
Cost-Efficiency of Decaying Wood as a Surrogate for Overall Species Richness in Boreal Forests

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Abstract: *Decaying wood is one of the most important elements for species richness in boreal forests. We tested how well reserve selection based on the amount and quality of decaying wood results in a representation of four ecologically different taxa (beetles, birds, wood-inhabiting fungi, and vascular plants). We also compared the cost-efficiency of the use of dead-wood indicators with comprehensive species inventory. Our database included 32 seminatural old-forest stands located in northern Finland. Decaying wood was a relatively good indicator of saproxylic species but not overall species richness. Even though dead wood did not reflect accurately overall species richness, our results indicated that the use of decaying wood as an indicator in site selection was more cost-efficient than using information from large-scale species inventories. Thus, decaying wood is a valuable surrogate for species richness, but other cost-efficient indicators that reflect the requirements of those species which are not dependent on decaying wood should be identified.*

Key Words: biodiversity, forest management, indicators of species richness, site selection

La Rentabilidad de la Madera en Descomposición como un Sustituto de la Riqueza Total de Especies en Bosques Boreales

Resumen: *La madera en descomposición es uno de los elementos importantes para la riqueza de especies en bosques boreales. Probamos como resulta la selección de reservas con base en la cantidad y calidad de madera en descomposición en la representación de cuatro taxa ecológicamente distintos (escarabajos, aves, hongos habitantes en la madera y plantas vasculares). También comparamos la rentabilidad del uso de indicadores de madera muerta con inventarios integrales de especies. Nuestra base de datos incluyó 32 sitios de bosque maduro seminatural localizados en el norte de Finlandia. La madera en descomposición fue un indicador relativamente bueno de especies saproxílicas pero no de la riqueza total. Aunque la madera en descomposición no reflejó la riqueza total con precisión, nuestros resultados indicaron que el uso de madera en descomposición como un indicador en la selección de sitios fue más rentable que el uso de información de inventarios de especies de gran escala. Por lo tanto, la madera en descomposición es un sustituto valioso de la riqueza de especies, pero se deben identificar otros indicadores rentables que reflejen los requerimientos de aquellas especies que no dependen de la madera en descomposición.*

Palabras Clave: biodiversidad, gestión de bosques, indicadores de riqueza de especies, seleccion de sitios

Introduction

Decaying wood is one of the most important elements for species richness in boreal forests. A recent survey

estimates that some 4000–5000 species, or 20–25% of all forest-dwelling species, depend on dead-wood habitats in boreal forests in Finland (Siitonen 2001). Regarding the entire boreal zone, several tens of thousands of

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species depend on dead-wood habitats. Because of these high numbers, decaying wood could perhaps be used in biodiversity management to indicate species richness in general.

Biodiversity indicators should represent key attributes of important ecological characteristics that are too difficult or expensive to be monitored directly. Several a priori 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 widely applicable, independent of sample size, and sufficiently sensitive to provide an early warning of change. Formal tests, however, are required to assess precisely how well the chosen indicators reflect the overall species richness.

The usefulness of an indicator depends on the final goals (i.e., what a given conservation project aims to protect) and, consequently, on what the indicator is supposed to indicate. Therefore, a test of indicators should be tailored according to the goals. Three different test approaches have been used: (1) correlated species counts, (2) coincidence of species hotspots, and (3) representativeness of species composition (Flather et al. 1997). The first approach is based directly on statistical examination of covariation in species richness among groups of organisms. The other two approaches are used in the context of site selection. Reyers and van Jaarsveld (2000) divide the coincidence approach further into two categories: degree of spatial overlap between reserve networks based on different taxa and comparison of selection order of sites within reserve networks. The representativeness technique investigates how well each reserve network, identified on the basis of an indicator, captures overall species richness in the region.

Results of several studies show a positive association between the amount of decaying wood (often called coarse woody debris [CWD]) and richness of species that depend on decaying wood (saproxylic species; e.g., Mac Nally et al. 2001; Siitonen 2001; Grove 2002). This is indicative of the tight link between habitat availability and species richness, the so-called species-area relationship (e.g., Rosenzweig 1995). It is not known whether dead wood is an indicator of overall species richness in forest ecosystems. Such a relationship would be expected if CWD is positively associated with ecological characteristics and conditions of sites that are important for species not directly dependent on dead wood. Large amounts and high diversity of dead wood quality usually signify low intensity of forest management. Therefore dead wood may be a surrogate for other ecologically important characteristics resulting from natural succession processes that are more difficult to perceive and measure than dead wood.

The usefulness of an indicator also depends on how difficult and costly it is to measure. Dead wood is clearly visible, relatively easy to measure, and probably much cheaper to assess than species richness. Full ecological

surveys of species composition of a site tend to be laborious, time-consuming, and, unlike CWD measurements, affected by temporal variation in species abundances and distribution. Coarse woody debris may therefore be a cost-efficient indicator of site quality for preserving species richness in forest ecosystems.

