REPORT

Incorporating threat in hotspots and coldspots of biodiversity and ecosystem services

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Abstract Spatial prioritization could help target conservation actions directed to maintain both biodiversity and ecosystem services. We delineate hotspots and coldspots of two biodiversity conservation features and five regulating and cultural services by incorporating an indicator of ‘threat’, i.e. timber harvest profitability for forest areas in Telemark (Norway). We found hotspots, where high values of biodiversity, ecosystem services and threat coincide, ranging from 0.1 to 7.1% of the area, depending on varying threshold levels. Targeting of these areas for conservation follows reactive conservation approaches. In coldspots, high biodiversity and ecosystem service values coincide with low levels of threat, and cover 0.1–3.4% of the forest area. These areas might serve proactive conservation approaches at lower opportunity cost (foregone timber harvest profits). We conclude that a combination of indicators of biodiversity, ecosystem services and potential threat is an appropriate approach for spatial prioritization of proactive and reactive conservation strategies.

Keywords Carbon sequestration · Carbon storage · Conservation management · Existence value · Recreation · Spatial priority setting

INTRODUCTION

Ecosystem services (ES) are the multiple contributions of ecosystems to human well-being. These can provide conservation arguments that go beyond intrinsic values of

biodiversity. Hence, the interest in finding common grounds and synergies between biodiversity and ES is increasing. While spatial priority setting has a long tradition in conservation biology (Margules and Pressey 2000; Sarkar et al. 2006), there is little, yet increasing awareness that spatial prioritization could also help to inform management aiming at sustained ES provision. Strategies could be found for conservation-compatible ES, especially regulating services, such as carbon sequestration and flood control, and cultural services, such as space for recreation and aesthetic appreciation (Chan et al. 2011; Schröter and Remme 2016). These types of ES are often associated with low levels of human interference and hence, provided by areas of potentially high biodiversity conservation interest.

A challenge to include ES in conservation planning is the different degrees of spatial congruence between areas with high biodiversity conservation value and ES provision (Cimon-Morin et al. 2013; Schröter et al. 2014b; Ricketts et al. 2016). A further challenge is the high opportunity cost of areas supplying high levels of provisioning services. These conflicts between conservation and ES provision are apparent for forests in Norway, especially in areas of high productive capacity of provisioning services (timber production), which are intensively managed and show low proportion of protected land (Sverdrup-Thygeson et al. 2014). Consequently, national indices measuring the condition of forest biodiversity show relatively low values (Storaunet and Framstad 2015). Among the main conservation features in decline are old trees and species associated with old-growth forest, dead wood, and wood decomposers, all directly related to forestry management practices. Logging of young trees and clear-cutting practices are the main causes of declining biodiversity (Framstad and Sverdrup-Thygeson 2015). There is also evidence that clear-cutting of forests has negative effects on a

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number of ES, in particular reducing the capacity to generate regulating and cultural services. For instance, carbon storage and sequestration can be reduced (Finér et al. 2003; Humphreys et al. 2006), and harvesting interventions on slopes can lead to open forests with low vegetation cover, which in turn increases the risk for snow slides (Bebi et al. 2001; Brang et al. 2006). Furthermore, large clear-cuts have a negative impact on the recreational experience by forest visitors (Gundersen and Frivold 2008; Tyrväinen et al. 2014). Based on these considerations, there is a need to rethink the criteria for prioritizing areas for conservation in Norwegian forests, in particular, in the light of targets to expand the area of protected land (i.e. Aichi targets of protecting 17% of land area, UNEP 2010).

A straightforward way to identify areas of high conservation priority is by means of hotspots. Biodiversity hotspots were defined as areas with high concentrations of endemic species and high level of threat in the seminal work of Myers (1990). Hence, threat has been included in biodiversity hotspot conceptualizations to delineate areas with higher risk of loss. This conceptualization has paved the way for further development of the hotspot concept, which often refers to other criteria of conservation value, including species richness and rarity, and have been used at local (Ceașu et al. 2015), regional (Trizzino et al. 2014) and global levels (Myers et al. 2000). So far, hotspots have been used to delineate important areas for ES provision only in a few cases and definitions of ES hotspots vary widely (Schröter and Remme 2016). While biodiversity hotspots have often integrated the degree of threat to species or habitats in setting priorities for conservation actions (Orme et al. 2005), threat to ES provision has so far not been considered in spatial delineation of hotspots (Schröter and Remme 2016).

