



Use of Inverse Spatial Conservation Prioritization to Avoid Biological Diversity Loss Outside Protected Areas

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Abstract: *Globally expanding human land use sets constantly increasing pressure for maintenance of biological diversity and functioning ecosystems. To fight the decline of biological diversity, conservation science has broken ground with methods such as the operational model of systematic conservation planning (SCP), which focuses on design and on-the-ground implementation of conservation areas. The most commonly used method in SCP is reserve selection that focuses on the spatial design of reserve networks and their expansion. We expanded these methods by introducing another form of spatial allocation of conservation effort relevant for land-use zoning at the landscape scale that avoids negative ecological effects of human land use outside protected areas. We call our method inverse spatial conservation prioritization. It can be used to identify areas suitable for economic development while simultaneously limiting total ecological and environmental effects of that development at the landscape level by identifying areas with highest economic but lowest ecological value. Our method is not based on a priori targets, and as such it is applicable to cases where the effects of land use on, for example, individual species or ecosystem types are relatively small and would not lead to violation of regional or national conservation targets. We applied our method to land-use allocation to peat mining. Our method identified a combination of profitable production areas that provides the needed area for peat production while retaining most of the landscape-level ecological value of the ecosystem. The results of this inverse spatial conservation prioritization are being used in land-use zoning in the province of Central Finland.*

Keywords: land-use zoning, land-use planning, site selection, spatial optimization, systematic conservation planning, Zonation software

Resumen: *La expansión global del uso de suelo por humanos establece un incremento constante en la presión para el mantenimiento de la biodiversidad y el funcionamiento de los ecosistemas. Para combatir la declinación de la biodiversidad, la ciencia de la conservación ha innovado métodos como el modelo operativo de planificación sistemática de la conservación (PSC), que se enfoca el diseño e implementación de áreas de conservación. El método usado más comúnmente en PSC es la selección de reservas que se concentra en el diseño espacial de redes de reservas y su expansión. Expandimos estos métodos mediante la introducción de otra forma de asignación espacial del esfuerzo de conservación relevante para la zonificación del uso de suelo a escala de paisaje que evita los efectos ecológicos negativos del uso de suelo por humanos afuera de áreas protegidas. Nuestro método se denomina priorización de conservación espacial inversa. Puede ser utilizado para identificar áreas adecuadas para el desarrollo económico al mismo tiempo que limitan los efectos ecológicos y ambientales de ese desarrollo a nivel de paisaje mediante la identificación de áreas con el mayor valor económico pero el menor valor ecológico. Nuestro método no se basa en objetivos definidos a priori, y como tal es aplicable a casos donde los efectos del uso de suelo sobre, por ejemplo, especies individuales o tipos de ecosistemas son relativamente pequeños y no violar objetivos de conservación regionales o nacionales. Aplicamos nuestro método a la asignación de uso de suelo para la explotación de turba. Nuestro método*

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identificó una combinación de áreas de producción rentables que proporcionan la superficie requerida para la producción de turba y al mismo tiempo retienen la mayor parte del valor ecológico del ecosistema a nivel de paisaje. Los resultados de esta priorización de conservación espacial inversa son utilizados en la zonificación de uso de suelo en la provincia de Finlandia Central.

Palabras Clave: optimización espacial, planificación de uso de suelo, planificación sistemática de la conservación, selección de sitios, software de zonificación, zonificación de uso de suelo

Introduction

The increasing human population sets universally high demands for land use (e.g., Foley et al. 2005; Millennium Ecosystem Assessment 2005; Polasky et al. 2008), and there is a constantly diminishing area remaining for the maintenance of biological diversity and ecosystem services (Chan et al. 2006; Fischer et al. 2007). Unfortunately, science has not, and may never, have an accurate answer to the question of how much area is enough to meet the varying goals for conservation of biological diversity and ecosystem functions (e.g., Svancara et al. 2005; Tear et al. 2005; Rondinini & Chiozza 2010). Despite apparent political will (Convention on Biological Diversity 2010), recent work shows that ecosystems are being degraded at alarming rates both outside and inside protected areas (Laurance et al. 2012).

