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Discussion

Optimal conservation resource allocation under variable economic and ecological time discounting rates in boreal forest

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ABSTRACT

Resource allocation to multiple alternative conservation actions is a complex task. A common trade-off occurs between protection of smaller, expensive, high-quality areas versus larger, cheaper, partially degraded areas. We investigate optimal allocation into three actions in boreal forest: current standard forest management rules, setting aside of mature stands, or setting aside of clear-cuts. We first estimated how habitat availability for focal indicator species and economic returns from timber harvesting develop through time as a function of forest type and action chosen. We then developed an optimal resource allocation by accounting for budget size and habitat availability of indicator species in different forest types. We also accounted for the perspective adopted towards sustainability, modeled via temporal preference and economic and ecological time discounting. Controversially, we found that in boreal forest set-aside followed by protection of clear-cuts can become a winning cost-effective strategy when accounting for habitat requirements of multiple species, long planning horizon, and limited budget. It is particularly effective when adopting a long-term sustainability perspective, and accounting for present revenues from timber harvesting. The present analysis assesses the cost-effective conditions to allocate resources into an inexpensive conservation strategy that nevertheless has potential to produce high ecological values in the future.

1. Introduction

In a world dominated by human impacts, where habitat degradation is reducing the space suitable for species, there are different alternatives to protect land when economical resources are limited (Polasky et al., 2008; Mönkkönen et al., 2011). Given the importance of habitat area and quality in conservation (Hodgson et al., 2011), taking two extremes, we can set-aside small selected areas of high quality habitats or we can set-aside as much area as we can, caring less for quality. In the former case we usually assume high habitat quality for species in these selected core areas; in the latter case we create a bigger reserve network that may compensate lower average habitat quality by increased area. Conceptually for boreal forest, setting aside large areas of presently lower quality habitat can be a long-term winning strategy, for at least three reasons. First, those areas will follow natural succession and improve in their quality through time. Second, the economic loss required to set aside this network may be much lower, thereby reducing conflict with stakeholders. This is assuming that lower habitat quality is correlated with lower economic value, as is the case specifically for the boreal forests in Fennoscandia that are focus of this study (Mönkkönen et al., 2014). Finally, choosing a few sites of high habitat quality (and high cost) can result in lower than expected long-term benefits: areas can be damaged by natural or human disturbance; a small protected area is likely to be unable to maintain spatial population dynamics leading to delayed extinctions via the extinction debt (Kuussaari et al., 2009). As a contrary

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argument, many species simply cannot survive outside high-quality late successional habitats, implying that such habitats must be included in any successful conservation area network (e.g., Hodgson et al., 2009; Mönkkönen et al., 2011).

In favor of protecting large conservation area networks is the species-area relationship, which states that there is a positive relationship between the area of a site and the number of species found on it. This relationship is one of the most general patterns observed in ecology (Rosenzweig, 1995). On the other hand, empirical observations show that species extinctions follow habitat loss, although often with a considerable time lag (Kuussaari et al., 2009). This implies that a conservation strategy opting for good quality habitats can maintain viable populations in the short term, but isolation and the small aggregate area of the sites could reduce the survival of populations in the long term. Both theory and practice suggest that successful conservation must aim at a balance between area and mean habitat quality (Hodgson et al., 2011).

Considering economics, the net present economic value of an area is combination of the revenue it can produce now and the time discounted revenue it could produce through time. Because future benefits are uncertain, future revenue is usually valued less than immediately available revenue. In contrast, the ecological value of the same area across time can be interpreted from different perspectives. From a utilitarian perspective, the area should have a higher ecological value at present, because the pleasure derived from the presence of biodiversity can only be fully appreciated at the present (Fuller et al., 2007). The conservation perspective assumes a higher ecological value to an area if it can ensure future persistence of species. These two perspectives base their rationale from alternative perceptions of nature as a balance or a flux (*sensu* Ladle and Gilson, 2009). From the sustainability perspective, transmitting ecological values to future generations is the key (Child, 2011).

The choice of the planning horizon or time window for evaluating ecological benefits is a key issue for conservation. Both economic and ecological benefits are dynamic: the former depend on the time an area provides valuable goods; the latter depend on the time the area is suitable for species of interest. Both are mediated through time by biological processes and are conditional on management taken (or lack of it) in the area. Consequently, it becomes necessary to jointly investigate the economic and ecological value of an area through time. However, future benefits of conservation may not be discountable in the same way as are economic values (Gollier, 2010; Kula and Evans, 2011; Guéant et al., 2012; Overton et al., 2013). Based on a logical scrutiny of economic discounting, Philibert (2003) argued that irreplaceable and non-reproducible environmental assets should be given a value growing over time at a pace close to the economic discount rate. A high net present value of future environmental benefits justifies increased immediate investment into conservation (Philibert, 2003). Future high net present value of biodiversity is amplified by the capacity of biodiversity to beget more biodiversity on longer time scales, if protected from factors causing decline (Overton et al., 2013). Long time spans (centuries) are justified in the evaluation of conservation benefits and ecological values, because these benefits are produced by functioning ecosystems and ecological processes and structures that take a long time to establish but can be lost very quickly due to human disturbance.