Hotspots can draw the attention of managers and decision-makers to areas of both high conservation importance and high vulnerability (Bagstad et al. 2016). Identifying hotspots is relatively straightforward, intuitive and sensitivity analyses on what threshold is considered “hot” can be easily performed in a transparent way. Parallel to the notion of hotspots, an antonym concept of coldspots has been proposed (e.g. Willemsen et al. 2010; Bagstad et al. 2016), however, with varying conceptualizations. While Bagstad et al. (2016) use coldspots for areas of low risk of anthropogenic change or conflict, Willemsen et al. (2010) define coldspots as areas with conflicts between two or more landscape functions. Other conceptualizations are used to either highlight the importance of going beyond species numbers in conservation, e.g. defining areas of low values of species richness being important for conservation (Kareiva and Marvier 2003), or to delineate areas of low importance for ES conservation, e.g. low values of ES (Timilsina et al. 2013; Locatelli et al. 2014). In our context,

the consideration of threat is crucial, and hence we define coldspots as areas with high biodiversity and ES values, but low threat values, i.e. low potential conflict. Such areas might cause less conservation conflicts due to low opportunity costs (Naidoo et al. 2006). Assessing levels of threat allows distinguishing conservation strategies that are either reactive (i.e. threat has already become evident) or proactive (i.e. taking action before threat becomes evident) (Brooks et al. 2006).

The aim of this study is to integrate threat into the delineation of priority areas for the conservation of biodiversity and forest-generated ES. We identify areas of high conservation importance under high threat—hotspots—and low threat—coldspots—defined by the probability of logging as an integrative indicator of threat. We apply this analysis to a case study in the forest area of Telemark, a province in southern Norway. We assess to which degree both hotspots and coldspots are spatially coinciding with the existing nature reserves. Based on the analysis, we discuss the usefulness of hotspots and coldspots, as well as the consideration of threat in proactive and reactive management strategies at a regional scale.

MATERIALS AND METHODS

Study area

Telemark, a province in southern Norway, covers about 15 300 km² (Fig. 1). With just 11 inhabitants per km², the area is sparsely populated, with most of the people living in the South-east. The climate varies between temperate conditions in the South and alpine conditions in the North-west. The main land cover is characteristic of coniferous and boreal deciduous forest (7995 km² or 52% of Telemark) and large inland lakes in the south and middle parts, whereas the northern part is covered by treeless alpine highland plateaus with bogs, fens and heathlands (Moen 1999). The analysis was conducted for the forest area of Telemark, excluding a small part (1.8% of the area) where data were lacking (cf. Figs. 1, 3). *Forest area* hereafter refers to this area of 7851 km².

Threat indicator

As threat indicator, we used a profitability model for timber harvest, assuming that higher profitability of an area for timber production leads to a higher likelihood to be logged, and hence a higher threat for biodiversity and ES (for details, see Blumentrath et al. 2013). The model uses data from the national forest inventory on forest stand quality, including timber stock volume, age, tree species and stand productivity, hence accounting for potential income from

Fig. 1 Study area: Telemark province, southern Norway, with four major land cover categories (aggregated classes from CORINE Land Cover 2012, v18.5.1). Hillshade is used for highlighting terrain properties

timber harvest (Blumentrath et al. 2013). It also accounts for harvest costs by considering factors of accessibility including distance to roads and slope of the harvested site. According to the model, highly productive, good-quality, highly accessible sites close to roads are more profitable than low-productive, remote and steep sites with low accessibility. The model measures net return in Norwegian kroner per hectare, corresponding to the resolution of the raster (100×100 m grid cells) covering the entire forest area. The grid values were normalized from 0 to 1.

Biodiversity index

We created a biodiversity index taking into account rarity and abundance (see below) of two categories of biodiversity features with relatively high area coverage: 10 priority habitats for conservation (Norwegian Environmental Agency 2013) and 40 old-growth forest types. Both datasets were rasterized to 10×10 m grid cells.

The priority habitats for conservation cover 93.3 km^2 or 1.2% of the forest area. Old-growth forest types cover

1363.7 km^2 or 17.4% of the forest area (details in Appendix S1).

