

Alternative targets and economic efficiency of selecting protected areas for biodiversity conservation in boreal forest

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Abstract We examine the relative merits of alternative forest biodiversity targets, which give different weights to species according to their conservation status and abundance. A site selection framework is used for choosing the habitat-protection strategy that maximizes biodiversity subject to an upper bound on funding with six alternative conservation goals. By using Finnish data on old-growth forests, we found that alternative conservation goals yield different benefit-cost tradeoffs. Goals relying on complementarity between protected stands result in great marginal costs at a high conservation level. Therefore, under these conditions it may not be economically efficient to establish a large conservation network to protect all species in a given area. In contrast, a large conservation network is more likely to be justified when the habitat-protection strategy focuses on species abundance. The trade-offs between alternative objectives are explicitly measured by incrementally varying the weights given to the species. We found that the targets for all species representation and species abundance can largely be met simultaneously. Protecting red-listed species reduces overall species coverage and species abundance particularly at low budget levels.

Keywords Biodiversity · Forest conservation · Forest management · Reserve site selection · Species representation

JEL Q20 · Q23 · Q57

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1 Introduction

In selecting reserves for biodiversity maintenance several alternative strategies addressing a range of interests and objectives can be used to guide decision makers towards choices society would be willing to accept (Williams and ReVelle 2002). In particular, multiple conservation objects reflect different attributes of biodiversity. Biodiversity has multiple facets and therefore explicit goals for conservation can be defined and measured at different levels of biological hierarchy (Noss 1990). There also are conflicting interests between benefits from biodiversity services and benefits from other land use purposes, such as forestry. To shed light on expected outcomes and trade-offs, we compare alternative site selection models aimed at efficient forest biodiversity maintenance.

Previous site selection studies have examined many alternative criteria for site selection (see Cabeza and Moilanen 2001; ReVelle et al. 2002; Rodrigues and Gaston 2002 for summaries of published studies). We will address four important aspects that have rarely been elaborated upon in previous studies.¹ First, most formulations include only a single objective, and therefore and unlike this paper these studies do not address the issue of how to meet several objects simultaneously and neither do they provide information on the efficient trade-offs between multiple conservation goals (but see Arthur et al. 2004).

Second, we extend the analysis to cover also species abundance, which can be considered a surrogate measure for species persistence because population extinction probability is an inverse function of population size (Hanski 1999). Species persistence has received much attention in the conservation literature but only lately has it been incorporated into the site selection literature (Church et al. 2000; Haight et al. 2000; Polasky et al. 2000; Rodrigues et al. 2000b, c; Williams and Araújo 2000; Haight et al. 2002; Lichtenstein and Montgomery 2003).

Third, most site selection studies assume that the costs of protecting sites of the same size are identical. This unjustified assumption may severely impede cost-effective conservation planning (Ando et al. 1998; Juutinen et al. 2004). Our work is based on heterogeneous site values.

Finally, in many site selection studies the chosen spatial scale may not be relevant for decision making in practice, and therefore the studies rarely provide useful guidelines for land managers. The spatial scale of the studies has often been much larger than the practical planning region in forest management and their results can be used to identify regions towards which conservation efforts should be aimed but not to identify the exact location of conservation areas (see e.g., Ando et al. 1998; Balmford et al. 2000).² Many earlier studies have also focused on arbitrary parcels of land such as grids (e.g., Cabeza et al. 2004) or hexagonal cells (Polasky et al. 2001; Arthur et al. 2004) to exemplify the outcomes of alternative site selection procedures. Even then, the size of the arbitrary parcels has often been much larger than a practical management unit, because the focus has been on methodology rather than

¹ Another important shortcoming of previous site selection studies is that they are typically static (see Nalle et al. 2004). Ideally one should use a dynamic approach to analyze the problem of biodiversity conservation, in particular, when forests are considered. Because this approach would entail large data requirements and there is still a lack of knowledge about several aspects of biodiversity maintenance, we adopt a static approach.

² In Fennoscandia, the average size of a forest stand (i.e., operative unit) is less than 10 ha. A landscape level forestry plan covers typically 10,000–100,000 ha.

application (Arthur et al. 2004). Emphasising the results of applications we consider a spatial scale which is relevant for actual decision making. Our data include 32 old-growth stands (a forest stand is the basic management unit) representing the whole spectrum of forest type variation in NE Finland within two landscape ecological forest planning areas (both covering about 40,000 ha).

We focus on species richness, which has been shown to be a good proxy for overall biodiversity reflecting also other aspects such as functional and genetic diversity, for example (Gaston 1996). However, species richness includes several aspects. One option is to favour threatened, endangered or rare species to identify the most valuable conservation areas, because these species need protection most urgently. Another possibility is to focus on species representativeness: reserves should contain sites that ideally represent the entire range of ecological variation within a given geographical area (Faith and Walker 1996). The third important aspect is species viability. Site selection based solely on representative rules does not explicitly incorporate information on species survival in the long run (Cabeza and Moilanen 2001). The ultimate goal of conservation is, however, to ensure species population persistence.

In this paper we ask how these alternative aspects of species richness affect ecological features and economic properties of a conservation area network when the site selection is made subject to a binding budget constraint. For that purpose we develop several budget-constrained site selection models. The models differ in terms of their specific goals whereby species are weighted according to three criteria: representation, conservation status, and abundance. We compare and discuss the pros and cons of achieving these alternative goals. More precisely, we first highlight the trade-offs between ecological and economic objectives within each conservation goal. It is important to identify if there is a range over which the marginal costs increase dramatically, because over this range one needs to measure the benefits of species conservation very accurately. After that we examine the trade-offs between conservation goals to identify in which circumstances can the goals be achieved simultaneously and when there are conflicts between them.

2 Models and empirical data

2.1 Alternative site selection goals

We define the alternative conservation goals in a model incorporating a binding budget constraint for site selection. This cost-effective solution is intended to cover as much biological diversity as possible by selecting reserve sites with a given budget since our conservation resources are limited. If a stand is protected, it causes opportunity costs due to the lost harvesting revenues, for example. These losses can not exceed the available budget for conservation.

