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Systematic targeting of management actions as a tool to enhance conservation of traditional rural biotopes

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Abstract

Traditional rural biotopes (TRBs), which are biologically and culturally valuable habitats maintained by low-intensity grazing and mowing, are a core element of biodiversity in Europe. During the last decades, TRBs have faced severe habitat loss and fragmentation due to agricultural modernization. Despite their well-known critical state, their conservation remains inadequate, thus raising a need to advance TRB conservation via spatial land-use planning. In this study we analyze a national GIS database on TRBs in order to examine how the current TRB network can be complemented in terms of conservation value based on known ecological characteristics. Given different target scenarios for the amount of managed TRBs, we demonstrate where management should be directed to both on protected and unprotected areas. We conclude that in current state, biodiversity depending on TRB management is not efficiently sustained in Finland. Substantial amount of TRB habitats and populations of threatened TRB species are left unmanaged. Based on our results, we suggest that to advance TRB conservation in Finland, the cover of managed TRBs should be rapidly extended to form ecologically functional networks. The expansion would prioritize additional management to the Baltic Sea coast and smaller clusters within inland Finland, double the cover of managed TRBs, and direct management subsidies in a more cost-effective way.

Abbreviations
AES, agri-environment scheme; TRB, traditional rural biotope

Keywords
Biodiversity conservation; Biodiversity management; Landscape management; Semi-natural habitats; Spatial prioritization; Zonation software

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1. Introduction

Although protection of biodiversity has been a fundamental tenet of conservation biology since its early beginning (Soulé, 1985), tight coupling of social and natural systems escaped conservation scientists' attention for a long time in many regions (Kareiva and Marvier, 2012). Recently, temporal changes in how conservation is perceived have raised global attention to a social-ecological approach in conservation (Corlett, 2014; Mace, 2014). In Europe, a significant proportion of biodiversity is situated in landscapes formed through a sequential overlay of traditional rural land-use systems (Plieninger et al., 2006). This process has continued for thousands of years, resulting in a rich diversity of cultural landscapes and associated species which are sustained by human land use (Batáry et al., 2015; Plieninger et al., 2006; Pullin et al., 2009).

Since low-intensity land use is important for existence of a lot of European biodiversity (Halada et al., 2011; Pullin et al., 2009), much of nature conservation aims to halt the loss of farmland biodiversity, and many protected areas are managed in ways that reflect traditional agricultural practices (Batáry et al., 2015; Linnell et al., 2015). Challenges, however, are substantial. Agricultural industrialization has caused a widespread decline in farmland heterogeneity and biodiversity (Benton et al., 2003; Strijker, 2005). Modern socioeconomy drives rural landscapes towards land abandonment and agricultural land-use intensification, centralization, and specialization (Beilin et al., 2014; Fjellstad and Dramstad, 1999; Knickel, 1990; Lambin et al., 2001). Therefore some of the most critical conservation issues today relate to the abandonment of traditional farming practices and the disappearance of biodiverse habitats dependent on them (Halada et al., 2011; Henle et al., 2008).

Traditional rural biotopes (TRBs) are heterogeneous disturbance-dependent grasslands and wood-pastures maintained through long-term grazing and mowing. The term "traditional rural biotope" refers to culturally influenced natural habitat complexes that are part of a traditional landscape formed through archaic rural livelihoods (Ministry of the Environment, 1992), and although its usage is specific to Finland, similar habitats are found throughout Europe (e.g. Bergmeier et al., 2010). Typical TRB habitats in Finland are grazed woodlands, sparsely wooded pastures, and mesic to moist meadows (Raunio et al., 2008). Management of TRBs is based on low-intensity raising of livestock on unfertilized vegetation growing on non-tilled soils, a practice that is especially valuable for biodiversity conservation across Europe (Beaufoy and Cooper, 2013). TRBs are among the most diverse and species-rich habitats of rural landscapes (Cousins and Eriksson, 2002; Fjellstad and Dramstad, 1999; Luoto et al., 2003), and they are mentioned as central elements of high-nature-value farmland (Heliölä et al., 2009; Plieninger et al., 2015). As ecosystems, TRBs are highly variable and dynamic. Their species assemblages depend on the interplay between active management, vegetation succession, and metapopulation dynamics (Allan et al., 2014; Halada et al., 2011; Hanski, 2011).

Ongoing TRB loss and fragmentation has serious ecological effects. TRB species' metapopulations lose their viability, because unoccupied habitat patches are not colonized at the same rate as extant populations disappear, i.e. they reach their extinction threshold (Hanski, 2011). Yet, some species – especially vascular plants – react slowly to land-use changes and persist on abandoned TRBs for long time periods (Cousins, 2009; Eriksson et al., 2002; Lindborg and Eriksson, 2004). Unless targeted habitat restoration and proper management actions are secured, species specialized in TRBs continue to decline and their populations face inevitable local extinctions (Cousins, 2009; Krauss et al., 2010; Kuussaari et al., 2009).

Loss of farmland biodiversity has created a need for agri-environment measures, which are incentives designed to encourage farmers to protect and enhance the environment on their farmland (Anonymous, 2005). Countries within European Union are increasingly funding habitat management and restoration actions through voluntary, contract-based subsidies within national agri-environment schemes (AESs) (Batáry et al., 2015; Kleijn and Sutherland, 2003). The AES contracts are the main tool for encouraging management of TRBs. However, the effectiveness of AESs has been questioned in TRB management and biodiversity conservation in general (Arponen et al., 2013; Batáry et al., 2015; Kleijn and Sutherland, 2003). In Finland, during the 20th century, over 99 percent of TRB cover disappeared as a consequence of agricultural modernization (Raunio et al., 2008; Salminen and Kekäläinen, 2000). Currently, TRBs are the most threatened of all Finnish habitat types (Raunio et al., 2008) and provide habitat for a total of 1 807 red-listed species (Rassi et al., 2010). Despite this, current conservation measures have been insufficient to tackle the situation.

Several reasons contribute to inefficient conservation of TRBs in Finland. These include capacity, knowledge, institutional, and ideological obstacles (cf. Bennett et al., 2016). Firstly, besides the AES, other funding sources for TRB management are scarce (Ministry of Agriculture and Forestry, 2013). Secondly, management actions have not been efficiently directed to biologically valuable sites (Arponen et al., 2013; Kemppainen and Lehtomaa, 2009), and thirdly, the dynamic and management-dependent character of TRBs challenges Finnish environmental authorities, who have mostly relied on establishing permanent set-asides to conserve natural habitats, aiming to exclude most or all human influence from them (Vuorisalo and Laihonen, 2000). In this sense, Finnish nature conservation has not followed the European tradition where nature and culture are intertwined, but rather a wilderness-oriented approach that separates people from nature (Linnell et al., 2015). In this context, the biological value of TRBs is deemed "semi-natural", and the motivation for conserving these "unnatural" habitats is undermined (Cronon, 1996; Mace, 2014).

As a result, TRBs are weakly represented in Finnish nature conservation policies. They have often been excluded from conservation networks such as Natura 2000 (Ministry of the Environment, 2015; Council of State, 1996; Vuorisalo and Laihonen, 2000). Although sole establishment of protected areas is insufficient for TRB conservation (Arponen et al., 2013; Bengtsson et al., 2003), there are valuable TRB sites on protected areas. However, the majority of them are unmanaged, and protection status is regularly based on conservation of other habitats (Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015).

