Do environmental diversity approaches lead to improved site selection? A comparison with the multi-species approach

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ABSTRACT

This paper suggests a new approach to select conservation areas cost-effectively according to the concept of complementarity and representation of focal natural features. The suggested environmental diversity (ED) site selection model maximizes ecological diversity, measured via ordination of the chosen taxa communities. Given their fundamental role in ecosystem functioning, vascular plants are chosen as the indicator taxa. We test the ED indicator model by contrasting it to the conventional site selection indicator (MS model), which maximizes the representation of species number in the indicator taxa. We demonstrate that the ED model is more cost-effective than the MS model. More importantly, while the ED selection is operative over the whole range of species, the MS selection does not work beyond the range of species, where all vascular plants become protected. Beyond that point MS indicator model cannot guide conservation efforts, which is a serious drawback. The ED model outperforms MS model also in terms of habitat conservation and taxonomic diversity. Thus, it provides an interesting selection framework for biodiversity.

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1. Introduction

Land areas set aside from commercial land use are the core of biodiversity conservation networks. The role of these reserves is to ensure that elements of biodiversity are maintained and disconnected from the anthropocentric processes that may threaten their existence in the wild. Reserves are chosen according to their representativeness, that is, according to the extent the focal natural features occur in the reserves (Faith and Walker, 1996). A practical ecological concept in promoting the representativeness is the concept of complementarity (May, 1990; Vane-Wright et al., 1991). It measures the contribution an area, or a set of areas, makes to an existing network of reserves in terms of unrepresented natural features (Margules and Pressey, 2000).

Most often site selections aim at promoting species representativeness, that is, the number of species included in the reserve network. Then, by complementarity, new sites should be chosen so that the increment in the number of species to the conservation area network is large. Large-scale species inventories are needed to facilitate the choice. Unfortunately, large-scale inventories encompassing many taxa are generally infeasible, because they are time-consuming and expensive (Juutinen and Mönkkönen, 2004; Juutinen et al., 2006). Ways to avoid increasing inventory costs include the use of indicator species to represent overall species diversity, or more generally, surrogate information for species-level diversity.

Finding indictor taxa or surrogate information that would well represent overall species diversity is difficult (Reyers et al., 2000). Even though spatial congruence within and among taxa in their species richness is consistently low (Prendergast et al., 1993; Oliver and Beattie, 1996; Kerr, 1997), sets of reserves selected using data on single taxa only can still be efficient—provided the choice is made according to the complementarity concept (Howard et al., 1998). The overall efficiency of a reserve network depends not only on their species richness but also on the degree of cross-taxon congruence in patterns of complementarity.

The most traditional approach in reserve selection problems has been to maximize species richness (MS approach) across taxa for which information exists or can be collected. It aims at the maximum representation of overall species richness. This approach has some disadvantages, however, the most obvious being the necessity for high quality data. In many cases reliable data on species distribution is non-existing. An alternative approach is based on the ecological principle that each species has a unique niche, i.e. species-specific habitat requirements differ at least along one important environmental gradient (Hutchinson,

1957). Consequently, maximizing the amount with which the existing ecological gradients become encompassed by the network of reserves would also maximize the number of critical resources available for different species, and thus species richness. This kind of thinking provides a basis for environmental diversity (ED) approach to conservation planning (Faith and Walker, 1996). ED is a surrogate framework where species data is linked with dissimilarities that indicate underlying environmental variation (Faith et al., 2003, 2004).

This approach would require two things. First, one has to decide, which ecological gradients are the most important. Obviously not all variation in ecological conditions can be incorporated, as the number of gradients may be infinite. Second, environmental diversity must be measured and expressed in terms of variables that are feasible to measure. In this paper we adopt the ED approach to site selection and apply it using one indicator taxa, vascular plants (the so-called species surrogate approach; Faith and Walker, 1996). It is based on the idea that maximizing variation in the vascular plant species composition (measured via ordination of plant communities) within the selected network would effectively encompass overall species diversity in boreal forest.

We select vascular plants as a surrogate group for several reasons. First, because of the fundamental role of vascular plants in ecosystem functioning it is likely that variation in plant species composition (rather than plant species richness) is important for overall species diversity. Second, the quantity, quality, and heterogeneity of resources affects the diversity of consumers, that is, plant species composition, and plant diversity influences the diversity at trophic levels higher up along the food chain (bottom-up control of diversity; e.g., Siemann, 1998). Third, previous studies suggest that vascular plants are likely good indicators of environmental variation, and hence useful in practical reserve selection problems in boreal forests (Virolainen et al., 2000; Saetersdal et al., 2004; Juutinen and Mönkkönen, 2004). These results are not surprising because net primary production is highly correlated with the diversity in plants (see e.g., Currie and Paquin, 1987; Wright et al., 1993) and is also reflected in the composition of plant communities (Tilman, 1990). The link between productivity and plant species composition forms a basis for the forest site type theory (Tonteri et al., 1990). In other words, compositional variation among sites in plant communities may well represent several gradients of environmental variation (productivity, moisture, soil properties) that are ecologically important for the whole ecosystem diversity. However, it is an untested hypothesis if the variation in plant community composition provides a useful surrogate for solving site selection problems in a cost-effective way.