Methods

General Outline

We used the representativeness approach to test how well reserve selection based on the amount and quality of decaying wood results in a representation of four ecologically different taxa (beetles, birds, wood-inhabiting fungi, and vascular plants) in boreal forest ecosystems. These taxa are ecologically dependent on very different resources. Our work is among the first quantitative tests in boreal regions to detect whether site selection based on decaying wood or any other structural indicator of forests also results in preserving species richness of a landscape. Siitonen et al. (2002) used CWD as one criterion in site selection for protection in a forest landscape in northern Finland, but they did not have data to assess how presence of CDW ensures that species richness is also encompassed by the selected network of stands.

To execute the test we followed the approach developed by Juutinen and Mönkkönen (2004) and integrated the ecological and economic aspects of the use of an indicator. We first ran the site-selection procedures with optimization algorithms tailored for maximizing the amount and/or diversity of decaying wood. Thus we developed site-selection models that take into account the quantity and quality of decaying wood because both these factors affect species composition and population viability in boreal forests. Second, to generate a benchmark (baseline) site selection with which CWD site selection can be compared, we carried out optimization procedures in which species richness was maximized with data on several species. The benchmark selection represents, by assumption, the maximum level of species richness that can be conserved in the region for a given amount of resources. These resources can be expressed in physical (i.e., an area constraint) or monetary terms (i.e., a budget constraint). A comparison between the site selections based on the optimization of CWD and the overall species composition under a given area constraint reveals how well decaying wood reflects overall species richness. Whereas a similar comparison with associated inventory and opportunity costs reveals how cost-efficiently species richness is protected when using information on the CDW indicator only. To interpret the results of these comparisons we executed several sensitivity analyses.

We used the number of species encompassed in the selected network of forest areas as the criterion for

biodiversity assessment in the benchmark models because one of the ultimate long-term goals of the present forest landscape 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 (e.g., genetic, taxonomic, functional) measures of biodiversity (Gaston 1996). We acknowledge, however, that species richness may not correlate with viability of individual or multiple species (Cabeza & Moilanen 2001; Arponen et al. 2005). Our data originate from 32 old-growth forest stands in northeast Finland within two areas of landscape-ecological forest management. We use lost harvesting revenues (commercial forest values) as opportunity costs of conservation.

Data

We used a database that included 32 seminatural 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] for a more detailed description of the study sites.) We sampled eight sets of stands representing each of the following four types of forest sites: xeric coniferous forests (*Vaccinium-Myrtillus/Empetrum-Vaccinium* type), mesic spruce forests (*Vaccinium-Myrtillus* type), spruce mires (a heterogeneous 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 gradient of forests in this region and represent a fertility gradient ranging from barren pine heaths to herb-rich forests.

We sampled each stand for beetles, birds, wood-inhabiting fungi, and vascular plants. We selected these taxa 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 5 window traps, set out as the 5 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 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 minutes/visit), between early and late June. Vascular plants were surveyed between mid-July and early August 1998 from 10 1-m² squares on each stand, located on a line 5 m apart approximately in the center of the stand.

To include the opportunity costs of conservation, we calculated the commercial forest value (timber and land value) for each stand with a forest-planning model called MELA (Siitonen et al. 1996). The data on detailed stand characteristics for these site-value calculations were taken from Metsähallitus (the Finnish Forest and Park Service) forestry files (Metsähallitus, unpublished data). Because the use of total timber and land values would automatically bias the selection of sites under a budget constraint toward small stands, we used unit forest values (€/hectare) and treated stands as having equal sizes in the optimization. (See Juutinen et al. 2004 for a more detailed description of the site values.)

We measured the amount and quality of dead wood in five circles (radius 10 m) at each study site (1570 m²/site; dispersion of circles similar to beetle traps). The quality of dead wood was categorized into one of five classes according to the stage of decay: (1) wood hard and all bark remaining; (2) wood soft on surface, bark partly or completely loose; (3) wood soft throughout; (4) burned wood; and (5) snags. Downed logs and standing dead trees were kept separate. Tree species included pine, spruce, birch, aspen, and other species. The size categories of decaying wood were <10 cm, 10–30 cm, >30 cm, according to diameter. Altogether, there were 114 combinations of the dead-wood quality classes out of 150 possible combinations.

Table 1 shows the key features of the data according to the forest types. The average age of the stands is 138 years; thus, stands have exceeded the optimal commercial harvesting age, which is about 80–120 years. The number of species in a stand was on average 156. The herb-rich forests and spruce mires typically had more species than the other forest types, but there was a rather large variation in the number of species within every forest type. Commercially, the most valuable forest types are herb-rich stands and the sites with lowest commercial value are spruce mires. The variation of the site value was rather large within every forest type, indicating there were both low- and high-cost stands within each type. The mean amount of decaying wood was 45.7 m³/ha. The decaying wood typically consisted of 29 quality classes in a stand. The forest types seemed rather similar regarding the number of quality classes of decaying wood.