Several means to enhance the conservation of TRBs have been proposed. These include establishing complementary management funding sources (Keränen et al., 2012), increasing AES uptake (Grönroos et al., 2007), and targeting funding to manage locations with high biodiversity (Arponen et al., 2013). Achieving a favorable TRB conservation status needs increasing their cover under protection, restoration, and active management alike. Because human influence essentially drives TRB ecology, TRB restoration requires reviving traditional social-ecological interactions. Therefore we refer to it as bio-cultural restoration (Egan et al., 2011).

In this paper we explore if and how conservation of TRBs could be improved by directing restoration and management actions spatially on a national scale. We began by evaluating the current management status of TRBs (Fig. 1). Then we explored how the current surveyed network of valuable TRBs can be complemented, assuming that the most important aim of network expansion is to secure the maintenance of threatened habitats and species dependent on TRB management. We answered the questions via a spatial prioritization analysis, where several layers of information contribute to the conservation value of a given habitat patch, and yield an optimized management network solution.

The purpose of the analysis was to inform management allocation on large scale instead of suggesting whether a specific site should be managed or not, and we did not aim to exclusively point out the most valuable individual TRB sites in whole Finland. Rather, we synthesized currently available spatial information. The quantified results provide a starting point for developing a national implementation strategy for further conservation action (Knight et al., 2006).

Given the national goal of securing management of all valuable surveyed TRBs and increasing the total cover of managed TRBs to 60 000 hectares (Kemppainen and Lehtomaa, 2009; Kotiaho et al., 2015; Salminen and Kekäläinen, 2000), we formulated a spatial prioritization solution for four nested management scenarios (A: surveyed TRBs, B–D: surveyed TRBs with a progressive addition of managed area). In each consecutive scenario, ca. 4 000 managed hectares were added, thus forming a realistic step-wise plan for expansion of the management network. The most extensive scenario (D) yielded a spatial allocation of nearly 45 000 hectares of managed TRBs.

2. Materials and methods

2.1. Data sets

We used existing GIS data derived from five different sources: (1) a national network of surveyed TRBs, covering ca. 30 300 ha; (2) AES subsidy contracts on TRB management in year 2014, ca. 19 200 ha; (3) habitat type inventories on protected and state-owned areas, ca. 4 620 200 ha; (4) database on protected private and state-owned TRBs, ca. 32 200 ha; and (5) 16 077 point occurrences of 133 TRB-specialized red-listed vascular plant species. The data sets are further described in Electronic appendix A. The Åland islands were excluded because of their self-governmental status. Without the Åland islands, the land area of Finland is 30 234 700 ha (National Land Survey of Finland, 2016).

We incorporated data on surveyed and protected TRBs in the analyses without modifications. AES contract sites outside surveyed TRBs or protected areas were omitted from spatial prioritization, as their biological value as TRBs has not been surveyed in the field, and according to our personal experience their quality varies from good to very poor. Habitat type inventory data is built on a nested structure, which was used to form GIS layers of different TRB habitats on two levels. Firstly, we derived an upper-level TRB habitat classification comparable to the assessed threatened habitat types (Raunio et al., 2008). Secondly, we categorized more strictly defined Natura 2000 -habitats (listed in the Habitats Directive Annex I: Council of Europe, 1992) as separate layers (Table 1). This allowed us to give increased weight on sites having high conservation value at the European level. However, the inventory did not cover all TRB sites. For these sites, a layer of undefined TRB habitat was formed, as there were no data on specific habitat types available.

We included certain complementary habitat layers because they contribute to TRB connectivity by sharing similar species communities. These were old traditional yards, reindeer gathering grounds, Sami camp sites, managed esker habitats, and dry, sandy sunlit dunes. In addition, occurrences of TRB specialist vascular plants may indicate undetected TRBs and act as source populations for nearby known TRB sites.

In order to control for biogeographical bias in species richness, we pooled existing red-listed species occurrences together according to their threat status. All species occurrences categorized as potentially or certainly disappeared were merged to form one data layer that reflected the historical range of TRB specialists.

2.2. Current management status

To estimate the amount of currently managed TRBs, we performed an overlay analysis by unioning the data on AES subsidy contracts, surveyed TRBs, and protected TRBs. The latter were divided according to landownership (either private or state-owned). Circa 2 500 hectares of managed TRBs are not subsidized (Kemppainen and Lehtomaa, 2009), but as there are no inclusive GIS data available on these sites, we were forced to exclude them. All GIS data handling were done with ArcGIS (ESRI® ArcMAP™ version 10.3.1).

2.3. Management scenarios

We used conservation prioritization software Zonation (version 4; C-BIG Conservation Biology Informatics Group, 2014) to produce spatial management scenarios. Starting from a full landscape, Zonation iteratively removes locations (cells or planning units) of least contribution to remaining biodiversity while minimizing marginal loss of overall conservation value following from the removal (Moilanen et al., 2005). Zonation accounts for connectivity measures and weights given for different biodiversity features, which are entered into the analysis as separate raster data layers. During prioritization, Zonation aims to retain a complementary-based balance across all features (Moilanen et al., 2011), and for each step, it calculates conservation performance as the average proportion remaining over all features within the analysis (Arponen et al., 2013).

Data layers and feature-specific weights used in the prioritization are listed in Table 1. Original data were rasterized with a cell size of 25 m × 25 m, as TRB sites and habitat patterns are small and highly fragmented. For computational reasons, initial cells were aggregated to binary 50 m × 50 m resolution. Total number of grid cells within the analysis was 307 072. We weighted habitat and species layers based on their red-list status (Rassi et al., 2010; Raunio et al., 2008), by giving a higher weight to a more threatened type. Critically endangered (CR), endangered (EN), vulnerable (VU), and near-threatened (NT) classes were given weights of 4, 3, 2, and 1, respectively. Additively, Natura 2000 habitats were weighted in respect to their importance according to the Habitats Directive (Council of Europe, 1992); priority habitats within the European Union were given a weight of 3 whereas other Natura 2000 habitats received a weight of 2. There were few exceptions based on national emphases on TRB management (Ministry of the Environment, 2013; Salminen and Kekäläinen, 2000): the weights of slash-and-burn areas and semi-natural dry grasslands and scrubland facies on calcareous substrates were raised by one unit; and the weight of boreal Baltic coastal meadows was lowered by one unit. Since species layers were fewer, we balanced the sum of their weights against the sum of weights of habitats (Lehtomäki and Moilanen, 2013). The final weights for species layers were: 32.4 for CR species, 21.6 for EN species, 10.8 for VU species, and 3.6 for NT species. We weighted remaining layers with the aim of producing weights that were as balanced as possible with the previously determined weights.

We chose the additive benefit function as the location removal rule. It is suitable for cases in which different co-occurring data layers are considered to provide additional value to each other, and the data is interpreted as indicating general conservation value rather than specific features (Moilanen, 2007). We assumed that TRBs with high heterogeneity (various TRB habitats), several species occurrences, and possibly an AES subsidy contract are the most important ones in conservational sense. Also, as we pooled the species data, it no longer represented specific species occurrences but reflected a general distribution of red-listed species dependent on TRBs.

Surveyed TRBs, protected unsurveyed TRBs, complementary habitat sites, and species occurrence sites were used as distinct planning units, because it was more purposeful to remove spatially separate sites rather than single cells from the landscape. We used a hierarchical removal mask to force all surveyed TRBs to the top fraction of the prioritization, thus forming management scenario A in our analysis. To determine subsequent management scenarios we utilized Zonation's hierarchical landscape zoning in which the order of site removal implies the conservational importance of different areas (Moilanen et al., 2011). We identified top-ranked residual unsurveyed TRBs corresponding to area targets within scenarios B–D to produce nested management networks.

