

Master of Science Thesis

**Management of boreal forest landscape for plant species
richness and timber revenues**

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ABSTRACT

One of the main reasons for the ongoing loss of biodiversity is habitat loss and degradation caused by human actions. The conflict between human actions and biodiversity is often caused by trade-offs between different land-use and land management objectives, e.g., commodity production versus biodiversity protection. In boreal forests, intensive forest management for timber has had negative effects on forest biodiversity, because it has changed the structure and dynamics of the forests. Sustainable forest management requires multi-objective management planning, where trade-offs between different objectives are minimized at the landscape level. In this study, I focused on the landscape level trade-offs between plant species richness and timber revenues, and the ways how to minimize them. I used a surrogate index of habitat suitability for plants as an estimate of plant species richness. Using seven alternative management options and a 50-year time frame, these surrogate indices and previously calculated timber revenues were optimized at landscape level to find management combinations that simultaneously optimize economic benefits and plant species richness in the landscape. The main goals were to find out 1) what is the potential of the landscape to simultaneously provide plant species richness and economic returns from selling timber, and 2) what combinations of management regimes maximize plant species richness with given levels of economic returns, and vice versa. The results show that there is a trade-off between plant species richness and timber revenues in the boreal landscape, but with optimal combinations of management regimes both objectives can be simultaneously maintained at high levels. Current management methods that are based on almost consistent application of the recommended management in turn yield substantially lower plant species richness. Maximizing plant species richness requires a mixture of many management regimes, which indicates that no management regime alone is optimal for plant species richness on all stands, and that landscape level heterogeneity is important for plant species richness.

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TIIVISTELMÄ

Ihmisen aiheuttama elinympäristöjen katoaminen sekä niiden laadun heikkeneminen ovat tärkeitä syitä luonnon monimuotoisuuden häviämiseen. Usein elinympäristöjen katoaminen ja laadun heikkeneminen johtuvat ristiriidoista eri maankäyttömuotojen välillä, kuten hyödykkeiden tuotannon ja monimuotoisuuden suojelun välillä. Borealisissa metsissä intensiivinen, puuntuotantoon tähtäävä metsänhoito on aiheuttanut muutoksia metsien rakenteeseen ja dynamiikkaan, millä on ollut negatiivisia vaikutuksia metsien monimuotoisuuteen. Metsien kestävä käyttö vaatii monitavoitteista suunnittelua, jossa ristiriidat eri käyttömuotojen välillä pyritään minimoimaan maisematasolla. Tässä tutkimuksessa keskityin puuntuotannosta saatavien tulojen ja kasvien lajimäärän välisiin ristiriitoihin sekä etsin ratkaisuja näiden ristiriitojen minimoimiseen. Arvioin kasvien lajimäärää metsissä surrogaatti-indeksillä, joka mittaa elinympäristön sopivuutta kasviyhteisöille. Nämä surrogaatti-indeksit sekä aiemmin lasketut, metsistä saatavat puuntuotantotulot optimoitiin maisematasolla käyttäen seitsemää eri metsänkäsittelytapaa ja 50 vuoden aikamittakaavaa. Tarkoituksena oli löytää käsittely-yhdistelmiä, joissa ristiriidat ekologisten ja taloudellisten tavoitteiden välillä olisivat mahdollisimman pieniä. Tutkimuksen päätavoitteet olivat selvittää: 1) millainen potentiaali maisemalla on tarjota samanaikaisesti suuri kasvien lajimäärä ja runsaat puunmyyntitulot, sekä 2) millaiset metsänkäsittely-yhdistelmät maksimoivat kasvien lajimäärän maisemassa eri puunmyyntitulotasolla, ja toisinpäin. Tuloksista nähdään, että borealisessa metsämaisemassa kasvien lajimäärän ja metsistä saatavien puunmyyntitulojen välillä on ristiriita, mutta molemmat tavoitteet voidaan pitää korkealla tasolla käyttäen optimaalisia metsänkäsittely-yhdistelmiä. Nykysuosituksen mukainen metsänkäsittely puolestaan tuottaa huomattavasti alhaisempia kasvien lajimääriä verrattuna optimaalisiin käsittely-yhdistelmiin. Kasvien lajimäärän maksimoimiseksi maisemassa tulisi yhdistää useita eri metsänkäsittelytapoja. Tämä kertoo, että mikään yksittäinen käsittelytapa ei ole optimaalinen kaikissa metsissä, ja että maiseman vaihtelevuus on tärkeää kasvien lajirikkuuden kannalta.

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1. INTRODUCTION

1.1. Biodiversity, ecosystem services and conservation planning in boreal forests

Biodiversity provides the basis for ecosystem functions, and thus it plays a key role in provisioning of the benefits that humans can obtain from nature (Millennium Ecosystem Assessment (MEA) 2005, Cardinale et al. 2012). These benefits are called ecosystem services, and they include nutrient cycling, water purification, climate regulation, production of food and other products, as well as spiritual and aesthetic values (MEA 2005). There is strong evidence about the existence of a relationship between biodiversity and certain supporting and regulating ecosystem services (e.g., Balvanera et al. 2006, Nelson et al. 2009, Quijas et al. 2010, Cardinale et al. 2012). Biodiversity can also be considered an ecosystem service or a good itself (MEA 2005, Mace et al. 2012). In a meta-analysis of biodiversity effects on ecosystem functioning and services by Balvanera and colleagues (2006), it was concluded that biodiversity has positive effects on most ecosystem services, especially on productivity, which is a supporting service that underpins provisioning services (e.g. food or wood). Biodiversity enhances also many other supporting and regulating services like erosion control, nutrient cycling, and decomposition. Because biodiversity is positively correlated with many ecosystem services, it is possible that the on-going loss of biodiversity has a negative effect on the goods and services that ecosystems can provide (Hooper et al. 2012).

One of the main reasons for the loss of biodiversity worldwide is habitat loss and degradation caused by human actions (MEA 2005). The conflict between human actions and biodiversity is often caused by trade-offs between different land-use and land management objectives, e.g., commodity production versus biodiversity protection. For example in boreal forests, intensive forest management for timber has had negative effects on forest biodiversity, as it has changed the structure and dynamics of the forests (e.g., Halpern & Spies 1995, Angelstam et al. 2001, Puumalainen 2001). At the landscape level, age structure and composition of forest stands have been simplified, so that the landscape is dominated by young, even-aged conifer monocultures, natural and old-growth forests remaining only in small, fragmented patches (Esseen et al. 1997). At the stand level, forest management has caused changes in tree species composition, stand structure, forest patch size and disturbance regime (Esseen et al. 1997, Puumalainen 2001). These changes in forest stands and landscapes have decreased habitat availability for many forest dwelling species, causing declines in many populations (Kuuluvainen et al. 2004). In Finland, changes in forested environments are the main reason for population declines for 693 red-listed species of fungi, plants and animals living in forests (30.8 % of all endangered species in Finland), and one of the reasons for additional 189 red-listed, forest associated species (Rassi et al. 2010). Moreover, about 100 species have already gone extinct. Thus, actions to combat this loss of forest biodiversity are urgently needed.

The main strategy to meet both economic and conservation needs has been to target land parcels for different uses, some for intensive commodity production and some for protection. Protected areas and managed land have been considered as separate units, where managed land does not contribute to conservation goals (Lindenmayer & Franklin 2002, Fischer & Lindenmayer 2006). However, as the land that can be targeted for protection is very limited, the potential of managed land to support biodiversity protection has awaked a lot of interest. Many forest dwelling species can indeed live outside reserves, and managed forests can serve as corridors between reserves (e.g., Franklin 1993, Lindenmayer & Franklin 2002, Kuuluvainen et al. 2004, Perhans et al. 2011, Driscoll et al. 2013). Due to their dominance in the landscape, managed forests also play a major role in providing various ecosystem services (Lindenmayer & Franklin 2002). With some changes

in prevalent management practices, the contribution of managed forests to biodiversity conservation and provision of ecosystem services can be increased substantially.

