Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics

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Abstract. In this study, the performance of biodiversity indicators used in the selection of boreal old-growth forest reserves is assessed. The indicators include beetles, birds, vascular plants, wood-inhabiting fungi, and a specified sub-group of assumed indicator species. We also analyze how well the amount and quality of decaying wood indicates overall species diversity. Our site selection procedure includes information both on ecological variables and on the economic costs incurred from the ecological survey and the opportunity costs of conservation. Complementarity and scoring procedures in site selection are compared. We show that the use of indicators likely results in a loss of species and, therefore, a complete inventory of biodiversity is necessary if the goal is to maintain all species in the landscape. However, the use of indicators seems to be an economically more efficient practice than to execute a large biodiversity survey for habitat protection in our case study. In general, birds and vascular plants seem better indicators than other taxa. A scoring approach performs better than a complementarity approach for indicator taxa containing a small number of species.

Key words: cost-efficiency, forest management, integer programming, site selection model

JEL classification: Q 23

1. Introduction

Setting aside forest areas that are particularly biodiverse is regarded as an efficient way to maintain biodiversity in forest landscapes under commercial use, because habitat loss is currently the most serious threat to species and ecosystems (see e.g. Fahrig, 2001). The protection of regional biodiversity requires that priority for the protection of individual areas be based on the contribution, which the area can make to represent overall biodiversity. However, it may be extremely costly to measure this contribution for all potential sites. Therefore, area selection procedures have to rely on surrogate measures of biodiversity (Faith and Walker, 1996). One standard approach is based on indicator groups of taxa. As a result, choosing the best possible indicators becomes a crucial step in biodiversity maintenance.

How is one to choose a good indicator? In general, indicators should represent key attributes of those ecological properties that are regarded important and that are too difficult or expensive to monitor directly. Several a priori suitability criteria have been proposed for the selection of indicators (Noss, 1990; McGeoch, 1998). For instance, the data for the indicator should be relatively easy to sample and sort, and the indicator should be sufficiently sensitive to provide an early warning of change, widely applicable, and be independent of sample size. These kinds of criteria can help the selection of indicators for species and higher taxa, but formal tests are required to assess how well the chosen indicators reflect the overall biodiversity.

In this paper, we search for indicators for biodiversity conservation. By using comprehensive background data, we test how well potential indicators perform when selecting boreal old-growth forest areas for protection. We address an ecological aspect, that is a representation of biodiversity in the broad sense of all species, and also focus on economic cost-efficiency. By cost-efficiency we mean biodiversity optimisation by selecting

a conservation network under a given budget constraint. As resources for conservation are limited, cost-efficiency is an important aspect of forest management and forest reserve selection for biodiversity maintenance (e.g. Haight, 1995). To our knowledge, the cost-efficiency of biodiversity indicators has been, until now, an unstudied issue (see Gaston, 1996, Flather et al. 1997, and McGeoch 1998, for reviews on indicator studies). Balmford and Gaston (1999) used, however, a rather similar approach to ours to assess the benefits of high quality biodiversity inventories.

We first study whether taxonomic groups can be used as indicators. We include beetles, birds, vascular plants, and wood-inhabiting fungi, and we test, for example, whether birds can be used as indicators for other taxa. These taxa represent a wide array of species ecologies, dispersal abilities and life-histories in boreal forests. Birds and vascular plants are rather well known taxa and may therefore be considered generally as potential indicators. Moreover, it is well known that some beetle and wood-inhabiting fungi species require certain structural characteristics of old-growth forests, and thus, these taxa may also be potential indicators. The second class we focus on is the occurrence of a specified sub-group of species (including species of birds, beetles and fungi), which earlier studies suggest to indicate old-growth forest conditions. We test whether or not they cover the variation in overall species diversity of old-growth forests. Third, we test how well reserve selection based on the amount and quality of decaying wood results in a representation of overall species diversity. Some 4000-5000 species, or 20-25 % of all forest-dwelling species, in boreal forests are dependent on dead wood habitats (Siitonen, 2001).

To test these indicators, we develop the following phased method by using site selection models. First, we run the site selection procedures using optimisation algorithms separately for different potential indicators. Second, we execute the optimisation for benchmark selection by using information of all species. Thus, the benchmark selection represents, by

assumption, the maximum level of biodiversity in the region at given resources devoted to conservation. Third, we compare the results from indicator-based area selection with the results from site selection based on information of all species to study how well biodiversity become conserved when using information of indicators only. On the basis of this comparison, we end up with a ranking of potential indicators. However, we execute the ranking by using two alternative site selection procedures, the ecological and integrated model. The ecological model uses information on species presence/absence only by maximising biodiversity under a given upper limit for a number of protected sites (Sætersdal et al., 1993; Dobson et al., 1997; Howard et al., 1998; Van Jaarsveld et al., 1998; Reyers et al., 2000; Virolainen et al., 2000), whereas the integrated model explicitly takes into account both economic and ecological aspects of biodiversity by maximising biodiversity under a given budget constraint (Ando et al., 1998, Balmford et al., 2000; Polasky et al., 2001; Juutinen et al., 2003). Comparisons between integrated and ecological selections allow us to see if the ranking remains same when the costs of biodiversity surveys, as well as the opportunity costs of conservation, are incorporated into the procedure.

We use the number of species encompassed in the selected network of forest areas as the criterion for biodiversity assessment in the benchmark models, since one of the ultimate long-term goals of the present forest management practices in Fennoscandia is to maintain viable populations of all naturally occurring species in a considered area (Mönkkönen, 1999). Moreover, species richness is a simple and transparent measure and it is often positively correlated with many other (genetic, taxonomic, functional, etc.) measures of biodiversity (Gaston, 1996). Our data originate from 32 old-growth forests stands in NE Finland within two landscape ecological forest management areas. We use lost harvesting revenues (forest values) as opportunity costs of conservation.

The rest of the paper is organized as follows. In Section 2.1, we present the site selection models, and explain how the tests can be executed by comparing the results of indicator models and benchmark models. Data is briefly described in Section 2.2. Section 3 includes results of indicator tests according to an ecological approach. Section 4 considers the cost-efficiency of indicator species. Section 5 is devoted to the assessment of the results. Finally, conclusions are in Section 6.

2. Framework and data

2.1. Biodiversity indicators in site selection

The goal of a forest manager is to select old-growth stands for a conservation network so that the biodiversity function is maximized with given resources available for conservation. A manager has a resource constraint, which can be expressed by a number of stands (or an area constraint) or a budget constraint. We use the former in the ecological and the latter in the integrated model. Cost-effective conservation under a given budget requires that a forest manager will take into account the differences of forest values e.g. in the form of harvest revenues. The ecological approach implicitly assumes that stands have equal forest values and partially neglects the economic costs of conservation.

