
A Cost-Efficient Approach to Selecting Forest Stands for Conserving Species: A Case Study from Northern Fennoscandia

Artti Juutinen, Erkki Mäntymaa, Mikko Mönkkönen, and Juha Salmi

ABSTRACT. We analyze cost-efficient conservation of boreal old-growth forests using three variants of the site selection framework. In all variants, the aim is to maximize biodiversity subject to a given resource constraint. Our benchmark, an integrated site selection model, takes into account both ecological and commercial values of the stands and defines a cost-efficient solution to conservation problems. The other two models are called the ecological and the penny-pincher models. The ecological model reflects current conservation practices and is based on ecological criteria. The penny-pincher model reflects an ad hoc preservation used earlier in many countries, which leads to selection of the stands having the lowest commercial value irrespective of their ecological features. Using Finnish data on forest dwelling species and commercial values of the stands, we demonstrate that the integrated model leads to 9–19% higher conservation cost-efficiency than the other two models. We also show that the xeric forest type may be underrepresented in the current old-growth forest preservation network in this region. *FOR. SCI.* 50(4):527–539.

Key Words: Biodiversity, forest management, integer programming.

LOSS AND FRAGMENTATION of natural habitats are considered the main reasons for certain species becoming extinct worldwide (Pimm et al. 1995). In Fennoscandia, a prime threat for species survival is commercial harvesting of forests, which leads directly or indirectly to habitat loss (Esseen et al. 1997, Rassi et al. 2001). The conflicts between timber and biodiversity production are obvious. Given that the forest industry is economically important in Nordic countries, biodiversity conservation imposes a great challenge: how is it possible to conserve biodiversity and economically use taiga forests?

A new type of management, called landscape ecological forest management, has been implemented in Fennoscandia during the past decade to tackle this problem. Under this paradigm, forest stands are not managed in isolation from the surrounding landscape, but entire landscapes, usually consisting of some tens of thousands of hectares, are con-

sidered a planning unit (Noss 1996, Mönkkönen 1999). The main tools used in this management planning system include mimicking natural disturbance regimes in harvesting, enhancing possibilities for species to move among habitat patches through increasing connectivity by designing movement corridors and stepping stones, and setting some stands aside from commercial harvesting either temporarily or permanently.

In forest conservation planning, the management of commercial forest and protected reserves should be considered together. Because less than 5% of productive forestland is currently protected in Fennoscandia, the vast majority of individuals of species indigenous to forests live outside protected areas. Therefore, biodiversity management in commercial forests is important for the persistence of many species along with larger protected areas. Thus, decisions about which stands are to be allocated to commercial forestry and which ones are to be

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protected are the basic choices in the landscape ecological planning. Therefore, maintaining biodiversity has to solve a typical site selection problem.

The site selection approach, where a land manager has to decide whether to harvest or protect a stand, is particularly useful when considering the protection of old-growth forests, because clear cutting combined with regeneration is the dominant silvicultural method in Fennoscandia. Because the remaining old-growth forests comprise considerable ecological value, setting aside at least some of the old-growth forest stands is a potentially effective way to maintain forest biodiversity. Clearly, forest managers have to set priorities and select the best targets for reserves taking into account their ecological value as well as the costs of conservation (Margules and Pressey 2000).

It is not easy to carry out a complete evaluation of the biodiversity value of forest stands, because biodiversity has multiple facets and can be measured in different ways at various levels of biological hierarchy (Noss 1990). Gaston (1996) surveyed the alternative biodiversity measures and concluded that species diversity is a reliable and practical surrogate for overall biodiversity (Gaston and Spicer 1998). We use species richness as a measure of diversity in our species representation approach, because it suits well to multispecies conservation.

The representation approach is often used in the biodiversity conservation literature (Sætersdal and Birks 1993, Kershaw et al. 1995, Csuti et al. 1997, Hacker et al. 1998, Snyder et al. 1999, Polasky et al. 2000), but in most cases, economical aspects are not adequately taken into account because sites are assumed to have equal value. This unjustified assumption may severely impede cost-efficient conservation planning. For example, using county-level data for the United States, Ando et al. (1998) showed that accounting for heterogeneity in land prices results in a notable increase in efficiency in terms of either the cost of achieving a fixed coverage of species or the coverage attained from a fixed budget. Similar results were also demonstrated in Balmford et al. (2000) in a global context and in Polasky et al. (2001) for the state of Oregon, USA. However, these studies, which we will call integrated site selection models, considered biodiversity maintenance at broader spatial scales than that of landscape ecological forest management.

Applications of the integrated site selection approach to old-growth forest are few.[1] To our knowledge, only Stokland (1997) has compared the efficiency of alternative selection strategies, with an aim at maximizing the number of species and also including the opportunity costs of conservation. Stokland found that the forests most valuable for forestry were also the most valuable for biodiversity conservation, and that the Norwegian network of forest reserves was seriously skewed toward less valuable sites. Nonetheless, generalizing from his results is difficult, because opportunity costs were not measured directly and only a narrow selection of taxa were used in the analysis.

In this article, we address the cost-efficiency of alternative site selection criteria. We integrate economic and ecological aspects to construct alternative forest preservation

networks that would maintain a maximum amount of diversity of species prevalent in old-growth forests under a given budget constraint. Our article differs from the previous work in two important respects. First, we consider a wide variety of species indigenous to forests.[1] Second, we measure the opportunity costs as forgone timber revenues defined in an optimal rotation solution for stand management, thus including both the land value and the value of standing timber.

The objective of the study is as follows. First, using site selection models, we compare alternative conservation models in terms of selected species, forest types, and associated costs, i.e., assess the relative performance of these methods. Second, we relate the ideal solution provided by these models to the current conservation network in the study region to make recommendations how to supplement the existing network in a cost-efficient way.