The question of how to manage boreal forest to protect biodiversity at the same time as getting economic revenues is becoming an interesting and challenging one. For example refraining from thinnings is a cost-efficient way to increase habitat availability for many species (Tikkanen et al. 2007, Mönkkönen et al. 2014). Other suggested management methods to increase the variety of ecosystem services and biodiversity in managed forests include maintaining defined structures, patterns or disturbance regimes, e.g. retention trees, decaying wood, gaps in forests via small-scale harvesting, tree species mixtures and small key-biotopes (e.g. wetlands, river and lake boundaries), as well as longer rotation cycles (Puumalainen 2001, Hynynen et al. 2005, Schwenk et al. 2012, Mönkkönen et al. 2014). However, the effectiveness of different methods must be carefully evaluated for achieving wanted objectives with minimum costs.

A prerequisite for evaluating different land-management options for ecosystem services and biodiversity is that there is available information about their distribution in the landscape. However, the establishment of a platform for systematic gathering of occurrence and distribution data on ecosystem services has only recently been established (TEEB 2010). Information on biodiversity is also rarely available or complete, since data is usually limited to the best-known taxa (Pimm 2000, Rassi et al. 2010). There might also be biases in sampling efforts, which will bias estimations about species distributions (Nelson et al. 1990, Lombard et al. 2003, Favreau et al. 2006). Detailed data about species distributions requires a lot of resources and is very time-consuming to collect (Favreau et al. 2006). This is why it is essential for decision making to have other ways to get information about the distribution of biodiversity.

1.2 Surrogates for biodiversity

1.2.1 Taxonomic and environmental surrogates

A widely used solution for the incompleteness of knowledge about biodiversity distributions is to use entities for which we do have distributional information as surrogates for spatial pattern of biodiversity. This reduces the amount of time, money and data required compared to detailed inventories for multiple species (Noss 1990, Margules & Pressey 2000, Favreau et al. 2006, Williams et al. 2006). Biodiversity surrogates can be roughly divided into taxonomic and environmental surrogates (Rodrigues & Brooks 2007, Grantham et al. 2010): *taxonomic surrogates* are based on biological data (well-known species or species groups); *environmental surrogates* in turn are based on physical data, often mixed with biological data.

Taxonomic surrogates predict distributions or abundances of other species using data about well-known species. These indicator species or taxa provide a way to estimate biodiversity based on the knowledge on a smaller number of species or on species that are easier to detect or identify than the target species (Caro & O'Doherty 1999, Kerr et al. 2000, Pearman & Weber 2007, Halme et al. 2008, Andrade et al. 2014). This approach relies on significant similarities in habitat requirements of indicator species and target species, and thus conservation efforts for surrogate species are thought to benefit target species as well (Caro & O'Doherty 1999, Ozaki et al. 2006, Lewandowski et al. 2010). Taxonomic surrogates can be species groups that do not overlap with target species (e.g. using diversity of one taxon to predict diversity of another), subgroups of target species (e.g. using threatened or rare species of a species group to predict diversity in the whole group), or partially overlapping with target species (Rodrigues & Brooks 2007).

The benefit of using *environmental variables* as surrogates is that they provide good geographical coverage, and they are much easier to assess than direct species abundance, since their measurement is easier and they can often be mapped using remote sensing data (Ferrier & Guisan 2006). If environmental surrogates can be related with existing species survey data, biological distributions can be extrapolated across large regions (Ferrier et al. 2002). In addition, if there is a correlation between surrogates and species diversity, surrogate data can be used not only for biodiversity assessments, but also to predict changes in populations resulting from environmental changes. Environmental surrogates have been used for example in predicting effects of forest management on biodiversity (e.g. Pitkänen 2000). Environmental surrogates can be discrete classes (ecological classifications or land types) or continuous data about factors that are correlated with biodiversity (Grantham et al. 2010).

The use of discrete ecological classifications, or land types, as surrogates, is based on the idea that these classes reflect variation in abiotic factors and/or vegetation characteristics that affect the distribution of species (Guisan & Zimmermann 2000). Classification of land area can be done using for example forest types, vegetation classes or classes based on environmental variables (Guisan & Zimmermann 2000, Lombard et al. 2003, Rodrigues & Brooks 2007, Grantham et al. 2010). For example, classifications of rainfall, temperature and lithology have been used in estimating plant species diversity (Trakhtenbrot & Kadmon 2005).

Continuous variables used in biodiversity distribution modelling include terrain indices, long-term average climate surfaces, edaphic variables, land-cover variables and spectral bands or indices (Ferrier & Guisan 2006). For example, stand basal area can be used as a surrogate in estimating understory plant species richness in forests (e.g., Pitkänen 2000). Another surrogate that has been used in plant diversity assessments is soil moisture, which is known to correlate strongly with plant species number (e.g., Zinko et al. 2005, Czarnecka & Chabudzinski 2014). Soil moisture can be modelled using wetness indices, which are based on the effect of landscape topography on the movement and accumulation of water in the soil (Zinko et al. 2005, Czarnecka & Chabudzinski 2014). Czarnecka & Chabudzinski (2014) concluded that topographic wetness index is one of the most important factors affecting plant species richness. In the study of Zinko et al. (2005), a topographic wetness index alone explained 30 % of the variation in plant species number in boreal forests from Sweden.

1.2.2 Reliability of biodiversity surrogates

Even though surrogates have been efficient in assessing biodiversity in many cases, there are some uncertainties associated to their use. The power of surrogates in predicting species diversity may not be consistent across geographic regions and/or at different spatial scales (Ricketts et al. 1999, Lawler & White 2008), and there are many studies that have found contrasting results in surrogacy effectiveness (e.g., Araújo et al. 2001). Surrogate effectiveness is also sensitive to chosen surrogate, test features, study area and testing methods (Grantham et al. 2010). This is why it has been argued that surrogates should only be used if their reliability has been appropriately tested (Lindenmayer 1999, Araújo et al. 2001). A review by Rodrigues & Brooks (2007) showed that, over 575 tests in 27 studies that estimated biodiversity distributions using surrogates, only 59 % showed positive surrogacy.

For environmental surrogates, about half of the tests reviewed by Rodrigues & Brooks (2007) had positive surrogacy, but their effectiveness was on average quite low. Of these tests, those that used abiotic data combined with species distribution data performed better than those that used only abiotic or species assemblage (e.g. forest types, vegetation

classes) data. Grantham and colleagues (2010) used forest ecosystems (classes based on forest types and floristic/environmental variation) and environmental units (classes based on four environmental variables) to estimate diversity in six groups of threatened species across two study areas, and concluded that overall these surrogates performed better than random in choosing areas for protection, but their effectiveness was somewhat poor, environmental units being slightly better than forest ecosystems. In general, environmental surrogates often have weaker surrogacy power than taxonomic surrogates (Rodrigues & Brooks 2007).

1.3. Biodiversity surrogates in multi-objective forest management planning

Forests are dynamic ecosystems, and thus some of the management practices that are applied have a long-term effect on the provisioning of ecosystem services and biodiversity habitats. Biodiversity surrogates are useful tools in predicting these long-term effects, since they provide a way to estimate how management-induced changes in forest structure affect biodiversity, and to compare different management options. Examples of this are species-habitat-models, which relate the effects of forest management with species' habitat requirements (e.g. Suchan & Baritz 2001, Hynynen et al. 2005, Mönkkönen et al. 2014). For example, Hynynen and colleagues (2005) simulated the effect of different forest management regimes on the diversity of three species groups (saproxylic beetles, polypore fungi and epiphytic lichens) using stand level variables (volume of dead wood, stand age and number of large deciduous trees) as surrogates. In a similar way, the changes in provisioning of different ecosystem services under various management options can be predicted by simulating the change in biophysical or social properties that can be correlated with ecosystem services (ecosystem service indicators) (de Groot et al. 2010). For example, simulated estimates of above-ground biomass under different management scenarios can be used as surrogates for carbon storage (e.g., Schwenk et al. 2012).

Because different species require different types of habitats, and the effects of management practices may differ among ecosystem services, there is no simple answer to the question of how to manage forests for biodiversity and ecosystem services, and the optimal management regime is different depending on the management goals (Schwenk et al. 2012, Mönkkönen et al. 2014). This is why ecologically, socially and economically sustainable forest management requires multi-objective planning, which aims to simultaneously maintaining timber production, other ecosystem services and biodiversity at sustainable levels at landscape scale.