In Fennoscandia, intensive timber extraction has led to decline of forest biodiversity, and there is a recognized need to expand forest conservation (Brumelis et al., 2011). Here, we investigate optimal allocation of resources between three alternative actions in boreal forests. First, our baseline is business-as-usual commercial forest management. Our second alternative is typical forest conservation enacted via setting aside of mature stands, which offers relatively high immediate ecological quality but with high per-area cost. The third alternative is setting aside of much larger areas of clear-cuts, which presently hold low economic and ecological value. Per-area costs of protecting clear-cuts are much lower than that of mature stands. The question becomes, can clear-cuts support enough ecological value through time to make them a viable complement for mature stands? While clear-cuts currently host few structures of biodiversity importance (Lundström et al., 2011), they can provide habitats for many species if they are allowed to develop via natural succession, including natural accumulation of dead wood (e.g. Junninen et al., 2006; Eräjää et al., 2010; Rudolphi and Gustafsson, 2011; Swanson et al., 2011). They can even host an equal or greater number of species than old-growth forests (e.g. Pykälä, 2004; Selonen et al., 2005).

The analysis done here was implemented using RobOff, a recently released software intended for the investigation of uncertain consequences of alternative (conservation) actions in different environments through time (Pouzols and Moilanen, 2013). A structurally similar analysis could be replicated for other areas or environments with different environmental response functions.

2. Methods

2.1. Outline

We first used a stochastic forest growth simulator (SIMA; Kellomäki et al., 1992) to simulate forest growth in three different habitat types under different management scenarios. From the simulated stands we estimated how economic returns from timber harvesting and habitat suitability indexes (HSI) for six focal species develop over three centuries. Time discounted economic and ecological returns were used to produce response functions that are basic building blocks of the next step, optimal cost-effective allocation of alternative actions using the RobOff framework and software (Pouzols et al., 2012; Pouzols and Moilanen, 2013). This analysis integrates species-specific responses to actions in different environments, uncertainty around these responses, costs of actions, availability of habitats suitable for different actions, and economical and ecological time discounting (Moilanen et al., 2009).

We compared three alternative management scenarios, Business-As-Usual (BAU), set-aside and protect as mature stand (SA), and clear-cut following set-aside and protect (CC + SA). By mature stands we do not mean mature old growth forests but commercially managed forests that have reached the mean diameter allowing clear cut. In Fennoscandia, mature old-growth-forests are available for conservation in very small areas only, and all of them naturally are first priority for conservation. In BAU, stands are managed according to the current widespread standard management recommendations. Since BAU has been developed for the needs of commercial forestry, we can assume that it approximates long-term revenue that is economically optimal. BAU represents a baseline for our primary comparison, which is between SA and CC + SA. In both set-aside scenarios (SA and CC + SA), natural succession was assumed to follow; in CC + SA after the forest first has been cleared during the first 30 years. This time span reflects the fact that the mature managed stands are cut earlier on more fertile soils (like OMT) and later on less fertile soils (like VT). Our chosen time frame, 300 years, corresponds to about four rotations, and is sufficient for a clear-cut to reach the status of an old growth forest stand. Even if stands managed with CC + SA scenario may be of low ecological quality in the beginning they will improve in quality through time. Details of management practices are provided in appendix S1.

2.2. Study areas

We chose for the parameterization of response functions 553 mature stands from the data available from the 9th National Forest Inventory (randomly chosen stands in the NFI containing 2816 stands all over Finland, 1996–2003) (Finnish Forest Research Institute, 2010). These stands are sampling plots of 100 m^2 distributed across southern Finland on c. 7 million privately-owned forest hectares (30.8% of the forested area in Finland). Each stand has been classified to one of the three main forest site types in southern Finland based on the ground vegetation of the site (Cajander, 1949). The site types are, in increasing fertility and water content (and by implication increasing productivity and land price), VT (Vaccinium Type; 57 stands), MT (Myrtillus Type; 301 stands), and OMT (Oxalis-Myrtillus Type; 195 stands). Silver birch and Norway spruce only occur naturally in OMT and MT sites but Scots pine also grows in the less fertile VT type forest. The same set of stands was simulated following each of our three management scenarios.

2.3. SIMA - forest simulations

We simulated forest dynamics with SIMA, an individual tree based ecosystem model that is a hybrid between a physiological and a statistical model (Kellomäki et al., 1992). Simulation details and limitations are described in Appendix S1.

2.4. Focal species and calculation of the stand's ecological value (habitat suitability indexes)

We chose six focal species (the capercaillie (*Tetrao uralensis*), the Hazel grouse (*Bonasia bonasa*), the three-toed woodpecker (*Picoides tridactylus*), the lesser-spotted woodpecker (*Dendrocopos minor*), the long-tailed tit (*Aegithalos caudatus*), and the flying squirrel (*Pteromys volans*)) to represent the most important dimensions of variation in boreal forest diversity and a wide spectrum of habitat associations, responses to management, and conservation and social values (Mönkkönen et al., 2014; Appendix S2).