To combat an overall decline in biological diversity, systematic conservation planning (SCP) was developed. This planning method focuses on both design and on-the-ground implementation of conservation (e.g., Sarkar et al. 2006; Margules & Sarkar 2007; Kukkala & Moilanen 2013). SCP offers tools to optimally design and expand reserves by identifying areas with the highest irreplaceability and complementarity (Sarkar et al. 2006; Pressey et al. 2007) and minimizing losses by considering spatial information on the probability of loss of ecological values in the landscape (e.g., Pressey et al. 2004; Nicholson et al. 2006; Visconti et al. 2011). Two target-based problem formulations, minimum-set and maximum-coverage planning, are integral to the SCP framework (Margules & Pressey 2000; ReVelle et al. 2002; Margules & Sarkar 2007). Minimum-set planning satisfies given ecological targets at minimum cost, and maximum-coverage planning satisfies as many targets as possible within the available budget when resources do not suffice to meet all targets. SCP can alleviate trade-offs between economic gains and ecological losses and improve conservation success because it maximizes the cost-effectiveness of conservation by minimizing area (and thus cost) needed for achieving a priori fixed ecological targets (Possingham et al. 2006).

Although SCP methods provide a systematic protocol for defining goals and targets for conservation (Pressey & Bottrill 2008; Carwardine et al. 2009), there is still uncertainty about whether the protected-area networks will ensure long-term persistence of populations and ecosystem functioning (e.g., Cabeza & Moilanen 2003;

Kuussaari et al. 2009; Laurance et al. 2012). In response to this uncertainty, a shift in focus from the design of protected-area networks to more holistic approaches that cover the entire landscape have been suggested (e.g., Maiorano et al. 2008; Mathur & Sitha 2008; Chazdon et al. 2009). Tools have also been developed that integrate conservation planning with the needs of other land uses (e.g., Gordon et al. 2009; Watts et al. 2009; Willis et al. 2012).

One important aspect of conservation outside protected areas is the avoidance of negative environmental and ecological effects of economic development projects (Cuperus et al. 2001; Ten Kate et al. 2004). We investigated the application of spatial prioritization methods to avoid landscape-level negative effects (e.g., decreasing ecosystem area and declining species populations) of development. This application differs from the typical use of spatial prioritization in reserve selection. We devised inverse spatial conservation prioritization, a process that identifies areas for economic development that are the least ecologically valuable.

Because target-based planning is the most typical planning mode in SCP (Sarkar et al. 2006; Margules & Sarkar 2007; Pressey & Bottrill 2008), we first summarize target-based inverse analogues of the minimum-set and maximum-coverage approaches. In the inverse minimum-set problem, each ecological feature is given a maximum loss limit, and the method identifies the set of areas that generate maximal joint income from alternative land uses without violating any feature-level ecological loss limit. In the inverse maximum-coverage problem, the objective is to provide stated economic benefits while violating as few ecological loss limits as possible. However, many planning projects are less than ideally suited for a completely target-based design. Negative effects on the environment caused by any single economic development project can be small and do not necessarily cause any landscape-wide feature-level targets to be violated. A target can indeed be set for economic return or area needed for development, but minimization of ecological losses over multiple features can sometimes be better implemented via an aggregate benefit-based approach rather than via targets (Moilanen & Arponen 2011; Laitila & Moilanen 2012).

We propose that trade-offs between conservation and economic development may be investigated in a more informative and flexible way when they are not restricted to target-based approaches. We illustrate nontarget-based

inverse spatial conservation prioritization by applying it to land-use zoning in the province of Central Finland. This zoning includes allocation of areas for peat mining. To satisfy the interests of stakeholders, a flexible preliminary target of 6000–12,000 ha for peat mining was considered. These areas were to be allocated so that ecological losses would be minimized. We used the Zonation approach to implement inverse spatial conservation prioritization. Zonation applies generic methods for how conservation value is aggregated across features, space, and time (Moilanen et al. 2009, 2011). Because our method operates without a priori targets and produces a continuous prioritization across the entire landscape, decision makers can examine the spatial and quantitative trade-offs between biological diversity features and peat mining before deciding how many and which areas will be allocated for peat extraction.

Methods

The focal landscape consisted of 306 partially ditched peatlands (36,503 ha). We excluded conservation areas and other unditched peatland areas from the analysis because they would not be allocated to peat mining in any case. Various stakeholders (peat mining companies, local energy company, nature conservation organizations, local and national environmental administration, and the Finnish Forest and Park Services) predetermined the areas included in the prioritization as possible candidates for peat extraction. However, not all stakeholders would choose the same set of areas for actual mining because the peatlands have variable peat-mining potential and contain different sets of biological diversity features.

Principles of Inverse Spatial Conservation Prioritization

We used the publicly available Zonation method and software (Moilanen et al. 2005, 2011, 2012) to perform land-use prioritization. Zonation identifies areas that are important for retaining environmental quality and landscape connectivity simultaneously for multiple features (species' populations, ecosystem types, etc.) in the landscape and thereby indirectly aims to retain persistence of all these features (e.g., Moilanen et al. 2005; Kremen et al. 2008; Moilanen et al. 2012).

