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Contributed Paper

Effects of preference heterogeneity among landowners on spatial conservation prioritization

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Abstract: *The participation of private landowners in conservation is crucial to efficient biodiversity conservation. This is especially the case in settings where the share of private ownership is large and the economic costs associated with land acquisition are high. We used probit regression analysis and historical participation data to examine the likelihood of participation of Danish forest owners in a voluntary conservation program. We used the results to spatially predict the likelihood of participation of all forest owners in Denmark. We merged spatial data on the presence of forest, cadastral information on participation contracts, and individual-level socioeconomic information about the forest owners and their households. We included predicted participation in a probability model for species survival. Uninformed and informed (included land owner characteristics) models were then incorporated into a spatial prioritization for conservation of unmanaged forests. The choice models are based on sociodemographic data on the entire population of Danish forest owners and historical data on their participation in conservation schemes. Inclusion in the model of information on private landowners' willingness to supply land for conservation yielded at intermediate budget levels up to 30% more expected species coverage than the uninformed prioritization scheme. Our landowner-choice model provides an example of moving toward more implementable conservation planning.*

Keywords: conservation opportunity, preference heterogeneity, private landowners, spatial prioritization, voluntary conservation

Efectos de la Heterogeneidad de Preferencias entre los Terratenientes sobre la Priorización de Conservación Espacial

Resumen: *La participación de los terratenientes privados en la conservación es crucial para la conservación eficiente de la biodiversidad. Este es el caso especialmente en escenarios en los que las porciones de propiedad privada son grandes y los costos económicos asociados con la adquisición de tierras son altos. Utilizamos el análisis de regresión probit y datos de participación histórica sobre los dueños de bosque danés en un programa de conservación voluntaria. Usamos los resultados para predecir espacialmente la probabilidad de participación de todos los dueños de bosque en Dinamarca. Incorporamos los datos espaciales con la presencia de bosque, información catastral sobre los contratos de participación, e información socio-económica a nivel individual sobre los dueños de bosque y sus hogares. Incluimos la participación pronosticada en un modelo de probabilidad para la supervivencia de las especies. Después, los modelos informados y desinformados (incluyendo a las características del terrateniente) fueron incorporados a una priorización espacial para la conservación de los bosques sin manejo. Los modelos de elección están basados en datos socio-demográficos de toda la población de dueños de bosque danés y en datos históricos sobre su participación en los esquemas de conservación. La inclusión dentro del modelo de la información sobre la disponibilidad de los terratenientes privados para proporcionar tierras para la conservación produjo, a niveles de presupuesto intermedio, hasta*

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30 % más cobertura de especies esperadas que el esquema desinformado de priorización. Nuestro modelo de elección del terrateniente proporciona un ejemplo de movimiento hacia una planeación de la conservación más posible de implementar.

Palabras Clave: conservación voluntaria, heterogeneidad de preferencias, oportunidad de conservación, priorización espacial, terratenientes privados

Introduction

Globally, the majority of biodiversity occurs on privately owned land (Rodriguez et al. 2012). Therefore, efficient biodiversity conservation requires policies designed to enhance landowners' engagement in conservation. A challenge of private-land conservation (PLC) is to attract sufficient numbers of landowners and to target the areas of highest conservation interest (Gallo et al. 2009). A number of studies have used so-called stated-preference techniques, in which landowners make choices over hypothetical scenarios, to identify the factors determining landowners' participation in PLC programs (Langpap 2004; Ma et al. 2012). These studies demonstrate that land and landowner characteristics are important. There is a growing conservation literature on georeferenced social data (Lechner et al. 2014) and their potential use in spatially explicit prioritization analysis to improve the feasibility of conservation action (Guerrero et al. 2010; Adams et al. 2014; Ives et al. 2015; Selinske et al. 2015). This development has contributed substantially to the understanding that social data are important in the design of effective conservation strategies. Disadvantages of applying social data derived from stated- or elicited-preference methods is the risk of receiving strategic responses from the landowners and failure to properly consider behavioral constraints. Landowners may state a willingness to participate that exceeds actual participation (Barrage & Lee 2010), making it hard to predict actual behavior if a conservation policy were implemented. Another challenge is that the collection of social data through surveys is often resource intensive and limited to a small subset of landowners, usually <1000 (e.g., Adams et al. 2014; Maslo et al. 2015; Selinske et al. 2015). If data on unsurveyed land and landowners are unavailable, it is hard to scale up the prediction of landowner behavior when dealing with thousands of landowners at a regional or national scale.

We examined, at a national scale, the extent to which species-based areas of conservation priority are spatially congruent or conflict with actual behavior measures of conservation feasibility (Knight et al. 2010; Moon et al. 2014), interpreted as forest owners' willingness to get involved in conservation schemes. We used national and detailed data on individual forest owners' socioeconomic and demographic attributes at the individual property level to develop a model for private-forest-owner participation in conservation programs. Further, we developed models to predict forest-owner participation based on actual participation and contractual data. Our use of actual participation data and extensive personal register data in the landowner participation model should minimize the risk of strategic biases. Access to predictor variables on individual forest owners and their property provided an opportunity to scale the analysis up to a national level. We included the predicted participation of all Danish forest owners in a national spatial-prioritization model. We prioritized areas at a national level to maximize species protection, minimize cost, and maximize likelihood of implementation by targeting willing landowners. We developed a simple model to evaluate individual species' survival probability as a function of forest area on private and public land. The cost-effectiveness of a model informed by landowner choice data was compared with a species-based conservation-priority framework, (hereafter uninformed model), for which we assumed all land was equally available for conservation. Finally, we considered how our methods and results may be useful in practice to target landowners if the Danish Nature Agency had access to high-resolution species data.