For this purpose, we develop three models and solve them numerically to guarantee that the best option with respect to objectives and restrictions is selected (Rodrigues et al. 2000a).[2] The first model is the integrated model, which we use as a benchmark. The second is the traditional ecological model, which represents recently adopted practices in landscape ecological forest management and is based on ecological arguments for reserve site selection. Our third model is called “shortcut selection” or “penny-pincher selection,” where the conservation network is established beginning with low-cost sites to get as large an area as possible under conservation and to avoid conflicts among land uses. This type of opportunistic selection may not seem a very rational conservation policy, but it corresponds to the fact that conserved areas in Fennoscandia are situated mainly on low productivity lands (Nilsson and Götmark 1992, Virkkala 1996, Stokland 1997, Pressey and Tully 1994).

Our data originate from 32 forests stands representing the whole spectrum of ecological variation in forest types in NE Finland within two landscape ecological forest management areas.[3] We include information concerning presence/absence of species (vascular plants, birds, beetles, and wood-inhabiting fungi) and the economic values of forests (timber values and land values). An optimization based on species presence/absence may result in a conservation network that will not ensure species persistence in the long run. Therefore, we also execute an optimization aiming to maximize species abundance to assess the robustness of our results.

Models and Empirical Data

Site Selection Models

In this section, we develop in detail the basic features of our integrated, ecological, and penny-pincher selection models. The models are based on the representation of chosen ecological features in a restricted optimization framework. We impose to all a binding, but different, resource constraint. The integrated model includes the conventional monetary budget constraint reflecting the fact that protected areas are either bought from private landowners or obtained by setting aside public forests—both being subject

to scarce public funds. The ecological and penny-pincher models have an area constraint representing a typical policy where the society fixes the target share of protected land, for example, by using ecological knowledge about the species-area relationship (Rosenzweig 1995).

We assume that each stand has only two management options: the stand is either clearcut or completely preserved from harvesting. Moreover, we use species diversity, namely the number of species, as a surrogate for overall diversity.[4] Given these standpoints, we adopt the following notation:

- $x_j = 1$ if stand j is selected and 0 otherwise;
- $y_i = 1$ if species i is contained in at least one of the selected stands and otherwise 0;
- N_i = the subset of candidate reserve stands that contains species i ;
- B = budget allowable for reserve network;
- b_j = opportunity costs of establishing a reserve stand j .

In the integrated model, the objective is to maximize the number of species that the selected stands can provide subject to the constraint that economic costs of conservation cannot exceed a given budget constraint. Thus, the integrated optimization problem is given by:

$$\text{Max}_{x, y} \sum_{i=1}^m y_i \quad (1)$$

s.t.

$$\sum_{j \in N_i} x_j \geq y_i, i = 1, \dots, m \quad (2)$$

$$\sum_{j=1}^n b_j x_j \leq B \quad (3)$$

$$y_i = (0, 1), i = 1, \dots, m \quad (4)$$

$$x_j = (0, 1), j = 1, \dots, n. \quad (5)$$

The objective function 1 sums up the number of species in the selected stands. Constraint set 2 ensures that species i is counted as being represented when at least one of the stands where it occurs is selected. Equation 3 is the budget constraint requiring that the sum of opportunity costs of the stands selected (having different opportunity costs) does not exceed the funds allowable for a conservation network. The constraint sets 4 and 5 simply indicate that the choice variables must be binary, and there are m species and n stands. Thus, the stands are either protected or harvested, and the species is represented or not represented, in their entirety.

In the integrated model, the stands are considered as a set, taking into account the interdependence among stands in terms of species representation.[5] The model selects stands that supplement each other from the viewpoint of species richness. Thus, to maximize species richness in the

network, it is optimal to select stands where the species composition differs as much as possible.

The ecological model differs from the integrated model by specifying the resource constraint in terms of the number of stands instead of the monetary budget constraint. The formal presentation of the ecological model is the following:

$$\text{Max}_{x, y} \sum_{i=1}^m y_i \quad (6)$$

s.t.

$$\sum_{j \in N_i} x_j \geq y_i, i = 1, \dots, m \quad (7)$$

$$\sum_{j=1}^n x_j \leq k, \quad (8)$$

$$y_i = (0, 1), i = 1, \dots, m \quad (9)$$

$$x_j = (0, 1), j = 1, \dots, n. \quad (10)$$

In the area constraint 8, k is the given upper limit for the number of stands in the conservation network. The approach is also called a site-constrained site selection problem (Polasky et al. 2001). Unlike the integrated model, ecological selection implicitly assumes the same opportunity costs for all stands. Therefore, stands are selected by ecological criteria only. Like in the integrated model, this model also takes into account the interdependence among stands and selects stands that complement each other as much as possible. Ecological models usually have multiple optimal solutions (with several sets of stands all containing the same number of species), and when this happens, we exemplify them with the minimum and maximum opportunity costs to show the variation in the results. The cases are named minimum and maximum cost solutions.

In the penny-pincher model, the manager minimizes the opportunity costs subject to the site constraint, which defines the lower limit for the number of protected stands:

$$\text{Min}_x \sum_{j=1}^n x_j b_j, \quad (11)$$

$$\sum_{j=1}^n x_j \geq k, \quad (12)$$

$$x_j = (0, 1), j = 1, \dots, n. \quad (13)$$

The objective function 11 sums up the opportunity costs of the selected stands. The area constraint 12 defines that the minimum number of selected stands must be at least k . The penny-pincher model is a minimization model, so it uses a lower limit for the number of protected stands instead of the ecological model's upper bound. The constraint set 13 indicates that the choice variables must be binary. Note that

the penny-pincher model does not have any choice variable for species, because here the stands are first ranked from the cheapest to the most expensive and then allocated in the network according to this rank. This implies that penny-pincher selection does not guarantee that the conservation network is diverse from the ecological perspective.

The objective functions 1, 6, and 11 are linear in the choice variables. Therefore, the problems can be solved using branch-and-bound algorithms, which guarantee the optimality of the solution (Csuti et al. 1997). With large applications, however, the solution time may become long, because the branch-and-bound process is computationally intense (McDill and Braze 2001). [6] We used a commercial spreadsheet optimization software named WB to solve these problems (What's Best! 2000). A Finnish forestry model, called MELA, was used to calculate the site value for each stand (Siitonen et al. 1996). MELA calculates the net present value of a forest by approximating Faustmann's formula.