The operational principle behind Zonation is to maximize the retention of range-size normalized occurrence levels of multiple features (species, ecosystems, etc.) according to their feature-specific weights, connectivity, and other considerations while retaining a complementarity-based balance across all features (Moilanen et al. 2011). Zonation starts from the assumption that in terms of ecological persistence it is best to conserve the entire landscape. Grid cells are iteratively removed (proposed to be allocated for economic land use) and

aggregate loss of biological diversity features is minimized according to their weights and abundance remaining after each removal. The order of removal of grid cells is recorded to produce a ranking for the prioritization of the grids.

Heuristically, Zonation balances the abundance, quality, and connectivity of ecological features. Zonation can also account for multiple direct or indirect costs of conservation. We defined cost as lost potential for peat mining, which we measured in units of area suitable for peat mining (Geological Survey of Finland 2011). This cost is an opportunity cost incurred when an area is conserved and thus not available for peat extraction. Grid cells that remained to the end of the ranking were mutually complementary and had generally high-weighted feature richness and rarity and low peat-mining potential. Focusing on the low-priority end of a Zonation priority ranking (first grid cells removed) allowed us to implement the inverse spatial conservation prioritization principle: identification of areas that have comparatively low ecological values but high utility for other land uses.

Analysis Structure

We used the additive benefit function method to aggregate conservation value (ABF) (parameter $z = 0.25$) (Moilanen 2007). The ABF assumes conservation value is additive across features, and representation of each feature is converted to a value with a benefit function such as the one used in the canonical species-area curve (Arponen et al. 2005; Moilanen et al. 2011):

$$V(S) = \sum_j w_j R_j(S)^{z_j}, \quad (1)$$

where $V(S)$ is the value of the remaining set of grid cells S , w_j is the weight of ecological feature j , and z_j is a feature-specific exponent. The quantity $R_j(S)$ is the normalized distribution of the feature remaining in set S . Initially, when the full landscape remains, $R_j(S) = 1$ for all features. As the ranking proceeds, $R_j(S)$ declines for all features as areas are removed from conservation. The ABF removes grid cells from the remaining landscape (S) so that loss of $V(S)$ are minimized. Range-size normalization causes narrow-range features to have a relatively high effect on prioritization. The concave shape of the function implies that a balance is retained across features—when the representation of a feature declines, marginal losses for the feature increase continuously.

We conducted the analysis in 7 stages with 7 combinations of ecological features, feature weights, and analysis settings for ranking the conservation priority of areas (Fig. 1 & Table 1). The groups of features and analysis settings increased in complexity: (1) ecosystem types, (2) ecosystem types + ecosystem-type weights, (3) ecosystem types + ecosystem-type weights + ecosystem condition weight, (4) ecosystem types + ecosystem-type