Methods

Study Area and Data

Our study area comprised 633 10×10 km grid cells covering Denmark. Forested areas (approximately 650,000 ha or 15% of total land area) were distributed among 53,942 properties; roughly 30% was publicly owned (Fig. 1 & Supporting Information). Danish forest is home to an estimated 26,000 species, of which 60% are forest obligates. We used presence-absence data on forest-obligate breeding birds, orchids, click beetles, butterflies, moths, hoverflies, and true bugs (179 species total; Supporting Information) to model species survival probabilities. The full data set represents the most complete species-distribution data for forest species in Denmark. Although the 10×10 km grain size may be suboptimal to real-world decision making at the property level, data aggregation for us was an indispensable analytical step for the following reasons. Exact point-occurrence data existed for all species and resulted in accurate presence-absence data. However, occurrence data were far from complete on the scale of forest estates or forest polygons within or shared by forest estates. For organisms with large home ranges or that formed metapopulations,

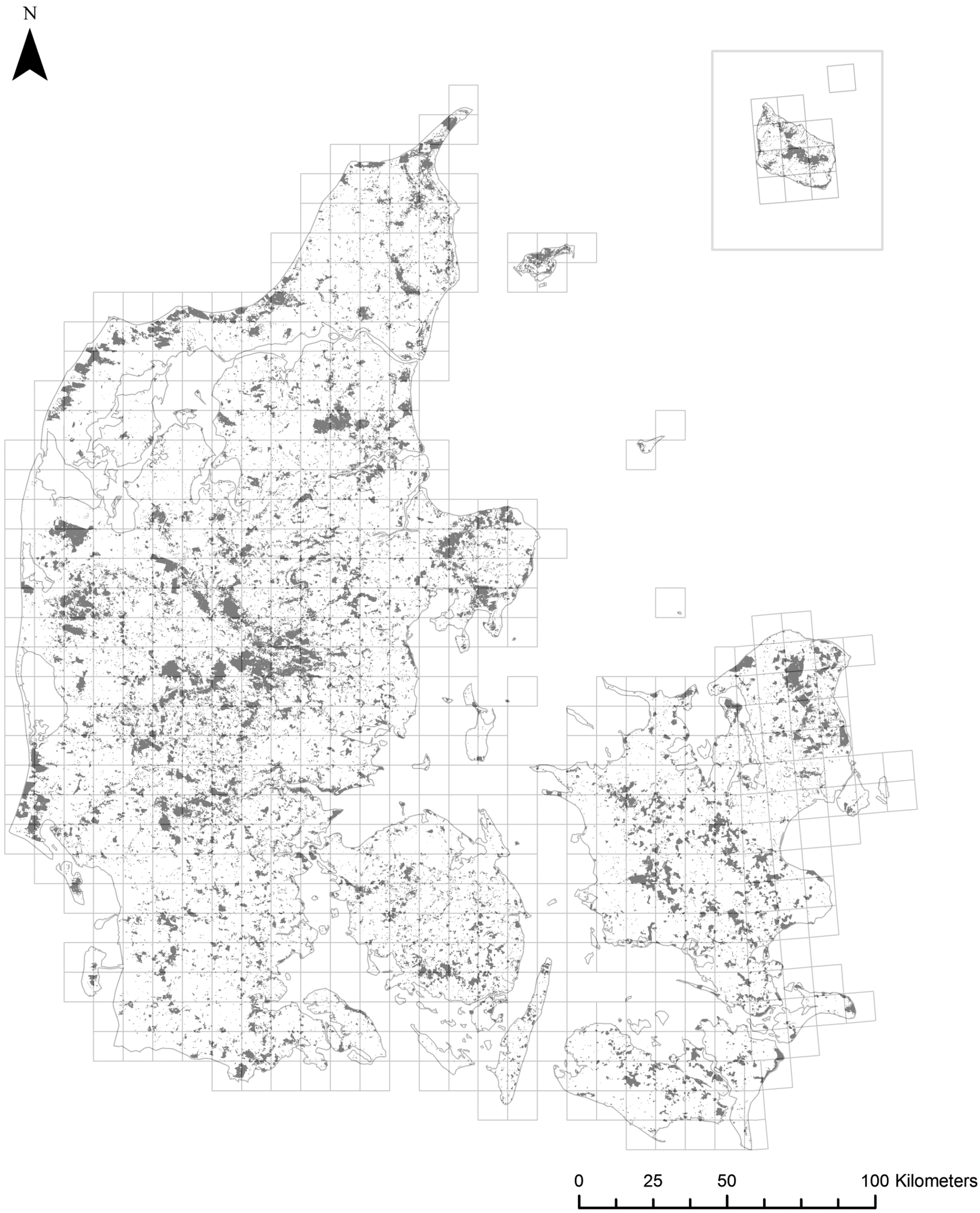

Figure 1. Network (10×10 km grid) of forested areas in Denmark.

neither single point occurrences nor occurrence data aggregated to forest estates were representative of the species' habitat (i.e., biologically meaningful). We illustrate this crucial point with data from the Biodiversity Map of Denmark (Ejrnæs et al. 2014). Use of our grid-cell-scale results at the level of individual properties is limited, as has been shown previously by, for example, Adams et al. (2014) and Guerrero et al. (2010).