Data Source

The database includes 32 seminatural old forest stands in two landscape ecological forest management areas (Puhos and Siikavaara, total area 80,000 hectares) in northeast Finland. Both areas are situated in the middle boreal forest vegetation zone (Kalela 1961). The forests in the study area are not totally intact old-growth stands, because the most valuable timber was removed during the 19th and early 20th century by selective harvesting. The study sites were chosen based on forestry files from the Finnish Forest and Park Service, and as natural and large stands as possible were selected. These stands were considered to be the best targets for the complementation of the Finnish old forest conservation network (Ministry of the Environment 1996). Also, they fulfilled the criteria of a biologically valuable forest: the age of the dominating trees was clearly above the average rotation period for the managed forests in the region (100–120 years), the canopy consisted of multiple layers and of several tree species, and decaying wood was a conspicuous element of the forest. The average tree age of the stands was 136 years, varying between 114–175.

We chose four forest site types and surveyed eight stands of each type: xeric coniferous forests (*Vaccinium-Myrtillus/Empetrum-Vaccinium* type), mesic spruce forests (*Vaccinium-Myrtillus* type), spruce mires (a heterogenous group of wet site types), and herb-rich, spruce-dominated

heath forest (*Geranium-Dryopteris* or *Vaccinium-Myrtillus/Geranium-Dryopteris* type). These site types cover the whole gradient of forests in the region and represent a fertility gradient ranging from barren pine heaths to herb-rich forests.

We sampled beetles (*Coleoptera*), birds (*Aves*), wood-inhabiting fungi (*Basidiomycetes*), and vascular plants (*Tracheophyta*) in each stand. These taxa were selected to cover a wide array of dispersal potential and life forms to yield general results. Beetles were sampled using window and pitfall traps. There were five window traps and 10 pitfall traps systematically distributed in each stand from the beginning of June until the end of August 1997. Birds were censused in June 1997 using the point count method (Hilden et al. 1991). Each stand was visited twice, in early and late June, and all birds seen or heard were tallied. In the analysis, we concentrated on forest birds. Wood-inhabiting fungi were sampled using manual sampling so that a standard area of 1570 m² was surveyed in mid-August to mid-September 1998. Each fruiting body was considered an individual. Percentage coverage of vascular plants was surveyed in 10 1 × 1 m² quadrates distributed systematically in each stand. Surveys were conducted between mid-July and early Aug. 1998. The data consists of 103 vascular plants, 30 forest birds, 64 wood-inhabiting fungi, and 435 beetle species, making a total number of species of 632. Table 1 describes the ecological features associated with forest types using mean values and coefficients of variation of species richness (for details of sampling procedures and data, see Similä et al. 2002).

The data on detailed stand characteristics for the forest value calculations were taken from the Finnish Forest and Park Service forestry files. Because the use of total timber and land values would automatically bias the selection of sites under a budget constraint toward small stands, we use unit forest values (US dollars/ha) and treat stands as having equal sizes in the optimization. Generally, the stands of the herb-rich heath forest type are the most costly options in the conservation of boreal old forest (Table 1). The xeric and mesic stand types also have rather high forest values. Spruce mire stands are clearly the cheapest options for reserve selection. However, the coefficient of variation of the forest value is rather large in every forest type (30–48%), indicating that there are both low- and high-cost stands within each type.

Table 1. Number of species observed and forest values of the site types in our study area. Figures are mean values across eight stands in each site type with the coefficient of variation (CV%) in parentheses.

	Forest type (<i>n</i> = 8)			
	Xeric	Mesic	Spruce mires	Herb-rich
Total number of species	153 (7)	143 (8)	166 (9)	163 (11)
Vascular plants	17 (23)	22 (20)	38 (25)	30 (11)
Wood-inhabiting fungi	11 (18)	11 (39)	9 (39)	14 (22)
Birds	12 (14)	12 (10)	11 (21)	11 (25)
Beetles	112 (7)	99 (10)	107 (11)	107 (15)
Forest values (US dollars/ha)	4,566 (30)	4,107 (48)	2,020 (45)	4,813 (48)

We compare the three models in terms of species coverage, opportunity costs, and forest types selected. We also discuss how the results depend on the taxonomic groups chosen. To assess species persistence and the robustness of the results, we also solve a maximization problem regarding species abundance.

Results

Species Representation

By varying the budget or the site constraint, we can plot the species coverage as a function of opportunity costs for all three models.[7] The target functions of the models are growing and discontinuous, and their shapes depend on the level of the opportunity costs (Figure 1).

When a low level of funds is devoted to conservation, the optimal species coverage of the integrated model is steeply increasing along with the number of stands included in the network. The budget size of 17,000 US dollars proved to be a critical threshold value. Below this threshold value, it is optimal to select the stands with the lowest opportunity costs and to establish as large a network as possible, because any increase in the number of stands rapidly increases the coverage of species. Above this threshold and given that the network includes eight stands, the complementarity of selected stands becomes more important than the size of the network as such. It is no longer optimal to select the nine cheapest stands, for example, because with this budget there is a combination of eight stands available covering a larger number of species. At this budget level, the target function becomes flatter and rather continuous. When almost all species are covered, the target function is nearly horizontal. The species not chosen yet are likely to be restricted to a single stand or very few stands. Also, these stands have,

naturally, rather high timber values. Therefore, saving the last few species is increasingly costly. In our data, covering all species requires that all stands are included in the conservation network.

A poorly designed selection of stands may result in a high loss of species and low cost-efficiency (Figure 1). The difference in the number of species between the integrated selection and the curve describing the worst possible selection is large, particularly at moderate levels of opportunity costs. Naturally, this lower bound curve also is increasing, indicating that a larger conservation area results in higher species richness.[8]

Ecological and penny-pincher selections lead to economic losses in terms of species representation. Usually, these selections cover fewer species than integrated selection. However, the differences in species numbers are small, but these models may still lead to considerable losses in cost-efficiency.

