Ecological Efficiency of Voluntary Conservation of Boreal-Forest Biodiversity

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Abstract: *Current networks of protected areas are biased in many countries toward landscapes of low productivity. Voluntary conservation incentives have been suggested as a socially acceptable way to supplement existing networks with more productive, privately owned areas of high priority for nature conservation. The limited resources committed to nature conservation demand cost-efficiency. Efficiency, however, depends not only on costs incurred to society from alternative ways of maintaining biodiversity but also on ecological values that can be captured. We examined the ecological efficiency of the new market-based voluntary program to preserve forest habitats on private land in southwestern Finland. We compared sites that have become protected (10-year contracts) in the program with managed forests, with sites that have been negotiated for protection for which no contract has been signed, and with the most ecologically valuable privately owned sites in the region that have not been offered for protection by forest owners. We surveyed sites for the amount of dead wood, wood-decomposing fungi, and epiphytic lichens to evaluate their ecological quality. Contracted sites had more features important for overall biodiversity than managed forests and negotiated sites with no contract. These results indicate that procedures used during site selection and negotiations were appropriate and not opportunistic. The contracted sites were also as valuable in ecological terms as the best, still-unprotected, privately owned forests in the region that have not been offered for protection. We conclude that voluntary conservation programs have the potential to yield ecologically valuable sites for protection if the site-selection procedures are appropriate. Reliance on completely voluntary programs, however, may entail uncertainties and inadequacies, for example, in terms of spatial configuration and persistence of the ecological values. Thus, such programs may often need to be supplemented with alternative methods such as land purchase to achieve an ecologically effective network of protected sites.*

Keywords: coarse woody debris, conservation programs, epiphytic lichens, polypore fungi, privately owned land, protected areas

Eficiencia Ecológica de la Conservación Voluntaria de la Biodiversidad de Bosques Boreales

Resumen: *En muchos países, las redes actuales de áreas protegidas están sesgadas hacia paisajes con baja productividad. Se ha sugerido que los incentivos para la conservación voluntaria son una manera socialmente aceptable de suplementar redes existentes con áreas privadas, más productivas y mayor prioridad para la conservación de la naturaleza. Los recursos limitados destinados a la conservación demandan rentabilidad. Sin embargo, la eficiencia no solo depende de los costos incurridos a la sociedad por formas alternativas de mantenimiento de la biodiversidad, sino también en los valores ecológicos que puedan ser capturados. Examinamos la eficiencia ecológica del nuevo programa voluntario, basado en el mercado, para preservar los hábitats forestales sobre terrenos privados en el suroeste de Finlandia. Comparamos sitios que se han protegido (contratos por 10 años) en el programa con bosques manejados, con sitios que se han negociado para protección para los que no se ha firmado contrato, y con los sitios privados ecológicamente más*

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valiosos en la región que no han sido ofrecidos para protección por los dueños. En cada sitio muestreamos la cantidad de madera muerta, hongos descomponedores de madera y líquenes epífitos para evaluar su calidad ecológica. Los sitios con contrato tenían más atributos importantes para la biodiversidad que los sitios manejados y los negociados sin contrato. Estos resultados indican que los procedimientos utilizados durante la selección y negociación de sitios fueron apropiados y no oportunistas. Los sitios contratados también fueron tan valiosos en términos ecológicos como los mejores bosques privados aun sin protección y que no han sido ofrecidos para protección. Concluimos que los programas de conservación voluntaria tienen el potencial para ceder en protección a sitios valiosos ecológicamente sí los procedimientos para la selección de sitio son adecuados. Sin embargo, la dependencia en programas completamente voluntarios puede entrañar incertidumbres e incompetencias, por ejemplo, en términos de la configuración espacial y la persistencia de los valores ecológicos. Por lo tanto, tales programas requieren ser suplementados con métodos alternativos, como la adquisición de terrenos, para lograr una red de áreas protegidas efectiva.