We calculated spatial rarity of each biodiversity feature according to the formula:

$$R_i = A_{\text{total},i}^{-1} \quad (1)$$

where $A_{\text{total},i}$ is the total area of feature i in the study area. R_i was also aggregated to 100×100 m cell size, and values were normalized from 0 to 1 over all features (old growth forest types and priority habitats), to ensure that rarity of each feature is independent of scale and standardized in relation to all others.

The biodiversity index was calculated according to the following formula:

$$\text{BDI} = \sum_{i=1}^n R_i \times A_{\text{grid},i} \quad (2)$$

where BDI is the biodiversity index value in each 100×100 m grid cell, R_i is the spatial rarity measure of feature i and $A_{\text{grid},i}$ is the area of feature i (i.e. abundance) calculated as the sum of 10×10 m grids in a

100 × 100 m grid cell with values from 1 to 100. Each feature corresponds to either one of the 40 old-growth forest types or one of the 10 priority habitats. After summing up all biodiversity features for each grid cell, we normalized the BDI from 0 to 1. We did not account for overlapping areas of old-growth forest and priority habitats for conservation due to the low share of the latter in old-growth forest area (19.4 km² of 1363.7 km² or 1.4%). However, this means that for this small percentage of forest, we account for both old-growth forest and priority habitat by summing up the respective BDI values. Due to limited spatial coverage of the input data, the BDI was calculated for 2756 km² or 35.1% of the forest area (cf. Fig. 2).

Ecosystem service indicators and index

We created an index covering the entire forest area and comprising standardized values of five ES: carbon storage and sequestration, snow slide prevention, recreational hiking and the existence of wilderness-like areas (for detailed model descriptions cf. Appendix S1 and Schröter et al. 2014a). We created the ES index weighing all five ES equally and summing the values of each ES per cell:

$$ESI = \sum_{i=1}^n ES_i \quad (3)$$

Fig. 2 Conceptual figure of spatial relation of the input data (*light grey* = ecosystem services index and threat index, corresponding to total forest area; *dark grey* = biodiversity index) and the derived hotspots/coldspots (*shaded*, cf. legend). *Note* size relations and overlays of *rectangles* do not correspond to actual numbers

where ESI is the ES index, n is the number of ES (5), and ES_i is the value of each ES in each grid cell, normalized from 0 to 100. This approach is a simplification, assuming that all ES are of equal importance. We normalized the ES index from 0 to 1.

Hotspots, coldspots and sensitivity analysis

We defined biodiversity and ES hotspots as areas with high levels of threat and high levels of biodiversity or ES. Joint biodiversity and ES hotspots (joint hotspots) represent areas of high biodiversity, ES and threat. We defined high levels as top deciles (10, 20, 30, 40, and 50%) of all cells and subjected them to a sensitivity analysis. Low levels of threat were defined as the lower five deciles (details in Appendix S1).

We created a feature space to illustrate the distribution of levels of threat, biodiversity and ES. For this, we randomly extracted 2% of all 100 × 100 m cells (15 702 cells) within the total forest area while accounting for a minimum distance of 500 m between grid cells to reduce spatial autocorrelation. For these cells, we extracted the values of threat, ESI and BDI and plotted threat against the ESI, indicating BDI values in the upper 50% quantile additionally. We furthermore intersected the 50%-quantile hotspot (top 50% quantiles for all indices, respectively) and coldspot areas (lower 50% quantile for threat and top 50% quantiles for ESI and BDI, respectively) with nature reserves (Norwegian Environmental Agency 2013). All spatial analyses were done with ArcGIS 10.2.2 (Esri) and independent Python scripts. Index data can be found in Appendix S2.

RESULTS

Spatial distribution of hotspots and coldspots

BDI, ESI and threat showed distinct spatial distribution patterns (Figs. 3, 4). There is a tendency of higher values of ESI on hillsides and of threat at lower and flatter areas throughout the province (cf. Figs. 1, 3). Joint hotspots showed a scattered spatial pattern (i.e. no large connected areas) in the South-east and along the valleys and hillside areas in the West, and clumped patterns on hillsides in the East and North (Figs. 1, 4). Hillside areas contribute both to snow slide prevention and carbon sequestration and storage, leading to a high ESI. Threat and ESI show a tendency of higher values toward the South-east. Low areas are mostly productive, accessible areas, leading to high profitability. BDI tended to be high on hillsides, primarily

Fig. 3 Spatial distribution of the ecosystem service index, biodiversity index and threat indicator

due to a higher number of rare old-growth forest types in close proximity to each other (different climatic zones, different productivity classes).