1.4. Multi-objective optimization in land-use planning

Careful land-use planning can substantially increase habitat availability for forest biodiversity with minor or no decrease in economic returns (e.g., Nalle et al. 2004, Polasky et al. 2005, Tikkanen et al. 2007, Mönkkönen et al. 2014). However, efficient land management that maintains multiple objectives at target levels while minimizing trade-offs between them requires optimization, which includes several different methods and approaches (Baskent & Keles 2005). One of them is to produce *production possibility frontiers (PPF)* (also called *efficiency frontiers*) that demonstrate the land use and land management patterns in which it is not possible to increase any objective without decreasing others (Calkin et al. 2002, Nalle et al. 2004, Polasky et al. 2005). PPF illustrates the nature of the trade-offs between different goals, and reveals possible inefficiency in current land use and land management helping to identify opportunities for improvement (Nalle et al. 2004, Polasky et al. 2008). Optimization methods provide potentially very useful tools for decision making as they produce concrete ways to reach desired objectives with minimum trade-offs.

Optimization has been used in many studies aiming to solve the conflict between timber production and biodiversity protection in forest landscapes (e.g., Nalle et al. 2004, Polasky et al. 2005, 2008, Tikkanen et al. 2007, Mönkkönen et al. 2014). In these studies, biodiversity is often modelled using forest features, such as stand basal area or amount of woody debris, as indicators of habitat quality for a species (e.g., Nalle et al. 2004), or a set of species (e.g., Tikkanen et al. 2007). Economic benefits are measured as the net present value of harvested timber. Altering combinations of different land use or land management options in the landscape (e.g., protection, prevailing management methods, no thinnings) changes habitat availability and timber revenues so that different combinations produce different outcomes considering different objectives. Of these outcomes, production possibility frontiers illustrate the set of management combinations for which neither habitat availability nor economic revenues can be increased without decreasing the other.

Spatial explicitness and temporal dynamism are important aspects of optimization models. Non-spatial models may easily over- or underestimate the productive capacity of a landscape and ignore actual conditions and spatial limitations on the ground (Nalle et al. 2004). Because forests are dynamic ecosystems, habitat distributions are not static in the landscape, and thus ignoring temporal change in optimization models may give misleading results. However, there are only few studies that use both spatially explicit and temporally dynamic modelling (Nalle et al. 2004, Mönkkönen et al. 2014). Mönkkönen et al. (2014) combined seven alternative management regimes to find land-use patterns that simultaneously maximize economic and ecological values on a dynamic forest landscape. They measured ecological values as habitat availability for six vertebrate species and four species groups of red-listed, dead-wood associated insects. Applying the same approach, I use a surrogate model for habitat suitability for plants to find optimal land-use patterns to maximize plant species richness and timber revenues in the landscape.

1.5. Understory plant species diversity in forests

The diversity of plants is an important aspect of biodiversity, because plants as primary producers form the basis for ecosystem functions (Gilliam 2007). Plant diversity contributes greatly to the provision of many ecosystem services (e.g., Balvanera et al. 2008, Quijas et al. 2010) and, given the dependence of other organisms on plant primary production, it can be assumed that diverse plant communities support diversity in other communities as well. In forests, the main factors affecting the variation in understory vegetation include site conditions, stand structure and disturbances (Hart & Chen 2006).

Site conditions, such as soil fertility and soil moisture, are important features affecting the variation of plant species diversity across landscapes. Vascular plants, particularly the herbaceous layer, are more diverse on productive sites (Chen et al. 2004). Even though soil fertility is mostly determined by soil type and topography, tree species composition has an influence on that as well: coniferous stands usually have higher carbon/nitrogen ratio, lower pH and lower nutrient content than hardwood stands (Barbier et al. 2008). Deciduous litter decomposes more rapidly than coniferous litter, increasing rates of nutrient cycling (Côté et al. 2000). Humus type, as affected by litter type, might also be an important factor in controlling herbaceous layer composition since many boreal herbaceous species root directly in the humus layer (Qian et al. 2003). Soil moisture is also a fundamental determinant for the spatial variation in plant species richness, water being an essential resource for plants. Especially on areas where topography is variable, spatial variation in ground water availability is an important factor affecting vegetation composition (Zinko et al. 2005, Czarnecka & Chabudzinski 2014).

Apart from the effects on litter type and thus soil attributes, stand structure also has other effects on understory vegetation. Trees compete with understory plants for resources,

such as light, water and nutrients (Riegel et al. 1992, Økland et al. 1999). In addition, trees modify the habitat conditions for understory plants by affecting microclimatic conditions (Augusto et al. 2003, Barbier et al. 2008). Light availability has been considered one of the most limiting factors for understory vegetation (Barbier et al. 2008). Because the effects on understory vegetation may be different for different tree species (e.g., Augusto et al. 2003, Macdonald & Fenniak 2007, Barbier et al. 2008), tree species composition is an important component in determining understory plant diversity. In general, hardwood and mixed forests have higher understory vascular species richness than pure coniferous forests (Saetre et al. 1997, Berger & Puettmann 2000, Pitkänen 2000, Barbier et al. 2008), with spruce dominated stands having more species-rich understories than pine dominated stands (Zinko et al. 2005).

Disturbances, such as fires, storms, or clear-cutting, may affect understory plant community directly via mortality and damage of plants, alteration of soil seed bank and changes in competitive relationships among plant species, or indirectly via changes in forest structure (Roberts & Gilliam 2003). Direct effects of forest management are associated with logging and site preparation, and indirect effects include changes in tree species composition, tree density, basal area, canopy structure and forest age, and thus may affect understory plant diversity by altering light and soil conditions (e.g., moisture level) of forest stands (Halpern & Spies 1995, Hart & Chen 2006). Even though direct effects may be important, they are considered to be temporary, since the populations of most understory plants recover before canopy closure (Halpern & Spies 1995). Thus indirect, long-term consequences of forest management are thought to be greater for plant species diversity than direct effects. However, although there are many studies about the initial effects of management on plant diversity (e.g., North et al. 1996, Vanha-Majamaa & Jalonen 2001, Lencinas et al. 2011), not many studies have focused on the long-term effects, and these studies show various results. For example, Battles and colleagues (2001) found plant species numbers to be higher under managed and shelterwood stands compared to unmanaged and single-tree selection stands, whereas Halpern & Spies (1995) found that plant species richness was higher in old-growth stands than younger successional stages. It has been suggested that plant diversity should be highest at intermediate levels of disturbance, and with management regimes creating more structural variation (Roberts & Gilliam 1995).

1.6. Study objectives

There are many studies about relationships between plant diversity and site and stand variables in forests (e.g., Pitkänen 2000, Laughlin et al. 2005, Zinko et al. 2005, Laughlin & Grace 2006, Czarnecka & Chabudzinski 2014), but to my knowledge no study before has aimed at finding landscape level management plans to simultaneously maximize timber revenues and plant species richness. In this study, multi-objective optimization methods were used to find these management plans using seven alternative management options, ranging from set-aside to intensive management according to current recommendations. I estimated plant species richness on these stands using a surrogate index of habitat suitability based on soil moisture and stand characteristics. These surrogate indices and timber revenues (calculated by Mönkkönen et al. (2014)) were optimized at landscape level to find management combinations that simultaneously optimize economic benefits and plant species richness in the landscape. The main questions in this study were: 1) what is the potential of the landscape to simultaneously provide plant species richness and economic returns from selling timber, and 2) what combinations of management regimes maximize plant species richness with given levels of economic returns, and vice versa. This study gives more insights to landscape level

conservation planning, and provides new information about trade-offs between plant species richness and forest management. Some relevant concepts concerning this topic are defined in Table 1.

Table 1. Relevant concepts and definitions.

Concept	Definition
Biodiversity surrogate	An indirect measure of biodiversity that estimates species richness or diversity, or distribution of a species. Can be, for example, distribution data of other species, or environmental data.
Multi-objective optimization	A mathematical method for multi-criteria decision making, when there are trade-offs between alternative objectives. Aim is to optimize multiple objectives simultaneously, so that these trade-offs are minimized.
Net present value of timber (NPV)	Net monetary value of timber over a given time period. Includes income from all timber assortments, minus silvicultural costs of required work. Future money flows are discounted to correspond their present value.
Pareto-optimal solution	A solution of multi-objective optimization, where no objective can be increased without decreasing others.
Species diversity	A measure of biodiversity, which includes not only number of species, but also their relative abundances.
Species richness	Number of species in a community.