We first formulate a general, multi-goal integer linear function, from which our specific models can be generated as special cases. We incorporate into the objective function both species representation and species abundance. Species representation is measured by the number of species in the selected conservation network.³ Species

³ It is possible to use also other diversity measures than just a weighted function of species numbers, such as measures of species genetic or taxonomic difference. For reviews of these approaches see, for example, Pearce and Moran (1994) and Gaston (1996).

abundance reflects species persistence, because the species with high abundance within the selected network is more likely to survive in the long run than the species with low abundance. We denote a species by h and weights for species representation and abundance by ω_h^1 and ω^2 , respectively. The former weight may differ between species reflecting their conservation status. The latter weight scales the abundances of species in relation to species representation depending on how much we value these aspects. By varying the weight parameters one can analyse the trade-offs between the alternative aspects of species conservation.

Formally, the objective function (1) is maximized subject to constraints (2)–(5):

$$\max_{x_j, z_h} \sum_{h=1}^k \left(\omega_h^1 z_h + \omega^2 \frac{\sum_{j=1}^n A_{hj} x_j}{T_h} \right) \tag{1}$$

subject to

$$\sum_{j \in N_h} x_j \geq z_h, \quad h = 1, \dots, k \tag{2}$$

$$\sum_{j=1}^n V_j x_j \leq B \tag{3}$$

$$z_h = (0, 1), \quad h = 1, \dots, k \tag{4}$$

$$x_j = (0, 1), \quad j = 1, \dots, n \tag{5}$$

where

ω_h^1 = weight attached to the presence of species h ($h = 1, \dots, k$),

ω^2 = weight attached to species abundance,

$x_j = 1$ if stand j is selected and 0 otherwise ($j = 1, \dots, n$),

$z_h = 1$ if species h is contained by at least one of the selected stands and otherwise 0,

A_{hj} = abundance of species h in stand j ,

T_h = maximum potential abundance in the h th species obtainable by protecting all stands,

N_h = subset of candidate reserve stands that contains species h ,

B = budget allowable for reserve network,

V_j = opportunity costs of establishing a reserve stand j .

The first part of the objective function (1) is a weighted sum of species presence and the second part is a weighted sum of species abundance in the selected conservation network. Abundance of each species is considered in relative terms, i.e., dividing the sum of abundances across selected sites by the maximum total abundance. More precisely, we define $T_h = \sum_{t=1}^p \sum_{j=1}^n A_{thj} x_{tj}, \forall h$, where A_{thj} is the maximum abundance A_{hj} across habitat types t for each stand j and species h , and there are p habitat types. Parameter x_{tj} denotes the stand j belonging to habitat type t . Thus, T_h describes the maximum potential abundance in the h th species that could be obtained by protecting all the stands. Species are often specialized with respect to a certain habitat type and therefore considerable differences may exist in species abundance among habitats (cf., Hof and Raphael 1993). Summing over habitat types

reflects this variation in the maximum abundances and for a given species describes the potential maximum abundance within a network of stands.⁴ As a result, the relative abundances of species h vary from 0 to 1. The advantage of this approach is that it treats species equally irrespective of their actual abundance. For example, protecting 500 individuals of one species may contribute just as much to its persistence likelihood as protecting 100 individuals of some other species contributes to this other species' persistence depending on the characteristic population sizes of the species.

The constraint set (2) ensures that species h is counted as being represented when at least one of the stands in which it appears is selected for the network. Equation (3) is the budget constraint assuring that the opportunity costs do not exceed the resources allowable for conservation network. By varying the budget one can trace the trade-offs between chosen biodiversity metrics and opportunity costs. The constraint sets (4) and (5) simply indicate that the choice variables are binary, and there are k species and n stands. Thus, the stands are either protected or harvested, and the species are represented in their entirety or not at all.⁵

We make the analysis in two phases. First we consider the alternative objectives separately, i.e., we analyse the trade-offs between ecological benefits and economic costs for each objective. Second, we reveal the trade-offs among ecological objectives. For the first phase we formulate three single-objective models and for the second phase three two-objective models from Eq. (1) as follows.

2.1.1 SR-model: species richness

This model focuses solely on species representation in the spirit of the classical Maximum Covering Location Problem (Church and ReVelle 1974).⁶ Therefore, we set ω^2 to zero so that the abundance in species is not considered and ω_h^1 to one to denote that all species are assumed to have equal importance. The SR-model follows the complementarity principle, i.e., that sites are selected into the network based on how much their inclusion enhances the total species richness of the network (May 1990; Vane-Wright 1991). Thus in order to maximize species richness in the network,

⁴ In other words, we implicitly assume that species persistence is a linear function of abundance. It is possible to use also a logistic functional form (e.g., Hof and Raphael 1993; Montgomery et al. 1994; Haigh 1995; Montgomery et al. 1999), but that would require nonlinear programming, which does not guarantee that the solution is optimal. Moreover, it is not straightforward to calibrate the logistic functions for multiple species.

⁵ This formulation is based on several previous studies. The weights are attached to species as suggested by Polasky et al. (2001) (see also Church et al. 2000; Rodrigues et al. 2000b). Church et al. (1996) proposed an additive objective function for assigning weights to species. Hof and Raphael (1993) used quite a similar approach as us regarding the species abundance in the context of timber scheduling problem (see also Bevers et al. 1995). Moreover, they presented a multiplicative objective function (joint viability) instead of additive form. Also Montgomery et al. (1999) and Polasky et al. (2001) presented a multiplicative nonlinear approach based on species abundance. Rodrigues et al. (2000a) introduced a linear site covering problem using information on species abundance.