We use an extensive empirical data on forest-dwelling species to quantify differences between MS and ED approaches. The data originate from 32 stands representing the whole spectrum of ecological variation in forest types in NE Finland within two landscape ecological forest management areas (Similä et al., 2002). We assume that the old-growth stands can either be conserved or harvested. The opportunity cost of biodiversity conservation is the net present value of harvest revenue lost. We include information on the presence/absence of species (vascular plants, birds, beetles and wood-inhabiting fungi) and the commercial values of forests (timber values and land values) in both indicator models. Furthermore, we include inventory costs and let the biodiversity conservation budget to vary.

MS site selection is run to maximize vascular plant species richness within the network. In the ED site selection we maximize the sum of dissimilarities (distances) in vascular plant species composition among the selected sites. We use ordination analysis of the vascular plant data (Gauch, 1982) to provide measurements dissimilarities among sites. In both models we examine how many species in total across all taxa become included, and which sites selected in the network of selected sites. The results of these surrogate approaches are then compared with the results from the benchmark model, which uses all available information and aims at maximizing total species richness.

We compare the MS, ED and the benchmark model from three angles. First, using conventional production possibility frontiers (PPF) we examine the cost-effectiveness of the three site selections. Second, we compare ED, MS and the benchmark models from the perspective of selected habitats. This is especially interesting, because, in most countries, biodiversity conservation planning and policy are rarely based on optimization but more often on recommendations to protect certain rare forest types and patches, e.g. key habitats. Third, we focus on differences between the models in terms of taxonomic diversity. Maximizing the number of species belonging to particular indicator taxa may happen at the expense of the number of species in other taxa. Thus, the selected conservation network may be biased towards the indicator taxa and under-represent species from other taxa. We are particularly interested if the ED model that aims at capturing variation along important gradients of the environment performs considerably better in representing overall taxonomic diversity than the MS model.

The ED and MS models are formulated using a linear formulation, so that they can be solved by methods that guarantee the optimality of solution. This has the advantage that the possible differences between the methods are not caused by the selection algorithm but by their alternative goals. To find precise optimal solutions to ED approach, we modify previous models developed to solve optimal clustering problem (the linear formulation of MS approach is well known by now). All the three site selection models are formulated as so-called integrated or ecological–economic models to simultaneously account for the ecological and economic features of the site (Ando et al., 1998; Balmford et al., 2000; Polasky et al., 2001; Juutinen et al., 2004).

The rest of paper is organized as follows. In the next section, we first present the site selection models for the alternative approaches. Then we present the data and describe how we executed the ordination analysis. Section 3 includes the empirical comparison of MS and ED selections. We collect our results under three sub-sections. In Section 3.1, we compare the cost-effectiveness properties of the site selections. ED and MS models are compared with each others and the benchmark model from the angle of selected habitats in Section 3.2. In Section 3.3, we focus on the differences between the models from the perspective of taxonomic diversity. In Section 4, we discuss the results.

2. Methods and material

2.1. Site selection models

Consider a given geographical area with n different old-growth stands. Each stand represents one site that possibly can be added to the conservation network. Denote the status of stands by x_j ($j = 1, \ldots, n$), which gets a value 1 if the stand is selected into the conservation network and 0 otherwise. Let c_j be the opportunity cost of conserving the stand j. The opportunity costs vary between the stands. The overall conservation budget is C. The problem of the society is to decide which stands to select into the conservation network, because all candidate stands cannot be protected due to the limited conservation budget. Species field inventories tend to be expensive, and therefore, reduce the conservation budget for compensating the opportunity costs (e.g. lost harvest revenue). Inventory costs can, however, be considerably reduced and the
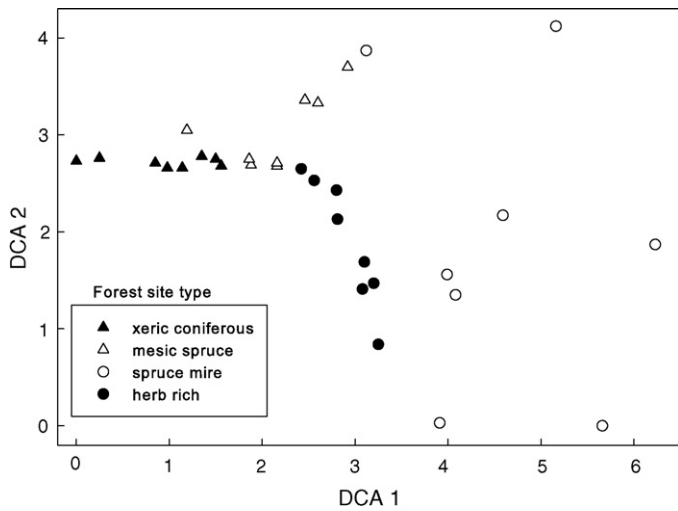
Fig. 1. DCA ordination of 32 forest stands based on their vascular plant assemblages. Eigenvalue of DCA1 axis is 0.521 and DCA2 0.329.

