

Dynamic animal populations in managed forests: species ecological requirements and sustainable harvesting

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Forest management has altered forested environments and provoked stress to many natural habitats and biodiversity. The goal of biodiversity management is the long-term persistence of populations in human-modified environments. We demonstrate a spatio-temporal modeling approach to address the relationship between various management objectives and population persistence in the long-term in a commercial forest landscape. We used the flying squirrel (*Pteromys volans*), the three-toed woodpecker (*Picoides tridactylus*) and the long-tailed tit (*Aegithalos caudatus*) as example species. They are all forest species but they have distinctly different habitat requirements. In the model, forest growth, forest clearing and regional population dynamics were simulated and operated simultaneously. We addressed regional population persistence by varying the conservation goal: First, there are no obligations to protect the species. Second, forest stands where the species occur are not cleared. Third, the entire species' habitat is preserved. The general message from our analysis is that the sustainable area cleared annually depends on the species' habitat requirements, and species' responses to management have various time lags.

Introduction

Utilization of natural resources and the production of commodities are frequently in conflict with the sustainable use and protection of natural systems (Nalle *et al.* 2004, Shan *et al.* 2009). In Finland, the national forest program (KMO) intends to enhance the extraction of timber and attempts to find novel production possibilities for timber. Intensive forest management puts pressure on many non-timber goods and benefits in forested environments. At the same time, there is an urgent need to maintain biodiversity and ecosystem services in natural systems (Cardinale

et al. 2012). Several international institutions have raised concerns regarding these issues, and inter-governmental agreements have set ambitious goals to improve the state of ecosystems worldwide. The European Union biodiversity strategy for 2020 (European Commission 2011) and the METSO program (Hildén *et al.* 2007) in Finland are the examples of attempts to maintain and restore natural environments. Sustainable use of natural resources entails a balance among economical, ecological and social objectives.

During the last six decades, modern forestry altered many natural forested habitats in terms of area and number (Raunio *et al.* 2008, Finnish

Statistical Yearbook of Forestry 2012). These large-scale changes in boreal landscapes have resulted in regional declines and local extinctions of many forest-dwelling species (Rassi *et al.* 2010). To combat these harmful trends in biodiversity and to mitigate negative consequences of forest clearing, action was taken to conserve valuable forest areas and to maintain many forest characteristics that are thought to be elementary for vulnerable species. Nowadays, during final harvesting it is common to leave many key habitats intact; retention trees such as aspen are not felled, and dead or dying trees are deliberately left in cleared sites (Päivinen *et al.* 2011, Junninen & Similä 2013, Metsätalouden kehittämiskeskus Tapio 2014). These actions to improve the living conditions of forest species have gained some success, but there are species that have not benefitted from harvesting designed to support them. For instance, it seems that the flying squirrel (*Pteromys volans*) has abandoned most of its breeding sites after forest felling despite detailed official instructions that outline harvesting restrictions in locations where it is present (Jokinen 2012, Santangeli *et al.* 2013).

The ecological goal of conservation is the long-term persistence of viable populations. Conservation planning must be based on adequate knowledge of a species' ecology and life-history features (Beissinger & Westphal 1998). This is seldom possible because of the lack of ecological information on most species that should be protected. We usually have no precise data on the spatial ecology of species and, therefore, occurrence data are commonly used to identify valuable sites for species (Cabeza & Moilanen 2003, Cerdeira *et al.* 2010, Schapugh & Tyre 2012, Schuster & Arcese 2013). However, management planning with occurrence data alone is insufficient to assess the effects of various management practices on species and their persistence in suitable forest sites. Therefore, projections of conservation actions with occurrence data are not definite for most species, particularly in human-modified landscapes (Lindenmayer *et al.* 2003).

We present a spatio-temporal modeling approach with which the relationship between various management objectives and long-term

population persistence in a commercial forest landscape can be assessed. In the model, forest growth, forest clearing and regional population dynamics are simulated and operated simultaneously. Using this modeling approach, we examined the flying squirrel (*Pteromys volans*), the three-toed woodpecker (*Picoides tridactylus*) and the long-tailed tit (*Aegithalos caudatus*) as example species. These species are all forest species, but they have distinctly different habitat requirements. Because these species are associated with different combinations of forest-stand characteristics, they exemplify the demanding task of forest management planning to maintain functional populations regionally for several species at the same time.

In this paper, we analyze the effects of the following three management strategies, in which forest clearing is allowed or restricted, on population persistence: (1) clear felling of a stand is allowed even if it is occupied or habitat is suitable for the species; (2) clear felling is prohibited if the stand is occupied by the species but can be harvested if it becomes unoccupied; and (3) clear felling of a stand is not allowed in stands where habitat is suitable for the species but can be harvested if it turns unsuitable with time. The forests in our study area are managed in accordance with these alternative guidelines to achieve the targeted level of harvested timber. We altered the area harvested (the amount of hectares clear-cut annually) to see when and how population persistence conflicts with timber extraction.

Material and methods

Study site

Our study area is located in central Finland (62°14'N, 25°43'E). The Finnish Forest Center in central Finland provided empirical stand information in GIS format. The main criterion in selecting the study area was that available data covered most of the area. The data set covered 65% of the forested land in the study area. We also avoided protected areas such as national parks in the study area to ensure that all stands are qualitatively equal and had been managed in the past. The missing 35% of forest data and gaps

in our GIS data were completed from the existing data set by randomly assigning a location on the map and extracting stand information from the data. New stands had sizes selected from a normal distribution, which followed parameters (mean and standard deviation) derived from the data. Forest data were based on field inventories in which tree structure was sampled and measured and, also, notes on biodiversity characteristics were made. The study area is 69 000 ha in size, and represents a boreal landscape where forest on mineral soils covers 55%, peat lands 13%, lakes 16% and farmland settlement some 15%. Pine, spruce and mixed stands dominate the forests, consisting of ca. 31 000 stands of an average size of 1.45 ha. Past forest management practices have resulted in a bimodal age structure of forest stands, with most of the stands being presently younger than 40 years. The other mode occurs near 80 years. For the present study, a subregion of 7908 ha (17.7%) was extracted. This subregion was the largest uniform forest area that could be extracted from the study area to avoid permanently open landscape features such as lakes, peatlands and fields. These features in the vicinity of forest stands affect the spatial dynamics of forest species. This subunit contained 5797 forest stands and was a sufficient spatial sample of the entire study area to achieve our research objectives.

Forest growth

Stand variables for forest growth modeling and habitat index calculations were extracted from the database administered by the Finnish Forest Centre. The initial data set was an empirical one, and had been collected in the field by staff of the Finnish Forest Center during several years. Forest stands were inventoried only on private land. Due to temporal differences in sampling and non-random sampling scheme, this empirical data set had inherent uncertainties and inaccuracies.

