1. INTRODUCTION

The unique biodiversity value of species rich semi-natural grasslands in Europe has long been recognized (Kull and Zobel, 1991; Eriksson et al., 2002; Pärtel et al., 2005; Ward et al., 2013; Dengler et al., 2014). In recent years, the Ecosystem Services (ES) framework has provided a new approach to assess the value and multi-functionality of these habitats (Bullock et al., 2011). Semi-natural grasslands provide a wide range of goods and services, including plant species diversity, carbon storage and sequestration, biomass production for grazing animals, flood reduction, habitat for migratory and breeding birds, water infiltration, purification and storage, erosion prevention and recreation amongst others. The cessation of moderate disturbance management re-establishes vegetation succession leading to scrub encroachment and a loss of grassland species diversity (Burnside et al., 2007; Pärtel and Helm, 2007; Sammul et al., 2008; Metsoja et al., 2011). As a result, land owners and managers are faced with a decision between maintaining the ecological benefits from grassland management as opposed to its economic costs. High plant species diversity provides a range of habitats for both breeding and migratory birds (Báldi et al., 2013). European grasslands are also estimated to store 5.5 Gt of carbon in the top 30 cm of soils (Lugato et al., 2014), which provides an important pedologic carbon store, particularly coastal grasslands (McLeod et al., 2011), and can exceed that of tropical rainforests (Pendleton et al*.,* 2012).

Throughout the second half of the twentieth century, semi-natural grasslands underwent a substantial decrease in area and connectivity in Europe (Critchley et al., 2004), mainly as a result of land marginalization and abandonment of the less productive or less accessible agricultural land in mountain regions (Hinojosa et al*.,*2016) and Eastern Europe (Henle et al., 2008). Soviet collectivization in Eastern Europe also accelerated the disappearance of semi-natural grasslands (Talvi and Talvi, 2012). Agricultural intensification in Western

Europe had the same effect (Bullock et al*.,* 2011). As well as abandonment, under-grazing has also been recognized as a threat to biodiversity in these habitats (Bagella et al., 2014). A decrease in the provision of certain ES such as pollination, cultural services associated to traditional farming practices and the aesthetic value of these grasslands and habitat for bird species occurs as a consequence of these processes. The effects of grassland abandonment in soil ES have been tested in different Bioclimatic regions. In some Mediterranean environments abandonment leads to a reduction in soil organic matter (SOM), total nitrogen and aggregate stability (Peco et al., 2017), whereas in parts of Central and Eastern Europe certain ES such as carbon sequestration, regulation of hydrological cycles in mountain areas, erosion control and habitat for large mammals may show an increase after abandonment (Navarro and Pereira, 2015). On the other hand, carbon storage in grasslands is sensitive to processes of intensification and conversion to arable land. Increased stocking density in semi-natural grasslands reduces soil carbon sequestration through less organic carbon being returned, and greater amounts of carbon being released as CO2 and CH4 and N being leached. (Soussana and Lemaire, 2014). Furthermore, the conversion of grassland into arable land leads to a decrease in soil carbon due to reduced carbon input from litter and carbon losses caused by tillage (Jones and Donnelly, 2004).

The most recent Common Agricultural Policy (CAP) reform (2014 – 2020) aims at improving the status of farmland biodiversity by introducing “greening” components in both Pillars I and II. However, it has been criticized for not being efficient in halting the decline of permanent grassland and lacking management criteria that includes habitat quality (Pe’er et al., 2014). Plieninger et al. (2012) argue that the ES framework could help design more flexible, targeted and context specific agri-environmental schemes, while at the same time assessing the environmental impact of the current CAP in a more holistic way.

In recent years there has been a major increase in scientific publications utilising a wide range of methodologies to estimate the provision of ES (Maes et al., 2012; Potschin and Haines-Young, 2016; Rabe et al., 2016), including the identification and mapping of hotspots (Schröter and Remme, 2015). Mapping ES hotspots involves a level of choice in the definition of thresholds, and this in turn influences the final patterns to a certain degree. Some studies set random cut-off points as top percentages of the overall dataset (Anderson et al., 2009). Others use data clustering algorithms that automatically generate thresholds based on the dataset structure (Liquete et al., 2015). Ideally, primary data on ES collected through field samples provides the highest level of precision. However, this approach entails significant costs when dealing with national projects. Thus, data availability has been identified as one of the major challenges to the development of ES mapping and assessment frameworks (Eigenbrod et al.,2010; Palomo et al., 2018). Surrogate models based on causal relationships have been suggested as a feasible alternative (Martínez -Harms and Balvanera, 2012; Zhang et al.,2017) when the lack of primary data is an obstacle.

Plant diversity and Soil Organic Carbon (SOC) pools have been identified as two key factors that underpin, or are directly linked, to the provision of several ES (Marks et al., 2008; Isbell et al., 2011; Lal, 2014). Previous studies address the link between biodiversity and ES in order to strengthen the arguments for ecological restoration and contribute to the management of protected areas (Haines-Young and Potschin, 2010; Harrison et al., 2014; Isbell et al., 2011; Nelson et al., 2009). Using plant species diversity and SOC as surrogate indicators for other ES helps overcome the challenge of primary data scarcity at nation-wide scales. Moreover, the spatial overlap of biodiversity and ES has been addressed by authors from different science, policy-making and management strategies perspectives (Anderson et al., 2009; Morelli et al., 2017; Quijas and Balvanera, 2013; Ren et al., 2016).

Within this study, the multi-functionality of semi-natural grasslands representing a range of common grassland habitats in Estonia is highlighted, and an ES assessment is undertaken considering particularly soil and biodiversity-related ES. In this regard, the study contributes to the implementation of nationwide scale ES assessments in Estonia. Although some isolated projects have been carried out evaluating ES in different habitats (Kimmel, 2010), only few have addressed the full extent of Estonia (Villoslada et al., 2018). At first, underlying environmental gradients (i.e. climatic factors, altitude and SOC) that underpin ecosystem functions and services are identified, and then related to plant species distribution patterns. Furthermore, the effects of management cessation in four semi-natural grassland types are assessed. Previous studies have focused on the relationship between biodiversity and management exclusively at regional (Burnside et al., 2007), and local (Liira et al., 2009) scales. Conversion to arable land was not considered since 72% of the semi-natural grasslands under study are within Natura 2000 areas and this trajectory of change is highly unlikely. Ultimately, hotspots for ES surrogate indicators SOC and plant species diversity in semi-natural grasslands are identified and mapped using plant diversity and SOC as surrogate indicators. The national scale of the present study posed a challenge in terms of data collection and as a result, existing databases were used for ES mapping and assessment.

Although this paper focuses on Estonia, very similar grassland abandonment trends have been observed throughout Europe (Cousins et al. 2007; Krauss et al., 2010; Pykälä et al., 2005; Strijker, 2005) and worldwide (Sala et al. 2000; Hoekstra et al. 2005). Halting biodiversity loss, land degradation and the resulting impacts on ES is increasingly becoming a challenge at local and global scales (Kremen and Merenlender, 2018). The methodology outlined in this paper contributes to a better understanding of these issues in Estonia and potentially other regions facing similar challenges.

2. MATERIALS AND METHODS

2.1. Study area

Estonia is located in the Baltic region between Latvia, Russia and Finland, in the border between the Boreal and Nemoral zones (Metzger et al., 2005). Despite its relatively small size (45228 km^2) Estonia exhibits a high geological, morphological, and climatic diversity (Arold, 2005).

Within Estonia, there are ten semi-natural grassland habitats, based on the Annex I Habitats Directive classification (Council Directive, 1992). Semi-natural grasslands in Estonia have exceptionally high levels of biodiversity, in particular wooded meadows (76 species/m^2; Kukk 2004, 1997), alvars (63 species/m^2; Partel et al*.,* 1999), floodplain meadows (50 species/m^2; Truus and Puusild, 2009), and coastal meadows (34 species/m^2; Burnside et al*.,* 2007), among the most species rich habitats in Northern Europe (Benstead et al., 1999).

Semi-natural grasslands are the result of long term, low-intensity management practices, in the form of grazing and mowing (Paal, 1998). In Estonia, some of these semi-natural habitats have been managed for centuries (Helm et al., 2005), leading to iconic landscapes such as the Laelatu wooded meadow (Sammul et al., 2003). The area of semi-natural grasslands in Estonia has decreased since the late 1950s (Kana et al., 2008). Between 1957 and 1960, 90 % of coastal meadows were grazed or mown, whereas between 1992 and 1995 only 35 % of coastal meadows remained in use (Kaisel et al*.,* 2004). Wooded meadows have also experienced a drastic decrease in area, from ca.

700000 ha in the 1940s to ca. 8000 nowadays (Sammul et al., 2008). A large proportion of the semi-natural grassland area has reverted to reed beds, scrubland and forest, through natural succession processes. Semi-natural grasslands in other parts of Europe have undergone similar changes. For instance, Cousins et al. (2007) describe a drastic decrease in the area of semi-natural grassland in south-eastern Sweden during the past 100 years due to the creation of larger fields, drainage of wetlands and the planting of commercial forestry amongst other drivers. Similarly, the area of mesic semi-natural grasslands decreased strongly in south-west Finland after abandonment of grazing in the 1960s (Pykälä et al., 2005). Beyond northern Europe and Scandinavia, comparable trajectories of change can be observed throughout Europe due to intensification on one hand and abandonment on the other (Strijker, 2005).

2.2 Conceptual framework

The ES cascade model (Potschin and Haines-Young, 2016) was partially adapted and utilized as the theoretical framework for the analysis. Addressing the different components of the *environment* section in the cascade model (Fig. 1) offers a comprehensive understanding of the complex linkages between environmental factors, ecosystem functions, anthropogenic pressures and final ES (see Fig. 1). In the present study, the analysis of the socio-economic domain of the cascade framework has not been specifically addressed in order to set the focus exclusively on the interconnections among structures, functions and services. Following a stepwise approach, the initial stage of the analysis involved identifying underlying environmental gradients (i.e. climatic factors, altitude and SOC) that underpin ecosystem functions and services, and then relating them to the species distribution patterns. Subsequently, the relationship between management status and species diversity, as well as presence of rare and protected species were also assessed. In the third and last step, five ES were mapped and assessed. Plant species diversity and SOC were tested as surrogate indicators for three regulation and maintenance, one provisioning and one cultural ES (ES categories according to the CICES V5.1 classification by Haines-Young and Potschin, 2018): Pollination, nutrient cycling, nutrient retention, biomass production and herbs for traditional medicinal use. The choice of ES related to plant species diversity and SOC was driven by the availability of databases and publications at the national scale. The categorization and naming of ES is compatible with CICES V5.1 (Table 1). In order to assess semi-natural grasslands multifunctionality and the coincidence and spatial patterns multiple ES supply, the spatial distribution of ES hotspots was mapped. Although the limited number of ES selected does not allow for a complete assessment of semi-natural grasslands, this approach constitutes the starting point for further analyses. The absence of grassland and management-related ES such as reared animals, forage quality or regulation of the chemical condition of fresh waters in the analysis calls for the collection of more detailed data.

Table 1. Overview of the selected ES and their correspondence to CICES V5.1 classification system

ES	Section (CICES V5.1)	Equivalent class (CICES V5.1)	Indicator	Surrogate indicator	Data sources
Pollination	Regulation & Maintenance	Pollination	Pollinators richness and abundance	Plant species diversity	Diaz Forero (2011). State Monitoring Program of Wildlife Diversity and Landscapes (Estonian
Nutrient cycling	Regulation & Maintenance	Weathering processes and their effect on soil quality	Microbial activity	SOC	State Monitoring Program of Wildlife Diversity and Landscapes (Estonian
Nutrient retention	Regulation & Maintenance	Regulation of the chemical condition of freshwaters by living processes	Total Nitrogen	SOC	State Monitoring Program of Wildlife Diversity and Landscapes (Estonian

Biomass production	Provisioning	Wild plants used for nutrition	Total biomass production (dry weight)	SOC	Heinsoo et al. (2010), Kull and Zobel (1991), Kupper (2007), Melts (2014), Neuenkamp et al. (2013), Rehme (2013), Saar (1996), Sammul et al. (2006), Sammul et al. (2011), Truus and Puusild
Herbs for traditional medicinal use	Cultural	Characteristics of living systems that enable activities promoting health, recuperation or	Wild medicinal and food plants	Plant species diversity	Kalle (2017)

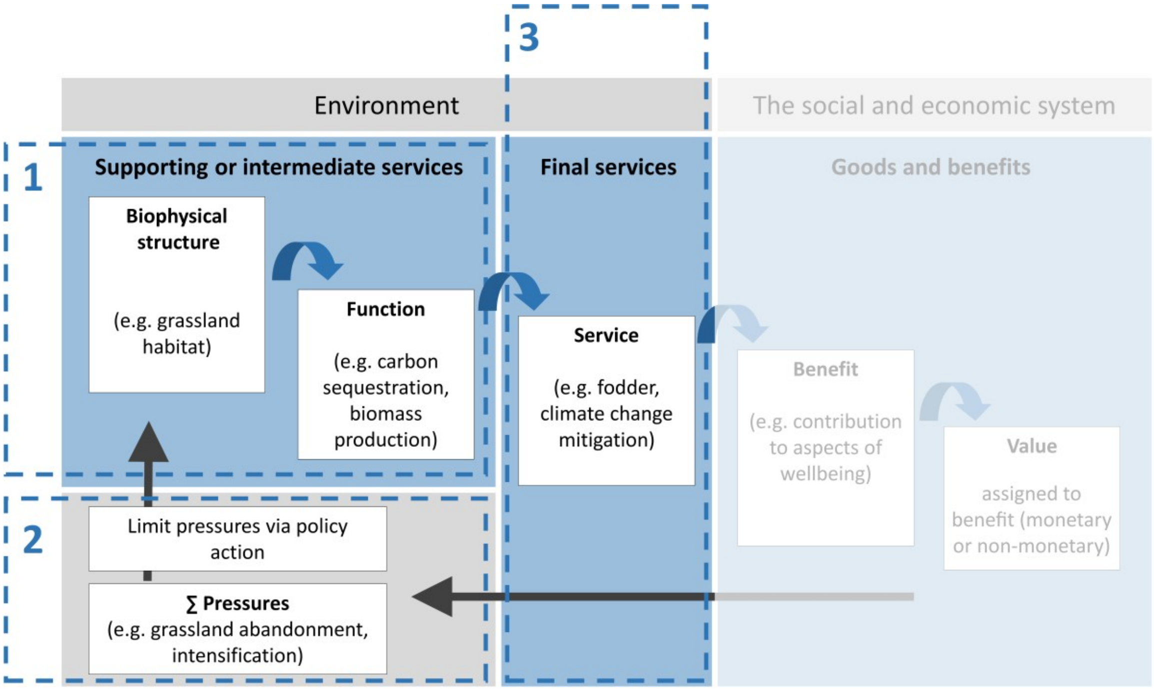


Fig. 1. The ES cascade model adapted from Potschin and Haines-Young (2016). Three cascade components were assessed within this study: (1) underlying environmental gradients determining species distribution in semi-natural grasslands, (2) effects of grassland abandonment and (3) the spatial distribution of ES hotspots in semi-natural grasslands. Although the cascade framework encompasses both the environmental and the socio-economic systems, only the environmental system was addressed in this study.