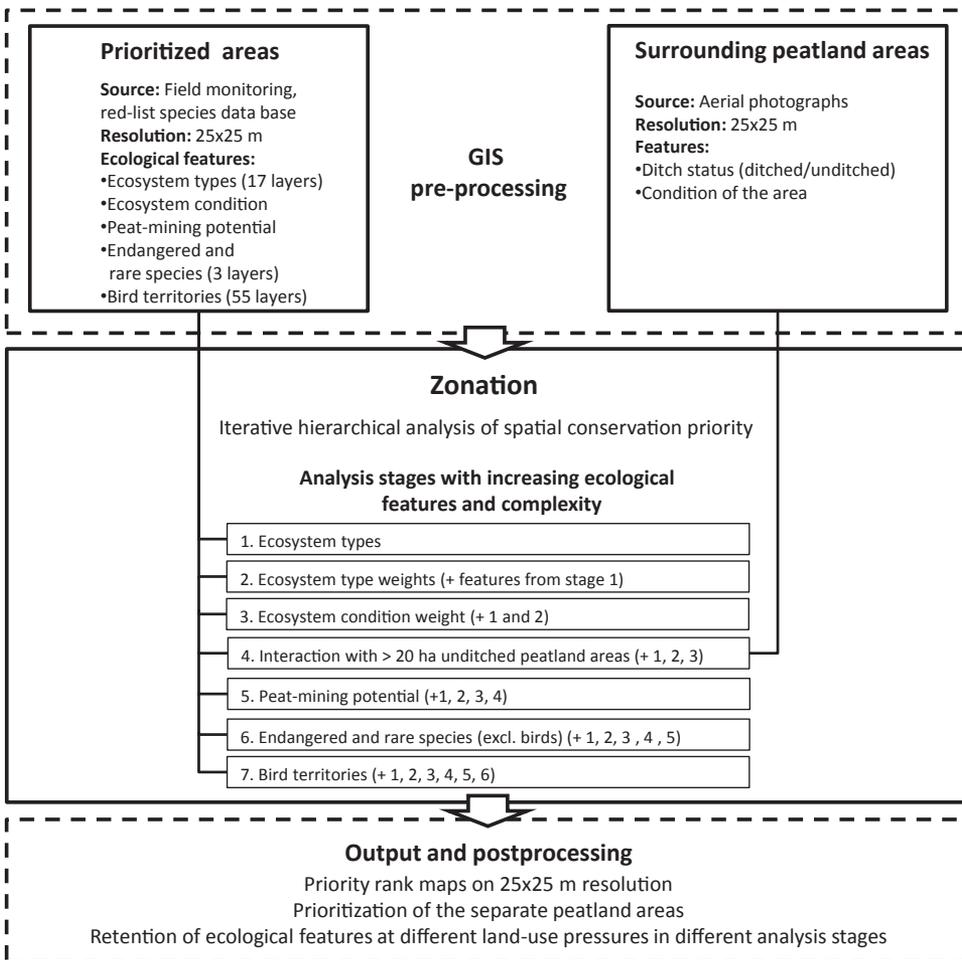


Figure 1. Process of the Zonation analysis that we used to perform the inverse spatial conservation prioritization for minimization of negative ecological effects of peat mining. Analysis stages include all the ecological-feature data used for conservation-priority ranking in the preceding stages together with new data or new analysis settings needed for the increasingly complex analyses (Table 1).

weights + ecosystem condition weight + connectivity interaction with unditched peatland areas >20 ha, (5) ecosystem types + ecosystem-type weights + ecosystem condition weight + connectivity interaction + peat-mining potential, (6) ecosystem types + ecosystem-type weights + ecosystem condition weight + connectivity interaction + peat-mining potential + red-listed and rare species, and (7) ecosystem types + ecosystem-type weights + ecosystem condition weight + connectivity interaction + peat-mining potential + red-listed and rare species + bird territories (see Supporting Information for details). We conducted analysis in stages so that we could verify the correctness of input data and analysis setup at each step.

We weighted ecological features according to an expert opinion on their relative importance (e.g., ecosystem types and condition were thought to best define the ecological value of peatland) (Table 1). Feature weights varied within and between feature groups (e.g., ecosystem types, endangered species occurrences, bird territories) (Table 1). We considered some core feature groups (e.g., ecosystem types) more important than other feature groups (e.g., bird territories), and some features within

each feature group were more important than others (e.g., nutrient-rich fens versus nutrient poor pine mires). We based the final weight of each ecological feature on its relative importance within the feature group and by the relative importance of the feature group to other feature groups. Although assigning weights may resemble target setting, the weights were only used to affect the balance among features, and they do not delineate how much of each feature should be conserved per se. For example, a low-weight feature can have a high representation level if it is highly correlated in space with other features. The built-in range-size normalization introduces a tendency for Zonation analyses to give high priority to areas with occurrences of narrow-range features (Moilanen et al. 2011).

We initially performed the prioritization at a 25×25 m grid resolution. For the purpose of zoning, we constructed the final prioritization with entire peatland entities (306 planning units) as planning units. We did this because when a peatland is mined, the drainage of the area usually affects the entire peatland, not just the individual grid cells where peat has been extracted. Nevertheless, in other types of land use, effects can

Table 1. Ecological-feature data layers, feature weights, and analysis settings used in different stages of the analysis to prioritize peatlands.