Despite the commitment to the EU 2020 Biodiversity Strategy, there is no coherent management plan for securing biodiversity in Danish forests. With large forested areas under private ownership and high opportunity costs of land acquisition (3–5 times more expensive than subsidy schemes with continued private ownership; N.S., unpublished data), conservation of forest biodiversity depends on voluntary conservation agreements on private land. Subsidy schemes are advertised in newspapers and landowner journals and can be applied for by all forest owners. From 1992 to 2009 the Danish National Budgets paid private forest owners approximately €11 million to set forest aside as unmanaged or to apply biodiversity-friendly management practices; <1.6% of the Danish private forest land was affected (Johannsen et al. 2013). For comparison, >5% of public forests are set aside. Because setting aside public forest areas for conservation also helps protect species, we included public conservation forests in the total expected supply of land for conservation. Setting aside 5% of public forests is assumed in the base-case scenario in which we ignored landowner participation probability but included species' survival probabilities. Planting, drainage, soil tillage, and wood extraction are the forest interventions that most negatively affect forest biodiversity (Müller & Bütler 2010). Government economic-support schemes aim to reduce drainage and convert commercially managed forests into unmanaged forest. Such actions will gradually allow for natural dynamics and increase the amount of dead wood and other habitats.

To assess the importance of incorporating information of private landowner participation in voluntary conservation programs, 3 data sets with a uniform spatial-grid resolution were combined into a spatial-prioritization model: estimates of opportunity costs of conservation when setting forest aside in perpetuity; supply of private and public conserved forest; and change in species survival probability in response to increased area of unmanaged forest. Opportunity costs were calculated as annual expected economic loss of foregone timber production, measured as loss of annual soil rent. Here, the soil rent is the net present value of the forest converted to constant annual rental values (Supporting Information). Opportunity costs represent economic loss to society and provided the social-regulator perspective in our study. A fraction of the loss was the compensation paid to the owner. Because forest management of public areas can be determined by the regulator, we assumed a share of public forests is set aside with 100% probability. We estimated expected supply based on predictions (see below) from a probabilistic model of private landowner participation.

Model of Landowner Participation

To examine private forest owners' willingness to participate in forest conservation, we investigated participation in the most comprehensive green-forest-management program implemented by the Danish Nature Agency from 1998 to 2009. The focus of the program was to safeguard natural forest and biodiversity and included leaving forest unmanaged. The program was regularly promoted in forestry journals, newspapers, and on the internet. All forest owners could apply and those selected by the agency were offered a contract under which the area would be protected permanently through juridical registration. Compensation was paid as an upfront lump sum. A total of 121 properties participated in the scheme. To examine the forest owners' participation choice, we merged GIS data on the presence of forest; cadastral information, including contract data; and individual-tract socioeconomic information about the forest owners and their households (retrieved from Statistics Denmark in 2013).

Out of the 121, we connected 92 properties to their owners and cadastral data (Supporting Information). For the nonparticipating forest owners, we connected 50,809 out of 53,942 to their properties. All forest owners were eligible. This left us with 92 participants in the program and 50,908 forest owners who could potentially apply. Participation is a rare, which could lead to bias and underestimation of participation probabilities (King & Zeng 2001). Therefore, we used choice-based sampling and randomly selected 92 nonparticipating forest owners and their properties (see Greene [2002] for a description). To get representative estimates, we based average results on 4,000 different sample draws and participation probabilities were weighted according to the original occurrence for prediction of participation for the full population. (Descriptive statistics for the full population, the participants, and the random draws of nonparticipants are in Supporting Information.)

We used STATA 13 for analysis of participation (StataCorp, College Station, Texas, U.S.A.). We used a probit model to assign a probability of participation in conservation for each property (Nagubadia et al. 1996; Langpap 2004) that included forest characteristics (area, production quality, number of hooved game shot in the region) and landowner characteristics (e.g., education, children in the household, number of co-owners, main occupation, age) as explanatory variables. These predictors were chosen based on a general model of economic and noneconomic motives of private landowners to participate in voluntary conservation programs and on previous empirical findings (Langpap 2004; Gren & Carlsson 2012). We expected participation likelihood to be smaller for owners with an occupation related to or education in forestry or farming because they might consider conservation a restriction on future generations use of the land (Miller et al. 2010). We expected younger owners would be more likely to participate (Kabii & Horwitz 2006). We included a dummy variable with a value of 1 if there were children under the age of 18 in the household of the landowner. The sign of the variable was ambiguous: positive because it could capture bequest values (Bengston et al. 2011) or negative because conservation may restrict the future opportunities of exploiting timber resources.