Forest growth in stands was modeled using the MOTTI stand simulator (Hynynen *et al.* 2005). MOTTI executes distance-independent tree-level models for natural regeneration, forest growth, tree mortality and effects of manage-

ment on tree growth (Salminen *et al.* 2005). These empirical models are based on data from permanent field experiments and forest inventory plots, thus allowing simulating stand development under various growth conditions in Finland (Hynynen *et al.* 2002). Here, we simulated forest growth for a 50-year period using two different management options: (1) a stand was grown and felled according to the official protocol, including one or two thinnings and a clear cut after the stand matured (Metsätalouden kehittämiskeskus Tapio 2014); and (2) the same as in option 1 but clear felling is not performed to allow a stand to grow old. We needed these two forest growth projections in our simulation since clear felling of a stand is performed randomly during the simulation after the stand has matured. Therefore, our management option 1 determined the minimum age for clear felling. For stands older than this age, stand development followed the forest growth projection of management option 2. Thus, all stands were allowed to mature, if they were not randomly harvested in the year of maturation. Thus, stands may become (much) older than their optimal final harvesting age.

In this study, we used 50-year forest growth projections because present forest growth models in the MOTTI stand simulator tend to overestimate forest growth if run over a long period and, especially, in old stands. Error and uncertainty in predictions increase considerably with time; 30 years is considered a reliable time span, while one rotation (60–70 years) gives overestimates in the oldest stands. On the other hand, if the simulation period is grossly extended, the entire data will change its nature: initial empirical data were entirely replaced by forest data, which were generated by the model during forest regeneration.

Harvesting

Area harvested (AH) in our study area was assessed from forest management statistics collected by the Finnish Forest Center in central Finland. During 2006–2011, annual clear felling area in our study area varied between 295 and 692 ha, with the average being 485.5 ha (1.08% of the total area). Here, we used 445 ha (~1%) as a baseline area harvested. This benchmark level

was then systematically increased or decreased to assess the effect of forest clearing on population size and to uncover the timber supply capacity within our study area. We changed area harvested moderately at intervals of about 12%. These changes were well within the range of observed forest management. Clear felling was assigned randomly to mature stands that were available at a given time period. If felling was not allowed because of protection, another stand was selected. Harvesting continued as long as the given harvested area was reached or no more felling was allowed. We assumed that all studied species respond similarly to clear felling and cannot persist in stands immediately after clear felling.

Habitat index

Stand variables can be combined to calculate the suitability of a stand for a given species (for details, see Mönkkönen *et al.* 2014). We scaled the indices between 0 and 1, with 0 being non-habitat and 1 the best possible habitat for the species. Species' habitat modeling was based on stand variables that are known to be associated with the species. Those stand variables have a minimum value after which the habitat becomes suitable for the species. After the minimum value, habitat quality increases linearly or follows an equation deduced from an empirical study. Similarly, we determined a ceiling value for the stand variables after which habitat was of the highest quality in our data. Habitat index (HI) is a product of two or more sub-utilities (w) to combine stand variables. Since our example species vary distinctively in their habitat demand and, therefore, habitat extent varies between species, we did not apply the same index threshold value to distinguish suitable sites from unsuitable ones. To be able to compare population trends among management strategies, the threshold value for each species was defined so that at the start of the simulation there were ca. 200 suitable sites in the study area, and half of them were randomly assigned as occupied. A common problem in habitat modeling at broader scales is that all necessary variables are not available in the data used for modeling. Resulting models are, therefore, perhaps not the most accurate ones but, never-

theless, are practical and serve many simulation approaches in an ecological study. Also, many species respond to habitat characteristics both at a stand scale and also at a local scale (e.g. the flying squirrel). Inclusion of these hierarchies requires more complicated habitat modeling than was executed in this study. Here, habitat index was used to label a certain habitat suitable for the given species, and to represent the potential breeding site as a core area of a species' range. Thus, in this study, a species' habitat was calculated at the forest-stand scale, their population dynamics at the local scale and forest management (area harvested annually) was measured at the study-area (subregion) scale.

The Siberian flying squirrel

The Siberian flying squirrel is found in mature spruce-dominated mixed forests. It requires large spruce for shelter, and aspen and other deciduous trees for feeding (Reunanen 2001, Selonen 2002).

Habitat of the Siberian flying squirrel was described with our data as:

$$w_{\text{sprucevol}} = \begin{cases} 0, & \text{if } v_{\text{spruce}} \leq 140 \\ 0.0286v_{\text{spruce}} - 4, & \text{if } 140 < v_{\text{spruce}} \leq 175, (1) \\ 1, & \text{if } v_{\text{spruce}} > 175 \end{cases}$$

where $w_{\text{sprucevol}}$ is the sub-utility for the spruce volume and v_{spruce} is the volume of spruce in a stand ($\text{m}^3 \text{ha}^{-1}$).

$$w_{\text{sprucep}} = \begin{cases} 0, & \text{if } p_{\text{spruce}} \leq 50 \\ 10p_{\text{spruce}} - 5, & \text{if } 50 < p_{\text{spruce}} \leq 60, (2) \\ 1, & \text{if } p_{\text{spruce}} > 60 \end{cases}$$

where w_{sprucep} is the sub-utility for the spruce proportion and p_{spruce} is the proportion of spruce of the total timber volume in a stand (%).

$$w_{\text{dec}} = \begin{cases} 0, & \text{if } v_{\text{dec}} \leq 12 \\ 0.34v_{\text{dec}} - 4, & \text{if } 12 < v_{\text{dec}} \leq 15, (3) \\ 1, & \text{if } v_{\text{dec}} > 15 \end{cases}$$

where w_{dec} is the sub-utility for the deciduous tree volume and v_{dec} is the volume of deciduous trees in a stand ($\text{m}^3 \text{ha}^{-1}$).

The habitat index for the flying squirrel (HI_{fs}) is the product of sub-utilities denoting the volume of spruce, its proportion in a forest stand and the volume of deciduous trees, and it was calculated as follows:

$$HI_{fs} = w_{\text{sprucevol}} \times w_{\text{sprucep}} \times w_{\text{dec}}. \quad (4)$$

Three-toed woodpecker

The three-toed woodpecker is widespread and fairly common in mature, often conifer-dominated forests. The species is a resident hole-nester. It feeds on bark beetles and other insects living in dead and decaying trees (Pakkala *et al.* 2002). Therefore, dead or dying trees are essential for the feeding and breeding success of the species. Roberge *et al.* (2008) calculated the presence of the three-toed woodpecker in a forest stand (in central Sweden) from the total basal area (BA; $\text{m}^2 \text{ha}^{-1}$) of recently dead trees with an equation:

$$w_{\text{dw}} = [1 + \exp(-3.55BA - 4.46)]^{-1} \quad (5),$$

where w_{dw} is the sub-utility for the dead wood.

In addition, Pakkala *et al.* (2002) found that stands with timber volume $< 60 \text{ m}^3 \text{ha}^{-1}$ are not suitable habitats for the three-toed woodpecker, which we included as follows:

$$w_{\text{vol}} = \begin{cases} 0, & \text{if } v_{\text{total}} < 60 \\ v_{\text{total}}/200, & \text{if } 60 \leq v_{\text{total}} \leq 200, \\ 1, & \text{if } v_{\text{total}} > 200 \end{cases} \quad (6)$$

where w_{vol} is the sub-utility for the total timber volume and v_{total} is the total volume of timber in a stand ($\text{m}^3 \text{ha}^{-1}$).