⁶ An objective based on global presence/absence can be justified on the basis that conserving the species someplace is necessary to preserve the genetic information and evolutionary potential of the species (Polasky et al. 2001). However, in a same manner one can state that an essential prerequisite for persistence is that biological diversity is appropriately represented in the local network in the first place (see Rodrigues et al. 2000a and references therein).

it is optimal to select stands that have (almost) non-overlapping representation of species.⁷

2.1.2 RL-model: red-listed species

In this model we give weights to the species (ω_h^1) according to their threatened status following the IUCN criteria (Rassi et al. 2001). The weight for red-listed species is one ($\omega_{RL}^1 = 1$) and the weight for other species, namely least concern species, is zero ($\omega_{LC}^1 = 0$). Moreover, we set ω^2 to zero neglecting the abundance in species. In other words, the RL-model maximizes the number of red-listed species.

2.1.3 AB-model: species abundance

In the AB-model, we set ω_h^1 to zero so that the number of species is not considered and ω^2 to one to denote that sites are selected in the conservation network according to the relative abundance of the species.

2.1.4 SR & RL-model: species richness and red-listed species

This model maximizes the number of species, but red-listed species are given a higher weight than other species. For that purpose we set ω^2 to zero so that the abundance in species is not considered. The weight ω_{LC}^1 is set to unity and ω_{RL}^1 takes four alternative values 1, 5, 10 and 100, allowing us to prefer red-listed species to other species.

2.1.5 SR & AB-model: species richness and species abundance

This model takes simultaneously into account species richness and species abundance in the site selection. Therefore, we set ω_h^1 to one and varied ω^2 between 1 and 100 to emphasize the importance of species abundance.

2.1.6 RL & AB-model: red-listed species and species abundance

In this model we set ω_{LC}^1 to zero and ω^2 to one. The weight ω_{RL}^1 is allowed to vary between 1 and 100 to increase the importance of red-listed species in the site selection.

We first used the single-objective models by varying the budget constraint. We then used the multi-objective models by varying the budget and the weight parameters for different objectives. However, it is not simple to present the results as we have several objectives. Therefore, we used each single-objective model in turn as a benchmark against which to compare the other models. This procedure ensures that all possible relationships between the objectives are considered but may produce some redundancy in the results. We first present these results in terms of cost differences between the objectives and then explicitly consider the trade-offs in

⁷ It is possible to add a restriction into this model which excludes that a species is accounted as represented when its abundance is less than a given threshold level (cf., Haigh et al. 2000; see also Polasky et al. 2000). The ecological knowledge regarding species is incomplete, however, so it is difficult to define accurate thresholds for species abundance.

ecological terms. We used branch-and-bound algorithm and commercial spreadsheet software to solve our linear integer problems (Lindo Systems 2000).

2.2 Data and calibration

The database includes 32 semi-natural old-growth forest stands located at the transition zone of the middle and northern boreal zones in northern Finland (Fig. 1). Drawing on their age and forest structure these stands were pre-selected as the best targets to complement the existing old forest conservation network in the region. We sampled four forest site types, each of which includes eight stands: 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 forests (*Geranium-Dryopteris* or *Vacciniuin-Myrtillus/Geranium-Dryopteris* type). These site types cover in practice the whole gradient of forests in this 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 in order to yield general results. The data consists of a total of 632 species including 103 vascular plants, 30 birds, 64 wood-inhabiting fungi, and 435 beetles. Abundance data for beetles and birds consists of the number of individuals or

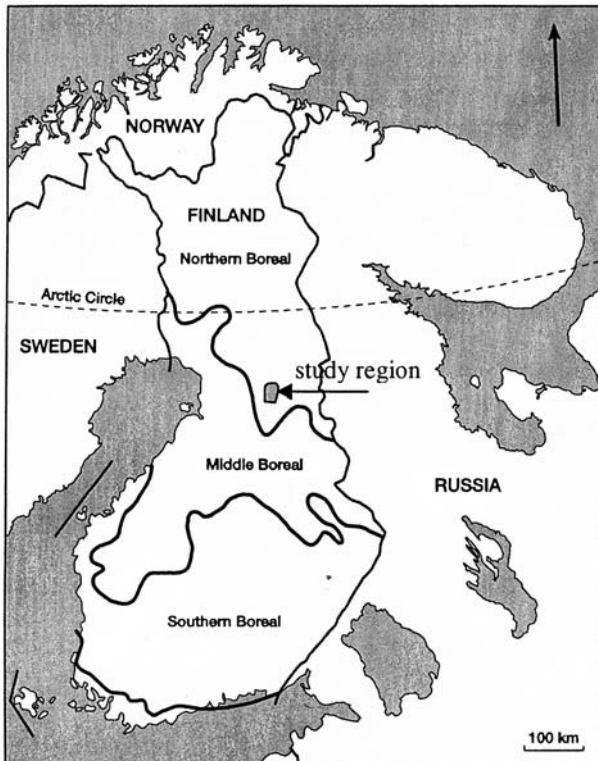


Fig. 1 Location of the study areas. The vegetation zones are based on Kalliola (1973)

breeding pairs, respectively, in the samples. The abundance of wood-inhabiting fungi is estimated by the number of fruiting bodies. For vascular plants, the percentage of coverage of each species within the sampling area was estimated. (See Similä et al. 2006 for a more detailed description of the study sites and sampling method.)

The data contain 18 red-listed species: 2 birds, 8 wood-inhabiting fungi and 8 beetles (Rassi et al. 2001; Similä et al. 2006). These are divided equally into vulnerable (VU) and near-threatened species (NT; see IUCN 1994 for a definition of Red List categories). Other species belong to the category of least concern (LC).

We calculated the maximum potential abundances (T_h) of species according to the highest number of individuals (beetles, birds, wood-inhabiting fungi) and the highest area cover (vascular plants) in each forest type. The database includes 160 unique species, i.e., present in one stand only. Thus, if a unique species is represented in the selected network, its relative abundance is 0.125, since the database consists of 8 stands for each habitat type. The species found in several stands may have lower figures if their number of individuals is relatively minor in the protected stands. The maximum value of relative abundance is always clearly less than one, because there are rather large differences in species abundance between stands within each forest type in the sample.

