

Modelling forest dynamics in a nature reserve: a case study from south-central Sweden

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ABSTRACT: This paper presents a modelling study on the forest dynamics in Helgedomen Nature Reserve (HNR) in Sweden. The main components of the forest transitions that occurred between 1930 and 2010 were described. The gradual conversion of Scots pine (*Pinus sylvestris* L.) dominated stands into stands with a high proportion of Norway spruce (*Picea abies* [L.] Karst.) was observed. Next, the capabilities of the modelling system (FORKOME) in predicting the future development of forests in the reserve were tested. The model was validated by simulating forest development from 1930 to 2010, and then it was applied to project the future development of forests in the reserve. Scenarios generated in the forecasting component of the model were (1) no intervention, (2) removal of spruce, and (3) prescribed burning. The FORKOME model was able to predict possible alterations of species composition, stem volume, total biomass in the next 100 years under these three scenarios. We argue that in the absence of natural fires, the active management of small reserves is required in order to maintain the major natural values. Prescribed burning is more effective than spruce removal for maintaining the pine-dominated character of the stands and to sustain the conservation value of the reserve.

Keywords: pine; spruce; computer simulation; ecological model

The application of computer models in ecology allows the prediction of the behaviour of complex systems to which forest ecosystems belong (SCHELLER, MLADENOFF 2007). However, taking into account the specific condition and arrangement of forests, the examination of their dynamics requires the use of particular tools (BUGMANN 2001). This role may be fulfilled by – adequately constructed – models of forest dynamics.

The two existing methods of forest modelling, growth-yield modelling (MOCHREN, KIENAST 1991; PRETZSCH et al. 2002; NAGEL, SCHMIDT 2006) and ecological modelling (SHUGART 1984; PRENTICE, LEEMANS 1990; BOSSEL 1991; BOTKIN 1993; BUG-

MANN 2001) evolved independently over a long period, both competing complementing each other.

Most existing forest growth-yield models focus on wood production and are not concerned with other aspects of the forest environment. Most empirical growth-yield models based on permanent plot data implicitly assume that the future will be like the past, in terms of most environmental factors (VANCLAY 1994). The growth-yield models are widely used in forestry, while the formerly widespread tabular statement of their results is now replaced by the corresponding regression models or integrated computer models of trees, such as SILVA (PRETZSCH et al. 2002) or BWINPro (NAGEL, SCHMIDT 2006).

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Ecological (process) models provide reasonable results reflecting the projected state of the environment. Linked to this is a wide field of applications of process models which relate both to the better understanding of the major biological processes that underpin the trees, as well as to forecasting the development of structurally complex natural stands and stands that are influenced by changing environmental conditions (including the future or past climate change). Descriptions of the theoretical and review of process models can be found in literature (SZWAGRZYK 1994; BUGMANN 2001; REYNOLDS et al. 2001; PORTE, BARTELINK 2002).

The FORKOME model (KOZAK et al. 2007) that contains elements of both ecological and growth-yield strategy has been specially designed for the conditions of Europe. In this article the FORKOME model was validated using historical data from the Helgedomen Nature Reserve (HNR) in Sweden on mixed stands with pine and was used to prognosticate the future role of Scots pine (*Pinus sylvestris* L.) under different treatment options. This is of high interest as pine starts to disappear because of Norway spruce (*Picea abies* [L.] Karst.) becoming more and more competitive under conditions where nutrients enter the system via the atmosphere and climate change and this may lead to, for example, conservation problems.

The sustainable forest management (SFM) supported by the international acts like the Forest Principles (UN 1992), Ministerial Conference on the Protection of Forests in Europe (MCPFE 2000), Montreal Process (MP 2009) and the EU Forest Action plan (COM 2006) aims to reach a suitable balance between the ecological, economic and social dimensions of sustainability (e.g. HYTÖNEN 1995; ANDERSSON et al. 2005). One of these is the maintenance of biodiversity using different measures including: nature conservation, consideration in production stands, and creation of nature reserves that support the threatened species and ecosystems in the long-term perspective (MIKUSINSKI et al. 2007; GUSTAFSSON, PERHANS 2010).

In boreal forest, the most important disturbance agent shaping the structural, compositional and functional diversity of these ecosystems in naturally dynamic landscapes is fire (HUNTER 1993). In Scandinavia, major forest fires have been virtually absent since the middle of nineteenth century due to active fire suppression as a part of forest management (ÖSTLUND et al. 1997). The absence of fire has led to several changes in boreal ecosystems. The tree species composition and structure of forests are changing, causing habitat loss for

many organisms which are dependent on different phases of post-fire succession (LINDER et al. 1997; ERICSSON et al. 2005; UOTILA et al. 2002). The recent trend in the management of forest biodiversity in the frame of sustainable forestry is to use prescribed fire to restore habitats for species dependent on this disturbance (e.g. HYVÄRINEN et al. 2006). These practices are gradually, but still in a very limited scale, being introduced in productive stands and also some attempts have been made to use them in reserves. Old Scots pine dominated stands are often considered as having a high conservation value due to their rarity in heavily managed landscapes, long continuity due to longevity of the species and finally because these harbour a high number of endangered species.