For this study, we assume that the only forest management option for biodiversity preservation is the protection of old-growth stands (non-treatment), so that the conservation problem can be formalized by using site selection models. Our models are presented in Table

1. They are classified into three model types named DIV, NUM and DW.[1] The DIV and NUM models are based on indicator taxa, and we develop several versions of these models depending on, which taxa are sampled for their diversity. The DIV model, which incorporates information on all species, is the benchmark model with which all the other models are compared. The third model type uses an environmental variable (decaying wood) as an indicator for overall species diversity.

[Table 1]

DIV models are species diversity models, where the aim is to maximize the number of species in the selected network subject to constraints 2, 5, and 3 or 4. In the target function (eq. 1), species richness Y is an aggregating function of binary variables y_i. Constraint set (2) ensures that species i is not counted as represented if no stand in which it occurs is protected. The EDIV model has a site constraint (eq. 3), where k is the given upper limit for the number of stands in the conservation network. The IDIV model has a budget constraint (eq. 4), which assures that the total costs of conservation, including the opportunity costs and inventory costs, do not exceed the funds allowable for a conservation network. Note that we treat inventory costs as fixed costs, because all the candidate stands have to be surveyed irrespective how many of them will be protected (see also Balmford and Gaston, 1999). Inventory costs depend only on the considered indicator so that they do not have a direct impact on the selection among stands since the relative values of the stands do not change. The constraint set (5) simply indicates that the choice variables must be binary. Thus the

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[1] The name DIV refers to species diversity. NUM indicates that, in this model, a given species is counted numerous times in the target function, if it is present on several protected stands. DW is an abbreviation from decaying wood.

stands are either protected or harvested, and the species are represented or are not, in their entirety.[2]

The presentation of DIV models is called a maximal coverage problem (MCP, Camm et al., 1996). The models are based on the complementarity concept of forcing to select stands those who supplement each other in terms of species richness.[3] Thus, the model type takes account the spatial interdependence between stands. The stands are considered as a set, and the model selects stands that supplement each other from the viewpoint of species richness, through the objective, the binary choice variable y_i, and an equation (2). Together, these guarantee that the choice variable is zero, if the considered species is not found on any of the selected stands. If the species exist on several selected stands, the choice variable gets always the value of unity. Thus, in order to maximize species richness, it is optimal to protect stands, which have different species. Note, however, that the model is not spatially explicit, as it does not take into account the spatial configuration of the selected stands. Hereafter, we use the concept of complementarity approach to refer to the DIV type models.

If species number in an indicator species group is small, all species may become included into the network after just a very few stands are selected. In such cases, the DIV models can no longer be used to select the remaining stands according to their conservation value. The

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[2] The optimisation with all species forms an unbiased benchmark for indicator testing. According to the benchmark model, maximizing the number of species results in solutions where all higher taxa (beetles, birds, fungi and plants) become represented from the very beginning proportionately to their overall relative species number (see Appendix 1). The event has a simple explanation. All stands foster species from all taxa and there is relatively little variation in the relative distribution of species among taxa between stands. On the other hand, the stands, which differ greatly from each other in terms of species distribution among taxa, are the most supplementary options and become selected one after the other.

[3] The ecological literature uses 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).

problem is avoided by using the NUM type model, where stands can be ranked even though all species are already covered by the existing conservation area network. In the target function of NUM models, species are counted as many times as they are present in the selected stands. Thus, the NUM models resemble a scoring procedure, and what follows, we use the concept of "scoring approach" to indicate the NUM type models. Scoring means that all stands are given some conservation value, which does not depend on the selected conservation network.[4] Thus, scoring omits that the stand are interdependent due to the biodiversity services.

The DW type models aims at maximizing the volume and/or quality of decaying wood in the selected network subject to the quality (eq. 2), resource (eq. 3 or 4), and binary (eq. 5) constraints. Decaying wood is potentially a very useful surrogate measure of biodiversity because it has been shown to correlate significantly with the species diversity in several taxonomic groups in boreal forests (Siitonen, 2001). Both the amount and quality of decaying wood can have an effect on species. The larger the volume, the more there is habitat for species associated with decaying wood. Different types of dead wood (e.g. snags vs. down logs) and decaying phases (e.g. freshly killed trees vs. well-rotten wood) represent different habitat types. Many species depending on decaying wood are specialists for a certain habitat type. These volume and quality aspects of decaying wood are incorporated into the target function of DW models. However, it is a value judgment to decide the relative importance of the volume and quality. Technically, the relative importance of these factors can be adjusted by varying the exogenous parameters a and b. If b is set to zero, only the volume of decaying wood affects the results. In this case, the stands that have the highest volume of decaying

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[4] Because INUM model has a budget constraint, it may not be possible to select the stands into the network according to a fixed rank. The stands having a high score cannot be protected, when their opportunity costs are too large with respect to a given budget. Therefore, in the INUM model, the ranking of stands varies according to the allowable budget, but, in the ENUM model, it is fixed.

wood (in the case of the IDW model, relative to their economic value) are the best targets for conservation. If a is set to zero, only the diversity of decaying wood types matters. In the analysis, we will use volume-only and quality-only as well as mixed approaches where the parameters are set such that both the volume and quality of decaying wood affects the selection of stands (used parameter values are a = 1 and b = 5 000).

The indicators can be tested with the following procedure. Denote species richness given by the benchmark and indicator models at a given resource constraint (B or k) by Y_{bench} and Y_{ind}, respectively. We are interested in the difference between Y_{bench} and Y_{ind}, which indicates species loss. In order to know Y_{ind}, we first have to use indicator models to maximize Z and find out the corresponding conservation network at a given resource constraint (B or k). For this comparison, we exclude the inventory costs from the integrated models, because those are treated as fixed costs. Otherwise, it would not be possible to compare indicator and benchmark results until the budget is high enough to cover the maximum inventory costs and the lowest forest value of the stands. The benchmark model has the biggest inventory costs, since it includes all the species. Therefore, in the ecological approach, we use this comparison to rank the indicators, but in the integrated approach, it only demonstrates whether the use of an indicator can result in species loss (or increased opportunity costs).[5] In the latter approach, it cannot be used to rank the indicators, because the economic rank depends also on the inventory costs. To rank the indicators in economic terms we compare conservation costs (C) at a given level of biodiversity. More precisely, using the previous notation for costs, C, we are interested in the difference between C_{bench} and C_{ind} at a given level Y. Both comparisons are, however, needed to see the differences between ecological and economical ranks.

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[5] This comparison is an interesting starting point for indicator testing also because it may be possible to use existing inventory data in the optimization meaning that the inventory costs can be excluded from the consideration. Moreover, previous studies basing on the ecological approach have used similar comparison (Howard et al., 1998; Pharo et al., 2000; Reyers et al., 2000; Virolainen et al., 2000).