A Finnish forestry planning model, called MELA, was used to calculate the site value for each stand (Siitonen et al. 1996). The site value represents the opportunity costs of protecting a given stand. MELA calculates the maximum net present value of a forest by approximating Faustmann's formula, so the site value consists of both timber and land values. More precisely, MELA first simulates the forest growths and feasible management schedules for given stands and then uses an optimization procedure to find the best schedule for the chosen objective which is maximizing future net revenues for each stand in this case. As our data consist of old-growth stands, the best timber management schedule always includes an immediate clear-cutting. The data on detailed stand characteristics for the forest value calculations were taken from Metsähallitus (Finnish Forest and Park Service) forestry files (Metsähallitus, unpublished data). 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 (€/ha) and treat stands as having equal sizes in the optimization (see Appendix).

3 Empirical results

3.1 Biodiversity conservation under single ecological objective

Selecting stands cost-effectively into the conservation network depends on two aspects: the contribution a stand provides to biodiversity conservation and the opportunity costs of protecting a stand. Therefore, to support the interpretation of the results we report the opportunity costs of considered stands in the Appendix. Recall that the opportunity costs measure the site value of each stand under efficient commercial forest management. A contribution a given stand provides to the biodiversity depends on the specific conservation goal and the features of other selected stands as will be examined next.

Figure 2 represents the level of biodiversity conservation in the selected conservation network for the chosen site selection models using relative metrics (actual

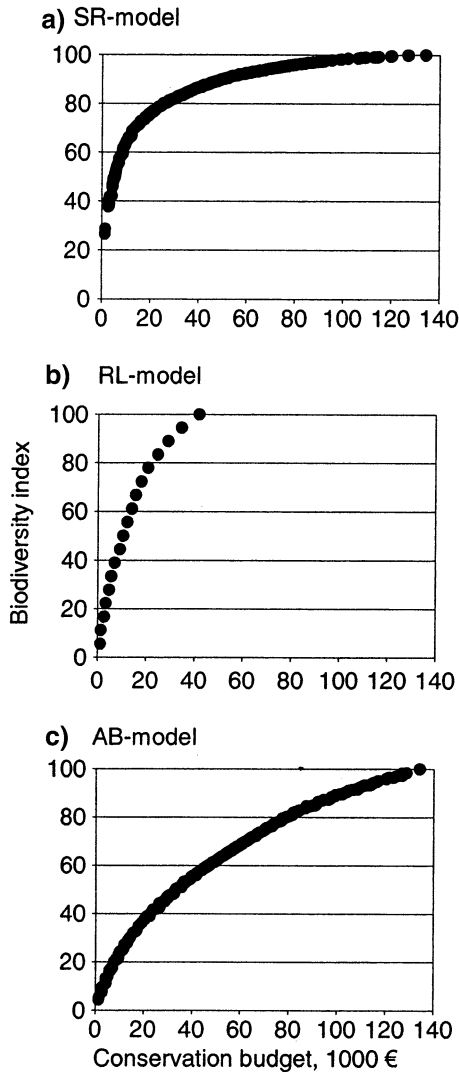


Fig. 2 The value of biodiversity index in the selected conservation network, plotted as a function of conservation budget, for the single-objective procedures. The biodiversity index is defined so that it takes a maximum value of 100 in each model when all the stands are protected

conservation level/conservation level when all stands are protected) for easy comparison. We plot this biodiversity measure as a function of the size of the conservation budget. The slope of this target curve reflects inversely the marginal costs of biodiversity conservation. It is obvious that the size of conservation budget affects the achievement of the ecological goals.

The relationship between the number of species represented and the conservation budget has some interesting properties (Fig. 2a). When a low level of funds is devoted to conservation, the optimal species coverage of the SR-model is steeply increasing along with the number of stands included in the network. The budget size

of € 16,000 proved to be a critical threshold value which divided the conservation strategy into two regimes.⁸ 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, since 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 to very few stands. These stands have, unsurprisingly, rather high timber values as the cheap ones were selected earlier. 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.

In the RL-model the focus is on red-listed species (Fig. 2b). When protected areas are selected by using the RL-model, the target function is rather steep indicating that it is typically more expensive to protect a red-listed species than a species belonging to the category of least concern. As there are only 18 red-listed species half of which are unique, the set of alternatives available for site selection in maximizing the number of red-listed species is quite small. Therefore, we are unlikely to find many low-cost stands harbouring red-list species. Consequently, about € 40,000 is needed to cover all red-listed species. The target function in the RL-model is only weakly concave. Hence, the marginal costs of protecting red-listed species rise rather steadily. Importantly, however, the rise of marginal costs would be very sharp also if red-listed species and other species were considered simultaneously in the site selection and red-listed species were given a high priority. In this case protecting one red-listed species yields the same benefits as protecting one hundred other species, for example, increasing the concavity of the target function.

The target function in the AB-model rises more slowly than in the SR- or RL-model (cf. Fig. 2a, b and c). This indicates that species abundance is rather evenly distributed among stands. Therefore, when the aim is to maximize the relative abundance of the species, the net benefits from conservation of alternative stands are rather equal. Moreover, one needs a large budget to achieve a high level of protection in terms of species abundance. The marginal costs rise quite steadily with increasing species abundance as the target function is only weakly concave.

It is obvious that the different objectives may result in different conservation networks, i.e., the same stands and habitat types are not protected. To consider this aspect in detail we first classify the potential stands denoted by squares according to the four habitat types, each of which includes eight stands, and then number the stands in each habitat type from 1 to 8 (Fig. 3). This order does not have any spatial interpretation, because the stands are not located closely side by side in the study region. The numbers just identify the stands (see Appendix). The protected stands are marked with grey colour. Moreover, the protected stands are showed in two columns according to the chosen budget levels and horizontally in three panels describing alternative selection methods.

⁸ We can expect that similar thresholds will emerge in many applications; its precise size will, of course, depend on the data in question. Hence, our finding has an important general message.

