Original Research Article

Red List updates and the robustness of sites selected for conservation of red-listed species

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A B S T R A C T

The long-term success of sites selected for species conservation depends on the persistence of target species. Red List species or threatened species lists are frequently defined as target species, but when Red Lists are updated, their species composition may change. Here we investigate the effects of Red List updates on the long-term robustness of fine-scale site selection. We used records of red-listed species (vascular plants, bryophytes, macrolichens, and polypore fungi) recorded in 1997−1998 in 1058 sample plots (50×50 m) from six forest landscapes in Norway, and four consecutive issues of the Norwegian Red List for species (1998, 2006, 2010, 2015). Sites were selected based on the first issue (1998) using both a scoring ("hotspot") approach and a complementarity approach, and the ability of selected sites to include red-listed species of later issues was measured. In four boreal forests the mean proportion of red-listed species included in selected sites were reduced by18% during the study period, whereas no such effect was found in two hemiboreal forests, where increased clustering of red-listed species in sites compensated for target species changes. Changing target species adds to earlier documented challenges caused by population dynamics, and we suggest that alternatives to using occurrences of target species in site selection should be considered, and particularly at finer spatial scales.

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1. Introduction

Tools for prioritizing sites for protection of species have been a major issue in conservation biology for decades, and methods for systematic conservation planning have been refined to include a range of ecological, technical, economical, and social aspects (e.g., Margules and Pressey, 2000; Bottrill and Pressey, 2012; Di Marco et al., 2017; Karimi et al., 2017). However, there are basic shortcomings associated with the use of species records for site selection (Brooks et al., 2004; Cowling et al., 2004). First, species data will be absent or incomplete for most taxa (Whittaker et al., 2005). Second, well-studied taxa will rarely function well as surrogate taxa for many other taxa (Prendergast et al., 1993; Hess et al., 2006; Sætersdal and Gjerde, 2011). Third, species data has limited lasting ability due to spatiotemporal dynamics of species (Margules et al., 1994;

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Williams, 1998; Virolainen et al., 1999; Rodrigues et al., 2000; Dornelas et al., 2014). Furthermore, such shortcomings tend to increase with finer spatial scales (Cowling et al., 2004). Here we focus on a related site selection problem that has received little attention in the literature, namely changes in the value of sites over time caused by changes in the prioritization of objects or features for conservation.

Although studies of threatened species are underrepresented in conservation science (Di Marco et al., 2017), red-listed species are frequently used as target species for conservation, particularly at finer spatial scales (Gustafsson et al., 1999; Gjerde et al., 2007; Hottola and Siitonen, 2008; Schmeller et al., 2014). Red Lists are updated regularly due to changes in population status and threats, but also because of new qualification criteria for assessments, revised taxonomy, new taxonomic groups evaluated, and recently discovered species. According to IUCN rules, species assessments become outdated after 10 years (IUCN, 2012; Rondinini et al., 2014), and as a result of updates some species are no longer considered threatened and others are added with new editions of Red Lists. If threat status of species is used as a value in site selection, areas selected and protected based on a certain issue of the Red List may not be the same areas as those based on a later issue of the Red List. Site selection based on one particular Red List may therefore be suboptimal for capturing red-listed species of later issues, and here we aimed at isolating this particular effect. The magnitude of this effect depends on the degree of changes in species composition of successive Red Lists, and how these changes are expressed in the spatial distribution of target species. Similar effects should be expected for changes in prioritization of other types of conservation objects. Assessments of the success of site selection for conservation require monitoring over time (Cabeza and Moilanen, 2001; Runge et al., 2016). To our knowledge, this is the first study attempting to quantify the effects of temporal change in target species composition on the effectiveness of site selection. The basic approach for site selection based on species data has either been a hotspot or a complementary approach (Gaston et al., 2001), and of these complementary selection is considered to be the most efficient way to include target species (Margules and Pressey, 2000; Justus and Sarkar, 2002).

Our main aim was to investigate on-the-ground effects of Red List updates on fine-scale site selection based on Red List species records. To explore this we used a large data set consisting of exhaustive species inventory data of vascular plants, bryophytes, macrolichens, and polypore fungi from six different forest areas in Norway (Gjerde et al., 2004, 2005), and four issues of the Norwegian Red List for species (1998, 2006, 2010, 2015). These data allowed us to investigate how national Red List updates changed the Red List species composition and their overall spatial distribution in the field. Specifically, four questions were asked: (i) what is the degree of compositional change of red-listed species when using different Red List issues, (ii) how is the spatial distribution of red-listed species in the field affected by successive updates of the Red List, (iii) what is the accumulated change in performance of site selection procedures based on hotspots and complementarity using a single Red List issue, regarding their ability to include red-listed species of later issues, and finally (iv) what is the relationship between changes in spatial distributions of red-listed species and the effectiveness of site selection? The implications of our findings are discussed in the light of general challenges for *in situ* conservation caused by spatiotemporal dynamics.