The data also included the costs of the species and decaying wood 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

Table 1. Key features of the stands used for the testing of decaying-wood indicators (mean \pm SD).

Forest type ($n = 8$)	Stand age (years)	No. of species	Site value (€/ha)	Amount of decaying wood (m^3/ha)	No. of quality classes of decaying wood
Xeric	128 \pm 9	153 \pm 11	4944 \pm 1499	42.2 \pm 17.0	29 \pm 6
Mesic	140 \pm 15	143 \pm 12	4447 \pm 2137	41.2 \pm 15.8	29 \pm 7
Spruce mires	137 \pm 20	166 \pm 15	2187 \pm 989	47.8 \pm 26.6	30 \pm 3
Herb rich	148 \pm 25	163 \pm 18	5211 \pm 2487	51.7 \pm 22.4	29 \pm 4
Total ($n = 32$)	138 \pm 19	156 \pm 16	4197 \pm 2150	45.7 \pm 20.3	29 \pm 5

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.

Site-Selection Models

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 is constrained by resources, which can be expressed as the number of stands (or an area constraint) or monetarily. We used the former in the ecological model and the latter in the integrated model. Cost-effective conservation under a given budget requires a forest manager to take into account the differences of commercial forest values (e.g., in the form of harvest revenues). The ecological approach implicitly assumes that stands have equal commercial forest values and partially neglects the economic costs of conservation.

We assumed that the only forest management option for biodiversity preservation is the protection of old-growth stands (nontreatment) so that the conservation problem can be formalized by using site-selection models. We used the following notation: Y , species richness; Z , surrogate biodiversity measure for species richness based on decaying wood; j, J , index and set of potential reserve sites, respectively; x_j , 1 if stand j is selected and 0 otherwise; i, S , index and set of species in the benchmark model, respectively; y_i , 1 if species i is contained in at least one of the selected stands, 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 species data; I_Q , inventory costs of decaying wood data; b, Q , index and set of quality classes of decaying wood, respectively; q_b , 1 if the decaying wood quality class b is contained in at least one of the selected stands, otherwise 0; M_b , subset of candidate reserve stands that contains the decaying wood quality class b ; v_j , volume of decaying wood in the stand j ; and a, b , weight parameters for the volume and quality factors of decaying wood, respectively.

The ecological benchmark model, presented as a maximal coverage problem (MCP; Camm et al. 1996), seeks to

maximize species richness in the selected conservation network subject to a given area constraint as follows:

$$\text{Max}_{\{x, y\}} Y = \sum_{i \in S} y_i, \quad (1)$$

$$\sum_{j \in N_i} x_j \geq y_i \quad \forall i \in S, \quad (2)$$

$$\sum_{j=J} x_j \leq k, \quad (3)$$

and

$$x_j, y_i \in \{0, 1\} \quad \forall i \in S, \forall j \in J. \quad (4)$$

The target function (1) sums the number of species in the selected stands. The constraint set (2) ensures that species i is counted as being represented when at least one of the stands where it occurs is selected. The model has a site constraint (3), where k is the given upper limit for the number of stands in the conservation network. The constraint set (4) indicates that the choice variables must be binary. Thus, the stands are either protected or harvested, and the species are represented in their entirety or not at all.

The ecological approach is also called a site-constrained site-selection problem (Polasky et al. 2001). Stands were selected by ecological criteria only. To maximize species richness in the network, it is optimal to select stands in which species composition differs as much as possible. Thus, the model selects stands that supplement each other from the viewpoint of species richness. In other words, this approach maximizes complementarity. The model is not, however, spatially explicit because it does not take into account the spatial configuration of the selected stands.

We tailored the site-selection model for the decaying wood. This model aims to maximize the volume and/or quality of decaying wood in the selected network subject to a given area constraint. The larger the volume, the more habitats there are for species associated with decaying wood. Different types of dead wood (e.g., snags vs. downed logs) and decaying phases (e.g., newly dead trees vs. well-rotted wood) represent habitats for different species. Many species depending on decaying wood are specialists with respect to certain habitat types. The model is as follows:

$$\max_{\{x, q\}} Z = a \sum_{j \in J} x_j v_j + b \sum_{b \in Q} q_b, \quad (5)$$

$$\sum_{j \in Mi} x_j \geq q_b \quad \forall b \in Q, \quad (6)$$

$$\sum_{j \in J} x_j \leq k, \quad (7)$$

and

$$x_j, q_b \in \{0, 1\} \quad \forall b \in Q, \forall j \in J. \quad (8)$$

The target function (5) sums the amount and different quality classes of decaying wood found in the selected conservation network. The relative importance of these factors was determined by the exogenous parameters a and b . The constraint set (6) ensures that the quality class b is counted as being represented when at least one of the stands where it occurs is selected. This model also has a site constraint (7), where k is the given upper limit for the number of stands in the conservation network. The constraint set (8) indicates that the choice variables must be binary. This implies that the stands are either protected or harvested and the quality classes are represented in their entirety or not at all. Therefore the quality aspect of decaying wood in this model is similar to the species richness in the previous model. As a result the decaying-wood model also takes into account the spatial interdependence of stands if quality is given a weight (i.e., $b > 0$). If only the amount of decaying wood is taken into account ($b = 0$) the model is similar to the so-called scoring procedure.