Stage	Ecological feature and analysis setting on which conservation-priority ranking is based ^a	Description (conservation status) ^b	Weight
1	Ecosystem types (separate layer for each type)	eutrophic fens (CR)	1
		eutrophic spruce fen mires (EN)	1
		springs (EN)	1
		mesotrophic fens (VU)	1
		mesotrophic spruce fens (VU)	1
		mesotrophic pine fens (VU)	1
		oligotrophic fens (VU)	1
		oligotrophic pine mires (VU)	1
		oligotrophic spruce fens (VU)	1
		oligotrophic pine fens (VU)	1
		swamps (NT)	1
		ombrotrophic fens (NT)	1
		ombrotrophic pine mires (NT)	1
		ombrotrophic pine fens	1
		moderately changed peatlands	1
		severely changed peatlands	1
peat mining sites	1		
2	Ecosystem-type weights	CR ecosystem types	5
		EN ecosystems types	4
		VU ecosystems types	3
		NT ecosystems types	2
		ombrotrophic pine fens	1
		moderately changed peatlands	0.5
		severely changed peatlands	0.1
		peat mining sites	0.001
3	Condition or state of peatland area: past loss of habitat condition was modeled as a local decrease in the occurrence level of the peatland ecosystem at the affected location	pristine	1.0
		near pristine	0.8
		moderately changed peatland	0.5
		severely changed peatland	0.2
		peat mining site	0.0
4	Unditched, >20 ha peatland areas: this information was used in connectivity calculation of prioritized sites	unditched peatland areas of Central Finland and their condition	NA
5	Peat-mining potential	proportion of each peatland area suitable for peat mining	-5
6	Endangered and rare species (excluding birds): one species group layer for each level of conservation priority; value of the occurrence given only to the grid cell it was observed in	vulnerable species (4 species/29 observations)	3
		near threatened species (19/52)	2
		regionally threatened and rare species (18 / 121)	1
7	Bird territories: individual layers for all observed bird species; value of each territory partitioned to the grid cells of the peatland area it was observed in	birds, high priority (21 species layers/264 territories)	0.5
		birds, moderate priority (16 species layers/320 territories)	0.25
		birds, low priority (18 species layers/1357 territories)	0.05

^aEach successive stage of the analysis includes all features of previous stages (e.g., condition or state of peatland area also includes ecosystem type and ecosystem-type weight).

^bAbbreviations: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened.

remain localized, in which case the grid-based solution can help identify small areas that are most important to conserve.

We used the feature-specific performance curves automatically created in Zonation to investigate the quantitative trade-off between ecological features and peat-mining potential. We compared the outcome of the full prioritization with a random allocation scenario and with a greedy selection scenario in which peat extraction was maximized without regard to ecological values.

Results

We created a prioritization over the entire landscape (Fig. 2) and successfully found a solution in which the need for peat mining areas can be satisfied without major loss of different ecosystem types, endangered species, or bird territories (Fig. 3a & Table 2). The spatial priority map created in the Zonation analysis showed the priority of different peatlands (Fig. 2). In the present case, the more pertinent information was in the