2. Methods

The community composition and distribution of species changes over time as a result of changing environmental variables and population dynamics, which in turn affects the success of site selected for conservation of species (Virolainen et al., 1999). In the present study, however, we aimed at isolating and measuring the magnitude and the effects of changing target species composition on the success of selected sites, and we did this by keeping the species composition constant, and alter target species in accordance with Red List updates.

2.1. Study areas and species data

We used species data collected in 1997−1998 from 1058 sample plots (50×50 m) in six forest areas that represented south-north (1350 km) and west-east (260 km) climatic gradients in Norway (Gjerde et al., 2005). Each study area was divided into a grid, and a sample plot was located in the south-eastern corner of each 100×100 m grid cell. The number of sample plots in the study areas varied between 134 and 197, covering 21−25% of the extent of study areas (Table 1). Two of the forest areas (Kristiansand and Kvam) included forest with European nemoral deciduous tree species like ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), and lime (*Tilia cordata*), and were classified as hemiboreal forest. The other four areas (Ringerike, Sigdal, Grong, and Målselv) were covered by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birch (*Betula pubescens*) forest, and classified as boreal forests. Hemiboreal and boreal study areas were treated separately in the analyses because of their different forest type composition. Vascular plants, bryophytes, macrolichens, and wood-inhabiting polypore fungi were recorded in sample plots by taxonomic experts, resulting in a data set containing 1295 species (Gjerde et al., 2004), from which red-listed species according to different Red List issues could be extracted (Appendix A1).

2.2. Changes in Red List species due to updates

We consulted four versions of the Norwegian Red List for species, the first one from 1998 and issued by the Norwegian Directorate for Nature Management (Direktoratet for Naturforvaltning, 1999), and three succeeding lists issued by the Norwegian Biodiversity Information Centre (Kålås et al., 2006, 2010; Henriksen and Hilmo, 2015). The last three Red Lists were compiled following the more recent IUCN criteria for national evaluation of species (Gärdenfors, 2001; IUCN, 2012), whereas

Table 1

Number of Red List species recorded in two hemiboreal and four boreal study areas, according to different issues of the Norwegian Red List for species. The lower part of the table shows accumulated number of species across all study areas and their distribution on species groups. 2SE = two standard errors.

Study area	Extent (hectares)	Sample plots	Number of Red List species			
			1998	2006	2010	2015
Hemiboreal						
Kristiansand	195	193	15	17	16	17
Kvam	147	134	15	15	14	17
Mean (2SE)	171	163.5	15(0)	16(2.00)	15(2.00)	17(0)
Boreal						
Ringerike	197	197	10	13	13	15
Sigdal	195	195	24	28	26	27
Grong	190	169	10	9	8	9
Målselv	200	170	10	10	10	10
Mean (2SE)	195.8	182.8	13.5(7.00)	15.0(8.83)	14.3(8.09)	15.3 (8.26)
All areas	1124	1058				
Overall# species			65	68	64	66
Vascular plants			2	4	4	6
Bryophytes			19	14	12	14
Macrolichens			16	20	20	21
Polypore fungi			28	30	28	25

the 1998 list was compiled following an earlier IUCN publication (IUCN, 1988). Thus there were some methodological differences in the compilation of the 1998 Red List and the others, for instance in the definition of threat categories. Red-listed species in the 1998 edition were defined as species in the categories "Declining/monitoring"(DM), "Declining/care demanding" (DC), "Rare" (R), "Vulnerable" (V), "Endangered" (E), and "Nationally extinct" (Ex) (Direktoratet for Naturforvaltning, 1999); and for the 2006, 2010, and 2015 issues red-listed species were defined as species in the categories: "Data deficient" (DD), "Near threatened" (NT), "Vulnerable (VU), "Endangered" (EN), "Critical endangered", and "Regionally extinct" (RE) (Kålås et al., 2006, 2010; Henriksen and Hilmo, 2015). The proportion of species red-listed among those assessed was relatively stable for different issues, and in the interval 20−30% for the species groups studied (Kålås et al., 2006, 2010; Henriksen and Hilmo, 2015).

Red List updates resulted in changing sets of species being defined as red-listed species in the different issues. We used Jaccard Distance (dissimilarity) index, r = 1- (X∩Y)/(X∪Y), where X and Y are the two sets of species compared (Levandowsky and Winter 1971), to calculate the degree of changes caused by each Red List update (2006, 2010, and 2015) for the lists of red-listed species recorded in each study area. To check if the degree of change in red-listed species composition in our study areas was comparable to that of the Norwegian Red List in general, we also calculated Jaccard Distance for all Red List species within the species group studied (vascular plants, bryophytes, macrolichens, and polypore fungi). An index value of 1 corresponds to no common species in the two sets, whereas 0 corresponds to equal species composition.

2.3. Changes in spatial distribution of red-listed species

If the identities of red-listed target species change as a result of Red List updates, the overall distribution of target species on sites may also change. Thus, when referring to changes in spatial distribution of species we are looking at shifting distribution patterns caused by shifting target species identities. The degree of clustering of species across sample plots and the frequency distribution of species occurrences are basic determinants of species distribution patterns, which in turn affect the effectiveness by which target species are included in sets of sites (Gjerde et al., 2004). We used the 0.25 ha sample plots as the units for investigating changes in spatial distribution of species defined as Red List species. The size of study areas and sample plots was originally chosen to study selection of fine-scale set-asides in managed forest landscapes (Gjerde et al., 2007). In each of the six study areas, we identified species that were red-listed according to the four Red List issues, and counted the number of plots they were recorded in. From these data we calculated two variables in each study area that indicated clustering and the frequency distribution of red-listed species, respectively.