2.3. A semi-natural grasslands database

Data concerning the location and area of semi-natural grasslands in Estonia was collected from three databases: the *Semi-Natural Habitats (SNH) on agricultural land (*Estonian Environmental Board), the *Estonian Semi-Natural Community Conservation Association (ESCCA)* and the *Estonian Fund for Nature* (EFN). The SNH comprises the location and extent of semi-natural grassland sites eligible for agri-environmental payments within the Pillar II subsidies system of the CAP, and represents all grassland types whereas the ESCAA contains records of the plant species composition of the sites included in the database (EFN & RDSFNC, 2001). Additionally, the EFN includes some of the Annex I semi-natural grassland habitat types (Paal and Leibak, 2011). In order to obtain the most precise estimate of the extent of semi-natural grassland habitats, it was necessary to merge the semi-natural grassland information contained in these databases into a single, unified geodatabase. The three databases use the Habitats Directive Annex I classification system to categorise the semi-natural grassland types used within this study.

In order to assess the predominant habitat types in Estonia the extent of each semi-natural grassland habitat was calculated (Table 2). The extents utilised in this study are broadly similar to previous estimates from other database sources (Kukk and Sammul, 2006). The unified database created within this project provides the most appropriate basis for ES mapping and assessment, as georeferenced data are needed to account for the complex spatial dimension of ES.

Table 2. Annex I habitats in Estonia and their extent based on the unified database. Shaded grassland habitats were selected for inclusion in this study.

Annex I habitat code	Grassland type	Unified database (% of total extent)
6450	Northern boreal alluvial meadows	27866 ha (25%)
1630	Boreal Baltic coastal meadows	22996 ha (21%)
6280	Nordic Alvars and precambrian calcareous flatrocks	16696 ha (15%)
6530/9070	Fennoscandian wooded meadows/pastures	11454 ha (10%)
6210	Semi-natural dry grasslands and scrubland facies on calcareous soils	9913 ha (9%)
6270	Fennoscandian lowland species-rich dry to mesic grasslands	7682 ha (7%)
6510	Lowland hay meadows	7584 ha (7%)
6430	Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	3790 ha (4%)
6410	*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils	1611 ha (2%)

TOTAL	109592 ha

Habitat types included in this study as the basis for the mapping and assessment of ES supplied by semi-natural grasslands were selected by extent and comprised all habitat types with an extent of at least 10% of the total semi-natural grassland area in Estonia (Table 2): Northern boreal alluvial meadows (6450, hereafter referred to as floodplain meadows), Boreal Baltic coastal meadows (1630, hereafter referred to as coastal meadows), Nordic alvars and Precambrian calcareous flatrocks (6280, referred to as alvars) and Fennoscandian wooded meadows and pastures (6530 and 9070 respectively, referred below as wooded meadows) represent the dominant semi-natural grassland types by area in Estonia (EFN and RDSFNC, 2001). Habitat types 6530 and 9070 are differentiated by management type and the species content and layer structure in wooded meadows and pastures are very similar (Paal, 2002). These grassland types were therefore combined for the purposes of this study. Fig. 2 shows the distribution of the selected semi-natural grassland habitats in Estonia regionalized by the Environmental Stratification of Estonia as described by Villoslada et al. (2016).

In order to assess the contribution of environmental factors to species distribution patterns, eight variables were selected as being representative of the overall environmental variability in Estonia. The extraction of environmental variables was carried out within the framework of the Environmental Stratification of Estonia (ESE) (Villoslada et al., 2016). The ESE is a statistical division of the environmental gradients in Estonia into homogeneous units, based on climatic and geomorphologic variables. The resulting strata help in the interpretation of climatic and environmental patterns and therefore, a better understanding of underlying ecological processes (Jongman et al., 2006). The ESE is constructed based on a Principal Components Analysis (PCA) that was used to generate a subset from a climate data set composed of 16 climate parameters interpolated from 31 Estonian (data obtained from the Estonian Meteorological and Hydrological Institute), Latvian, Russian and Finnish weather stations covering a period of 30 years (Haylock et al., 2008).

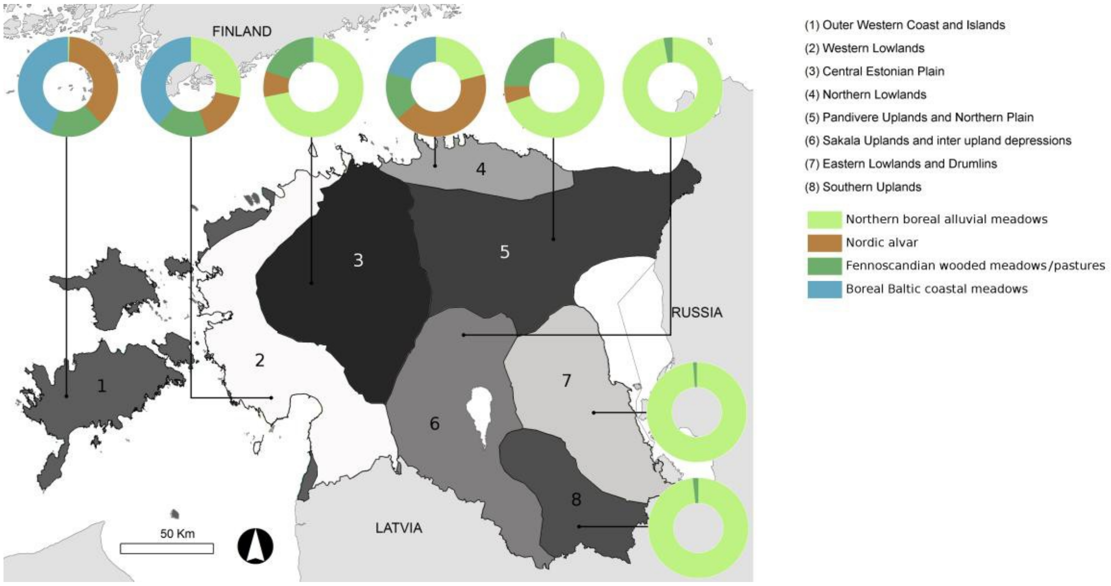


Fig. 2. Distribution of the principal semi-natural grassland types in Estonia by the regions of the Environmental Stratification of Estonia as developed by Villoslada et al. (2016).

2.4. Environmental factors and species distribution

A Canonical Correspondence Analysis (CCA) was used to analyse the relationship between species, grassland habitats and the associated environmental variables identified in the ESE. CCA has been widely used in similar studies (Krause and Culmsee, 2013**;** Mota et al., 2018; Ward et al., 2016a). The CCA incorporated the presence/absence of 876 vascular plant species combined with the eight environmental variables (mean precipitation in July, mean precipitation in January, mean precipitation in October, mean sunshine in July, minimum temperature in January, minimum temperature in April, maximum temperature in October, and elevation) derived from Villoslada et al. (2016), plus

SOC, grouped by grassland type, for all 2312 sites selected for the analysis. The climate parameters selected in the ESE capture the majority of environmental variation in Estonia. SOC was included in the CCA because of its pivotal role on soil-related ES (Lal, 2011; Lal, 2014) and its high variability between different semi-natural grassland types. SOC data were derived from Kõlli et al. (2007). CCA axis scores were analysed for correlations using Pearson's test for correlation at the 0.05 level and the statistical analysis was performed in CANOCO 5 (Ter Braak and Šmilauer, 2012).

2.5. Assessment of the effect of grassland abandonment on species diversity

In order to provide a full overview on the effects of grassland abandonment on plant species diversity, it was necessary to combine two spatial datasets since none of the datasets used in this study provides all the necessary information individually. The SNH database, containing information on grassland management and management years was combined with the ESCCA database, containing information on plants species composition and sampling year. Both databases were created based on the Estonian Base Map (1:10000) and orthophotos and both cover the whole extent of Estonia. In order to evaluate the effect of management cessation, plant species diversity within each habitat type was compared between abandoned grasslands and those being grazed or mowed in 830 grassland plots across Estonia (the number of plots per grassland type is described in Table 4) using Student's t-tests at the 0.05 level. To achieve this, join queries between both databases were built based on spatial overlaps, sampling year in the ESCCA and last year of claimed agri-environmental payment in the SNH. The criteria for abandonment was grasslands for which payments have never been claimed in the SNH and grasslands indicated as managed 10 or more years ago in the ESCCA. Additionally, the effect of abandonment on rare and protected meadow plants within each habitat type was also analysed using a Chi-Square test at the 0.05 level, i.e. the proportion of grassland plots in which rare and protected species occur was compared between managed and abandoned grasslands within each habitat type. Rare and protected species were identified using the EU Habitats Directive (Annex II) (Council Directive, 1992), protected species under Estonian Nature Conservation Act and the Red Data Book of Estonia (Eesti Punane Raamat, 2008). Information on the year of management initiation and duration was extracted from the SNH database and combined at the site level with the number of species, derived from the ESCCA database in order to perform the statistical analyses. For the purposes of these analyses, semi-natural grasslands for which agri-environmental payments have not been claimed since 2007 were considered abandoned.

2.6. Plant species diversity and soil organic carbon as surrogate indicators for other ecosystem services

The relationship between plants species diversity and two ES (pollination and herbs for traditional medicinal use) were tested using Pearson product-moment correlations at the 0.05 level. Plant resources for food and medical uses is still an important cultural asset in Estonia (Kalle, 2017). Although it is often regarded as a provisioning service, it is addressed in this study as a cultural ES. Data on pollinators was compiled from Diaz Forero (2011) and the State Monitoring Program of Wildlife Diversity and Landscapes, subprogram on Pollinators Monitoring (Estonian Environment Agency).

In Estonia, SOC and SOM pools in semi-natural grassland soils have been determined by sampling soil profile horizons in 82 grassland experimental areas (Kõlli et al., 2007). The data were compiled between 1967 and 1985 and subsequently updated in 1985-1995 and 1999-2002. The Tjurin method (Vorobyova, 1998) was used to determine the carbon concentration in each soil horizon. The carbon content used in the present study was estimated for the whole soil (the depth reaches the parent material) and has been found to be comparable with data from other sources (Ward et al., 2014, Ivask et al., 2012). The depth of the analysis varied considerably depending on the soil type, from 16 cm in skeletic leptosols to 77 cm in haplic, endogleyic and glossic albeluvisols (Kõlli et al., 2007). The soil classes contained in the Soil Map of Estonia (1:10.000) were updated with the SOC data obtained from Kõlli et al. (2007). Subsequently, SOC was tested as a surrogate for three additional ES (nutrient cycling, nutrient retention and biomass production) using Pearson product-moment correlations ($p < 0.05$) between SOC and three ES indicators (microbial activity, total N and aboveground biomass production respectively). The choice of ES and functions that can be related to SOC in the present study is constrained by the availability of data. Data on biomass production in semi-natural grasslands were collected from several previous studies (Heinsoo et al., 2010; Kull and Zobel, 1991; Kupper, 2007; Melts, 2014; Neuenkamp et al., 2013; Rehme, 2013; Saar, 1996; Sammul et al., 2006; Sammul et al., 2011; Truus and Puusild, 2009) and combined with the SOC geodatabase. In order to avoid interferences of the management regime in the results, only actively managed meadows were selected for this analysis. Data on total nitrogen (TN) and soil microbial activity was obtained from the State Monitoring Program of Wildlife Diversity and Landscapes (Estonian Environment Agency).

2.7. Mapping ES hotspots

SOC and plant species diversity were classified into coldspots, range and hotspots and mapped. Following the definitions by Egoh et al. (2009), “range’’ are understood as areas where a particular service is produced in meaningful quantities and ‘hotspots as areas which provide large components of a particular service. Subsequently, multiple ES hotspots were mapped in order to assess their spatial distribution in relation to semi-natural grassland habitats and these were assessed in terms of eligibility for agri-environmental schemes by overlaying the resulting hotspots with the SNH database. In the framework of this study, multiple ES hotspots are understood as areas where surrogate indicators hotspots (species diversity and SOC) overlap (Gos and Lavorel, 2012).

Plant species diversity and SOC were reclassified into three ranks from minimum to maximum using a Jenks Natural Breaks algorithm. This algorithm was specifically developed for segmenting geographic datasets into discrete categories by minimizing variation within classes and maximizing variation between classes (Slocum, 1999). In order to account for environmental heterogeneity, the ranking of values of species diversity and SOC were regionalized, using the minimum and maximum values within each of the strata in the Environmental Stratification of Estonia (Villoslada et al., 2016). This procedure avoids regional minimum-maximum ranges being masked by the overall environmental variability of Estonia. The reclassified plant species diversity and SOC maps were combined in order to find grasslands where the hotspots overlap for the extent of the ESCCA database. All the spatial analysis were performed in Esri's ArcGIS ® 10.3 (http://www.esri.com/software/arcgis).

3. RESULTS

3.1. Distribution of species along environmental gradients

The CCA highlighted associations between species, grassland type and the nine environmental variables (mean precipitation in July, mean precipitation in January, mean precipitation in October, mean sunshine in July, minimum temperature in January, minimum temperature in April, maximum temperature in October, elevation and SOC) (Fig. 3). Axis 1 accounted for 47.37%, and axis 2 17.41% of the variation in the data. Table 3 provides the correlations between the canonical axes and the environmental variables in order to better interpret the ordination plot (Fig. 3). Axis 1 was significantly correlated with *average precipitation in July*, *average sunshine in July*, *minimum temperature in January*, *minimum temperature in April*, *maximum temperature in October*, *elevation* and *SOC* whereas axis 2 was significantly correlated with *average precipitation January* and *average precipitation October*. Each grassland type is separated from the others in the CCA, although overlaps occur (Fig. 3). Four clusters of species are present, each corresponding to the habitats under study. Species associated with shallow soils (e.g. alvars and coastal meadows) are clustered in two groups, whereas species from deeper soils and/or higher elevations (i.e. alluvial meadows and wooded meadows/ pastures) are similarly clustered in two groups. The CCA also highlights associations between the climate variables and the species distribution.

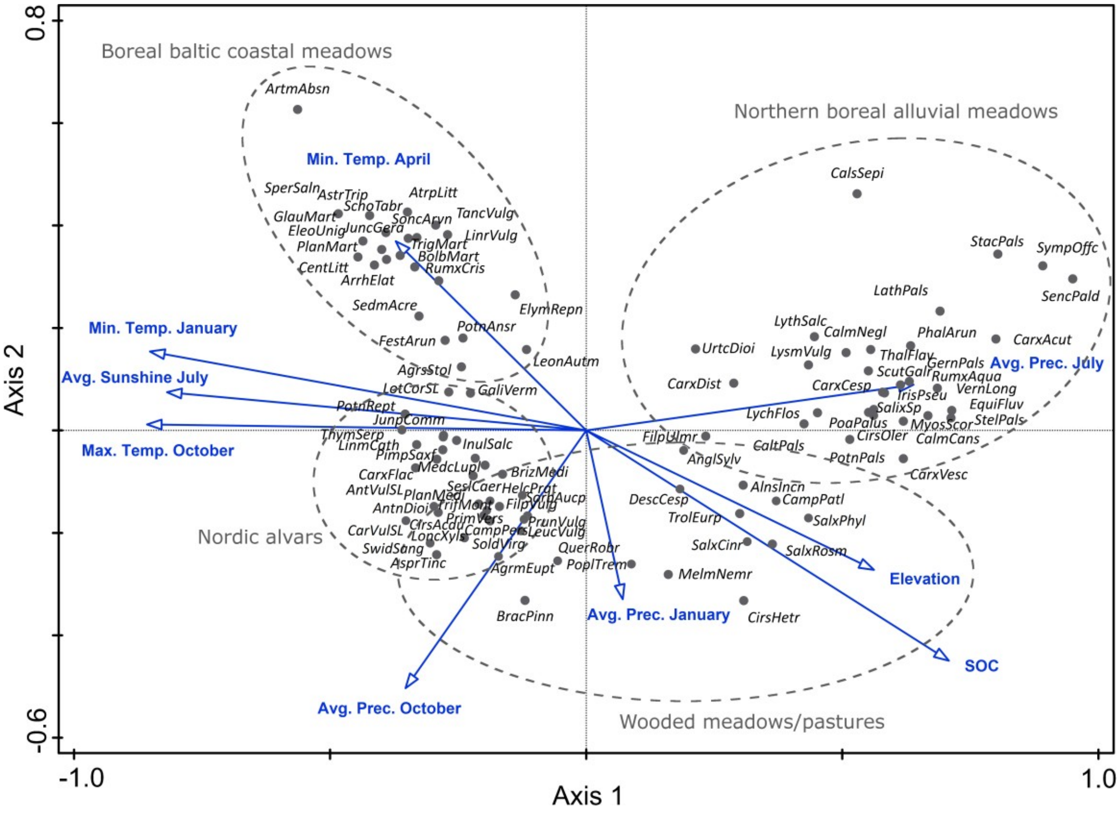


Fig. 3. Canonical correspondence analysis ordination plot showing grassland type, 90 most common species, and environmental vectors. The dashed lines represent the grassland types under study and group the most common species in each grassland type.