We conducted separate analyses with and without landscape connectivity measures. While other feature-specific parameters were kept the same, we added interaction connectivity (Rayfield et al., 2009) by including a positive contribution of protected TRBs and complementary habitats for surveyed TRBs. We ran two connectivity analyses utilizing distribution smoothing with 2 km (according to Arponen et al., 2013) and 5 km mean dispersal distances. To determine whether including connectivity significantly affected the prioritization, we analyzed the rank orders of sites from the prioritizations with Wilcoxon signed rank test in R 3.3.0 (R Core Team, 2015).

In ArcGIS, we extracted management scenarios from the prioritization rank map, and further examined their spatial patterns with average nearest-neighbor analyses. As our main interest was to locate the most optimal solution for the expansion of surveyed TRB network regionally, we created generalized prioritization maps, in which each scenario was combined and mapped with a resolution of 10 km × 10 km.

2.4. Assumptions and limitations

There are several assumptions related to our data and the analyses, which affect the interpretation of the results:

1) Surveyed TRB sites are more valuable than unsurveyed ones.
2) Sites within habitat type inventory are more valuable than sites without habitat information.
3) Sites with many TRB habitats are more valuable than sites with only one TRB habitat type.
4) Unmanaged sites retain some value as TRBs despite the level of vegetational changes after abandonment.

We acknowledge that the national data on surveyed TRBs are not up-to-date for each individual site. Also, the AES subsidy contract data do not include all managed TRBs. The database on protected TRBs was formed by merging several different data sets into a collection of all sites with some value as TRBs (Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015). It includes sites where lack of management has launched successional substitution of a TRB habitat by another habitat type, as disturbance-dependent vegetation changes rapidly after management ceases. The database includes also fjell and shore grasslands, where natural disturbances maintain populations of TRB specialists. As a result, all sites within the prioritization may not be in need of active management. Species occurrence data are dependent on sampling effort, and the habitat data are similarly spatially restricted, as only protected TRB sites are covered by habitat type inventory. For the sake of our research questions these assumptions and limitations are not major problems.

3. Results

3.1 Current management status

Subsidized TRB management spread over different TRB categories (Table 2). Altogether 19 225 hectares received AES subsidy for TRB management. Of the total subsidized area, 42.8 % comprised of unprotected and unsurveyed sites located on private land.

Protected TRBs covered 38.0 % of the subsidized area. Among them, surveyed sites were more often managed than unsurveyed sites. Also, there were more managed private than state-owned TRBs.

Despite their substantial total area, unprotected privately-owned surveyed TRBs were rarely managed. They covered 19.2 % of the total subsidized area.

3.2 Spatial allocation of TRB management

Accounting for connectivity changed site ranking (Wilcoxon signed rank test, $n = 25\,136$, $p < 0.001$ for both 2 km and 5 km scales). Also the connectivity analyses differed from each other ($p = 0.04$). However, conservation performances of prioritization analyses were quite similar (Table 3). We derived management scenarios from the analysis with 2 km connectivity, which had the highest average performance. In each scenario, a fifth of the total area was under AES-funded management. Site pattern in all scenarios was spatially significantly clustered.

Scenario A, which consisted of surveyed TRBs, encompassed 52.4 % of the analysis landscape and 0.1 % of the total land area of Finland. Area-wise the scenario centered on SW Finland and the large river valley close to Swedish border (Fig. 2, A). There were surveyed sites throughout the country, but in Lapland and near the Russian border the spatial distribution was sparse. Protected sites comprised 24.0 % of scenario A (Table 3).

The prioritization analysis targeted TRB management especially to Baltic Sea coast, but also other distinct clusters in parts of Southern, Central, and Northern Finland emerged in the results (Fig. 2, B–D). When compared to the current extent of TRB management (Fig. 2, E), the core areas along the western coast were strengthened, and management allocation within Lapland and inland was increased. Along the western coastline the prioritized unsurveyed TRBs were mostly located on protected areas (Fig. 2, F). Inland areas expressed a more fragmented pattern where management was largely targeted according to TRB specialist species occurrences (Fig. 2, G).

3.3 Red-listed vascular plant species specialized in TRBs

Most of the existing occurrences of TRB specialists within the analysis were located on unprotected and unsurveyed sites. Only 3.8 % (501 out of 13 038 occurrences) were managed through an AES contract (Table B.1). Surveyed TRBs (scenario A) hosted 1 123 occurrences of 58 threatened and 33 near-threatened species. This included 68.4 % of all species in the data, but only 8.6 % of their occurrences (Fig. 3). Targeting management actions according to scenario B included a total of 122 red-listed species (with 8 422 existing occurrences), with a focus on threatened species. Half of scenario B's additional management effort was allocated to unprotected sites indicated by occurring specialist species (Table 3). Extending management according to scenario C incorporated 127 species (11 668 occurrences). It especially increased management of populations of near-threatened species. Scenario D did not cover any additional species, and the rise in the amount of species occurrences was small (168 additional occurrences).

3.4 TRB habitats on protected areas

The majority of scenario A consisted of sites without specific habitat information, including all unprotected surveyed sites (Table C.1). On protected areas, different TRB habitats were unevenly represented when compared to their total coverages (Fig. 4A). The pattern was somewhat similar when Natura 2000 -habitats were explored (Fig. 4B). Areal summaries (Tables C.1 and C.2) showed that the most frequent habitats on protected TRBs in scenario A were moist to mesic meadows, wooded pastures, or grazed woodlands, whereas other TRB types were rare.

Scenarios B–D hosted increasing proportions of different TRB habitats (Fig. 4A and 4B). Scenario B emphasized habitat rarity and it included the scarcest TRB habitats, except for heaths. Scenario C especially increased the total area of mesic and moist meadows, heaths, and grazed woodlands. Considering Natura 2000 -habitats, scenario C included over 90 % of all types other than wooded pastures, coastal meadows, and dry heaths. Scenario D covered nearly all TRB habitats on protected areas. Only moist meadows were left to 68.8 % representation. Similarly, coastal meadows were the only Natura 2000 -habitat left under 90 % representation within scenario D (exact coverage 87.8 %).

4. Discussion

Our results show that the conservational status of TRBs remains ecologically inadequate in Finland. We demonstrated that the overall cover of TRBs managed through an AES contract has decreased to less than 20 000 hectares in ten years (from ca. 24 500 ha in 2005–2007 according to Kemppainen and Lehtomaa, 2009). In 1950s, TRB cover was over 2.1 million hectares (Raunio et al., 2008). Thus we conclude that after the collapse during late 20th century, the total cover of managed TRBs is further declining. Although our data on the general management status of TRBs were deficient, the change is clear and we doubt that more accurate data would change the interpretation. With such prevalent habitat loss, both the low amount of remaining habitat and the high degree of fragmentation will strongly reduce remaining species richness (Rybicki and Hanski, 2013). In the long term, habitat loss and fragmentation also lead to genetic and evolutionary changes in remnant populations of specialized species, often reducing their viability (Hanski, 2011).