Participation may decrease as the number of co-owners increases because the more owners involved, the more difficult it could be to agree on management decisions. Alternatively more co-owners may indicate the property is not owned for production purposes only, which would increase the likelihood of participation and make the expected sign ambiguous. We also included a proxy of residence. Most forest owners are not allowed to build and live on their land, but those living near or on the property may better capture private nonmonetary values (e.g., recreational use or aesthetic values). Recreational values are expected to increase as proximity between residence and recreational sites increases (Bateman et al. 2006). Less participation may result if the residence value is compromised by further restrictions and governmental interference on the land. Therefore, the expected sign of the coefficient is ambiguous. The variable was measured as a dummy and indicated whether the forest property and residence of the forest owner was located in the same municipality. We expected participation to increase as income increased (Raymond & Brown 2011). Other psychological predictors, not included in the household data, may influence participation probability (Boon et al. 2010). Finally, we estimated the average marginal effects for the statistically significant explanatory variables. The model predictions and individual-level register data were applied to scale the results up to the entire population of private forest owners. This means each owner (*m*) of a forest in grid cell *j* is represented by an individual participation probability (p_{mj}) based on the physical characteristics of the property and their socioeconomic status.

The expected area supply of private forest for conservation in each grid cell j is $a_{\text{private},j} = \sum_{m\in M} p_{mj} a_{\text{private},mj}$, where M is the entire set of forest owners. We assumed a percentage area share (5%, 15%, 25%, or 100%) of public forests participated for sure, and we set the probability of participation for these forests to 1, $a_{\text{public},j} = \sum_{m\in M} a_{\text{public},mj}$; the total expected supply for each grid cell was calculated as $a_j = a_{\text{public},j} + a_{\text{private},j}$.

Species Survival Probability Model

Species survival probability was modeled using data on presence and absence of a set of 179 obligate forest species compiled for all grid cells. The model was parameterized with data per grid cell on current forest area, amount of broadleaved forest, and current area of unmanaged forest. We assigned grid cells to 6 regions that represented gross climate and soil variation. We estimated survival probability for all species in all grid cells and used the model to predict changes in species' survival probability in each grid cell given a change in the area of unmanaged forest.

The model relies on a 2-component estimate of species' survival probability, $p_{ij} = \xi_{ij}(a_j)\gamma(a_j)$, that is current probability of a given species $i \in I$ being present in grid cell $j \in J$, $\xi_{ij}(a_j)$, and a survival probability function $\gamma(a_j)$, where a_j is the expected forest area supplied on private and public land to be set aside as unmanaged forest in grid cell j.

We estimated $\xi_{ij}(a_j)$ with a probit model in which the current presence-absence distribution of species depended on current forest area, the share of broadleaved forest cover, a regional effect, and current area of unmanaged forest for each species $i \in I$ in each grid cell $j \in J$. We estimated the average marginal effect, how changes in the amount of unmanaged forest set aside, a_j, affects the species persistence probability $p_{ij}(a_j)$, and hence how responsive a species is to changes in supply of private and public forest for conservation. If a species group is not present in a grid cell, the persistence probability was zero.

We modeled the long-term species' survival probability function, $\gamma(a_j)$, with a Gompertz function that we assumed followed a sigmoidal function of area set aside (Fahrig 2001; Huggett 2005). Approximately 2000 ha of unmanaged forest (20% of the area of a grid cell) was the maximum amount (i.e., threshold). In the absence of empirical threshold estimates for the study system and because empirical estimates sometimes deviate from the sigmoid shape (Ranius & Fahrig 2006), we also ran models with a smooth, approximately linear function (Fig. 2).

Spatial Optimization Model

Species persistence may be uncertain and related to the stochastic nature of habitat quality as well as management. Following the approach described above, we estimated the probability that species $i \in I$ persists at grid cell $j \in J$, $p_{ij}(a_j)$ $[0 \leq p_{ij}(a_j) \leq 1]$. Making the simplifying assumption that probabilities are independent between grid cells, the probability, s_i, that species i does not persist in any of the grid cells, x_j, can be estimated as

$$s_i = \prod_{i\in I} (1 - p_{ij}(a_j))^{X_j} \quad \forall \quad i \in I. \tag{1}$$

The spatial-optimization model selected grid cells (with their respective total expected area a_j) that maximized the total expected species persistence, $W = \sum_{i\in I} (1 - s_i)$, subject to a budget constraint. Because the problem is nonlinear, we used Arthur et al.'s (2004) procedure and ILOG-CPLEX 9.0 to solve the problem (Supporting Information).

