term sustainable biomass of pendulous lichens. Further, the merging of LIBSEM with other spatially explicit forest models as, e.g. LANDIS (Mladenoff and He, 1999; Shifley et al., 2000) or LEEMATH (Li et al., 2000) will increase the usefulness of LIBSEM as a tool in forest management planning. For example, LIBSEM might be improved by including other harvesting methods, such as partial cutting, and natural disturbances, such as forest fire and wind throw. An integration of LIBSEM with economic forest models as e.g. LEEMATH (Li et al., 2000) will enable decision makers to evaluate proposed forest management regimes from both an economic and ecological point of view.

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Appendix A

LIBSEM is a grid-based simulation model that describes the interactions of the relevant processes determining the biomass of epiphytic lichens over time in dynamic forest landscapes. The model basically consists of two parts, a dynamic forest landscape model given as annual maps of forest age, and a lichen model describing the dynamics of lichen biomass within the landscape. Below we give the key algorithms of the model and describe the relevant processes in detail.

A.1. Lichen biomass dynamics

Based on an estimated initial lichen biomass $B_{t=0}$ in a forest cell (50×50 m^2), the change in biomass ΔB is calculated in annual time steps ($\Delta t = 1$) based on annual growth G and litterfall L. The surrounding cells contribute to the biomass of the focal cell ('center' cell) by local dispersal of a certain amount of lichen fragments I. Each cell also gains a constant annual input of regional dispersed lichen propagules R. The lichen biomass B at time t in each cell approaches the lichen carrying capacity K of the forest cell using a standard logistic function. The annual change in lichen biomass (Eq. (A.1)) is thus calculated as

$$\frac{\Delta B}{\Delta t} = (G - L + I + R)\left(1 - \frac{B}{K}\right) \qquad \text{(A.1)}$$

A.1.1. Carrying capacity

The maximum possible biomass in each cell, the 'carrying capacity' K (Eq. (A.2)), is a function of the forest age (AGE) in the cell and the maximum possible carrying capacity $K_{\max}$ anywhere in the modelled landscape (Fig. 7). Further, K is lowered by edge effects E, due to e.g. changes in light, wind speed and humidity in the edge zone. It has been shown that epiphyte abundance is lower in old stands bordering young stands or clear-cuts (e.g. Sillett, 1995; Esseen and Renhorn, 1998b). Therefore, edge effects E only affects cells with old forest that directly adjoin cells with younger forest. E has always a negative effect and reduce the carrying capacity K to a minimum of 50%, using a linear function, i.e.

$$K = f(K_{\max}, \mathrm{AGE})E \qquad \text{(A.2)}$$

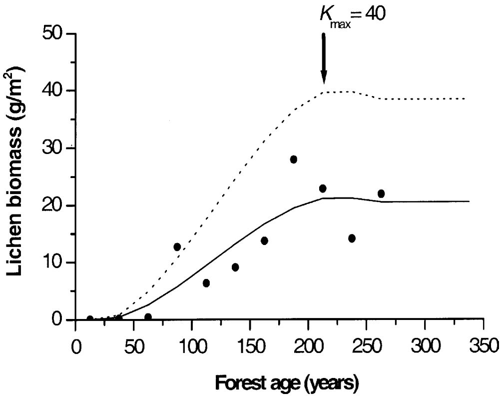

Fig. 7. Estimated initial lichen biomass and carrying capacity. A cubic function (—) was fitted to field data (●), representing the initial lichen biomass in relation to forest age. The carrying capacity K (- - -) is obtained by linear scaling of the initial biomass function up to a maximum $K_{\max}$ (here e.g. 40 g/m^2). Both functions were kept constant for forest ages greater than 250 years. Based on pooled data (25-year-classes) from Dettki and Esseen (1998).