First, clustering (K) of red-listed species among sample plots was calculated for each study area and Red List issue as the mean number of observed species pairs (P_o) in sample plots divided by the mean number of species pairs in the same number of sample plots for a random distribution (P_r), the latter obtained by averaging the results of 1000 randomly generated species distributions using the same number of occurrences for each species as for the observed data. This index measures the degree of clustering for a given collection of species and their occurrences across a set of sites of similar size, with 1 corresponding to a random distribution and the maximum K value (depending on the species abundance distribution) corresponding to a completely nested species distribution with all species present in the most species-rich plot(s) (Gjerde et al., 2004). The frequency variable was selected to indicate the proportion of rare species in the red-listed species abundance distribution, and for this we used the proportion of singleton species (here defined as species recorded in a single sample plot within a study area).

2.4. Effectiveness of hotspots and complementary sites

The ability of sites selected based on a specific Red List issue to include red-listed species of later issues was investigated by conducting an initial site selection by using occurrences of red-listed species in sample plots according to the 1998 list. We then investigated to what degree the selected plots included species red-listed according to the three following Red List issues. Thus, species defined as Red List species changed, whereas species distribution data was extracted from the same survey. For these analyses red-listed species from all taxonomic groups were pooled, representing a general use of red-listed species as target species.

To study the robustness of site selection to changes in target species we applied two generic site selection approaches. There are two main types of basic site selection approaches: scoring/ranking procedures and complementarity procedures (Gaston et al., 2001). One common version of the scoring procedure is to rank sites for conservation based on the number of target species (e.g., Prendergast et al., 1993). The complementarity procedure, on the other hand, typically maximizes species representation for a set of sites, or minimizes the area needed in a conservation plan (Kirkpatrick, 1983). We employed both a scoring procedure (set of sample plots consisting of the highest ranked plots regarding the number of Red List species found there, hereafter termed the "hotspot approach") and a site selection procedure based on complementarity (set of sample plots with the highest cumulative number of Red List species, hereafter termed the "complementarity approach").

Our algorithm based on complementarity solved the maximal coverage problem (e.g., Camm et al., 1996; Pressey et al., 1997), by using a "greedy" heuristic procedure (e.g., Moilanen et al., 2009) where the objective was to find the solution that satisfies the maximum number of red-listed species for a certain selection level (proportion of area selected).

We measured the effectiveness (*sensu* Rodrigues et al., 1999) of the selected sites as the proportion of red-listed species in the area included by selecting 2.5% and 5% of the sample plots, respectively. Selection levels above 5% were not used because of the limited number of red-listed species. For higher selection levels all species would be included and changes in effectiveness would not be detected. When ties occurred among ranked sample plots (plots with similar number of red-listed species for hotspots, and plots with similar number of not yet included species for complementary selection) we ran 1000 random selections of sample plots from ties to complete the sets, and calculated the mean effectiveness for all iterations. Both selection algorithms (Appendix B) were conducted in R (R Core Team, 2017).

2.5. Relationships between the effectiveness of selected sites and the composition and distribution of target species

The proportion of red-listed species included by the originally selected sites may change owing to the degree of change in Red List composition (Jaccard Distance), clustering of Red List species occurrences (K), and their frequency distribution (Proportion of singletons). All variables were measured at the study area level, i.e. there was one value for each Red List issue and area. We investigated the relationship between the effectiveness of sites and these variables by simple regression (squared correlation coefficients). The main purpose was to explore how and to what extent changes caused by Red List updates affected site selection effectiveness, but tests of statistical significance was not conducted due to the dependency between species lists of different Red List issues.

In addition, to investigate if the spatial distribution of red-listed species within the study areas changed with changing Red List composition, we included a spatially explicit modelling of richness distributions of red-listed species for one hemiboreal and one boreal study area by using species counts from sample plots and by estimating a spatial Gaussian Markov Random Field (Lindgren et al., 2011; Blangiardo and Cameletti, 2015) (Appendix C). From this we constructed heat maps showing the distribution of richness of red-listed species in Kvam and Sigdal according to the 1998 and the 2015 Red Lists, as these two areas demonstrated opposite temporal trends in the degree of clustering of red-listed species across sample plots. By including this part, we were able to investigate changes in clustering of red-listed species on a larger spatial scale than sample plots.

2.6. Statistical analyses

Although data from a large number of sample plots were used in our study, the focus was on results that pertain to the study area scale, reported from two hemiboreal and four boreal forest landscapes. Because of the limited number of landscape replicates and the inherent dependency between different Red List issues, we present our results using different types of descriptive statistical tools, only.