2. MATERIALS AND METHODS

2.1. Study area and source data

My study area is located in Central Finland (62° 14' N, 25° 43' E), and it covers 68 700 ha. It represents a typical boreal landscape with 55 % of the total area covered by forest on mineral soils, 13 % by peat lands, 16 % by lakes and 15 % by farmland settlement. There are no protected areas such as national parks in the study area. Forested area consists of 29 706 pine, spruce and birch dominated stands of an average size of 1.45 ha. Past forest management practices have resulted in bimodal age structure of forest stands with a large proportion being less than 40 years of age, and the other mode occurring near 70-90 years.

The stand structure and economic value data used in this study are simulated data produced by Mönkkönen and colleagues (2014), which originates from the forestry data administered by the Finnish Forest Centre. Mönkkönen and collaborators (2014) simulated the growth of the forest stands 50 years forward with 5-year intervals under seven alternative management regimes and calculated the net present value (NPV) for each stand and management regime. I used these stand structure data to calculate habitat suitability index for plants (HSI). Both HSI and NPV were used for the optimization. Geographic data needed for calculating topographic wetness index (TWI) (part of the HSI model) is a freely available digital elevation model data by the National Land Survey of Finland. Choices of predictor variables and their coefficients to calculate HSI were based on the study by Zinko and colleagues (2005).

2.2. Forest management options

Seven alternative management regimes were applied for each forest stand (Table 2; for detailed description of the regimes and growth simulations see Mönkkönen et al. 2014). Of these regimes, the two extremes are *business as usual* (BAU), where a stand is managed according to the current recommendations, and *set aside* (SA), where a stand is permanently protected. *Extended rotations* (EXT10 and EXT30) represent temporal conservation strategies, with final harvest delayed by 10 and 30 years, respectively. *Green tree retention* (GTR30) represents a conservation-oriented management attempting to mimic and restore natural disturbance regimes, with an increased amount of retention trees left at the final harvest compared to BAU. In addition, there are two regimes with no thinnings, one with similar final harvesting criteria to BAU, resulting in extended rotation time (*no thinnings with long rotation*, NTLR), another with adjusted final harvesting criteria to achieve the equal rotation length to BAU regime (*no thinnings with short rotation*, NTSR).

Table 2. Management regimes applied on the forest stands (adapted from Mönkkönen et al. 2014).

Management regime	Acronym	Description
Business as usual	BAU	Recommended management: rotation length 80 years; site preparation, planting or seeding trees; 1-3 thinnings, final harvest with green tree retention level 5 trees/ha
Set aside	SA	No management
Extended rotation (10 years)	EXT10	BAU with postponed final harvesting by 10 yrs; rotation length 90 years
Extended rotation (30 years)	EXT30	BAU with postponed final harvesting by 30 yrs; rotation length 115 years
Green tree retention	GTR30	BAU with 30 green trees retained/ha at final harvest; rotation length 80 years
No thinnings (final harvest threshold values as in BAU)	NTLR	Otherwise BAU regime but no thinnings, therefore forests grow more slowly and final harvest is delayed; rotation length 86 years
No thinnings (minimum final harvest threshold values)	NTSR	Otherwise BAU regime but no thinnings; final harvest adjusted so that rotations do not prolong: rotation length 77 years

2.3. Habitat Suitability Index (HSI)

The purpose of habitat suitability index (HSI) is to act as a surrogate for plant species numbers on a given forest site by approximating habitat quality. Habitat quality is modelled using predictor variables known to be associated with plant species richness.

Zinko and colleagues (2005) have shown that plant species richness in the Swedish boreal forests is strongly positively correlated with soil moisture, which can be described using topographic wetness index (TWI): in their study, TWI alone explained 30 % of the variation of plant species numbers. Forest stand characteristics, soil variables and altitude also showed some surrogacy power. Of forest stand characteristics, the basal area of pine (*Pinus sylvestris*) was the most important in determining plant species richness, with species numbers decreasing as basal area of pine increases. Basal areas of spruce (*Picea abies*) and deciduous trees in turn had positive effects on plant richness. In this study, the results of the study by Zinko and colleagues (2005) were used as the base for choosing predictor variables to calculate a habitat suitability index that illustrates potential plant

species richness in a given forest site. We used the original data from Zinko and colleagues (2005) and fitted curvilinear relationships between plant species richness and the predictor variables.

The criteria for the choice of predictor variables were that 1) they were important for explaining plant species richness, 2) they were easily available for the study area, 3) they were interesting considering the study questions, and 4) they were not significantly collinear. Using these criteria, the variables chosen in the model were TWI and basal areas of pine, spruce and deciduous trees. Because of the high dominance of two birch species (*Betula pendula* and *B. pubescens*) in deciduous trees of the study area, only basal areas of these two species were included. Altitude was, despite its important effect on plant species numbers and availability for the study area, left out of the model because altitudinal variation in the data was small and only slightly overlapping with the variation in the data of Zinko and colleagues (2005). Thus including altitude could have caused some bias in the model. Of the predictor variables, TWI value of a stand was constant over the 50-year time frame, whereas basal areas of trees varied with time and management regime.

Topographic wetness index (TWI) is an index that is used to predict movements and accumulation of water in the landscape using topographic properties of the landscape. It is a function of specific catchment area per unit width orthogonal to the flow direction (α) (measure of how much water drains through a certain location) and slope angle (β) (measure of how quickly water drains from that location) (Beven & Kirkby 1979). The index is formulated as

$$TWI = \ln(\alpha/\tan\beta).$$

Moore and colleagues (1993) have shown that TWI is positively correlated with many soil attributes, such as horizon depth ($r = 0.55$), silt percentage ($r = 0.61$), organic matter content ($r = 0.57$) and phosphorus ($r = 0.53$). For this study, TWI has been calculated with an ArcGIS algorithm provided by J. Evans (<http://arcsripts.esri.com/details.asp?dbid=11863>). TWI is a-dimensional and its values range from less than 1 (dry conditions) to greater than 20 (wet conditions). It was calculated with a grid size of 25 x 25 m², so that TWI value per forest stand is the average value of the grids that it encloses.

The relationships between predictor variables and plant species richness in the data by Zinko and colleagues (2005) were explored using the curve fitting tools included in the statistical software SPSS 20.0 (IBM Corp. 2011). The curves that best explained variation in plant species richness were chosen. These functions represent the partial contributions of each predictor variable on habitat suitability for plants. The final habitat suitability index is the product of these contribution values, and is rescaled so that it takes values between 0 (least suitable habitat, i.e. low species richness) and 1 (best quality habitat, i.e. high species richness). To sum up, habitat suitability index of a forest stand is calculated as follows:

$$HSI = \prod_{i=1}^3 f(x_i) = f(TWI) * f(BA_{pine}) * f(BA_{spruce}) * f(BA_{deciduous}),$$

Where HSI is the habitat suitability index for plants, ranging from 0 to 1, $f(TWI)$ is the contribution of topographic wetness index on habitat suitability, and $f(BA_{pine})$, $f(BA_{spruce})$ and $f(BA_{deciduous})$ correspond the contributions of the basal areas of trees. The functions for these partial contributions for each explanatory variable, their capacity of explaining variance in species richness (Adj. R²), and their level of fit to the data (F, P) are described in Table 3. In general, increasing TWI and basal areas of spruce and deciduous trees increase habitat suitability for plants, and increasing basal area of pine in turn decreases it. I calculated HSI for each stand, management option and time step. The final habitat

suitability value per forest stand and management option is the average over 50 years (i.e. 11 time steps). Calculations of HSI were performed using the statistical software R version 3.0.2 (R Development Core Team 2013).

Table 3. Description of the functions for explanatory variables of the HSI model: type of relationship (function and equation), explanatory variables (x), model coefficients (a, b), adjusted coefficients of determination (Adj. R²) and F- and P-values. The response variable ($y = f(x)$) for each function is species richness of plants, rescaled from 0 to 1.