2.2. Data

The database includes 32 semi-natural old-growth forest stands in the middle boreal forest vegetation zone in Finland. We sampled four forest site types including eight replicates of each: 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 whole gradient of forests in this region and represent a fertility gradient ranging from barren pine heaths to herb rich forests. The sampled species in each stand are beetles (Coleoptera), birds (Aves), wood-inhabiting fungi (Basidomycetes) and vascular plants (Tracheophyta). 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 103 vascular plants, 30 birds, 64 wood-inhabiting fungi, and 435 beetle species. The total number of species is 632. In order to include the opportunity costs of conservation (lost revenue from alternative uses) into the consideration, we calculated the forest value for each stand by using a forest model called MELA (Siitonen et al., 1996). 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 (€/ha) and treat stands as having equal sizes in the optimization. (See Similä, et al. 2002a, and Juutinen et al., 2003, for a more detailed description of the study sites, sampling method, and forest values, see also acknowledgements.)

From the total species set, we separated a subgroup of old-growth forest indicator species based on their known status as old-growth forest specialists. The indicator group includes a

total of 42 species of which 14 are wood inhabiting-fungi (Kotiranta and Niemelä, 1996), 5 birds (Väisänen et al., 1998), and 23 beetles (J. Siitonen, pers. comm.).

We measured the amount and quality of dead wood in five circles (radius 10 m) at each study site (1570 m^2/site). The quality of dead wood was classified into five classes according to the stage of decay. Downed logs and standing dead trees were kept separate. Tree species included pine, spruce, birch, aspen, and other species. The size of decaying wood had three categories, <10 cm, 10 cm< x <30 cm, >30 cm, according to the diameter. Altogether, there were 114 combinations of the dead wood quality classes out of 150 possible combinations.

The models also include the inventory costs of the particular species group. The inventory costs are based on the actual time and effort spent to collect the data for that particular group including the travel costs, materials, and working hours for field work and species identification. These costs cannot be calculated for each stand separately because all 32 stands should have been inventoried anyway. 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 are presented in Table 2.

[Table 2]

3. Ecological properties of the indicators

In this section, we test indicators from a purely ecological perspective by analysing how their use in the ecological models is reflected in corresponding overall species diversity. The results are presented in Figures 1–3. The ecological models often result in multiple optima. With a given site constraint, there may be several alternative conservation networks available,

which cover the same number of indicator species. In that case, our results include the average of (all) the species representations of these solutions.

Figure 1 represents number of species in the selected network compared to benchmark selection for chosen indicator species groups, plotted as a function of the number of protected sites. The stands were selected by using the EDIV model (complementarity approach). Beetles and vascular plants seem to be the best indicators, since by using these groups, the selected networks also cover most of the other species. Understandably, beetles cannot be a poor indicator group, when economic costs are left out, since about 68 % of the species are beetles in our sample and the aim is to maximize species richness (cf. vascular plants in Pharo et al., 2000). Vascular plants are a good indicator group, because spruce mires and herb rich forests are the most important forest types in ecological optimisation for all species, and these types have a high diversity of vascular plants (see Juutinen et al., 2003). Birds and the old-growth forest indicator species seem to perform the worst as overall indicators of total species richness.

[Figure 1]

It is not straightforward to rank the species groups, because their operative ranges vary.[6] For example, birds are fully covered by protecting six sites (Figure 1). Thus, it is not possible to set priorities for sites by using birds, if we want to protect more than six sites. Therefore, we cannot compare birds with other indicators when over six sites are selected. This problem can be avoided by using the ENUM models (e.g. scoring approach), where species presence is

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[6] The operative range of an indicator is the range of conservation costs or number of sites, in which the indicator species are not all represented in the selected conservation network. After the indicator species are fully represented, the remaining unprotected stands cannot be selected by using the indicator.

still kept track of even if all the species in a particular group are included into the network. The results based on ENUM model are represented in Figure 2. The EDIV and ENUM models result in same ranking of the indicator species (cf. Figures 1 and 2). However, the scoring model outperforms the complementarity model for birds and old-growth forest indicator species, the groups in which the number of species are the smallest.[7]

[Figure 2]

Figure 3 shows the results of using decaying wood as a surrogate for overall species diversity. The volume of decaying wood is in general a more effective surrogate for species diversity than quality based measures, particularly at higher levels of conservation. However, the differences between the mixed indicator, which includes both a volume and quality component of decaying wood, and the volume indicator are small. In relation to species indicators, the selection of sites based on decaying wood does not result in an effective species representation (cf. Figures 1, 2 and 3). Particularly, using beetles and vascular plants with the EDIV procedure seems to work better than decaying wood surrogates.

[Figure 3]

4. The cost-efficiency of indicator species

The ecological test does not consider the differences in the inventory and opportunity costs between alternative indicators, thus we next incorporate these into the analysis. Because

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[7] The effectiveness of EDIV and ENUM models can be compared only in the range where EDIV model is operative. The ENUM model is inevitably relatively effective, when the majority of the stands are protected.

the economic test of decaying wood ended with results very similar to the ecological test, we focus solely on indicator species. We start by considering how well they perform in terms of species protection when species inventory costs are omitted from the analysis. Then we compare the indicators in terms of conservation costs, also taking inventory costs into consideration.

Figures 4a–d represents the number of species in the selected network compared to the benchmark for the alternative indicator species group, plotted as a function of opportunity costs. The results are based on the IDIV model. Clearly, IDIV models usually covers all the species less than the benchmark model at any fixed budget level, when inventory costs are excluded from the consideration. However, the species loss is minor, when beetles are used as the target group in optimization (Figure 4a). On the average, calculated over the whole operative range of beetles by varying the budget, species loss is less than 1 %. Unfortunately, beetles are a poorly known taxonomic group, and they have been rarely inventoried, so that it may be impossible to avoid inventory costs in practice. The selection based on vascular plants seems to also protect most of the other species (Figure 4b). By using vascular plants in the IDIV model, it is on the average possible to cover almost 96 % of all the species of the benchmark model. The mean species coverage is about 91 % when using wood inhabiting-fungi as a target (Figure 4c). Birds (Figure 4a) and old-growth forest indicator species (Figure 4d) seem to perform less well as overall indicators of total species richness. The average coverage regarding birds attains to 85 % and the mean value for old-growth forest indicator species is about 84 %. These results are similar to the results of ecological tests, indicating that the differences in the opportunity costs between indicators do not have a strong affect on their ranking (cf. Figures 1-2 and 4).

[Figure 4]

An interesting view can be obtained by considering the operative range of each indicator. The operative range of vascular plants in the IDIV model ends when the budget is about 50 500 € and all vascular plants are covered in the selected network (Figure 4b). However, there still are many unprotected stands left, which cannot be selected by using the vascular plants indicator. It costs almost 134 500 € to protect all of the 32 stands without considering inventory costs. Also birds (Figure 4a), wood-inhabiting fungi (Figure 4c) and old-growth forest indicator species (Figure 4d) have a rather narrow operative range, since their number of species is relative small. Noteworthy, the operative range of wood-inhabiting fungi (64 spp.) is larger than that of vascular plants (103 spp.), even though the latter group has more species. This indicates that wood-inhabiting fungi species are a relatively demanding group from conservation perspective, as covering all the species in this group requires some 90 000 €.