We extracted species-specific habitat suitability responses from SIMA simulations. We translated structural characteristics of stands into habitat suitability indexes (HSI, ecological value) that develop through time as a function of the management scenario applied in the habitat (Fig. 1), and responses of other focal species (Fig. S3.1). HSI indexes vary between 0 (unsuitable) and 1 (optimal habitat) and are a proxy for species population density (see Mönkkönen et al. (2014), for calculation of the HSIs). We used a quasi-hyperbolic model with a constant rate for discounting ecological values (Laibson, 1997).

2.5. Calculation of the stand's economic value

Under the Business-As-Usual scenario, the economic value (Net Present Value, NPV) of a forest stand depends on the stumpage prices of timber (saw log and pulpwood) and on the costs of site preparation after clear-cut and planting new saplings (Finnish Forest Research Institute, 2010). The NPV is calculated as the sum of the economic return obtained for each year by an annual discount rate r,

$$NPV = \sum_{k=1}^{8} \sum_{t=1}^{300} [y_{kt} \times p_k - c_t] e^{-rt}.$$

In this calculation, timber yield y_{kt} is the harvested volume (m^3/ha) for each timber assortment k and time period t. Timber price, p_k, is the stumpage price in euros/m^3 for eight different timber assortments (K = 8, i.e. sawlog and pulpwood of four tree species). Management cost, c_t is the cost of management actions (including natural regeneration, seedling, planting, tending of seeding stands, and cleaning of sapling stands) (€/ha) expected in time period t, and r is the discount rate. We divided the 300 year period into 30 decades. We assume that NPV remains constant over the short period of time forest is purchased for protection.

In the set-aside scenario, there are neither revenues nor costs across the 30 decades, because the stands are not cut, planted or managed. In case of the clear-cut followed by set-aside scenario, all the stands are harvested during the first three decades (with accumulation of revenue), but there are no costs thereafter because forests are allowed to regenerate via natural succession. The economic value of stands is a function of the forest type and of the discount rate (Fig. 2).

2.6. Time discounting economic and ecological value

Different discount rates were applied both to the HSIs and to the economic value to deal with differential time preferences for economic and ecological values. Present time economic returns from timber harvesting are generally valued higher than returns that can be harvested sometime in the future. (This is obvious from the low market price of clear-cuts.) Accordingly, we only allowed positive discount rates for economic value, +1%, +3%, and +5%. In contrast, opinions about ecological discounting vary, and it has been proposed that the future could be valued equally or even higher than present (Gollier, 2010; Kula and Evans, 2011). However, as there are several ways to determine the ecological (=social) discount rate (see e.g., Boardman et al., 2006) a sensitivity analysis was attempted by applying a wider range of discount rates for ecological value (−5%, −3%, −1%, −0.5%, 0%, +0.5%, 1%, 3%, 5%). With negative discount rates, the future is valued more than the present. As the impact of the choice of discount rate may have different outcomes (e.g., Davidson, 2014), it is reasonable to consider different types of discount functions for different objectives (Overton et al., 2013). For this reason we used the exponential model for discounting NPV and a quasi-hyperbolic model with a constant rate for discounting ecological values (Laibson, 1997; Green and Myerson, 2004).

2.7. RobOff - optimal allocation of resources to management options

The core of the RobOff framework and optimization software (Pouzols et al., 2012; Pouzols and Moilanen, 2013) emphasizes the uncertain responses of different biodiversity features to alternative scenarios in different habitat types or environments. Responses over time of biodiversity features to different management actions are the main input of RobOff. These were obtained as the trends of the HSI values for the six focal species. The responses were specified in a RobOff framework setup as estimated values and upper and lower uncertainty envelopes (calculated as 95% confidence intervals from a t distribution, accounting for inter-stand variability) for each decade across 300 years (Fig. 1; Fig. S3.1).

The three alternative management options applied in three different forest types were modeled as nine different pairs of actions and forest type, each having different costs and producing different responses of biodiversity features. Thus, a total of 54 different responses were defined (six focal species × three forest types × three management scenarios). Additional data objects considered are the costs of conservation actions (or NPV values of alternative management options), and the budget available. We used a 182 million Euros budget (and its multiples), equaling the Finnish government's resolution to allocate this amount of funding