Sensitivity of hotspot and coldspot areas

Quantile levels considerably influence the size and relative proportion of hotspots and coldspots (Tables 1, 2). Relatively few hotspots of ES, BD or both (joint), were delineated within the whole forest area of Telemark by applying small top quantiles of threat (e.g. 10, 20%). A fifth of the BDI area was delineated as joint hotspots at 50% quantile levels (Table 1).

The sensitivity analysis for coldspots showed a small percentage of the forest area with high levels of biodiversity and ES and low levels of threat (e.g. 0.8% of the area at the 30% quantile level, Table 2). Overall, the area covered by coldspots is smaller than that covered by hotspots.

Proactive versus reactive conservation

A large number of randomly selected points (33% of the sample) present low threat and low ESI values (bottom-left quadrant in Fig. 5). In contrast, a relatively low number of the sampled points in this quadrant show BDI values in the upper 50% quantile (17% of all grid cells with BDI value above zero). These are marginal areas, situated in relatively remote and high-elevation forests with a below average potential for conducting proactive biodiversity and ES conservation. The bottom-right quadrant is characterized by low levels of threat and high ESI values (20% of the area), and a relatively high proportion of biodiversity rich areas (30% of all grid cells

with a BDI value above zero). This quadrant contains areas with a high potential for proactive conservation of both ES and biodiversity and a relatively low conflict potential given the low threat. The top right quadrant contains ES hotspots (31% of the area) and the identified joint hotspots (36% of all grid cells with a BDI value above zero) (cf. also Fig. 3; Table 1). The top left quadrant contains highly threatened areas of relatively low importance for ES (17% of the area) and a relatively low number of biodiversity hotspots (17% of all grids cells with a BDI value above zero). Both top quadrants contain search areas for reactive conservation approaches. Note that the data presented in Fig. 5 is of correlational nature and does not provide information about causality between threat levels and biodiversity and ES.

Spatial congruency with nature reserves

Hotspots for ES, biodiversity and joint hotspots (at the top 50% quantile) are under-represented in nature reserves (Table 3). Both ES and biodiversity hotspots cover only 9.7% of protected forest, while they can be found in 29.8 and 11.2% of the total forest area, respectively. Joint hotspots account for 7.1% of the total forest area, while in nature reserves they only account for 4.5%. In contrast, joint coldspots comprise only 3.4% of the forest area, but are overrepresented in nature reserves with 10.5%. ES and biodiversity coldspots, considered separately, are also overrepresented in nature reserves. Note that the timber harvest profitability model (threat indicator) was independent of the presence of a nature reserve and did not take harvest restrictions into account for the calculation of level of threat.

Fig. 4 Map of biodiversity and ecosystem services hotspots and coldspots in Telemark. Indices of ecosystem services, biodiversity and threat as red–green–blue (RGB) composite. The RGB colour scheme also indicates the delineation of joint hotspots and coldspots. Detail map A illustrates how different hotspots and coldspots but also high levels of threat alone can occur in close proximity to each other. Detail map B highlights a concentration of ecosystem service hotspots at different threat levels (range of yellow hues) with some areas tending towards joint hotspots where colours get bright

Table 1 Percentage of forest area identified as ecosystem service hotspot (light grey), biodiversity hotspot (white) and joint hotspot (dark grey) with varying top quantiles as a result of the sensitivity analysis. Numbers in brackets indicate percentage of the BDI area (cf. Fig. 2). *TQ* top quantile

[%]		Ecosystem service hotspot, biodiversity hotspot									
Threat	TQ ¹	10%		20%		30%		40%		50%	
	10%	1.5	0.3 (0.9)								
		0.1 (0.3)									
	20%			6.3	2.4 (6.9)						
				0.4 (1.1)							
	30%					11.7	3.7 (10.6)				
						1.4 (4.0)					
	40%							19.7	7.0 (20.0)		
								3.4 (9.7)			
	50%									29.8	11.2 (32.0)
7.1 (20.3)											