Next, we assess the indicators from the conservation costs side. Figure 5 gives the absolute costs of conservation by terms of the costs functions of the benchmark and the IDIV models. The cost functions include two parts, the inventory costs and opportunity costs of conservation. Because the inventory costs are independent of the level of conservation, at low levels of conservation, the share of inventory costs from total costs is high, and they may dominate the cost pattern. This is clearly the case when we consider the benchmark or the costs of using beetles (Figure 5a) or old-growth forest indicator species (Figure 5d) as an indicator group. In other groups, the inventory costs do not seem to have strong effects on cost functions. Especially, at a low level of conservation, the absolute cost difference between the benchmark model and the IDIV models for vascular plants (Figure 5b), wood-inhabiting fungi (Figure 5c), and birds (Figure 5a) is rather big. It is typical for all the models that the opportunity costs increase exponentially as the species coverage increases, e.g. the marginal

costs of conservation are increasing. However, we can note that the cost functions of the indicator models are not increasing all the time, because they were not optimised in terms of all species coverage in contrast to the benchmark model. If a particular species group is a poor indicator, its use will increase the opportunity costs of conservation relative to better indicators, however, this is difficult to notice in terms of absolute costs.

[Figure 5]

In order to rank the indicators, we calculated the relative cost differences between indicator models (IDIV) and the benchmark to Table 3. Vascular plants seem to be the best indicator group from a relative cost point of view. The mean cost difference between the benchmark and vascular plants is bigger than the differences for other groups at every level of species represented. On the average, the conservation costs are about 68 % larger in the benchmark case than using vascular plants as an indicator group in the operative range of vascular plants. The old-growth forest indicator species are surprisingly the poorest surrogate measure, as their mean cost difference is the lowest. The protection decisions based on old-growth forest indicator species incur even more costs than the benchmark when the range of species represented is 61-80 %. Beetles also have a low mean cost difference, 14 %. The figure for wood-inhabiting fungi is 56 %, respectively. Birds, as an indicator, are operative only within a narrow range of conservation (the maximum species representation is less than 71 % of the total) because the number of bird species is small and all birds become included at a relatively low level of conservation, and therefore provide no information for site selection procedures thereafter. A general pattern in the results is that the wider the operative range of an indicator, the smaller is the cost difference because of fixed inventory costs.

Consequently, the average cost difference of birds is the highest 79 %, but birds are, clearly, an inferior indicator group relative to vascular plants.[8]

[Table 3]

In Table 4 are the relative cost differences between the INUM models and the benchmark. In general, the scoring procedure seems to be more effective than the complementarity models (cf. Tables 3 and 4). Only for beetles, where the number of species is rather high, the INUM model is poorer than the IDIV model. According to the INUM optimisations, birds are the best indicators, and vascular plants are almost as good as birds. Beetles and old-forest indicators are the poorest indicators.

[Table 4]

5. Assessing the results

Our analysis suggests that using indicator species may result in a loss of overall biodiversity (see Flather et al., 1997; Oliver et al., 1998; Van Jaarsvelt et al., 1998; Chase et al., 2000; Reyers et al., 2000). Also Similä et al. (2002b) found that there are in general only weak correlations in the diversity among different boreal forest taxa across forest stands. In contrast, Virolainen et al. (2000) found that the use of one taxonomic group captured the species richness of all groups with the same efficiency as using information on all taxa at once

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[8] We compared indicators also to benchmark, which does not include inventory costs. In that case, the rank according to mean cost difference was vascular plants, wood-inhabiting fungi, birds, beetles and old-growth forest indicator species in descending order (the detailed results are available from the authors).

in taiga forests. Howard et al. (1998) had similar findings from a tropical forest in Uganda. However, both Virolainen et al. (2000) and Howard et al. (1998) used a heuristic optimization procedure, and therefore, there is no guarantee that optimal solutions were found (see e.g. Pressey et al., 1997). Our findings support the statement made by Howard et al. (1998) that temperate (and also boreal) regions may be too homogenous and relatively species poor, and therefore, complementary areas for indicator taxon may not capture diversity in other groups. Also in Virolainen et al. (2000), the considered areas were very heterogeneous including 16 old-growth forests from Finland and Sweden, which were situated on islands or the mainland.

However, in our case, the use of indicators usually costs less than the benchmark, except with the old-growth forest indicator species, suggesting that a wide inventory of species is not cost-efficient. Whether this result can be generalized, is an open question. We have a small number of stands and we treated the stands as having equal size in the optimizations. Although the inventory cost function is unknown, it is likely that the curve for unit inventory costs is U-shaped. The unit costs are very high when only few areas are inventoried. Gradually, the unit costs decrease when the scale of inventory increases, but they start to rise again when the scale of inventory is further increased. Moreover, the contribution of inventory costs to total expenditure would be minor, if the number (or area) of protected stands, i.e. opportunity costs, were larger. In that case, we would likely see more clear trade-offs in benefits between the use of indicators and large-scale species inventory. The use of an indicator costs less than extensive species inventories at a low level of conservation, but at a higher level, such inventories may be reasonable by reducing the opportunity costs of conservation due to a more efficient selection of protected areas (Balmford and Gaston, 1999).

Ecological models lead to a different ranking of indicators compared with the integrated models, thus it is very important to include opportunity and inventory costs into the analysis.

However, according to our findings, there seems to be no indicator group which would be unambiguously better than any other group. Beetles turned out to be a good indicator group relative to the other groups at a high level of conservation, despite the high inventory costs. Thus, it may be reasonable to execute an expensive inventory for beetles, when the task is to complement a large existing conservation network which already covers less species rich taxa. Beetles are good indicators also in the absence of inventory costs. These results support the view that the inclusion of invertebrates into biodiversity surveys may offer cost savings (see Oliver et al., 1998). Vascular plants seem to be the best indicator, although they are not usually considered as a potential indicator group for species diversity in boreal old-growth forests, because usually vascular plant diversity is low in coniferous boreal forests (Esseen et al., 1997).[9] One explanation for our findings might be the fact that the diversity of vascular plants is highest in stands with the lowest opportunity costs (spruce mires forest type, see Juutinen et al. 2003, see also Section 3.) Birds are also relatively good indicators when the selection of protected stands is based on the INUM model. Inventory costs are low, and scoring algorithms ensure that enough information is available for ranking all stands despite of the low number of species of birds.[10] Wood-inhabiting fungi seems to be a rather demanding group to protect, and it is a rather poor indicator for overall species diversity. Also the so-called old-growth forest indicator species are relatively poor indicators for all species richness. It is likely that low species richness, combined with relatively high inventory costs, reduce the effectiveness of this group.

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[9] Regional studies in Australia, South Africa and United States have also found, that vascular plants may be a useful indicator taxon (Panzer and Schwartz, 1998; Pharo et al., 2000; Reyers et al., 2000).

[10] Respectively, Reyers et al. (2000) found that in South Africa birds were a better indicator group in hot spot selection than in complementary selection, even though the number of bird species was the largest among the considered taxonomic groups (birds, butterflies, mammals, and vascular plants).