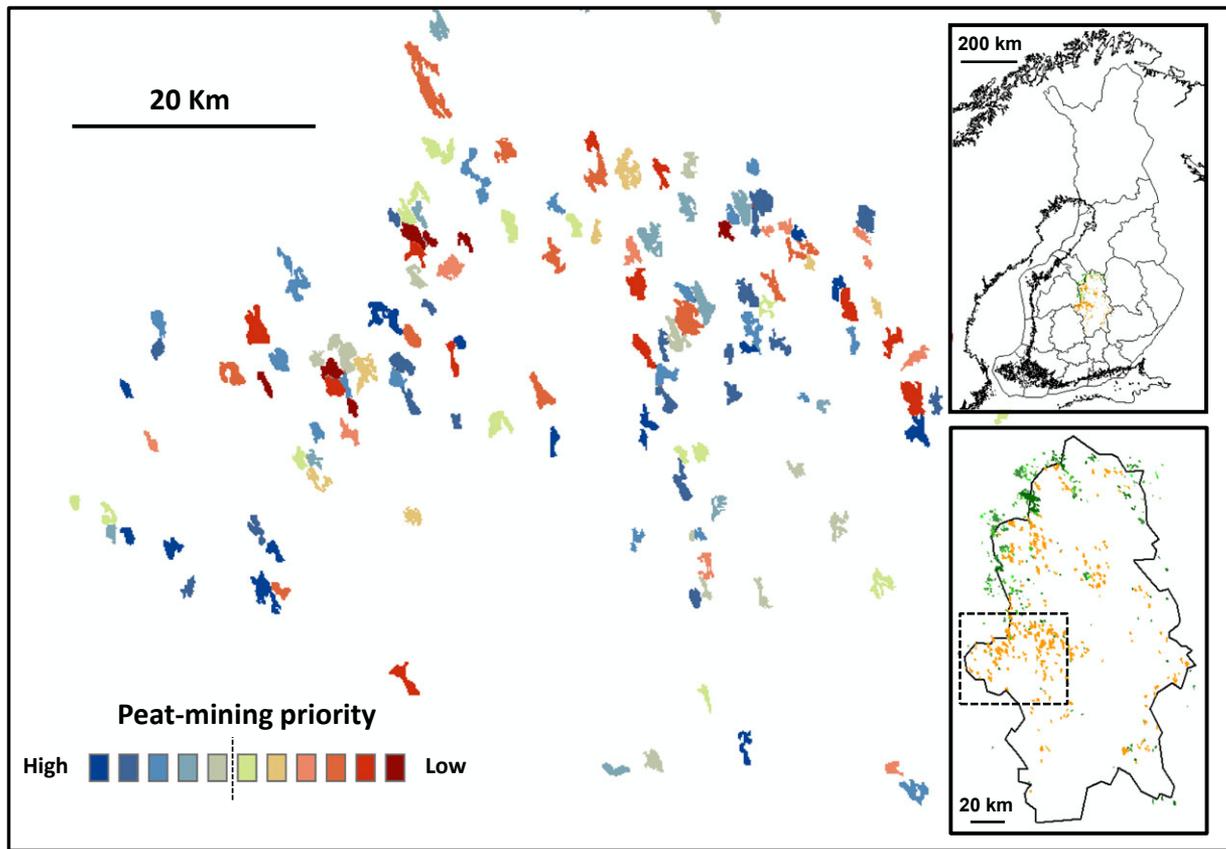


Figure 2. Close up of the inverse spatial conservation prioritization of peatlands under consideration for peat mining (high, high priority for peat mining; low, low priority for peat mining; line dividing priority color scheme, 7000 ha realized peat-mining potential). The upper inset shows the location of the study area in Finland, and the lower inset shows the spatial distributions of >20 ha of unditched peatland (green) and the candidate areas for peat mining we included (brown). Map outlines are from the National Land Survey of Finland (2010).

performance curves, which showed the status of each ecological feature (or feature group) throughout the prioritization (Fig. 3 & Table 2). The distributions of most of the ecological features remained at high levels up to the loss of approximately 42% of peatlands (Fig. 3a & Table 2). Thereafter, the retention of ecological features declined substantially (Fig. 3a). With 42% (approximately 15,200 ha) loss of the total peatland area, 47% (approximately 7000 ha) of the total peat-mining potential was achieved, and on average 82% of the distributions of biological diversity features were retained in the rest of the landscape (Fig. 3a & Table 2).

When no prioritization was used (i.e., spatial allocation of mining areas was random), the decrease in distributions of ecological features and the increase in realized peat-mining potential were on average in direct proportion to total area allocated for peat mining (see the decrease of nonprioritized features' distributions in greedy selection in Fig. 3b). In the scenario of random allocation of peatlands to peat mining, 47% of the peat-mining potential was achieved in 47% of the total area, leaving, on average, 53% of the ecological value, with

potentially large random differences between individual features. Consequently, the inverse spatial conservation prioritization resulted in, on average, retention of 54% more of the ecological value (82% versus 53%) (Table 2) than random allocation of peatlands. The aggregate benefit of spatial prioritization was that ecological losses were reduced by, on average, 62% relative to random allocation.

In the economically realistic greedy-selection scenario, peatlands were allocated to mining in decreasing order of peat content (amount per area) without consideration of biological diversity features (Fig. 3b). In this scenario, 47% of peat-mining potential (approximately 7000 ha of peat-mining area) was achieved in 34% of the total peatland area, a significantly smaller area than that required by full prioritization or random allocation. Due to the high overall reduction in total area, the greedy scenario produced an ecologically better outcome than the random-allocation scenario. Because there was no strong correlation between the ecological features and peat-mining potential, ecological value declined in direct proportion to area, but there were relatively large