Table 2 Percentage of forest area identified as ecosystem service coldspot (light grey), biodiversity coldspot (white) and joint coldspot (dark grey) with varying top quantiles for ESI and BDI and lower quantiles for threat. Numbers in brackets indicate percentage of BDI area (cf. Fig. 2). *TQ* top quantile (for ecosystem services and biodiversity), *LQ* lower quantile (for threat)

[%]	Ecosystem service coldspot, biodiversity coldspot									
Threat	TQ/LQ ¹	10%		20%	30%	40%	50%			
	10%	1.0	0.2 (0.6)							
		0.1 (0.3)								
	20%			3.9	0.9 (2.6)					
				0.4 (1.1)						
	30%					8.5	1.9 (5.4)			
						0.8 (2.3)				
	40%							12.6	3.6 (10.3)	
								1.6 (4.6)		
	50%									17.7
								3.4 (9.7)

Fig. 5 Value distribution of 15 702 randomly selected cells of the total forest area in Telemark. *Black points* represent high biodiversity values (top 50% quantile; threshold value 0.035). *Red lines* indicate the threshold between the top and lower 50% quantiles of the ecosystem services index and the threat indicator and divide the feature space into four quadrants. For each quadrant, different land management options are suggested

Overall, 1.9% of the forest area in Telemark is located in nature reserves. Accordingly, a low percentage of ES hotspots (0.6%), biodiversity hotspots (1.7%), and joint hotspots (1.2%) is protected. Joint coldspots, on the other hand, are protected to a proportionally higher degree (6.0%), indicating the application of a proactive conservation approach. Irrespective of the level of threat, 78% of the nature reserves contain relatively high biodiversity and ES values (Table 3).

DISCUSSION

Spatial congruence of ecosystem services and biodiversity in hotspots and coldspots

Analysing spatial congruence of biodiversity and ES has taken a prominent position in discussing multiple values of

nature as arguments for conservation (Cimon-Morin et al. 2013; Ricketts et al. 2016). In this paper, we went one step further by testing how conservation priority setting based on threat translates into joint hotspots of biodiversity and ES. For the whole forest area of Telemark, we found low spatial congruence of high levels for biodiversity, ES and threat. Furthermore, spatial congruence was low across varying levels of biodiversity and threat for the whole forest area. However, relative to the area covered by the BDI, the overlap between high levels of threat and biodiversity is high. Moreover, irrespective of threat, around 60% of BDI areas are also supplying high levels of services (Fig. 5). These mixed results are in accordance with the current literature on the relationship between ES and biodiversity, which suggests complex patterns depending on the methodology and indicators of ES and biodiversity as well as on the functional relationship between biodiversity and ES in each particular case (Ricketts et al. 2016). For

Table 3 Proportion of hotspots and coldspots in total forest and in forest protected by nature reserves (forest area in nature reserves accounts for about 60%). For hotspots, top 50% quantiles for BDI, ESI and threat were set, respectively. For coldspots, top 50% quantiles for BDI and ESI and the lower 50% quantile for threat were set

Forest status type	Proportion in total forest area [%] (cf. Tables 1, 2)	Proportion in nature reserve forests [%]	Proportion of nature reserve forest in the respective forest status type [%]
Total forest	(100)	(100)	1.9
Ecosystem service hotspot	29.8	9.7	0.6
Biodiversity hotspot ^a	11.2	9.7	1.7
Joint hotspot ^a	7.1	4.5	1.2
Ecosystem service coldspot	17.7	40.0	4.3
Biodiversity coldspot ^a	6.3	18.7	5.7
Joint coldspot ^a	3.4	10.5	6.0

^a This hotspot/coldspot builds upon the BDI, covering 35.1% of the total forest area (cf. Fig. 2)

instance, the areas of mismatch could be due to the set of ES included in the analysis and the actual presence of beneficiaries using these ES within a respective area. While wilderness-like areas, carbon sequestration and storage are independent of the spatial pattern of beneficiaries, snow-slide prevention and opportunities for recreation are strongly coupled to the number of beneficiaries in the vicinity of the areas where ES are provided, or, as is the case for recreation, influenced by the distribution of access infrastructure (Schröter et al. 2014a).