conservation budget expanded provided that the planner uses a good biodiversity indicator that reflects accurately the ecological features that are regarded as important. The use of indicator taxa (vascular plants) reduces inventory costs (I) in the ED and MS models, while the benchmark model must pay the full cost of inventing all species.

ED and MS models specify the selection problem differently. We first describe the ED method needed to formalize ED selection. We first run detrended correspondence analysis (DCA) ordination on the vascular plant data to arrange the 32 stands along axes based on their vegetation (data and results of DCA ordination are described in the next section). DCA arranges stands in n-dimensional space so that stands that foster similar vascular plant assemblages (the same species with similar abundances) are situated close to each other in space, and stands that differ in their plant species composition are far apart. The axes summarize the information in plant species composition so that the first axis includes the largest amount of variation, second axis the second largest amount, etc. DCA was performed with PC-ORD on log-transformed data to normalize the distribution of species data with rescaling the axis with 26 segments (McCune and Mefford, 1999). Positions of each stand on the first two axes were then used to calculate all pairwise ecological (Euclidean) distances between stands in two-dimensional space (see Fig. 1). We denote these distances by e_{ij} for stands i and j. We use an auxiliary binary variable y_{ij}, which obtains a value 1 if the distance e_{ij} from the stand i to stand j is selected (see Rosing and ReVelle, 1986; Klein and Aronson, 1991). Given this notation, the goal of the society is to maximize the sum of ecological distances in the selected conservation network over all stands,

$$\max_{x_i, y_{ij}} \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} y_{ij} e_{ij}. \qquad (1)$$

The target function (1) sums the ecological distances among the selected stands. This selection is constrained by the conservation costs and budget, as well as technical requirements. We define them as follows:

$$\sum_{j=1}^{n} c_j x_j + I_E \leq C \qquad (2)$$

$$x_i + x_j \geq 2 y_{ij} \qquad i = 1, \ldots, n-1, \quad j = i+1, \ldots, n \qquad (3)$$

$$x_i, y_{ij} = (0, 1) \quad \forall \, i, ij \qquad (4)$$

Eq. (2) is the budget constraint indicating that the sum of opportunity costs and inventory costs (I_E) is not allowed to exceed the conservation budget. Inventory costs are fixed costs. We assume that all stands must be surveyed irrespective how many of them will be protected (see also Balmford and Gaston, 1999). Inventory costs depend only on the considered indicator, thus they do not have a direct impact on the selection among stands since the relative values of the stands do not change. The role of constraint set (3) is to ensure that if the distance between stands i and j is included in the target function, the stand i and j are selected as protected areas and vice versa. The constraint set (4) indicates simply that the choice variables must be binary.

According to ED model, it is optimal to select stands so that ecological distance to the other protected stands becomes as large as possible as was suggested in the seminal works by Weitzman (1992, 1993). This implies that the focal ecological features of the selected stands supplement each other; doing so the model takes into account the interdependence among stands in their plant species composition. Consequently, the selected conservation network represents focal ecological features effectively.

The MS approach seeks to maximize species richness in the selected conservation network subject to a given budget constraint. Denoting the index and set of species by h and the subset of candidate reserve stands that contains species h by N_h, the MS model can be expressed as follows:

$$\max_{x_j, y_h} \sum_{h=1}^{m} y_h \qquad (5)$$

s.t.

$$\sum_{j \in N_i} x_j \geq y_h \quad h = 1, \ldots, m \qquad (6)$$

$$\sum_{j=1}^{n} c_j x_j + I_S \leq C \qquad (7)$$

$$x_j, y_h = (0, 1) \quad \forall \, i, h \qquad (8)$$

The target function (5) sums the number of species in the selected stands. Constraint set (6) ensures that species h is counted as being represented when at least one of the stands where it occurs is selected. The budget constraint is given in (7), where I_S denotes inventory costs. The constraint set (8) simply indicates that the choice variables must be binary; the stands are either protected or harvested, and the species are represented in their entirety or not at all.