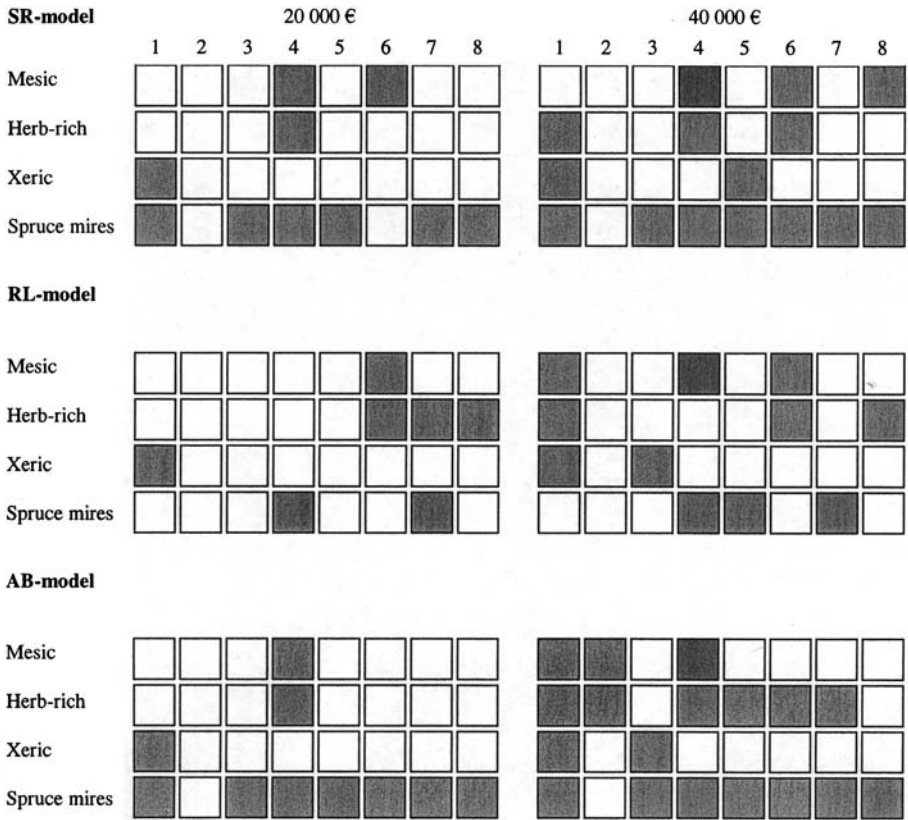


Fig. 3 Protected stands (gray squares) and habitat types picked by using single-objective models with different budget levels

At low budget levels, the selected conservation network is almost the same when stands are picked by the SR- or AB-model (Fig. 3). Spruce mires are the dominating forest type in these selections. As the budget increases from € 20,000 to € 40,000, the share of the herb-rich forest type in the selected conservation network is larger when using the AB-model than using the SR-model. Nevertheless, these selections are still quite similar as 12 of 15 protected stands picked by the SR-model are also selected when using the AB-model. The outcome of the RL-model differs clearly from the other two models. With the € 20,000 budget, the herb-rich forest type is dominating in the selection based on maximizing the number of red-listed species. At the € 40,000 budget level all forests types have almost an equal share in the selected conservation network revealing that red-listed species are found in every forest type.

It also interesting to compare the number of selected stands between the models at a given budget level (Fig. 3). At a low budget level the SR- and AB-model protect equal numbers of stands, though the chosen stands are not exactly the same. At the € 40,000 level, however, the number of stands is larger when using the AB-model than using the SR-model. Thus, cheaper stands are protected when the AB-model is used compared with the SR-model at the € 40,000 budget level. The number of

stands is the lowest when the RL-model is used indicating that relatively expensive stands are needed to protect red-listed species.

3.2 Biodiversity conservation under multiple ecological objectives

We next examine the trade-offs between different ecological objectives. First, consider how protecting the abundance of species and protecting the number of red-listed species impacts upon the coverage of all species. For that purpose we depict conservation costs as a function of the number of species represented in the selected conservation network picked by alternative conservation strategies (Fig. 4). There are two ways of interpreting these outcomes. The vertical distance between the costs curves measures the cost of increasing species abundance or the number of red-listed species, while maintaining the level of the number of all species. The horizontal distance measures the trade-off between the alternative objectives in terms of the number of species at a given cost level (size of the budget).

It seems that there is only a small conflict between maximizing the number of species and species abundance (Fig. 4, left panel). These strategies result in similar cost levels under a given number of species represented. The cost differences are minor even if the sites are selected using single-objective SR- or AB-models instead of using multi-objective SR & AB-model (the bottommost results of left panel in Fig. 4). The AB-model generates on average 4.5% higher costs than the SR-model when the number of species is used as a benchmark in the comparison. Recall that the number of protected stands is larger in the AB-model than in the SR-model with a given budget level (Fig. 3). Thus, the number of species in the selected conservation network picked by the AB-model is quite high, most likely because of the positive association between area (number of stands) and species even though the complementarity between selected stands may not be the best possible.

The conflict is more evident with respect to maximizing the number of all species and the number of red-listed species (Fig. 4, right panel). The cost difference between these objectives is large when areas are selected by using single-objective SR- and RL-models (the bottommost results of right panel in Fig. 4) except when only a few stands are selected in the conservation network. This exception indicates that some red-listed species are found in stands having low opportunity costs and these stands supplement each other in terms of the number of species. The cost difference is minor with a low weight for red-listed species and it is obvious only when most of the species are represented in the selected conservation network. This means that to cover all red-listed species by the network almost all other species needs to be protected. However, increasing the weight for red-listed species increases the cost difference and the difference becomes marked also at a lower number of species.

The pattern of trade-offs between the ecological objectives does not change much if we use species abundance as a benchmark instead of using the number of species (cf. Figs. 4 and 5). It seems, however, that almost the maximum species abundance can be achieved by using the SR & AB-model when the weight for abundance is set at a value of 10 or larger. Another interesting outcome is that the average cost difference between the SR-model and AB-model is larger when the benchmark is species abundance (6.1%) than when the number of species is used as a benchmark (4.5%). The trade-offs between species abundance and red-listed species are very similar to the trade-offs between species richness and red-listed species.