3. Results

3.1. Changes in Red List species due to updates

Updates of the 1998 Norwegian Red List in 2006, 2010, and 2015 did not result in substantial changes in the mean number of red-listed species present in our study areas, and on average 16 red-listed species were recorded in the hemiboreal study areas, and 15 species in the boreal study areas (Table 1). Although the numbers of red-listed species recorded in the study areas were approximately the same for different Red List issues, species composition changed considerably (Table 2). These changes were mainly due to changes in assessed threat status of individual species. The change in species composition

(Jaccard Distance) among red-listed species between the 1998 and 2015 issues, that were recorded in the study areas, was on average 0.52 and 0.44 for the hemiboreal and the boreal forests, respectively (Table 3). Change in species composition for all red-listed species within the same species groups was found to be on average 0.55 between the 1998 and 2015 issues. In most areas the changes were largest in the eight year interval between 1998 and 2006, coinciding with the shift in Red List assessment criteria.

3.2. Spatial distribution of red-listed species

The proportion of sample plots with records of red-listed species increased in five of six study areas (Appendix A1), and increased on average from 50% in 1998 to 63% in 2015. This change was mainly due to the inclusion of several locally abundant species from the 2006 Red List issue and onward (Appendix A2). A high proportion of plots with red-listed species was found particularly among the boreal forest areas. The inclusion of the abundant species on the Red Lists did not result in a lower proportion of singleton species in boreal forests. In the hemiboreal forests, however, the proportion of singletons decreased in both areas between 1998 and 2015 (Table 3).

The distribution of records of red-listed species among plots, measured as clustering K in each study area, also changed between the Red List issues. On average, clustering increased in the hemiboreal areas from 1.95 to 3.19 between 1998 and 2015, and decreased from 1.69 to 1.24 for the boreal areas in the same period (Table 3).

3.3. Effectiveness of hotspots and complementary sites

Because the ratio of the number of selected sites to the number of target species affects the effectiveness of selected sites, we here focused on the relative changes in effectiveness with Red List updates for each study area. Besides the expected lower effectiveness (proportion of red-listed species included in selected sites), the 2.5% selection level showed the same patterns of changes in effectiveness with Red List updates as the 5% selection level (Fig. D1), and for simplicity only the results of the 5% selection level are presented in Fig. 1. The overall trend found for the hemiboreal study areas was an unaltered or slightly increasing effectiveness with successive updates of the Red List from 1998 to 2015 (Fig. 1a). In contrast, the main trend found for the boreal study areas was a decreasing effectiveness with successive updates, amounting to a mean reduction in effectiveness of 18% (Fig. 1b). For both forest types and selection levels, complementary selection performed better than hotspot selection (Fig. 1 and Table 3).

3.4. Relationships between the effectiveness of selected sites and the composition and distribution of target species

Fig. 2 shows the relationships between effectiveness of sites selected based on the 1998 Red List and variables related to changes in Red List species and their distributions. The relationship between effectiveness and differences between Red Lists (Jaccard Distance) showed a negative trend for boreal forests and a positive trend for hemiboreal forests (Fig. 2a and b). This is in accordance with the results of Fig. 1, showing that the increasing differences in target species composition with successive Red List updates was not sufficient to reduce the effectiveness in the hemiboreal forests over time. For selection at the 2.5% level no clear relationship was found for either selection approach (Appendix D2). Clustering of red-listed species was positively correlated with the effectiveness in hemiboreal areas (Fig. 2c and d, Appendix D2), whereas clustering in boreal areas showed only minor variation between Red List issues (Table 3), and are therefore not shown in Fig. 2. Modelling of richness of red-listed species for Kvam and Sigdal (Fig. 3) showed that hotspot areas remained mostly in the same parts of study areas, whereas the characteristics (range and field variance) of the patterns changed with time (Fig. 3). The increased clustering found in the hemiboreal area Kvam was due to a proportionally higher increase in number of red-listed species in the same parts of the area that had the highest number of red-listed species from the start, whereas the reduced clustering in Sigdal was due to decreased difference between the original hotspots and the rest of the area. Finally, the effectiveness was

Table 2
Changes in composition of red-listed species in two hemiboreal and four boreal study areas as a result of Red List updates in 2006, 2010 and 2015, when comparing with the 1998 list. Species that were removed (out), species added to the list (in), and the number of species that were on both lists (same) are shown. These numbers were used to calculate dissimilarity between lists (Jaccard Distance), see Table 3.