Nevertheless, we identified some spatial overlap between biodiversity features with conservation importance and high ES provision, which opens opportunities for synergies between the protection of ES and biodiversity. In Norway, approximately 25% of the endangered species occur in forests, and for instance 200 beetle species associated with forests occur in Telemark and are listed in the Norwegian Red List 2015 (Henriksen and Hilmo 2015). The lowland areas in the South-east of Telemark are characterized by high forest productivity, leading to higher growth rates and profitability, and hence, to higher levels of threat. Besides, lower extraction costs are promoted by high accessibility due to higher population density and well-developed infrastructure. These areas also correlate with high levels of some ES. For instance, accessibility enables direct use (recreational hiking), and high productivity corresponds with higher rates of carbon sequestration.

Another reason for the relatively small area of joint hotspots may lie in our conservation planning approach and priority setting criteria. Hotspot and coldspot approaches do not aim at optimizing complementarity of features in the process of establishing priority areas. Other approaches to conservation planning, such as systematic conservation planning (Margules and Pressey 2000) which search for solutions based on optimization of multiple objectives are likely to be more suited to identify sets of multifunctional areas (Schröter et al. 2014b; Vallecillo et al. in revision).

Incorporating threat in hotspot and coldspot delineation

While threat has been considered regularly in spatial priority setting for biodiversity conservation, this is less the case for ES (Schröter and Remme 2016). As Brooks et al. (2006) point out, threat has been implicitly or explicitly included in approaches of prioritizing conservation areas. ES can be compromised by a variety threats (Allan et al. 2013; Maron et al. 2017). In the case of Norwegian forests, the economic exploitation of trees is a main threat to biodiversity, and to regulating and cultural services (e.g. Humphreys et al. 2006; Gundersen and Frivold 2008; Framstad and Sverdrup-Thygeson 2015). Similarly to marine reserve planning where fisheries exploitation is the main concern (Klein et al. 2013), timber harvest represents both an opportunity cost and a potential provisioning service. This raises challenges for management and reveals trade-offs between non-extractive, i.e. cultural and regulating services, and extractive provisioning services (Lee and Lautenbach 2016).

Hotspots and coldspots can offer a straightforward way to deal with the problem of prioritizing sites for different management options. However, inherent to the approaches of hotspots and coldspots is a decision of what is considered “hot” or a high value of a feature of conservation importance, and also to define the level of threat. This remains arbitrary and thresholds have been set differently in the literature on ES hotspots, ranging from 5 to 30% (Schröter and Remme 2016).

Despite the inability to identify multifunctional areas, hotspots and coldspots are simple, compelling and understandable indicators for conservation. The characteristic of an indicator to be easy to communicate and understandable for decision-makers and stakeholders is one recurring criterion of appropriate indicators (Brown et al. 2014). Hotspots and coldspots could help identify different and complementary conservation strategies protecting larger areas at low cost, and smaller areas of high value, that require more efforts and a suit of approaches engaging

stakeholders to avoid conflict and ensure a legitimate and fair process. In sum, hotspots and coldspots could provide a less costly approach for dialogue to achieve consensus than a map generated from a conservation planning algorithm where the levels of potential conflict may be less evident.

Management implications of hotspots and coldspots

Hotspots and coldspots allowed us to distinguish a proactive and a reactive approach to forest management. The proactive approach prioritises coldspots, areas that show low levels of threat and high levels of biodiversity (Bryant et al. 1997), ES or both. Thus, coldspots of high biodiversity values can be considered as low conflict areas for conservation with ES as a side-benefit. This approach is conflict-avoiding and cost effective, as high opportunity costs in terms of foregone forestry income or cost for conflict-solving can be avoided, and proactive management can be implemented with higher acceptance of concerned stakeholders. There is also a lower chance that these areas will be harvested in the near future, so relatively undisturbed ecosystems and ecological functions can be identified. In contrast, the reactive approach prioritises hotspots, areas with high levels of threat and high levels of ES or biodiversity or both. Here, timber harvest should be accompanied by reactively protecting biodiversity in selected places (top-left quadrant of Fig. 5) through implementing forestry practices aiming to improve the conditions for organisms under threat (Gough et al. 2014; Sverdrup-Thygeson et al. 2014). A similar approach has been proposed by Allan et al. (2015) for prioritizing restoration options for threatened cultural ES. The distinction between hotspots and coldspots is, however, not dichotomous, as conservation approaches will take place along a gradient of threat and high conservation values.