It is a value judgment to decide the relative importance of the volume and quality of CWD. 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 wood are the best targets for conservation. If a is set to zero, only the diversity of decaying wood types matters. In the analysis we use volume-only, quality-only, and mixed approaches, where the parameters are set such that both the volume and quality of decaying wood affect the selection of stands (parameter values used are $a = 1$ and $b = 10, 25, 50$).

These models can be easily transformed into the integrated models by replacing the area constraints (3) and (7) with following budget constraints (9) and (10), respectively:

$$\sum_{j \in J} b_j x_j + I_s \leq B \quad (9)$$

and

$$\sum_{j \in J} b_j x_j + I_Q \leq B. \quad (10)$$

A budget constraint ensures that the total costs of conservation, including the opportunity costs and inventory costs, do not exceed the funds allowable for a conservation network. The opportunity costs may vary between stands. We treated inventory costs as fixed costs and implicitly assumed that all the candidate stands have to be surveyed irrespective of how many of them will be protected (Balmford & Gaston 1999). Inventory costs depended only on the considered indicator so that they did not have a direct impact on the selection among stands because the relative values of the stands did not change. The benchmark model had typically greater inventory costs than the decaying wood model because it was more expensive to execute broad species inventories than to measure decaying wood.

If inventory costs are treated as fixed costs, it is likely that they will have a strong effect on the results, in particular when only a few stands (compared with the number of potential stands) are protected. Therefore we also used the following linear formulation of inventory costs in the analysis:

$$\sum_{j \in J} b_j x_j + \frac{I_s}{n} \sum_{j=1}^n x_j \leq B \quad (9')$$

and

$$\sum_{j \in J} b_j x_j + \frac{I_Q}{n} \sum_{j=1}^n x_j \leq B, \quad (10')$$

where n denotes the number of potential stands available for conservation. In these budget constraints we implicitly assumed that only the protected stands have to be inventoried because the unit inventory costs are multiplied by the number of protected stands. This is an unrealistic assumption because in practice one always has to inventory more stands than can be selected for the conservation network to find the best targets. With our approach, however, we can reveal the lower bound for the total conservation costs and assess the sensitivity of the results regarding the alternative treatments of inventory costs.

The indicators were tested with the following procedure. We denoted species richness as that given by the benchmark and decaying-wood models at a given resource constraint (B or k) by Y_{bench} and Y_{ind} , respectively. The difference between Y_{bench} and Y_{ind} indicates species loss based on the ecological approach and the area constraints. To determine Y_{ind} we first used decaying-wood models to maximize Z and identify the corresponding conservation network and species included at a given area constraint (k). To test the use of decaying wood as an indicator from the economic perspective we compared conservation costs (C) at a given level of species richness with the integrated approach. More precisely, using the previous notation for costs, C , we determined the difference between C_{bench} and C_{ind} at a given level Y . These

comparisons demonstrate the differences between ecological and economic approaches. We used commercial spreadsheet optimization software to solve our linear integer problems (Lindo Systems 2000).

It is not straightforward to express the outcomes of the decaying-wood models in terms of the number of species. For instance, the decaying-wood model, which is based only on the quality aspect and has an area constraint, usually has multiple optimal solutions (with several sets of stands all containing the same number of quality classes). Naturally, these alternative conservation networks may cover different numbers of species. In what follows, we used the average number of species calculated over the multiple optimal solutions to present the species coverage of this model. The variation behind these average results may be quite large, particularly when only a few stands are selected.

Similarly, the integrated decaying-wood models may have many solutions that contain the same number of species but have different conservation costs because they are not optimized with respect to species richness. When this happened, we used the average conservation costs calculated over these similar solutions to present the conservation costs of integrated models at every particular level of species coverage.

Selecting sites for protection using surrogates should lead to a higher level of species richness protected than in an equal number of randomly selected sites. We therefore formed random sets of sites for each level of the number of sites protected to provide a comparison with respect to dead-wood indicators. The number of random sets of sites at each level of the number of sites protected was 1000.

Our sample included many species (163 beetles and 64 wood-inhabiting fungi species) that are dependent on decaying wood. By removing these species from the species set and repeating the optimizations, we assessed how well the decaying-wood indicators represent those species that are not directly dependent on decaying wood. Similarly, we executed optimizations also for species dependent on decaying wood only.