The habitat index for the three-toed woodpecker (HI_{two}) is the product of these two sub-utilities denoting the basal area of fresh dead wood and the timber volume that exceeds $60 \text{ m}^3 \text{ha}^{-1}$, and it was calculated as follows:

$$HI_{\text{two}} = w_{\text{dw}} \times w_{\text{vol}}. \quad (7)$$

Long-tailed tit

The long-tailed tit is a semi-resident species

feeding on small invertebrates. According to Jansson and Angelstam (1999), its habitat is dominated by middle-aged to mature deciduous stands composed of *Alnus* spp. and *Betula* spp. These researchers reported that occupied forests had a minimum basal area of all living trees of $11 \text{ m}^2 \text{ha}^{-1}$ (mean $18 \text{ m}^2 \text{ha}^{-1}$) and at least 21% deciduous trees (mean 66%). Using this information, we formulated three following sub-utility functions for a habitat index:

$$w_{\text{age}} = \begin{cases} 0, & \text{if age} < 30 \\ 0.033 \times \text{age} - 1, & \text{if } 30 \leq \text{age} < 60, \\ 1, & \text{if age} \geq 60 \end{cases} \quad (8)$$

where w_{age} is the sub-utility for the stand age and 'age' is the stand age in years.

$$w_{\text{BA}} = \begin{cases} 0, & \text{if BA} \leq 10 \\ 0.02 \times \text{BA} - 2, & \text{if } 10 < \text{BA} \leq 15, \\ 1, & \text{if BA} > 15 \end{cases} \quad (9)$$

where w_{BA} is the sub-utility for the stand basal area and BA is the total basal area in a stand ($\text{m}^2 \text{ha}^{-1}$).

$$w_{\text{dec}} = \begin{cases} 0, & \text{if } p_{\text{dec}} \leq 20 \\ 2.5 p_{\text{dec}} - 0.5, & \text{if } 20 < p_{\text{dec}} \leq 60, \\ 1, & \text{if } p_{\text{dec}} > 60 \end{cases} \quad (10)$$

where w_{dec} is the sub-utility for the deciduous tree proportion and p_{dec} is the proportion of deciduous trees of the total timber volume in a stand ($\text{m}^3 \text{ha}^{-1}$).

The habitat index for the long-tailed tit (HI_{tit}) is the product of these three sub-utilities denoting the stand age, the total basal area in a stand and the proportion of deciduous trees in a forest stand, and it was calculated as follows:

$$HI_{\text{tit}} = w_{\text{age}} \times w_{\text{ba}} \times w_{\text{dec}}. \quad (11)$$

Population dynamics

Our population modeling was based on the incidence function method proposed by Hanski (1994). Our modeling approach was kept conservative, and details of species' behavior were not included in the present project. To assess

the capacity of our study area to support viable populations, we assumed that only one closed population occupied our study area. Population dynamics take place in a patchwork of suitable forest stands. A forest stand is labeled suitable if its habitat index exceeds a threshold value. A collection of these stands constitute the current patchwork for the population at each time step. Colonization of a stand depends on the location and size of suitable stands in the neighborhood. For simplicity, we assumed that large good-quality forest stands most probably remained occupied and empty sites were colonized eagerly if there were occupied sites nearby. Stand extinction probability, E , depends on its size as follows:

$$E = \text{MIN}[1, A_{\text{min}}/(A^{0.85})], \quad (12),$$

where A is the stand size (ha, $A_{\text{min}} = 0.2$ ha). Stands that are smaller than 0.15 ha always remain unoccupied. The average size of stands in our subregion was 1.63 ha with a population extinction probability of 0.13. Here, we assumed that small sites may become occupied for a short period of time (i.e. one time unit) but they were not capable to support longer continuous occupancy.

Colonization of an empty, suitable stand depends on the number of occupied stands in its neighborhood within a 500-m search radius. This is an edge-to-edge distance, which results in somewhat different search areas depending on stand size. However, despite the varying area, distances between stands remain the same. All occupied stands within or at the border of the search area were included in the calculation of colonization potential:

$$m = \sum A_j \exp(-d_{ij}), \quad (13),$$

where m is the colonization potential of a vacant forest stand, and A_j is the size of the neighboring occupied stand, and d_{ij} is the distance (in hectometers) between them. Colonization probability, c , was then calculated as

$$c = m/(m + y), \quad (14),$$

where y is a parameter ($y = 0.3$).

We applied the same population model to all species since we had no valid data to adjust the models for each species. This is a shortcoming of the study, but it allowed for the comparison of species with dissimilar habitat requirements. Therefore, our study shows species' occupancy dynamics in a habitat network rather than represents a true population study. A search distance of a constant 500-m may seem a limited one, but considering the size of the subregion, and changes in habitat availability in our study area during the simulation, area of colonization was relevant for our approach. There was no movement outside the subregion nor were individuals moving in from outside the study area.

Spatio-temporal modeling

Computer simulations were carried out with the SELES (spatially explicit landscape event simulator) software. SELES is a domain-specific computer language for modeling landscape dynamics (Fall & Fall 2001). SELES enables dynamic simulations of landscape models that operate on digital maps from real landscapes (e.g. classified remote sensing images). Models built using SELES may incorporate a variety of submodels of landscape processes simultaneously (forest succession, disturbance events, etc.). Additionally, the location of animal and plant populations and movement of individuals in the landscape and among populations can be explicitly simulated (Fall *et al.* 2001), which allows for more realistic understanding of species ecology in dynamic heterogeneous environments than static models.

Our simulation encompassed three subroutines: (1) species habitat modeling which was based on a forest growth schedule; forest growth data, in turn, were derived from the MOTTI forest stand simulator; (2) population dynamics among suitable forest stands; and (3) final harvesting of forests from forest statistics. Subroutines were run in a sequence of 5-year intervals. Simulation at each time interval started with the habitat model. Forest growth was updated and the current habitat index for all stands was calculated. Suitable stands for the given species were mapped as a spatial variable. After habitat modeling, extinc-

tion and colonization probabilities were calculated. Each suitable stand was visited again and checked for its present status by comparing the probabilities of E and c (Eqs. 12 and 14) with a random probability number. After these subroutines, clear felling was performed. A given total area of stands was felled. All runs were replicated ten times to produce average trends and to explore variation in the resulting trends.

Our modeling scheme was rather conservative and makes many assumptions. Our study area did not contain protected areas or refuges for the species but it could be managed entirely. We assumed there was only one landowner since a stand selected to be harvested must be compensated with another one if constrained by the species to achieve the given management objective. In addition, we assumed that the system was closed and there was no population flow from outside the study area. These assumptions were to some degree unrealistic but they helped to avoid overly-detailed analysis in order to uncover the general, emerging trends. The interpretation framework of the results of this study covers the study area and the 50-year time span. With this research design, it was meaningless to look at single forest stands or periods since the 50-year time range attempted to cover most of the rotation length, and resulting trends were specific to this study area only. Therefore, one should pay attention to emerging population trends and compare occupied stand numbers with their initial number. Absolute numbers are simulation specific and change if models and assumptions are modified.