Costs Comparisons

The cost differences of the models are presented in Figure 2. Overall, there are 32 observations of cost differences in every comparison, because the ecological and penny-pincher models have site constraints and our application includes 32 stands. In addition, the minimum and maximum cost solutions of the ecological model are separated to highlight the range of opportunity costs in ecological selection.

At a low conservation level, where the number of species represented is less than 370, ecological selection can be very expensive. It costs 16–72% more than integrated selection. By contrast, penny-pincher selection is as good as integrated selection at low levels of conservation. At higher levels of

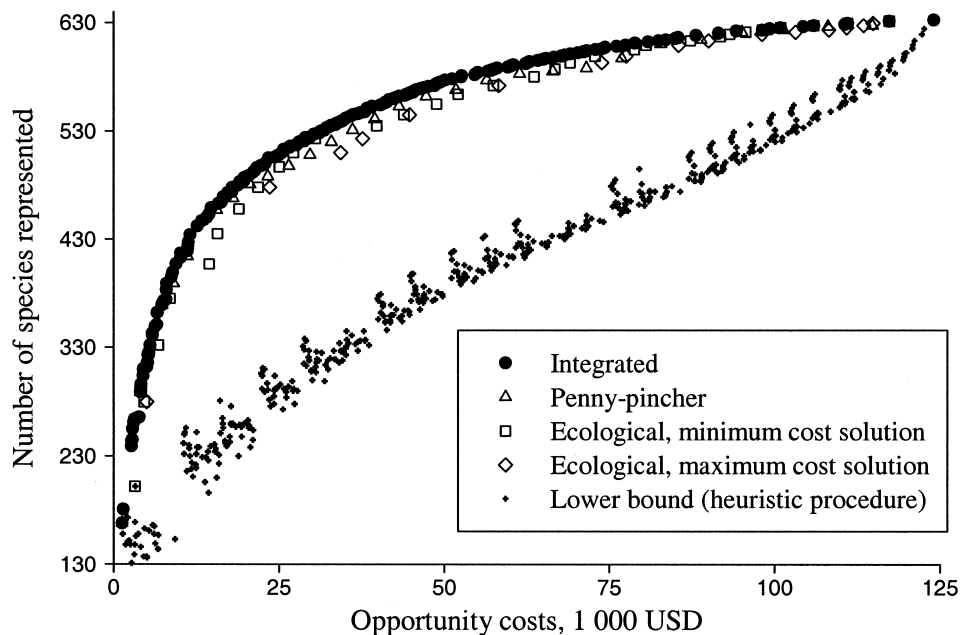


Figure 1. The number of species represented in the selected conservation network, plotted as a function of opportunity costs, picked by alternative priority-setting methods. When the minimum and the maximum cost solutions of ecological selection are the same, for clarity, only the minimum cost solution is plotted.

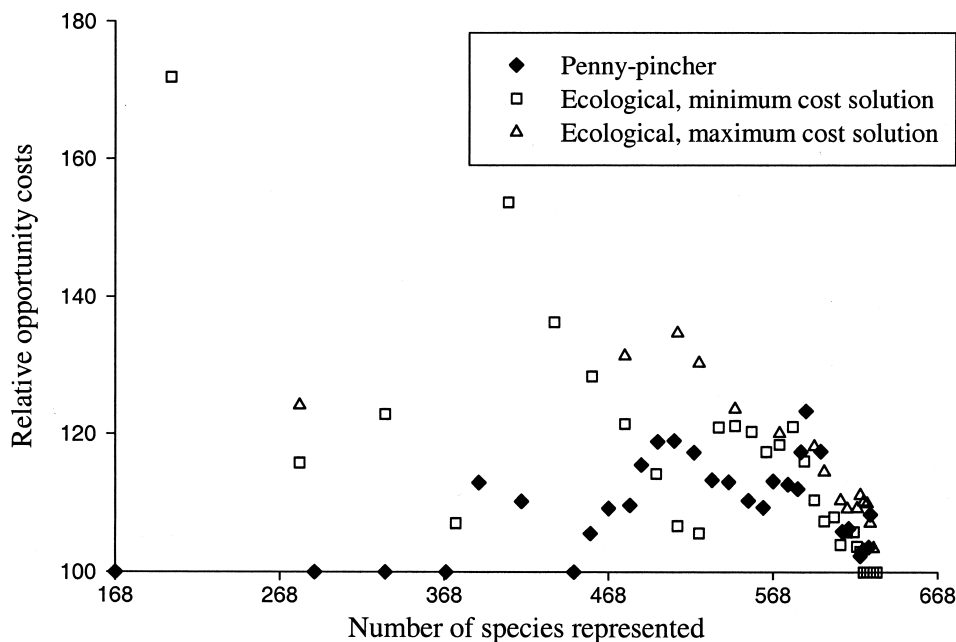


Figure 2. The relative opportunity costs of ecological and penny-pincher selections, plotted as a function of the number of species represented in the selected conservation network. The costs of integrated selection are designated as a benchmark, with a value of 100; thus, a value of 150 for another selection method means 50% higher costs than in integrated selection. When the minimum and the maximum cost solutions of ecological selection are the same, for clarity, only the minimum cost solution is plotted.

conservation, ecological and penny-pincher selections are both more expensive than integrated selection. The difference in opportunity costs between penny-pincher and integrated selections is at the highest, 23%, when the conservation network covers about 93% of the species. Ecological selection costs about 6–53% more than integrated selection at the medium level of conservation (370–600 species represented). There is much variation in the costs of ecological selection between the minimum cost solutions and maximum cost solutions. When almost all species are covered, the cost differences among the methods are minor, because nearly all stands are already selected into the network.

We next calculate the mean values of cost differences over the whole range of species represented (168–632). Penny-pincher selection costs, on average, 9% more than integrated selection. The respective figure for ecological selection varies between 15–19% depending on whether the minimum or the maximum cost solutions are considered. Thus, the integrated selection method saves considerable amounts of money relative to the other two selections. Interestingly, penny-pincher selection can provide the same number of species as ecological selection but with lower average costs.