We used a step-wise approach to calculate the difference in cost-effectiveness between the uninformed and the informed scenarios. First, we ran a so-called uninformed base-case scenario for increasing budgets in which we ignored landowner participation probability but included species' survival probabilities. The uninformed scenario rested on the assumption that the entire forest area within a grid cell is available for conservation. Next, we calculated the total available area

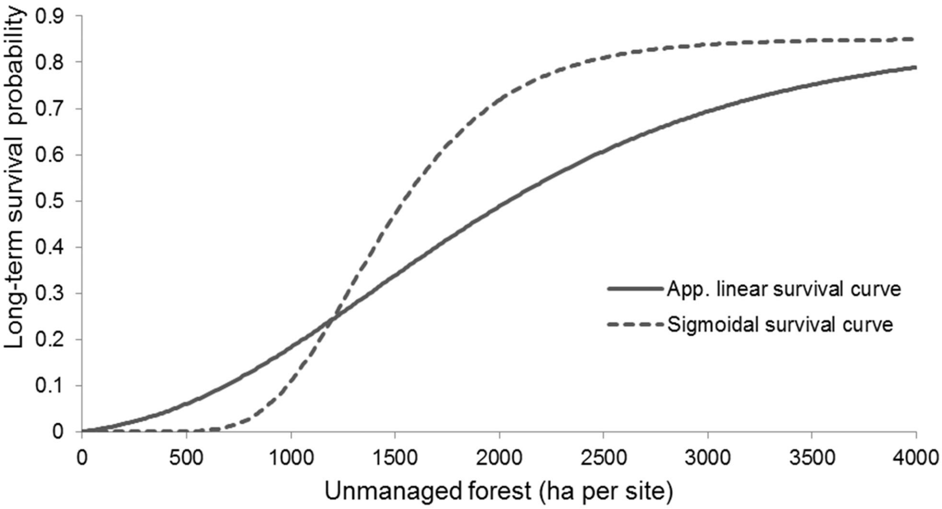

Figure 2. Functional forms of assumed long-term survival probability of species in relatively untouched forested areas (app., approximate).

in the informed scenario as the sum of expected area supplied by private landowners and the public forest and evaluate the total expected species persistence and the realized opportunity cost of that solution. Then the total opportunity cost of the (realized) expected enrolled area was used as budget constraint in the informed scenario, which maximized expected species persistence. Finally, we calculated efficiency gain as the difference between the expected coverage of the informed and uninformed scenarios. It was calculated for various budget levels from 0.15 to 240 million DKK/year. Public forests, which account for roughly 30% of the Danish forest area, could in principle be set aside through a governmental edict. We evaluated the importance of certainty of public participation by designating a fraction of all public forest within each grid cell as set-asides. We varied the fraction of set-aside forest reserves as 5%, 15%, 25%, and 100% of all public forest land within each grid cell. We estimated the sensitivity of efficiency gains of a relatively linear species-survival model compared with a sigmoidal survival model. We assumed the opportunity cost of conservation, the value of lost timber production per hectare, was the same in private and public forests.

Results

Forest-Owner Participation

We estimated the marginal effect for the explanatory variables that had significant parameters. Forest-owner participation increased significantly as area of forest property increased, decreased significantlyas owner age increased, and was lower for owners professionally occupied in agriculture or forestry than for owners who were not professional foresters or farmers (Table 1). The estimated pseudo R^2 of 0.092 appears low but corresponds to an R^2 of 0.27 (a relatively good fit [Hensher et al. 2015]). Explanatory variables had a minimal effect on participation probability. For instance, an increase in forest property area of 10 ha increased the participation probability by 3.42 percentage points (pp; pp, 10 ha x 0.00342%/ha), and a 10-y increase in owner age reduced the participation probability by 0.14 pp. An owner's occupation in agriculture or forestry had a minor impact on participation probability (0.5 pp); thus, large differences in forest property area would account for the majority of the explanation of the forest owners' participation choice.

Acknowledging the uncertainty in private land supply sharply reduced the forest area available for conservation (Fig. 3). The total private forest area was 473,599 ha of which 130,586 ha was expected to be part of the conservation program. Therefore, when including probability of participation forest supply was reduced by 343,013 ha (72%).

Species Survival Probability

Overall, the 179 models for obligate forest species revealed a positive and on average large effect of forest cover per grid cell on species' survival probability. Two species were not significantly affected by forest cover. For the remaining species, a 1% increase in forest cover increased the average probability in a grid cell by 6.7 pps. Ninety-eight species were significantly influenced by the proportion of broadleaved forest. For these species, an increase of 1% in broadleaved forests increased survival probability by 0.26 pp. Even fewer species were responsive to the availability of unmanaged forest areas. In total, survival of 36 species correlated significantly with unmanaged forest cover. The average increase in survival probability was 0.26 pp for a 1% increase in the unmanaged forest area (Supporting Information).

Table 1. Parameter estimate coefficients in the model of participation of forest landowners in conservation.*

Variable	*Parameter estimates (p, SE)*	*Marginal effects*
Physical attributes		
forest area on property (ha)	0.85 (<0.0001, 0.137)	0.00342
area of high productivity: yes, 1; no, 0	−0.39 (0.236,0.329)	
number of hooved game shot in municipality	−0.0001 (0.999,0.009)	
Socioeconomic attributes		
agricultural education: yes, 1; no, 0	−0.302 (0.313, 0.299)	
occupied in agricultural sector: yes, 1; no, 0	−1.230 (<0.0001,0.306)	−0.00494
children in the household under 18: yes, 1; no, 0	−0.149 (0.634,0.313)	
age of owner	−0.035 (0.007,0.013)	−0.000140
number of owners	−0.318 (0.170,0.232)	
log-transformed total income of household (1000 DKK)	−0.206 (0.130,0.136)	
forest and residence in the same municipality: yes, 1; no, 0	−0.596 (0.106,0.364)	
Constant	0.734	1.384
Observation	184	
Pseudo R^2	0.344	
Log likelihood	−431,721	

Data are simulated with 4000 runs to get stable estimates.