Study areas	1998/2006			1998/2010			1998/2015		
	out	in	same	out	in	same	out	in	same
Hemiboreal									
Kristiansand	3	5	12	5	6	10	4	6	11
Kvam	4	4	11	5	4	10	6	8	9
Boreal									
Ringerike	1	4	9	2	5	8	2	7	8
Sigdal	3	7	21	4	6	20	5	8	19
Grong	2	1	8	3	1	7	4	3	6
Målselv	2	2	8	2	2	8	3	3	7

Table 3

Changes in Red List species composition (Jaccard Distance, where 1 correspond to no species in common) due to Red List updates in two hemiboreal and four boreal forest areas, when compared to the 1998 Red List issue, and how these changes affected the later distribution of red-listed species (proportion of singletons and clustering K of records on sample plots). Effectiveness of complementary (E_{CS}) and hotspot (E_{HS}) selection when using the 1998 Red List was measured as the proportion of species of Red List issues included by selecting 2.5% and 5% of sample plots.

| Study area	Forest type	Red List issue	Jaccard D.	Prop. of singletons	Clustering K	Effectiveness			
						$E_{CS\ 2.5}$	$E_{CS\ 5}$	$E_{HS\ 2.5}$	$E_{HS\ 5}$
Kristiansand	Hemiboreal	1998	—	0.93	0.88	0.40	0.73	0.28	0.39
Kristiansand	Hemiboreal	2006	0.400	0.81	1.59	0.39	0.66	0.39	0.45
Kristiansand	Hemiboreal	2010	0.476	0.73	1.88	0.45	0.67	0.48	0.57
Kristiansand	Hemiboreal	2015	0.476	0.75	1.89	0.44	0.68	0.45	0.55
Kvam	Hemiboreal	1998	—	0.27	3.01	0.52	0.71	0.44	0.63
Kvam	Hemiboreal	2006	0.368	0.47	2.65	0.52	0.67	0.47	0.60
Kvam	Hemiboreal	2010	0.474	0.21	2.86	0.57	0.72	0.50	0.64
Kvam	Hemiboreal	2015	0.571	0.21	4.48	0.67	0.79	0.62	0.69
Ringerike	Boreal	1998	—	0.30	1.31	0.70	0.99	0.60	0.62
Ringerike	Boreal	2006	0.357	0.23	1.21	0.67	0.92	0.62	0.63
Ringerike	Boreal	2010	0.429	0.23	1.23	0.66	0.85	0.62	0.62
Ringerike	Boreal	2015	0.529	0.27	1.23	0.57	0.80	0.53	0.53
Sigdal	Boreal	1998	—	0.42	2.00	0.66	0.89	0.41	0.70
Sigdal	Boreal	2006	0.323	0.36	1.29	0.63	0.83	0.51	0.67
Sigdal	Boreal	2010	0.333	0.35	1.27	0.63	0.83	0.49	0.65
Sigdal	Boreal	2015	0.375	0.37	1.23	0.60	0.80	0.50	0.63
Grong	Boreal	1998	—	0.50	2.13	0.70	0.99	0.60	0.70
Grong	Boreal	2006	0.273	0.56	1.28	0.67	0.99	0.56	0.67
Grong	Boreal	2010	0.364	0.50	1.28	0.71	0.99	0.63	0.75
Grong	Boreal	2015	0.538	0.56	1.28	0.57	0.78	0.44	0.56
Målselv	Boreal	1998	—	0.60	1.32	0.60	0.99	0.32	0.47
Målselv	Boreal	2006	0.333	0.70	1.97	0.44	0.80	0.24	0.35
Målselv	Boreal	2010	0.333	0.70	1.91	0.44	0.80	0.24	0.34
Målselv	Boreal	2015	0.333	0.70	1.21	0.44	0.80	0.22	0.33
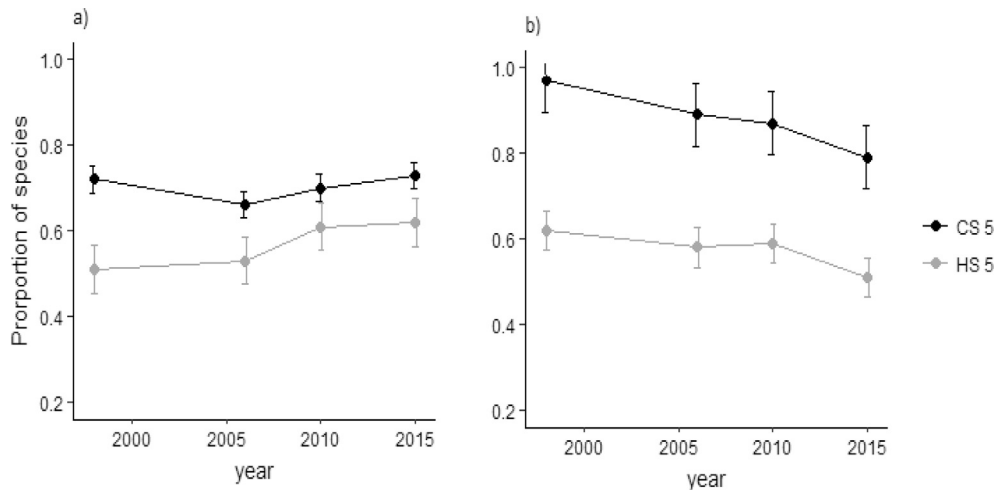
Fig. 1. Changes in the effectiveness of site selection based on the initial Red List (1998) and calculating the proportion of red-listed species included of the initial list and of the three successive issues of the Red List (2006, 2010, and 2015). Results are shown for hotspot (HS) and for complementary selection (CS), using 5% selection levels. (a) Hemiboreal forest areas, (b) boreal forest areas. Error bars indicate ±2SE.

negatively correlated with the proportion of singletons, the effect mainly appearing for proportion of singletons above 0.5 (Fig. 2e and f, Appendix D2).