We treated all species as equally important in the benchmark, assuming that the aim of conservation is to protect all naturally occurring species in the region. However, threatened and rare species are often primary targets in conservation (e.g. Kershaw et al., 1995) and it is possible that wood-inhabiting fungi and old-growth forest indicator species would be better indicators for threatened and rare species than for overall species diversity (see e.g. Similä et al., 2002b). Also population viability is an important aspect of conservation (Cabeza and Moilanen, 2001). Viability is a function of the number of individuals, and therefore, the abundance of species in addition to their presence/absence could be used as a surrogate measure (e.g Montgomery et al., 1999, see also Noss, 1999). However, here we may end up with similar problems as with presence/absence data that the viability of one species populations may not be a reliable indicator of overall species viability. Our ecological knowledge is far too limited for identifying such umbrella species, whose viability would ensure the persistence of species diversity more generally. An example of one potential umbrella species in boreal forests is the white-backed woodpecker. Martikainen et al. (1998) found that the presence of the woodpecker clearly indicated high species richness of threatened beetle species as well.

According to our results, the scoring models (INUM) were generally better than the models based on complementarity (IDIV). Previous studies have suggested that the scoring procedure results in biased conservation, because redundant sites may become selected (Pressey and Nicholls, 1989; Sætersdal et al., 1993). However, our approach differs from fixed scoring because we also considered conservation costs and the allowable budget for conservation. When scoring models include a budget constraint, they seem to have properties similar to the integrated complementarity models, which take the species composition of the stands into account (see Juutinen et al., 2003).

Our results, that decaying wood is not very effective indicator of overall species diversity in boreal forests, match well with the earlier findings that dead wood, in general, does not predict overall species diversity very accurately. Similä et al. (2002b) found that the number of wood-inhabiting fungi species was correlated with the amount and diversity of dead wood, but in other taxa, only weak correlations were found. Only wood-inhabiting fungi of the species groups in this study are completely dependent on decaying wood. Of the other taxa, only beetles contain a considerable proportion of species (163 species, 37%) that are saproxylic, i.e. directly dependent on dead wood. The quality of decaying wood has been found to be a reliable surrogate of species diversity for many saproxylic species groups (for review, see Siitonen, 2001).

We found decaying wood to be relatively unimportant as an indicator, because a large proportion of the boreal forest species in our study are not directly dependent on dead wood. Moreover we did not select the stands for this study to specifically test the role of decaying wood, and therefore, the variation among stands in the amount of dead wood was not pronounced (14- 93 m^3/ha). In particular, we did not have any stands with very low amounts of dead wood. We also found that the cost-efficiency of decaying wood as an indicator for overall species diversity in boreal forests was relatively low despite of low inventory costs. The usefulness of decaying wood as an indicator depends on the goal of conservation, and it may be a cost-efficient surrogate for threatened saproxylic species (see Siitonen, 2001), but the overall performance in our study was less than desired.

Given that the use of an indicator seems to result in a loss of overall diversity, this also brings up many important general issues. Is the loss real? Our ecological knowledge is incomplete and we are dealing with several measurement problems. If the loss is likely, are we ready to accept it and consider the trade-offs between biodiversity benefits and other

benefits? Assessing these questions involves value judgments, which reflect social preferences for ecological risks and biodiversity benefits versus the costs of conservation.

6. Summary and conclusions

We tested how effective species indicators and an indicator based on the structural characteristics of forests are for all species diversity by using both an ecological (E) and integrated (I) approach. Moreover, we used models based on complementarity (DIV) and scoring (NUM). Our main conclusion is not too positive: there seems to be fairly few alternatives for a complete inventory of biodiversity if the goal is to maintain populations of all species in the landscape. The use of site selection based on individual taxonomic groups, species set of old-growth forest indicator species and decaying wood all seem to result in a loss of overall biodiversity, as has been found also in previous studies (Pantzer and Schwartz, 1998; Pharo et al., 2000; Reyers et al., 2000; Virolainen et al., 2000). Therefore, it is very important to consider trade-offs between conservation costs and diversity loss when assessing the goodness of an indicator. Considerable conservation costs may be incurred from using surrogate measures, although the use of indicators seems to cost less than a broad species inventory for optimisation in our small case study. More studies, however, are needed to reveal whether, in general, it is more beneficial to use an indicator or to execute a broad species inventory (cf. Balmford and Gaston, 1999). According to our findings, vascular plants and birds are the most cost-efficient indicators for species diversity in boreal old-growth forests in the given region, particularly if the INUM model is used for the site selection. This is partly because obtaining data for these species groups is relatively cheap. Thus, they may be suitable indicators for overall species diversity to be used in landscape ecological forest management. If decaying wood is used as a surrogate for species diversity, it seems that the

volume of decaying wood is more important than the quality. However, decaying wood may only be a suitable indicator for certain species associated with dead wood, rather than for overall biodiversity. Threatened species are particularly numerous within saproxylic species (Rassi et al., 2001).

The results demonstrated that the efficiency of a considered indicator is dependent on several factors, and therefore, the comparison between indicators is not straightforward. First, inventory costs strongly affect efficiency. In general, small inventory costs result in high efficiency. In practice, inventory costs can vary widely due to the different sampling methods (Balmford et al., 1996; Oliver and Beattie, 1996; Howard, 1998; Lawton et al., 1998; and Oliver et al., 1998). Secondly, the use of an indicator may increase the opportunity costs of conservation compared with cost-effective protection. However, this may vary at different budget levels (cf. Balmford and Gaston, 1999). Thirdly, the optimisation procedure also affects the results (cf. Reyers and Van Jaarsveld, 2000). The scoring approach (NUM) was suitable for small taxonomic groups and the complementarity model (DIV) for large species groups. Moreover, when the number of species is small in the group under consideration, the operative range of the indicator is narrow, because the considered species may be all protected with a rather small budget. Overall, the results support the view that the selection of an indicator depends ultimately on the goals and the constraints of a conservation study (Caro and O'Doherty, 1999; Reyers et al., 2000; Reyers and Van Jaarsveld, 2000). It is therefore very important to set explicit goals in the forest planning process (see Noss, 1999).

Finally, we caution against straightforwardly generalizing our results to other regions and forest areas, but emphasize the need for local knowledge on species composition and ecological conditions. We stress the importance of taking opportunity and inventory costs into account if the aim is cost-effective protection. Moreover, in order to find cost-effective surrogates for overall species diversity, we should develop cheaper sampling methods,

particularly, for taxa having a large number of species, such as beetles. An alternative would be to identify taxon-specific indicators (Oliver and Beattie, 1996; Oliver et al., 1998; Panzer and Schwartz, 1998) For example, Similä et al. (2002b) found that species richness in a set of wood inhabiting fungi indicator species correlated strongly with the species diversity of these fungi more generally. To conclude, we developed a method for testing biodiversity indicators in the ecological and economic context simultaneously and recommend that this integrated approach would be used instead of the ecological tests used previously.