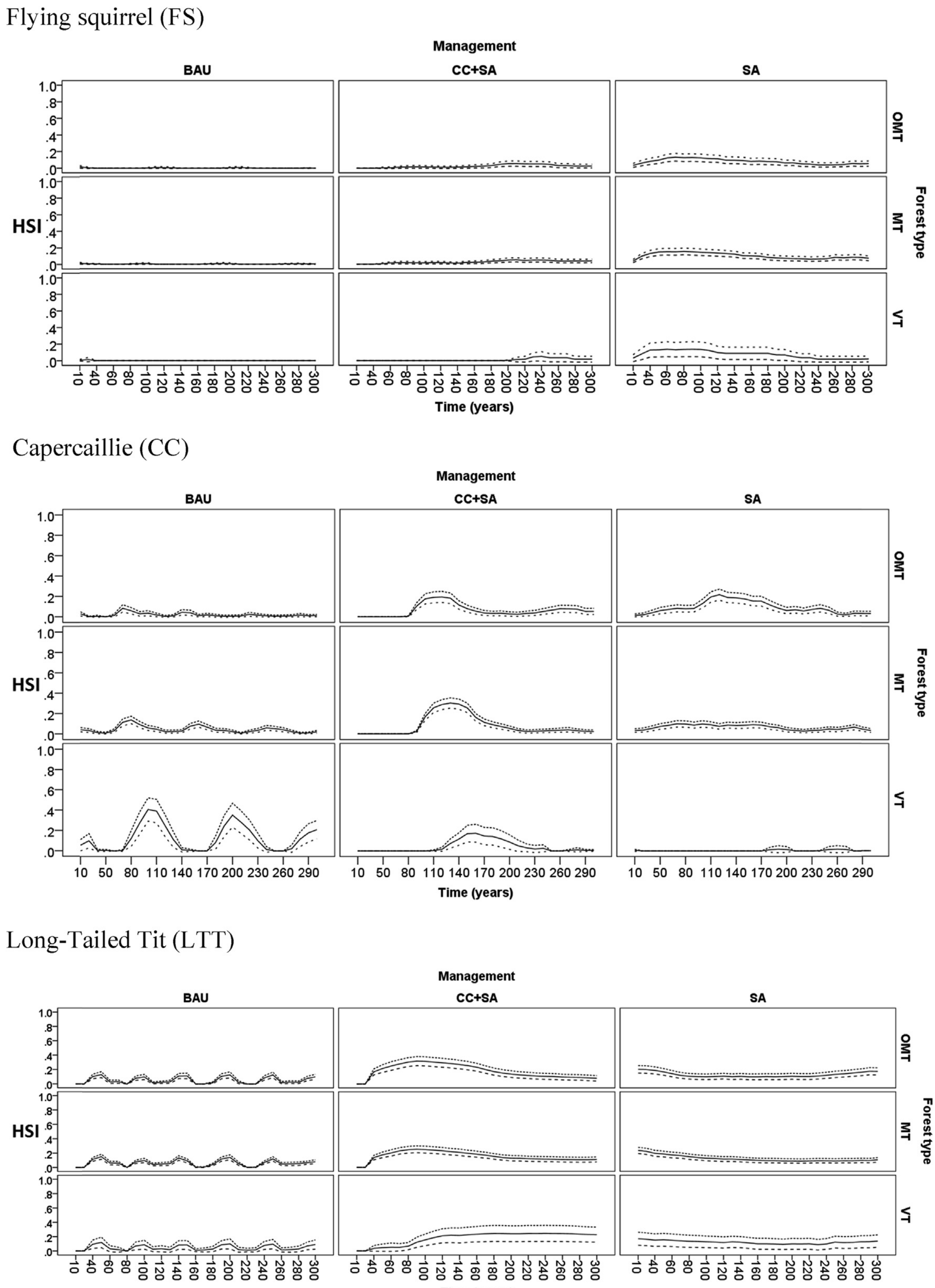

Fig. 1. Contrasting habitat suitability (HSI) for three of the focal species in three major forest types of southern Finland. Responses of HSI (y-axes) through time (x-axes) are used by RobOff, and they are given for three management scenarios: business-as-usual (BAU), clear-cut followed by set aside (CC + SA), and set aside of mature forest (SA). The lines show the mean, and upper and lower 95% confidence intervals of HSI. FS = Flying squirrel; CC = capercaillie; LTT = long-tailed tit.

for additional forest conservation in southern Finland through the METSO II program over a period of five years (Ministry of the Environment, 2008). According to a recent government resolution, this program will continue at least until 2020.

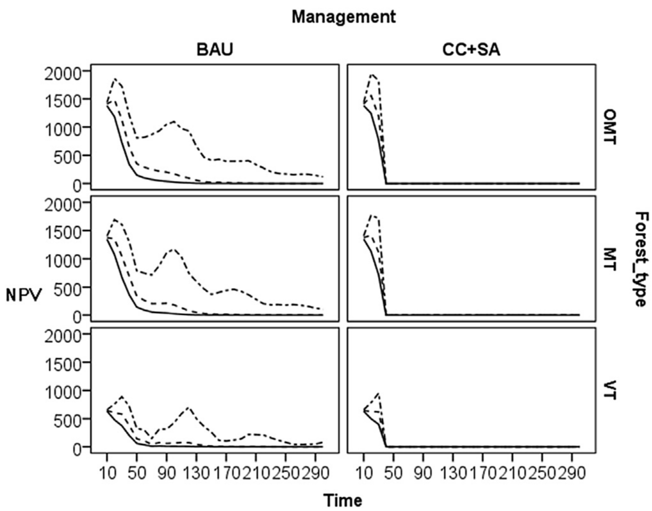

Fig. 2. Trends of discounted net present forest value (NPV, €/ha) for business-as-usual (BAU) and clear-cut followed by set-aside (CC + SA), for forest types (OMT, MT, VT, in decreasing order of productivity). NPV is shown as function of economic discount rate (+1%, dashed-dotted line, +3%, dashed line, +5%, solid line). NPV is always zero for set-aside of mature forest.