Our study built upon three analytic components: (1) the analysis of changes occurring in the present area of Helgedomen Nature Reserve (HNR) through the period of 1930 to 2010; (2) validating the FORKOME model with historical data from the reserve; (3) carrying out predictions (until the year 2110), with the use of models, of the possible changes of species composition, stem volume and number of stems, total biomass in three scenarios: no intervention, removal of spruce and prescribed burning.

MATERIAL AND METHODS

The study site HNR is located in south-central Sweden (40 km to the north from Orebro). It has been protected since 1937 as an especially designed set-aside area embedded within intensively managed forest land owned by the state. In 1996 it was transformed to a reserve with the main goal of conserving the old pine dominated stand with long temporal continuity and an associated community of species dependent on such forest. The area of HNR is 26 ha and consists of a mosaic of forest (about 10 ha) and mires (about 16 ha). In this study we analysed with the use of the FORKOME model plots within the forest stands of the reserve located on mineral soil (stands Nos 28–31, 33, 35, 36, 38, 56, 57, 58–60, 61, 63).

In each of the 15 analysed stands up to 4 sample plots each of 25 × 25 m in size were analysed. In each plot all living trees, snags, stumps, and logs with a diameter larger than 4 cm were measured and mapped. The height of all living trees was measured. Seedlings, defined as tree specimens of between 0.1 and 1.3 m in height, were also mapped. Soil depths, soil texture, soil moisture, occurrence

of subsurface water flow and ground vegetation types were analysed for each plot. The data from each of those plots concerning DBH (diameter at breast height), height and crown projection of each living tree were used to initialize the model, parameter estimation and model calibration.

FORKOME computer model belongs to the same type of gap models as JABOWA (BOTKIN et al. 1972), JABOWA 3 (BOTKIN 1993) and FORET (SHUGART, WEST 1977; SHUGART 1984) models. Since this model was analysed in detail in previous publications (KOZAK, MENSHTUKIN 2002; KOZAK et al. 2003, 2007), only a simple description of the model is required here.

FORKOME belongs to the family of ecological models which simulate the forest stand dynamics, allowing single tree research, and herein it is divided into blocks. The options of selecting tree felling modes and temperature and humidity conditions are available in certain scenarios (KOZAK, MENSHTUKIN 2002; KOZAK et al. 2003). The Monte Carlo statistical method allows the simulation of up to 200 variants for each scenario. The model provides the average number and average biomass of trees with the standard variation in each year.

The FORKOME model is an object system with the following basic components (1) AREA – denotes the current patch (gap) and (2) TREE – gives a single tree. The Area object has characteristic properties defining factors including the dimensions, habitat and climate conditions. Here, the user interface simplifies the modification of patch properties. The Area object contains an almost unlimited number of Tree objects, representing currently existing trees.

In the FORKOME model, the “growth block” simulates the actual annual tree growth on the studied area. The FORKOME model trees are also described by species-specific growth functions, with the main parameters of diameter at breast height (DBH), height (H) and age, together with the external conditions of the individual patch area (Table 1). This approach simplifies growth simulation and allows growth-function activation and implementation in current conditions. The basic simulation consists of the tree diameter calcula-

tion, where the annual diameter increase ranges from the minimal value of 0 to the maximum value for each species under ideal conditions. Here, the following equation is used:

$$\delta(D^2H) = rLa \left(1 - \frac{DH}{D_{\max}H_{\max}} \right) \quad (1)$$

where:

- r – species constant, describing photosynthetic productivity of assimilation apparatus,
- La – relative tree leaf area in m^2/m^2 ,
- D – tree diameter measured in cm 1.30 m above ground level,
- H – tree height in cm,
- D_{\max} – species maximum diameter in cm,
- H_{\max} – species maximum height in cm,
- $\delta(D^2H)$ – tree volume increase in cm^3 .

The influence of external conditions is factored into the annual tree volume increase process. The actual tree increase results from the optimal increase and tree growth inhibiting conditions f_p, f_2, \dots, f_j , where the value of each tree growth-inhibiting factor ranges from 0 to 1.

In FORKOME, light availability is calculated with consideration to light radiation loss (KOZAK et al. 2003). This loss is caused by the total shading by the leaf area of higher trees. The available light function describes the amount of light available for specific tree leaves, and it is calculated according to the equation:

$$Q(h) = Q_{\max} e^{-kLA(h)} \quad (2)$$

where:

- $Q(h)$ – height, h, measured radiation,
- Q_{\max} – solar radiation measured on the tree-tops,
- e – exponent,
- k – constant value – 0.25,
- $LA(h)$ – total tree-leaf area in the patch, above height h .