Function	Equation	x	a	b	Adj. R ²	F	P
Power	$a+[b*\ln(x)]-1$	TWI	0.853	0.254	0.29	36.4	<0.001
Exponential	$a*e^{[b*(x+1)]}-1$	BA_Pine	1.484	-0.009	0.19	21.8	<0.001
Inverse	$a+[b/(x+1)]$	BA_Spruce	1.495	-0.156	0.05	5.5	0.021
Power	$a+[b*\ln(x)]-1$	BA_Deciduous	1.298	0.072	0.16	17.1	<0.001

2.4. Optimization

Each combination of applied management regimes on forest stands makes a *management plan*. The *outcome* of a management plan is a vector of timber revenues and habitat suitability values associated with that plan. Optimization was used to find the set of management plans that are Pareto-optimal, i.e. neither of management objectives can be increased without decreasing the other. This set of outcomes forms the production possibility frontier (see introduction). In this study, a production possibility frontier was produced and used to study trade-offs between habitat suitability for plants and economic revenues in the forest landscape. Mathematical formulation of the optimization method can be found in the article by Mönkkönen and colleagues (2014). Finally, a general framework about this study is presented in Figure 1.

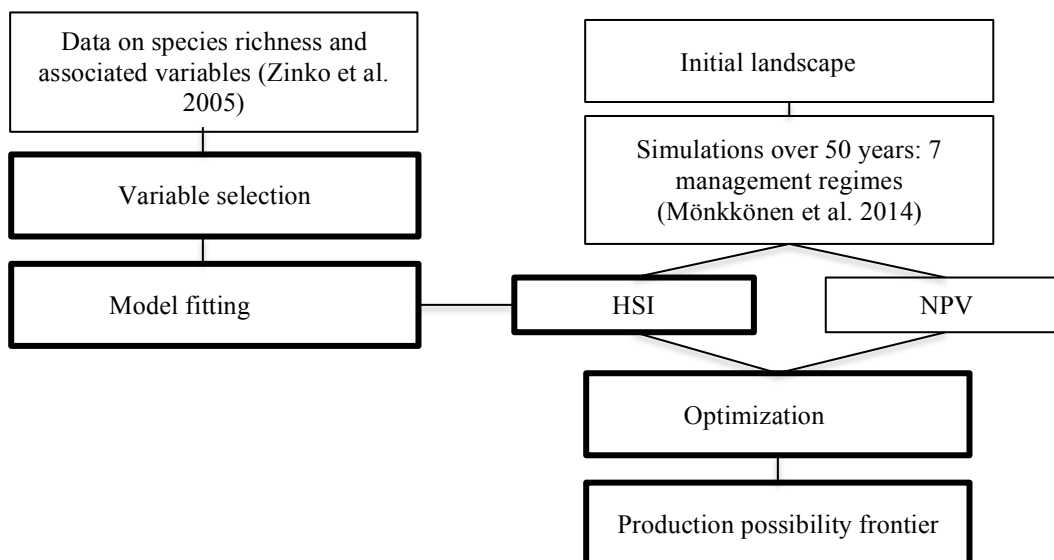


Figure 1. Model framework. The model parts included in this study are in bold.

3. RESULTS

3.1 Habitat suitability for plants in the landscape

Across all management regimes, the minimum habitat suitability index value per stand was 0 and the maximum was 0.78 (average of 11 time steps over 50 years). The distributions of

habitat suitability indices on forest stands had very similar pattern in all management regimes, having one peak at zero, two others around 0.1 and 0.2, and a long tail towards higher values. These distributions are shown in Figure 2.

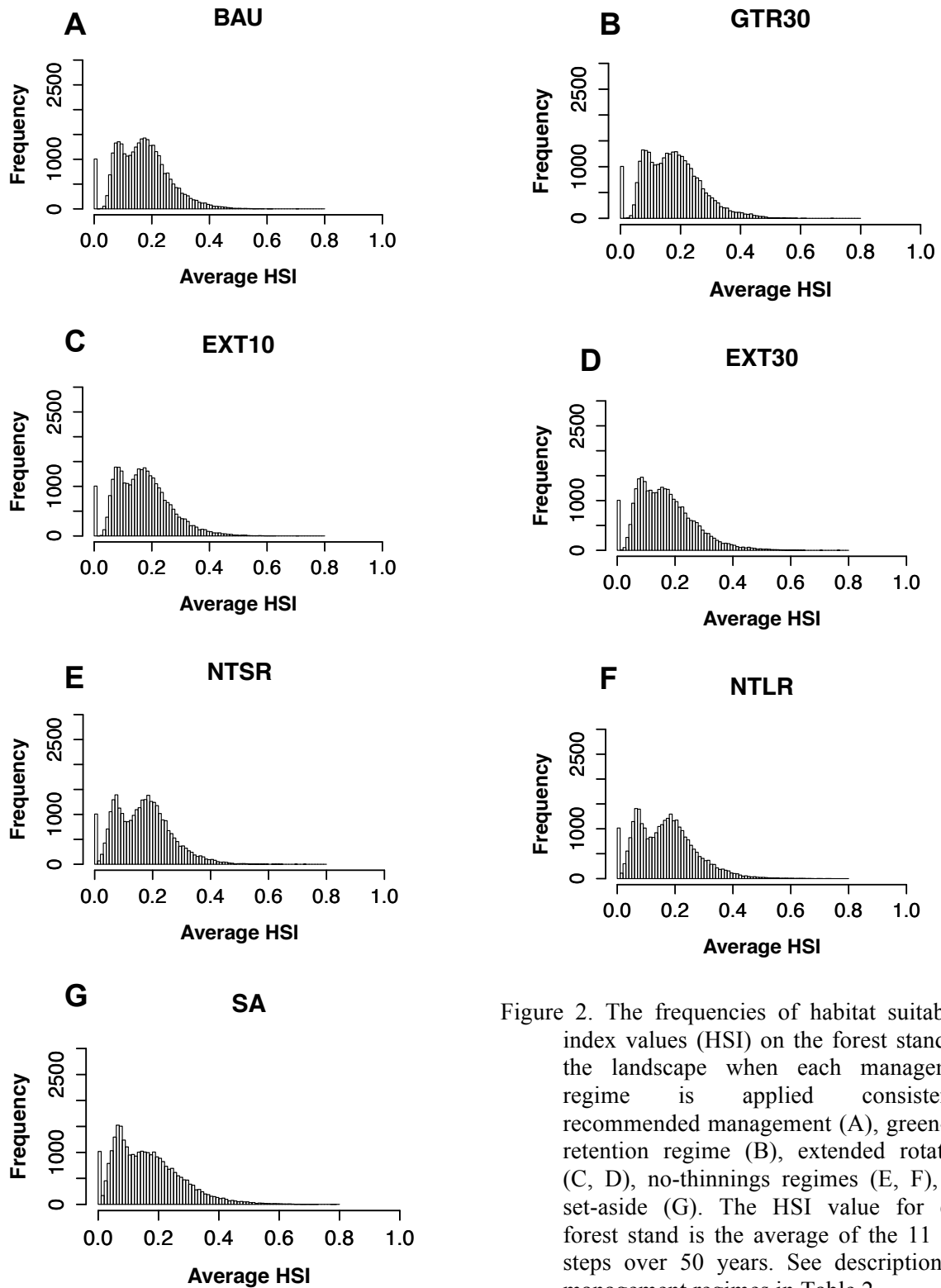


Figure 2. The frequencies of habitat suitability index values (HSI) on the forest stands in the landscape when each management regime is applied consistently: recommended management (A), green-tree retention regime (B), extended rotations (C, D), no-thinnings regimes (E, F), and set-aside (G). The HSI value for each forest stand is the average of the 11 time steps over 50 years. See descriptions of management regimes in Table 2.

3.2. Potential of boreal forest landscapes to provide plant species richness and timber revenues

The results show that there is a trade-off between habitat suitability for plants and economic income in boreal forest landscape (Figure 3). With management combinations where neither habitat suitability for plants nor timber revenues can be increased without decreasing the other (i.e. management plans in the Pareto-optimal set), maximal habitat suitability for plants is 7 % units bigger than in the situation where landscape is managed for maximal timber revenues (range of HSI in the Pareto-optimal set from 7 467 to 8 041). The difference between minimum and maximum timber revenues over 50 years in the Pareto-optimal set in turn is 20 % (40 M€). Thus the trade-off is bigger for economic revenues than for plant species richness.

The relationship between habitat suitability for plants and timber revenues is not linear: starting from the minimum habitat suitability and maximum timber revenues, the first increments in habitat suitability for plants are inexpensive but maximizing it has high economic costs (Figure 3). For example, as 93 % of the maximum habitat suitability is attained when forests are managed for maximum timber revenues, a 5 % decrease in economic income increases habitat suitability for plants to 98 % (i.e. 5 % increase in HSI) (Figure 4, Appendix 1). Maximizing habitat suitability in turn is more expensive, as increasing it from 98 % to 100 % decreases NPV to 80 % of maximum (i.e. 20 % decrease in NPV).