Results

Ecological Aspect

The use of decaying wood as an indicator for overall species richness resulted in a loss of some species because decaying wood does not reflect the presence of species that are dependent on other resources (Fig. 1). The areas selected using the information on decaying wood, however, typically covered 90% or more of the species found in those areas that were selected based on species inventory information.

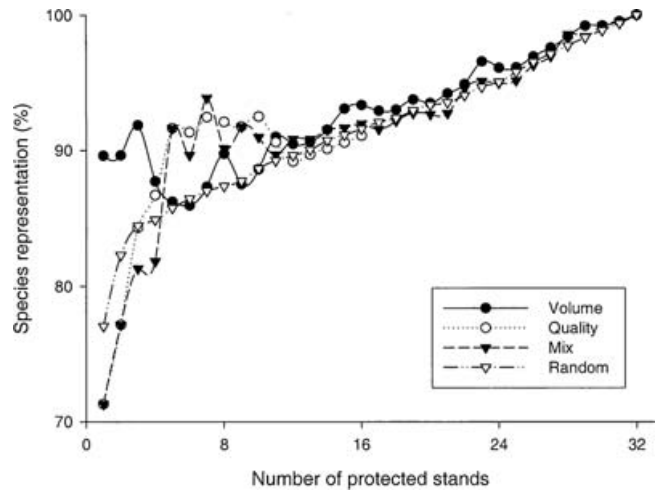


Figure 1. Mean species representation (%) of the decaying-wood indicators (volume, quality, volume + quality [mixed], random) compared with the benchmark model ($\epsilon = 100$, maximum level of species richness conserved in a region given amount of resources), plotted as a function of the number of protected sites and based on the ecological site selection. The parameter value $b = 25$ (b , weight parameter for quality indicator) was used in the mixed model. Random refers to relative species representation in randomly selected sets of sites at each level of number of protected stands.

The differences between species representations among the models were largest when only a few stands are selected. The difference lessened gradually as more areas became protected. Finally, the differences disappeared when all the stands were selected. It was not possible to select all the stands using the pure quality approach, however, because all the quality classes were covered when 16 stands were selected. On the contrary, when the volume aspect was incorporated into the site selection, all the stands could be prioritized because an extra unit of decaying wood always increased the ecological value of the conservation network.

The volume of decaying wood seemed a more effective surrogate for species richness than quality-based measures, particularly when a large number of stands were protected. The differences, however, between the mixed indicator, which included both the volume and the quality component of decaying wood, and the volume indicator alone were small. Also, the quality and mixed selections seemed to work better than the volume selection in ranges where some 5–10 stands were protected (Fig. 1). Overall, the selection based on decaying wood volume covered on average 93% of the species included in the benchmark. The mixed and quality-based selections covered 92% and 88% of the species, respectively. The latter figure was calculated over the range of 1–16 stands

and was therefore smaller than the two other figures. The comparative figures for this range of protected stands (1–16 stands) for the volume and mixed models were 90% and 88%, respectively.

On average random sets of sites covered 91% of the species included in the benchmark and 87% over the range of 1–16 stands. Therefore, dead-wood indicators in general performed only slightly better than random selection. Volume of dead wood was a relatively good indicator compared with random selection when only a few sites (1–4) were selected (Fig. 1). The quality and mixed model, on the other hand, performed markedly better than random selection at intermediate levels of protection (5–10 sites protected).

Another way to demonstrate the performance of the models is to consider how many stands are required to cover a certain number of species. To cover, for example, 500 species one needed to protect 10 stands picked by species richness, but 14 stands were required when the volume of decaying wood was used as a base for site selection. In other words, site selection based on information on decaying wood increased opportunity costs of conservation in terms of lost harvesting revenues.

Next we investigated how well the decaying wood indicators represent those species that are not directly dependent on decaying wood. The site selection based on decaying wood volume covered on average 90% of species compared with the benchmark (Fig. 2). The mixed and quality-based selections covered 88% and 83% of species, respectively. Thus, the species representation was lower

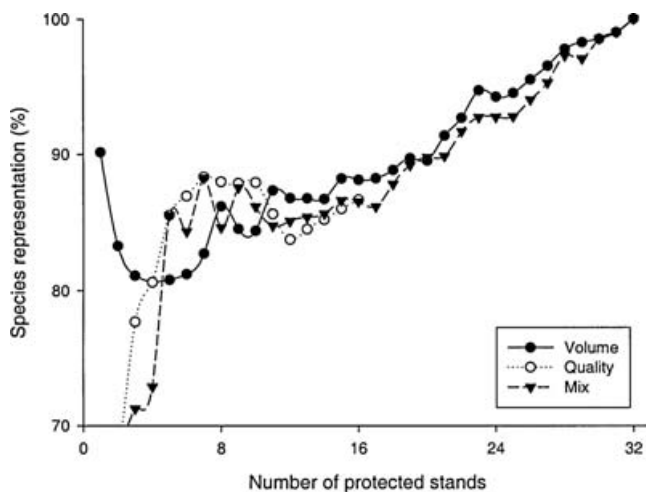


Figure 2. Mean species representation (%) of the decaying-wood indicators compared with the benchmark model ($= 100$), plotted as a function of the number of protected sites and based on the ecological site selection, excluding the species that depend on decaying wood. The parameter value $b = 25$ was used in the mixed model. (See Fig. 1 legend for more complete description of elements.)