Results

If there is no harvesting at all in the study area, the amount of habitat, and concomitantly, the number of occupied stands in all species increased (Fig. 1). Population growth depended on the regional forest structure and the temporal capacity of our study area to provide habitat for the species. However, the response curves were distinctly variable because of species habitat requirements. Deviation between lines suggests how quickly the population responded to an increase in the amount of habitat in our study area.

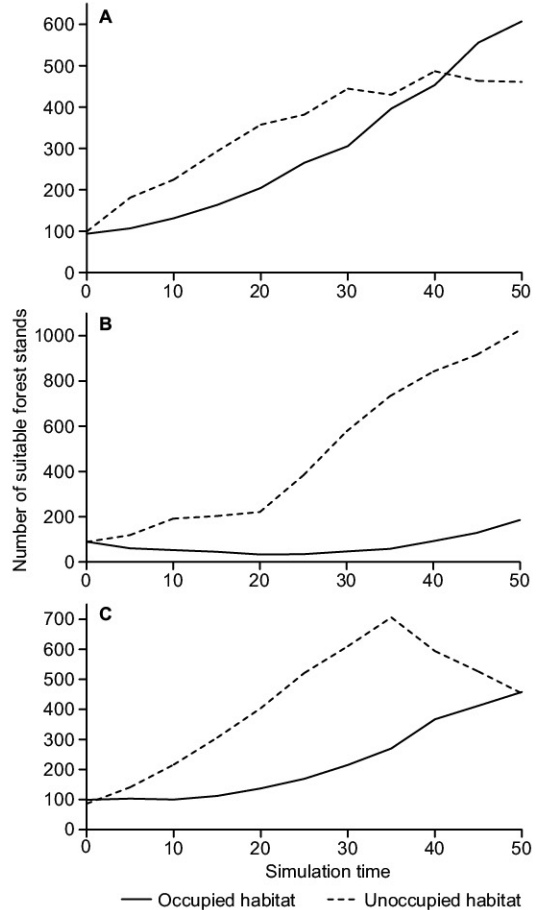


Fig. 1. Habitat availability for the three focal species if no clear felling is permitted. (A) Flying squirrel, (B) three-toed woodpecker, and (C) long-tailed tit. Resulting trend lines are almost deterministic after the forest management subroutine was switched off. Therefore, error bars are not included.

The parallel increase in the number of occupied and unoccupied stands that are suitable for the flying squirrel showed that the species tracks habitat almost without time lags and was capable to use emerging habitat effectively (Fig. 1A). By contrast, the three-toed woodpecker showed a considerable population decrease during the first few decades of the simulation, and the number of stands occupied by the species reached a minimum level of 33 stands in year 20. Recovery from the early decline took time, and slow recovery started to take effect only after habitat became more common in the study area (Fig. 1B). If no area is clear felled, the number

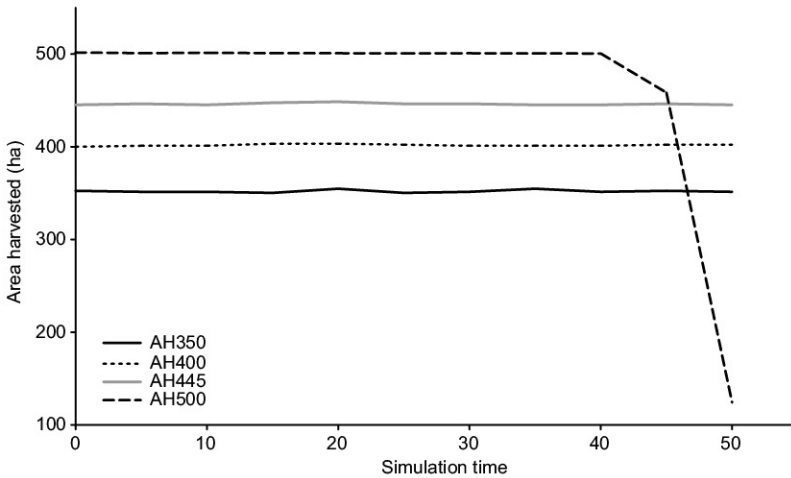


Fig. 2. Area felled annually (AH) when clear felling is assigned to stands, ignoring species occupancy and their habitat requirements. Horizontal lines represent sustainable level of area felled, whereas declining trends indicate that the given level cannot be sustained throughout the 50-year period. AHs refer to different levels in the annual clear felling area.

of occupied stands at the end of the simulation approximately doubled as compared with the initial number of occupied stands in the study area. For the three-toed woodpecker, the lack of recently dead woody material due to tree mortality in forests caused a habitat bottleneck for the species. The long-tailed tit seemed to become more abundant with a longer time lag than that of the flying squirrel (Fig. 1C). The reason for this lag was a higher turnover of its habitat (i.e. premature middle-aged forests). Deciduous-rich forests occupied by the long-tailed tit were without exception thinned and thus the change in vital characteristics in its habitat did not allow long-term occupancy within any forest stand.

If management planning and subsequent clear felling was carried out without paying attention to species requirements, we can explore the capacity of our study area to provide timber over the 50-year time frame (Fig. 2). We see that if the area felled was raised from a baseline level of 445 ha, the constant management protocol cannot be maintained in the long run. In our study area, the current baseline level is rather close to the upper sustainable long-term management objective.

When clear felling in the study area was maintained at the current annual level or increased and the species' occurrence and/or habitats were ignored, the number of stands occupied by the flying squirrel declined. However, when the area felled annually was reduced from 455 to 350 ha, the number of occupied stands remained approximately at the initial level or increased during the

simulation (Fig. 3A). Persistence of the flying squirrel in our study area depended strongly on the extent of clear felling.

When clear felling was applied in the study area without regard to species requirements, the number of stands occupied by the three-toed woodpecker decreased by 75% during the first 25 years, irrespective of the area felled annually (Fig. 3B). Only during the second half of the simulation did the population start to recover at a rate that depended on the area felled annually. At lower than the current level of annual felling (350 ha year⁻¹), the population recovered to ca. 65% of the initial level. Because habitat of the three-toed woodpecker included also immature forests where the amount of dead wood and total tree volume were high, the conflict between clear felling and habitat availability was not as direct as in the case of the flying squirrel. In our simulations, all thinnings were performed periodically and suitable habitat for the woodpecker mainly emerges after the last thinning and may last for a long time after that. Natural, dead, woody material from self-thinning accumulated only with time and provided limited quantities of dead wood to support the three-toed woodpecker.