Palabras Clave: áreas protegidas, hongos poliporaceos, líquenes epífitos, programas de conservación, restos leñosos gruesos, tierras de propiedad privada

Introduction

Habitat loss is a major global threat to biodiversity, and efficient tools are needed to prevent any further loss. Supplementing existing protected-area networks is one of these tools. The history of protected-area establishment in many global regions has produced a network that is biased toward infertile landscapes that are not economically valuable for production (Pressey 1994; Balmford & Whitten 2003). This is also the case in Fennoscandia, where the majority of protected areas are located at high elevations and high latitudes, or in remote landscapes with low economic value (Nilsson & Götmark 1992; Virkkala 1996; Stokland 1997). Protected-area networks in more productive regions of Fennoscandia appear to be inadequate, and there is an imminent need to protect more productive sites, particularly forests (Angelstam & Andersson 2001; Hanski 2005).

As a consequence of bias toward landscapes of low productivity, areas of high priority for nature conservation tend to be located on unprotected private lands (Knight 1999). Protecting privately owned land for biodiversity involves many challenges. For example, traditional obligatory approaches, such as government compulsory acquisition of land, have resulted in intense resistance by landowners (e.g., Wätzold & Schwerdtner 2005). In particular, obligatory approaches do not provide motivation to landowners to produce biodiversity services on their land and may even generate incentives to deliberately destroy features of conservation value on their land to avoid coercive protection and thereby financial loss (Innes et al. 1998).

Voluntary protection is assumed to be better accepted by landowners than compulsory land acquisition (Segerson & Miceli 1998) and may reduce expensive conflicts among parties and promote positive attitudes toward environmental protection. Furthermore, a voluntary program may motivate landowners to produce biodiversity services and cooperate with environmental managers (Smith & Shogren 2002).

In line with these arguments, a new voluntary pilot program to protect privately owned forests in Satakunta, southwestern Finland, was launched in 2003. This new program, in which landowners and the Finnish government enter into a fixed-term contract, is called Trading in Natural Values (TNV). The TNV pilot project is based solely on landowners' initiatives.

Landowners offer to participate in the program. If the site a landowner offers is deemed valuable enough and fulfills the biological criteria of nature protection (Anonymous 2003) on the basis of information available and collected during a short field survey, the value of the site is calculated with a valuation mechanism (Juutinen et al. 2008). During the field surveys, ecological values (e.g., large broadleaved trees and pines, dead or burned trees, signs of management actions) are not measured in detail; rather, they are estimated roughly and placed in categories. Each category is assigned a predetermined monetary value. The government authority uses the conservation value as a guideline in negotiations to compare different targets and offers. Finally, the authority and the landowner negotiate the compensation payment. If an agreement is reached, a contract is signed for a period of 10 years. According to the contracts, the forest owners produce biodiversity services on their lands and receive a compensation payment. This payment includes a capitalized value for the loss due to delayed harvesting (with 1% interest rate) and due to expected decay of wood as well as payment for the ecological values. Thus, from forest owners' perspective, the agreements are probably more beneficial than ordinary forestry. After the 10-year period, the landowner is free to choose whether the contract is renewed or not.

Efficiency of the program does not depend only on public acceptance or costs incurred to maintain biodiversity; it also depends on the ecological value that can be captured. Thus, to fully evaluate effectiveness of the method, it is important to assess biodiversity benefits of voluntary approaches.

We consider an approach ecologically efficient if it encompasses areas that contain the most ecologically valuable features in the region. We compared biodiversity values among site categories representing (1) TNV sites, (2) managed forests, (3) sites that were offered to TNV and negotiated but not contracted, and (4) the ecologically most valuable privately owned forests known in the region. In particular, we examined whether sites that have become protected under the TNV program have more ecologically valuable features than managed forests in the region. Protected sites should also be ecologically more valuable than those that have been negotiated but for which no contract has been signed because, for example, the authority considers the compensation claim too high. Our comparisons tested whether the procedures used during site selection and negotiations were appropriate and efficient. Furthermore, sites that have become protected should be at least equally valuable in ecological terms to the best privately owned sites in the region that have not been offered by forest owners. If the sites protected by TNV program have less biodiversity value than the best sites in the region, TNV is inefficient and results in a suboptimal network of protected sites. In this case, compulsory land acquisition could be more efficient at capturing the remaining sites of ecological value in the landscape.