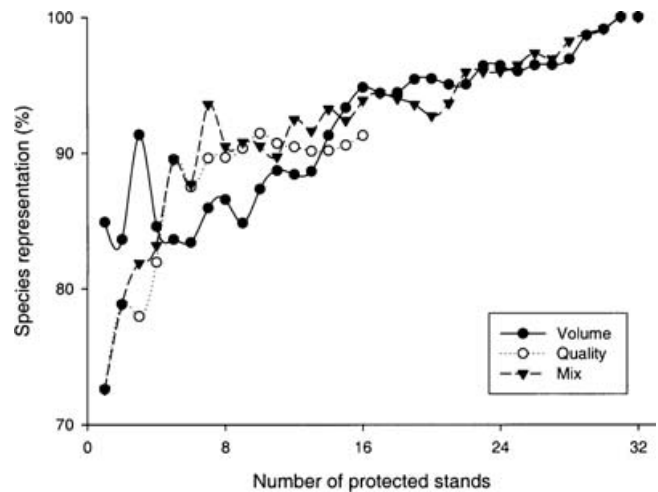


Figure 3. Mean species representation (%) of the decaying-wood indicators compared with the benchmark model ($= 100$), plotted as a function of the number of protected sites and based on the ecological site selection, including the species that depend on decaying wood only. The parameter value $b = 25$ was used in the mixed model. (See Fig. 1 legend for more complete description of elements.)

in these optimizations than in the original optimizations; otherwise, the patterns of the different models were quite similar (cf. Figs. 1 & 2).

We also executed optimizations for species dependent on decaying wood only (Fig. 3). Not surprisingly, dead-wood indicators performed relatively better, with minor exceptions, for species dependent on dead wood than for species not dependent on dead wood. In particular, the quality of decaying wood was more important to the species dependent on decaying wood than to the other species. Moreover, it seemed that the efficiency of indicators depended on the size of the sample (cf. Figs. 1 & 3).

It seemed that the results regarding species representation were not sensitive to the values of the weight parameters used in the mixed model (Eq. 5). We repeated the mixed optimizations with alternative values for the weight parameter b ($b = 10, 25, 50$) and found there was no consistent pattern; thus, any value of b (relative to a) performed better than others in terms of species representation.

Economic Aspect

We examined whether or not it is economically justified to select conservation areas by using information on decaying wood compared with information on species presence. Therefore, we examined two opposite hypotheses: (1) the use of decaying wood as an indicator increased the opportunity costs of conservation because decaying wood did not reflect fully the overall species richness as

was shown in the previous section and (2) the use of decaying wood reduced inventory costs compared with the use of large-scale species information.

First we present how much the use of decaying wood as an indicator in site selection increased the opportunity costs. For clarity, the results of mixed model are not presented, but they were similar to the results of the volume model. The volume of decaying wood seemed to be a more cost-efficient surrogate for species richness than the quality-based measure, particularly when a large number of stands were protected and the species coverage was high (Fig. 4). In contrast to previous findings (Fig. 1), there were no subranges, where the quality selection clearly worked better than the volume selection. Overall, the selection based on decaying wood volume increased opportunity costs on average 27% compared with the benchmark selection. In contrast to previous findings, the mixed model worked a little bit better than the volume model and increased opportunity costs by 25%. The selection based on the quality of decaying wood increased opportunity costs on average 42% compared with the benchmark selection. This figure was calculated over the range of 168–534 species, whereas in the other models the range was 168–632 species; therefore it was distinctively larger than the figures of the volume and mixed models. It is interesting that the mixed model worked better than the volume model, although the quality model seemed to work rather poorly in the integrated approach.