In order to maximize species richness in the network, it is optimal to select stands so that increment in species richness, i.e. marginal benefit, is as high as possible. Thus, the MS model selects stands that supplement each other from the perspective of species richness and therefore takes into account the interdependence between stands.

We first apply the ED and MS models to data on vascular plants only to provide the conservation network (protected stands and habitats) and protected species at a given budget constraint. Given that both models use the same indicator taxa, inventory costs in ED and MS models are identical, that is $I_E = I_S$ in Eqs. (2) and (7). We then apply the MS approach to the whole dataset including all taxa to produce a benchmark against which to compare the ED and MS indicator taxa models. As this benchmark model uses data on larger set of species, it entails higher inventory costs than the ED and MS indicator models. Cost-effectiveness is defined as the ratio of the number of species protected to the conservation costs. The model with a higher ratio is more cost-effective. Varying the budget constraint produces a (discontinuous) function indicating

how the costs of conservation and number of species relate to each other in ED and MS models.

We express the cost-effectiveness properties of the models using the production possibility frontiers (PPFs). A PPF describes the maximum quantity of one good (diversity) that can be produced given the quantity of the other good produced (timber). We assume that old-growth stands can be used to produce either timber or biodiversity. In other words, the joint production of the two goods is not possible at stand level. Following Calkin et al. (2002), Boscolo and Vincent (2003) and Lichtenstein and Montgomery (2003), we measure the production of timber in monetary terms, whereas production of biodiversity is measured by the number of species (including vascular plants, birds, beetles and wood-inhabiting fungi) in protected stands. Given that timber production is measured in money and biodiversity in physical unit, just by redefining the vertical axis (to indicate revenue lost, instead of revenue obtained) PPF can be turned to express the cost function of species conservation. Recall, the benefit-cost ratios indicate differences in ecological and economic characteristics between the stands. If the characteristics of the stands were same, then the PPF would be a straight line, because the stands are either protected or harvested (Boscolo and Vincent, 2003). We use What's Best! spreadsheet optimization software to solve our linear integer problems (Lindo Systems, 2000).

2.2. Materials

We used a database that included 32 semi-natural old forest stands located in Pudasjärvi at the transition zone of the middle and northern boreal zones in northern Finland (see Similä et al., 2002). Eight sets of stands were surveyed representing the following four types of forest sites: 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 in practice the entire spectrum of forest site types in this region and represent a fertility gradient ranging from barren pine heaths to herb-rich forests.

Beetles, birds, wood-inhabiting fungi, and vascular plants were sampled on each stand. These taxa were selected so as to cover a wide array of dispersal potential and life forms and thus gain general results. The data from our sampling consisted of 103 vascular plants, 30 birds, 64 wood-inhabiting fungi, and 435 beetle species. The total number of species was 632.

Sampling effort per stand was constant irrespective of stand size. Beetles were sampled using window and pitfall traps. There were five window traps, set out as the five points in a dice, and 10 pitfall traps, 2 per window trap, on each stand making 160 window traps and 320 pitfall traps in total. The distance between window traps (and pitfall trap duets) was about 40 m. The trapping period lasted from the end of May to the beginning of September in 1997. On each stand five circles (radius 10 m; in total 0.16 ha/stand; configuration similar to beetle traps) were surveyed for polyporous fungi between mid-August and mid-September 1998. Fruit bodies of polypores were recorded from all living trees and decaying wood with a minimum length of 1 m and minimum basal diameter of 5 cm. Birds were censused with the point count method in June 1997. Each stand contained one point count station that was visited three times (5 min per visit), between early and late June. Vascular plants were surveyed between mid-July and early August in 1998 from ten 1 m^2 squares on each stand, located on a line 5 m apart approximately in the center of the stand.

DCA ordination shows that the first axis arranges stands from xeric heaths on the left to spruce mires on the right end of the axis,

and can be interpreted to represent moisture gradient (Fig. 1). The second axis tends to position herb-rich sites on the lower end of the axis, and clearly shows the heterogeneity in plant species composition among spruce mire stands, and correlates negatively with the total plant species richness. Thus, we interpret axis 2 as the gradient correlated with site productivity.

A Finnish forestry planning tool, 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 maximizes future net revenues for each stand. 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). We use unit forest values (€/ha) and treat stands as having equal sizes in the optimization (see Juutinen and Mönkkönen, 2007).

The data also included the costs of the species surveys. We based inventory costs on the actual time and effort spent collecting the data for that particular group, including the travel costs, materials, and working hours for field work and species identification. All 32 stands were inventoried by a joint effort, so there is no point in calculating these costs for each stand separately. Likewise, it is not reasonable to express these costs per hectare because each stand irrespective of its size was sampled with equal effort. The inventory costs for vascular plants and for all species were 3868€ and 46,756€, respectively.