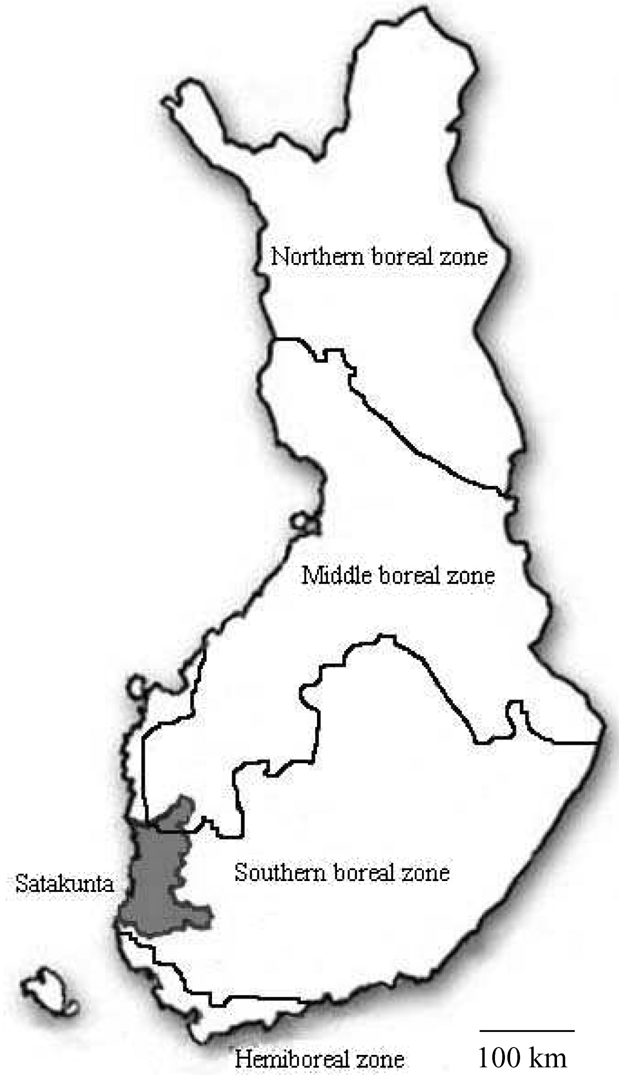

Figure 1. Location of the study region in southwestern Finland (gray) in relation to boreal forest zones.

Methods

Study Region

Our study region was in southwestern Finland (Fig. 1). Most of the sites were in the southern boreal zone, but 5 were in the middle boreal zone. About 65% of the total area is forestry land, and over 95% of that is privately owned. The Satakunta region has a long history of forestry, and resource extraction started in the 17th century, first for tar production, later for saw timber, and finally in the 20th century for the pulp industry. Practically all forests in the region have been under commercial use, and no genuine old-growth forests remain. Currently, <1% of forest land is protected in this region (Virkkala et al. 2000). The most ecologically valuable sites are overly mature stands that have not received any silvicultural treatments for several decades. In southern Finland overly mature forests that have not been treated for 30 years comprise about 4.5% of productive forest land.

Sites

During the first 2 years (2003–2004) of the TNV program, over 150 forest owners with some 1400 ha contacted the Forest Centre. Contracts were made with 62 landowners with a total of 552 ha.

We included only mature heath (upland) forests in the study, and there were 4 site categories. First, we included sites for which a protection agreement was made (TNV sites). The second category consisted of sites offered by the forest owner to TNV program, but for which no contract was negotiated because they were managed forest and had little ecological value (value determined during the preliminary field survey) (MF). Because sites in the second category were offered by the forest owners, they did not represent a random sample of managed forests and were likely of slightly better quality than the average managed forests in the region. The third category consisted of sites of ecological value, but for which no contract was negotiated because of a disagreement over the amount of compensation for a 10-year

Table 1. Number of sites and total area surveyed according to site category and year in a study of ecological efficiency of voluntary conservation.