Table 3. Pearson correlation coefficients for all environmental variables, axis eigenvalues, cumulative percentage of axis explanation, and pseudo canonical correlation of the axes for the canonical correspondence analysis in Fig. 3

Variables	Axis 1	Axis 2
SOC	0.6062***	-0.2771***
Average precipitation July	0.5472***	0.055***
Elevation	0.481***	-0.1678***
Maximum temperature October	-0.7343***	0.0073
Minimum temperature April	-0.3184***	0.2277***
Minimum temperature January	-0.7293***	0.0951
Average precipitation January	0.061	-0.2033***
Average precipitation October	-0.3021***	-0.3103***
Sunshine July	-0.7008***	0.0461
Pseudo canonical correlation	0.8561	0.6166
Eigenvalues	0.3196	0.1174
Cumulative percentage	47.37	64.78

*** = $p < 0.001$

3.2. Effect of abandonment on species diversity, and rare and protected species

The Student's T-tests reveal significantly lower species diversity following abandonment in three of the four grassland types under study (Table 4). Only Nordic alvars did not show a significant change in the number of species ($p = 0.083$).

Table 4: Student's t-test results for the differences between the average number of plant species in managed grasslands and abandoned grasslands for all habitats, where N is the number of abandoned and managed sample grasslands. Significance level was set at p < 0.05.

Grassland type	N	*p*-value	Mean number of species Abandoned	Managed
Boreal Baltic Coastal Meadows	28/33	0.023	29.64	46.24
Nordic alvar and precambrian calcareous flatrock	92/92	0.083	43.67	48.66
Northern boreal alluvial meadows	136/136	0.000	27.5	38.7
Fennoscandian wooded meadows/pastures	150/163	0.000	31	45

The occurrence of rare and protected species was significantly lower (p=0.02) after abandonment in northern boreal alluvial meadows (Fig. 4), whereas in alvars, coastal meadows and wooded meadows and pastures there is no significant difference in the occurrence of rare and protected species between abandoned and managed sites (p=0.28, p=0.39 and p=0.24 respectively).

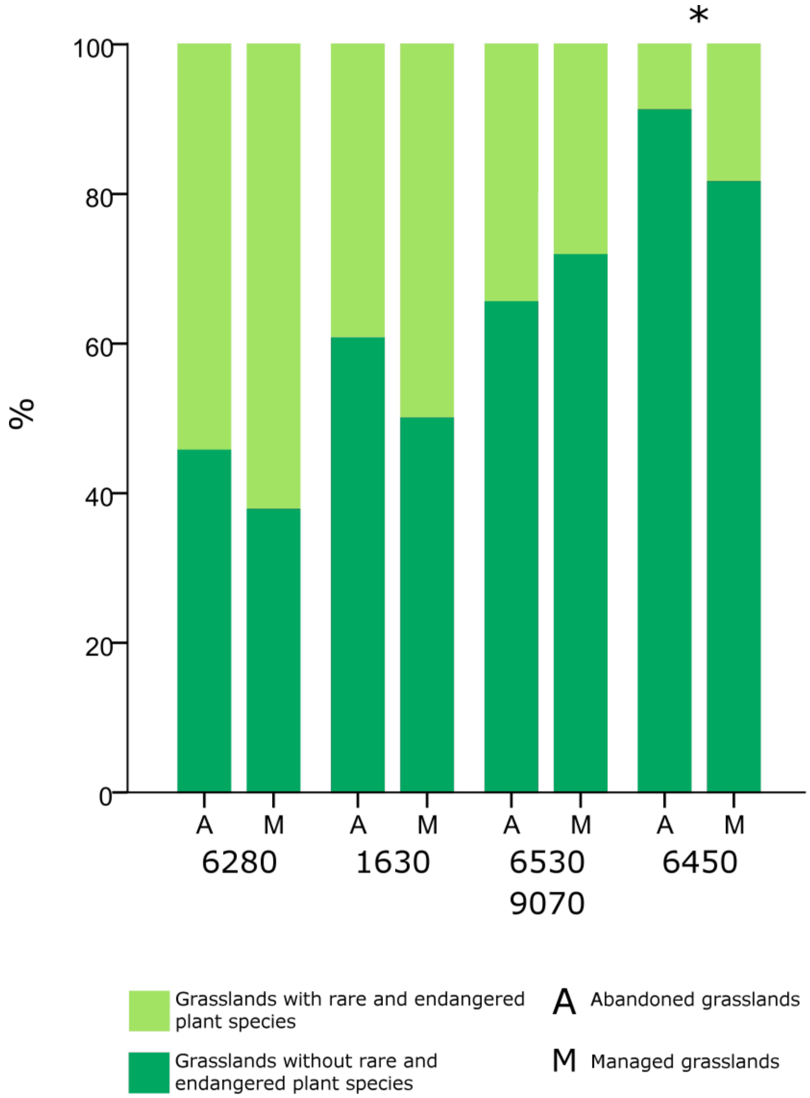


Fig. 4. Percentage of grasslands with and without rare and protected vascular plant species in abandoned and managed grasslands in all habitats, including 6530/9070: Fennoscandian wooded meadows/pastures, 6280: Nordic Alvars and precambrian calcareous flatrocks, 1630: Boreal Baltic coastal meadows, 6450: Northern boreal alluvial meadows. * = $p < 0.05$

3.3. Correlation between plant species diversity, SOC and ecosystem services

Significant positive correlations were found between plant species richness and pollinator species richness and abundance and herbs for medicinal use (Table 5). Different pollinator groups show different correlations, wasps, bees and hoverflies richness are most strongly correlated with flowering plant species richness. SOC shows moderate to strong correlations with aboveground biomass, TN and microbial activity (Table 6).

Table 5. Pearson's correlation coefficients between flowering plant species richness and different groups of pollinators richness and abundance and herbs for traditional medicine. Significance level was set at $p < 0.05$.

Variables	**r**	***p*-value**
Plant species richness & Wasps, bees & hoverflies richness	0.712	0.000
Plant species richness & Wasps, bees & hoverflies abundance	0.559	0.007
Plant species richness & Bumblebees richness	0.620	0.002
Plant species richness & Bumblebees abundance	0.644	0.001
Plant species richness & herbs for medicine	0.87	0.000

Table 6. Pearson's correlations between SOC and different ES indicators. Significance level was set at $p < 0.05$.

Variables	**r**	***p*-value**
Soil organic carbon & Biomass production	0.45	0.01
Soil organic carbon & Nitrogen(%)	0.99	0.000
Soil organic carbon & Microbial activity	0.96	0.000

3.4 ES hotspots map

The results from the SOC and plants species diversity hotspots are presented in Fig. 5. A high share of alvars area falls within range and hotspot values for plant species diversity (47% and 40% respectively), whereas alluvial meadows show the highest share of plant species diversity coldspots. Conversely, alluvial meadows and wooded meadows and pastures account for most of the SOC hotspots (43.1% and 43.6%) and show very similar values for range and coldspots. Most of the coastal meadows area belongs to SOC coldspots and range (78.2 and 21.1% respectively).

Fig. 6 shows the coldspot, range and hotspots maps of SOC and vascular plant species diversity maps used to obtain multiple ES hotspots maps.

Soil organic carbon and species diversity were tested for correlations in order to detect possible synergies or trade-offs between these ES; however, no significant correlations were found (r = -0.062, p = 0.033).

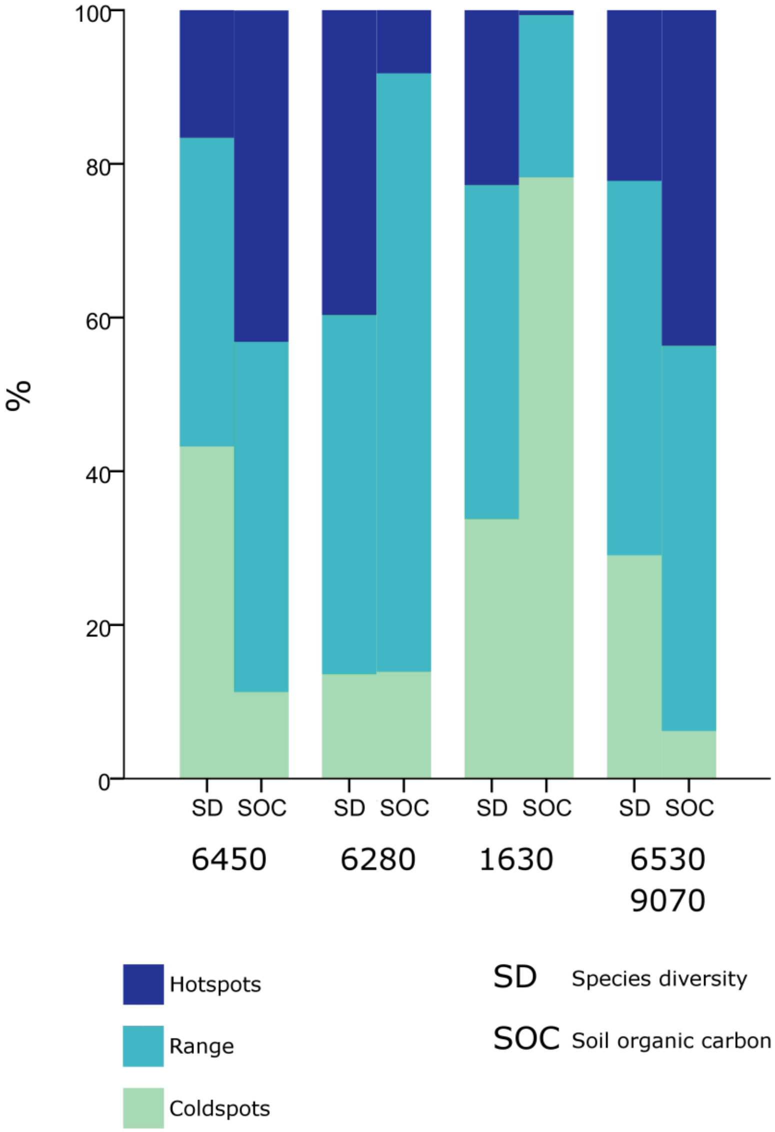


Fig. 5 Percentage of SOC and plant species diversity coldspots, ranges and hotspots within each grassland type analyzed in the study. 6530/9070: Fennoscandian wooded meadows/pastures, 6280: Nordic Alvars and precambrian calcareous flatrocks, 1630: Boreal Baltic coastal meadows, 6450: Northern boreal alluvial meadows.

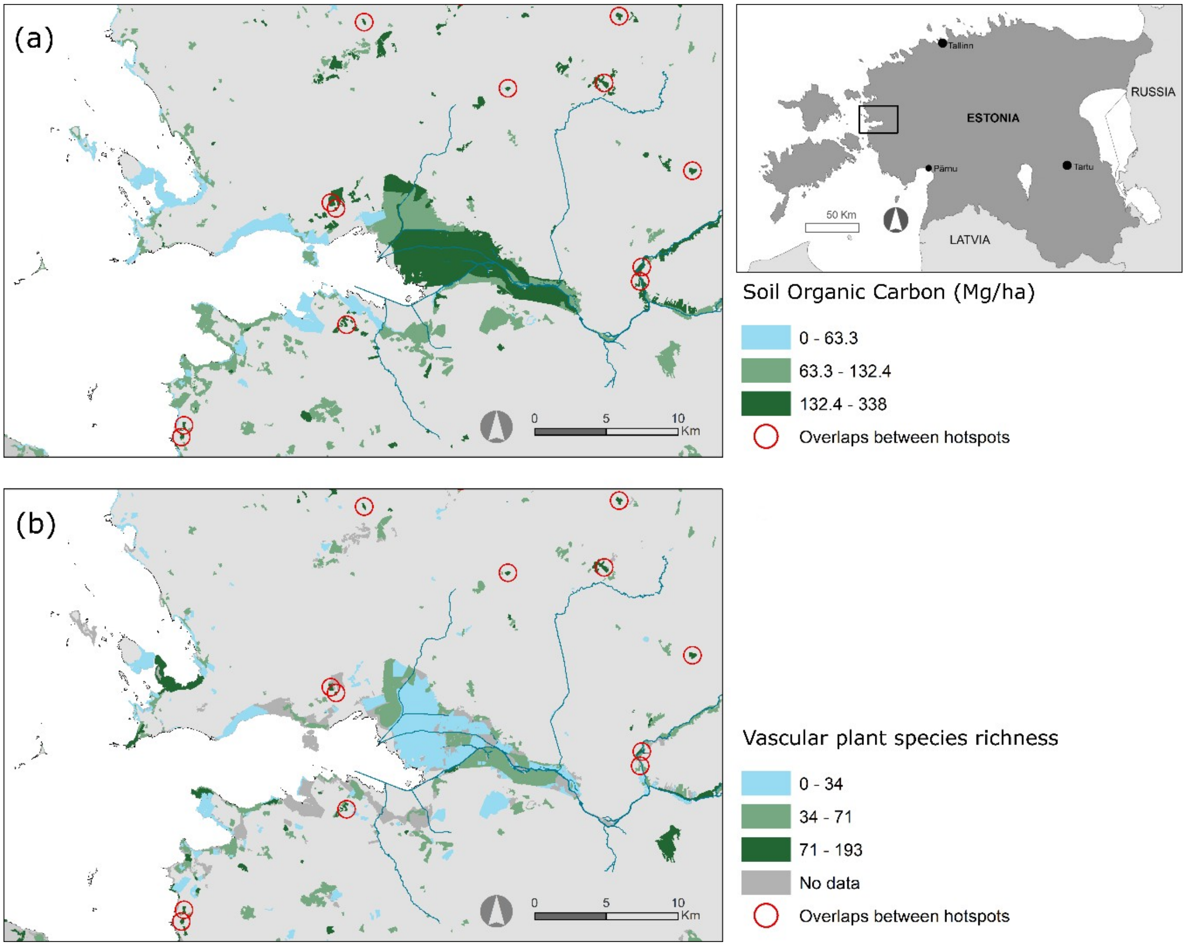


Fig. 6. A close-up view of Matsalu bay in Western Estonia. The reclassified SOC (a) and vascular plant species diversity (b) maps are overlapped in order to map ES hotspots. The spatial coincidence of SOC and species diversity maximum reclassified values constitutes multiple ES hotspots.