Trees are divided into the following three types, dependent on their light tolerance index: sun-tolerant, medium and shade-tolerant. The tree-growth inhibiting light index is called the light re-

Table 1. Example of some parameters used in FORKOME model

Tree species	H_{\max} (m)	D_{\max} (cm)	Age _{max} (year)	DGD_{\min}	DGD_{\max}
<i>Pinus sylvestris</i>	45	120	340	150	2,000
<i>Picea abies</i>	55	120	360	0	1450
<i>Betula pendula</i>	35	100	100	0	2,000

action function, and it is calculated in two different ways, depending on the tree light toleration index. Light-demanding and medium species have the same equation:

$$r = 2.24(1 - e^{-1.136[Q(h) - 0.08]}) \quad (3)$$

while shade-tolerant trees have the following equation:

$$r = 1 - e^{-4.64[Q(h) - 0.05]} \quad (4)$$

where:

r – the light reaction function – growth light reduction,
 e – exponent,
 $Q(h)$ – individual height radiation.

Thermal conditions of this model are described by the addition of annual effective temperatures above 5°, and the temperature index inhibiting tree growth can be calculated by the following equation (BOTKIN 1993).

$$t = \frac{4(DGD - DGD_{\min})(DGD_{\max} - DGD)}{(DGD_{\max} - DGD_{\min})^2} \quad (5)$$

where:

t – growth inhibiting index,
 DGD – sum of effective temperatures for a particular site,
 DGD_{\min} – minimal sum of effective temperatures needed for species occurrence,
 DGD_{\max} – maximal sum of effective temperatures for species occurrence.

The model was initially run with climate data for Orebro. In prognosis/scenarios over the next 100 years we added some “anomalies” to the corresponding monthly temperature and/or precipitation data: temperature change in °C for December, January and February as 5.1; March, April and May as 4.0; June, July, August as 2.2; September, October and November as 3.8; and the respective precipitation change in mm·day⁻¹ 0.4; 0.6; 0.7; 0.5 (PRENTICE et al. 1993).

The FORKOME model also considers leaf transpiration, and this depends not only on the meteorological conditions but also on the tree species like in other patch models. There also exist relationships between tree species and groundwater level, and tree growth rate and the availability of groundwater implemented in the model structure. The block is created by the following basic water balance equation:

$$W(t + 1) = W(t) + \text{Prec}(t) - \text{Trans}(t) - \text{Evapor}(t) \quad (6)$$

where:

$W(t)$ – groundwater amount in the time period t ,
 $\text{Prec}(t)$ – precipitation,
 $\text{Trans}(t)$ – transpiration,
 $\text{Evapor}(t)$ – soil surface water evaporation.

In the FORKOME model a tree can perish in the following two ways: (1) randomly, or (2) if it does not reach the minimum diameter increment size. The model asserts that if the tree does not increase its diameter every year for ten years, then there is only a 1% chance that the tree will survive that period. The MORTAL statistical probability for annual tree death is 0.386 (normatively set value). The FORKOME model is able to confirm the tree's minimal increment. If the minimum value is not exceeded, then it is assigned its random probability from 0 to 1, and when that value is greater than 0.386, the tree is removed. Random tree mortality is based on the theory that only some healthy trees live to their maximum age, and the FORKOME assumption states that 2% reach their maximum age (BOTKIN 1993). In addition, the sapling number was generated separately for each light-tolerance reading, and a polynomial function was used for nutrient blocks (WEINSTEIN et al. 1982). In FORKOME, we simulated the transition phase between the establishment of seedlings and young trees using the tree height of 1.3 m. The functioning of the block BIRTH is based on the rule that the influence of environmental factors on regeneration is considered first, then the list of possible tree species that may regenerate is established and finally the number of tree individuals of each species is provided.

The FORKOME model provides the ability to define forest-felling scenarios. The interface helps to determine the time and sequence of felling, and also the tree species diameter. Besides the already mentioned blocks, the FORKOME model in its latest version also includes a recently created and intensively developed block of natural disturbances, including the effects of forest fires. As a result, it is possible to simulate potential changes caused by their activity and finally predict via simulations the impact of those fires on forest conditions and stand regeneration. The predicted impact of fire on trees is based on DBH, height of flames, wind velocity, temperature, fire intensity, and the degree to which trees are mineralized. It concerns the trees, understory and forest floor (SIDOROFF et al. 2007). In our case, the limitations of DGD_{\min} , DGD_{\max} , $PRECIP_{\min}$, $PRECIP_{\max}$ were not important since fire was prescribed so the probability of its occurrence was 100%.