	2004		*2005*		*Total*	
*Category**	*number*	*area (ha)*	*number*	*area (ha)*	*number*	*area (ha)*
TNV	9	49.5	11	53.1	20	102.6
CD	9	53.6	6	39.9	15	93.5
MF	9	49.5	7	43.6	16	93.1
PS	9	50.7	10	57.0	19	107.7
Total	36	203.3	34	193.6	70	396.9

**Abbreviations: TNV = sites in the Trading in Natural Values program; CD = sites that were negotiated but no agreement was made because of a compensation disagreement; MF = sites that were offered but not negotiated (managed forests); PS = potentially valuable sites that were not offered to TNV.*

agreement (compensation disagreement, CD). For these 3 categories, information on site location, area (ha), and volume of living trees was provided by the Southwestern Finnish Regional Forest Center. The fourth site category included privately owned forests, which were not offered to TNV, but which very likely represented the best as yet unprotected forests in Satakunta region (potential sites, PS). Information on their location and site characteristics were collected in mid-1990s by the Satakunta Nature Conservation League (Satakunnan luonnonsuojelupiiri). This field survey was a comprehensive inventory of the remnant seminatural forest patches in southwestern Finland and included all potential sites that still remained (had not been cut) and for which we could get permission to conduct the survey from the landowner.

We surveyed 70 forest sites in this study, for a total area of about 400 ha. The area of the sites varied between 1 and 20 ha (mean 5.7 ha), and there were no significant differences in the average size among site categories ($F_{3,66} = 0.20$, $p = 0.899$). We also surveyed approximately an equal total area in each category (Table 1).

Sampling

We surveyed sites for 3 ecological features that are considered valuable for biodiversity: dead wood, richness and abundance of wood-inhabiting species of fungi (Polypores), and occurrence of epiphytic lichens. We estimated the amount of dead wood at sites because it is considered one of the most important elements for biodiversity in boreal forests. Some 6000–7000 species in Fennoscandia depend on dead-wood habitats (Stokland et al. 2004). Wood-inhabiting fungi are considered good indicators of dead-wood continuity and naturalness of a forest area (Bader et al. 1995). Polypores are often used as indicators of conservation value in boreal forests (Kotiranta & Niemelä 1996) and of the species diversity in some other dead-wood-associated taxa (Jonsson & Jonsell 1999; Similä et al. 2006). Occurrence of epiphytic lichens has also been proposed as an indicator of forest continuity and conservation value in boreal forests (Kuusinen 1995; Esseen et al. 1996). Several epiphytic lichen species are confined to old-growth habitats with long continuity (e.g., with old living trees), and their biomass tends to be considerably higher in old-growth than in managed forests (McCune 1993; Esseen et al. 1996). Thus, wood-inhabiting fungi, in terms of dead wood and dead-wood-associated species, and lichens, in the terms of living trees, can be considered indicators of the conservation value of an area.

The field work was carried out in June–August 2004 and 2005. We surveyed the sites with systematic line sampling (line width 8 m). We held sampling effort per unit area constant by surveying 100 m of line per hectare of a stand. We measured dead wood and examined lichens in the first 50 m of every 400 m (i.e., one 400-m^2 area was sampled for every 4 ha). If the site was under 4 ha, we sampled one area in approximately the middle of the site to minimize the edge effect.

We identified the species of standing dead trees and downed pieces of dead-wood species and measured their diameter (breast height [dbh] for entire trees and in the middle of snags and pieces of downed wood) and length. We took the measurements only from dead-wood items that were at least 1 m long or $\geq$10 cm base diameter. We report only results on total amount of dead wood because other dead-wood variables (such as dead-wood diversity) tended to strongly correlate with this. We examined all living trees >10 cm dbh within the 400-m^2 sampling area up to the height of 2 m for epiphytic lichens. Lichen taxonomy was in accordance with Vitikainen et al. (1997) and Ahti et. al. (1999).

We examined the whole transect area for polypores (poroid Basidiomyceta). In addition, 2 corticoid fungi that are old-growth forest indicators were included in the survey (*Asterodon ferruginosus* and *Pseudomerulius aureus*). We included only species that form perennial fruiting bodies or could be detected with the same reliability throughout the survey time. We identified or took a sample for later identification of all visible fruiting bodies on standing and downed trees that were at least 1 m long or 10 cm in diameter at the base. Species taxonomy of polypores followed Niemelä (2005). We assigned fungi and lichen species into threat categories (indicator and red-listed species) on the basis of Kuusinen (1995), Kotiranta and Niemelä (1996), and Rassi et al. (2001).