Fig. 7 shows the spatial distribution and habitat type of multiple ES hotspots in semi-natural grasslands in Estonia. Although wooded meadows and pastures have the highest proportion of ES hotspots (816 ha), this habitat only accounts for 10% of the semi-natural grassland cover (Table 1). ES hotspots belonging to alluvial meadows are spread throughout mainland Estonia, and have the second highest proportion of ES hotspots after wooded meadows/pastures.

The area of ES hotspots in semi-natural grasslands eligible for agri-environmental support is only 50% in the case of alvars and less than 50% in the case of northern boreal alluvial meadows (Table 7). Some of the hotspots that are not eligible for agri-environmental support may have already been converted to arable land or overgrown by shrubs, due to the time frame in which plant species diversity data was recorded. There are several reasons why a fraction of the hotspots identified in the present study are not eligible for agri-environmental support. In the case of wooded meadows and pastures, the eligibility criteria for CAP support for permanent pastures in Estonia excludes many wooded meadows due to limitations in the number of trees per hectare. Moreover, any semi-natural grassland that is located out of a Natura 2000 site is not eligible for agri-environmental support, even if it is actively managed.

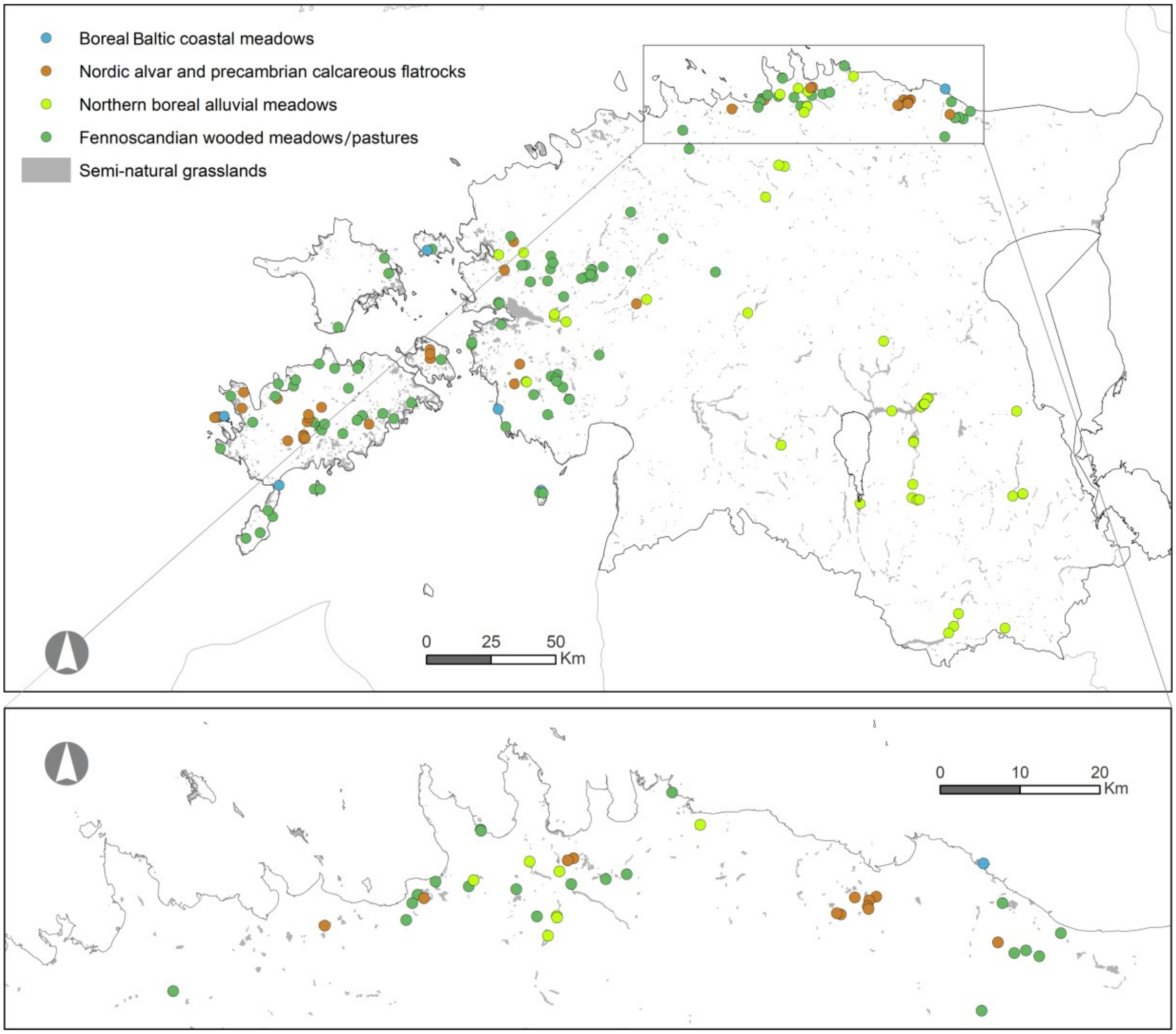


Fig. 7. Distribution of ES services hotspots in semi-natural grassland habitats in Estonia. The zoomed area shows the northern cluster of multiple ES hotspots, including Lahemaa National Park.

Table 7. Total area of multiple ES hotspots per grassland type and area of hotspots not eligible for agri-environmental support.

Habitat	**Total hotspot area (ha)**	**Area without agri-evironmental support (ha)**	**Area without support (% of total hotspot area)**
Boreal Baltic coastal meadows	101	26	25%
Nordic Alvars	398	198	50%
Northern boreal alluvial meadows	594	316	53%
Wooded meadows and pastures	816	317	39%
Total	1909	857	45%

4. DISCUSSION

Despite the wide selection of ES mapping methods currently available, several authors (Eigenbrod et al., 2010; Palomo et al., 2018) have identified the lack of data as one of the main obstacles in the process. Thus, the use of proxy data or surrogates becomes relevant in national scale ES assessments, especially for *regulating and maintenance* services (Maes et al., 2012). The collection of primary data on ES provision at national and regional scales may become a challenging and costly process that could hinder the success of the ES mapping and assessment process. In order to overcome the lack of primary data on ES, two variables were tested in this study as surrogate indicators for a wider selection of ES provided by semi-natural grasslands, following a three-step process.

Concerning the adopted methodological framework, the cascade model (Potschin and Haines-Young, 2016) connects ecosystems to human wellbeing in a structured way and illustrates the flow of ES. Although the analysis in this study is restricted to the *environment* component of the cascade, it is necessary to further incorporate benefits and socio-cultural values and perceptions in order to fully understand the ways society benefits from nature. In this regard some studies have addressed landowners' values and perceptions in order to elicit ES trade-offs (Torralba et al., 2018), motivations for semi-natural habitat management (Birge and Herzon, 2014) or perceived provision of grassland ES by stakeholders (Lamarque et al., 2011).

Environmental variables and species distribution

The CCA highlighted the soil fertility requirements of different species along the SOC gradient. Relatively young and shallow soils in coastal areas are generally more mineral rich and have less organic matter (Ward et al., 2016a). Within the coastal meadows cluster, a gradient occurs between very shallow soils, inundation-tolerant species

(*Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani*) and those characteristic of higher elevation above mean sea level and higher nutrient content soils (*Elytrigia repens, Potentilla anserina*). Very thin soils typical of alvar grasslands also show very low content of SOC (32 Mg/ha) (Kõlli et al., 2007). An overlap can be observed between alvars and wooded meadows due to the fact that many wooded meadows in Western Estonia are located on calcareous and relatively thin soils similar to alvar habitats. Conversely, riverside soils with a peat epipedon are characterized by very high SOC content. Within the alluvial meadows cluster, SOC defines a gradient between sedge meadow species in old riverbeds (i.e. *Carex acuta*) and tall forb meadows at higher elevations of the floodplain (i.e. *Filipendula ulmaria*) (Neuenkamp et al., 2013).

Differences regarding the climatic requirements of plants species can also be observed in the CCA ordination plot. For instance, alvars and alluvial meadows can be significantly impacted by high intensity rainfall during the growing season. Therefore, two clusters of species (corresponding to alvars and alluvial meadows) are found along the vector defined by mean precipitation in July. The minimum temperature in April is related to the onset of the growing season and the sensitivity of plant species to late frost events, which influences the coastal meadow species.

The results of this analysis provide a better understanding of the biophysical factors that define the ecological functions of Ecosystem Service Providers (ESP) (i.e. habitats) (Kremen et al., 2005) and also highlight the complex interrelations between ecosystems structure, functions and services. For instance, the maintenance or increase of SOC pools plays a crucial role in the context of climate change mitigation. Additionally, the persistence of SOC is an ecosystem property that integrates several inherent soil properties strongly correlated with key regulation and maintenance ES (Schmidt et al., 2011; Vågen and Winowiecki, 2013). On the other hand, plant species number and composition influence SOC accumulation (Fornara and Tilman, 2008).

Effect of grassland abandonment on species diversity

Abandonment resulted in a significantly lower plant species diversity in three of the four grassland types under study, as well as a significant decrease in rare and protected species in Northern boreal alluvial meadows. Similar results have been found in wooded meadows in Sweden (Mitlacher et al., 2002) and alluvial and coastal meadows throughout Europe (Joyce, 2014). Alvar grasslands showed no significant change in plant species diversity after abandonment, which could be explained by the fact that these grasslands show a rapid decrease of plant species diversity with a shrub cover over 70% (Kasari et al., 2013) and the encroachment process is spatially heterogeneous due to the diverse soil conditions in alvars (Pärtel et al., 1999; Pärtel and Helm, 2007). Helm et al. (2005) found a slow response of remnant alvar plant communities to reduced area and connectivity.

The major loss of biodiversity associated with grassland abandonment processes may in turn lead to shifts in functional traits composition and modify derived ES (Díaz et al., 2005). Abandonment can also result in changes in primary productivity, root depth, soil biota and the dynamics of nutrient cycling and carbon storage. Specifically, grassland abandonment and fragmentation have been previously identified as having a considerable impact on the provision of ES like pollination (Fontana et al., 2014; Nilsson et al., 2013) and herbs for traditional medicine (Fontana et al., 2014).

Surrogate indicators and ES hotspots

The roles of both biodiversity and soils in the context of ES have been discussed in the scientific literature (Harrison et al., 2014; Isbell et al., 2011; Pereira et al., 2018). The results of this study indicate that in semi-natural grasslands, an increase in SOC results in increased biomass production, nutrient cycling and nutrient retention, indicating soil function may be higher and the delivery of soil-related ES improved. Strong correlations were found between SOC and microbial activity and TN (indicators of nutrient cycling and nutrient retention respectively). Soil organic carbon is the main resource for the soil microbial community, which decomposes organic matter and releases nutrients (Williams and Hedlund, 2013). The correlation between SOC and biomass production was only moderate (r = 0.45, p = 0.01) because other factors such as inter-annual climate variability, plant community canopy and root structure differences and halted succession influence this relationship. These were not addressed within this study due to lack of data. Heinsoo et al. (2010) detected very large variability in biomass yield within the same grassland in several locations in Estonia, most likely as a result of differing environmental conditions.

Soils are a key component of ecosystem functioning and provide and regulate several ES (Pereira et al., 2018). Within the complex dynamics of soils, carbon sequestration and storage is an important ES as an agent for soil formation and functioning (Kõlli et al*.,* 2007) as well as due to its importance in climate change mitigation, particularly for coastal soils (Chmura et al*.,* 2003). In addition, increased SOC is strongly linked to soil-related processes and ultimately, ES such as soil structure, water retention capacity, nutrient retention capacity, diversity of soil flora/fauna (Lal, 2011; Lal, 2014), pollutant attenuation (Abdalla et al., 2018) and erosion prevention (Gardi et al., 2016). In this regard, moderate grazing regimes have been shown to increase SOC concentrations (Hewins et al., 2018; Wang et al., 2014).

Plant species diversity was used as a surrogate indicator for two ES: Pollination and plants for traditional medicine. Correlations between plant species diversity and these two ES were strong and positive. In previous studies, plant species diversity has been directly related with a number of ecosystem functions and services including: primary productivity

(Hooper et al., 2012), forage quality and pest control (Soliveres et al., 2016), nutrient cycling (Maestre et al., 2012), SOC accumulation (Fornara and Tilman, 2008), and pollinator abundance and richness (Diaz Forero, 2011; Batáry et al., 2010; Ebeling et al., 2008). Although there is still much deliberation regarding the role of biodiversity within the ES framework (Jax and Heink, 2015), the relationship between biodiversity and ES must be addressed in order to develop appropriate conservation policies and strategies.

Landcover-based proxy methods have been criticized for being crude estimates of actual ES and for being poorly representative of wider ranges of ES (Eigenbrod et al., 2010). The methodology presented in this paper partially overcomes the errors derived from uniquely linking ES values to landcover classes by accounting for biophysical heterogeneity (SOC) and biodiversity within the grassland types under study. The proposed methodology provides an integral overview on the location and extent of semi-natural grasslands hotspots where potentially several ES are provided. The results show that alvars contribute greatly to plant species diversity ranges and hotspots. Although alvars are not the largest grassland type, they are very species rich (Pärtel et al., 1999). Regarding SOC, alluvial meadows and wooded meadows and pastures encompass the greatest proportion of hotspots. Alluvial meadows are generally located on gleysols and fluvisols with rather thick organic horizons (Paal et al., 2007), characterized by high input of sediments and high microbial activity in shallow flooding water (Truus, 1998), and therefore a higher SOC content. On the other hand, wooded meadows and pastures are generally characterized by thicker organic horizon soils with a higher input of plant litter from the tree layer (Ivask et al., 2012). The multiple ES hotspots (overlaps between SOC and plant species diversity hotspots) are mostly grouped in two clusters in the North and the West of Estonia. A third group of hotspots comprises alluvial meadows, which are also distributed in the South West of Estonia. The greatest proportion of multiple ES hotspots belongs to wooded meadows and pastures (Table 7), characterized by high levels of SOC and a large species pool due to the high niche diversity. Alluvial meadows show the second highest proportion of ES hotspots (594 ha). The distribution of ES hotspots also reflects the present distribution of the remaining patches of some semi-natural grassland types (i.e. alvars and wooded meadows and pastures), with the highest grassland area in the West and North. No significant correlations were found between SOC and species diversity, indicating that the multiple ES hotspots are not the result of a synergetic interaction between the surrogate indicators but rather, a spatial co-occurrence of high levels of multiple ES.

The hotspots approach can assist in identifying and prioritizing relevant areas for the provision of ES and targeting conservation and agri-environmental measures. Kremen and Merenlender (2018) highlight the degradation and loss of rangelands worldwide and propose Mediterranean dehesas and montados as an example of land management that both protect biodiversity and enhance the supply of ES. Similarly, Torralba et al. (2018) address the coproduction of ES in wooded pastures across Europe, revealing complex ES interactions and concluding that there is a need for policies oriented towards enhancing provisioning, regulating and cultural ES through the regulation of both intensity of management and multifunctionality of agroecosystems. In the context of a global loss of biodiversity, holistic approaches aimed at securing ES supply and landscape multifunctionality can benefit from analyses of ES hotspots like the one presented in this paper, as they set the path towards identifying priority areas for policy action and decision support.