When clear felling of stands in the study area was carried out disregarding the species' occurrence or habitats, the number of stands occupied by the long-tailed tit increased, and the increase was prominent even if the area felled annually was increased from the current level (Fig. 3C). Thus, the long-tailed tit persistence did not

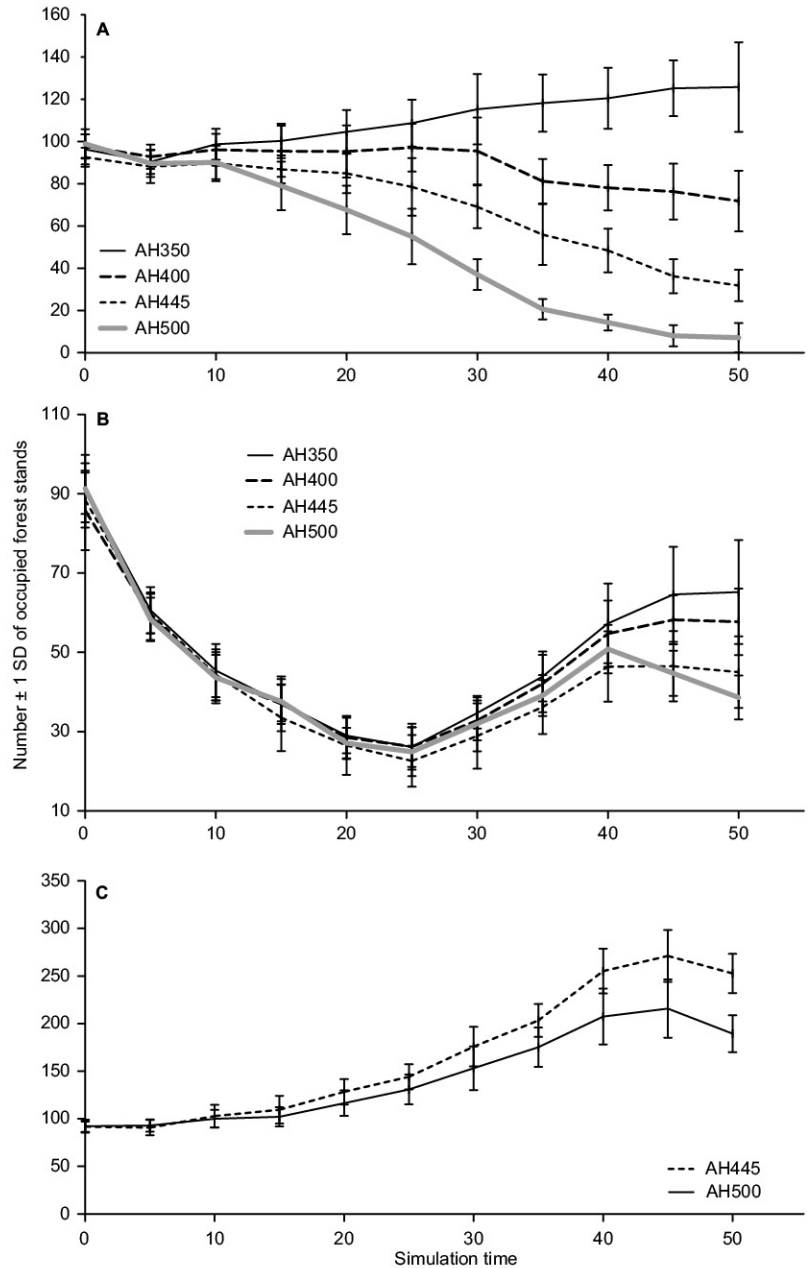


Fig. 3. Number of occupied stands by the three focal species under alternative harvesting levels when clear felling is assigned to stands ignoring species occupancy and their habitat requirements: (A) flying squirrel, (B) three-toed woodpecker, and (C) long-tailed tit. Vertical bars depict standard deviation in the ten simulation runs.

depend on the extent of clear felling. Stands where deciduous trees comprise a substantial proportion of the timber volume are common in the study area even at the elevated level of annual area felled.

Preservation of forest stands if they are occupied by the focal species is but one method to improve species persistence. The number of stands occupied by the flying squirrel increases

if clear felling was not permitted in occupied stands (Fig. 4A). Even at an elevated level of area felled annually, the number of occupied stands first increased and then remained at a constant level that is higher than the initial level. However, after the first 15 years harvest area higher than the current area felled could not be maintained and harvesting was severely constrained by occupancy by the flying squirrel

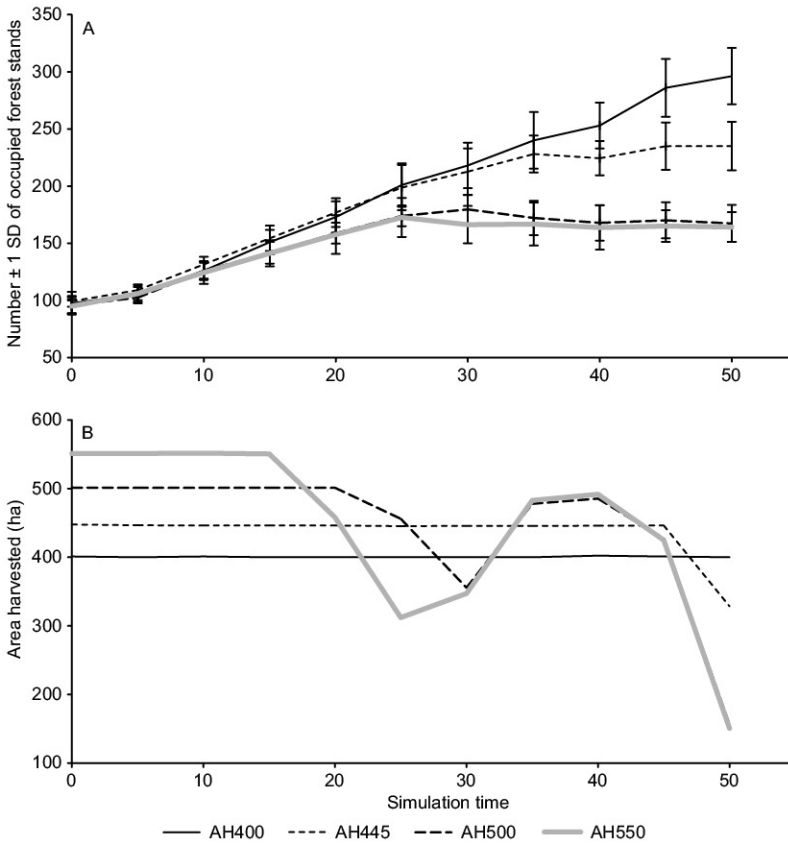


Fig. 4. (A) Number of stands occupied by the flying squirrel under alternative management objectives if clear felling is not allowed in occupied stands. (B) Annual area clear felled when no clear felling is allowed in stands occupied by the flying squirrel.

(Fig. 4B). Even the current area felled could not be maintained during the entire 50-year period.

When clear felling was not executed in suitable habitat for the flying squirrel, the number of occupied stands increased rapidly (Fig. 5A) at the current and reduced levels of area felled. This population increase entailed that the current area of clear felling could not be sustained for longer than 20 years, and only a reduced level of clear felling (350 ha year⁻¹) was sustainable in the long run (Fig. 5B).