In its present version, the model FORKOME (written in DELPHI language) contains newly introduced blocks to co-operate with averaged data originating from forest stands. Based on these data (mean DBH, mean H, mean age, and number of trees for each stand) it is possible to make prognosis concerning the tree species composition, tree numbers, volume and biomass. The size

of the unit (length and width) and number of trees are specified. Next, the percentage of particular tree species should be provided (e.g. pine 90% = 9; spruce 10% = 1) followed by mean values of DBH (with the use of DBH distribution on control sample plots), age and height of trees (e.g. pine 32 cm, 205 years and 26 m, respectively). After putting the values into the model for spruce, the simulation for the forest stand may be performed. We performed Monte Carlo simulations for all studied units (200 simulations for each unit starting from the same initial conditions). The number of trees predicted by FORKOME model was validated in unit No. 61: in 1930 there were 280 trees.ha⁻¹ of pine and 130 of spruce; 359 pines and 107 spruces in 2010; and in FORKOME simulation from 1930 to 2010 there were 351 ± 12 pines and 109 ± 9 spruces in 2010.

The analysis of historical inventory data concerning the initial state in 1930 was done. Average diameter, height, age and tree numbers in forest stands were used for the simulation in terms of start values.

RESULTS

The analysis of changes that occurred in Helgödomen Nature Reserve during the period of 1930 to 2010 indicated the gradual conversion of Scots pine dominated stands into stands with a high proportion of Norway spruce. The number of spruce trees clearly exceeded the number of pine trees in 2010. The timber volume of spruce in 1930 was only 11% (Fig. 1a) and in 2010 it increased to 25% (Fig. 1b). Changes in DBH for forest stands confirm an increase of spruce in 2010 compared to the inventory data in 1930. During the last 80 years spruce has increased more in formerly pine dominated forests (stands No. 28, 30, 31, 33, 36, 38, 56, 60, 61). The FORKOME model validation on the inventory

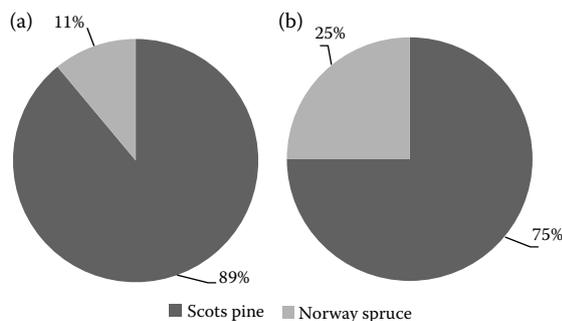


Fig. 1. Stem volume inventory data: (a) in 1930, (b) in 2009

data from 1930 also showed an increase in spruce in 2010, very similar to inventory data in 2010 (Table 2).

A multi-sized diameter distribution of living trees in sample plots (created in 2010) in forest stands indicates that pine was mostly confined to larger diameter classes, while spruce was generally found in smaller classes.

Forecasting changes from the year 2010 to 2110 shows that according to scenario 1 (no intervention) the total biomass of pine would be lower than that of spruce in 2110 (Fig. 2a). According to scenario 2 (initial removal of spruce) the total biomass of spruce will continue to grow after removal and in 2110 the proportion of spruce would also be higher than that of pine (Fig. 2b). On the contrary, in scenario 3 (prescribed burning) the proportion of spruce would be quite low (Fig. 2c). Due to the lack of space we do not provide accurate results for each of the plots separately (these results were obtained on the basis of 200 model simulation runs carried out in 100 years for each of the plots established in each forest stand). Instead, we described observed trends in summary, illustrated by the example of sample plot No. 1 from unit 61. For trend analysis only those simulations were utilized where the standard deviation was within 5–10%.

In scenario 1 (no intervention), stand density, stand volume, and total biomass will alter from pine domination to spruce within the next 100 years. It was also noticed that in pine stands with a higher average age of trees in 2010, pines can quickly be replaced by spruce. The total biomass of pine will decrease by half, and the total biomass of spruce will increase from 20% to 55%. After 90 years,

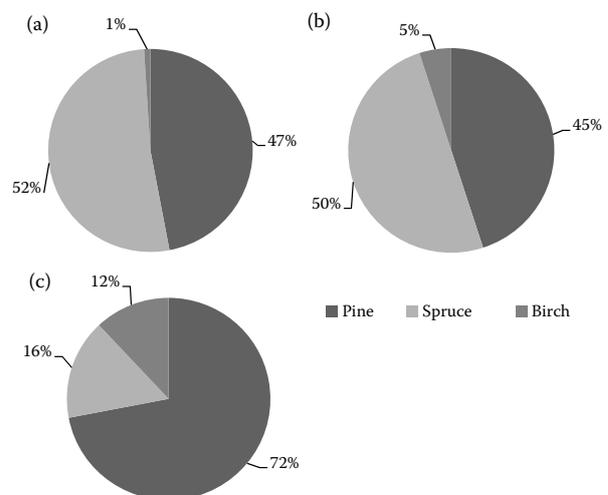


Fig. 2. Percentage of tree biomass in the year 2110 predicted by FORKOME model: (a) no intervention, (b) removal of spruce, (c) prescribed burning