4. Discussion

Comparison of four consecutive issues of the Norwegian Red List for species showed that approximately one-half of the joint list of all species red-listed in 1998 or 2015 (within the groups vascular plants, bryophytes, wood-inhabiting polypore fungi, and macrolichens) were not shared between the two lists, and that a similar degree of mean change in species composition (Jaccard Distance = 0.47) was found for red-listed species within the same groups recorded in six forest
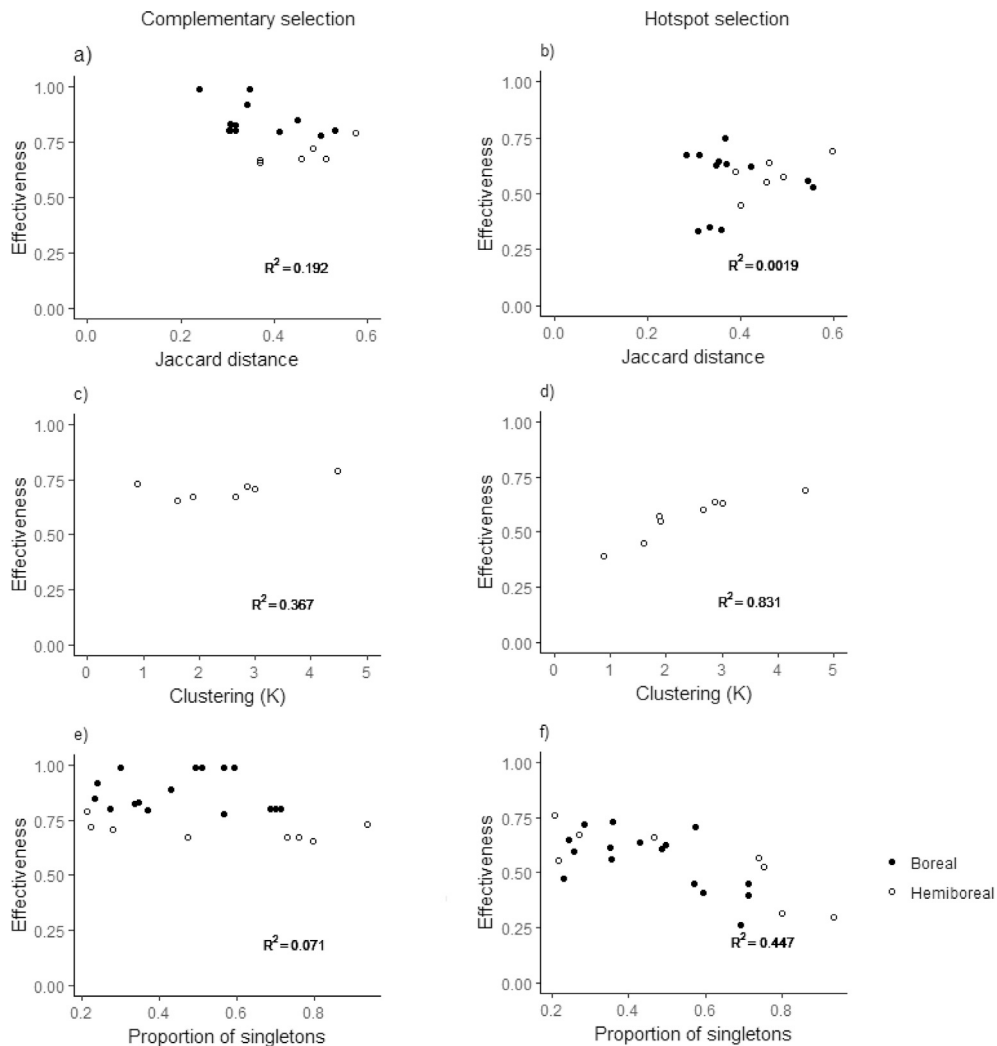
Fig. 2. Relationships between effectiveness (proportion of species included in 5% of sites) and variables potentially affecting the spatial distribution of red-listed species. In each graph a point corresponds to an observation of a variable in an area for a certain red List issue plotted against the effectiveness of initial sites to include these species (see Table 3 for data used). For the degree of clustering (K) of occurrences of red-listed species on sample plots, only observations in the two hemiboreal study areas are shown, due to lack of variation of K in boreal areas.

landscapes. These results illustrate that although the proportion of species red-listed among those evaluated may be stable, the difference in composition of red-listed species may accumulate with successive Red List updates.