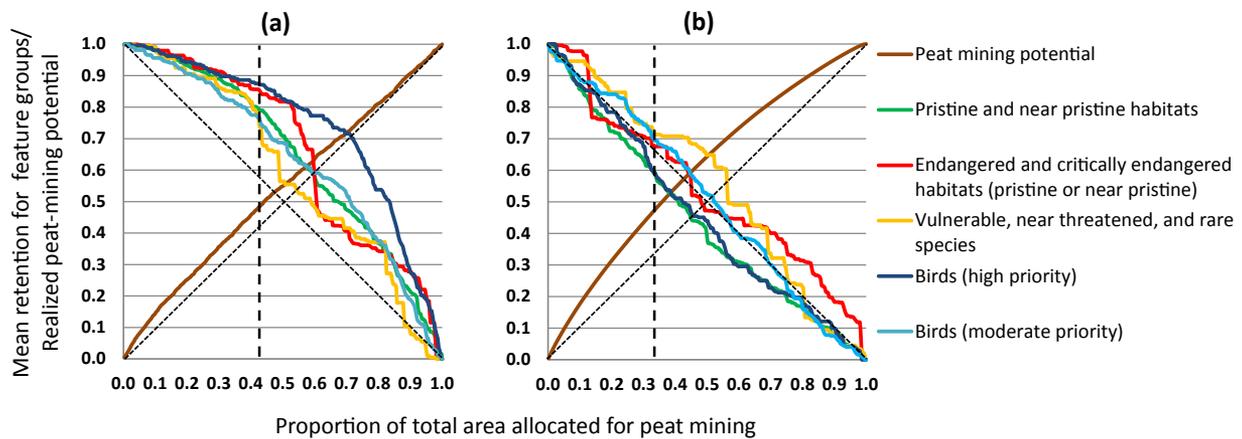


Figure 3. Performance curves for prioritizations of peatlands: (a) baseline analysis including all major ecological feature groups and peat-mining potential and (b) simple greedy selection (peatlands allocated to mining in decreasing order of proportion of area suitable for peat mining). Each declining line shows the average proportion remaining across features within one major biological diversity feature group, plotted as a function of declining area available for conservation. The thick increasing line shows the proportion of maximal peat-mining potential realized as a function of the proportion of area outside conservation. For example, 0.8 proportion remaining for birds of high priority means that on average 80% of the territories of these birds are in peatlands saved from peat mining. The thin black diagonal lines represent expected decrease in ecological values (Table 1) and expected increase in realized peat-mining potential if areas are randomly allocated into peat mining (i.e., the random selection scenario). The dashed vertical lines mark the 7000-ha realized peat-mining potential (Table 1).

difference among features. This resulted in relatively high and unnecessary losses of ecological value. For example, 44% of the pristine and near-pristine peatland area was lost as 42% of the distributions of high-priority bird species. On average, approximately 65% of the distributions of biological diversity features were

retained in this scenario (Fig. 3b), which compares unfavorably with the approximately 82% retained by full prioritization of multiple ecological features (Fig. 3a). These figures are naturally case specific, but they illustrate the quantitative benefits generated by the propose analyses.

Table 2. Biological diversity gains with inverse spatial conservation prioritization with approximately 7000 ha of suitable area for peat mining realized.*

Biological diversity feature	Distribution size in full study area	Remaining in full analysis	Remaining in random selection	Remaining in greedy selection	Gain compared with random selection	Gain compared with greedy selection
Total area (ha)	36503	0.58 (21,040)	0.53 (19,347)	0.65 (23,864)	0.10 (1975)	-0.11 (-2,542)
Pristine and near pristine peatland area (ha)	4531	0.80 (3629)	0.53 (2401)	0.56 (2537)	0.51 (1228)	0.43 (1092)
Critically endangered and endangered areas (pristine and near pristine) (ha)	300	0.86 (257)	0.53 (159)	0.68 (204)	0.62 (98)	0.26 (53)
Endangered and rare species (occurrences)	202	0.78 (158)	0.53 (107)	0.71 (143)	0.48 (51)	0.10 (15)
Birds, high priority (territories)	264	0.88 (231)	0.53 (140)	0.58 (153)	0.65 (91)	0.51 (78)
Birds, moderate priority (territories)	320	0.77 (246)	0.53 (170)	0.68 (217)	0.45 (76)	0.13 (29)
Average remaining proportion (excluding total area)		0.82	0.53	0.64		
Average relative gain of the full analysis (excluding total area)					0.54	0.29

*Retention and gain (full analysis compared with random and greedy selections) are expressed as fractions of total. Where relevant, absolute amounts corresponding to fractions are in parentheses.

Discussion

Our method of inverse spatial conservation prioritization balances economic requirements of one or several stakeholders while minimizing ecological loss aggregated over multiple biological diversity features. The spatial solutions derived from this method delineates areas ideal for avoidance of negative ecological effects. Our results demonstrated that the negative effects of human land use can be successfully avoided because we found that over 80% of the known ecological values of the planning area could be saved with a reasonable trade-off for peat-mining interests. In fact, when the peat-mining potential of areas was included in the analysis, the expected efficiency of peat mining increased relative to random allocation of areas to peat mining. Inverse spatial conservation prioritization also resulted in significant ecological savings compared with a greedy selection scenario, which only minimized the total area needed. On the basis of our results and other considerations, including negotiations with various stakeholders, the Regional Council of Central Finland decided that approximately 7000 ha of area suitable for peat mining will be allocated for peat extraction in the final land-use zoning plan. According to our analysis 7000 ha of suitable peat-mining area can be derived with 42% of the total peatland area allocated to peat mining and over 80% of the known ecological values of the planning area retained.