We prove that while a majority of remaining conservationally valuable TRBs is unmanaged, over 40 % of area under AES management consists of sites whose biological value is not documented. This finding confirms the earlier notion that Finnish authorities have been unsuccessful in targeting TRB management according to the conservational value and connectedness of the sites (Arponen et al., 2013; Kemppainen and Lehtomaa, 2009). AES policies have compensated for management costs without accounting for effects on biodiversity (Arponen et al., 2013). We suggest that these unsurveyed and unprotected sites should be inspected by authorities in order to determine their value as TRBs.

Building a management network that best benefits biodiversity is challenging with limited resources (Kotiaho et al., 2015). If appropriate, reallocation of management funding should be considered. It is essential that future subsidies are systematically directed to sites that either are biologically representative or will develop into such. Targeting management funding spatially in a more optimal manner would increase the effectiveness of TRB management both economically and ecologically (Arponen et al., 2013).

Our spatial prioritization produced management scenarios that reflect the distribution of TRB-related conservation value. In all scenarios, the South-West–West coastal region receives most of the prioritized management effort. Spatial coordination of management actions promotes habitat connectivity and the associated ecological functions, such as population densities, dispersal, and outbreeding (Arponen et al., 2013; Hanski, 2011). Targeting additional TRB management and restoration primarily to the Baltic Sea coast would promote the extent and connectedness of TRB habitats and support species populations' viability. Within this core area, a 30 % cover of TRB habitat should be locally pursued in order to maintain a large fraction of specialist species (Hanski, 2011). This target, however, calls for large-scale bio-cultural restoration of abandoned TRBs. The success of TRB restoration, in turn, is dependent on the successional vegetation changes following management abandonment. Remnant species, interactions, and TRB structures compose an ecological memory that makes ecosystem reorganization possible (Bengtsson et al., 2003). Occurrence of TRB specialists makes it possible to discriminate restorable TRBs from sites that are difficult to restore.

According to the prioritization, small clusters of inland sites with red-listed TRB specialist species should be managed in a network-like manner. The observed spatial clustering of prioritized TRBs serves as a good platform for strengthening species' metapopulations. It counteracts the fragmentation effect and enables creation of new high-quality habitat patches via restoration and management reinitiation, therefore relaxing populations' extinction threshold (Eriksson and Kiviniemi, 1998; Rybicki and Hanski, 2013).

Management scenarios B and C would substantially improve the conservational status of TRB-dependent species. Our analysis took into account 133 vascular plants, but it should be noted that there are a vast number of TRB specialists also in other red-listed taxa (Rassi et al., 2010). Majority of these are insects living on dry meadows, especially butterflies and beetles, but unfortunately records on their populations are scattered (Rassi et al., 2010). In addition, bird species breeding on coastal and alluvial meadows have faced population declines due to habitat degradation, and many of them are categorized as threatened (Rassi et al., 2010).

Because of spatial segregation between species occurrences and TRB habitat sites and higher weights given to species data, the prioritization process emphasized species over habitats. However, different TRB habitats became well represented within the largest management scenario (D). Scenario D encompasses nearly all protected sites with TRB habitats of European level conservation interest (Halada et al., 2011). We conclude that the order of scenarios A–D serves as an initiative and a guideline for prioritization of additional TRB management in Finland. Realization of the national target of 60 000 managed hectares of TRBs needs further increase in available resources and their purposeful allocation. Without systematic targeting of field surveys, management planning, and restoration it is impossible to achieve a two- to threefold increase in the total amount of managed area when compared to the current situation.

Our work is the first nation-wide attempt to advance TRB conservation on the basis of ecological functionality instead of administrative categorizations (see Fig. 1 and Table 2). Although surveyed TRBs (scenario A) provided a basis for management network building, we demonstrated the conservational potential of TRB management on unsurveyed sites. Protected and unprotected TRBs, in turn, complement each other by forming habitat networks within the landscape (Bengtsson et al., 2003).

Our suggestions for future work concern effective ways to advance TRB conservation. The systematic assessment presented here is only one part of conservation planning, and its results should be critically evaluated (Knight et al., 2006). Because conservation of TRBs is dependent on collaboration between authorities, landowners, and managers, we propose adoption of and research on modern systematic conservation strategies, which are based on promoting resilience and cooperation. These include multi-use conservation landscapes (Hanski, 2011), dynamic reserves (Bengtsson et al., 2003), contract-based temporary conservation (Moilanen et al., 2014), and adaptive co-management (Berkes, 2007).

As a final note, we argue that current incoherent governance of TRB conservation hinders promotion of TRB management and more efficient utilization of management funding. This finding is based on an observation we gained through our data collection process. There are several Finnish authorities involved in TRB-related decision-making, none of which carries a clear responsibility on coordinating TRB conservation (Ministry of the Environment, Ministry of Agriculture and Forestry, Finnish Environment Institute, Metsähallitus Parks & Wildlife Finland, Agency for Rural Affairs, and 15 regional ELY centres). Also elsewhere in Europe disintegration to static, isolated, and monosectoral conservation strategies has proven to be inefficient in tackling the biodiversity loss in rural landscapes (Plieninger and Bieling, 2013). Individual organizations and structural institutions shape how the environment is governed, and often impede integrative conservation practice (Bennett et al., 2016). This should be taken into account while our results are implemented.

5. Conclusions

Throughout Europe, traditional rural biotopes and their species are declining. This has caused substantial biodiversity loss. We noticed two main challenges in TRB conservation. On the one hand, the total area under management is too small to safeguard TRB-dependent biodiversity. On the other, management actions are not targeted to sites that are conservationally most important. As a solution, we present a nation-wide and spatially explicit management network optimization. It introduces ecological functionality into systematic promotion of TRB management and targeting of management funding, and can be implemented in a step-wise manner.

Allocating additional management and large-scale restoration actions to Baltic Sea coastal region emerges as a strategic starting point. This would create a large, well-connected core area for a Finnish TRB habitat network. In addition, reviving populations of red-listed TRB species requires that smaller inland clusters of TRB sites are managed in order to promote habitat connectivity. However, as current policies are failing in sustaining biodiversity dependent on TRBs, we stress that implementation of targeted TRB management calls for adopting new perspectives on their conservation and governance.

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Table 1. Analysis layers. "No." refers to continuous numbering of data layers. For each layer, also name, weight value, and distribution are listed. Base layers (1–3) included site-level information on survey and management status. Habitat type inventory data was used to form layers 4–14 and 16–28. TRB habitat layers 4–11 are comparable with the Finnish assessment on threatened habitats (CR: critically endangered, EN: endangered, NE: not evaluated; according to Raunio et al., 2008). Natura 2000 -layers are listed according to the TRB habitats in directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Council of Europe, 1992). Habitats marked with an asterisk (*) are classified as priority habitats within the European Union. Undefined TRB habitat (layer 15) includes all area that is not covered by habitat type inventory. Species layers include information on the occurrence of red-listed vascular plant species specialized in TRB habitats. Transformed layers (34 and 35) were included only in the analyses with landscape connectivity measures. Weight sums were balanced between layers 1–28 and 29–33. Cell size in the analysis was 0.25 ha (50 m × 50 m).