3. Results

3.1. Cost-effectiveness

We present the PPFs of the ED and MS indicator taxa models together with the benchmark in Fig. 2. Fig. 2a neglects the inventory costs but they are added in Fig. 2b (for the indicator models inventory costs are identical). By definition, the farther away from origin of the graph a data point locates the more efficient is the production of the two goods and the more cost-effective is the selection of sites.

The first observation is that all PPF-curves are strictly concave. A socially optimal combination of the two outputs could be identified, if values to society were known for the both timber and biodiversity. The optimum would be the point at which the slope of PPF is equal to the social indifference curves indicating value society places on timber relative to biodiversity. The strict concavity of PPFs indicates that the socially optimal combination of the two outputs hardly results in corner solutions where all stands are either protected or allocated to timber production. Instead, some of the stands are used for biodiversity and some other stands for timber production.

Interpreting PPFs in cost terms further illustrates this outcome. Recall, the marginal opportunity costs are increasing with the number of stands added to the conservation network. For example, in the benchmark model the marginal opportunity costs increase from 7€ for the first two (smallest) units to 7267€, for the last two (largest) units, that is, marginal costs increase three orders of magnitude. Thus, the more areas are protected, the more timber production one has to give up to gain an additional species represented in the selected conservation network.
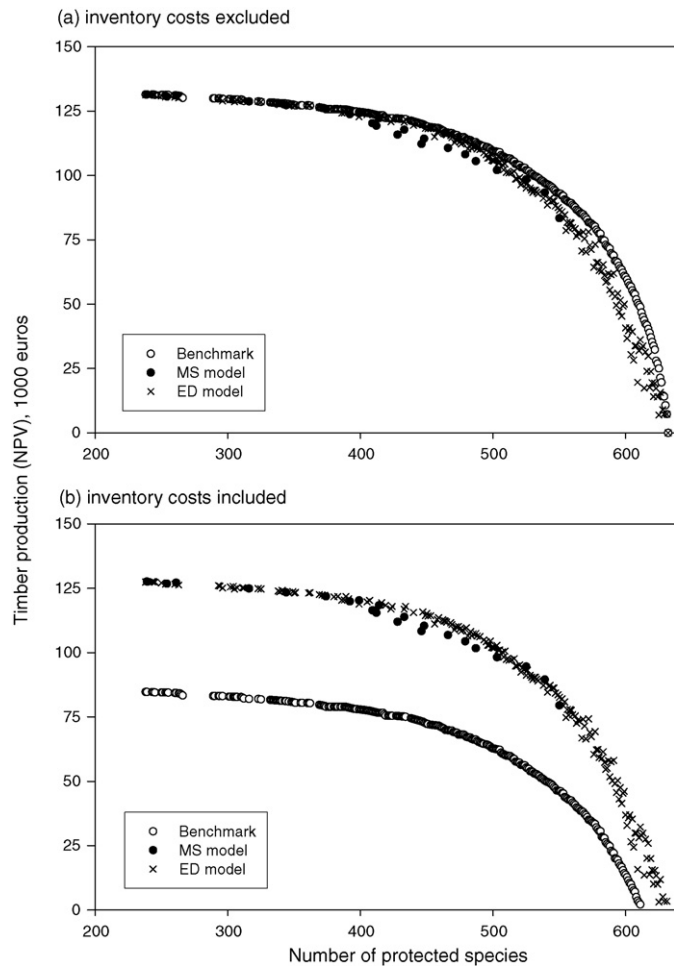
Fig. 2. Production possibility frontiers of the different site selection strategies.
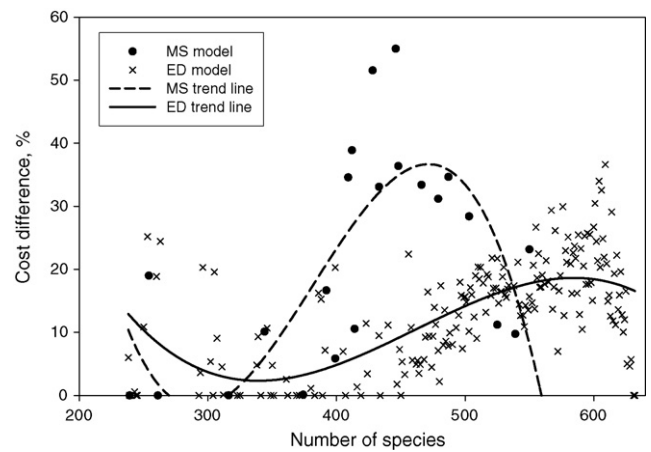

Fig. 3. The relative costs of ED and MS models, plotted as a function of the number of species represented in the selected conservation network. The costs of the benchmark model have a value of 0. Thus, a value of 50 for another selection method means 50% higher costs than in benchmark selection.