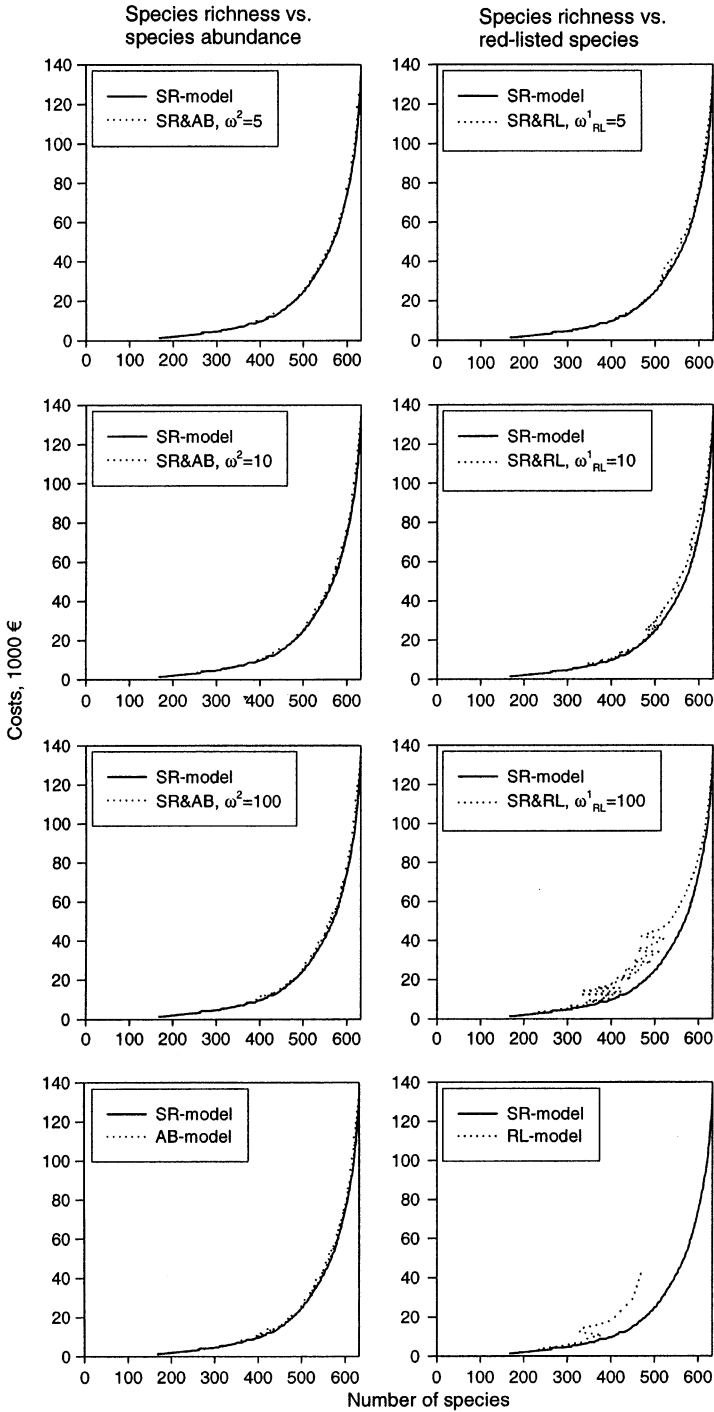


Fig. 4 Costs occurred at given levels of number of species represented in the selected conservation network under alternative conservation strategies