As expected, effectiveness was higher for complementary selection than for hotspot selection. The compositional change in the Red Lists from 1998 to 2015 translated into an 18% reduction in effectiveness of sites selected based on the 1998 Red List to include species on the 2015 Red List, when using complementary selection in boreal forest areas. However, changes in Red List composition due to updates do not necessarily erode the performance of a site selection based on an outdated Red List, as the performance will depend on how changes in Red List species composition affect the spatial distribution of target species. If new red-listed species tend to occupy the same sites as the old ones, selected sites will be robust to Red List updates. This was shown in our hemiboreal forest areas, where a mean change in Red List composition corresponding to Jaccard Distance 0.54 actually resulted in a similar or slightly increased effectiveness regarding 2015 Red-listed species compared to the 1998 Red List. This was caused by an increased clustering of red-listed species in parts of the landscape (broad-leaved forest with elm, lime, and ash in landscapes dominated by pine forest), i.e. forest sites selected based on the 1998 list became even more important with Red List updates despite Red List dynamics. With a more clustered distribution of target species on mainly the same sites, effectiveness tends to increase. Thus, contrary to in the boreal forest areas increased clustering of target species in the hemiboreal areas compensated for the changes in target species composition.

A higher degree of effectiveness of complementary site selection compared to hotspot site selection was expected as the complementarity approach is designed to pick up as many target species as possible that are not already represented in a set
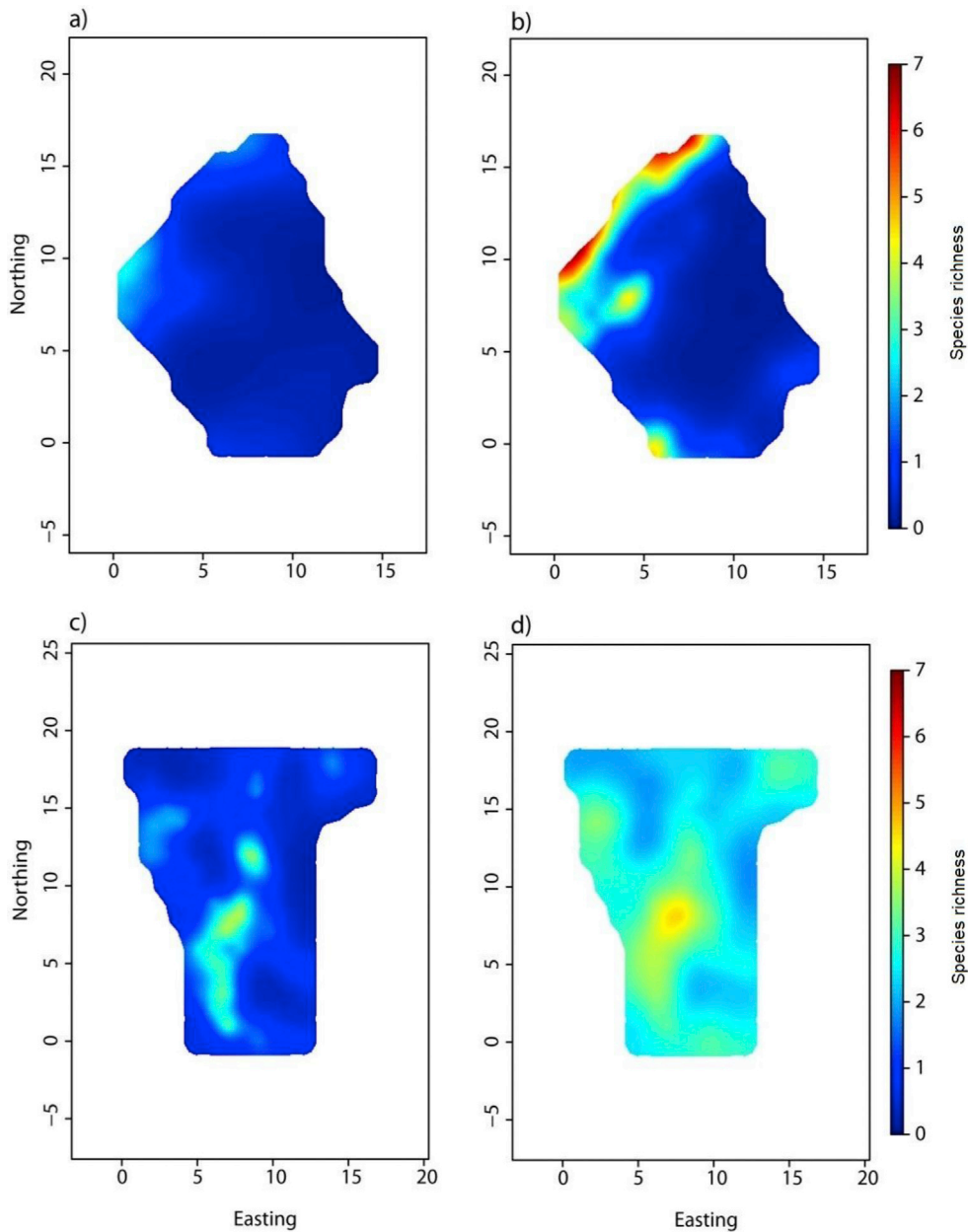
Fig. 3. Red List species richness distribution in the study areas Kvam (upper panels) and Sigdal (lower panels) according to the 1998 (left) and the 2015 (right) Red Lists. The Maps are based on spatial Gaussian Markov Random Field models, and the scale unit is 0.1 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of sites (Pressey et al., 1993; Sætersdal et al., 1993; Margules and Pressey, 2000; Justus and Sarkar, 2002). However, the difference in success between complementarity and hotspot sites varied, and under certain conditions the effectiveness of the complementarity approach may be more susceptible to changes in species composition than the hotspot approach. For instance, if Red List updates mainly remove singletons species from the list, and these species are being replaced by other singleton species present in other sites, the effectiveness of the originally selected complementary sites to include species of later Red List issues may be reduced more than the effectiveness of hotspot sites. Our field data only permitted a small proportion of sites to be selected until the recorded local pool of red-listed species had all been included by complementary selection. Although our inventory data was rather extensive, we only investigated species groups comprising approximately 15% of all red-listed forest species (Gjerde et al., 2004). If all remaining species could have been included, comparison at higher selection levels would have been possible. However, we consider our species a fairly representative sample of Norwegian red-listed species as they belonged to a broad spectrum of forest habitats (ground-living species, species on rock