In Estonia, a substantial area of semi-natural grasslands is located outside of the limits of Natura 2000 sites and is therefore excluded from Pillar II CAP support (Lepmets, 2015). In addition, many semi-natural habitats outside Natura 2000 (mainly wooded pastures/ meadows and alvars) are not eligible for Pillar I CAP payments due to eligibility rules that are based exclusively on the density of trees per hectare (in Estonia, a parcel is eligible if there are less than 50 trees per hectare). The ES framework has been proposed as a holistic solution for setting agri-environmental payments schemes, by targeting the provision of multiple ES (Ekroos et al., 2014; Prager et al., 2012). In this regard, any future efforts directed at protecting valuable semi-natural grasslands located outside Natura 2000 areas could benefit from an ES hotspots-based prioritization.

In the context of ES research, hotspot-based approaches may prove useful in setting priority areas for direct data collection. Tiered approaches have been proposed as a flexible and nested multi-method tool for mapping and assessment of ES (Grêt-Regamey et al., 2015). Within tiered toolsets, hotspot maps can highlight focus areas for applying data-intensive methods of higher tiers and therefore improve the overall efficiency of the ES mapping and assessment process. The methodology and results outlined in this paper can be therefore used as a starting point for further research on ES.

5. CONCLUSIONS

Climatic variables and SOC were significantly correlated with the species composition of grassland types under study. This results are essential to understand how species fill environmental niches and sets the basis for future assessments of impacts of global change on the distribution of species and related ES. Additionally, coastal meadows, alluvial meadows and wooded meadows/pastures showed significantly lower species diversity after abandonment. The occurrence of rare and protected species was also significantly lower after abandonment in alluvial meadows. This results show that the cessation of management activities can have an effect in biodiversity-related ES in certain grassland types.

Plant species diversity and SOC were significantly correlated with five ES: Pollination, herbs for traditional medicinal use, nutrient cycling, nutrient retention and biomass production. The overlap between surrogate indicators hotspots show that wooded meadows and pastures comprise the highest proportion of multiple ES hotspots, although this grassland type only accounts for 10% of the semi-natural grassland cover.

The present paper demonstrates the potential use of surrogate indicators for spatially identifying and quantifying semi-natural grasslands ES hotspots when there is a lack of primary data. However, applying the same methodology for different policy, planning or management objectives would require careful consideration of what thresholds constitute a hotspot and the underlying assumptions should be carefully tested.

6. ACKNOWLEDGEMENTS

This work was supported by institutional research funding IUT21-1 at the Estonian Ministry of Education and Research, This study was funded by Estonian Ministry of Science and Education. We especially thank Dr. Pablo Scodeller for his inestimable help and support.

7. REFERENCES

Abdalla, M., Hastings, A., Chadwick, D., Jones, D., Evans, C., Jones, M., Rees, R. M., Smith, P., 2018. Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. Agr. Ecosyst. Environ. 253, 62-81. doi:10.1016/j.agee.2017.10.023

Anderson, B. J., Armsworth, P. R., Eigenbrod, F., Thomas, C. D., Gillings, S., Heinemeyer, A., Roy, D. B., Gaston, K. J., 2009. Spatial covariance between biodiversity and other ecosystem service priorities. J. App. Ecol. 46(4), 888-896. doi:10.1111/j.1365-2664.2009.01666.x

Arold, I., 2005. Estonian landscapes. University of Tartu, Tartu

Bagella, S., Caria, M. C., Farris, E., Rossetti, I., Filigheddu, R., 2014. Traditional land uses enhanced plant biodiversity in a Mediterranean agro-silvo-pastoral system. Plant Biosyst. 150(2), 201-207. doi:10.1080/11263504.2014.943319

Báldi, A., Batáry, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary – analysing assemblages of 1200 species. Agr. Ecosyst. Environ. 166, 28-34. doi:10.1016/j.agee.2012.03.005

Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F., Kleijn, D., 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. Agr. Ecosyst. Environ. 136(1-2), 35-39. doi:10.1016/j.agee.2009.11.004

Benstead, P., Jose, P., Joyce, C., Wade M., 1999. European Wet Grasslands: Guidelines for management and restoration. RSPB, UK.

Birge, T., Herzon, I., 2014. Motivations and experiences in managing rare semi-natural biotopes: A case from Finland. Land Use Pol. 41, 128–137. doi: 10.1016/j.landusepol.2014.05.004.

Brickhill, D., 2015. Ecosystem services and Biodiversity. In-depth report 11 produced for the European Commission, DG Environment. Technical Report. European Commission, Brussels. Available from: http://eprints.uwe.ac.uk/25914

Bullock, J. M., Jefferson, R. G., Blackstock, T. H., Pakeman, R. J., Emmet, B. A., Pywell, R. J., Grime, J. P., Silvertown, J., 2011. Semi-natural grasslands. UK National Ecosystem Assessment. Understanding nature's value to society. Technical Report. UNEP-WCMC, Cambridge.

Burnside, N. G., Joyce, C. B., Puurmann, E., Scott, D. M., 2007. Use of vegetation classification and plant indicators to assess grazing abandonment in Estonian coastal wetlands. J. Veg. Sci. 18(5), 645. doi:10.1658/1100-9233(2007)18[645:uovcap]2.0.co;2

Chmura, G. L., Anisfeld, S. C., Cahoon, D. R., Lynch, J. C., 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochem. Cy. 17(4). doi:10.1029/2002gb001917

Costanza, R., Groot, R. D., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., Grasso, M., 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosyst. Serv. 28, 1-16. doi:10.1016/j.ecoser.2017.09.008

Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (1992); http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:31992L0043.

Cousins, S. A. O., Ohlson, H., Eriksson, O., 2007. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. Land. Ecol. 22(5), 723-730. doi: 10.1007/s10980-006-9067-1

Critchley, C., Burke, M., Stevens, D., 2004. Conservation of lowland semi-natural grasslands in the UK: A review of botanical monitoring results from agri-environment schemes. Biol. Conserv. 115(2), 263-278. doi:10.1016/s0006-3207(03)00146-0

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: A synthesis. Agr. Ecosyst. Environ. 182, 1-14. doi:10.1016/j.agee.2013.12.015

Díaz, S., Tilman, D., Fargione, J., Chapin, F. S., Dirzo, III, R., Kitzberger, T., Gemmill, B., Zobel, M., Vilà, M., Mitchell, C., Wilby, A., Daily, G. C., Galetti, M., Laurance, W. F., Pretty, J., Naylor, R., Power, A., Harvell, D., 2005. Biodiversity regulation of ecosystem services. 297–329 in Hassan, H., Scholes, R., & Ash, N. editors. Ecosystems and human well-being: current state and trends. Island Press, Washington, D.C., USA.

Díaz Forero, I., 2011. Influence of biotic and abiotic factors at patch and landscape scale on bumblebees (Bombus spp.) in semi-natural meadows. Estonian university of Life Sciences, Tartu, Estonia.

Ebeling, A., Klein, A., Schumacher, J., Weisser, W. W., Tscharntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos, 117(12), 1808-1815. doi:10.1111/j.1600-0706.2008.16819.x

Eesti Punane Raamat, 2008. Retrieved from http://vana.elurikkus.ut.ee

EFN & RDSFNC., 2001. The inventory of semi-natural grasslands in Estonia 1999-2001: Final report. Estonian Fund for Nature and Royal Dutch Society for Nature Conservation, Estonia

Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D. M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol Cons 142(3), 553-562. doi:10.1016/j.biocon.2008.11.009

Eigenbrod, F., Armsworth, P. R., Anderson, B. J., Heinemeyer, A., Gillings, S., Roy, D. B., Thomas, C. D., Gaston, K. J., 2010. The impact of proxy-based methods on mapping the distribution of ecosystem services. J. App. Ecol. 47(2), 377-385. doi:10.1111/j.1365-2664.2010.01777.x

Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F. Smith, H.G., 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? Biol. Conserv. 172, 65-71

Eriksson, O., Cousins, S. A., Bruun, H. H., 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. J. Veg. Sci. 13(5), 743-748. doi:10.1111/j.1654-1103.2002.tb02102.x

Estonian Environment Agency. State Monitoring Program of Wildlife Diversity and Landscapes. Retrieved from: seire.keskkonnainfo.ee

EU FP7 OpenNESS Project. Wijnja, H., van Uden, G., Delbaere, B., 2016. Ecosystem services in operation: case studies. European Commission FP7. Available at: https://issuu.com/ecnc.org/docs/openness_casestudies_brochure

Fontana, V., Radtke, A., Walde, J., Tasser, E., Wilhalm, T., Zerbe, S., Tappeiner, U., 2014. What plant traits tell us: Consequences of land-use change of a traditional agro-forest system on biodiversity and ecosystem service provision. Agr. Ecosys. Environ. 186, 44-53. doi:10.1016/j.agee.2014.01.006

Fornara, D. A., Tilman, D., 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. J. Ecol. 96(2), 314-322. doi:10.1111/j.1365-2745.2007.01345.x

Gardi, C., Visioli, G., Conti, F. D., Scotti, M., Menta, C., Bodini, A., 2016. High Nature Value Farmland: Assessment of Soil Organic Carbon in Europe. Front. Env. Sci., 4. doi:10.3389/fenvs.2016.00047

Gos, P., Lavorel, S., 2012. Stakeholders expectations on ecosystem services affect the assessment of ecosystem services hotspots and their congruence with biodiversity. Int. J. Biodiv. Sci. Ecosyst. Serv. Man., 8(1-2), 93-106. doi:10.1080/21513732.2011.646303

Grêt-regamey, A., Weibel, B., Kienast, F., Rabe, S., Zulian, G., 2015. A tiered approach for mapping ecosystem services. Ecosyst. Serv. 13,16–27.doi: 10.1016/j.ecoser.2014.10.008

Haines-Young, R., Potschin, M., 2010. The links between biodiversity, ecosystem services and human well-being. In: Raffaelli, D. & C. Frid (eds.): Ecosystem Ecology: a new synthesis. BES Ecological Reviews Series, CUP, Cambridge

Haines-Young, R., Potschin, M.B., 2018. Common International Classification of EcosystemServices (CICES) V5.1 and Guidance on the Application of the Revised Structure. Available from www.cices.eu

Harrison, P., Berry, P., Simpson, G., Haslett, J., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamănă, N., Geertsema, W., Lommelen, E., Meiresonne, L., Turkelboom, F., 2014. Linkages between biodiversity attributes and ecosystem services: A systematic review. Ecosyst. Serv. 9, 191-203. doi:10.1016/j.ecoser.2014.05.006

Haylock, M.R., Hofstra, N., Klein Tank, A. M. G., Klok, E.J., Jones, P. D., New, M., 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation. J. Geophys. Res-Atmos. 113 (D20), 119. doi:10.1029/2008JD10201

Heinsoo, K., Melts, I., Sammul, M., Holm, B., 2010. The potential of Estonian semi-natural grasslands for bioenergy production. Agr. Ecosyst. Environ. 137(1-2), 86-92. doi:10.1016/j.agee.2010.01.003

Helm, A., Hanski, I., Partel, M., 2005. Slow response of plant species richness to habitat loss and fragmentation. Ecol. Lett. 0(0), 051109031307003. doi:10.1111/j.1461-0248.2005.00841.x

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, McCracken, T., Moritz, F.A.R., Niemelä, J., Rebane, M., Wascher, D., Watt, A., Young, J., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe–A review. Agr. Ecosyst. Environ. 124(1-2), 60-71. doi:10.1016/j.agee.2007.09.005

Hewins, D. B., Lyseng, M. P., Schoderbek, D. F., Alexander, M., Willms, W. D., Carlyle, C. N., Chang, S. X., Bork, E. W., 2018. Grazing and climate effects on soil organic carbon concentration and particle-size association in northern grasslands. Sci. Rep-UK., 8(1). doi:10.1038/s41598-018-19785-1

Hinojosa, L., Napoléone, C., Moulery, M., Lambin, E.F., 2016. The “mountain effect” in the abandonment of grasslands: Insights from the French Southern Alps. Agr. Ecosyst. Environ. 221, 115-124. doi: 10.1016/j.agee.2016.01.032

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett., 8, 23–29. doi.org/10.1111/j.1461-0248.2004.00686.x

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L., O’Connor, M. I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature, 486(7401), 105-108. doi:10.1038/nature11118

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., Van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. Nature, 477 (7363), 199-202. doi: 10.1038/nature10282

Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., Binder, S., 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. P. Natl. Acad. Sci. 110 (29), 11911-11916; doi:10.1073/pnas.1310880110

Ivask, K., Kuu, A., Truu, M., Kutti, S., Meriste, M., Peda, J., 2012. Earthworm Communities in Soils of Estonian Wooded Meadows. Balt. For. 18 (1), 111-118

Jax, K., Heink, U., 2015. Searching for the place of biodiversity in the ecosystem services discourse. Biol. Conserv. 191, 198-205. doi:10.1016/j.biocon.2015.06.032

Jones, M. B., Donnelly, A., 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO2. New Phytol. 164(3), 423-439. doi:10.1111/j.1469-8137.2004.01201.x

Jongman, R. H., Bunce, R. G., Metzger, M. J., Mücher, C. A., Howard, D. C., Mateus, V. L., 2006. Objectives and Applications of a Statistical Environmental Stratification of Europe. Land. Ecol. 21(3), 409-419. doi:10.1007/s10980-005-6428-0

Joyce, C.B., 2014. Ecological consequences and restoration potential of abandoned wet grasslands. Ecol. Eng. 66, 91-102. doi.org/10.1016/j.ecoleng.2013.05.008.

Joyce, C. B., Simpson, M., Casanova, M., 2016. Future wet grasslands: Ecological implications of climate change. Ecosystem Health and Sustainability, 2(9). doi:10.1002/ehs2.1240

Kalle, R., 2017. Change in Estonian natural resource use: The case of wild food plants. Estonian University of Life Sciences, Tartu, Estonia.

Kahmen, S., Poschlod, P., Schreiber, K., 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. Biol. Conserv. 104(3), 319-328. doi:10.1016/s0006-3207(01)00197-5

Kaisel, K., Mägi, E. Paakspuu, T., 2004. Development of coastal grasslands for bird fauna in Matsalu wetland. Loodusevaatlusi, 3, 35-40

Kana, S., Kull, T., Otsus, M., 2008. Change in agriculturally used land and related habitat loss: A case study in eastern Estonia over 50 years. Est. J. Ecol. 57(2), 119. doi:10.3176/eco.2008.2.04

Kana, S., Otsus, M., Sammul, M., Laanisto, L., Kull, T., 2015. Change in Species Composition during 55 Years: A Re-Sampling Study of Species-Rich Meadows in Estonia. Ann. Bot. Fenn, 52(5-6), 419-431. doi:10.5735/085.052.0525

Kasari, L., Gazol, A., Kalwij, J. M., Helm, A., 2013. Fertilising semi-natural grasslands may cause long-term negative effects on both biodiversity and ecosystem stability. TUEXENIA 33(1), 293-308.