Analyses

We calculated the amount of dead wood for each area. These data were log transformed to homogenize variances among categories. Forest age (average age of dominant trees) and total volume of living trees were taken from forestry files. Data for forest age and volume of living trees were available for only 56 of the total 70 sites.

We examined whether there were differences among categories in the amount of dead wood, forest age, and total tree volume with analysis of variance (ANOVA) with least significant difference (LSD) post hoc comparisons.

We used ANOVA to test whether polypore and epiphytic lichen species richness or the number of records differed among site categories. For polypore and lichen species richness, we also fitted general linear models (GLM) in which we first entered the area of the site as a covariate. We log transformed species richness and area because on log–log scale, there is an expected linear species-area relationship (Rosenzweig 1995). For polypores, we then entered log-transformed volume of dead wood to test whether polypore species richness is a function of the amount of dead wood, as suggested by earlier studies (Bader et al. 1995; Junninen et al. 2006). For epiphytic lichen species richness, we entered forest age and total tree volume into the models because many epiphytic macrolichens species require stable substrates (i.e., old, large trees for their existence; Kuusinen 1995; Dettki & Esseen 2003). We finally entered the site category into the models as a fixed factor to test whether the species richness differed among categories for a given area and substrate amount.

We analyzed numbers of polypore and lichen records with GLM models. We used untransformed variables because abundance was expected to be a linear function of area provided that density (individuals per unit area) remained constant. Otherwise models were identical with species-richness analyses.

We lumped together species and record numbers of indicator and red-listed polypore and lichen species because their frequencies were too low to allow separate analyses. For this species group, we ran GLM models similar to those described earlier. We first entered area (log transformed for species richness) into the model. We exploratively entered one by one the total amount of dead wood, age of living trees, and the total volume of living trees to see whether any of these significantly explained the species richness or the number of records in this species group. Finally, we entered site category to test for among-category differences for a given area and substrate availability.

Results

There were significant differences in the volume of dead wood among site categories ($F_{3,66} = 9.23$, $p < 0.001$); TNV (average 19 m^3/ha) and PS (32 m^3/ha) sites contained significantly more dead wood than MF (8 m^3/ha) or CD (9 m^3/ha) sites. The PS sites tended to contain more dead wood than TNV sites (LSD post hoc test, $p = 0.077$). All sites contained roughly equal amounts of small-diameter (<10 cm) dead wood (on average 5 m^3/ha); therefore, among-site category differences reflect

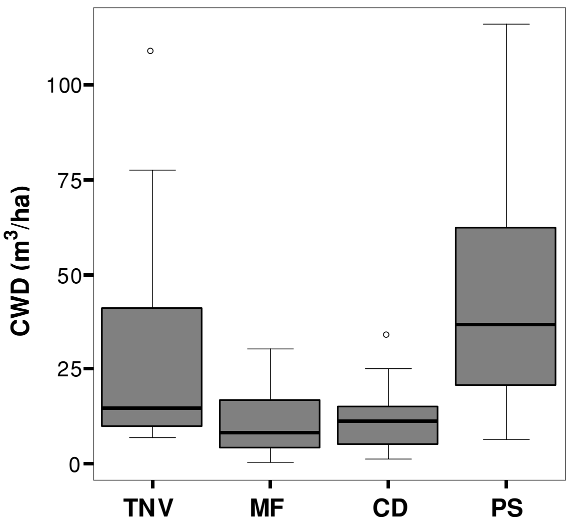

Figure 2. Total amount of coarse woody debris in each boreal forest site category (TNV = sites in the Trading in Natural Values program; CD = sites negotiated but no agreement was made because of a compensation disagreement; MF = sites offered but not negotiated [managed forests]; PS = potentially valuable sites not offered to TNV) Black horizontal lines are median values, boxes show 25 and 75% quartiles, and whiskers denote minimum and maximum values, except for outliers, which are shown with open dots.

variation in the amount of coarse woody debris. Nevertheless, there was much variation in the amount of dead wood within each site category (Fig. 2). The average age of trees and the total volume of living trees at the sites differed among site categories (age: $F_{3,55} = 3.38, p = 0.025$; tree volume $F_{3,55} = 9.06$, $p < 0.001$) and were higher in TNV and PS sites than in MF or CD sites (Table 2).