When inventory costs are excluded the ED and MS models are not as efficient as the benchmark model, because the benchmark model yields PPF that is farthest from the origin in Fig. 2a. This means that the used indicators in ED and MS models do not reflect fully the species richness of wide array of species. However, the differences between the models are minor. In contrast, when inventory costs are included both indicator models yield more cost-effective selections than the benchmark model (Fig. 2b). Large inventory costs of the benchmark model reduce the size of its production possibility set considerably, because a share of conservation budget funds has to be allocated to the species inventory and less money is available for establishment of conservation networks.

It is obvious in Fig. 2 that PPFs of the ED and MS models are almost identical at low levels of protected species. At the interval of 400–555 species ED model clearly yields a more efficient (more cost-effective) selection. Importantly, beyond 555 species the MS model does not provide any selection, because all vascular plant species (103 species) are already represented in the selected network. The conservation budget required to select 555 species is roughly 51,000€. This implies that the MS selection no longer guides biodiversity conservation beyond this level. This is a serious drawback of the MS indicator model. In contrast to the MS model, the ED model performs well over the entire range of species numbers (632 in total). ED model can be used to guide biodiversity conservation also at higher levels of conservation budget if the society aims at very high levels of conservation.

We represent the relative differences in the opportunity costs as a function of species represented in the selected conservation

network by both indicator models relative to the benchmark selection in Fig. 3. For a given number of species protected, the benchmark costs are set to zero and the vertical axis thus illustrates the relative cost difference between the benchmark and the indicator models. To make the cost differences clearer between the models, Fig. 3 also includes the trend curves for ED and MS selections. The trend curves are obtained by fitting a cubic linear regression model to the observed cost differences by using Sigma-Plot software (Systat Software Inc., 2006). The cubic functional form was selected as it performed better than quadratic or peak (Gaussian) form according to the Schwartz information criteria.

Fig. 3 confirms that the ED model is more cost-effective than the MS model in the range of 400–500 species. The average cost differences to the benchmark across the entire range of species numbers are 13.4% and 22.0% for the ED and MS models, respectively. Although there is a quite large variation in the cost differences, the 95% confidence intervals for these two average figures (ED 12.2–14.6%; MS 14.7–29.2%) are not overlapping. Also, the deviation in the average cost differences between the models increases if we consider only the range were the MS model is operative. In this case the average relative cost difference of ED model is 10.1% with the confidence interval 8.8–11.4%. The trend lines demonstrate that the cost patterns of the two selections considerably differ at different levels of species conserved. A notable feature is that the cost difference increases for the ED model for species between 500 and 600. Although the cost difference is deeply decreasing for the MS model, recall, it ceases to work in this range. Cost differences tend to zero as all potential stands and species have been selected.

3.2. Habitats

Recall, our data includes four forest types. To examine which forest types become protected by each model, we depict the proportions of the forest types at different levels of opportunity costs in the benchmark, ED, and MS models in Fig. 4a–c.

Interestingly, the benchmark and the ED model yield similar outcomes in terms of protected habitat types (Fig. 4a and b). The spruce mire type is the dominant type in the network, particularly at small budget levels. An obvious explanation for this outcome is the fact that the stand values (the opportunity cost) of spruce mires are generally the lowest. The proportions of the other forest types vary rather randomly under a small conservation budget, except that the mesic forests are disproportionately selected. When the
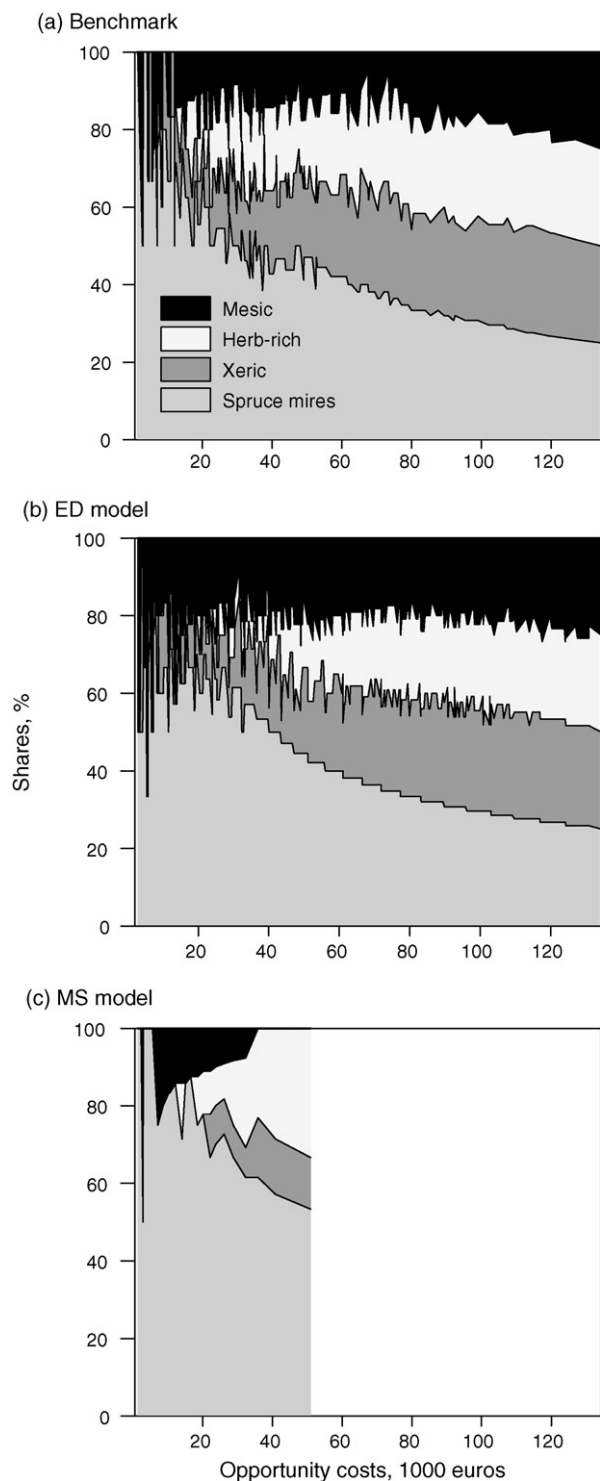
Fig. 4. The forest types in the selected conservation network, plotted as a function of opportunity costs: (a) benchmark model, (b) ED model and (c) MS model. The Y-axis describes the proportion of protected stands: the number of selected stands of the respective forest type/the number of all selected stands × 100.