Kimmel, K., 2009. Ecosystem services of Estonian wetlands. Dissertationes Geographicae Universitatis Tartuensis 38. Tartu University Press, Tartu

Krause, B., and Culmsee, H., 2013. The significance of habitat continuity and current management on the compositional and functional diversity of grasslands in the uplands of Lower Saxony, Germany. Flora - Morphology, Distribution, Functional Ecology of Plants, 208(5-6), 299-311. doi:10.1016/j.flora.2013.04.003

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, K., Lindborg, R., Ockinger, E., Partel, M., Pino, J., Poyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett., 13, 597-605. doi:10.1111/j.1461-0248.2010.01457.x

Kremen, C., 2005. Managing ecosystem services: What do we need to know about their ecology? Ecol Lett, 8(5), 468-479. doi:10.1111/j.1461-0248.2005.00751.x

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 2018, 362, eaau6020. doi: 10.1126/science.aau6020

Kukk, T. and Kull, K., 1997. Wooded Meadows (Puisniidud). Estonia Maritima 2, 1–249

Kukk, T., 2004. Pärandkooslused. Õpik-käsiraamat. Tartu: Pärandkoosluste kaitse Ühing

Kukk, T. and Sammul. M., 2006. Loodusdirektiivi poollooduslikud kooslused ja nende pindala Eestis. Eesti Looduseuurijate Seltsi aastaraamat, 84, 114-159

Kull, K. and Zobel, M., 1991. High species richness in an Estonian wooded meadow. J. Veg. Sci. 2(5), 715-718. doi:10.2307/3236182

Kupper, T., 2007. Loopealse sammalkatte dünaamikast levisepanga, häiringute ja ilmastikutingimuste mõjul. Tart, Estonia: University of Tartu

Kõlli, R., Köster, T. Kauer, K., 2007. Organic matter of Estonian grassland soils. Agro. Res. 5, 109-122.

Lal, R., 2011. Sequestering carbon in soils of agro-ecosystems. Food Policy. 36. doi:10.1016/j.foodpol.2010.12.001

Lal, R., 2014. Soil conservation and ecosystem services. International Soil and Water Conservation Research. 2(3), 36-47. doi:10.1016/s2095-6339(15)30021-6

Lamarque, P., Tappeiner, U., Turner, C., Steinbacher, M., Bardgett, R.D., Szukics, U., Schermer, M., Lavorel, S. 2011. Stakeholder perceptions of grassland ecosystem services in relation to knowledge on soil fertility and biodiversity. Reg Environ Change. 11, 791–804. doi:10.1007/s10113-011-0214-0

Leito, A., Elts, J., Mägi, E., Truu, J., Ivask, M., Kuu, A., Ööpik, M., Meriste, M., Ward, R., Kuresoo, A., Pehlak, H., Sepp, K., Luigujõe, L., 2014. Coastal grassland wader abundance in relation to breeding habitat characteristics in Matsalu Bay, Estonia. Ornis Fennica. 91 (3): 149-165.

Lepmets, E., 2015. Country report on the implementation of the new CAP and its possible effects on permanent pastures: ESTONIA. European Forum on Nature Conservation and Pastoralism

Liira, J., Issak, M., Jõgar, Ü, Mändoja, M., Zobel, M., 2009. Restoration Management of a Floodplain Meadow and Its Cost-Effectiveness — the Results of a 6-Year Experiment. Ann. Bot. Fenn. 46(5), 397-408. doi:10.5735/085.046.0504

Liquete, C., Kleeschulte, S., Dige, G., Maes, J., Grizzetti, B., Olah, B., Zulian, G., 2015. Mapping green infrastructure based on ecosystem services and ecological networks: A Pan-European case study. Environmental Science & Policy. 54, 268-280. doi:10.1016/j.envsci.2015.07.009

Liquete, C., Cid, N., Lanzanova, D., Grizzetti, B., Reynaud, A., 2016. Perspectives on the link between ecosystem services and biodiversity: The assessment of the nursery function. Ecol. Ind. 63, 249-257. doi:10.1016/j.ecolind.2015.11.058

Lugato, E., Panagos, P., Bampa, F., Jones, A., Montanarella, L., 2013. A new baseline of organic carbon stock in European agricultural soils using a modelling approach. Glob. Change Biol. 20(1), 313-326. doi:10.1111/gcb.12292

Maes, J., Egoh, B., Willemen, L., Liquete, C., Vihervaara, P., Schägner, J. P., Grizzetti, B., Drakou, E., La Notte, A., Zulian, G., Bouraoui, F., Paracchini, M. L., Braat, L., Bidoglio, G., 2012. Mapping ecosystem services for policy support and decision making in the European Union. Ecosyst. Serv. 1(1), 31-39. doi:10.1016/j.ecoser.2012.06.004

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., et al. 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science, 335(6065), 214-218. doi:10.1126/science.1215442

Marks, E., Aflakpui, G. K., Nkem, J., Poch, R. M., Khouma, M., Kokou, K., Sagoe, R., Sebastià, M., 2008. Conservation of soil organic carbon, biodiversity and the provision of other ecosystem services along climatic gradients in West Africa. Biogeosciences Discussions. 5(6), 4413-4452. doi:10.5194/bgd-5-4413-2008

Martínez-Harms, M. J. and Balvanera, P., 2012. Methods for mapping ecosystem service supply: A review. International Journal of Biodiversity Science, Ecosystem Services & Management, 8(1-2), 17-25. doi:10.1080/21513732.2012.663792

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Silliman, B. R., 2011. A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Environ. 9(10), 552-560. doi:10.1890/110004

Melts, I., 2014. Biomass from semi-natural grasslands for bioenergy. Estonian University of Life Sciences, Tartu, Estonia.

Metsoja, J., Neuenkamp, L., Pihu, S., Vellak, K., Kalwij, J. M., Zobel, M., 2011. Restoration of flooded meadows in Estonia - vegetation changes and management indicators. Appl. Veg. Sci. 15(2), 231-244. doi:10.1111/j.1654-109x.2011.01171.x

Metzger, M. J., Bunce, R. G., Jongman, R. H., Mücher, C. A., & Watkins, J. W., 2005. A climatic stratification of the environment of Europe. Global Ecol. Biogeogr. 14(6), 549-563. doi:10.1111/j.1466-822x.2005.00190.x

Metzger, M. J., Schröter, D., Leemans, R., Cramer, W., 2008. A spatially explicit and quantitative vulnerability assessment of ecosystem service change in Europe. Reg. Environ. Change. 8(3), 91-107. doi:10.1007/s10113-008-0044-x

Mitlacher, K., Poschlod, P., Rosén, E., Bakker, J., 2002. Restoration of wooded meadows - a comparative analysis along a chronosequence on Öland (Sweden). Appl. Veg. Sci. 5, 63-73. doi:10.1111/j.1654-109X.2002.tb00536.x

Morelli, F., Jiguet, F., Sabatier, R., Dross, C., Princé, K., Tryjanowski, P., Tichit, M., 2017. Spatial covariance between ecosystem services and biodiversity pattern at a national scale (France). Ecol. Indic. 82, 574-586. doi:10.1016/j.ecolind.2017.04.036

Mota, G. S., Luz, G. R., Mota, N. M., Coutinho, E. S., Veloso, M. D., Fernandes, G. W., Nunes, Y. R., 2018. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. Flora. 238, 32-42. doi:10.1016/j.flora.2017.03.010

Navarro, L. M., Pereira, H. M., 2015. Rewilding Abandoned Landscapes in Europe. In: Pereira H., Navarro L. (eds) Rewilding European Landscapes. Springer, Cham

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, M.K., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front. in Ecol. Environ. 7(1), 4-11. doi:10.1890/080023

Neuenkamp, L., Metsoja, J., Zobel, M., Hölzel, N., 2013. Impact of management on biodiversity-biomass relations in Estonian flooded meadows. Plant Ecol. 214(6), 845-856. doi:10.1007/s11258-013-0213-y

OPERAs. (2016). OPERAs- Ecosystem Science for Policy & Practice (http://www.operas-project.eu/)

Pettersson, L., Nilsson, S., Franzén, M., 2013. Land-use changes, farm management and the decline of butterflies associated with semi-natural grasslands in southern Sweden. Nat. Conserv. 6, 31-48. doi:10.3897/natureconservation.6.5205

Paal, J., 1998. Rare and threatened Estonian plant communities. Biodivers. Conserv. 7: 1027-1049.

Paal, J., 2002. Estonian forest types in terms of the Habitats Directive. Balt. For. 8(1), 21-27

Paal, J., Rannik, R., Jeletsky, E., Prieditis, N., 2007. Floodplain forests in Estonia: Typological diversity and growth conditions. Folia Geobot. 42(4), 383-400.

doi:10.1007/bf02861701

Paal, J. and Leibak, E. 2011. Estonian mires: inventory of habitats. Publication of the Project “Estonian Mires Inventory completion for maintaining biodiversity”. Regio, Tartu

Palomo, I., Willemen, L., Drakou, E., Burkhard, B., Crossman, N., Bellamy, C., Burkhard, K., Campagne, C., Dangol, A., Franke, J., Kulczyk, S., Le Clec'h, S., Abdul Malak, D., Muñoz, L., Narusevicius, V., Ottoy, S., Roelens, J., Sing, L., Thomas, A., Van Meerbeek, K., Verweij, P., 2018. Practical solutions for bottlenecks in ecosystem services mapping. One Ecosystem 3: e20713. https://doi.org/10.3897/oneeco.3.e20713

Pe’er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., Collins, S., Dieterich, M., Gregory, R. D., Hartig, F., Henle, K., Hobson, P. R., Kleijn, D., Neumann, R. K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W. J., Turbe, A., Wulf, F., Scott, A. V., 2014. EU agricultural reform fails on biodiversity. Science, 344(6188), 1090-1092. doi: 10.1126/science.1252254

Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, W.A., Sifleet, S., Craft, C., Fourqueran, J.W., Kauffman, J.B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D. and Balder, A., 2012. Estimating Global “Blue Carbon” Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. PLoS ONE 7(9): e43542.

Pereira, P., Bogunovic, I., Muñoz-Rojas, M., Brevik, E. C., 2018. Soil ecosystem services, sustainability, valuation and management. Curr. Opin. Env. Sci. Health. 5, 7-13. doi:10.1016/j.coesh.2017.12.003

Plieninger, T., Schleyer, C., Schaich, H., Ohnesorge, B., Gerdes, H., Hernández-Morcillo, M., Bieling, C., 2012. Mainstreaming ecosystem services through reformed European agricultural policies. Conserv. Lett. 5(4), 281-288. doi:10.1111/j.1755-263x.2012.00240.x

Potschin, M. and Haines-Young, R., 2016. Defining and measuring ecosystem services. In: Routledge Handbook of Ecosystem Services (pp. 25-44). New York, NY: Routledge

Prager, K., Reed, M., Scott, A., 2012. Encouraging collaboration for the provision of ecosystem services at a landscape scale—Rethinking agri-environmental payments. Land Use Policy. 29(1), 244-249

Pykälä, J., Luoto, M., Heikkinen, R. K., Kontyla, T., 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic Appl. Ecol. 6, 25-33. doi: 10.1016/j.baae.2004.10.002

Pärtel, M., Kalamees, R., Zobel, M., Rosén, E., 1999. Alvar grasslands in Estonia: Variation in species composition and community structure. J. Veg. Sci. 10(4), 561-570. doi:10.2307/3237190

Pärtel, M., Bruun, H. H., & Sammul, M., 2005. Biodiversity in temperate European grasslands: origin and conservation. In Grassland Science in Europe (Vol. 10, pp. 1-14). Grassland Science in Europe

Pärtel, M. and Helm, A., 2007. Invasion of woody species into temperate grasslands: Relationship with abiotic and biotic soil resource heterogeneity. J. Veg. Sci. 18(1), 63. doi:10.1658/1100-9233(2007)18[63:iowsit]2.0.co;2

Quijas, S., and Balvanera, P., 2013. Biodiversity and Ecosystem Services. Encyclopedia of Biodiversity, 341-356. doi:10.1016/b978-0-12-384719-5.00349-x

Rabe, S., Koellner, T., Marzelli, S., Schumacher, P., Grêt-Regamey, A., 2016. National ecosystem services mapping at multiple scales: The German exemplar. Ecol. Ind. 70, 357-372. doi:10.1016/j.ecolind.2016.05.043

Rehme, K., 2013. Matsalu rahvuspargi lamminiitude peamiste taimkattetüüpide rohtse biomassi produktsioon 2012. Aastal ja selle varumise otstarbekus 2008-2012. Tartu, Estonia, Tallinn Technical University (Tartu College)

Ren, Y., Lü, Y., Fu, B. 2016. Quantifying the impacts of grassland restoration on biodiversity and ecosystem services in China: A meta-analysis. Ecol. Eng. 95, 542-550. doi:10.1016/j.ecoleng.2016.06.082

Saar, K., 1996. Vilsandi loopealsete liigiline mitmekesisus ja biomass. Tartu, Estonia: University of Tartu

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M., Wall D.H., 2000. Biodiversity—Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. doi:10.1126/science.287.5459.1770

Sammul, M., Kull, K., Tamm, A., 2003. Clonal growth in a species-rich grassland: Results of a 20-year fertilization experiment. Folia Geobot. 38(1), 1-20. doi:10.1007/bf02803124

Sammul, M., Oksanen, L., Mägi, M., 2006. Regional effects on competition-productivity relationship: A set of field experiments in two distant regions. Oikos, 112(1), 138-148. doi:10.1111/j.0030-1299.2006.13378.x

Sammul, M., Kattai, K., Lanno, K., 2008. Wooded meadows of Estonia: Conservation efforts for agricultural landscape. Agr. Food Sci. 17(4), 413. doi:10.2137/145960608787235513

Sammul, M., Kauer, K., Köster, T., 2011. Biomass accumulation during reed encroachment reduces efficiency of restoration of Baltic coastal grasslands. App. Veg. Sci. 15(2), 219-230. doi:10.1111/j.1654-109x.2011.01167.x

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Koegel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature. 478, 49-56.

Slocum, T. A., 1999. Thematic cartography and visualization. Upper Saddle River, NJ: Prentice-Hall.

Soliveres, S., Plas, F. V., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., et al., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature, 536(7617), 456-459. doi:10.1038/nature19092

Schröter, M., and Remme, R. P., 2015. Spatial prioritisation for conserving ecosystem services: Comparing hotspots with heuristic optimisation. Landscape Ecol. 31(2), 431-450. doi:10.1007/s10980-015-0258-5

Soussana, J., and Lemaire, G., 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. Agr. Ecosys. Environ. 190, 9-17. doi:10.1016/j.agee.2013.10.012

Strijker, D., 2005. Marginal lands in Europe-causes of decline. Basic Appl. Ecol. 6(2) 99-106. doi: 10.1016/j.baae.2005.01.001

Talvi, T. and Talvi, T., 2012. Semi-Natural Communities. Preservation and Management. Ministry of Agriculture, Tallinn

Ter Braak, and C.J.F., Šmilauer, P., 2012. CANOCO reference manual anduser’s guide: software for ordination (version 5.0). Microcom-puter power, Ithaca, New York

Torralba, M., Fagerholm, N., Hartel, T., Moreno, G., Plieninger, T., 2018. A social- ecological analysis of ecosystem services supply and trade-offs in European wood- pastures. Sci. Adv., 4, eaar2176. doi:10.1126/sciadv.aar2176

Truus, L., 1998. Influence of management cessation on reedbed and floodplain vegetation on the Kloostri floodplain meadow in the delta of the Kasari River, Estonia. P. Est. Acad. Sci. Biology, Ecology, 47 (1), 58−72

Truus, L. and Puusild, E., 2009. Species richness, biomass production and recent vegetation changes of Estonian floodplain grasslands. Pol. J. Ecol. 57, 33-45.

Vågen, T.G., Winowiecki. L.A., 2013. Mapping of soil organic carbon stocks for spatially explicit assessments of climate change mitigation potential Environ. Res. Lett. 8, 1-9. doi: 10.1088/1748-9326/8/1/015011

Van Swaay, C. A. M. et al., 2013. The European grassland butterfly indicator 1990–2011. European Environmental Agency, Copenhagen, Denmark.