Thirty-three polypore and 46 lichen species and 2201 and 5133 records, respectively, were observed (see Supporting Information; Table 2). Polypore species richness differed among site categories and was higher in TNVs and PSs than in CD or MF sites (Table 2, $F_{3,66} = 7.63$, $p < 0.001$). When the area of sites and the amount of dead wood were entered into models, this difference among site categories still remained (Table 3). The TNV and PS sites had about 30% more species for a given area and amount of dead wood than CD or MF sites.

The number of polypore records also differed among categories ($F_{3,66} = 3.46$, $p = 0.021$, Table 2), but after entering the area and the amount of dead wood as covariates, significant differences among categories disappeared (Table 3). Without the site category in the model, the volume of dead wood was significantly and positively related to the number of polypore records ($F_{1,66} = 8.64$, $p = 0.005$).

Table 2. Average tree age, total tree volume of living trees, and the number of polypore and lichen species and records observed in this study in total across forested sites and on average according to site categories (defined in Table 1).

	Site category				
Feature	*TNV*	*MF*	*CD*	*PS*	*Total*
Age (years)	102	88	80	107	93
Volume of living trees (m^3/ha)	254	166	163	283	209
Polypore species richness					
total	25	22	18	28	33
average	5.0	3.9	2.7	5.7	4.5
Polypore records					
total	834	223	202	938	2201
average	41.7	14.0	13.5	49.5	31.4
Lichen species richness					
total	34	26	28	30	46
average	9.7	7.1	7.6	8.0	8.2
Lichen records					
total	2012	766	858	1497	5133
average	100.6	47.9	57.2	78.8	73.3
Indicator species richness					
total	25	13	12	15	29
average	2.6	1.6	1.5	2.1	2.0
Indicator records					
total	162	60	123	169	514
average	8.1	3.8	8.2	8.9	7.3

Lichen species richness did not differ among site categories ($F_{3,66} = 0.92$ $p = 0.435$, Table 2). None of the variables explained significantly the variation in lichen species richness when entered into the same model, but lichen species richness tended to be a positive function of tree age (Table 3).

The number of lichen records differed among site categories ($F_{3,66} = 5.64$, $p = 0.002$) and was higher in TNV and PS sites compared with CD and MF sites (Table 2). When the site category, forest age, and tree volume were entered into the same model, significant differences among categories disappeared and only tree volume significantly explained variation in the number of lichen records (Table 3).

The highest numbers of indicator and red-listed species and records occurred in TNV and PS sites (Table 2), but none of the differences were statistically significant (species richness, $F_{3,66} = 1.25$, $p = 0.30$; number of records, $F_{3,66} = 0.80, p = 0.50$). Modeling results showed that species richness was a positive function of forest age and that the number of records increased with increasing area and forest age (Table 4). Regression coefficients (Table 4) showed that each 10-year increment in forest age was associated with an increase of one species and one record of indicator or red-listed species.

Table 3. Results for polypore and lichen species richness and number of records from generalized linear modeling.*

	F	*df*	p	R^2	B
Polypore species richness (ln transformed)					
model	12.65	5	<0.001	0.497	
ln (area)	28.12	1	<0.001	0.305	0.333
ln (CWD)	10.18	1	0.002	0.137	0.174
category	3.29	3	0.026	0.134	
Polypore records					
model	5.77	5	<0.001	0.311	
area	18.78	1	<0.001	0.227	5.58
CWD	2.61	1	0.111	0.039	0.41
category	1.53	3	0.214	0.067	
Lichen species richness (ln transformed)					
model	1.56	6	0.179	0.160	
ln (area)	1.87	1	0.178	0.037	0.124
age	2.88	1	0.096	0.056	0.006
tree volume	0.72	1	0.401	0.014	0.001
category	0.94	3	0.429	0.053	
Lichen records					
model	8.80	6	<0.001	0.519	
area	31.35	1	<0.001	0.390	8.00
age	0.05	1	0.827	0.001	0.07
tree volume	6.51	1	0.014	0.117	0.25
category	1.97	3	0.130	0.108	