A.1.2. Growth and litterfall

For the annual lichen growth rate g (in %; Eq. (A.3)) we assume that g is constant over the whole life of a lichen thallus, i.e. independent of the age or size of the lichen thallus.

$$G = gB \qquad \text{(A.3)}$$

$$L = nB^{1.5} \qquad \text{(A.4)}$$

The calculation of annual litterfall L (Eq. (A.4)) follows McCune (unpublished data). The constant n can be parameterised with lichen dynamics in steady-state condition, i.e. when annual growth G equals annual litterfall L. This is the case when the standing lichen crop B reaches the carrying capacity K, i.e. $B = K$. From Eqs. (A.3) and (A.4) follows:

$$gK = nK^{1.5} \qquad \text{(A.5)}$$

$$L = gK^{-0.5}B^{1.5} \qquad \text{(A.6)}$$

A.1.3. Dispersal

The total annual dispersal is modelled as the sum of a constant regional dispersal R and the local, distance dependent dispersal D. While R can be any type of lichen propagule (e.g. soredia or thallus fragments), it is assumed that D is composed by thallus fragments which re-establish successfully in the same cell or

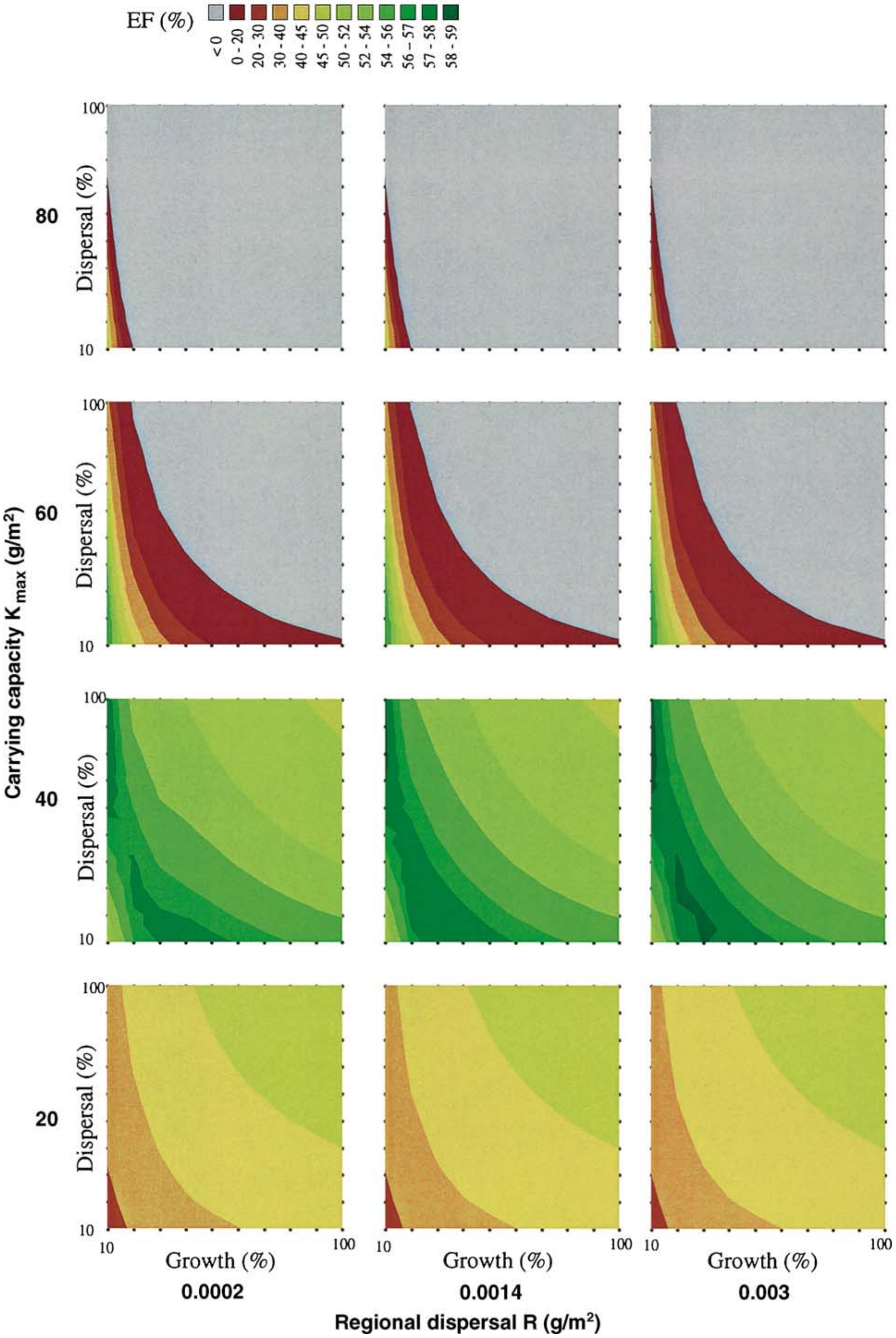

Fig. 8. Sensitivity analysis (modelling efficiency EF) for different combinations of lichen growth, local dispersal, regional dispersal, and maximum carrying capacity in a managed forest landscape (5 km × 5 km) in northern Sweden. Based on field data from Dettki and Esseen (1998).

neighbouring cells. The model assumes that R is constant over time (McCune, unpublished data) and independent of any landscape pattern. The local dispersal D is estimated as a percentage d of the total annual litterfall L (McCune, unpublished data; Esseen, personal communication; Eq. (A.7)).

$$D = d\,L = d\,g\,K^{-0.5}B^{1.5} \tag{A.7}$$

D is dispersed over distance with infinite small portions D_{dist} following the inverse power law (Eq. (A.8)). The dispersal curve is parameterized from field data (Dettki, 1998).

$$D_{\text{dist}} = a\,\text{dist}^{-x} \tag{A.8}$$

where $a =$ constant and $x = 0.6039$.

Integrating over distance for a circle around the centre cell (annulus calculations, cf. Fahrig, 1992) Eq. (A.9) can be derived. Based on Dettki (1998) we assume a maximum dispersal distance $r_{\max}$ of 200 m for local dispersal. The area b of a cell is 2500 m^2 (50 m × 50 m).

$$D_{r1\rightarrow r2} = D\frac{(r_2^{(2-x)} - r_1^{(2-x)})b}{\pi r_{\max}^{(2-x)}(r_2^2 - r_1^2)} \tag{A.9}$$