RobOff finds the allocation of resources into alternative actions such that conservation value is maximized in a robust manner (considering the uncertainty envelopes in the input responses). Conservation value is aggregated through time, different forest types, focal species, and alternative management scenarios (Pouzols et al., 2012). Results shown here are robust in the sense that, for the uncertainty bounds provided as inputs, conservation outcomes are guaranteed to be equal to or greater than those expected from the lower 95% confidence interval of the HSI predictions. Optimization was performed by the exhaustive search method which is deterministic and guarantees solutions that are optimal at a given budget resolution (minimum unit of resource allocation; we used 0.5%).

3. Results

3.1. Conservation resource allocation across species

We find that optimal allocation of resources between clear-cut followed by set aside (CC + SA) and setting aside of mature forests (SA) strongly depends on discount rates assumed for economic and ecological returns (Fig. 3). With the present budget CC + SA becomes relevant already with economic discount rates >2% (Fig. 3), a rate lower than generally accepted in economics. Differences in allocation result in varying fractions of the landscape under conservation; this area is large when resources mostly go into CC + SA, which has relatively low costs per hectare. With the actual budget level, highest investment into CC + SA occurs when we emphasize immediate economic returns (i.e. high economic discount rate) and distant ecological returns (i.e. negative ecological discount rate) (Fig. 3, upper and middle rows, left panel). Then, a maximum of 4.2% of the focal landscape could be set aside. With increasing emphasis on immediate ecological returns (i.e. increasing ecological discount rate) the relative utility of setting aside mature forests increases (Fig. 3, lower left panel), but simultaneously, total area under protection decreases dramatically, and only a maximum of 1.4% could be set aside with the current budget (Fig. 3, upper left panel). Decreasing economic discount rates always result in less area set aside due to increased per-area costs of conservation via higher NPV.

With an increasing conservation budget, more total area could be placed under conservation, but also the relative utility of setting aside clear-cuts and mature forests changes (Fig. 3). When the budget is increased to 10 times the original, maximally 49% of the total area could become protected, and it remains optimal to allocate most of the budget into setting aside clear-cuts when the emphasis is on short-term economic returns and long-term ecological returns. Only after the current conservation budget is (unrealistically) multiplied by 100, setting aside mature stands becomes the dominant strategy for most combinations of discount rates (Fig. 3).

The results can also be investigated with respect to allocation into different types of forests. With positive ecological discount rates the vast majority (>95%) of mature forest protected is of low-productivity VT type, where opportunity costs are lower (1 × budget). For negative ecological discount rates, all resources would be allocated into medium-productivity MT type. On the other hand, for CC + SA most of the budget (>90%) is allocated into high-productivity OMT areas, except for very low ecological discount rates (−3 to −5%) in which case all resources go into MT areas. These results are explained by the different costs of action in different forest types and different delays in ecological responses. MT forests have a more favorable combination of long-term average conservation value and land/opportunity cost than other forest types.

3.2. Species specific conservation resource allocation

The relative utility of setting aside clear-cuts and mature forests varies significantly between the species, reflecting species-specific habitat requirements (Fig. 1; Fig. S3.1). We illustrate this variation by showing the optimal allocation for three species: the flying squirrel, for which set-aside of mature stands provided highest average HSI values; the capercaillie, for which there were no significant differences in HSI values between scenarios; and the long-tailed tit, for which CC + SA provides highest HSI values.

The largest total area becomes protected when the economic discount rate is high and the ecological discount rate is negative (Figs. 3 and 4). The relative utility of setting aside mature forests vs. clear-cuts varies markedly between species (Fig. 4). At the current budget level, setting aside clear-cut remains a part of the conservation tool-box for all species (Fig. 4). When the focal species has a strong association with mature forests (e.g., the flying squirrel) it is optimal to allocate only a low fraction of resources into clear-cuts (Fig. 4) and only under limited combinations of ecological and economic discounting. For other species, optimal allocation into CC + SA is overall higher (e.g. long-tailed tit) or takes place under a wider combination of discount rates (capercaillie).