Villoslada, M., Bunce, R. G., Sepp, K., Jongman, R. H., Metzger, M. J., Kull, T., Raet, J., Kuusemets, V., Kull, A., Leito, A., 2016. A framework for habitat monitoring and climate change modelling: Construction and validation of the Environmental Stratification of Estonia. Reg. Environ. Change. 17(2), 335-349. doi:10.1007/s10113-016-1002-7

Villoslada, M., Vinogradovs, I., Ruskule, A., Veidemane, K., Nikodemus, O., Kasparinskis, R., Sepp, K., Gulbinas, J., 2018 A multitiered approach for grassland ecosystem services mapping and assessment: The Viva Grass tool. One Ecosystem. 3 e25380. doi: 10.3897/oneeco.3.e25380

Vorobyova, L. A., 1998. Chemical analysis of soils. Moscow University Press. Moscow.

Wang, X., Vandenbygaart, A., Mcconkey, B. C., 2014. Land Management History of Canadian Grasslands and the Impact on Soil Carbon Storage. Rangeland Ecol. Manag. 67(4), 333-343. doi:10.2111/rem-d-14-00006.1

Ward, R. D., Burnside, N. G., Joyce, C. B., Sepp, K., 2013. The use of medium point density LiDAR elevation data to determine plant community types in Baltic coastal wetlands. Ecol. Ind. 33, 96-104. doi:10.1016/j.ecolind.2012.08.016

Ward, R. D., Teasdale, P. A., Burnside, N. G., Joyce, C. B., Sepp, K., 2014. Recent rates of sedimentation on irregularly flooded Boreal Baltic coastal wetlands: Responses to recent changes in sea level. Geomorphology, 217, 61-72. doi:10.1016/j.geomorph.2014.03.045

Ward, R. D., Burnside, N. G., Joyce, C. B., Sepp, K., 2016a. Importance of Microtopography in Determining Plant Community Distribution in Baltic Coastal Wetlands. J. Coastal. Res. 321, 1062-1070. doi:10.2112/jcoastres-d-15-00065.1

Ward, R., Burnside, N., Joyce, C., Sepp, K. Teasdale, P. A., 2016b. Improved modelling of the impacts of sea level rise on coastal wetland plant communities. Hydrobiologia Wetlands Biodiversity & Processes: 1-14.

Williams, A., and Hedlund, K., 2013. Indicators of soil ecosystem services in conventional and organic arable fields along a gradient of landscape heterogeneity in southern Sweden. App. Soil Ecol. 65, 1-7. doi:10.1016/j.apsoil.2012.12.019

Zhang, L., Lü, Y., Fu, B., Dong, Z., Zeng, Y., Wu, B., 2017. Mapping ecosystem services for China's ecoregions with a biophysical surrogate approach. Landscape Urban Plan. 161, 22-31. doi:10.1016/j.landurbplan.2016.12.015

FIGURE CAPTIONS

Fig. 1. The ecosystem services cascade model adapted from Potschin and Haines-Young (2016). Three cascade components were assessed within this study: (1) underlying environmental gradients determining species distribution in semi-natural grasslands, (2) effects of grassland abandonment and (3) the spatial distribution of ecosystem service hotspots in semi-natural grasslands.

Fig. 2. Distribution of the principal semi-natural grassland types in Estonia by the regions of the Environmental Stratification of Estonia as developed by Villoslada et al. (2016).

Fig. 3. Canonical correspondence analysis ordination plot showing grassland type, 90 most common species, and environmental vectors. The dashed lines represent the grassland types under study and group the most common species in each grassland type.

Fig. 4. Percentage of grasslands with and without rare and protected vascular plant species in abandoned and managed grasslands in all habitats, including 6530/9070: Fennoscandian wooded meadows/pastures, 6280: Nordic Alvars and precambrian calcareous flatrocks, 1630: Boreal Baltic coastal meadows, 6450: Northern boreal alluvial meadows. * = $p < 0.05$

Fig. 5 Percentage of SOC and plant species diversity coldspots, ranges and hotspots within each grassland type in Estonia.

Fig. 6. A close-up view of Matsalu bay in Western Estonia. The reclassified SOC (a) and vascular plant species diversity (b) maps are overlapped in order to map ES hotspots. The spatial coincidence of SOC and species diversity maximum reclassified values constitutes multiple ES hotspots.

Fig. 7. Distribution of ES services hotspots in semi-natural grassland habitats in Estonia. The zoomed area shows the northern cluster of multiple ES hotspots, including Lahemaa National Park.

Table 1. Overview of the selected ES and their correspondence to CICES V5.1 classification system

ES	Section (CICES V5.1)	Equivalent class (CICES V5.1)	Indicator	Surrogate indicator	Data sources
Pollination	Regulation & Maintenance	Pollination	Pollinators richness and abundance	Plant species diversity	Diaz Forero (2011). State Monitoring Program of Wildlife Diversity and Landscapes (Estonian Environment
Nutrient cycling	Regulation & Maintenance	Weathering processes and their effect on soil quality	Microbial activity	SOC	State Monitoring Program of Wildlife Diversity and Landscapes (Estonian Environment
Nutrient retention	Regulation & Maintenance	Regulation of the chemical condition of freshwaters by living processes	Total Nitrogen	SOC	State Monitoring Program of Wildlife Diversity and Landscapes (Estonian Environment
Biomass production	Provisioning	Wild plants used for nutrition	Total biomass production (dry weight)	SOC	Heinsoo et al. (2010), Kull and Zobel (1991), Kupper (2007), Melts (2014), Neuenkamp et al. (2013), Rehme (2013), Saar (1996), Sammul et al. (2006), Sammul et al. (2011), Truus and Puusild
Herbs for traditional medicinal use	Cultural	Characteristics of living systems that enable activities promoting health, recuperation or	Wild medicinal and food plants	Plant species diversity	Kalle (2017)

Table 2 Annex I habitats in Estonia and their extent based on the unified database. Shaded grassland habitats were selected for inclusion in this study.

Annex I habitat code	Grassland type	Unified database (% of total extent)
6450	Northern boreal alluvial meadows	27866 ha (25%)
1630	Boreal Baltic coastal meadows	22996 ha (21%)
6280	Nordic Alvars and precambrian calcareous flatrocks	16696 ha (15%)
6530/9070	Fennoscandian wooded meadows/pastures	11454 ha (10%)
6210	Semi-natural dry grasslands and scrubland facies on calcareous soils	9913 ha (9%)
6270	Fennoscandian lowland species-rich dry to mesic	7682 ha (7%)

	grasslands	
6510	Lowland hay meadows	7584 ha (7%)
6430	Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	3790 ha (4%)
6410	*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils	1611 ha (2%)
TOTAL		109592 ha

Table 3. Pearson correlation coefficients for all environmental variables, axis eigenvalues, cumulative percentage of axis explanation, and pseudo canonical correlation of the axes for the canonical correspondence analysis in Fig. 3

Variables	Axis 1	Axis 2
SOC	0.6062	-0.2771
Average precipitation July	0.5472	0.055
Elevation	0.481	-0.1678
Maximum temperature October	-0.7343	0.0073
Minimum temperature April	-0.3184	0.2277
Minimum temperature January	-0.7293	0.0951
Average precipitation January	0.061	-0.2033
Average precipitation October	-0.3021	-0.3103
Sunshine July	-0.7008	0.0461
Pseudo canonical correlation	0.8561	0.6166
Eigenvalues	0.3196	0.1174
Cumulative percentage	47.37	64.78

Table 4: Student's t-test results for the differences between the average number of plant species in managed grasslands and abandoned grasslands for all habitats, where N is the number of abandoned and managed sample grasslands. Significance level was set at p<0.05.

			Mean number of species	
Grassland type	**N**	***p*-value**	**Abandoned**	**Managed**
Boreal Baltic Coastal Meadows	28/33	0.023	29.64	46.24
Nordic alvar and precambrian calcareous flatrock	92/92	0.083	43.67	48.66
Northern boreal alluvial meadows	136/136	0.000	27.5	38.7

Fennoscandian wooded meadows/pastures	150/163	0.000	31	45

Table 5. Pearson's correlation coefficients between flowering plant species richness and different groups of pollinators richness and abundance and herbs for traditional medicine. Significance level was set at p<0.05.

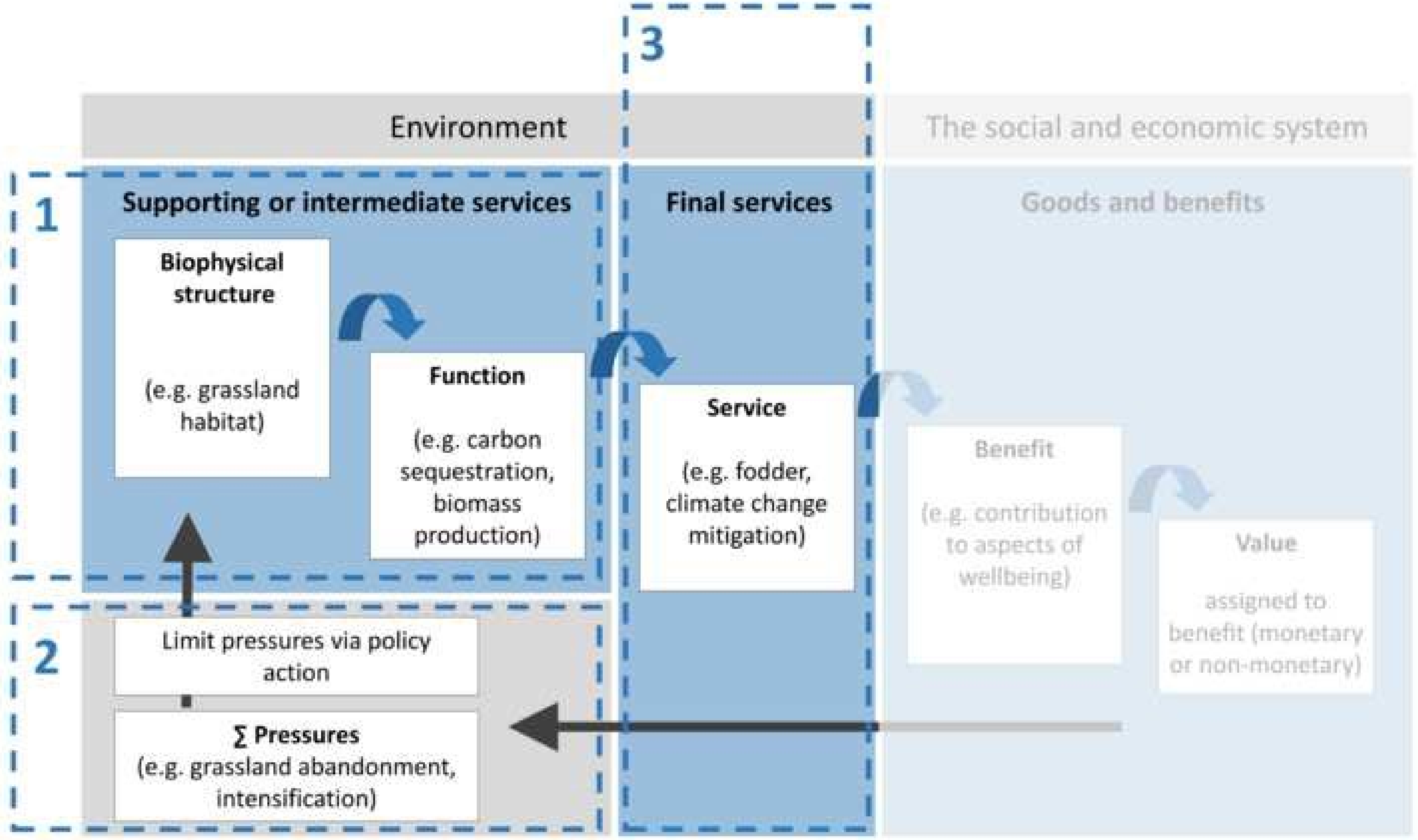
Variables	**r**	***p*-value**
Plant species richness & Wasps, bees & hoverflies richness	0.712	0.000
Plant species richness & Wasps, bees & hoverflies abundance	0.559	0.007
Plant species richness & Bumblebees richness	0.620	0.002
Plant species richness & Bumblebees abundance	0.644	0.001
Plant species richness & herbs for medicine	0.87	0.000

Table 6.Pearson's correlations between SOC and different ES indicators. Significance level was set at p<0.05.

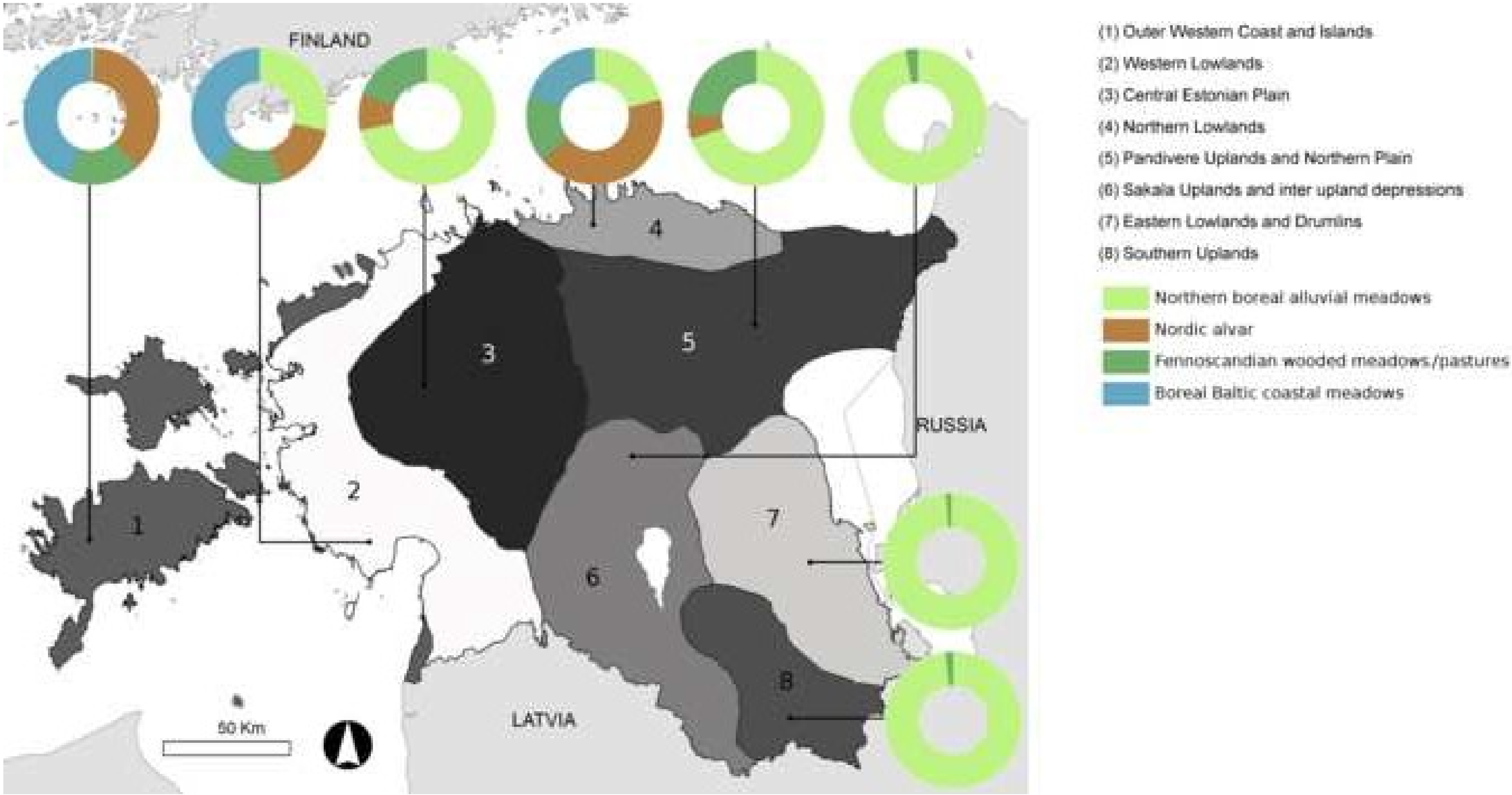
Variables	**r**	***p*-value**
Soil organic carbon & Biomass production	0.45	0.01
Soil organic carbon & Nitrogen(%)	0.99	0.000
Soil organic carbon & Microbial activity	0.96	0.000