Acknowledgements

Appendix 1: Pattern of species representation in the selected network, plotted as a function of the opportunity costs, based on the benchmark model (IDIV).
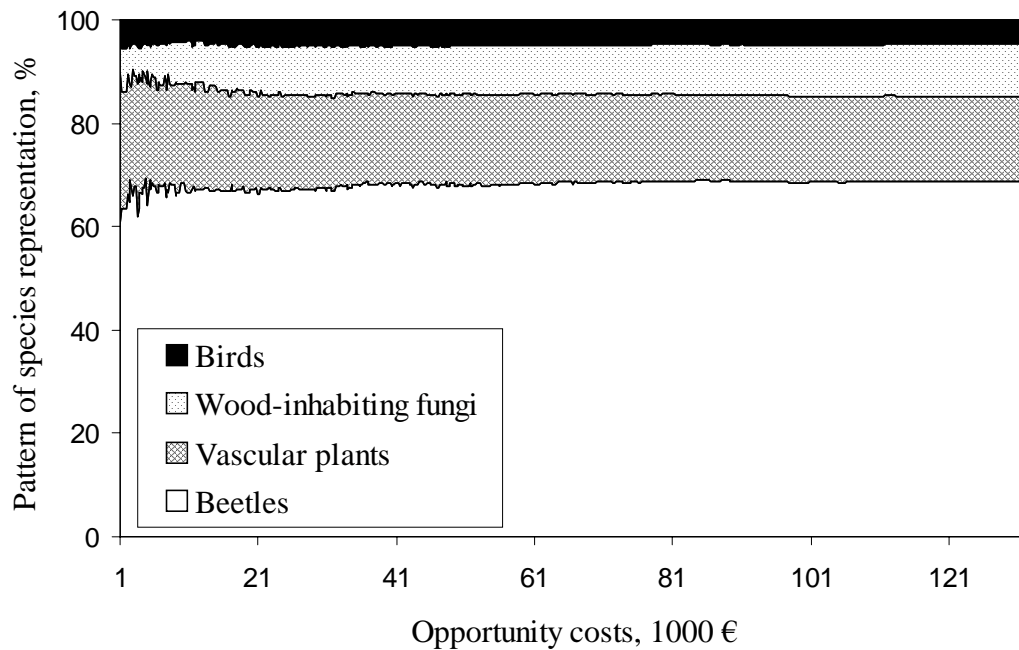
Appendix 2: The notation used in Table 1.

Z Surrogate biodiversity measure,

j, J index and set of potential reserve sites,

x_j 1 if stand j is selected and 0 otherwise,

i, Z_s index and set of species in the indicator model,

y_i 1 if species i is contained in at least one of the selected stands and otherwise 0,

y_{ij} 1 if species i is contained in the stand j and otherwise 0,

N_i the subset of candidate reserve stands that contains species i,

k number of sites allowable for reserve network,

B budget allowable for reserve network,

b_j opportunity costs of establishing a reserve stand j,

I_s inventory costs of surrogate measure,

i, Q index and set of quality classes of decaying wood,

q_i 1 if the decaying wood quality class i is contained in at least one of the selected stands and otherwise 0,

M_i subset of candidate reserve stands that contains the decaying wood quality class i,

v_j volume of decaying wood in the stand j,

a, b   weight parameters for the volume and quality factors of decaying wood.

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Table 1. Site selection models. Site constraint is used in the ecological models (E), and a budget constraint in the integrated models (I). Notation is explained in Appendix 2.

EDIV* & IDIV**	ENUM* & INUM**	EDW* & IDW**	
$\underset{\{x,y\}}{Max}\,Z = \sum_{i \in Zs} y_i$	$\underset{\{x\}}{Max}\,Z = \sum_{i \in Zs}\sum_{j \in J} y_{ij}x_j$	$\underset{\{x,q\}}{Max}\,Z = a\sum_{j \in J} x_j v_j + b\sum_{i \in Q} q_i$	(1)

Subject to

$\sum_{j \in Ni} x_j \geq y_i \quad \forall i \in Zs$		$\sum_{j \in Mi} x_j \geq q_i \quad \forall i \in Q$	(2)
$\sum_{j=1}^{n} x_j \leq k$	$\sum_{j=1}^{n} x_j \leq k$	$\sum_{j=1}^{n} x_j \leq k$	(3)*
$\sum_{j=1}^{n} b_j x_j + I_s \leq B$	$\sum_{j=1}^{n} b_j x_j + I_s \leq B$	$\sum_{j=1}^{n} b_j x_j + I_s \leq B$	(4)**
$x_j, y_i \in \{0,1\} \quad \forall i \in Zs, \forall j \in J$	$x_j \in \{0,1\} \quad \forall j \in J$	$x_j, q_i \in \{0,1\} \quad \forall i \in Q, \forall j \in J$	(5)

Table 2. Total inventory costs for different indicators.

Inventory costs	€
Beetles (435 spp.)	34 479
Birds (30 spp.)	2 691
Vascular plants (103 spp.)	3 868
Wood-inhabiting fungi (64 spp.)	5 718
Old-growth forest indicators (42 spp.)*	31 788
Decaying wood (amount in 114 quality classes)	4 205

* Include all inventory costs of beetles, birds, and wood-inhabiting fungi, except that the costs of species identification were reduced to correspond to the lower number of considered old-growth forest species.

Table 3. Mean cost difference $(=(C_{bench}-C_{ind})/C_{bench}*100)$ between indicator species groups and benchmark at different levels of species represented in the selected network relative to total species number (%), based on the IDIV models. The last row includes the mean cost difference calculated over the whole range, where the particular indicator is operative. The mark (–) indicates the range, where the indicator is not operative.

Range of species represented	IDIV models				
	Vascular plants	Wood-inhabiting fungi	Birds	Beetles	Old-growth forest indicator species
1-60 %	84	79	83	24	20
61-70 %	69	60	63	20	-3
71-80 %	55	38	-	17	-27
81-90 %	45	15	-	13	-
91-100 %	-	-	-	7	-
1-100 %	68	56	79	14	12

Table 4. Mean cost difference (=(C_{bench}-C_{ind})/C_{bench}*100) between indicator species groups and benchmark at different levels of species represented in the selected network relative to total species number (%), based on the INUM models. The last row includes the mean cost difference calculated over the whole range, where the particular indicator is operative. The mark (–) indicates the range, where the indicator is not operative.