Avoiding clear felling in stands occupied by the three-toed woodpecker (Fig. 6) or in all suitable stands (Fig. 7) did not completely remove the population bottle-neck, but the number of occupied stands decreased approximately to one third of the initial level almost irrespective of the area felled annually. However, population recovery depended both on the area felled annually and on the way clear felling was assigned to stands. Within the 50 years, recovery to the initial level of occupied stands was not com-

plete when only occupied stands were set aside from clear felling (Fig. 6A). In contrast, the initial level of occupancy could be attained if all suitable habitats for the three-toed woodpecker were set aside from clear felling (Fig. 7A). This took place also with the current rate of the area felled. If clear felling was avoided in stands that were either occupied or suitable for the species, harvesting areas higher than the current area harvested was not sustained during the 50-year period (Figs. 6B and 7B).

Discussion

Our simulations show that species respond differently to harvesting and responses have dissimilar time lags. The habitat of the flying squirrel overlaps with mature forests and the population distribution responded readily to variation in habitat availability. Consequently, the species is vulnerable to more intensive harvest manage-

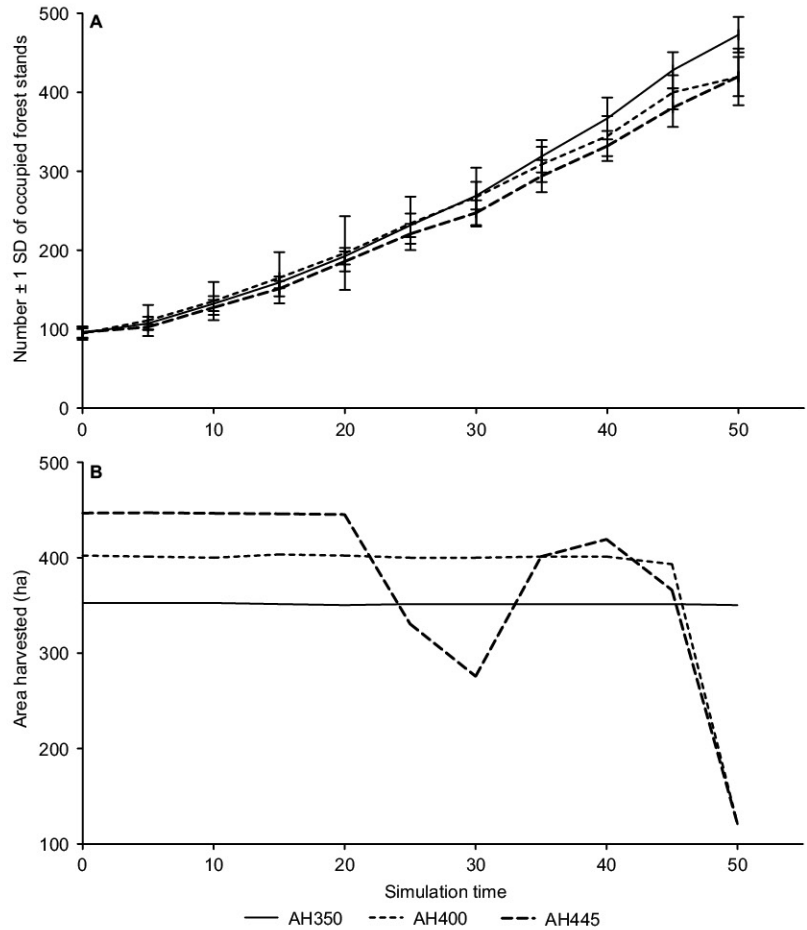


Fig. 5. (A) Number of stands occupied by the flying squirrel under alternative management objectives if clear felling is not allowed in suitable stands for the species. (B) Annual clear felled area when no clear felling is allowed in suitable stands.

ment objectives. Protection of occupied stands enhanced the population and it allowed felling of an even larger area annually than currently without negative effects on the population. However, harvest levels greater than the current area felled can only be sustained for the first two decades after which the occurrence of the species starts to limit harvesting potential. When all suitable habitats, in addition to occupied stands, were preserved from clear felling, the population distribution increased, but harvest potential in such a case becomes rapidly limited even at the current level of area felled. Thus, for the flying squirrel, a reasonable strategy for planning forest management to resolve the conflict between species habitat availability and economically-sustainable forestry is to leave occupied stands unharvested. Preserving all suitable habitats seems too restrictive, and strongly constrains harvesting potential.

Habitat for the three-toed woodpecker in our simulations strongly declined during the first half of the simulation period most likely because of the thinning of stands, which efficiently removes self-thinning mortality and thereby reduces the amount of dead wood (Tikkanen *et al.* 2012). This is evident from the trajectory of the number of occupied stands when thinning, but not clear felling, was applied in forest management (Fig. 1B). The bottleneck results from the stand age distribution that is distorted towards younger stands at the initial state of the simulation. These stands become gradually suitable for the three-toed woodpecker after 20–30 years. By this time, suitable habitat in older stands is harvested and its amount declines constantly. After the bottleneck, the species started to recover when forests mature and accumulate dead woody material. An increase in suitable

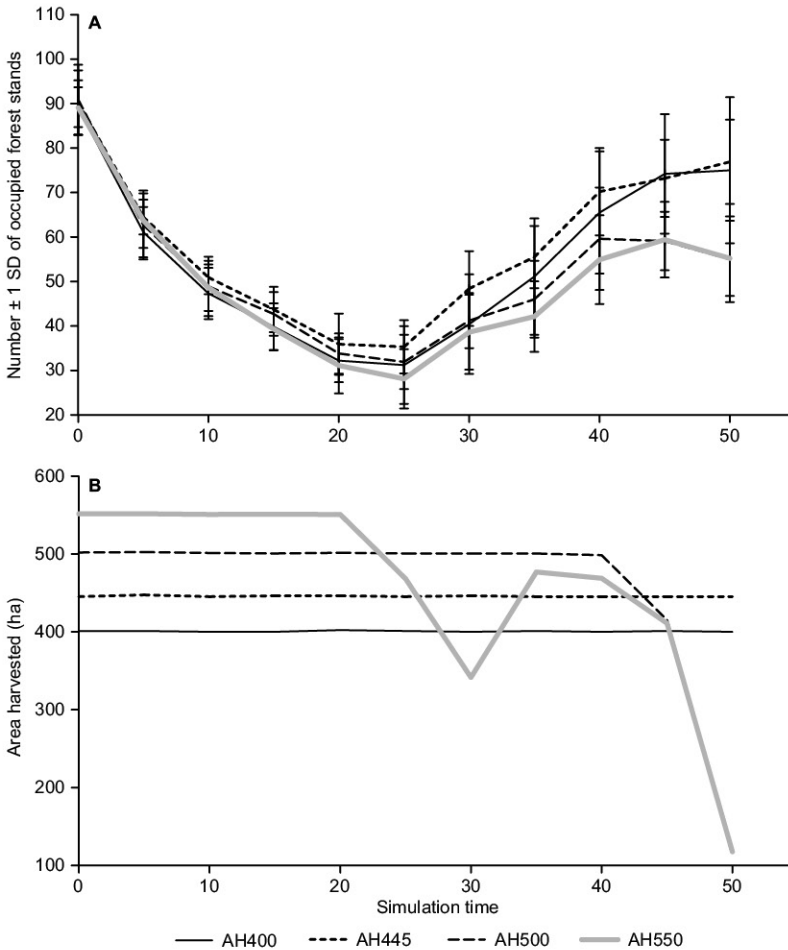


Fig. 6. (A) Number of stands occupied by the three-toed woodpecker under alternative management objectives if clear felling is not allowed in occupied stands. (B) Annual clear felled area when no clear felling is allowed in stands occupied by the three-toed woodpecker.