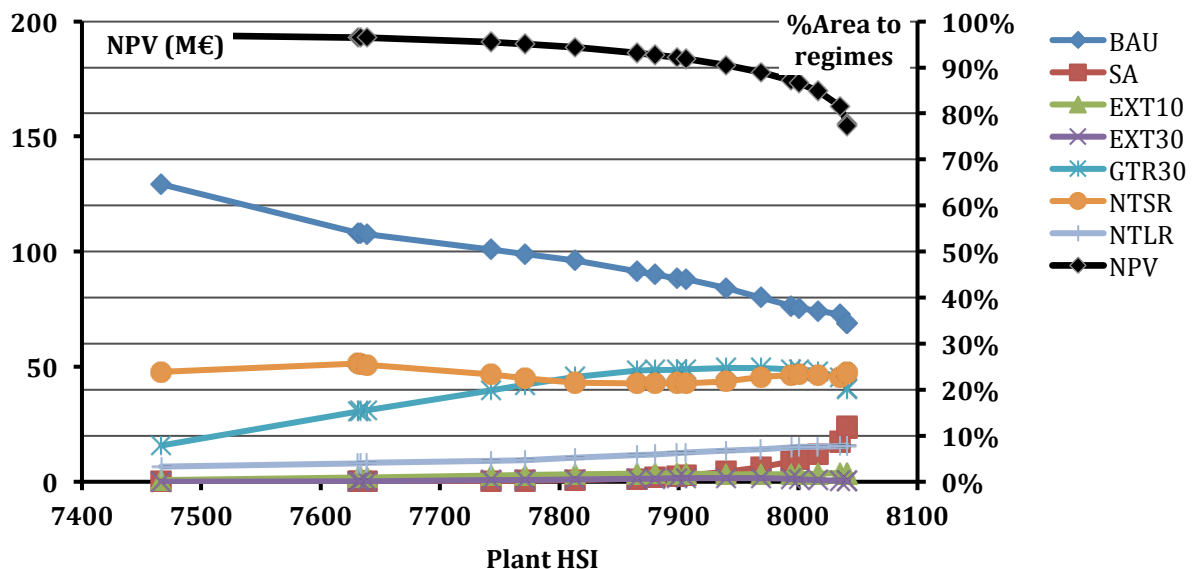


Figure 3. Curves representing the trade-off between habitat suitability for plants and net present value of timber in the forest landscape, and the proportions of forest management regimes applied in Pareto-optimal solutions. NPV is the sum of economic revenues over 50 years, and Plant HSI is the sum of stand specific index values across the landscape.

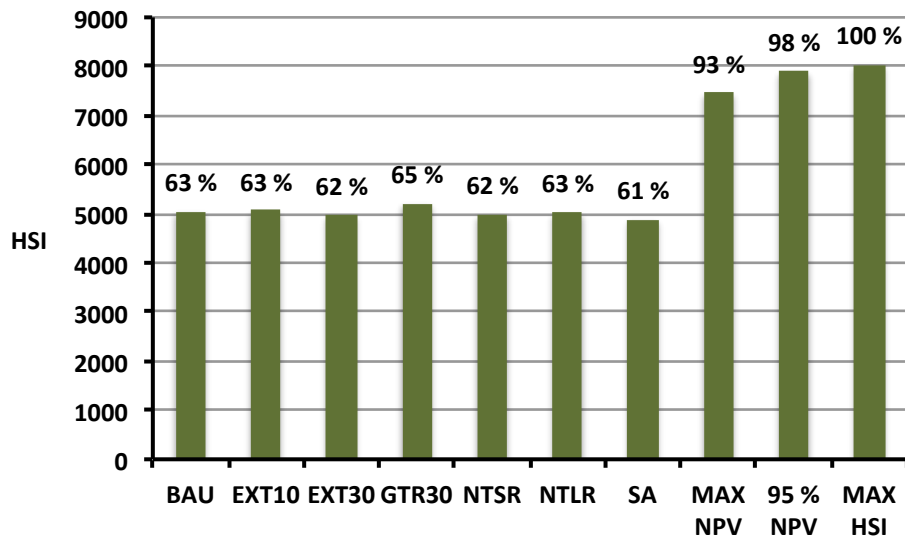


Figure 4. Habitat suitability index (HSI) values summed across the landscape. BAU, EXT10, EXT30, GTR30, NTSR, NTLR and SA represent cases where each management regime is applied consistently in the landscape (see descriptions of management regimes in Table 2). MAX NPV represents the case where forests are managed for maximal timber revenues, and MAX HSI the case where forests are managed for maximal habitat suitability for plants. 95 % NPV represents the case with optimal management for HSI with 5 % reduction in timber revenues.

3.3. Management regimes and their optimal combinations

When applied consistently, all the management regimes are almost as good as another considering habitat suitability for plants, green tree retention regime (GTR30) performing slightly better than the others (Figure 4). However, even the green tree retention regime produces only 65 % of maximum HSI that can be achieved with a combination of management regimes in the set of Pareto-optimal management plans. This indicates that maintaining high plant species richness requires combining multiple management regimes in the landscape.

The most important management regimes to maximize timber revenues in the landscape are recommended management (BAU, 65 %), no-thinnings regime with short rotation (NTSR, 24 %) and green-tree retention regime (GTR30, 8 %)(Figure 3). Increasing habitat suitability for plants requires decreasing the proportion of recommended management, and increasing the proportions of green-tree retention regime, set-asides and no-thinnings regime with long rotation (Figures 3, 5). In the optimal management plan for maximal habitat suitability for plants the most important management regimes are recommended management (BAU, 34 %), no-thinnings regime with short rotation (NTSR, 24 %), green-tree retention regime (GTR30, 20 %), set-aside (SA, 12 %) and no-thinnings regime with long rotation (NTLR, 8 %). The contributions of management regimes with extended rotations (EXT10 and EXT30) to both economic returns and plant species richness is very minor in the Pareto-optimal set: no matter the objective, the proportion of EXT10 is less than 2 %, and that of EXT30 stays below 1 %.

As can be seen in Figure 3, consistent application of the recommended management (BAU) does not maximize timber revenues in the landscape. Mönkkönen and colleagues (2014) showed that consistently applying recommended management results in a policy cost of 5 % compared to the maximum timber revenues that could be gained with an optimal combination of management regimes. Consistently applying recommended management yields 63 % of maximum habitat suitability for plants. Interestingly, with the

same 95 % level of timber revenues that can be attained in consistent application of recommended management, managing forests according to the Pareto-optimal solution habitat suitability for plants could be increased to 98 % of maximum (i.e. 35 % increase in HSI) (Figure 4). In addition, even managing forests for maximum timber revenues, i.e. increasing timber revenues from the present situation, would increase habitat suitability for plants to 93 % of maximum.

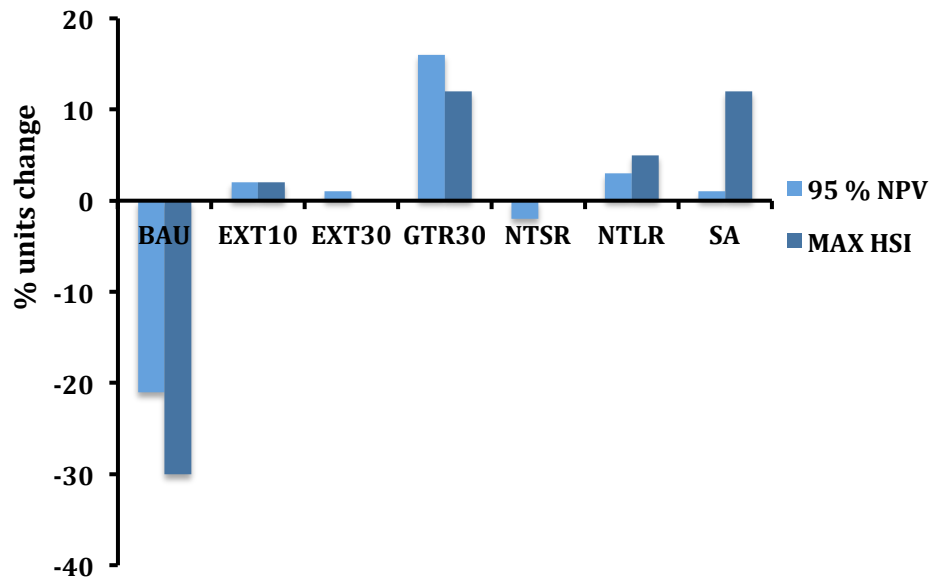


Figure 5. Changes in the proportions of management regimes in the landscape with different objectives. Zero (0) is the reference line, which is the case where the landscape is managed for maximal timber revenues (93 % of maximum habitat suitability for plants attained): 65 % of forests managed with BAU regime, 24 % with NTSR, 8 % with GTR30, 3 % with NTLR, and 0 % with EXT10, EXT30 and SA (see descriptions of alternative regimes in Table 2). 95 % NPV refers to a situation with a 5 % reduction in timber revenues (98 % of habitat suitability attained), and MAX HSI is the optimal management combination for maximal habitat suitability for plants (80 % of maximum timber revenues gained). Bars represent the direction and amount of change in the proportions of regimes compared to the reference case.