We call the principle applied here inverse spatial conservation prioritization because, in contrast to typical spatial prioritization, the idea is not to identify (for protection) areas with the highest ecological values. Rather, the objective is to identify the inverse end of the landscape, that is, areas with the lowest ecological values that are simultaneously the most appropriate for economic land uses (here peat mining). Of course one still needs to decide where to draw the line of acceptable ecological loss (Fig. 3). Estimation the consequences of this decision is plagued by uncertainty arising from incomplete data and understanding of ecological dynamics and, perhaps more importantly, changing political will. However, we believe, and others agree, that decision making is better justified and more acceptable when the trade-offs between economic gain and ecological loss are first examined quantitatively (e.g., Wilhere 2008).

It has been suggested that avoidance of negative ecological effects should be the primary goal of conservation efforts that counter development effects that may threaten the environment (Cuperus et al. 2001; Ten Kate et al. 2004). Even so, avoidance of negative effects is rarely discussed or properly applied in the context of land-use planning in unprotected areas that are not perceived to hold any great ecological value (e.g., Maiorano et al. 2008; Mathur & Sitha 2008; Chazdon et al. 2009). Nevertheless, it is known that even partially degraded unprotected areas can provide ecosystem services

or hold ecological value that substantially supplement conservation-area networks (e.g., Fischer & Lindenmayer 2002; Bengtson et al. 2003; Laita et al. 2010). Integrating the inverse spatial conservation prioritization principle to global land-use planning could avoid a multitude of individually small ecological losses and could indirectly generate huge conservation gains at regional and global scales.

The proposed approach differs from previous related work that focused on targeting of protection measures to valuable sites that would experience substantial loss of biological diversity value in the absence of protection because we focused on ecologically low-value sites. One well-known approach to loss avoidance is to use a combination of vulnerability and irreplaceability to determine protection priorities for ecological features of interest (Gaston et al. 2002). Pressey et al. (2004) introduced the principle of maximal retention of biological diversity by loss minimization, which combined loss rates and presence of biological diversity in one measure. Ban and Vincent (2009) turned traditional target-setting around by setting targets for fishery yields and then minimizing the area (ecological cost) needed to satisfy these economic targets, thus working inversely from classic SCP problem formulations. The approach Ban and Vincent (2009) used allows spatial prioritization in which multiple target features are balanced with a single cost (i.e., a many-to-one structure). In their case, this was multiple targets for economic components (yields of separate fisheries to be satisfied with minimum area) and a single aggregate layer for area (area as a surrogate for biological diversity value), the allocation of which to fishery use was minimized as a cost. Instead of balancing distributions of multiple features with a single cost, our method has a computational structure in which multiple biological diversity features may be balanced against multiple costs (Moilanen et al. 2011), which is a major advantage because biological diversity value need not be represented by a single layer.

Recently, Klein et al. (2010), Weeks et al. (2010), Wilson et al. (2010), and Grantham et al. (2013) applied an approach that allows sites to be placed into one of several different planning zones, and the zone designation has different effects on economic gains and biological diversity features. All these authors focused on zoning with balanced benefits across multiple stakeholders. For example, Grantham et al. (2013) set separate protection targets for species, ecosystems, and coverage of communal fishing grounds, thereby identifying a solution that produces prespecified economic benefits across stakeholders while retaining target levels of biological diversity.

As a distinguishing feature, our work does not require a priori setting of targets, which is a practical and conceptual advantage (Laitila & Moilanen 2012). Here, an acceptable trade-off between production and nonproduction areas is quantified after prioritization with performance

curves. This is in the reverse order of the common practice of SCP (Margules & Pressey 2000; Cawardine et al. 2009). The target-free inverse approach bypasses overall inefficiency that can arise from the target-setting model and processes because a poorly set target can consume a disproportionate fraction of resources and lead to inferior aggregate conservation performance (Moilanen & Arponen 2011; Di Minin & Moilanen 2012; Laitila & Moilanen 2012). This is a real possibility when many targets need to be set for different types of biological diversity features. Our work offers a different and flexible approach to balancing economic benefits and ecological effects of development through the use of spatial-prioritization tools.

Conservation prioritization should be flexible in the sense that it does not lose its effect when facing real life considerations (Margules & Pressey 2000; Cabeza & Moilanen 2006; Sarkar et al. 2006; Knight et al. 2008; Arponen et al. 2010). We contend that this flexibility requirement should apply to other forms of land use planning as well. Fortunately, prioritization outside protected areas does not have to be an either/or battle between ecological values and economic returns (Polasky et al. 2005; Polasky et al. 2008; Perhans et al. 2011). Inverse spatial conservation prioritization, as used here, can be successful in identifying profitable production areas while simultaneously safeguarding ecological values in an all-inclusive approach to land use decisions.

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Supporting Information

Information on the data and analysis stages we used are available online (Appendix S1). 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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