stands enhances stand colonization thus mitigating the recovery of the species. Avoidance of clear felling in occupied stands had a positive effect on recovery. If all suitable stands for the woodpecker were left intact, recovery was obvious. In this case, the population almost regained its initial level by year 50. Regarding the potential management gain, the two strategies did not differ considerably and, therefore, avoiding clear felling in all suitable habitat of the three-toed woodpecker seems an ecologically meaningful management strategy. However, because the species also occupies premature forests, the conflict between habitat availability and forest clear felling is not as severe as in the case of the flying squirrel. Therefore, the best strategy to maintain viable three-toed woodpecker populations would be to partly refrain from thinnings in the man-

agement of young forests rather than refraining from final clear felling at all suitable sites for the species (Mönkkönen *et al.* 2014).

In our study, there was not any marked conflict between forest clear felling and habitat availability of the long-tailed tit. The population in our study area will increase even at a harvesting level higher than the current level of forest clear felling. This is likely because the long-tailed tit tolerates clear felling of mature forest stands. Immature, mid-successional forests with plenty of deciduous trees were common in our study area, and these stands provided ample habitat for the long-tailed tit. However, mid-successional stands are temporary in nature and provide only short-term occupancy for the species. Mönkkönen *et al.* (2014) suggested that a cost-efficient way to secure long-tailed tit

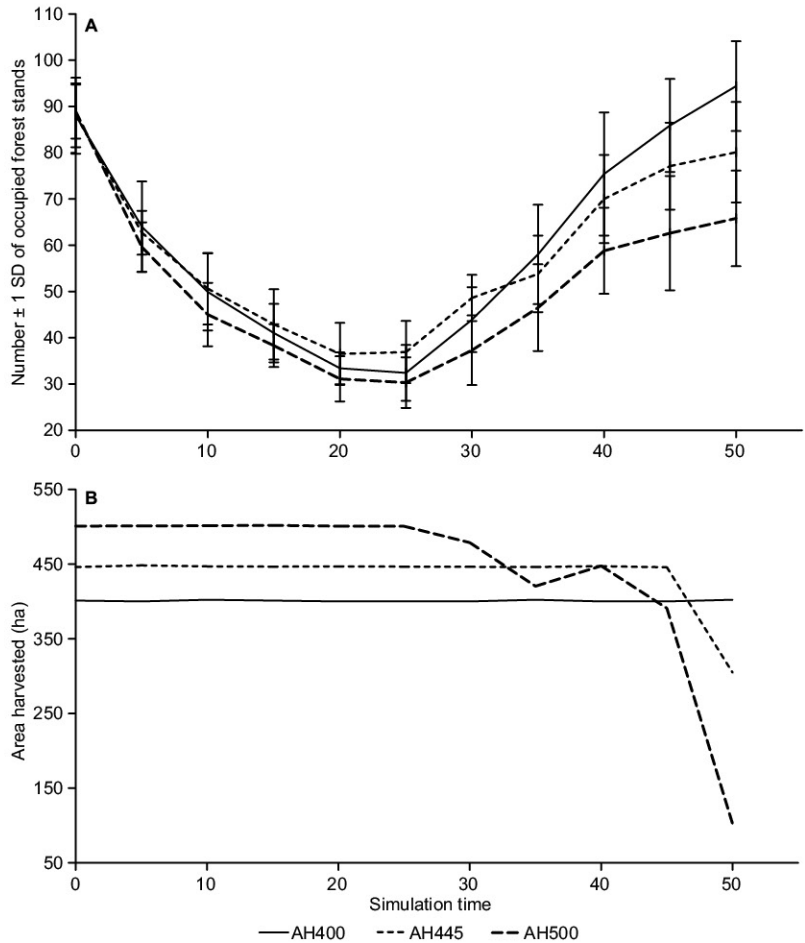


Fig. 7. (A) Number of occupied stands by the three-toed woodpecker under alternative management objectives if clear felling is not allowed in stands that are suitable for the species. (B) Annual clear felled area when no clear felling is allowed in suitable stands.

habitats is to refrain from thinnings, i.e. not to remove all deciduous trees when managing young forests.

Common and abundant species do not require extra attention whereas species depending on certain habitat attributes, such as microhabitat or site type, need population-level management to allow their regional long-term persistence. Successful management planning supports populations in the long run and does not unnecessarily restrict harvesting. To meet their commitments, forest managers should have all the necessary information available to plan management accordingly. Depending on biodiversity-conservation goals, management objectives and their timing may vary among geographic locations. There is no one particular management objective that covers all forest biodiversity, but protection requires objec-

tives that vary depending on species, and they should also be prioritized locally, regionally and temporally (Reunanen *et al.* 2010).

Corrently, it is common to leave retention trees, dead and dying trees or key habitats unharvested in the final clearing (Metsätalouden kehittämisskeskus Tapio 2014). These methods are likely to be effective for some species since they may provide habitat for them. However, for many mobile vertebrates, such as birds and mammals, such residual structures may provide some resources but they are not large enough to offer shelter or breeding sites. For instance, the flying squirrel is sensitive to harvesting in occupied sites (*see also* Jokinen 2012, Santangeli *et al.* 2013). In managed forest landscapes, many habitats are in short supply and some habitat characteristics cannot be promoted simply by

leaving key forest elements unharvested during final clearings. The three-toed woodpecker requires dead and dying trees. Sufficient quantities of dead woody material accumulates in middle-aged, managed forests. However, such stands are regularly thinned throughout, which effectively diminishes habitat for the woodpecker at a broad scale. In our study, the effect of thinning operations can be seen as a rapid decrease in the number of occupied stands, which seems not to be linked with the protection of mature stands.

In spatio-temporal computer simulations with a limited time horizon, the single most decisive factor affecting future projections is the initial state of the system. The state of the forest landscape in the beginning crucially defines the forest growth trajectories and thus, the supply of timber and habitat during the simulation time. However, stochastic population behavior in this spatio-temporal context cannot be accurately assessed from the initial state of the system alone since it depends on several independent and partly dependent processes. Dynamic populations need to adapt to forest succession and management, as well as to local stochastic extinctions. Stochastic occupancy patterns hamper forest management planning that aims at functional populations at a regional scale. Therefore, the need for management of animal populations calls for new harvesting strategies, such as partial harvesting of a stand, that can be applied widely and at all stages of forest management during the rotation.

The general message from our analysis is that the sustainable level of area clear felled annually varies among the three focal species. Thus, strategies to reconcile timber harvesting and population persistence are species-specific. Sustainable management depends first of all on the degree to which forest management objectives overlap with habitat requirements of the species. Forest management is restricted by many obligations to maintain biodiversity, habitats and other values beside commercial timber production. Strict terms to maintain biodiversity in forest management inevitably limits harvesting possibilities. On the other hand, adequately informed regional planning of forest management that adopts multiple objectives simultaneously may result in considerable benefits for biodiversity with low economic costs (Mönkkönen *et al.* 2014).