4. DISCUSSION

4.1. Potential of boreal forest landscape to provide plant species richness and timber revenues

The results of this study show that there is a trade-off between plant species richness and economic revenue from timber in boreal forest landscape, though this trade-off is smaller for plant species richness than for timber revenues. However, with optimal management combinations both ecological and economic values can be maintained on very high levels simultaneously, but maximizing either of them causes reductions on the other. Maximizing either of the two objectives studied here requires combining multiple management regimes in the landscape, and applying any one management regime consistently produces inferior outcomes.

Trade-offs between biodiversity and economic values in boreal forests have been found also in other studies. Landscape level conflicts between these two objectives have

been documented at least for birds and mammals (e.g., Nalle et al. 2004, Mönkkönen et al. 2014), dead-wood associated insects (e.g., Tikkanen et al. 2007, Mönkkönen et al. 2014) and red-listed fungi (Tikkanen et al. 2007). To my knowledge, this is the first study where these conflicts have been revealed for plants. However, compared to many other species and species groups, the trade-off between plant species richness and economic values is quite small, as the difference in habitat suitability for plants between optimal management plans for timber revenues and for habitat suitability is only 7 % units. For comparison, the same difference for red-listed, dead-wood associated species is 34–42 % units, depending on habitat quality threshold (Tikkanen et al. 2007). In general, there is a more pronounced trade-off between timber production and habitat availability for species that are dependent on dead-wood than for species that are not, because dead-wood associated species and timber production compete on the same resource (Mönkkönen et al. 2014). The trade-off between plant species richness and timber revenues is in turn a question of whether the kind of forest management that yields the highest economic income creates also a good environment for a species-rich plant community. Thus the trade-off between them is likely to be smaller.

4.2. Optimal forest management for plant species richness and timber revenues

When applied consistently, all the management regimes produce very similar levels of habitat suitability for plants. The similarity of the regimes may be because there is no management regime that would produce high levels of habitat suitabilities on all stands, but stands differ on which regime produces the best result. Thus the sums of habitat suitability values across the landscape show no difference between alternative regimes when they are applied consistently. This is supported by the fact that a combination of management regimes produces substantially higher overall habitat suitability for plants than any regime alone. It is, however, possible that differences between regimes would be more pronounced with a longer time frame, when especially the effects of the extended rotations and setting aside stands could be seen better (Hartig & Drechsler 2008). For example, on forest stands that are less than 30 years old in the initial situation, in 50 years there is no difference between the recommended management (BAU), green-tree retention (GTR30) or extended rotation (EXT10, EXT30) regimes because stands are not yet mature for final harvesting. Likewise, there would be no difference between no-thinnings regimes (NTSR, NTLR) and set-aside (SA). However, the further into the future the growth of forests is simulated, the more uncertainties there would be in the simulation outcomes.

Applying one management regime consistently in the landscape can even at its best provide only 65 % of the maximum habitat suitability for plants in the landscape. This indicates that different stands should be managed differently for optimal outcomes, and thus maximizing plant species richness on the forest stands requires a combination of regimes. As can be seen in my results, and also noted before by Mönkkönen and colleagues (2014), the same is true for economic income from the forests, as even consistently applying the most intensive and generally applied management regime (BAU) only yields 95 % of the maximum economic income. The policy cost of applying the recommended management consistently has been shown to be even more pronounced for biodiversity (Mönkkönen et al. 2014). Assuming that timber revenues in consistent application of the recommended management regime represent the present timber revenues in the landscape, according to my results it is possible to substantially increase plant species richness on the forest stands with no costs: as current forest management provides only 63 % of maximum habitat suitability for plants, with the same economic income 98 % of maximum HSI could be gained using an optimal combination of management regimes.

The optimal management combinations to apply in the landscape depend on wanted objectives. Maximizing timber revenues requires large portions of forest stands managed with recommended management (BAU, 65 %), no-thinnings, short rotation regime (NTSR, 24 %) and green-tree retention regime (GTR30, 8 %). Maximizing plant species richness in turn requires more diverse combination of regimes, with decreased proportion of recommended management and increased proportions of other regimes. The most important management regimes to maximize plant species richness with least economic costs are recommended management (BAU, 34 %) no thinnings with short rotation (NTSR, 24 %) and green tree retention (GTR30, 20 %) regimes, with some stands set aside (SA, 12 %) and managed with no thinnings, long rotation (NTR, 8 %) regimes.

The objectives of the recommended management regime (BAU) are solely economic, and thus it is generally thought to have negative impacts on biodiversity. This is indeed true for many forest dwelling species and species groups, indicated by the declining populations of a number of species in Finnish forests (Rassi et al. 2010). However, for plant species richness, forest management using the current recommendations does not seem to be a bad option, as it should be applied on one third of the forest stands to maximize plant species richness in the landscape. This might be because plant species richness has been shown to be highest in young forests (e.g. Tonteri 1994, Widenfalk & Weslien 2009), and thinnings often increase plant species richness due to increased light availability and decreased competition of resources with trees (Widenfalk & Weslien 2009).

The high percentages of no-thinnings regimes are in opposition to the initial expectations, as in dense forests there is less light reaching forest floor, and light is one of the most limiting resources for understory plants (Barbier et al. 2008). Empirical stand scale studies also suggest that unthinned forests tend to have lower number of understory plant species (e.g., Thomas et al. 1999, Augusto et al. 2003, Økland et al. 2003). On the other hand, low plant species numbers have been reported especially on dense spruce forests (e.g., Augusto et al. 2003, Økland et al. 2003), and thus might not be generalizable. In addition, the results of Widenfalk & Weslien (2009) suggest that thinning only has a positive effect on plant species richness on young forests, and not on mature stands. This effect also depended on site fertility. In the study of Zinko et al. (2005), total basal area of the forest did not explain variation in plant species richness, but the effect depended on tree species. It might be that in some cases unthinned stands retain soil moisture better than thinned stands, thus promoting high species richness. Refraining from thinnings has been found to be a cost-efficient way to increase biodiversity for other species and species groups as well, such as many red-listed, deadwood associated species (Tikkanen et al. 2007, Mönkkönen et al. 2014).

To maximize plant species richness in the landscape, 20 % of the forest stands should be managed with green tree retention regime (GTR30). Studies about the effects of green-tree retention on plant species richness so far have mostly focused on the short-term effects, which usually do not significantly differ from the negative effects of clear-cut on plant species richness (e.g., Vanha-Majamaa & Jalonen 2001, Rosenwald & Löhmus 2008). However, Halpern and colleagues (2012) found that retention harvests increased total herb richness 6 and 10 years after harvest, species numbers being the highest with 15 % retention level and dispersed retention. Also, North and colleagues (1996) found that 16 months after harvesting understory species number was higher on stands with retention trees than on clear-cut stands, or even un-cut stands. They suggested that this might be caused by the greater variation of habitats on retention stands compared to continuous forest or clear-cut. It is possible that retention trees create vertical variation in the forest canopy, promoting higher light levels in the understory (Van Pelt & Franklin 2000), and

thus possibly higher species richness. In general, habitat heterogeneity has been considered one of the main factors supporting high species richness (Tilman & Pacala 1993).