Table 2. DBH inventory and FORKOME validation data in Helgedomen

Stands No.	Inventory data (DBH in 1930)		Inventory data (DBH in 2010)		FORKOME simulation data (DBH in 2010)	
	pine	spruce	pine	spruce	pine	spruce
28	7	3	28	23	27.3 ± 1.1	23.5 ± 1.4
29	17	13	34	25	33.9 ± 2.1	26.2 ± 2.4
30	25	7	40	21	41.2 ± 2.6	22.3 ± 2.1
31	40		36	17	35.7 ± 3.1	17.4 ± 1.1
33	13	5	32	16	32.0 ± 2.8	17.1 ± 1.2
35	5	3	33	22	33.1 ± 3.1	22.8 ± 2.3
36	33	12	43	25	42.3 ± 2.7	25.9 ± 2.4
38	14	10	34	23	34.5 ± 3.1	23.7 ± 2.1
56	32	4	42	19	41.3 ± 2.7	20.2 ± 2.1
61	32	14	43	27	42.2 ± 3.6	28.1 ± 2.5
63	15	7	34	25	34.2 ± 3.3	25.9 ± 2.9
57	9	6	29	18	29.6 ± 2.5	18.2 ± 2.1
58	20		28		29.2 ± 2.2	
59	9	6	26	17	26.7 ± 2.5	18.5 ± 2.1
60	25	5	36	19	36.4 ± 2.9	20.2 ± 2.8

spruce total biomass will dominate in comparison with pine total biomass (Fig. 3). Although the number of spruce trees will be greater than that of pines in the control scenario, we see that the dominance of spruce is still possible within 100 years from now. In all pine-dominated plots there was a plenty of spruce seedlings while pine seedlings were very uncommon. The problem with the lack of pine regeneration in the Helgedomen Nature Reserve is highly noticeable.

In scenario 2 (removal of spruce) spruce biomass will slowly increase (Fig. 4), however with delay in time; in this scenario we can achieve a decrease in the amount of spruce trees in contrast to the control scenario, nonetheless we will not gain an increase in

the number of pine stems. Furthermore, in this scenario the model does not predict the emergence of juvenile pine trees. The only difference in the control scenario will be the time delay. Cutting of spruce in this scenario provokes an increase in the proportion of old pines in total, however, there is no enhancement in the recovery of this species.

In scenario 3 (prescribed burning) the model has predicted an increase in biomass and number of birch trees (Fig. 5). By the end of the simulation (thus within the next 100 plus years) pine will slowly restore its dominant position concerning biomass. In this scenario, by the end of the prognosis, the total biomass of pine is going to increase up to 98 t·ha⁻¹.