Site Selection by Forest Types

Above we considered species coverage at different levels of opportunity costs. Next we analyze how different forest types are represented in the selected conservation network. Figure 3 presents the proportions of the selected forest types at different levels of opportunity costs for integrated and ecological site selection procedures.

The spruce mire is the dominant forest type in the integrated selection, particularly at low budget levels, because spruce mires have, on average, the lowest forest value (Table 1). The proportions of the other types vary rather widely at low budget levels. Also, mesic forest stands become selected rather early. Above the opportunity costs of about 17,000 US dollars, it is optimal to initially include at least one stand of each type in the network. As funds increase, the share of xeric and herb-rich forests increases, while that of spruce mires decreases.

The shares of forest types are not very sensitive to the forest values (Figures 3a and 3b). We repeated the integrated optimization by using the mean values of forest types (the values are given in Table 1), and these results are very similar to the original integrated selection.[9] As Figure 3b shows, the rank of the forest types is very clear. Spruce mires contribute disproportionately to the cost-efficient biodiversity conservation network. Also, xeric and herb-rich forests have remarkable shares in the conservation network. The mesic forest type is less important. Generally, all forest types are represented in the network, even at a low level of conservation. Thus, the selected network is diverse also in terms of forest habitat types.

Forest type selection looks rather different in the ecological model (Figure 3c). The most important forest types for biodiversity conservation are the herb-rich forests and the spruce mires. Xeric forests also contribute much to the optimal conservation network, with mesic forests clearly showing the lowest contribution. Mesic forests become selected only when about half of the total conservation budget is used. Interestingly, in ecological selection, all forest types

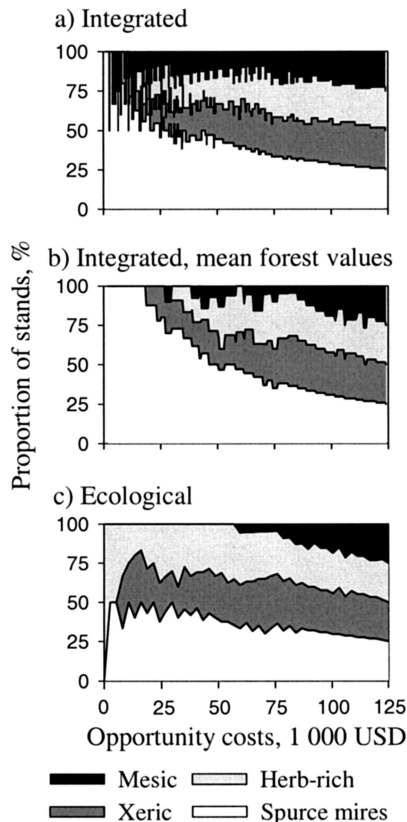


Figure 3. The pattern of the forest types in the selected conservation network, plotted as a function of opportunity costs, picked by (a) integrated selection, (b) integrated selection by using mean forest values of the forest types instead of using separate values for each stand, (c) ecological selection (including the minimum and the maximum cost solutions). The y-axis describes the proportion of protected stands: the number of selected stands of the respective forest type/the number of all selected stands*100.

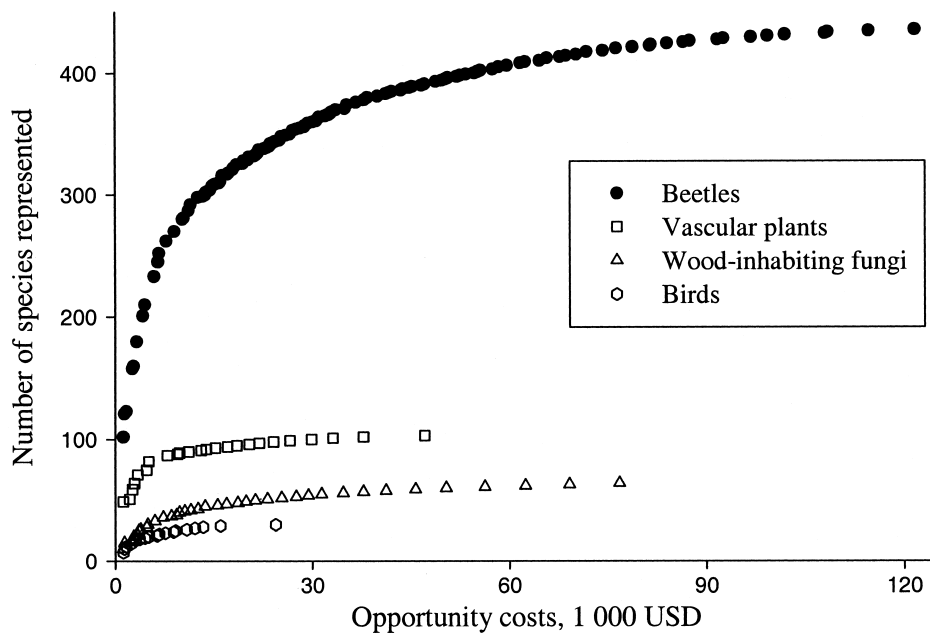


Figure 4. The number of species represented in the selected conservation network, plotted as a function of opportunity costs, picked by an integrated selection using different taxonomic subgroups.

do not become represented in the optimal network until conservation efforts are at a high level.

Taxonomic Groups

Our material includes four taxonomic groups representing a wide array of taxa inhabiting boreal old forests. It appears that our results depend on the selected groups. Obviously, taxa with a relatively high number of species, such as beetles, have a strong effect on the results. However, the size of the taxa is not the only factor contributing to the results. Another crucial factor is the stringency of living requirements of various subgroups. To clarify this aspect, we repeated the integrated optimization separately for different taxa (Figures 4 and 5).