Overall, it seems that a mixture of management regimes is important for plant species richness in the forest landscape. Varying intensities of disturbance may create a heterogeneous landscape with a mosaic of different habitat patches, enhancing high species richness in the landscape (Roberts & Gilliam 1995). For example, variation in gap sizes creates spatial and temporal variation in forest vegetation (Burton et al. 2014). Heterogeneous landscapes have indeed been considered one of the main factors in maintaining forest biodiversity (Lindenmayer et al. 2006). However, it must be noted that stand structure attributes only measure indirect effects of management, and thus are not direct measures of land-use intensity (Gossner et al. 2014).

4.3. Model assumptions

Modelling work inherently involves a number of assumptions, which have important consequences on the results and their validity. Models are always simplifications of the real world phenomena that they represent, and thus they always include some uncertainties. There are probably a multitude of factors that affect plant species diversity of a site, including soil variables, location, history and species interactions, to name some. Small-scale variation of habitats inside forest stands probably has an impact on the number of species found on a site. However, there is not enough data of these variables, and their contributions to plant species richness are not well understood. Thus it is necessary to use very simplified and general models, which, however, can provide a rough estimate of the suitability of the forest stand for harbouring multiple species. Anyway the scope of this study is not to predict exact species numbers for any given forest site, but to get general insights into landscape level trade-offs in ecological and economic values of boreal forest landscape.

In this study, plant species richness was maximized for each stand, and maximum landscape level species richness considered to be achieved when the sum of stand level habitat suitability indices reached maximum. However, in reality, maximizing stand level species richness might not actually maximize landscape level species richness, if community compositions are not taken into account. It might be that lower habitat suitability index values may not always just tell about less diverse communities compared to higher values, but also tell about a different species composition. Constantly maximizing habitat suitability index on each stand may produce a lot of similar habitats in the landscape, whereas landscapes providing more heterogeneous habitats would actually have higher total species richness (Honkanen et al. 2010). Thus, instead of only maximizing index values, considering variation in them across landscapes might also be interesting.

The main goal for biodiversity conservation is to maintain the natural patterns of biodiversity distributions (Kuuluvainen et al. 2004). This is why maximizing species richness may not actually be the optimal goal for conservation purposes. For example, even though younger forests often have higher species richness than older stands, it is often because there are more rural and generalist species, or even non-native, invasive species (Esseen et al. 1997, Haeussler et al. 2002). On the contrary, old-growth forests may foster specialist species that are not found on younger stands. In addition, the results of the study by Scheller & Mladenoff (2002) suggest that forest management also changes the spatial pattern of understory plant communities, old-growth forests having smaller community patch size and thus spatially more heterogeneous understories than managed forests. Indeed, it might be that the effects of forest management on species composition and

community structure may be more important than to species richness (Moora et al. 2007, Duguid & Ashton 2013).

The data that was used to build a model for habitat suitability for plants is from a study that was performed in Sweden (Zinko et al. 2005). Sweden and Finland belong to the same bio-geographical area, so their forest landscapes and species compositions can be assumed to be very similar, and thus relationships between plant species numbers and forest site variables measured in Sweden applicable also in Finland. Of course these relationships may not be exactly the same and thus may cause some uncertainty in the model. There are not many studies about factors affecting understory plant species richness conducted in Finland, but at least plant species richness has been found to be higher on more fertile sites (fertility being partly correlated with TWI (Moore et al. 1993, Seibert et al. 2007)), and in forests with a mixture of birch (Tonteri 1994, Pitkänen 1997, 2000). Age of the forest stand was also found to explain variation in plant species richness (Tonteri 1994, Pitkänen 2000). Stand age might illustrate changing forest structures with time after disturbance, because plants are probably more dependent on the structures that modify their environment than stand age itself. These results are congruent with the results of Zinko et al. (2005).

Environmental surrogates have been criticized for low effectiveness in predicting distributions of biodiversity, and surrogates in general should not be used unless their reliability has been appropriately tested (Lindenmayer 1999, Araújo et al. 2001, Rodrigues & Brooks 2007). The effectiveness of the surrogate used in this study to predict plant species richness has not been empirically tested, but the model is based on the results of an empirical study (by Zinko et al. 2005). It is assumed that the predictor variables have a direct effect on habitat quality for plants and thus are effective predictors for plant species richness. Provided that the relationships between chosen explanatory variables and plant species richness are generalizable, the habitat suitability model should be an effective surrogate of plant species richness. In addition, Carmel & Stoller-Cavari (2006) showed that at a local scale, environmental surrogates can be as good or even better estimates of species richness than taxonomic surrogates.

4.4. Conclusion

The aim of this study was to study trade-offs between two important functions of boreal forest landscapes: provisioning of timber and maintenance of plant species richness. The main result was that despite there is a trade-off between these functions, both can be maintained on high levels through optimal combinations of management regimes in the landscape. Maximizing plant species richness on the forest stands also requires a combination of regimes. By combining alternative management regimes optimally, plant species richness in the landscape could be increased substantially with no costs compared to the present situation where forests are mainly managed according to current recommendations.

Managing forests for multiple objectives is a challenging task, as optimal forest management solutions depend on objectives. Thus careful landscape level planning is required to maintain biodiversity and timber revenues on sustainable levels. Being the first study that aims to find optimal management combinations for plant species richness and timber revenues, the results of this study provide more insights to the question of how to minimize trade-offs between economic and ecological objectives in boreal forest landscape. This kind of information is essential for developing forest management practices for more sustainable land-use. How to combine information about sustainable management for multiple aspects of biodiversity and ecosystem services in practical

landscape level management planning is a challenging but very important question that still remains to be answered.

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APPENDIX 1

Absolute and relative values of habitat suitability and net present value of timber in the Pareto-optimal solution, and proportions of alternative management regimes to be applied on different levels of the two considered objectives.

HSI	HSI %Max	NPV	NPV %Max	BAU	SA	EXT10	EXT30	GTR30	NTSR	NTLR
7466.67	92.86%	193.99	100.00%	64.63%	0.08%	0.37%	0.00%	7.81%	23.86%	3.24%
7631.26	94.91%	193.02	99.50%	54.02%	0.11%	0.87%	0.12%	15.23%	25.64%	4.01%
7633.57	94.93%	192.99	99.48%	53.93%	0.11%	0.90%	0.12%	15.33%	25.59%	4.02%
7638.88	95.00%	192.91	99.45%	53.81%	0.11%	0.91%	0.13%	15.49%	25.44%	4.10%
7742.88	96.29%	190.90	98.41%	50.42%	0.16%	1.33%	0.35%	19.91%	23.25%	4.58%
7771.25	96.65%	190.12	98.00%	49.48%	0.21%	1.51%	0.39%	21.15%	22.53%	4.72%
7813.18	97.17%	188.70	97.27%	48.03%	0.34%	1.67%	0.47%	22.79%	21.52%	5.18%
7865.10	97.81%	186.33	96.05%	45.66%	0.68%	1.80%	0.66%	24.09%	21.36%	5.75%
7880.11	98.00%	185.47	95.61%	45.04%	0.89%	1.84%	0.71%	24.23%	21.32%	5.98%
7898.47	98.23%	184.29	95.00%	44.23%	1.22%	1.75%	0.77%	24.36%	21.48%	6.18%
7905.58	98.32%	183.78	94.74%	43.98%	1.35%	1.74%	0.78%	24.42%	21.44%	6.28%
7939.45	98.74%	180.98	93.30%	42.13%	2.16%	1.68%	0.82%	24.72%	21.77%	6.71%
7968.79	99.10%	177.85	91.68%	40.02%	3.18%	1.61%	0.72%	24.67%	22.73%	7.06%
7994.28	99.42%	174.24	89.82%	38.25%	4.37%	1.61%	0.61%	24.48%	23.21%	7.47%
8000.72	99.50%	173.12	89.25%	37.79%	4.79%	1.65%	0.52%	24.43%	23.27%	7.55%
8016.52	99.70%	169.78	87.52%	37.07%	6.14%	1.69%	0.32%	23.99%	23.16%	7.63%
8035.12	99.93%	163.32	84.19%	36.37%	8.67%	1.85%	0.17%	22.58%	22.65%	7.71%
8040.91	100.00%	155.44	80.13%	34.42%	11.65%	1.83%	0.21%	20.27%	23.72%	7.90%
8040.92	100.00%	154.48	79.64%	34.38%	12.08%	1.82%	0.21%	20.13%	23.62%	7.76%