Range of species represented	INUM models				
	Vascular plants	Wood-inhabiting fungi	Birds	Beetles	Old-growth forest indicator species
1-60 %	81	78	84	24	26
61-70 %	71	66	72	20	19
71-80 %	58	56	61	17	7
81-90 %	41	41	46	12	1
91-100 %	26	18	26	5	-3
1-100 %	48	44	53	13	8
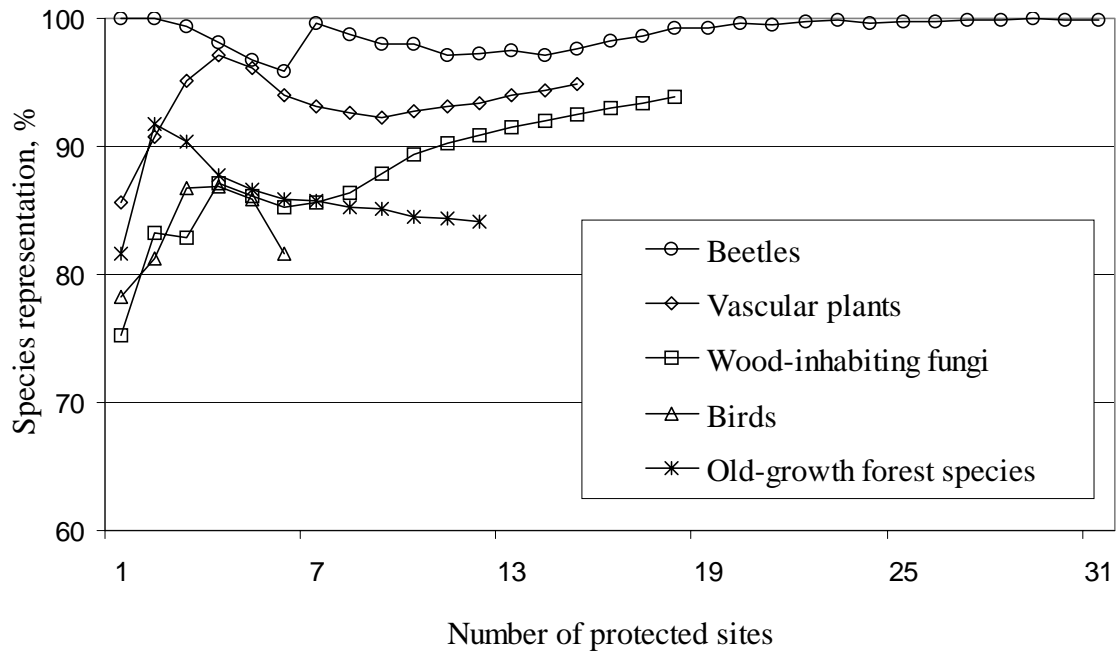
Figure 1. Mean species representation (%) of the taxonomic group indicators compared to the benchmark model (=100), plotted as a function of the number of protected sites, based on the EDIV model.
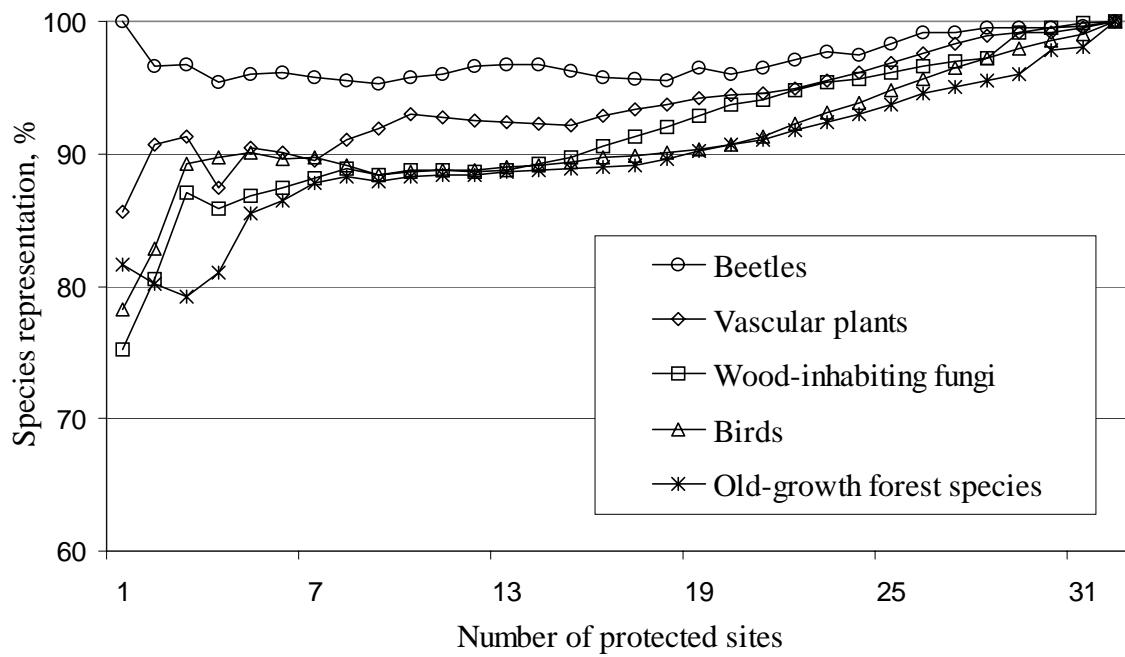
Figure 2. Mean species representation (%) of the taxonomic group indicators compared to the benchmark model (=100), plotted as a function of the number of protected sites, based on the ENUM model.
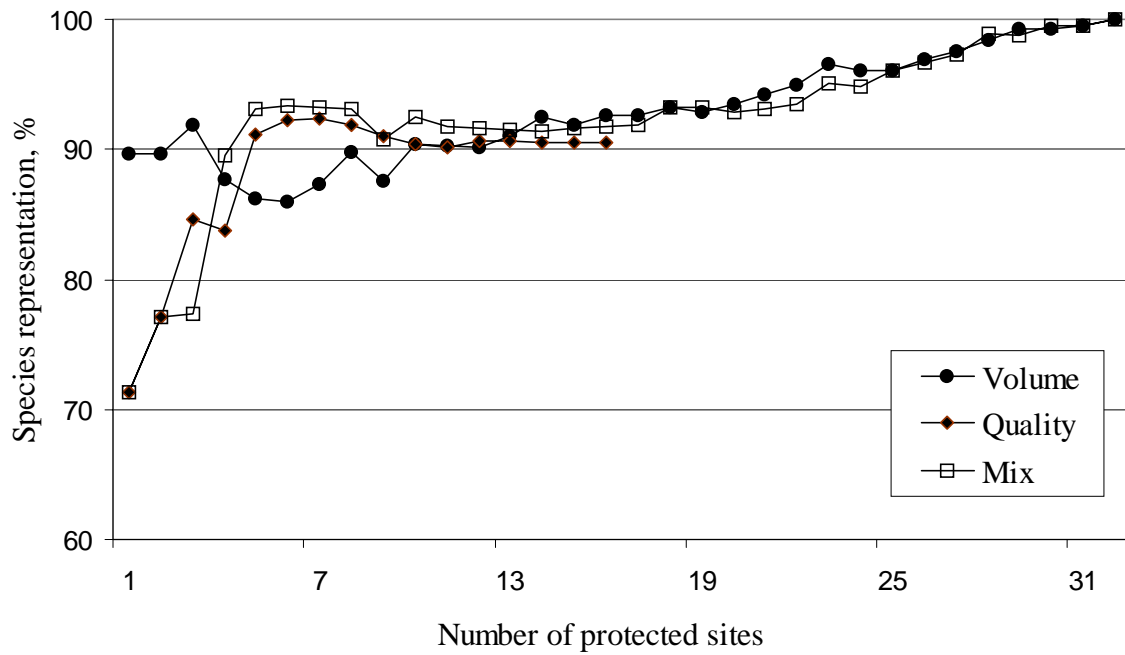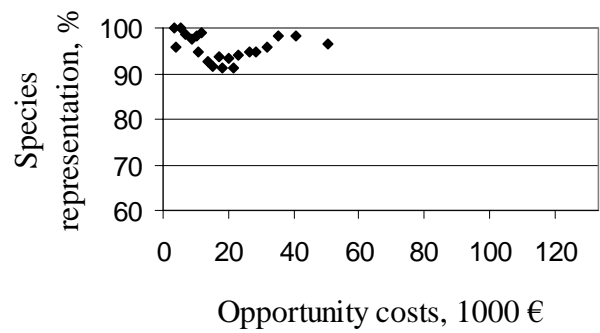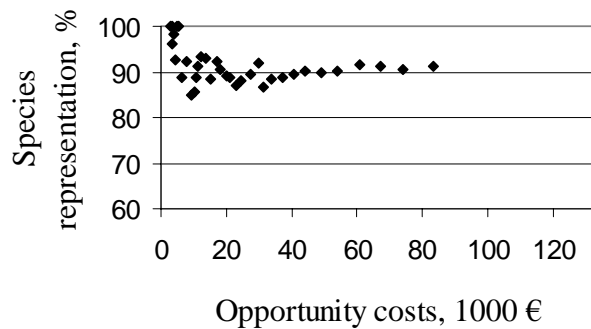
Figure 3. Mean species representation (%) of the decaying wood indicators compared to the benchmark model (=100), plotted as a function of the number of protected sites, based on the EDW model.