Fig. 5. Proportions of vascular plant species (the number of vascular plants/the number of all species × 100) in the selected conservation network, plotted as a function of the opportunity costs.

The contribution of forest types to the conservation network looks rather different when the MS model is applied (Fig. 4c). First, the range of budgets that can be considered is restricted, because all vascular plant species become included in the network of selected sites at rather low budget levels. The dominant forest type with the MS model selection is, again, the spruce mires. The share of other forest types varies along the size of the budget. From ecological perspective it is notable that mesic forests are not needed at all to protect all vascular plant species. This is because the mesic forest stands did not foster any vascular plant species unique to this site type. Thus, maximizing the number of vascular plant species may result in a conservation network, which does not represent all existing habitat types (environmental diversity) in a region.

3.3. Taxonomic diversity

To examine how the use of indicator models affects the species representation in the selected conservation networks, we first examine how large proportion of the total species richness vascular plants comprise at different levels of opportunity costs, resulting from the alternative site selection models (Fig. 5). To make the differences clearer between the models, Fig. 5 also includes the trend curves for the selections. Trend curves are derived by fitting an exponential regression model to the observations (Systat Software Inc., 2006). We then calculate the average proportions of all taxa to further examine the potential bias in species representation in the selected conservation network (Table 1).

Again, the benchmark and the ED model are rather similar in terms of representing vascular plants in the selected conservation network except when the budget is very low and only one or two stands are selected (Fig. 5). At low budget levels the proportion of vascular plants varies much in all the models. The MS model results

Table 1
Average proportion of species (%) in the selected conservation networks

Taxa	Benchmark	ED model	MS model
Vascular plants	19.1 (18.8–19.4)	19.0 (18.8–19.2)	22.7 (21.5–23.9)
Beetles	67.4 (67.2–67.5)	67.6 (67.5–67.8)	65.4 (65.4–65.5)
Birds	5.0 (4.9–5.0)	4.9 (4.8–4.9)	5.1 (4.8–5.2)
Wood-inhabiting fungi	8.6 (8.4–8.8)	8.5 (8.4–8.6)	6.8 (6.3–7.3)

The 95% confidence interval of the mean is in the parentheses. Figures are calculated over the budget range where MS model is operative.