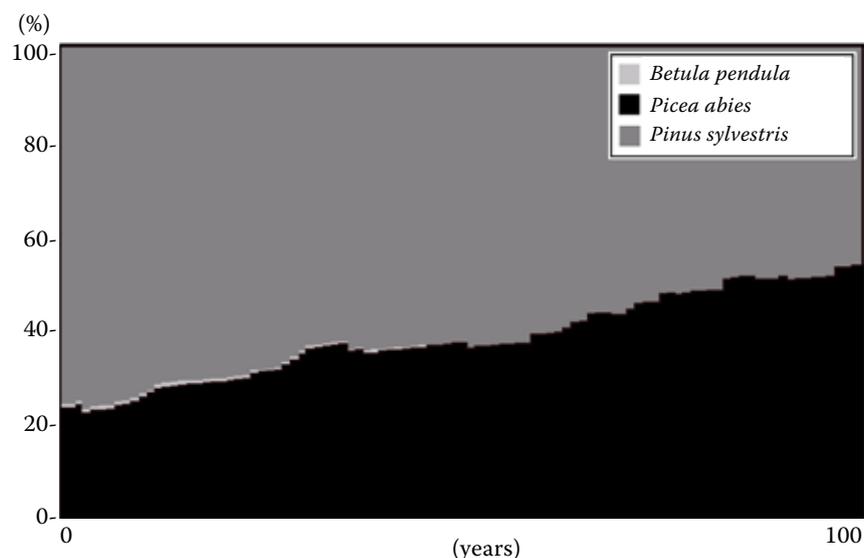


Fig. 3. Percent biomass prediction in the control scenario

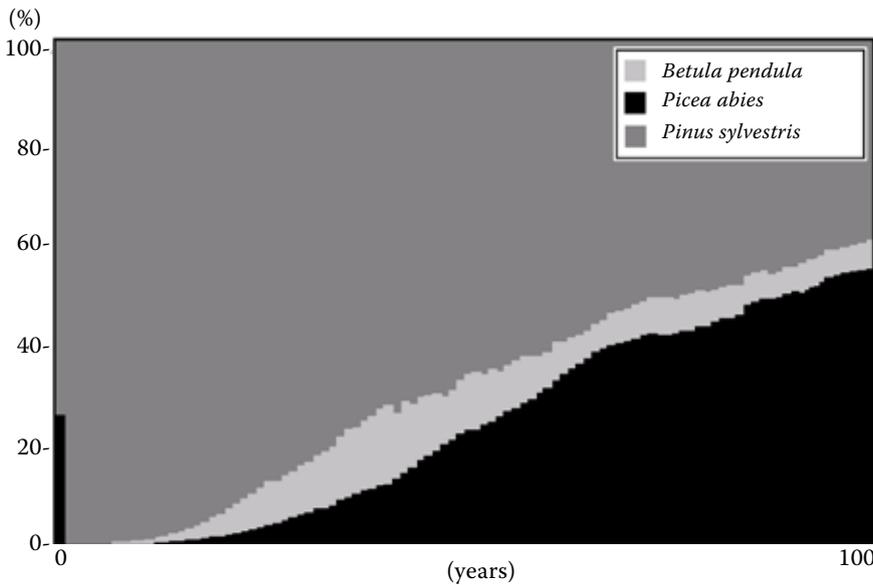


Fig. 4. Percent biomass prediction in scenario 2

DISCUSSION

The application of the FORKOME model to forests in Sweden has shown the effectiveness of uniting these growth-yield and ecological strategies in forest modelling. Furthermore, the FORKOME model application shows the necessity of using future hybrid models which contain elements of both growth-yield and ecological factors. Using the FORKOME model we were able to demonstrate how to predict the development of forest conditions in a nature reserve according to three different scenarios. Such modelling has been rarely attempted in the case of small nature reserves since the main emphasis was put on production forests or entire landscapes. Since most of the nature reserves in production landscapes are of that sort (i.e. small, isolated ones lacking natural disturbances), we argue that our work illustrates an important

problem; small areas without active management will continuously evolve towards environments not necessarily preserving the values they were created for.

The model confirmed that succession trends of change from pine-dominated forests into spruce forests in the absence of fire, observed historically in the study site and elsewhere (e.g. LINDER et al. 1997), will continue. Most probably, without active management, the HNR will change towards spruce-dominated forest and thereby the original conservation values linked to old-growth pine character will be lost. This change will be especially pronounced in moist sites. The immediate cause of this process is a lack of pine regeneration due to limited access to light. The active removal of spruce will slow this process but most probably it will not improve the situation for young generations of pine. In contrast, the scenario with the use of prescribed

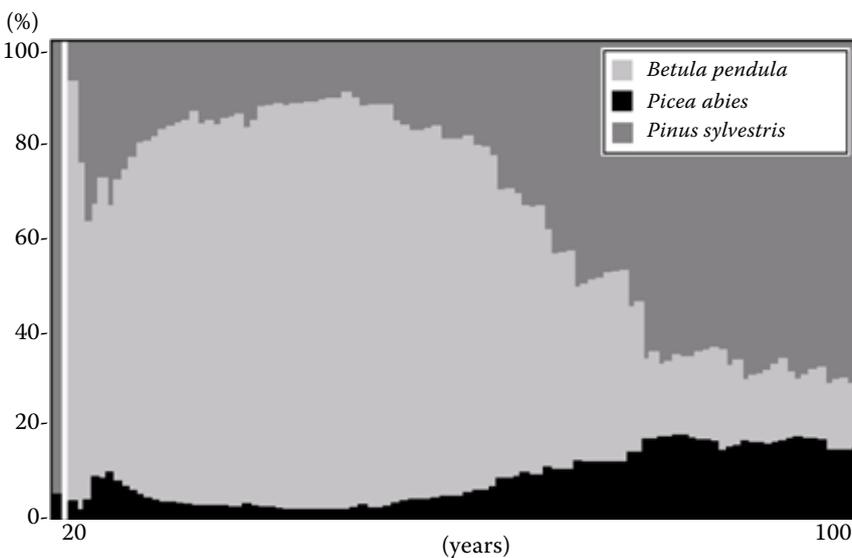


Fig. 5. Percent biomass prediction in scenario 3

fire as a management tool predicts that, after short birch dominance, pine will maintain its dominance in the HNR. In drier sites, the maintenance of old-growth pine forest character appears to be easier to attain.

The analyses of stand characteristics presented here indicate that the process of succession may cause serious negative changes highly undesirable from a conservation standpoint. This process exemplified here in HNR is relevant for similar, rather small and isolated old-growth pine stands in Sweden and elsewhere. The same trends were detected for example in other virgin forest stands where forest fires were suppressed (LINDER 1998). The simulation by the model FORKOME allowed us to understand the extent of these changes with a longer perspective. Therefore, the maintenance of natural values in forests similar to HNR apparently requires active conservation measures. Through simulations, we demonstrated that the use of prescribed burning is much more effective than the removal of spruce. It has been confirmed empirically that prescribed burning enhances the regeneration of Scots pine in Scotland (HANCOCK et al. 2009). LINDER et al. (1997) suggested that management plans for forest reserves should include management practices that maintain or mimic the natural disturbance regimes in a certain way.