Figure 3. The expected supply of forest conservation areas for the (a) uninformed scenario (all private forest [473,599 ha] is assumed to be enrolled in the conservation program) and (b) informed scenario (130,586 ha of private land is assumed to be enrolled in the program).

Spatial Optimization

Not including predictions of participation, the risk of not achieving the potential conservation gains was considerable (Fig. 4). The risk was relatively small when budgets were either very low or very high. For intermediate budgets, the potential efficiency gains were substantial, peaking at spending of approximately 30 million DKK/year. The number of expected surviving species increased when the percentage of public forest area conserved with certainty increased (Fig. 4). The efficiency loss was still significant but much smaller when we assumed species survival was a linear function of unmanaged area in a grid cell (Fig. 4). The number of expected surviving species increased as public forest area conserved increased and

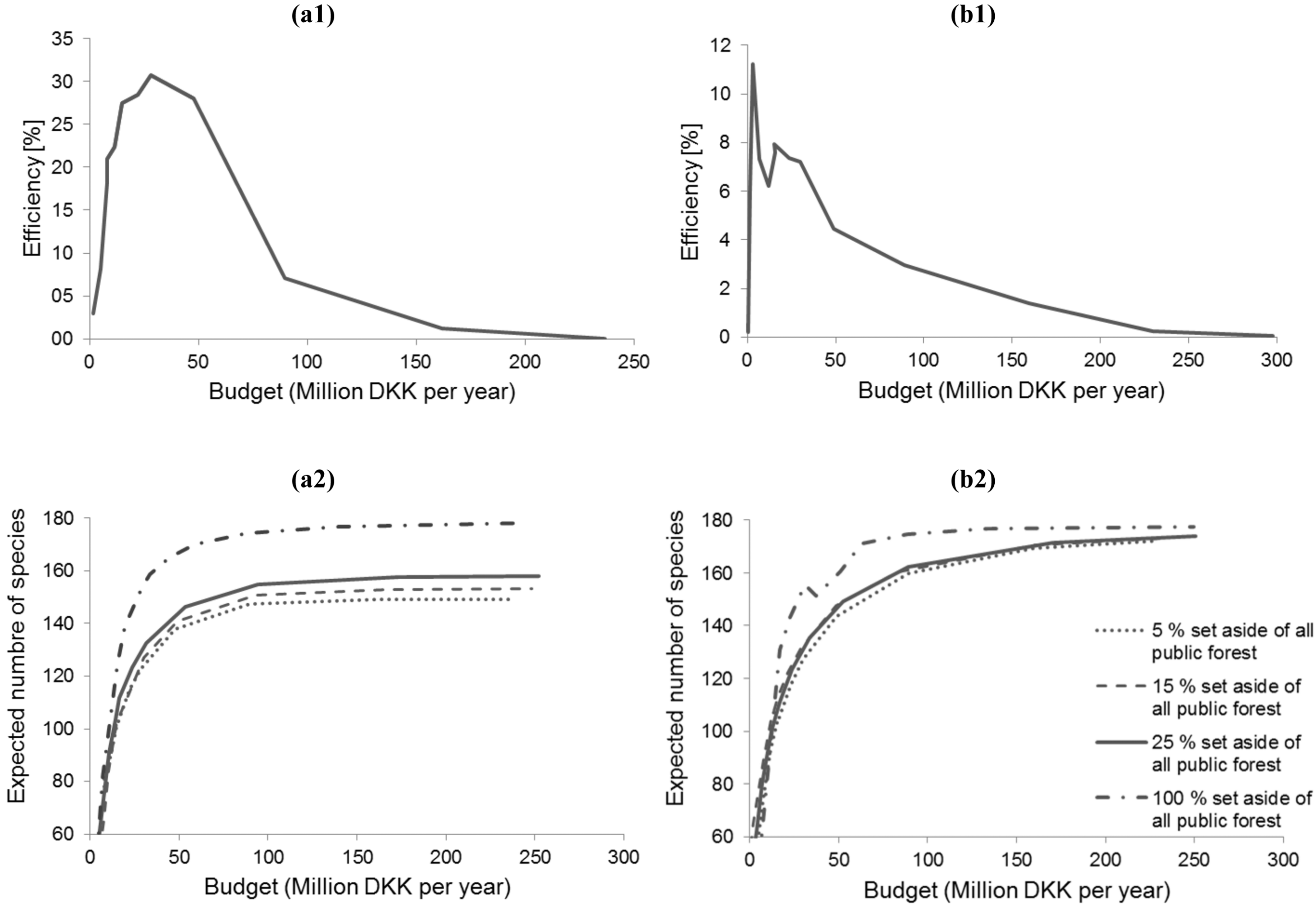

Figure 4. The expected efficiency gains of the informed scenarios for (A1) sigmoidal and (B1) linear probability functions. We assumed 5% of public forest is conserved with certainty. The expected efficiency gains were estimated as the difference between the expected coverage of the informed and uninformed scenarios. Estimates of the total expected species survival in (A2) sigmoidal and (B2) linear probability functions for different percentages of public forest set aside as untouched forest.

increased in the linear species-survival scenario, although to a lesser extent (Fig. 4).