**Models include all the listed variables together. Statistical terms:* R^2 *= coefficient of variation of the total model and partial eta-squared for individual terms;* B *= regression coefficient for covariates. Variables: area-total area of sites in hectares; CWD = coarse woody debris; category = site category (defined in Table 1); age = average age of dominant trees; tree volume = total volume of living trees.*

Discussion

Our results showed that TNV sites had more features important to overall biodiversity than managed forests (MF) and sites that had been negotiated but for which no

Table 4. Results from generalized linear modeling for species richness and the number of records of indicator and red-listed polypores and lichens.*

	F	*df*	p	R^2	B
Indicator species richness (ln transformed)					
model	2.36	5	0.053	0.191	
ln (area)	2.38	1	0.129	0.045	0.152
age	6.94	1	0.011	0.122	0.009
category	0.20	3	0.896	0.012	
Indicator records					
model	2.46	5	0.046	0.197	
area	4.64	1	0.036	0.085	0.574
age	4.08	1	0.049	0.075	0.109
category	0.78	3	0.510	0.045	

**Models include all the listed variables together. Statistical terms and abbreviations are defined in Table 3.*

contract had been signed (CD). This indicates that procedures used during site selection and negotiations are appropriate and not opportunistic. The TNV sites were also as valuable in ecological terms as the potential sites (i.e., the best still-unprotected privately owned forests in the region not offered by owners to the TNV program). Nevertheless, the amount of dead wood tended to be higher in PS than in TNV sites. These results suggest that the highest-quality sites in terms of dead wood were not necessarily offered to TNV program, but in general, the voluntary-based TNV program can be considered efficient and not likely to result in a seriously suboptimal network of protected sites, particularly if sites selected for protection are the highest quality among those offered by owners. Because the TNV was a pilot project in the region, it is possible that not all forest owners with the most ecologically valuable sites received information; thus, some of the most valuable sites may not have been offered. We emphasize the need for comprehensive dissemination of information with regard to the goals and opportunities of voluntary conservation programs. The large variation in the amount of dead wood among TNV sites (Fig. 2) and the fact that some TNV sites contained very little dead wood further emphasize the importance of carefully comparing the ecological quality of the offered sites for optimal site selection.

The average volume of coarse woody debris (diameter > 10 cm) in MF sites (3.9 m^3/ha) and CD sites (4.3 m^3/ha) are comparable with typical managed forests in southern Finland, which according to National Forest Inventory contain 2.4 m^3/ha coarse woody debris (Tonteri & Siitonen 2001). In addition, protected forests in southern Finland include rather low volumes of coarse woody debris (average 7.5 m^3/ha), which reflects their management history. Compared with these values, both TNV (13.9 m^3/ha) and PS (28.8 m^3/ha) sites can be considered valuable in terms of coarse woody debris. Nevertheless, even these volumes lag behind of the amount of coarse woody debris in natural old-growth forests in the southern boreal zone, which on average contains 60–90 m^3 of deadwood per hectare (Siitonen 2001). Ecological research suggests that the amount of coarse woody debris should be at least 20–30 m^3/ha for more demanding dead-wood-associated species to occur (Martikainen et al. 2000; Penttilä et al. 2004). We observed values >20 m^3/ha on 6 TNV sites (30% of the TNV sites), 1 MF site (6%), 2 CD sites (13%), and 14 PS sites (74%).

Polypore species richness was higher in TNV and PS sites than in other categories, even if the amount of dead wood was controlled for, but the between-site category differences in the number of polypore records disappeared when dead wood was entered into the model. Thus, polypore abundance, but not species richness, was mainly determined by the amount of dead wood. These results confirm earlier findings that stand management history affects polypore species richness, so polypore species richness is not dependent only on dead-wood volume (Bader et al. 1995; Sippola & Renvall 1999; Sippola et al. 2001). There is also evidence that long-lasting and large-scale forestry decreases polypore species richness through fragmentation and dispersal failure at the regional scale (Penttilä et al. 2006). The lower abundance of dead wood in CD and MF sites likely correlates with their more intensive management history; thus, the local species pool at these sites has become depauperate. Hence, even though the amount of dead wood has lately increased, either the quality of dead wood is not suitable for all species or some species have not been able to recolonize the sites.