The complete conservation of the taxa can be achieved at different budget levels (Figure 4). We need 31 of 32 stands to include all of the beetles. The same numbers for vascular plants, birds, and wood-inhabiting fungi are 15, 7, and 18, respectively. The opportunity costs of complete representation of subgroups differ in the same manner. It is worth noting that there are less wood-inhabiting fungi species than vascular plants, but complete conservation of fungi still incurs higher costs than the full coverage of vascular plants. Thus, the wood-inhabiting fungi are relatively the most demanding subgroup to cover. Its representation requires many herb-rich forests, which generally have high forest values. Moreover, the complete representation of wood-inhabiting fungi requires many stands, which reflects a large variation in species composition among stands.

The results of the subgroup optimizations show differences in selected forest types among the taxonomic groups (Figure 5). The results for beetles correspond most closely to the original results, because almost 70% of species in the

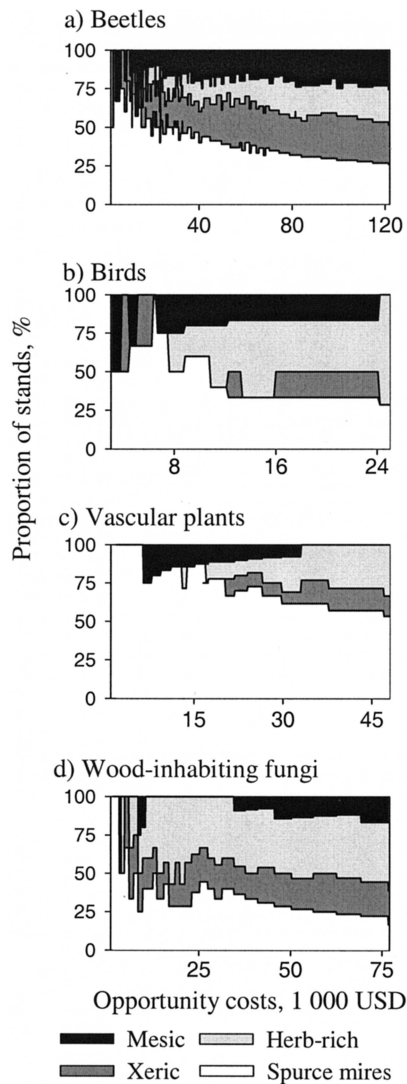


Figure 5. The pattern of the forest types in the selected conservation network, plotted as a function of opportunity costs, picked by an integrated selection using (a) beetles, (b) birds, (c) vascular plants, (d) wood-inhabiting fungi. The y-axis describes the proportion of protected stands: the number of selected stands of the respective forest type/the number of all selected stands*100.

total material are beetles (Figures 3a and 5a). Some differences, however, exist. If only beetles are considered, the herb-rich forest types have a small share, while the mesic heath forest type has a large share in the optimal conservation network relative to the results from optimization with all taxa. The pattern of protected forest types varies considerably in the results for birds (Figure 5b). Obviously, however, spruce mires are the most important forest type for birds. All bird species are eventually represented by selecting only spruce mires and herb-rich forests. For vascular plants, spruce mires are very important at every level of conservation (Figure 5c). In regard to the other forest types, the results are twofold. The mesic type is selected at a small budget level, but it is not needed at all for the complete representation of all vascular plants. When we consider only the wood-inhabiting fungi, the herb-rich forest type is em-

phasized, indicating that the protection of fungi is relatively expensive (Figure 5d). Nevertheless, all forest types are needed for complete conservation.

Species Persistence and Spatial Considerations

Our analysis has omitted many important ecological factors related to the maintenance of biodiversity in boreal old-growth forests. They include issues such as the size and the location of protected stands and an uncertainty of the effects of habitat conservation due to the stochasticity and disturbances (e.g., fires and storms) of natural processes (see Spies and Franklin 1996 for a more detailed discussion about the diversity and maintenance of old-growth forests). In the long run, these issues are closely connected to species survival. Even though a lack of adequate data prevents us from formulating a comprehensive analysis of these issues, we try to tackle this question indirectly. This broader ecological scale can be, at least partly and indirectly, brought into consideration by using the species abundance information in the site selection.

Maximizing just the number of species subject to a budget constraint may result in a network of areas that cannot support species persistence in the long run (Viro-lainen et al. 1999, Rodrigues et al. 2000b). Thus, it is advisable to compare the selection with results from different methods, as Kershaw et al. (1995) suggested.

In the absence of population level information, one way to assess the outcome of a selection of conservation areas is to use surrogate measures for species viability. One commonly used surrogate is species abundance, because the risk of extinction increases with a decreasing population size. Therefore, in area selection, forest stands having high species abundance should be preferred to stands with low abundance. To assess the validity of our previous results, we executed an optimization aiming to maximize the abundance of each species in the selected network subject to a budget constraint.[10] Because representation and persistence goals may conflict, an additional trade-off to consider is whether a network that represents more species with lower persistence is worth more to a decision maker than a network that represents fewer species with higher persistence (Haight et al. 2000).

In our case study, the conflict between species richness and abundance was minor. Total abundance (relative abundance of each species varying between 0 and 1, summed overall species) in the network, selected by using a species richness-based model, was generally almost as high as in the network, where abundance was maximized. The difference in the total abundance between these area selection methods was quite low, 3% on the average. The two methods did not differ noticeably from each other in terms of representation of forest types. In both cases, spruce mires dominated the selected network at low budget levels, and at high budget levels all forest types became selected (see Figure 3 for the original results). Therefore, it seems that the representation approach based on presence-absence data effectively controls also for species abundance. This may stem from the

pattern that species richness often correlates with species abundance (Rosenzweig 1995).

The two methods, however, differed with respect to the cost differences among the three selection models. When abundance was included as a goal in selection, the difference between integrated and ecological selection increased to an average of 25% from 15–19% in the original approach, but the penny-pincher model was almost as cost-effective as the integrated model, the difference being only 3% on average (9% in the original approach).