An interesting feature of the present study is the use of historical site data from 1930 to validate the model. Quantitative assessment of how well the model did at predicting forest conditions in 2010 based on the 1930 conditions is an important aspect if we are to have confidence in the predictions of the model from 2010 to 2110. Computer simulations that were conducted on various scenarios of changes not only demonstrated methodological applicability of computer modelling studies in studying forest dynamics, but also allow the future assessment of these trends in order to study biodiversity and nature conservation policy. We add empirical patterns to the FORKOME model that are also used in Swedish forestry that enabled us to take advantage of current literature achievements in the form of empirical data for trees in Sweden.

The presented FORKOME model, in addition to the scientific elements, also has an attractive work environment based on three-dimensional graphics, which are subject to a change during the simulation process. It may be interesting to present the changes occurring in forests, future shading calculations and other processes as presented, for example, in ZELIG model (URBAN 1990).

CONCLUSIONS

The FORKOME model simulates the fast change of pine stands into spruce-dominated stands. Prescribed burning is more effective than spruce removal for maintaining the pine-dominated character of the stands. Prescribed burning is the best option to sustain the conservation value of the reserve.

After completing the prognosis of forest selective spruce cutting and burning scenarios and analysing the results, the FORKOME model proved to be a useful and reliable tool for this research. This model is a simple and inexpensive tool used in current forest studies and in forecasting forestry needs. It can be used to simulate the development of actual forest conservation areas and also to answer questions about their appropriate management. Predictive research using the FORKOME model will facilitate a better comprehension of forest development of natural systems and improve their future management. The FORKOME model, applied to different site conditions and different climate scenarios, could contribute to a better understanding of the different future pathways of mixed pine forests.

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References

- ANDERSSON F., ANGELSTAM P., FEGER K.H., HASENHAUER H., KRÄUCHI N., MARELL A., MATTEUCI G., SCHNEIDER U., TABBUSH P. (2005): A Research Strategy for Sustainable Forest Management in Europe. COST Action 25. Technical Report 5. Paris, Groupement d'Intérêt Public Ecosystèmes Forestiers: 149.
- BOSSEL H. (1991): Modelling forest dynamics: moving from description to explanation. *Forest Ecology and Management*, **42**: 129–142.
- BOTKIN D.B. (1993): *Forest Dynamics: An Ecological Model*. Oxford, New York, Oxford University Press: 309.
- BOTKIN D.B., JANAK E.J., WALLIS J.R. (1972): Some ecological consequences of computer model of forest growth. *Journal of Ecology*, **60**: 649–873.
- BUGMANN H. (2001): A review of forest gap models. *Climatic Change*, **51**: 259–305.