This interpretation has 2 practical implications. First, management history seems important to take into account when selecting sites for protection among possible sites of similar current forest structure, particularly if time and funds are limited to conduct species survey. Second, the amount of dead wood alone—even though it usually correlates with species richness—may in some instances be a poor predictor of polypore species richness and an inadequate surrogate for the integrity of polypore assemblages. Thus, to get exact information on polypore species richness and composition, there may be no good substitutes for detailed species surveys (Juutinen et al. 2006; Halme et al. 2008).

None of the measured variables was significantly associated with the species richness of epiphytic lichens, but there was a tendency that species richness increased with forest age. Lichen abundance, on the other hand, was a positive function of total tree volume. After the tree volume was entered into the model as a covariate, all differences among site categories disappeared. These results suggest that present substrate availability is capable of explaining variation in the abundance of lichens, and differences in management history among site categories are not as important for lichen abundance as for polypores.

Substrate availability and stability (slow growth rate of trees) are important factors for epiphytic macrolichens (Dettki & Esseen 2003). Our results indicate that to maximize lichen diversity and abundance, forest managers should give a priority to sites with old trees and large timber volume. In the present case, the stands of forest on the TNV and PS sites were about 20 years older and contained about 100 m^3/ha more timber than the stands in the other 2 categories; therefore, site-selection procedures had been rather successful for lichens.

Our main conclusion is that TNV programs, and voluntary agreements in general, have the potential to yield ecologically valuable sites for protection if site-selection procedures are appropriate. In the TNV program, sites were not selected with systematic site-selection tools (sensu Margules & Pressey 2000), even though this was strongly recommended in many studies (Pressey 1994; Ando et al. 1998), but the site selection still resulted in a set of sites that was by and large ecologically sound. In the real world, the site selection of protected areas is a product of multiple factors that are typically neither measurable nor predictable. These factors include, for example, available funding, institutional capacity, political defensibility, and land tenure and strongly affect which sites become available for protection and are eventually protected (Knight & Cowling 2007). This suggests that well-reasoned site selection—even if not based on systematic tools—is defensible particularly if there are multiple goals, some of which may be difficult to measure (e.g., social benefits such as acceptance and positive attitudes toward nature conservation). Moreover, as suggested earlier (Juutinen & Mönkkönen 2007; Mönkkönen et al. 2008), the complementarity principle of systematic site selection becomes more important for cost-efficiency after a considerable network of conservation areas has been established. In the current situation, where only a small fraction of forest land (<1%) is protected, a reasonable strategy is to combat habitat loss by protecting a maximum total area of ecologically high-quality sites.

From an ecological perspective, voluntary agreements, including TNV-type programs, have strengths and weaknesses. First, general acceptance of voluntary agreements may ensure the persistence of ecologically valuable sites even if sites are not included in protected areas because land owners do not have incentives to manage their property in a way that is harmful to biodiversity. The TNV offers forest owners an alternative to timber harvesting to gain profits from their property, and this may encourage some owners to actively manage their forests for biodiversity protection.

On the other hand, temporary agreements, such as those used in the TNV program, do not guarantee that ecological values will be maintained beyond the first contract period. Many habitat features that are important for biodiversity—such as large-diameter living and dead trees—develop over long periods of time. Therefore, temporary agreements are not likely the most effective way to ensure their persistence in the landscape. Moreover, a network of protected areas built on voluntary agreements tends to constitute a fragmented set of sites because typically privately owned forests are not large (on average 35 ha in Finland) and seldom is an entire property protected. A network of small, isolated sites is not optimal for population persistence of species that specifically need protected areas (Hanski 2005). To balance these uncertainties, projects such as the TNV must be supplemented with additional means. These include, for example, land purchase and contracts of longer than 10 years for the most valuable sites. Fragmentation can be combated by targeted pleas to forest owners to offer sites with specific features or location and by landscape-level planning to achieve an ecologically effective network of protected sites. Temporality of agreements, on the other hand, provides flexibility for both the forest owner and the conservation manager to reconsider protection, if needed, when economic pressures or conservation priorities change. Voluntary protection programs should not be viewed as a substitute for more traditional protection methods; rather, they should be a part of a larger palette of programs used to maintain biodiversity in managed forest landscapes.

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Supporting Information

A list of lichen and polypore species and their numbers of records detected in this study is available as part of the online article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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