	No.	Layer name	Weight	Distribution (cells)
Base layers:	1	Nationally and regionally surveyed traditional rural biotopes on private and state-owned land (corresponds to scenario A)	2	160 830
	2	Protected TRBs on private and state-owned land: extended network	1	166 457
	3	AES management contract areas (on layers 1 and 2)	2	65 745
Habitat layers:	4	Heaths (CR)	4	5 950
	5	Dry meadows (CR)	4	2 834
	6	Mesic meadows (CR)	4	7 625
	7	Moist meadows (CR)	4	35 640
	8	Wooded meadows (CR)	4	215
	9	Wooded pastures (CR)	4	3 630
	10	Grazed woodlands (EN)	3	7 364
	11	Slash-and-burn areas (NE)	4	188
	12	Old traditional reindeer gathering grounds	1	163
	13	Old traditional yards and Sami camp sites	1	1 204
	14	Dry sandy sunlit dunes and eskers	1	3 302
	15	Undefined TRB habitat	2	242 034
Natura 2000 layers:	16	Boreal Baltic coastal meadows (1630) *	2	19 502
	17	European dry heaths (4030)	2	4 207
	18	Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210)	3	24
	19	Species-rich *Nardus* grasslands on siliceous substrates (6230)*	3	7
	20	Fennoscandian lowland species-rich dry to mesic grasslands (6270)*	3	1 792
	21	Nordic alvar and precambrian calcareous flatrock (6280)*	3	60
	22	*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (6410)	2	1
	23	Hydrophilous tall herb fringe communities (6430)	2	1 227
	24	Northern boreal alluvial meadows (6450)	2	3 905
	25	Lowland hay meadows (6510)	2	190
	26	Mountain hay meadows (6520)	2	93
	27	Fennoscandian wooded meadows (6530)*	3	146
	28	Fennoscandian wooded pastures (9070)	2	3 979

Species layers:	29	Critically endangered (CR) plant species inhabiting TRBs	32.4	34
	30	Endangered (EN) plant species inhabiting TRBs	21.6	1 816
	31	Vulnerable (VU) plant species inhabiting TRBs	10.8	5 213
	32	Near threatened (NT) plant species inhabiting TRBs	3.6	5 213
	33	NT, VU, EN, or CR plant species historically inhabiting TRBs; disappeared or potentially disappeared locations	3.6	2 936
Transformed layers:	34	Contribution of protected TRBs (layer 2) to connectivity of surveyed TRB network (layer 1)	5	166 457
	35	Contribution of dry sandy sunlit dunes and eskers (layer 17) to connectivity of surveyed TRB network (layer 1)	2	3 299

Table 2. Management status of traditional rural biotopes in Finland (in hectares and percents) in year 2014. Note that managed TRBs include only sites where management is funded through national agri-environment scheme. For unmanaged sites, private unprotected and unsurveyed sites are excluded, as there is no existing data on them. Original vector data were used in the analysis.

		Managed (ha)	Unmanaged (ha)	Managed (%)
Protected:	State-owned surveyed	1 122.0	2 946.6	27.6
	State-owned unsurveyed	1 460.7	14 555.2	9.1
	Private surveyed	1 531.2	1 739.4	46.8
	Private unsurveyed	3 199.9	6 468.3	33.1
Unprotected:	Private surveyed	3 681.8	19 237.2	16.1
	Private unsurveyed	8 229.8	N.A.	N.A.
Total (protection status):	Protected	7 313.8	25 709.4	22.1
	Unprotected	11 911.5	N.A.	N.A.
Total (survey status):	Surveyed	6 335.0	23 923.2	20.9
	Unsurveyed	12 890.4	N.A.	N.A.
Grand total:		19 225.4	N.A.	N.A.

Table 3. A summary of spatial prioritization from Zonation analysis. Rows 1–3 give conservation performances of different prioritization analyses in terms of average proportion of conservation value remaining within the prioritized landscape of given size. Nested management scenarios were further investigated only for connectivity analysis with 2 km dispersal distance (rows 4–12). Original vector data were used in the calculations instead of raster data from the analysis. However, the coverage of species point occurrences outside of surveyed traditional rural biotopes or protected areas was estimated from rasterized data (cell size 0.25 ha). Currently managed area is derived from agri-environment scheme contracts on TRB management in year 2014. ANN refers to Average Nearest-Neighbor analysis conducted for each scenario.

	Scenario A (surveyed TRBs)	Scenario B (A + 5 000 ha)	Scenario C (A + B + 5 000 ha)	Scenario D (A + B + C + 5 000 ha)
Conservation performance (without connectivity)	0.333	0.719	0.865	0.940
Conservation performance (with 5 km dispersal distance)	0.335	0.722	0.864	0.937
Conservation performance (with 2 km dispersal distance)	0.345	0.727	0.866	0.939
Additional area (ha)	0.0	4 362.6	8 256.5	12 133.1
Total area within scenario (ha)	30 258.1	34 620.7	38 514.6	42 391.2
Coverage on protected areas (ha)	7 258.8	9 194.4	12 280.6	16 150.1
Coverage on unprotected areas (ha)	22 999.3	25 426.4	26 234.0	26 241.1
Currently managed area (ha)	6 335.0	6 740.2	7 752.5	8 851.7
ANN: observed mean distance (m)	1 254.7	926.0	833.8	801.1
ANN: expected mean distance (m)	4 311.5	2 950.4	2 650.0	2 587.9
ANN: z-score	-122.2	-175.7	-196.6	-202.8
ANN: p-value	<0.001	<0.001	<0.001	<0.001

Figure legends

Fig. 1. A framework for categorizing traditional rural biotopes from a governance perspective. Key determinants are management, protection, and survey statuses. Information on management status is mainly available through AES contracts. Protected TRBs are located both on private and state-owned land. A recognized network of valuable sites is based on nationally and regionally conducted surveys on TRBs. The management and protection statuses of surveyed TRBs are variable. Ecologically, TRBs are detected via distinct structural features such as the occurrence of TRB habitat specialist species, whether the site is managed or not. On national level, the data on TRBs vary in quality. The level of knowledge positively correlates with the ability of Finnish environmental authorities to influence management of TRBs belonging to different categories. Data sets utilized in detecting sites belonging to each category are listed in italic (for detailed descriptions of data, see Electronic appendix A).

Fig. 2. Distribution of surveyed traditional rural biotopes (management scenario A; panel A) and allocation of cumulative TRB network expansion according to management scenarios B, C, and D (panels B–D, respectively). For comparison, the distributions of currently managed TRBs (according to AES contracts; panel E), protected TRBs (surveyed and unsurveyed; panel F) and TRB-specialist vascular plant species occurrences (panel G) are also shown. Note that the Åland islands were excluded from the analyses.

Fig. 3. The proportional increase in the number of specialist vascular plant species (A) and their occurrences (B) according to nested management scenarios (A–D, on x-axis). Curves are drawn according to red-list status: CR: critically endangered; EN: endangered; VU: vulnerable, and NT: near-threatened. The numbers of occurrences per species are summarized in Table B.1.