surfaces, epiphytic species, and wood-decomposing species). Furthermore, the rate of change in Red List composition was representative for all species within the species groups studied. We therefore believe that a higher selection level based on all red-listed species in our areas would have given similar trends regarding changes in effectiveness of sites due to Red List updates.

As our study probably is the first to investigate the effects of changing Red List composition on effectiveness of site selection on the ground, it is difficult to evaluate how representative our results are for other spatial scales and locations. Our goal was mainly to explore the relationships between the effectiveness of site selection and the spatial distribution of target species, and such relationships should be highly relevant for any locations and spatial scales where lists of target species change over time. However, further studies are needed to identify conditions where initial site selection is particularly susceptible to species dynamics, and how different site selection approaches perform under varying scales and spatial distributions. Simulations where such variables can be manipulated seem to be a promising next step.

Species dynamics and persistence in sites selected for conservation is a major challenge for the discipline (Cabeza and Moilanen, 2001), and has been thoroughly discussed in the literature (e.g., Virolainen et al., 1999; Rodrigues et al., 2000; Araújo et al., 2002; Gaston et al., 2002; Guitiérrez, 2005; Felinks et al., 2011; Ikin et al., 2016; Haupt et al., 2017). As shown by the present study, changes in target species may add to these concerns. The dynamics of Red List composition following Red List updates generates similar challenges to those that are due to spatiotemporal population dynamics of target species, but solutions to mitigate the effect of moving targets on effectiveness may not apply to both types of dynamics. For instance, long-term performance of selected sites increases if sites are selected according to population density or local abundance (Rodrigues et al., 2000). Although a promising strategy for persistence of species in sites, it will not apply to the challenge of changing Red Lists. Furthermore, changes in Red Lists may generate their own dynamics. If new knowledge and assessments change the threat status of species associated with particular habitat types (for instance related to climate change, introduced species, or land use), this will change the spatial distribution of red-listed species accordingly. In our study, increased clustering of red-listed species in hemiboral forests due to Red List updates may indicate increasing concern about the conditions for species in broad-leaved forests with ash, elm, and lime.

Multiple species inventories repeated over several years may better reveal the most important sites for protection (Ikin et al., 2016; Haupt et al., 2017; Webb et al., 2017). Such data series may help identify core areas that retain high value for target species over time and during population bottlenecks (Runge et al., 2016), and may also help to detect habitats that are less affected by changes in species composition than others. In other cases multiple data series from an area may not only continuously add new species (Gaston and Blackburn, 2000) but also new sites with species, resulting in an increasing size of reserve network needed to include sites where target species have been recorded. For changing Red Lists the equivalent to such a dynamic would be that new species on the list are found mainly in new sites.

Selection of a set of optimal sites for future conservation based on target species data is in principle an application of a model predicting that the set of sites will continue to host the target species in the future. The value of the model prediction will depend on its temporal transferability (Houlahan et al., 2017). Stochastic spatiotemporal dynamics of species tend to undermine such predictions (Lawton, 1999; Sætersdal et al., 2005; McGill, 2010). Changes in Red List species composition, or changes in composition of other target species, may further erode the transferability of the predictions. Multiple inventories may improve temporal transferability, but the cost of such inventories for multiple taxa of red-listed species will be very high in most cases (e.g., Cowling et al., 2009).

Prioritizing sites for conservation based on species data only, becomes a big challenge when the aim is to preserve a broad spectrum of taxa within the same conservation plan (Cowling et al., 2004). Lack of species data for many taxa (Whittaker et al., 2005), shortcomings of surrogate taxa (Sætersdal and Gjerde, 2011), spatiotemporal dynamics (Dornelas et al., 2014), and changing identity of target species (this study) all contribute to this. Alternative models for site selection should therefore be considered when many taxa are involved, and particularly at finer spatial scales. With an accumulating understanding of species associations with habitat conditions, and the developments of species distribution models (e.g., Guisan et al., 2013), one alternative may be to scale up from species to the level of habitat types, and preserve sets of habitats with complementary target species compositions (e.g., Gjerde et al., 2007). Provided there is a sufficient match in spatial resolution, this may be a fruitful way to combine species data and environmental data for site selection at finer scales.

Declaration of interests

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00454.

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