where $D_{r1\rightarrow r2}$ is the cell fraction of the total dispersed biomass D onto the annulus with radius r_1 and r_2 corresponding to the area fraction of the cell inside the annulus. The fraction dispersed into the centre cell (i.e. dist = 0) is simply the difference between total dispersed biomass D and biomass dispersed due to Eq. (A.9) to the adjacent cells. In this model dispersal from a centre cell to the surroundings equals the ‘potential immigration’ I from the surroundings into each centre cell. Therefore, Eq. (A.9) calculates for each cell the potential fragment immigration I into the cell instead of the dispersal loss from each cell.

A.2. Initial biomass

The initial biomass $B_{t=0}$ in a forest cell (Fig. 7) was estimated using litterfall data from Dettki and Esseen (1998) and Dettki (1993). The relation between biomass B and forest age is described by a cubic function. As the carrying capacity K is the maximum possible lichen biomass in a certain cell, it is assumed that the dependency of K on forest age follows a linear transformation of the cubic function with a maximum at $K_{\max}$ (Fig. 7).

A.3. Sensitivity analysis

Sensitivity analysis was conducted for growth rate g, dispersal rate d, regional dispersed biomass R and the maximum carrying capacity in the landscape $K_{\max}$ for a wide range of parameters (Fig. 8) using field data from Dettki and Esseen (1998).

Validation of the model for one managed 5 km × 5 km forest landscape in northern Sweden shows that the model, in decreasing order, is most sensitive to changes in carrying capacity $K_{\max}$, growth rate g and dispersal rate d, and somewhat less sensitive regarding changes in the amount of regional dispersal R (Fig. 8). Further, the incorporation of edge effects only marginally improves the model at this scale (Dettki, 2000). The results show a ‘best fit’ of the model with 59% modelling efficiency EF for the following parameter combination: annual growth rate $g = 8\%$, dispersal rate $d = 100\%$, regional dispersal $R = 0.003$ g/m^2 and a maximum carrying capacity in the landscape $K_{\max}$ of 42 g/m^2. For biological relevant parameter values taken from literature (cf. Dettki, 2000) modelling efficiency was highest with 54% for $g = 32\%$, $d = 10\%$, $R = 0.0798$ g/m^2 and $K_{\max} = 30$ g/m^2.

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