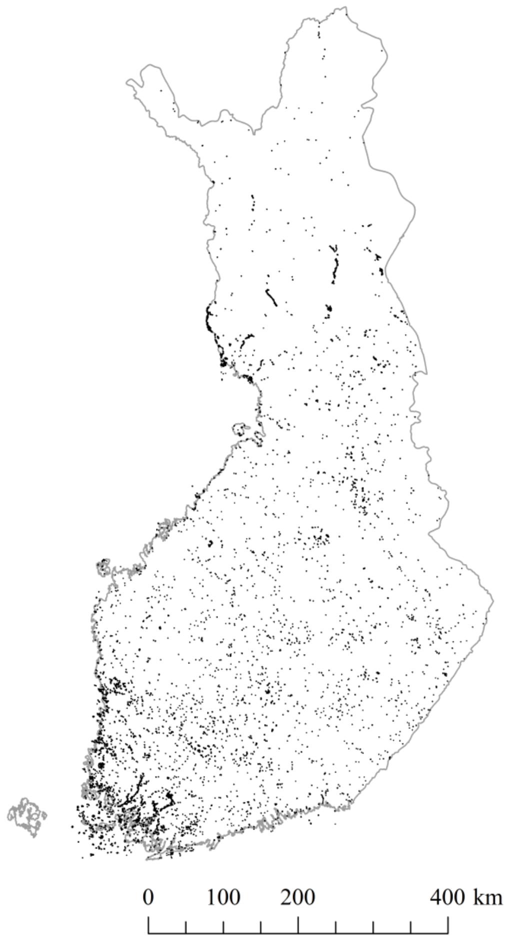
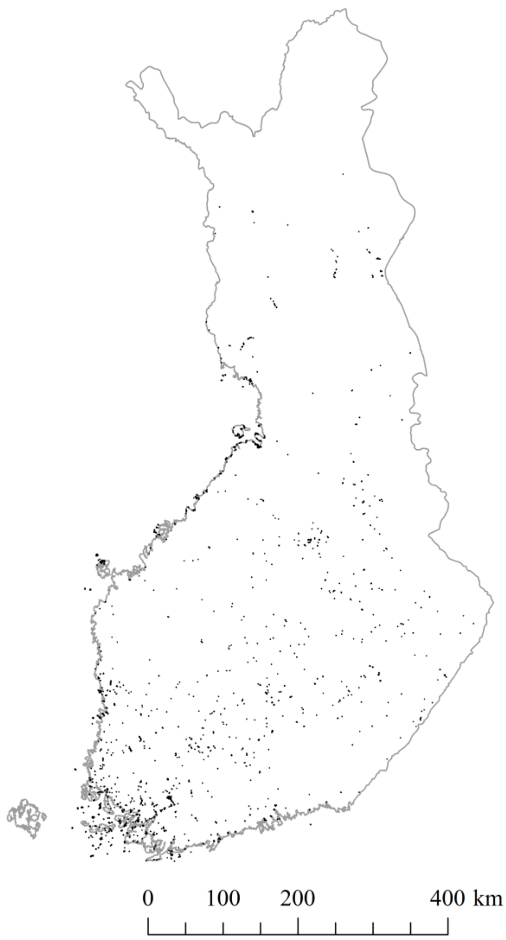
Fig. 4. The increase in the proportion of different habitat types included in the nested management scenarios (A–D; represented in grayscale). Panel A shows upper-level habitat type inventory classes. In panel B more specific Natura 2000 -habitats are depicted (codes in brackets). The numeric data are provided in Tables C.1 and C.2. Only sites located on protected areas are included.

[1]: complementary habitats

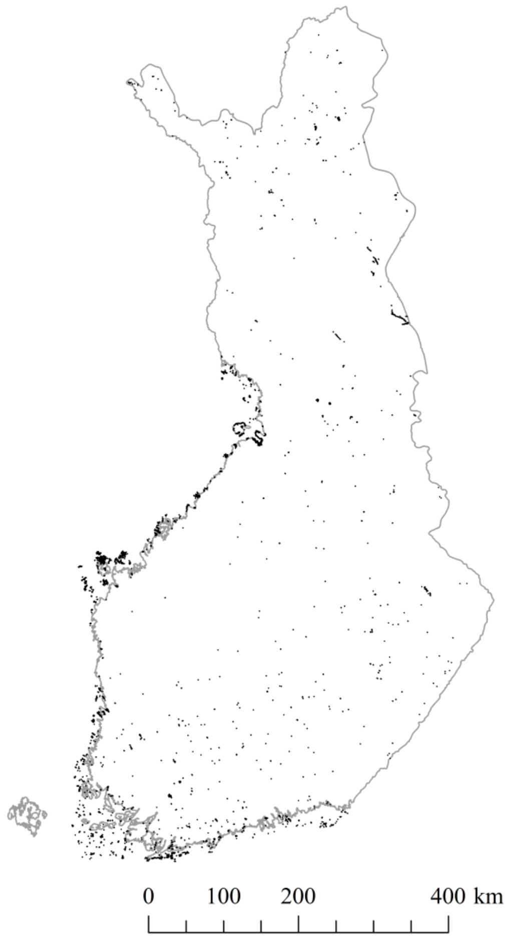
[2]: sites without habitat information, including all unprotected TRBs

*: priority habitats within the European Union

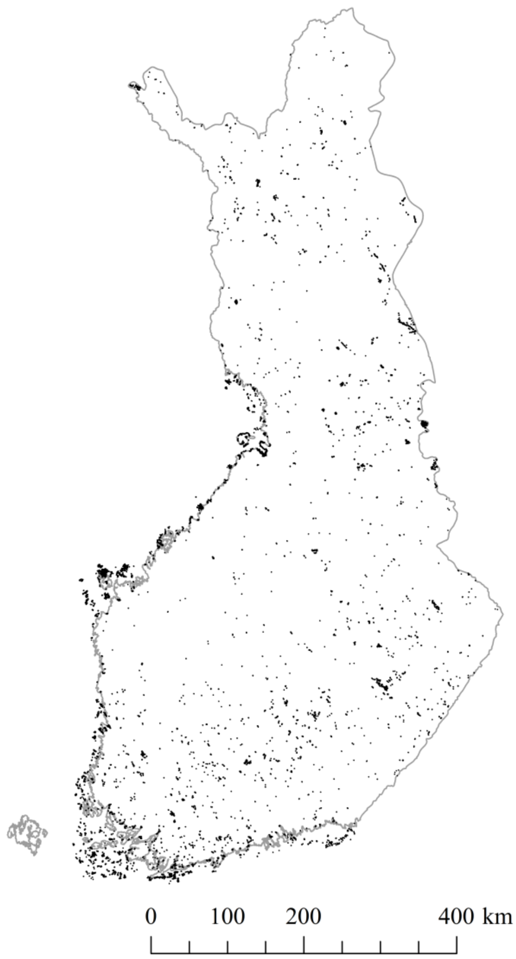
Appendix A.

Original vector data sets used in the analysis:	Snapshot:
1. Surveyed traditional rural biotopes *Type*: Polygon *Description*: Includes site-level geometries and attributes of TRBs detected in field surveys by environmental authorities (regional ELY Centres). Sites are classified as nationally, regionally, and locally valuable (with sub-classes). Also sites classified as restorable are included. Database is compiled and updated by the Finnish Environment Institute. Originally, the national survey on Finnish TRBs was conducted during 1992–1998. It covered 18 640 hectares of TRBs classified as biologically valuable. After that, additional surveys and follow-ups have been done regionally, and the database has been updated accordingly (latest update in summer 2014). The coverage of the data is 30 258 ha. Because the data is combined from several sources, it is heterogeneous and its accuracy varies spatially and temporally. *Extent*: Nationwide data *Date of acquisition*: November 4th 2014. Field data are collected during a time period 1992–2014. *Source*: Finnish Environment Institute *References*: (Kemppainen and Lehtomaa, 2009; Raatikainen, 2009; Vainio et al., 2001)	
2. Agri-environment scheme contract areas *Type*: Polygon *Description*: Plot-level geometries of five-year AES subsidy contracts on TRB management. Only contracts valid on year 2014 were included. The combined coverage of the data is 19 225 ha. *Extent*: Nationwide data *Date of acquisition*: June 19th 2014. Continuously updated. *Source*: Ministry of Agriculture and Forestry	