4. Discussion

We quantitatively investigated optimal conservation resource allocation in boreal forests in Finland. Our analysis showed that when a longer time perspective is adopted, unconventional decisions, such as allocating resources into an inexpensive conservation action (setting aside and protecting clear-cuts) that has potential to produce high ecological values in the future, may make sense. This is true in particular when the conservation budget is limited, present revenues from timber extraction are preferred, and, following guidelines of sustainability and intergenerational equity, both present and future ecological benefits are valued. Importantly, we note that we are not advocating for clear-cutting forestry, but in a context that is already about 98% dominated by intensive forestry with clear-cut final harvesting, allocating a proportion of conservation resources for protecting clear-cut areas

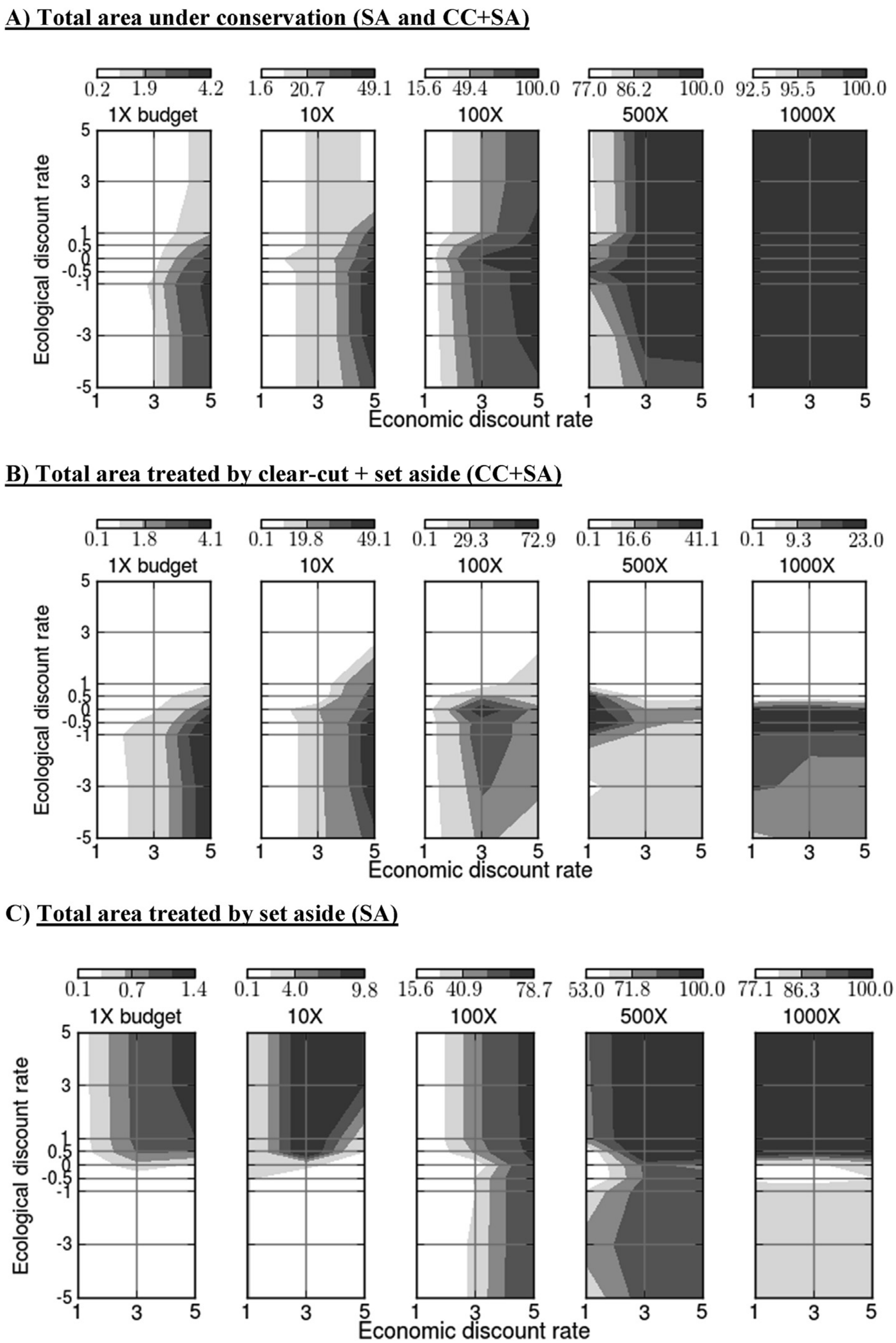

Fig. 3. Effect of time discounting and available budget on optimal allocation of actions, expressed as percentage of area (out of c. 7 M ha total) allocated for conservation. This percentage varies primarily because much more area could be afforded via clear-cut + set aside compared to set aside of mature stands. The upper row gives the total area under conservation; the middle row gives area treated by clear-cut + set aside; the bottom row is for set-aside of mature forest. Area not allocated for conservation (complement of percentage allocated) would be managed following business-as-usual practice. The gray scale indicates allocation at different discount rates; note that its interpretation (scale bars) differs between rows and columns. At the present 1 × budget level and within a range of plausible discount rates, the majority of conservation area would go into CC + SA.

would be a cost-efficient policy in the long-run. Consequently, the Finnish environmental administration (and neighboring countries) could consider setting aside a larger area of clear-cuts as a valid alternative to the purchase of old managed stands (Lundström et al., 2011). Note that only part of the budget should be used for clear-cuts (Fig. 3), and that clear-cuts should be left alone to follow natural succession (Rudolphi and Gustafsson, 2011; Swanson et al., 2011).