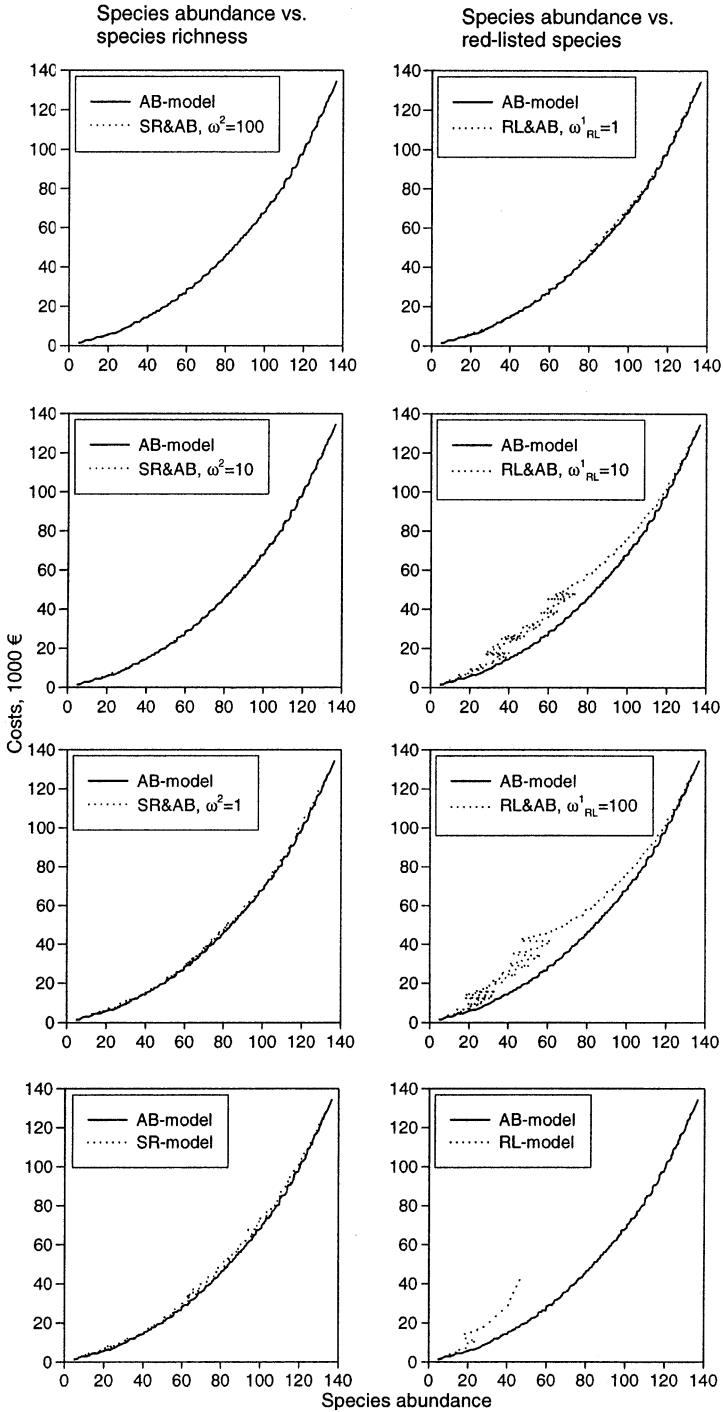


Fig. 5 Costs occurred at given levels of species abundance in the selected conservation network under alternative conservation strategies

Using red-listed species as a benchmark in analysing trade-offs between ecological objectives shows clearly how the objectives conflict (Fig. 6). The cost differences are very large when single-objective models are compared (the bottommost results in Fig. 6). The differences narrow as red-listed species are preferred to other species in multi-objective models, but quite a large weight for red-listed species is required before the cost difference becomes small. One can note that the cost differences are larger when red-listed species are compared with species richness than when red-listed species are compared with species abundance with a given weight for red-listed species (compare left and right panels in Fig. 6). This is feature simply reflects the absolute values of the number of species and species abundance. The former is bigger than the latter. For example, the maximum values for the number of species and species abundance are 632 and 136.7, respectively. Thus, roughly speaking a weight of $\omega_{RL}^1 = 10$ used in the SR & RL-model equals a weight of $\omega_{RL}^1 = 2.2$ used in RL & AB-model.

The above outcomes reveal that the strongest conflict is between protecting red-listed species and the other two objectives. Next we examine this feature in more detail. For that purpose we plot the number of species represented in the selected conservation network as a function of the number of red-listed species at different budget levels (Fig. 7).

At all budget levels the conflict is evident between red-listed species and total species richness, so that maximizing either one of them reduces the other objective (Fig. 7). An optimal solution is likely in a range where both objectives can be achieved at a relatively low trade-off. For example, at € 40,000 budget level increasing the coverage of red-listed species from 16 to 17 reduces total species richness only by 3% from 538 species to 522 species. Thus, an appropriate weight for red-listed species could be about 10–20 to one indicating that the benefits from protecting one red-listed species equals to the benefits from protecting 10–20 least concerned species.

4 Discussion

We examined alternative conservation targets representing different aspects of species protection in an economic context by using six budget-constrained site selection models. We found that the trade-off between conservation costs and biodiversity value in terms of selected conservation targets differs considerably between the alternative selection methods as well as the marginal costs of conservation. More precisely, while the marginal costs are increasing in all models, the increase is the sharpest in models that take into account the complementarity between forest stands in terms of species richness. This confirms the results in Ando et al. (1998), Balmford et al. (2000), and Polasky et al. (2001). Our finding supports the hypothesis that it is likely to be economically inefficient to protect all the species in every region or planning area, but different planning areas should have different ecological targets in practice (Sætersdal et al. 1993; Mykrä and Kurki 1999; Noss 1999).

Conservation based on threatened or rare species may not protect many other species when reserves are selected by using hot spot or scoring approaches (Pressey and Nicholls 1989; Prendergast et al. 1993; Williams et al. 1996; Kerr 1996). According to our results the number of uncovered species is, however, minor if the