3. Habitat type inventory
Type: Polygon
Description: Includes plot-level geometries and attributes on habitats located on private protected areas and all state-owned land. Geometries are formed with a high level of accuracy and habitat information is categorized within a multi-level database structure, where general habitat classes are further divided into more detailed Natura 2000 -habitat classes and/or vegetation classes. In total, the inventory covers 4 620 235 ha (including water bodies). For Zonation analysis, geometries without TRB-related attributes were discarded, leaving a data set covering 11 143 ha (depicted in the right-hand map).
Extent: Protected and state-owned areas
Date of acquisition: December 4th 2012 (privately-owned protected areas) and June 11th 2014 (state-owned areas). Inventories started in year 2001, and most of the field work was conducted during 2003–2006. The database is continuously updated.
Source: Metsähallitus, Parks & Wildlife Finland
References: Airaksinen and Karttunen, 2001; Metsähallitus, 2010; Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015



4. Protected traditional rural biotopes
Type: Polygon
Description: Geometries and attributes of surveyed and unsurveyed TRB sites located on protected areas (either private or state-owned) and unprotected state-owned land. Database was compiled from the national survey on TRBs, existing and expired AES contracts on TRB, landscape, and biodiversity management, NTI data, and additional GIS data on managed and unmanaged TRBs on protected areas available during years 2012–2014. The information level of the database varies according to the original data source, and it includes sites whose value as TRBs is unsure. Total coverage of the data is 32 229 ha.
Extent: Protected private and all state-owned areas
Date of acquisition: September 17th 2014.
Source: Metsähallitus, Parks & Wildlife Finland
References: Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015



5. Occurrences of vascular plant species specialized in traditional rural biotopes

Type: Point

Description: Includes existing and historical occurrences of red-listed TRB-dependent vascular plants derived from national Hertta database. Species are listed in table B.1. Species were selected according to their specialization in TRB habitats, and this information was based on the national survey guide for TRBs (Raatikainen, 2009) and the 2010 Red List of Finnish Species (Kalliovirta et al., 2010). Compilation of the data set is described in Pakkanen et al. (2015) and Raatikainen and Raatikainen (2015). Oldest observations of the data are from 19th century herbariums, and in recent years environmental authorities have recorded their red-listed vascular plant observations routinely to the database. Only occurrences with at least 100 meter accuracy were included. Number of currently existing occurrences within the data is 13 038. In addition, there are 3 039 historical occurrences that are categorized as potentially or certainly disappeared.

Extent: Nationwide data

Date of acquisition: June 2nd 2014. Continuously updated.

Source: Finnish Environment Institute

References: Kalliovirta et al., 2010; Ryttäri et al., 2012

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Appendix B.

Table B.1. Red-listed vascular plant species specialized in traditional rural biotopes and a summary of their occurrence data. The red-list statuses are according to Kalliovirta et al. (2010) and the nomenclature follows Hämet-Ahti et al. (1998). Columns 3–5 present the number of existing occurrences of the species on different TRB sites, column 6 lists all occurrences within the data, and column 7 summarizes the number of occurrences located on TRB management subsidy contract areas. Note that surveyed TRBs are equivalent to scenario A in the prioritization analysis. Scenarios B–D, however, allocate additional management to unsurveyed TRB sites without accounting for protection status.

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
CR	*Anthyllis vulneraria* subsp. *polyphylla*			9	9	
CR	*Armeria maritima* subsp. *intermedia*			7	7	
CR	*Asperula tinctoria*	2			2	
CR	*Botrychium simplex*	4		2	6	2
CR	*Pimpinella major*	4		3	7	
CR	*Thalictrum lucidum*			1	1	
CR	*Veratrum album* subsp. *lobelianum*			2	2	
EN	*Agrimonia pilosa*	12		27	39	
EN	*Anagallis minima*	1		4	5	
EN	*Androsace septentrionalis*			19	19	
EN	*Arctium nemorosum*	14	1	8	23	12
EN	*Armeria maritima* subsp. *elongata*	5	4	6	15	
EN	*Asplenium ruta-muraria*	1	3	88	92	
EN	*Botrychium matricariifolium*	12		18	30	2
EN	*Carex hartmanii*			1	1	
EN	*Carex hostiana*			1	1	
EN	*Carex vulpina*			2	2	
EN	*Carlina biebersteinii*	3	3	28	34	
EN	*Crepis praemorsa*			8	8	
EN	*Epilobium lamyi*	1		5	6	
EN	*Epipactis palustris*			18	18	
EN	*Euphrasia micrantha*			1	1	
EN	*Euphrasia rostkoviana* subsp. *fennica*	4		36	40	
EN	*Galium saxatile*	7		6	13	
EN	*Gentianella amarella*	12	2	149	163	9
EN	*Gentianella campestris*	28	2	56	86	9
EN	*Gentianella uliginosa*	4			4	3
EN	*Hippuris tetraphylla*	11	103	88	202	35
EN	*Lithospermum arvense*	7	1	26	34	
EN	*Lonicera caerulea*	1	19	38	58	
EN	*Malaxis monophyllos*	1	5	75	81	
EN	*Ophrys insectifera*			3	3	
EN	*Orchis militaris*			3	3	
EN	*Persicaria foliosa*	13	6	266	285	3
EN	*Potentilla anglica*	11	2	10	23	9
EN	*Potentilla tabernaemontani*			1	1	
EN	*Primula stricta*	1		189	190	
EN	*Pulsatilla patens*		2	262	264	
EN	*Rosa sherardii*	4			4	2
EN	*Sagina maritima*	4	1	6	11	1
EN	*Salicornia europaea*	3	18	6	27	18
EN	*Samolus valerandi*			27	27	
EN	*Saxifraga adscendens*	5	3	39	47	
EN	*Scleranthus perennis*			5	5	