These differences must not be interpreted to mean decaying wood would not be a cost-efficient indicator for species richness. The total costs (including both the opp-

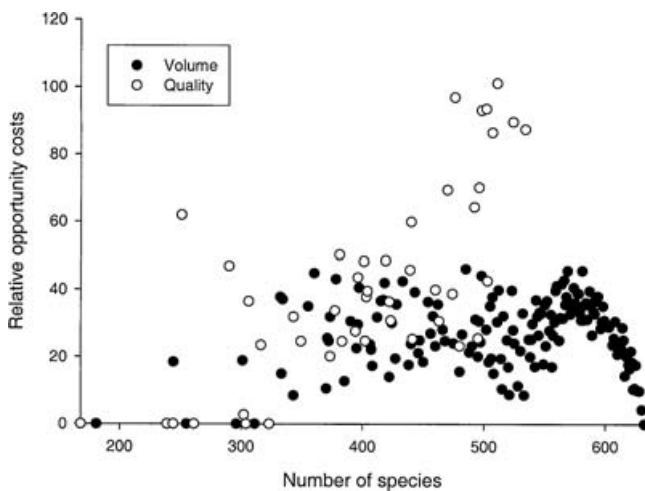


Figure 4. The relative opportunity costs of the decaying-wood indicators (volume, quality), plotted as a function of the number of species represented in the selected conservation network. The costs are compared with the benchmark selection (see Fig. 1 legend). Thus, a value of 50 for another selection method means 50% higher costs than in benchmark selection.

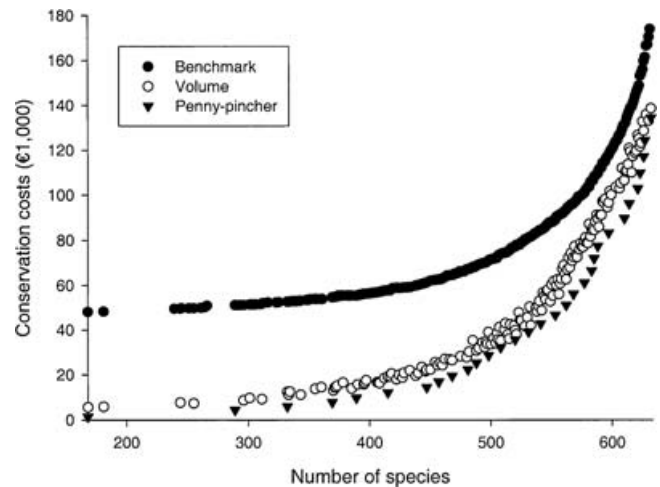


Figure 5. Conservation costs (including opportunity and inventory costs) of the volume, benchmark (see Fig. 1 legend), and penny-pincher selections, plotted as a function of the number of species represented in the selected conservation network. In the penny-pincher selection the aim is to minimize the opportunity costs of conservation subject to a given lower bound for the number of protected areas.

portunity and inventory costs) of the benchmark model were always higher than the costs of the volume model (or the other two decaying-wood models; Fig. 5). Thus, it was economically more efficient to use information on decaying wood in the site selection than to use information on species compositions when inventory costs were included. Altogether, the species survey cost €46,756. The costs for beetles, birds, vascular plants, and wood-inhabiting fungi were €34,479, €2,691, €3,868, and €5,718, respectively. The decaying wood survey cost €4,205. Hence, the species survey costs were about 11 times more than the decaying wood survey, primarily because of difficulty in surveying and identifying the beetles.

Using decaying wood as an indicator, however, may not be cost-efficient either (Fig. 5). For example, the site selection, hereafter termed penny-pincher selection, where the conservation network was established beginning with the lowest-cost sites to get as large an area as possible under conservation with given funds available for conservation, always incurred lower costs than the decaying-wood-volume-based selection (see Juutinen et al. 2004 for a more detailed description of penny-pincher selection). The penny-pincher selection did not need ecological information after the potential areas were identified and therefore incurred no inventory costs.

In the previous analysis, we implicitly assumed that all the potential stands had to be inventoried no matter how many of them would be protected. Naturally, therefore, the fixed inventory costs had a dominating role in the results, particularly at low levels of species coverage

(Fig. 5). Accordingly, it was economically more efficient to use information on decaying wood in the site selection than to use information on species compositions. This conclusion, however, did not depend on whether we inventoried all potential stands or only the selected stands. The same pattern emerged in the optimizations, which used linear inventory costs (Eqs. 9' & 10') instead of fixed costs (Eqs. 9 & 10). The cost differences between the alternative selections were, however, quite small, and there were 2 out of 165 possible solutions in which the conservation costs were slightly larger in the dead-wood-volume-based model than in the benchmark model. Thus, if one has to make inventories on more stands than can be protected eventually, the cost differences of the alternative selection methods would automatically get larger and the benchmark model would have the largest costs.

Discussion

Our result, that decaying wood is not a comprehensive indicator of overall species richness in boreal forests from an ecological viewpoint, matches well with the earlier findings that dead wood, in general, does not predict overall species richness very accurately. For instance, Similä et al. (2005) found that the number of species of wood-inhabiting fungi correlates with the amount and diversity of dead wood, but there are only weak correlations among dead wood and other taxa. Only wood-inhabiting fungi of the species groups in this study were completely dependent on decaying wood. Of the other taxa, only beetles contained a considerable proportion of species (163 species, 37%) that are saproxylic (i.e., directly or indirectly dependent on dead wood).