Our analyses also found differences between optimal allocations of resources into forests of different productivity. When mature stands are protected, the preference should be on low-productivity low-cost VT types, with lower cost per area, whereas with clear-cuts more productive forest land should be preferred (Lundström et al., 2011).

Current conservation investments in Finland are not enough for achieving the Aichi conservation targets, which require protection of at least 17% of terrestrial areas by 2020 (European Commission, 2010). Presently, approximately 10% of the terrestrial areas of

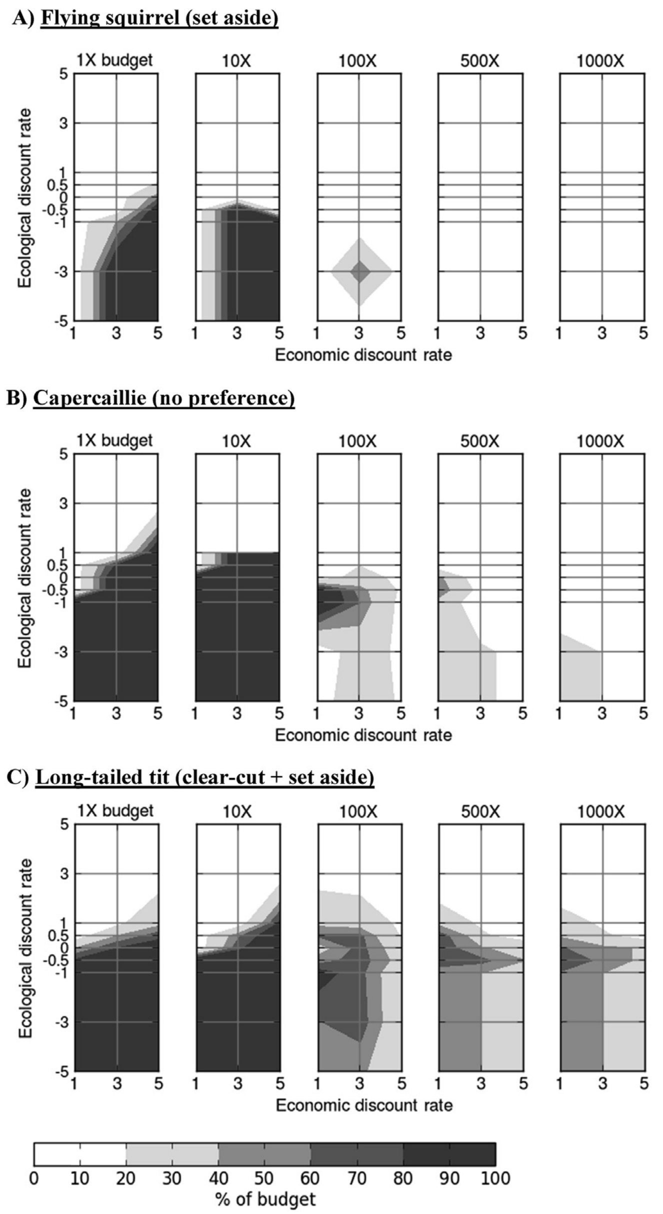

Fig. 4. As Fig. 3, but now showing optimal allocation (percentage of budget) of money into clear-cut + set aside, if planning was for one species only: the flying squirrel (FS), capercaillie (CC) or long-tailed tit (LTT). Here, the complementary percentage becomes allocated for setting aside mature stands. The management scenario most suitable for the species is given in parentheses.

Finland belong to public and private protected areas, implying that a further 7% of the territory should additionally be protected, which in South-Finland converts into an expansion of about 483 000 ha of forest conservation areas. Therefore, the actual present forest conservation budget could achieve up to 59% of the Aichi target (about 282 900 ha) if used to set-aside clear-cuts, but only up to 20% of the Aichi target (about 96 600 ha) if setting aside only mature stands. According to the present analysis, the Aichi target would be achieved with a balance of mature stands and clear-cuts under a quota of approximately ten times the actual current forest conservation budget.