Maximizing abundance in addition to diversity does not guarantee species persistence. Population viability is a function of population demography, dispersal, and landscape structure (Beissinger and Westphal 1998) further complicated by demographic (e.g., birth and death rates, mating) and environmental (e.g., catastrophes) stochasticity, especially afflicting small populations (Caughley and Gunn 1996). Spatial configuration of protected stands may be an important issue in fragmented landscapes where individual dispersal among habitat patches is limited, and a rule-of-thumb recommendation is to spatially aggregate selected areas whenever possible (Wilson and Willis 1975). Spatially explicit modeling is a way to include spatial goals and population viability into site selection, but more work is needed to make realistic and practical site selection procedures, particularly to meet multispecies conservation objectives (Haight et al. 2000, Cabeza and Moilanen 2001). In boreal forest landscapes, where forest succession continuously alters stand and landscape characteristics, there is not much evidence that fragmentation affects species persistence (Schmiegelow and Mönkkönen 2002). Therefore, habitat availability, not the spatial configuration, is the primary concern (Andrén 1994, Fahrig 1998).

Habitat availability is not, however, a linear function of the total size of protected stands (measured in hectares, for example). Maximizing the spatial extent of protected areas may not be the most efficient way to maintain biodiversity. From a species perspective, a more important aspect is often the availability of certain forest structures, such as decaying wood, and therefore, small stands also may possess large biodiversity values (Martikainen et al. 2000). The complex question of the relevant size distribution of protected stands is, however, outside the focus of this article (see Lomolino 1994 for further discussion about the issue).

Evaluation of the Results

Integrated selection, as demonstrated also in previous studies, is clearly more efficient than the other selection methods (Ando et al. 1998, Balmford et al. 2000, Polasky et al. 2001). The trade-off between the number of species represented and the opportunity costs highlights that it is increasingly expensive to cover the last few species (Montgomery et al. 1994, Haight 1995, Ando et al. 1998, Balmford et al. 2000, Polasky et al. 2001). This finding supports the idea that it may be impossible or impractical to maintain all species within one landscape ecological management area (Sætersdal et al. 1993). Thus, different forest planning areas should have different ecological targets according to

the intrinsic characteristics that define an area's ecological potential (and socioeconomic constraints) (Mykrä and Kurki 1998, Noss 1999).

The spruce mires and herb-rich forests are commonly considered biodiversity "hotspots" in Fennoscandian boreal forests (Hörnberg et al. 1998), so they are given high priority in conservation. This is in line with our results regarding spruce mires. In contrast, herb-rich forests may be low ranking sites using the integrated site selection procedure, because their forest value is, on average, high. This, however, depends on species entities and the amount of turnover among and within forest types. Earlier analyses of the beetle and vascular plant data showed high levels of turnover in species composition both within and among forest types (Similä et al. 2002). This emphasizes the role of spatial interdependence among stands and suggests that plain hotspot-oriented conservation will result in biodiversity loss (Prendergast et al. 1993, Williams et al. 1996, Reid 1998).

According to our results, it seems that xeric forest types are also important targets in the conservation of boreal old forests. In contrast, Stokland (1997) found pine-dominated forest types to extend a relatively small contribution to the protection of old forests in Norway when considering birds. We similarly found that the xeric forest type is quite unimportant regarding bird species coverage, but for beetles, for example, pine heaths comprise a distinctive habitat type rich in species (Similä et al. 2002). Clearly, protection based on a single-species group (indicator approach) can result in inefficient selection and a loss of other species. This shortcoming has been demonstrated in many other studies (Flather et al. 1997, McGeoch 1998).

The following three issues are crucial for the validity and value of these findings. First, the field data can include "random" species, which are not typical of a given habitat type (see Sætersdal et al. 1993 for discussion about rare species). [11] Our data is not likely to include many atypical species. All nonforest bird species were excluded from data analysis. All vascular plants and wood-inhabiting fungi species in our material are truly indigenous to forests. Only the beetle sample may contain some vagrant individuals from other habitats in the surrounding landscape, but excluding such species is problematic because the habitat requirements of beetle species are poorly known. However, in passive sampling studies on animals, very rare species may go unnoticed. Some rare and threatened species were probably not detected even if they were present in some stands. Such species (e.g., many saproxylic beetles) require species-specific surveying techniques to be reliably sampled (Martikainen 2001). In this sort of multispecies approach, such uniquely tailored sampling techniques are not feasible. Nevertheless, the presence of atypical and absence of rare species may not be a serious problem in the present study, because we focused on total species richness treating all species as equally important.

Second, the calculation of forest values by the forestry model involves the problem of assessing uncertain future costs and revenues of timber production, but there is no

reason to assume that the values would be systematically biased among the forest types. Thus, the results are reliable from this perspective. This narrow focus on harvest revenues only neglects the other benefits of the joint products associated with forest protection, such as amenity values (Hartman 1976, Swallow and Wear 1993, Pukkala et al. 1995). Unfortunately, it is not straightforward to assess how the nontimber values are related to harvesting and how the nontimber values will change when a forest stand is designated as a biological reserve (Lewandrowski et al. 1999). For example, in distant areas, the establishment of conservation areas usually increases the amenity values. In contrast, near urban areas, biodiversity and recreation production can conflict with one another because of heavy tramping. In our analysis, it is likely that the other values would not notably impact the relative cost differences of the selection methods or the selection of the site types, because nontimber values may not differ considerably across old-growth forest types, and timber values constitute a large part of the total benefits.

Third, the spatial scale in our study was small, because there were only 32 stands included and they are all located in a spatially restricted landscape of some tens of thousands of hectares. Earlier studies analyzing the cost differences between site selection methods have considered far larger regional scales where land values can vary widely, for example, according to pressures for land development for housing or agriculture (Ando et al. 1998, Balmford et al. 2000, Polasky et al. 2001). Also, species composition varies more at larger spatial scales. Consequently, the cost differences between methods were relatively small in our study as compared with the other analyses. Our study was carried out on a spatial scale considered to be a reasonable planning unit (Montgomery et al. 1999). Therefore, our results may be quite useful estimates for cost savings of the use of the integrated approach in conservation planning.