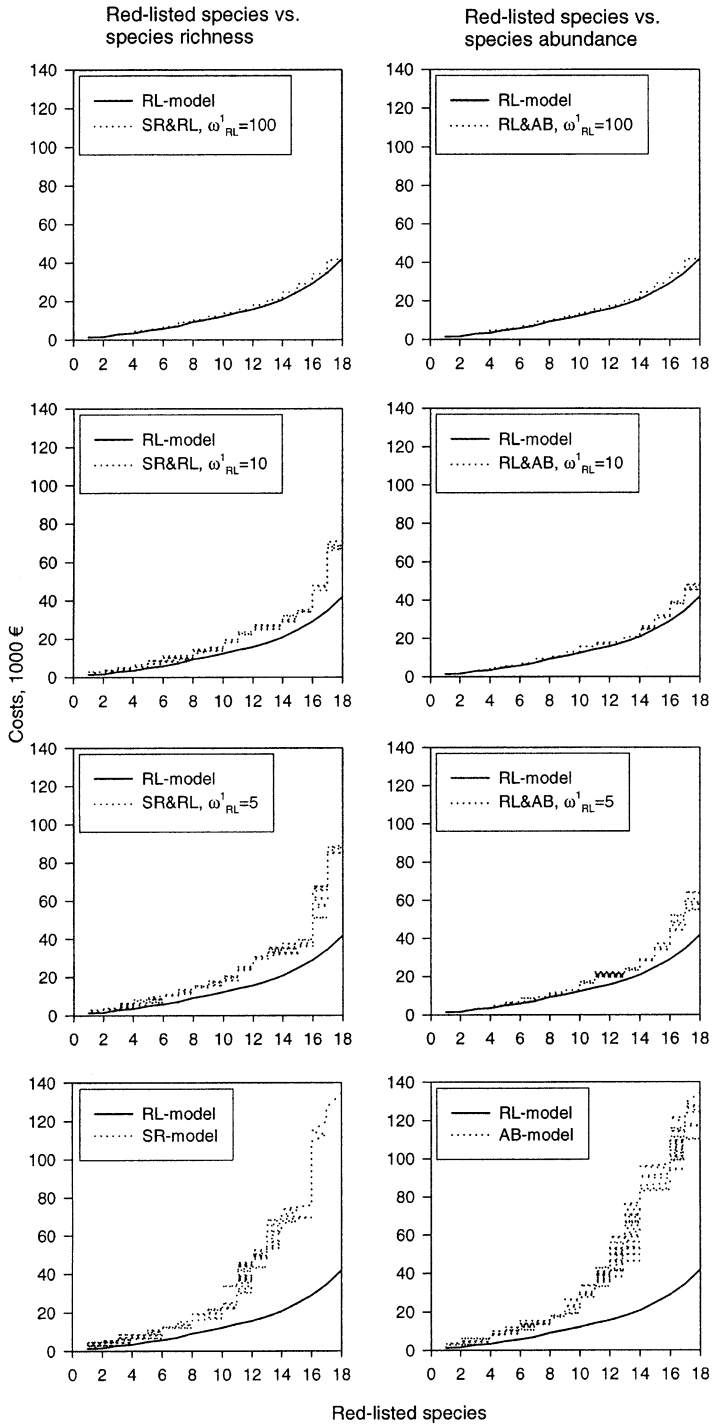


Fig. 6 Costs occurred at given levels of number of red-listed species represented in the selected conservation network under alternative conservation strategies

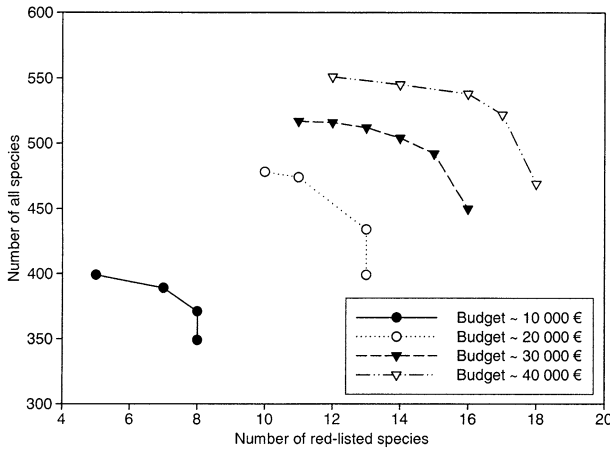


Fig. 7 Feasible trade-offs between number of all species and number of red-listed species with a given budget

protected areas are selected by using a method which takes into account the complementarity between areas and prefers to some extent the red-listed species to the other species. Also Arthur et al. (2004) found that with larger budgets both a strategy to cover as many species as possible and a strategy focused on protecting endangered species will tend to converge on the same priority areas for conservation. Thus, it may be reasonable to favour threatened species in setting targets for boreal forest conservation provided that protected areas complement each other, for example, in terms of the number of species. These species need conservation the most urgently.⁹

Two conflicting features emerged from our analysis. First, if red-listed species are given a high weight in conservation, it is likely optimal to protect most of the species, but not all, because the marginal cost of conservation is increasing strongly (and marginal benefits are likely decreasing) at a high level of conservation. From the practical viewpoint this implies that the conservation may end up at a level where all red-listed species are protected, but it is difficult to enlarge conservation to protect other species. It is presumably difficult to get general acceptance for environmental policy, which requires a lot of funds but does not seem to result in remarkable improvements. Second, because total abundance was a monotonically increasing function of the conservation budget, it is apparent that the size of the conservation network is an important factor for species persistence. Many earlier studies support this result (Margules et al. 1988; Rodrigues et al. 2000b, c; Williams and Araújo 2000). Consequently, when the objective is to maximize species abundance, the marginal benefits can be considerable also at a high level of conservation, and an incentive for an extensive conservation network may exist. These findings emphasize that it is important to examine how the benefits of biodiversity services depend on these phenomena.

⁹ Some earlier studies considering tropical habitats (neglecting the economic aspect) have not yielded similar results. For example, Kersaw et al. 1995 found (by using data on Afrotropical antelopes) that in sub-Saharan Africa conservation emphasizing threatened species covered only about 76% of species that were covered according to species richness-based selection (see also Hacker et al. 1998).

To conclude, the budget for conservation is usually determined through a political process. The size of this budget reflects the size of the conservation network. Our results indicate that if the budget is very low it may be reasonable first to make a pre-selection using available ecological information to determine the potential targets and then select the cheapest areas into the conservation network within the budget. This feature emerges from the species-area-relationship, i.e., that species richness is a strongly concave function of area (see e.g., Rosenzweig 1995), and may indicate that the old-growth boreal forests are relatively uniform in terms of biodiversity contribution. If the budget exceeds a case-specific threshold value, then it is important to take into account the complementarity between stands in the site selection. This is likely to require specific field inventories in practice. However, at this budget level it may be reasonable to prefer red-listed species to common species, because they need protection the most urgently. Also, it is justified to protect sites where species abundance is high. If the budget is large enough, then complementarity may not be so important an aspect anymore, while persistence should be given the highest priority. In practice, this could mean, for example, that protected areas are selected to avoid fragmentation of forest landscape, i.e., improving possibilities for species to move among habitat patches through increasing connectivity by designing movement corridors and stepping stones.

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Appendix The opportunity costs of stands, €/ha

Habitat type	Number	€/ha	Habitat type	Number	€/ha
Xeric	1	2,312	Spruce mires	1	1,552
Xeric	2	6,589	Spruce mires	2	4,453
Xeric	3	3,964	Spruce mires	3	1,904
Xeric	4	5,411	Spruce mires	4	1,370
Xeric	5	6,416	Spruce mires	5	1,928
Xeric	6	3,617	Spruce mires	6	2,443
Xeric	7	5,422	Spruce mires	7	1,542
Xeric	8	5,819	Spruce mires	8	2,307
Mesic	1	7,267	Herb-rich	1	5,045
Mesic	2	4,901	Herb-rich	2	6,823
Mesic	3	5,508	Herb-rich	3	10,022
Mesic	4	1,506	Herb-rich	4	3,479
Mesic	5	7,257	Herb-rich	5	3,479
Mesic	6	2,752	Herb-rich	6	3,479
Mesic	7	2,948	Herb-rich	7	2,686
Mesic	8	3,434	Herb-rich	8	6,677

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