size of the budget increases, it is optimal to include first at least one stand of all forest types in the network. Thus, the selected network is diverse also in terms of forest habitat types. In the ED model the herb-rich forest types become selected at a little bit higher budget level than in the benchmark, however. Finally, all stands are selected and the forests types necessarily have equal shares as our data includes eight stands for each forest type.
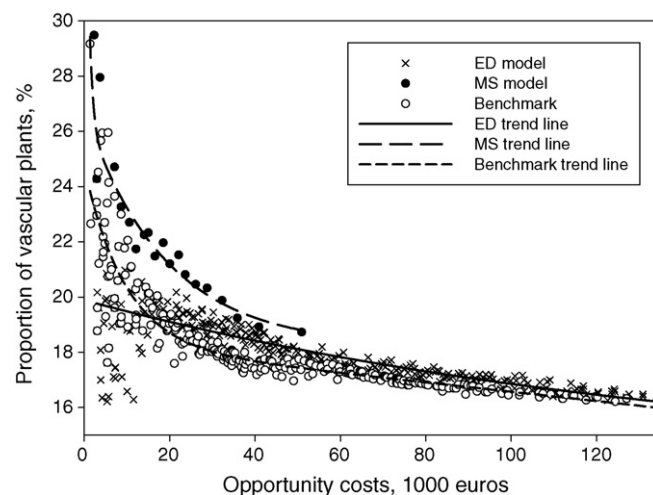
in a conservation network where the vascular plants are over-represented compared with the benchmark at all levels of conservation budget. The higher proportion of vascular plants in MS model reduces the representation of beetles and wood-inhabiting fungi species in the selected conservation network but has no effect on birds (Table 1). In general, even though the differences in the pattern of species representation among the models are rather small the MS model results in a larger bias than the ED model.

4. Discussion and conclusions

This paper demonstrated a new approach (ED model) to select conservation areas according to the concept of complementarity and representation of focal ecological features and tested its cost-effectiveness by contrasting it to the conventional site selection indicator model (MS model). Many important features were found. First, the ED model was clearly more cost-effective than the MS model. More importantly, ED selection was operative over the whole range of species in the data and at all required conservation budget levels, whereas the MS selection worked only on a restricted range of budget levels and numbers of species. The obvious weakness of the MS model resulted from the fact that all vascular plant species became protected well before the network of selected sites comprehensively encompassed total species richness. Once all species in an indicator group become protected, MS indicator model cannot guide conservation efforts at higher conservation levels. This is a serious drawback, as the application of MS model becomes very sensitive to the chosen indicator (Juutinen and Mönkkönen, 2004). By virtue of being based on species composition, the ED model does not have this weakness, because ecological diversity measured as a distance can be defined over all stands as long as the sites are not totally identical to each.

Second, differences between ED and MS model persisted also as regards to representation of habitat and taxonomic diversity. In particular, MS model provided selections of stands that did not cover the whole existing habitat variation (forest types) and that tended to be biased towards the indicator group (vascular plants). It is therefore likely that MS approaches in general do not capture the environmental and ecological variation as comprehensively as the ED approach. This is likely because of the fact that there tends to be only little cross-taxon congruence in species richness, i.e. sites rich in species in one species group tend to be different from those rich in species in other taxa (Prendergast et al., 1993; Similä et al., 2006). By contrast, ecological gradients capturing variation in species composition in one species group, and particularly in primary producers, may more likely be also relevant for other taxa. This is not only because of direct links between heterotrophic organisms and their basic resources (plant diversity and productivity). In our case, only a minority of species was directly dependent of specific plant species, e.g. by being specialist herbivores. We suggest that the relatively good performance of the ED site selection model may reflect more general similarity in compositional variation among species groups. When underlying abiotic conditions change, this triggers a change in the structure of biological communities that is of similar magnitude across a wide range of taxa. We interpreted our DCA axes (Fig. 1) to represent forest moisture and fertility. It remains to be tested if site selection based directly on measurements of these two environmental gradients would also turn out as cost-effective as ED site selection based on vascular plant composition.

Third, if inventory costs are high, both indicator models outperform the benchmark model. This further emphasizes the importance of carefully selected biodiversity surrogates because otherwise a considerable proportion of limited funds may be used in mere information collection (Juutinen and Mönkkönen, 2004; Sarkar et al., 2006; Mönkkönen et al., in press).

We suggest ED approach as a viable strategy in site selection problems. Particularly the rapid development in quality and availability of remotely sensed data provide interesting and potentially cost-effective possibilities for ED site selection approach. We used here actual data on vascular plant species composition to produce ecologically relevant environmental gradients. Relevant environmental gradients, however, can be produced using many different data sources (Faith, 2003) but their usefulness needs to be properly tested (Araujo et al., 2001).

An important issue for future work also is to include spatial attributes such as connectivity into the analysis. There are several possibilities to extend site selection models to cover spatial features (Williams et al., 2005). The ultimate goal is, however, to develop spatially explicit models for conserving multiple species, models that take into account the spatial function of selected conservation network (Arponen et al., 2005; Cabeza and Moilanen, 2006). These models require species-specific data, and at the moment are infeasible for large set of species. Meanwhile, ED approach provides a promising and a cost-effective alternative to traditional MS models. By maximizing just the number of species the MS model does not aim at species survival in the long run (Nalle et al., 2004) but may in fact maximize species extinction (Cabeza and Moilanen, 2001). The ED model explicitly takes into account species abundances along with species richness, because it uses information on species compositions. Therefore, it may result in better outcome than the MS model in terms of species persistence.

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