Discussion

Conservation Participation

Inclusion of socioeconomic properties of landowners appeared to improve conservation efficiency relative to a strategy that did not consider socioeconomic factors. Efficiency gains were highest at intermediate budget levels. We assumed the survival probability of all species in all grid cells was known. This condition cannot be met in almost all real-world situations and results in potentially much larger efficiency loss if social information on landowners is excluded. When applying a sigmoid function of conservation area within a grid cell, the informed strategy would most likely target grid cells with large public forest areas (provided with certainty) and private land holdings with either a large forest area or large landowner willingness to participate in conservation. We ignored transaction costs of negotiation, which are expected to increase nonlinearly as the number of owners increases (Wuenscher et al. 2008).

Both forest-property characteristics and socioeconomic attributes of the owner were significant determinants of participation. Size of property had the largest positive marginal effects on participation, which is well supported (Mäntymaa et al. 2009; Gren & Carlsson 2012). This result may reflect that the relative size of opportunity cost of setting aside a part of the forest for conservation may decrease when more forest is owned (Nagubadia et al. 1996; Langpap 2004). Further, we assumed factors that characterize past participation also explain future participation. Other studies show that future participation can be affected by crowding-out effects or other psychological motives (Primmer et al. 2014).

Species Survival

At the grid-cell level, species' survival probabilities increased significantly as forest area increased. Given an expected positive relationship between habitat area and population size, this finding is what one would anticipate. Because most of the modeled species rarely occur in large populations throughout entire forests, we considered this relationship resulted from an increase in the probability of the occurrence of particular microhabitats as forest area increases. For example, the larval stages of all included click beetles and some hover flies are exclusively associated with rotting and other types of cavities in large old (mainly broadleaved) trees. Trees presenting such microhabitats are rare in plantation forests, but their incidence is likely to increase as forest area increases. Large effects of forest margin on birds (Supporting Information) may reflect a more direct relation between habitat area and population size. In a similar vein, we considered the positive effect of proportion of broadleaved to coniferous forest on species' occurrence probability was due to a relatively high probability of occurrence of certain microhabitats of importance to the modeled species (Petersen et al. 2016).

The rather modest effect of unmanaged forest on species' presence probability was unsurprising. First, in Denmark unmanaged forests are a small percentage of the entire forested area, and data used to parameterize our model contained grid cells with areas of unmanaged forest area ranging from none to very small. The long-term species persistence in larger set-aside areas may therefore be higher than we estimated. Consequently, the certainty of estimates based on extrapolating such a model may be low. Second, although the actual whereabouts of declared unmanaged forest areas are well known, many small areas of de facto unmanaged forest occur in relatively inaccessible or marginal pockets in plantation forests and are unrecognized. Such areas may, however, be very important to the modeled organisms.

Long-term survival of species will depend not only on the current location of species but also on sufficient habitat area to support long-term population viability. Consequently, we modeled long-term viability by using a Gompertz function based on the assumption that there is an approximately linear and a sigmoid relation between forest area set aside as unmanaged and species' survival probability. This assumption is restrictive in 2 ways. First, using one functional form for all species may not be justified because species may differ in their dependence on the area of forest left unmanaged. Second, the actual functional form for each species is unknown as is the impact our results. We modeled 2 different assumptions on the functional form to highlight the assumption sensitivity, but further research that may untangle this functional form is warranted. A sigmoidal relationship between large forest areas and high species survival correlates with high participation probability. Further, forests in Denmark are highly fragmented, and we assumed probabilities were independent between grid cells. If species persistence is spatially autocorrelated, it is relevant to include such spatial relationships in future studies.

Owners of large forest properties were more likely to participate than owners of small forests. However, due to returns to scale, owners of large properties are also more likely to manage their forest for timber, which has negative effects on biodiversity (Boon et al. 2010). Small, private forest holdings are therefore expected to have elevated species' survival probabilities per unit area. Lack of data on the actual forest management prevents more detailed modeling of this aspect. Nevertheless, governmental agencies should worry about habitat area and quality of the land enrolled in conservation programs. This suggests the need for multiple-action planning and contract designs that motivate both owners of small and large forest properties. We assumed planners had complete knowledge of species' survival probabilities. In reality, this is not nearly the case; hence, the impact of owner willingness on efficiency could be even larger than we found.

Making the Willingness Modeling Applicable to Practice

The Danish Nature Agency is the governmental body charged with managing nature-protection schemes in Denmark. Private forest owners may apply to participate in conservation schemes. In general, the agency does not systematically target owners of forests of high conservation value. In rare cases, the agency contacts forest owners to initiate negotiations. Such initiatives are likely to benefit strongly from knowledge about forest owners. Such data could be gathered through face-to-face interviews with landowners (Guerrero et al. 2010). Compilation of accurate data would be expensive to acquire and would require a prohibitive number of people be interviewed. Our methods may provide a cost-effective way to predict which landowners to approach. Increased focus in governmental bodies on evaluating the performance and participation in implemented voluntary conservation programs and a coherent data-registration strategy to enhance spatial targeting of conservation efforts could increase the potential for this kind of analysis. Such a registration strategy would reduce measurement errors and increase knowledge of private-landowner motivations for conservation.