- COM (2006): Communication from the Commission to the Council and the European Parliament on the EU Forest Action Plan. Commission of the European Communities. COM 302, Brussels: 13.
- ERRICSSON T.S., BERGLUND H., OSTLUND L. (2005): History and forest biodiversity of woodland key habitats in south boreal Sweden. *Biological Conservation*, **122**: 289–303.
- GUSTAFSSON L., PERHANS K. (2010): Biodiversity conservation in Swedish forests: Ways forward for a 30-year-old multi-scaled approach. *Ambio*, **39**: 546–554.
- HANCOCK M.H., SUMMERS R.W., AMPHLETT A., WILLI J. (2009): Testing prescribed fire as a tool to promote Scots pine *Pinus sylvestris* regeneration. *European Journal of Forest Research*, **128**: 319–333.
- HUNTER Jr. M.L. (1993): Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation*, **65**: 115–120.
- HYTÖNEN M. (1995): History, evolution and significance of the multiple-use concept. In: HYTÖNEN M. (ed.): *Multiple-use Forestry in the Nordic Countries*. METLA, The Finnish Forest Research Institute, Helsinki Research Centre, Helsinki: 43–65.
- HYVÄRINEN E., KOUKI J., MARTIKAINEN P. (2006): Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology*, **20**: 1711–1719.
- KOZAK I., MENSHTUKIN V. (2002): Predictions of Spruce Forest Dynamics in the Polish Bieszczady and Ukrainian Bieskidy Using the Computer Modelling. *Baltic Forestry*, **8**: 28–34.
- KOZAK I., CHŁODEK D., ZAWADZKI A., KOZAK H., POTACZAŁA G. (2007): Symulacja przebudowy drzewostanów świerkowych w Bieszczadach za pomocą modelu FORKOME. [Conversion simulation of spruce stands in the Bieszczady mountains with the aid of FORKOME model.] *Leśne prace badawcze*, **2**: 7–26.
- KOZAK I., MENSHTUKIN V., FERCHMIN M., POTACZAŁA G., JÓŻWINA M., KOZAK O. (2003): Prognozowanie zmian lasu sosnowego w obszarze ochrony ścisłej Nart w Kampinoskim Parku Narodowym z wykorzystaniem modelu FORKOME. [Pine forest prognosis with use of FORKOME model in the Kampinoski National Park] *Parki Narodowe i Rezerwaty Przyrody*, **22**: 483–497.
- LINDER P. (1998): Structural changes in two virgin boreal forest stands in central Sweden over 72 years. *Scandinavian Journal of Forest Research*, **13**: 451–461.
- LINDER P., ELFVING B., ZACKRISSON O. (1997): Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management*, **98**: 17–33.
- MCPFE (2000): General Declarations and Resolutions Adopted at the Ministerial Conferences on the Protection of Forests in Europe. Strasbourg 1990 - Helsinki 1993 - Lisbon 1998. Ministerial Conference on the Protection of Forests in Europe (MCPFE). Liaison Unit Vienna, Vienna: 88.
- MIKUSIŃSKI G., PRESSEY R. L., EDENIUS L., KUJALA H., MOILANEN A., NIEMELÄ J., RANIUS T. (2007): Conservation planning in forest landscapes of Fennoscandia and an approach to the challenge of Countdown 2010. *Conservation Biology*, **21**: 1445–1454.
- MOCHREN G.M.J., KIENAST F. (1991): Modelling forest succession in Europe. *Forest Ecology and Management*, **42**: 1–2.
- MP (2009): Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests. Available at http://www.rinya.maff.go.jp/mpci/2009p_4.pdf (accessed September 21, 2012).
- NAGEL J., SCHMIDT M. (2006): The Silvicultural Decision Support System BWINPro. In: HASENAUER H. (ed.): *Sustainable Forest Management*. Berlin, Springer: 59–63.
- ÖSTLUND L., ZACKRISSON O., AXELSSON A.L. (1997): The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**: 1198–1206.
- PORTE A., BARTELINK H.H. (2002): Modeling mixed forest growth: a review of models for forest management. *Ecological Modeling*, **150**: 141–188.
- PRENTICE I.C., LEEMANS R. (1990): Pattern and process and the dynamics of forest structure: a simulation approach. *Journal of Ecology*, **78**: 340–355.
- PRENTICE I.C., SYKES T., CRAMER W. (1993): A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling*, **65**: 51–70.
- PRETZSCH H., BIBER P., DURSKEY J. (2002): The single tree-based stand simulator SILVA: Construction, application and evaluation. *Forest Ecology and Management*, **162**: 3–21.
- REYNOLDS J.F., BUGMANN H., PITELKA L.F. (2001): How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations and potentials. *Climatic Change*, **51**: 541–557.
- SHELLER R.M., MLADENOFF D.J. (2007): An ecological classification of forest landscape simulation models: Tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology*, **22**: 491–505.
- SHUGART H.H. (1984): *Theory of Forests Dynamics*. New York, Springer: 278.
- SHUGART H.H., WEST D.C. (1977): Development of an Appalachian deciduous forest model and its application to assessment of the impact of the chestnut blight. *Journal of Biogeography*, **5**: 161–179.
- SIDOROFF K., KUULUVAINEN T., TANSKANEN H., VANHAMAJAMAA I. (2007): Tree mortality after low-intensity prescribed fires in managed *Pinus sylvestris* stands in southern Finland. *Scandinavian Journal of Forest Research*, **22**: 2–12.
- SZWAGRZYK J. (1994): Symulacyjne modele dynamiki lasu oparte na koncepcji odnawiania drzewostanu w lukach. [Simulation models of forest dynamic based on concept of stand gap regeneration] *Wiadomości Ekologiczne*, **40**: 57–75.

- UN (1992): Non-legally Binding Authoritative Statement of Principles for a Global Consensus on the Management, Conservation and Sustainable Development of All Types of Forests. Report of the United Nations Conference on Environment and Development, Rio de Janeiro 3–14 June 1992. United Nations, New York. Available at <http://www.un.org/documents/ga/conf151/aconf15126-3annex3.htm> (accessed September 21, 2012).
- UOTILA A., KOUKI J., KONTKANEN H., PULKKINEN P. (2002): Assessing the naturalness of boreal forests in eastern Fennoscandia. *Forest Ecology and Management*, **161**: 257–277.
- URBAN D.L. (1990): A versatile model to simulate forest pattern: a user's guide to ZELIG version 1.0. Charlottesville, VA: University of Virginia, Environmental Sciences Department. *Forest Ecology and Management*, **42**: 95–110.
- VANCLAY J.K. (1994): *Modelling Forest Growth and Yield. Applications to Mixed Tropical Forests*. Wallingford, CAB International: 312.
- WEINSTEIN D.A., SHUGART H.H., WEST D.C. (1982): *The Long-term Nutrient Retention Properties of Forest Ecosystems: A simulation Investigation*. Oak Ridge, Tennessee, Oak Ridge National Laboratory: 214.

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