Conclusions

We analyzed cost-effective properties of three alternative site selection models—the integrated, ecological and penny-pincher models—in terms of the number of species represented, opportunity costs, and selected forest types. Furthermore, we investigated the dependence of the results in relation to taxonomic group considerations and species abundance.

The following new results were derived. First, a cost-efficient integrated selection saves conservation costs on average of about 9–19% compared with the other selection models. Thus, there seems to be great potential for cost savings in applying the integrated approach.[12] Second, the xeric forest types may be an important target for conservation along with spruce mires and herb-rich forests.[13] This indicates that these types may be underrepresented in the current conservation network in the study area. Third, the integrated site selection procedure is a cost-efficient way to select areas for conservation, and we recommend its use in the planning of landscape ecological forest management, because even though our investigation exhibits many area-

specific features, the cost-efficiency property is a general result. Finally, and interestingly, the integrated model seems to result in a more diverse conservation network than the ecological model in terms of selected forest types, and the penny-pincher model seems to be more efficient than the ecological model in our application.

Our analysis contains some simplifying assumptions. Most importantly, we approach biodiversity using species richness, which is just one aspect of biodiversity. We also neglected spatial aspects of forest protection, such as enhanced connectivity or decreased fragmentation of habitats. Relaxing these assumptions in future work would be interesting. Finally, a multispecies approach may not often be feasible in practice because broad inventories of species are expensive. Finding cost-effective surrogate methods for species representation and persistence is desirable, including the use of indicator groups/species or environmental variables.

Endnotes

- [1] There are also other related studies devoted to the economic potential, costs, and benefits of ecological forest management (Montgomery et al. 1994, Haight 1995, Montgomery 1995, Haight and Travis 1997, Bevers and Hof 1999). These studies integrate timber production and species viability for forest management. The viability is based on species population dynamics (growth and dispersal), which is affected by harvesting. Montgomery et al. (1999) also used an approach which integrates species viability and the opportunity costs of conservation, but their study also included other land uses than forest management.
- [2] Note that the conservation level in a cost-effective solution produced by a site selection model may not be optimal in an economic sense. According to economic theory, the optimal level of conservation is achieved when its marginal costs equal the marginal benefits. Unfortunately, the valuation of biodiversity has proven to be a difficult task (Pearce and Moran 1994, Jakobsson and Dragun 1996).
- [3] Our application draws on the typical features of Scandinavian forests. For the readers interested in North American forestry, we would like to recommend related studies by Hof and Raphael (1993), Montgomery et al. (1994), Haight and Travis (1997), Ando et al. (1998), Montgomery et al. (1999), Snyder et al. (1999), Church et al. (2000), Haight et al. (2000), Polasky et al. (2001), Haight et al. (2002), and Ruliffson et al. (2003).
- [4] There are also other measures for species diversity (May 1990, Vane-Wright et al. 1991, Eiswerth and Haney 1992, Faith 1992, Weitzman 1992, Solow et al. 1993, and Humpries et al. 1995).
- [5] The ecological literature uses the word complementarity in this context (May 1990, Vane-Wright et al. 1991). According to economic concepts, it is, however, a matter of substitutability or total independence (Koskela and Ollikainen 2001, Amacher et al. 2004). Taking into account the ecological interdependence among stands is consonant with landscape ecological forest management, because protected stands are not selected in isolation from the surrounding landscape.
- [6] When problems are too large to be solved in a reasonable time by algorithms, which guarantee solution optimality, there are several heuristic practices available (Csuti et al. 1997, Pressey et al. 1997). However, a non-optimal solution, probably produced by a heuristic practice, can be costly for a decision-maker. Moreover, it may not be so easy to find intuitively good heuristic algorithms for the complex problem at hand (see Rodrigues et al. 2000a).
- [7] The ecological model does not explicitly include opportunity costs, but the costs can be calculated, of course, after we know which stands are selected. Respectively, the penny-pincher model does not explicitly include species, but the species representation can also be seen when the selected stands are known.
- [8] The curve for the worst possible selections is not smooth, but at the lower bound, the number of species represented is very sensitive to opportunity costs jumping up and down. Because of this feature, the lower bound was calculated using a heuristic procedure similar to a greedy algorithm (see Church et al. 1996 and references therein for a more detailed description of the greedy style heuristics).

- [9] Note, however, that the share of mesic forest type is smaller in Figure 3b than in Figure 3a. This difference is caused by one mesic forest stand, which has exceptionally low forest value compared with the other mesic stands.
- [10] The aim was to maximize

$$\sum_{i=1}^m \left(\sum_{j=1}^n \frac{a_{ij}}{a_{is}} x_j \right),$$

where a_{ij} denotes species' i abundance in the stand j and a_{is} species' i abundance summed over all 32 stands. Otherwise, the notation is similar to the previous models.

- [11] If a species can survive in habitat types other than old-growth forest, it is very restrictive to assume that there are only two management options (clear cutting or protection) and to value the biodiversity of these other forests at zero. Moreover, a generalist species will not need protection at all, as it can manage in different habitats. We should exclude these species from the total species list. It is not straightforward, however, to classify species according to habitat types, because the biology of many species is not understood well enough to identify what the habitat requirements of a given species are. One possibility is to include this uncertainty into the site selection model (Haight et al. 2000, Polasky et al. 2000, Williams and Araújo 2000).
- [12] In order to illustrate the level of the absolute saving potential, we may value the current conserved state-owned Finnish forests (479,834 ha) by using our mean forest values of the forest types. According to this valuation and using the average saving potential percentages (9–19%), the economic loss of inefficient conservation may be about 160–320 million US dollars.
- [13] The proportion of xeric heath forests of the current conservation network area is less than 11%, although it is a rather common forest type in the region (Ministry of the Environment 1996). Herb-rich and spruce mires forest types have currently been given a high conservation priority according to the Finnish forestry legislation. Thus, we may assume that in regard to these forest types, the Finnish conservation policy is going in the right direction.

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