It is a limitation that the current spatial-conservation-prioritization framework is based on nationwide 10×10 km grid data on biodiversity. It is well-known that spatial conservation prioritization on a fine scale is more cost-effective than coarse-scale prioritization (Arponen et al. 2012). However, our presence–absence data set is the most comprehensive in Denmark. High-resolution data for forest estates are unavailable. However, a national

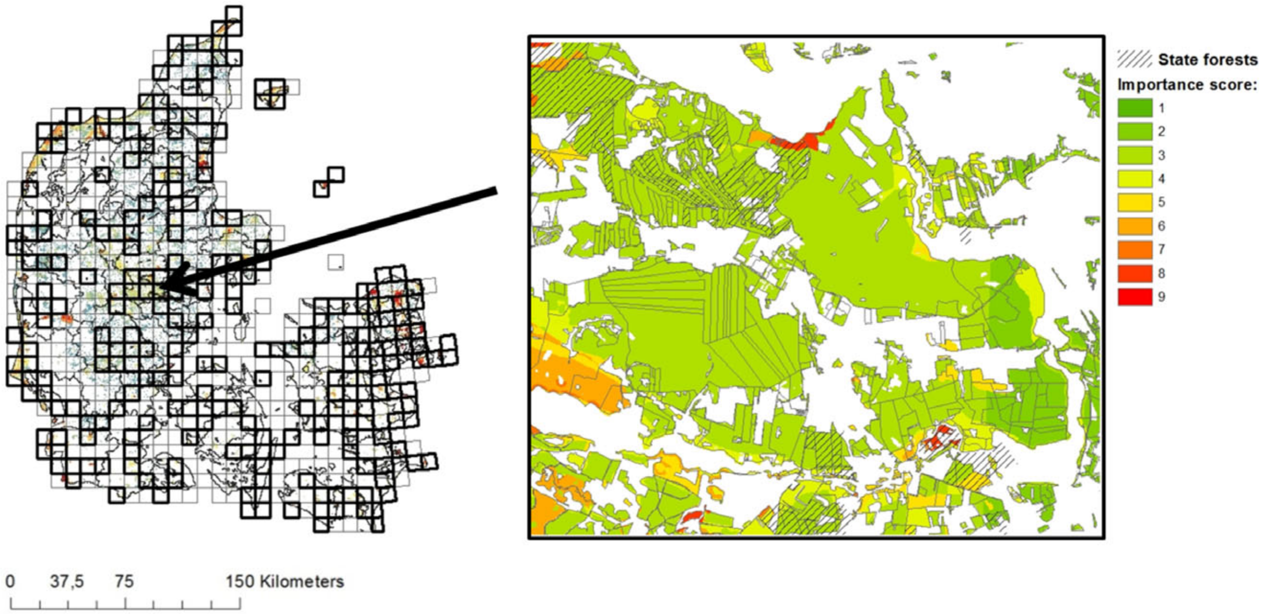

Figure 5. Example of a 10×10 km grid cell superimposed on a cadastral map of state-owned (hatched) and private (thin black lines) forest estates. Importance scores (1, lowest; 9, highest) are based on protection of nationally red-listed species (Ejrnæs et al. 2014).

map of biodiversity-importance scores, based on red-listed species and expert judgment, has been created (Ejrnæs et al. 2014; Fig. 5).

Species on the map represent approximately 20% of the national forest species data set. Despite not all species being assessed, we suggest importance scores be used for high-resolution analyses aimed at pinpointing forest polygons to target in conservation schemes. The national priority analysis based on forest-owner participation models could then be applied prior to screening of 10 × 10 km squares for areas of high conservation value. Then, all state-owned forests (hatched areas in Fig. 5) with a sufficiently high conservation-importance score could be set aside for protection and restoration (e.g., reestablishment of natural hydrology by closing ditches). The privately owned forests could subsequently be targeted, starting with forest polygons with sufficiently high importance scores and a maximum likelihood of participation based on our model (Table 1). Statistics Denmark did not allow us access to data with which we could have examined spatially explicit relations between importance scores and data on likelihood of landowner participation at the forest polygon level (personal register data protection). However, the Danish Nature Agency could apply their local knowledge and spatially explicit information from this study to target owners of large forests, who are relative young and not employed in forestry or agricultural sectors. Such a sequential approach illustrates that combining participation models based on revealed behavior with spatial-optimization and scale-adapted conservation priorities may increase conservation efficiency. We demonstrated the importance of using social data, based on real participation data, to predict effective conservation priority areas.

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Supporting Information

The complete descriptions of the landowner (Appendix S1), species-survival (Appendix S2), and opportunity-costs data (Appendix S3) and spatial-optimization models

(Appendix S4) are available online. The authors are solely 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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