We showed that the area suitable for a reactive approach is larger than the area providing opportunities for proactive conservation (at 30–50% top/lower quantiles, Tables 2, 3). However, applied to Telemark, none of the prioritization approaches comes close to achieving the international conservation target of 17% of protected area (UNEP 2010). Thus, conservation targets would need to be achieved through a combination of proactive and reactive strategies. Priority for protection and management should be given to areas of overlap between high values of biodiversity and ES. We found that areas of low threat are better protected than areas of high threat, hence established nature reserves have focused on low threat, and likely low conflict areas. This result is in line with previous analyses at global level pointing out the opportunistic placement of many protected areas in areas that are less attractive to other uses (Joppa

and Pfaff 2009). It is often argued that the inclusion of ES in prioritization can offer new impetus to designate protected areas (Cimon-Morin et al. 2013). An example for our case are wilderness-like areas, which we considered here a cultural ES. Such wilderness-like areas have turned into a policy instrument preventing subsidies for building roads for timber extraction and hence keeping timber harvest profitability at low levels (Sverdrup-Thygeson et al. 2014).

Methodological limitations

Several limitations of our approach are related to the input data that we used and that could affect the distribution of hotspots and coldspots. Distribution data for vertebrates or plants and their status such as rarity or vulnerability represent widely used criteria associated with conservation value (Myers et al. 2000; Ceaşu et al. 2015). However, such data are frequently difficult to obtain, expensive (Pierson et al. 2015) or not representative for different aspects of biodiversity (Westgate et al. 2014). As species data of relevant resolution were also missing for our area, we used instead habitat indicators proposed by local environmental institutions. Habitat proxies are used in many cases to characterize biodiversity value (Lindenmayer et al. 2014). Habitats are easier to map and monitor, compared with species inhabiting them, and they represent the ecological conditions that support occurrence of more than one species. Heterogeneous age and structural composition, e.g. the presence of dead wood, are considered important for forest biodiversity, especially for fungi and invertebrates species (Seibold et al. 2016). However, habitat and species metrics do not always lead to the same priorities for conservation (Kati et al. 2004).

Other factors strongly influencing our results are the set of ES considered, the ability of the chosen indicators to accurately represent them, and the aggregation method. Only two of the ES models (carbon sequestration and recreational hiking) could be validated and showed varying levels of accordance with validation data (Schröter et al. 2014a). For other ES indicators, the question arises how well they are able to reflect the indicated object. For instance, given the multiple ways to indicate wilderness-like areas (Ceaşu et al. 2015), other indicators for this ES might result in a different spatial distribution or other place-based adaptations of the concept of wilderness might lead to different results. Validation is often not done in ES mapping and modelling and this led to calls to better measure uncertainties involved in these models (Schulp et al. 2014). Furthermore, the number of ES considered is

likely to influence the location of highly important areas depending on the spatial distribution of the chosen ES. Moreover, future studies should focus on the effect of weighting and different ways to measure the relative importance of ES to concerned social groups, which could inform spatial priority setting in a better way.

CONCLUSION

We used Telemark province in Norway to demonstrate an innovative approach of spatial delineation of joint biodiversity and ES hotspots and coldspots by incorporating timber harvest profitability as a measure of threat. We accounted for three regulating and two cultural services and two types of biodiversity indicators. We found relatively few areas that concomitantly showed high levels of biodiversity, ES and threat (joint hotspots). These areas could be used in the context of reactive conservation approaches to search for valuable areas that have relatively high opportunity costs of conservation but are in danger of being lost. Furthermore, areas of high levels of biodiversity and ES that face low levels of threat (coldspots) can be used as search corridors for proactive conservation approaches. We conclude that incorporating threat into measures of hotspots and coldspots is a simple and intuitive way to delineate areas for different management strategies. The knowledge on spatial distribution of biodiversity and ES has been increasing recently. If common threat indicators for biodiversity and ES can be defined, this method would be applicable to other landscapes. Remaining challenges are a representative choice of indicators for biodiversity, ES and threat, in particular in data-scarce regions, and the choice of threshold levels for what is deemed ‘hot’ or ‘cold’.

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