One factor strongly influencing decisions over long time periods is balancing of immediate versus distant gains and losses, which we implemented via time discounting (Green and Myerson, 2004). We used separate time discounting for economic and ecological values. Arguments in favor of dual discounting are based on the fundamentally different characters of environmental benefits and monetary costs. At least three reasons have been proposed for the use of zero or even negative discount rates for ecological values: (i) partial non-substitutability of ecological and biodiversity values by economic growth/consumption, (ii) guaranteeing of intergenerational equity, and (iii) providing an adequate basis for long-term persistence of biodiversity (Gollier, 2010; Kula and Evans, 2011). The lower the growth rate of environmental quality (or the larger its rate of decline), and the lower the elasticity of substitution between environmental quality and produced goods, the lower the ecological discount rate should be (Hoel and Sterner, 2007). Our results also show that setting aside clear-cuts becomes especially effective when the economic discount rate is >2%. It is not possible to find a single general discount rate for forestry investments but realistic rates have typically been >2% (e.g. Grege-Staltmane and Tuherm, 2010; Finnish Forest Research Institute, 2010). If we accept the widely held assumption that ecological discount rates should be well below the economic ones (Gollier, 2010; Guéant et al., 2012), decision makers should apply ecological discount rates closer to zero or negative. The strategy of CC + SA indeed seems a cost-efficient option for a plausible range of time discount rates for economic and ecological benefits. On the other hand, setting aside clear-cuts is not a cost-efficient option, when ecological discount rate is positive. However, the choice of discount rate is a controversial issue. Private discount rate (PDR), such as a market interest rate, is an appropriate selection to discount cost and revenues of timber production when the purpose of simulations is assess how actions of private forest owners impact forest biodiversity. More generally, biodiversity conservation is a social investment, and therefore, a social discount rate (SDR) is needed to evaluate impacts of social conservation project or policy. There are several ways to determine the SDR (see e.g., Boardman et al., 2006). Hence, it is not possible to find a single general discount rate to value present vs. future economic and biodiversity benefits. As it is not possible to determine the correct discount rate we performed a sensitivity analysis, rerunning analyses using varying discount rates for both economic and biodiversity benefits with a number of alternative combinations, and checking how sensitive results are to this variation.

Some assumptions and choices were made to facilitate the present analysis. For example, because species have different responses it makes a difference which ones are included in analysis (Fig. 4; Fig. S3.1). The six species included here are associated with mid-seral or late-seral forest stages, and as such are considered indicators of high-quality boreal forest (Mönkkönen et al., 2014). Nevertheless, a different choice towards early-seral species associated with young forests could lead to a different optimal resource allocation, which by necessity will be more biased towards setting aside of clear-cuts. Overall, the strategy of partial investment into clear-cuts seems a robust strategy: CC + SA produces habitats that support many species in the long run and large areas could be afforded. Indeed the long-term benefits of CC + SA in terms of HSI are as highly certain as the favorable short-term responses from SA, conditional on natural succession been allowed through the establishment of permanent reserves (Mönkkönen et al., 2011).

A simplification of the present analysis is that RobOff does not account for spatial patterns, which however is not a major impediment for the applicability of the results. Survival of species obviously depends on the overall structure of the landscape. Once we have identified the relevance of setting-aside clear-cuts, it is a simple matter to purchase these from the neighborhood of the remaining old-growth forests, almost all of which already are under protection. Thus, it is possible to ensure adequate connectivity and colonization potential. Also, all our focal taxa are vertebrates capable of long-distance dispersal and recolonization of empty habitat. However, in some cases (e.g., sessile short distance dispersers) when species may not able to track suitable habitat patches or could go extinct before the required habitat quality is available, models accounting for meta-population dynamics should be applied (c.f., Snäll et al., 2004). Making the present analysis fully spatial would on the other hand be highly expensive in terms of data and computational demands. As another limitation, our analysis only considered two strategies (BAU and SA) widely applied in Fennoscandian boreal forests. Alternative strategies have recently been suggested, such as selective logging (Hjälten et al., 2012), partial harvesting (Thorpe et al., 2010), or uneven-aged management (Kuuluvainen et al., 2012) but little is currently known about their effects on biodiversity. Subsequent improved analysis could also include additional focal guilds, such as forest dwelling beetles and polypore fungi, which have well-known habitat requirements (Tikkanen et al., 2006), and whose occurrence is related to forest management (Siitonen, 2001; Mönkkönen et al., 2011).

While the present analysis focuses on and is highly relevant for boreal forests in Finland, and by extrapolation in the neighboring areas of Fennoscandia, the insights gained could be extrapolated to different environments with similar relationships between opportunity costs and environmental responses. We anticipate that setting aside forests where timber has been extracted can be a part of a long-term conservation tool-box in all forest biomes where the total area of forests is not diminishing but a large proportion of area is under human influence. We do not recommend applying this strategy in less resilient ecosystems where natural succession is not likely to restore ecological values or in ecosystems where remaining natural areas are declining rapidly. In such cases it would be unrealistic to assume that species would persist until degraded areas regain their suitability via natural succession.

5. Conclusions

The present multi-dimensional analysis summarizes effects of alternative conservation actions on the occurrence of priority fauna in different types of boreal forests through time. It is among the first major studies that integrate both economic and ecological discounting in conservation resource allocation. We quantitatively identified sets of actions that produce high conservation value that is balanced across features, forest environments and time, guided by costs and budget availability. Our results suggest that protection of clear-cuts preferably nearby existing high-quality forest conservation areas would be a feasible conservation strategy in boreal forests. This suggestion is contrary to presently accepted conservation management in Finland. Put simply, per-area costs of protecting clear-cuts are very low, and the forests that will naturally develop in these areas will grow into valuable conservation areas to be enjoyed by future generations.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2016.05.057.

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