a) Beetles and birds
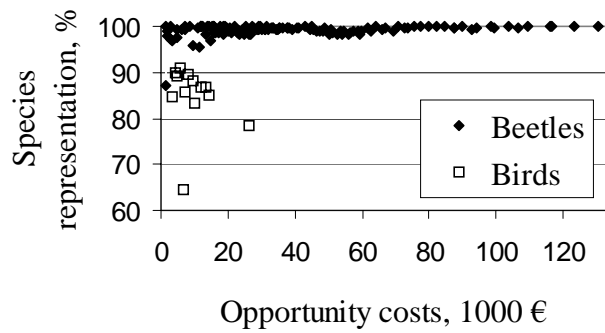
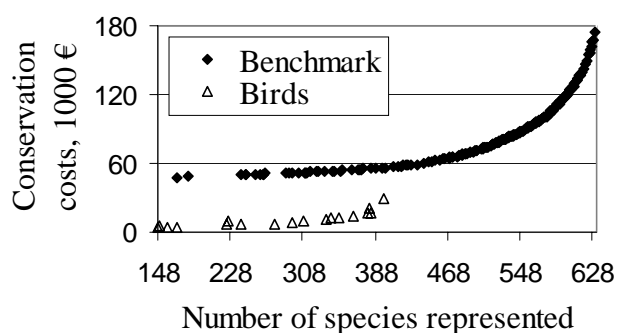b) Vascular plants

c) Wood-inhabiting fungi

d) Old forest species
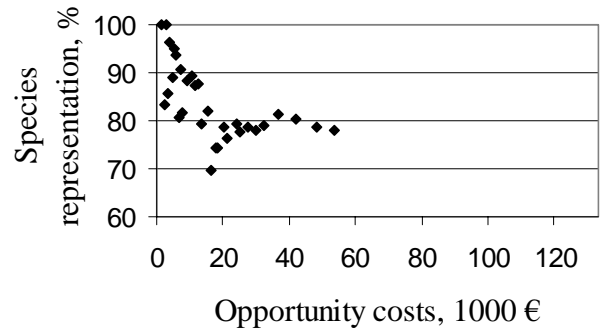
Figure 4. Relative number of species represented (= $(1-(Y_{bench}-Y_{ind})/Y_{bench})*100$) in the selected conservation network, plotted as a function of opportunity costs, based on the IDIV model excluding inventory costs using (a) beetles and birds, (b) vascular plants, (c) wood-inhabiting fungi, and (d) old-growth forest indicator species.
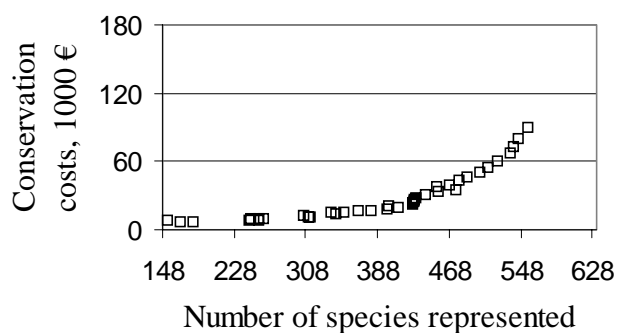
a) Benchmark and birds

b) Beetles and vascular plants
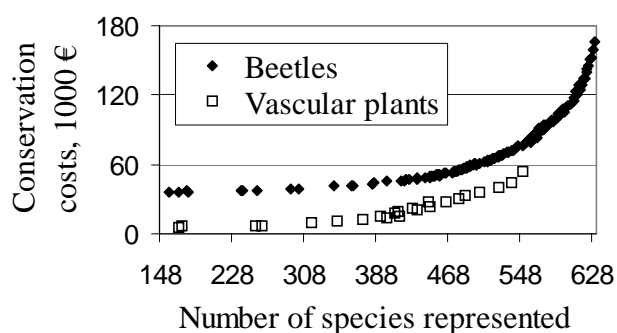
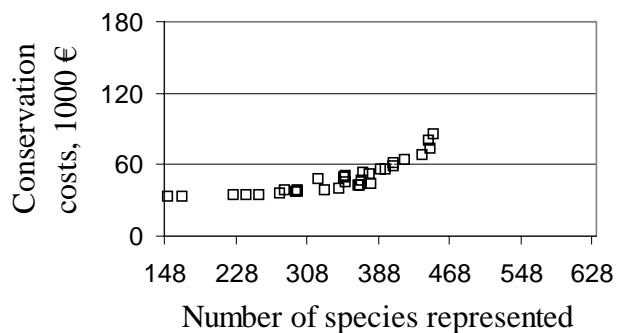c) Wood-inhabiting fungi

d) Old forest species

Figure 5. Conservation costs plotted as a function of the number of species represented in the selected conservation network, based on the IDIV model using (a) benchmark (all species) and birds, (b) beetles and vascular plants, (c) wood-inhabiting fungi, (d) old-growth forest indicator species.