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References

- Beissinger, S. R. & Westphal, M. I. 1998: On the use of demographic models of the population viability in endangered species management. — *Journal of Wildlife Management* 62: 821–841.
- Cabeza, M. & Moilanen, A. 2003: Site-selection algorithms and habitat loss. — *Biology* 17: 1402–1413.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. 2012: Biodiversity loss and its impact on humanity. — *Nature* 486: 59–67.
- Cerdeira, J. O., Pinto, L. S., Cabeza, M. & Gaston, K. J. 2010: Species specific connectivity in reserve-network design using graphs. — *Biological Conservation* 143: 408–415.
- European Commission 2011: *European Parliament resolution of 20 April 2012 on our life insurance, our natural capital: an EU biodiversity strategy to 2020*. European Commission 2011/2307(INI).
- Fall, A. & Fall, J. 2001: A domain-specific language for models of landscape dynamics. — *Ecological Modeling* 141: 1–18.
- Fall, A., Daust, D. & Morgan, D. 2001: A framework and software tool to support collaborative landscape analysis: Fitting square pegs into square holes. — *Transactions in GIS* 5: 67–86.
- Finnish Statistical Yearbook of Forestry 2012: Finnish Forest Research Institute.
- Hanski, I. 1994: A practical model of metapopulation dynamics. — *Journal of Animal Ecology* 63: 151–162.
- Hildén, M., Syrjänen, K., Koskela, T., Kumela, H. & Fredrikson, J. 2007: *Metsien monimuotoisuuden turvaaminen – Keinot ja niiden kohdentaminen [Focusing conservation measures for biodiversity protection]*. Suomen ympäristö 17, Suomen ympäristökeskus, Helsinki. [In Finnish with English summary].
- Hynynen, J., Ahtikoski, A., Siitonen, J., Sievänen, R. & Liski, J. 2005: Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. — *Forest Ecology and Management* 207: 8–15.
- Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H. & Haapala, P. 2002: Models for predicting stand development in MELA system. — *Finnish Forest Research Institute Research Papers* 835: 1–116.

- Jansson, G. & Angelstam, P. 1999: Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. — *Landscape Ecology* 14: 283–290.
- Jokinen, M. 2012: *Liito-oravan lisääntymis- ja levähdyspaikka- ja leikkauksen vaikuttavuus lajin suojelualueella* [Effectiveness of breeding and resting site delimitations as a conservation method for the Siberian flying squirrel]. — Suomen ympäristö 33, Suomen ympäristökeskus, Helsinki. [In Finnish with English summary].
- Junninen, K. & Similä, M. (eds.) 2013: *Metsien ennallistamisen ja luonnonhoidon opas* [Guide for habitat restoration and management]. — *Metsähallituksen Luonnonhoitojulkaisuja*, Sarja B 157: 1–19. [In Finnish with English summary].
- Lindenmayer, D. B., Possingham, H. P., Lacy, R. C., McCarthy, M. A. & Pope, M. L. 2003: How accurate are population models? Lessons from landscape-scale tests in a fragmented system. — *Ecology Letters* 6: 41–47.
- Metsätalouden kehittämiskeskus Tapio 2014: *Hyvän metsänhoidon suositukset*.
- Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H. & Tikkanen, O.-P. 2014: Spatially dynamic forest management to sustain biodiversity and economic returns. — *Journal of Environmental Management* 134: 80–89.
- Nalle, D. J., Montgomery, C. A., Arthur, J. L., Polasky, S. & Schumaker, N. H. 2004: Modeling joint production of wildlife and timber. — *Journal of Environmental Economics and Management* 48: 997–1017.
- Pakkala, T., Hanski, I. & Tomppo, E. 2002: Spatial ecology of the three-toed woodpecker in managed forest landscapes. — *Silva Fennica* 36: 279–288.
- Päivinen, J., Björkqvist, N., Karvonen, L., Kaukonen, M., Korhonen, K.-M., Kuokkanen, P., Lehtonen, H. & Tolonen, A. 2011: *Metsähallituksen metsätalouden ympäristöopas*. — Metsähallituksen metsätalouden julkaisuja 67: 1–215.
- Rassi, P., Hyvärinen, E., Juslen, A. & Mannerkoski, I. (eds.) 2010: *Suomen lajien uhanalaisuus — Punainen kirja 2010* [The 2010 red list of Finnish species]. — Ympäristöministeriö ja Suomen ympäristökeskus, Helsinki. [In Finnish with English summary].
- Raunio, A., Schulman, A. & Kontula, T. 2008: *Suomen luontotyyppien uhanalaisuus 1–2* [Endangered habitats in Finland, parts 1–2]. — Suomen ympäristö 8: part 1 page 264, part 2 page 572. Suomen ympäristökeskus, Helsinki. [In Finnish with English summary].
- Reunanen, P. 2001: Landscape responses of the Siberian flying squirrel (*Pteromys volans*) in northern Finland — the effect of scale on habitat patterns and species incidence. — *Acta Universitatis Ouluensis A* 371: 1–39.
- Reunanen, P., Fall, A. & Nikula, A. 2010: Biodiversity and ecological forest-cover domains in boreal landscapes. — *Biodiversity and Conservation* 19: 665–678.
- Roberge, J.-M., Angelstam, P. & Villard, M.-A. 2008: Specialised woodpeckers and naturalness in hemiboreal forests — deriving quantitative targets for conservation planning. — *Biological Conservation* 141: 997–1012.
- Salminen, H., Lehtonen, M. & Hynynen, J. 2005: Reusing legacy FORTRAN in the MOTTI growth and yield simulator. — *Computers and Electronics in Agriculture* 49: 103–113.
- Santangeli, A., Wistbacka, R., Hanski, I. K. & Laaksonen, T. 2013: Ineffective enforced legislation for nature conservation: a case study with the Siberian flying squirrel and forestry in a boreal landscape. — *Biological Conservation* 157: 237–244.
- Schapaugh, A. W. & Tyre, A. J. 2012: Bayesian networks and the quest for reserve adequacy. — *Biological Conservation* 152: 178–186.
- Schuster, R. & Arcese, P. 2013: Using bird species community occurrence to prioritize forests for old growth restoration. — *Ecography* 36: 499–507.
- Selonen, V. 2002: *Spacing behaviour of the Siberian flying squirrel — effects of landscape structure*. — Ph.D. thesis, University of Helsinki.
- Shan, Y., Bettinger, P., Cieszewski, C. J. & Li, R. T. 2009: Trends in spatial forest planning. — *International Journal of Mathematical and Computational Forestry and Natural-Resource Sciences* 1: 86–112.
- Tikkanen, O.-P., Matero, J., Mönkkönen, M., Juutinen, A. & Kouki, J. 2012: To thin or not to thin — bio-economic analysis of two alternative practices to increase amount of coarse woody debris in managed forests. — *European Journal of Forest Research* 131: 1411–1422.