The stands in this study, however, were not originally selected 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 m³/ha). In particular, we did not have any stands with very low amounts of dead wood. It is likely that species richness would be lower in stands with low amounts of dead wood than in the stands with high amounts of dead wood (Martikainen et al. 2000). In these circumstances indicators would perform better at separating effectively the high-quality stand from low-quality stands (Howard et al. 1998; Virolainen et al. 2000).

From an ecological viewpoint, it seems that the volume of decaying wood was a more important surrogate for overall species richness than the quality of decaying wood. At the intermediate levels of site selection, however, the quality and mixed models performed better than volume, and random selection performed as well as dead-wood models when a higher number of sites were selected. The “saturation effect” may explain the phenomenon: at the beginning of the selection the in-

crease of dead-wood quality, or the quality and volume together, effectively selected sites with high saproxylic richness. When most of these sites were included in the conservation network, selection of sites with nonsaproxylic species increased the species representation as effectively as dead-wood indicators.

When the dead-wood indicator was used in selection of saproxylic species, the applicability of the quality of decaying wood was even better than for all other species (cf. Figs. 2 & 3). This supports earlier studies in which the quality of decaying wood was a reliable surrogate of species richness for many saproxylic species groups (for a review, see Siitonen 2001).

Thus, decaying wood seems a more suitable indicator for species richness of species associated with dead wood than for overall species richness. In particular, it may be a useful indicator for many threatened species (Berg et al. 2002), which are numerous among saproxylic species (Rassi et al. 2001). It has to be remembered, however, that the quality model we used takes into account only the number of decaying-wood quality classes and not differences in the decaying-wood quality per se, which are important for many threatened saproxylic species (Speight 1989; Samuelsson et al. 1994; Rassi et al. 2001).

Juutinen and Mönkkönen (2004) tested how alternative species groups work as indicators for overall species richness and how cost-efficient their use is. Compared with these earlier findings it seems that decaying wood was a slightly less cost-efficient indicator of overall species richness than vascular plants or birds but better than beetles or wood-inhabiting fungi. For example, the average cost of the decaying-wood volume model was about €56,000, whereas the average cost of models based on birds and vascular plants was €46,000 and €52,000, respectively, calculated over the whole range of 1 to 32 sites protected. From a practical viewpoint, decaying wood may, however, be more useful than vascular plants or birds because it may be easier to integrate the inventory of decaying wood into the ordinary forest inventory than to integrate species inventories that require specialists to identify species.

Although decaying wood does not accurately reflect overall species richness, our results indicate that the use of decaying wood as an indicator in site selection was more cost-efficient than using information from large-scale species inventories. This is interesting because some researches have argued that it is worthwhile to make such inventories (Balmford & Gaston 1999). It is not straightforward, however, to compare these findings with our results because the methods used in the analysis are different. Studies with a larger variation in species groups and wider variation in decaying wood volumes are needed to reveal whether, in general, it is more beneficial to use decaying wood as an indicator or to execute a broad species inventory. Many species groups such as spiders or lichens are laborious to survey and difficult to identify; therefore,

it is unlikely that including these species in the analysis would have changed the results.

Our results also indicate that we should develop cheaper sampling methods, particularly for taxa with a large number of species, such as beetles. Even with moderate inventory costs, however, using an indicator in the site-selection process may be a worse option than selecting the cheapest areas to conserve (i.e., the penny-pincher model described in Juutinen et al. 2004) without using detailed information on each areas' ecological properties. Because of the plain species-area relationship (Rosenzweig 1995), species accumulate with an increasing number of sites selected and selecting the cheapest areas to conserve may be cost-efficient. One must bear in mind, however, that most old forest stands in our study region are ecologically valuable (i.e., including characteristics of old-growth forests) because they have been undisturbed since the early 1900s. Thus the penny-pincher model operated on sites of relatively high conservation value and our conclusions must not be generalized to areas and data with more variation in ecological quality. Howard et al. (1998) concluded that in relatively homogeneous environments indicators do not perform well. It seems that in cases like ours the use of species and dead wood data will be useful only if these data already exist or can be collected with minor inventory costs.

Decaying wood is a valuable surrogate for species richness, but one should also find other cost-efficient indicators to reflect the requirements of those species that do not depend on decaying wood. Some earlier studies indicate that the species compositions in vascular plants covary with the species compositions of several other nonsaproxylous species groups (Saetersdal et al. 2003) and that the group is also a cost-efficient indicator of overall species richness (Juutinen & Mönkkönen 2004). Thus, the combination of decaying wood and vascular plants might form a cost-efficient and ecologically representative group of indicators. More data are needed, however, to reveal whether this combination works in different habitats and regions because large variation in correlations of species richness among taxa has been observed (e.g., Jonsson & Jonsell 1999; Berglund & Jonsson 2003; Siitonen et al. 2003).

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