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
EN	*Stellaria crassifolia* var. *minor*	1		3	4	1
EN	*Vicia cassubica*			6	6	
EN	*Viola persicifolia*	2		29	31	1
EN	*Viola uliginosa*			5	5	
VU	*Alchemilla hirsuticaulis*	1		5	6	
VU	*Antennaria nordhageniana*			15	15	
VU	*Antennaria porsildii*		1	32	33	
VU	*Botrychium boreale*	29	21	200	250	12
VU	*Botrychium lanceolatum*	27	10	168	205	7
VU	*Campanula cervicaria*	14	17	487	518	3
VU	*Carex caryophyllea*	8		22	30	
VU	*Carex pulicaris*			1	1	
VU	*Carex viridula* var. *bergrothii*	1	1	108	110	
VU	*Carlina vulgaris*		1	1	2	
VU	*Cirsium oleraceum*			2	2	
VU	*Crassula aquatica*	5	9	144	158	4
VU	*Crataegus monogyna*	7	3	4	14	6
VU	*Crataegus rhipidophylla*	6	7	10	23	
VU	*Dactylorhiza incarnata* subsp. *cruenta*	13	30	318	361	11
VU	*Dactylorhiza incarnata* subsp. *incarnata*	5	17	1 241	1 263	3
VU	*Dactylorhiza traunsteineri*	1	4	395	400	
VU	*Drosera intermedia*			67	67	
VU	*Elymus fibrosus*	7	10	77	94	3
VU	*Epipactis atrorubens*		1	82	83	
VU	*Erigeron acris* subsp. *decoloratus*	3	6	32	41	
VU	*Eriophorum brachyantherum*	1		105	106	
VU	*Fragaria viridis*	6		1	7	6
VU	*Galium verum*	28	2	77	107	9
VU	*Gymnadenia conopsea* var. *conopsea*	43	4	136	183	12
VU	*Gypsophila muralis*			32	32	
VU	*Leersia oryzoides*	2		78	80	
VU	*Lythrum portula*			23	23	
VU	*Malus sylvestris*	34	12	65	111	19
VU	*Melampyrum arvense*	2	1	5	8	1
VU	*Melampyrum cristatum*	19		10	29	12
VU	*Ononis arvensis*		2	13	15	
VU	*Polygala amarella*	11		8	19	10
VU	*Polygala vulgaris*	7		10	17	1
VU	*Potentilla neumanniana*	26		2	28	23
VU	*Primula nutans* subsp. *finmarchica*	67	165	530	762	84
VU	*Sorbus intermedia*	3		2	5	2
VU	*Thalictrum simplex* subsp. *simplex*	26		39	65	8
VU	*Ulmus laevis*	5	2	292	299	1
NT	*Ajuga pyramidalis*	2		8	10	1
NT	*Alchemilla samuelssonii*			3	3	
NT	*Allium schoenoprasum* subsp. *alpinum*	3	1	5	9	
NT	*Allium ursinum*	1	4	7	12	
NT	*Anchusa officinalis*	3		7	10	
NT	*Antennaria dioica*	18	21	260	299	1
NT	*Antennaria villifera*			11	11	
NT	*Anthyllis vulneraria* subsp. *lapponica*			62	62	
NT	*Blysmus rufus*	7			7	2
NT	*Botrychium lunaria*	169	74	585	828	50
NT	*Botrychium multifidum*	103	26	485	614	26
NT	*Carex acutiformis*			15	15	

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
NT	*Carex atherodes*	8	1	66	75	2
NT	*Carex glareosa*	5			5	2
NT	*Carex paleacea*		1	1	2	
NT	*Carex rhynchophysa*			14	14	
NT	*Carex riparia*		1	45	46	1
NT	*Catabrosa aquatica*	11	5	133	149	8
NT	*Cerastium glutinosum*	5		1	6	3
NT	*Cynoglossum officinale*			10	10	
NT	*Cypripedium calceolus*	1	17	1 565	1 583	1
NT	*Dactylorhiza fuchsii*	2	1	63	66	
NT	*Dactylorhiza sambucina*	14	4	25	43	3
NT	*Dianthus deltoides*	64	13	339	416	21
NT	*Draba muralis*	13		3	16	8
NT	*Euphrasia bottnica*	3	2	6	11	2
NT	*Geranium bohemicum*	2		19	21	
NT	*Helianthemum nummularium*	2		2	4	1
NT	*Leontodon hispidus*	3	1	17	21	
NT	*Melica picta*	1		1	2	
NT	*Mentha aquatica* var. *litoralis*	1		1	2	
NT	*Myosotis nemorosa*	26		55	81	3
NT	*Nardus stricta*	18	5	106	129	4
NT	*Orchis mascula*			2	2	
NT	*Phleum phleoides*			1	1	
NT	*Phleum pratense* subsp. *serotinum*	2		1	3	
NT	*Prunus spinosa*			3	3	
NT	*Sesleria caerulea*	5			5	5
NT	*Stellaria fennica*	4	1	118	123	
NT	*Thalictrum minus* subsp. *kemense*	6		24	30	
NT	*Thymus serpyllum* subsp. *serpyllum*		1	332	333	
NT	*Trifolium aureum*	5	3	118	126	1
NT	*Trifolium fragiferum*	4		1	5	4
NT	*Trifolium montanum*	2		1	3	
NT	*Trifolium spadiceum*	25		279	304	8
NT	*Valerianella locusta*			1	1	
	Total:	**1 123**	**683**	**11 232**	**13 038**	**501**

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Appendix C.

Table C.1. Cumulative cover of different habitat types located on prioritized sites included in the nested management scenarios (A–D). In addition, total coverage of each habitat type within the analysis is given. Note that areas are derived from rasterized data, which somewhat overestimates total coverages. Due to generalization into 50 × 50 m cell size, the covers of different habitat classes overlap. The data are represented proportionally in Fig. 4A. Habitat data were available only from protected sites covered by habitat type inventory. All sites without habitat information, including all unprotected sites, are classified as undefined TRB habitat.

	Scenario A (surveyed TRBs)	Scenario B (incl. A)	Scenario C (incl. A and B)	Scenario D (incl. A, B, and C)	Total coverage (ha)
Heaths	101.2	728.9	1 352.1	1 425.0	1 487.5
Dry meadows	139.6	497.4	651.8	690.8	708.5
Mesic meadows	549.0	1 031.3	1 551.7	1 763.3	1 906.3
Moist meadows	1 318.7	2 076.0	3 483.8	6 130.1	8 910.0
Wooded meadows	43.8	53.8	53.8	53.8	53.8
Wooded pastures	451.0	675.2	832.2	891.2	907.5
Grazed woodlands	629.6	784.3	1 259.2	1 741.6	1 841.0
Slash-and-burn areas	7.8	47.0	47.0	47.0	47.0
Old traditional reindeer gathering grounds	8.6	40.8	40.8	40.8	40.8
Old traditional yards and Sami camp sites	54.8	174.0	280.8	289.9	301.0
Dry sandy sunlit dunes and eskers	11.6	158.5	385.5	806.5	825.5
Undefined TRB habitat	11 920.2	21 541.0	34 429.3	48 527.8	60 508.5

Table C.2. Cumulative cover of Natura 2000 -habitats located on prioritized sites included in the nested management scenarios (A–D), and total coverage of each habitat type within the data. Note that areas are derived from rasterized data, which somewhat overestimates total coverages. Due to generalization into 50 × 50 m cell size, the covers of different habitat classes overlap. Habitats marked with an asterisk (*) are classified as priority habitats within the European Union. The data are represented in Fig. 4B. Only sites located on protected areas are included.

	Scenario A (surveyed TRBs)	Scenario B (incl. A)	Scenario C (incl. A and B)	Scenario D (incl. A, B, and C)	Total coverage (ha)
Boreal Baltic coastal meadows (1630) *	975.1	1 399.3	2 233.0	4 280.7	4 875.5
European dry heaths (4030)	43.1	670.0	935.0	992.9	1 051.8
Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210)	3.3	6.0	6.0	6.0	6.0
Species-rich *Nardus* grasslands on siliceous substrates (6230)*	1.0	1.8	1.8	1.8	1.8
Fennoscandian lowland species-rich dry to mesic grasslands (6270)*	232.5	395.6	425.6	438.6	448.0
Nordic alvar and precambrian calcareous flatrock (6280)*	6.8	15.0	15.0	15.0	15.0
Molinia meadows on calcareous, peaty or clayey-silt-laden soils (6410)	0.0	0.3	0.3	0.3	0.3
Hydrophilous tall herb fringe communities (6430)	51.2	207.7	284.1	294.5	306.8
Northern boreal alluvial meadows (6450)	153.3	455.9	943.1	962.6	976.3
Lowland hay meadows (6510)	33.8	47.3	47.3	47.3	47.5
Mountain hay meadows (6520)	17.5	22.7	22.7	22.7	23.3
Fennoscandian wooded meadows (6530)*	29.5	36.5	36.5	36.5	36.5
Fennoscandian wooded pastures (9070)	483.4	700.3	879.4	956.0	994.8