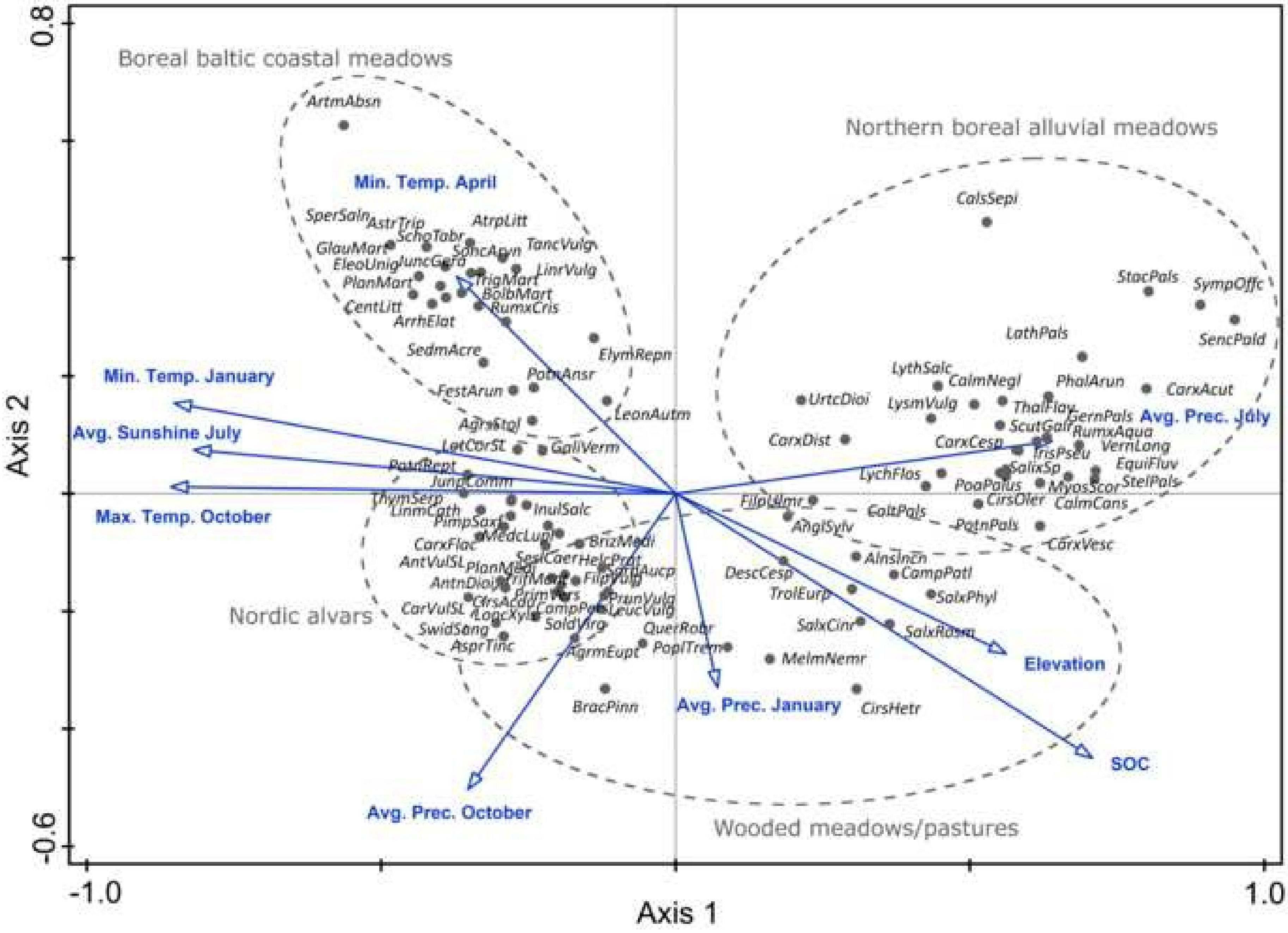
Table 7. Total area of multiple ES hotspots per grassland type and area of hotspots not eligible for agri-environmental support.

Habitat	**Total hotspot area (ha)**	**Area without agri-evironmental support (ha)**	**Area without support (% of total hotspot area)**
Boreal Baltic coastal meadows	101	26	25%
Nordic Alvars	398	198	50%
Northern boreal alluvial meadow	594	316	53%
Wooded meadows and pastures	816	317	39%
Total	1909	857	45%


3
Environment
The social and economic system
1
Supporting or intermediate services
Final services
Goods and benefits
Biophysical structure
(e.g. grassland habitat)
Function
(e.g. carbon sequestration, biomass production)
Service
(e.g. fodder, climate change mitigation)
Benefit
(e.g. contribution to aspects of wellbeing)
Value
assigned to benefit (monetary or non-monetary)
2
Limit pressures via policy action
∑ Pressures
(e.g. grassland abandonment, intensification)

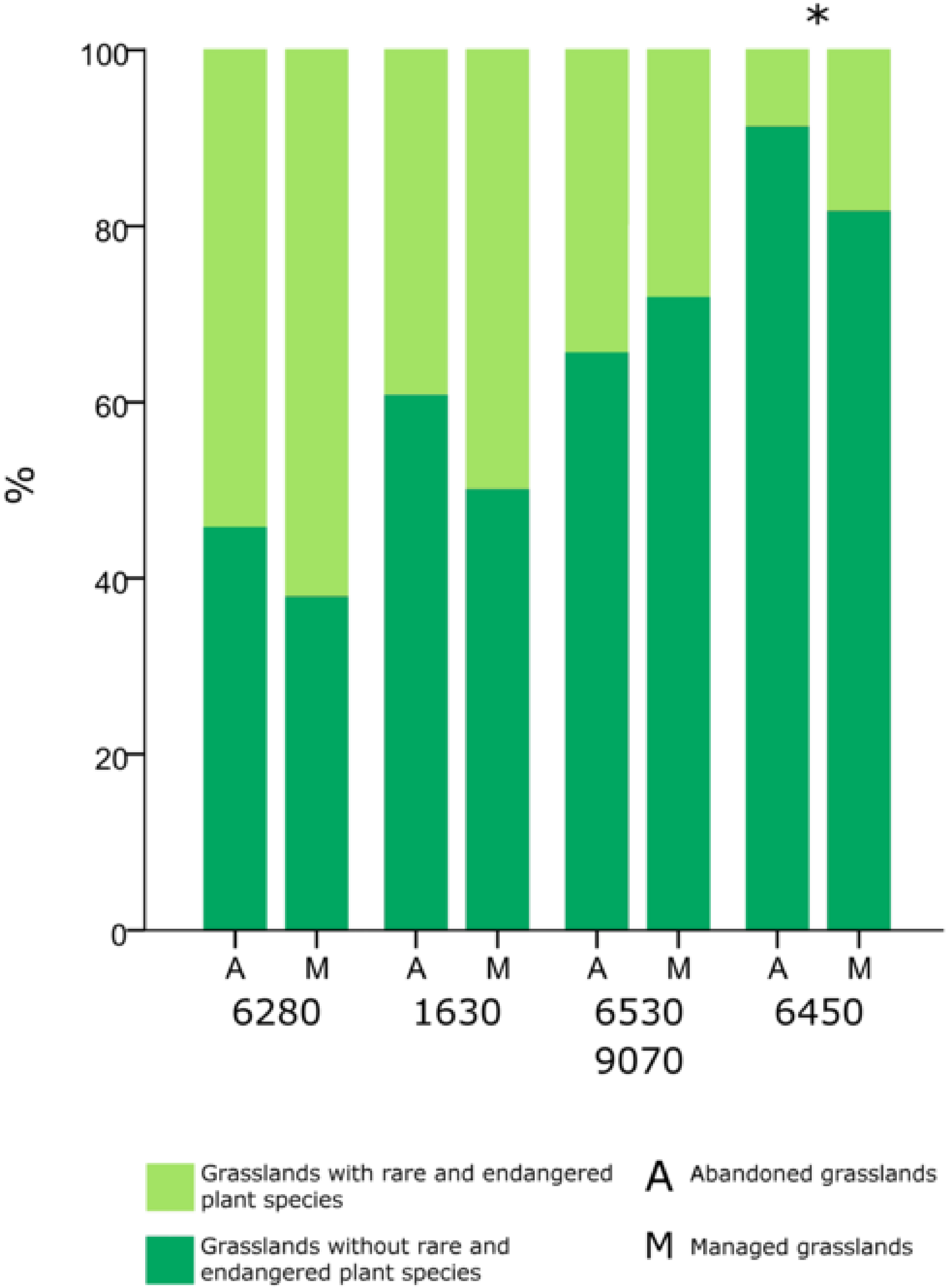
Figure


FINLAND
RUSSIA
LATVIA
1
2
3
4
5
6
7
8
50 Km
(1) Outer Western Coast and Islands
(2) Western Lowlands
(3) Central Estonian Plain
(4) Northern Lowlands
(5) Pandivere Uplands and Northern Plain
(6) Sakala Uplands and inter upland depressions
(7) Eastern Lowlands and Drumlins
(8) Southern Uplands
Northern boreal alluvial meadows
Nordic alvar
Fennoscandian wooded meadows/pastures
Boreal Baltic coastal meadows


Boreal baltic coastal meadows
Northern boreal alluvial meadows
Nordic alvars
Wooded meadows/pastures
Min. Temp. April
Min. Temp. January
Avg. Sunshine July
Max. Temp. October
Avg. Prec. October
Avg. Prec. January
Elevation
SOC
Avg. Prec. July
ArtmAbsn
SperSaln
AstrTrip
SchoTabr
AtrpLitt
GlauMart
SoncArvn
TancVulg
EleoUnig
JuncGerd
LinrVulg
PlanMart
TrigMart
BolbMart
CentLitt
RumxCris
ArrhElat
SedmAcre
ElymRepn
PotnAnsr
FestArun
LeonAutm
AgrsStol
LotCorSt
GaliVerm
PotnRept
JuncComm
ThymSerp
LinmCath
InulSalc
PimpSaxf
MedcLupl
CarxFlac
BrizMedi
SeslCaer
HelcPrat
AntVulSL
PlanMedi
TrifMont
FiliVulg
SorbAucp
AntnDioi
PrimVers
PrunVulg
CarVulSL
CirsAcau
CampPers
LeucVulg
SwidSang
LoncXylo
SoldVirg
AsprTinc
AgrmEupt
QuerRobr
PoplTrem
BracPinn
CalsSepi
StacPals
SympOffc
SencPald
LathPals
LythSalc
CalmNegl
PhalArun
CarxAcut
UrtcDioi
LysmVulg
ThalFlav
GernPals
ScutGalr
RumxAqua
CarxDist
CarxCesp
IrisPseu
VernLong
SalixSp
EquiFluv
LychFlos
PoaPalus
MyosScor
StelPals
CirsOler
CalmCans
FiliUlmr
CaltPals
AnglSylv
PotnPals
CarxVesc
AlnsInch
CampPatl
DescCesp
TrolEurp
SalxPhyl
SalxCinr
SalxRosm
MelmNemr
CirsHetr
0.8
-0.6
-1.0
1.0
Axis 1
Axis 2

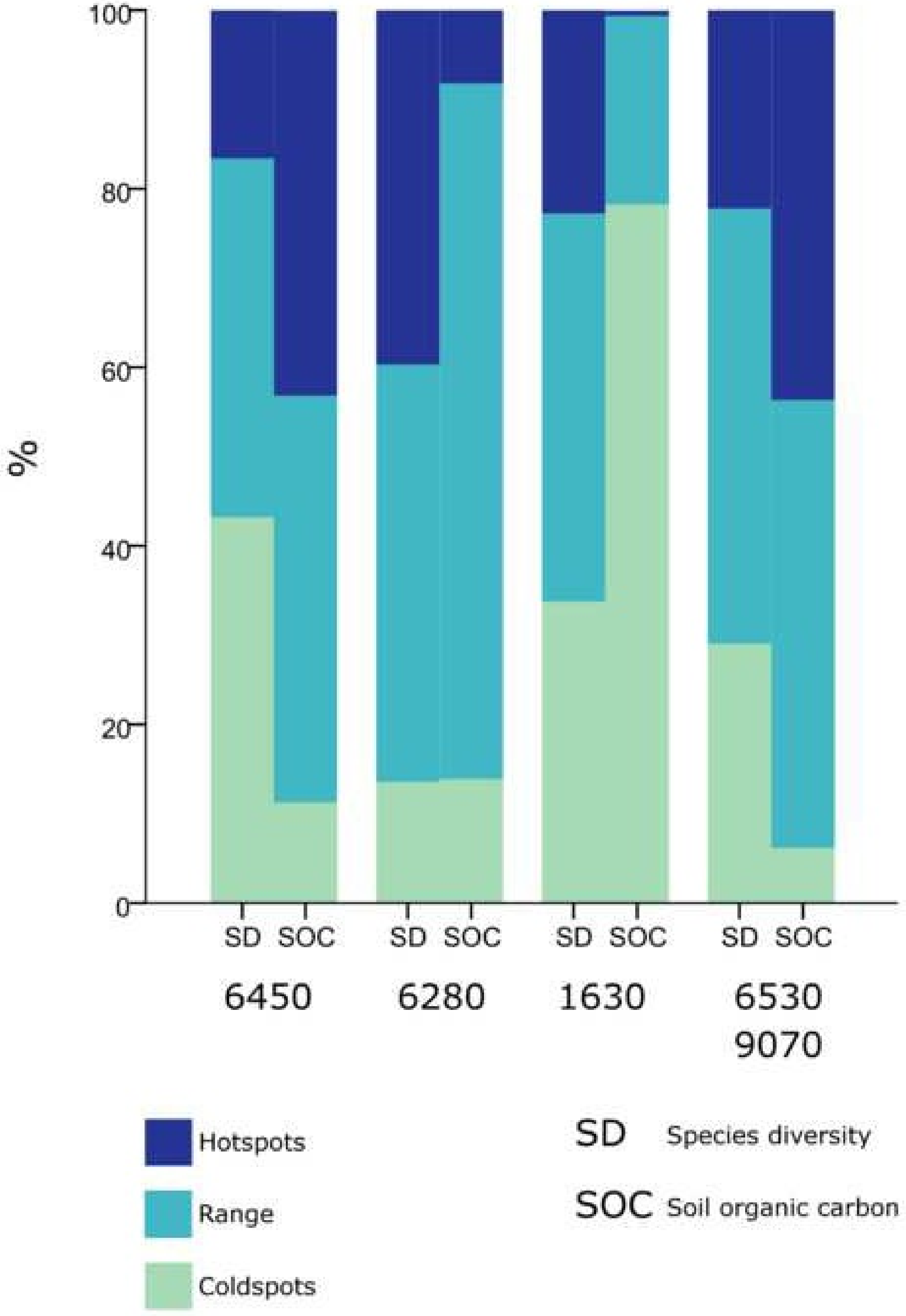
Figure

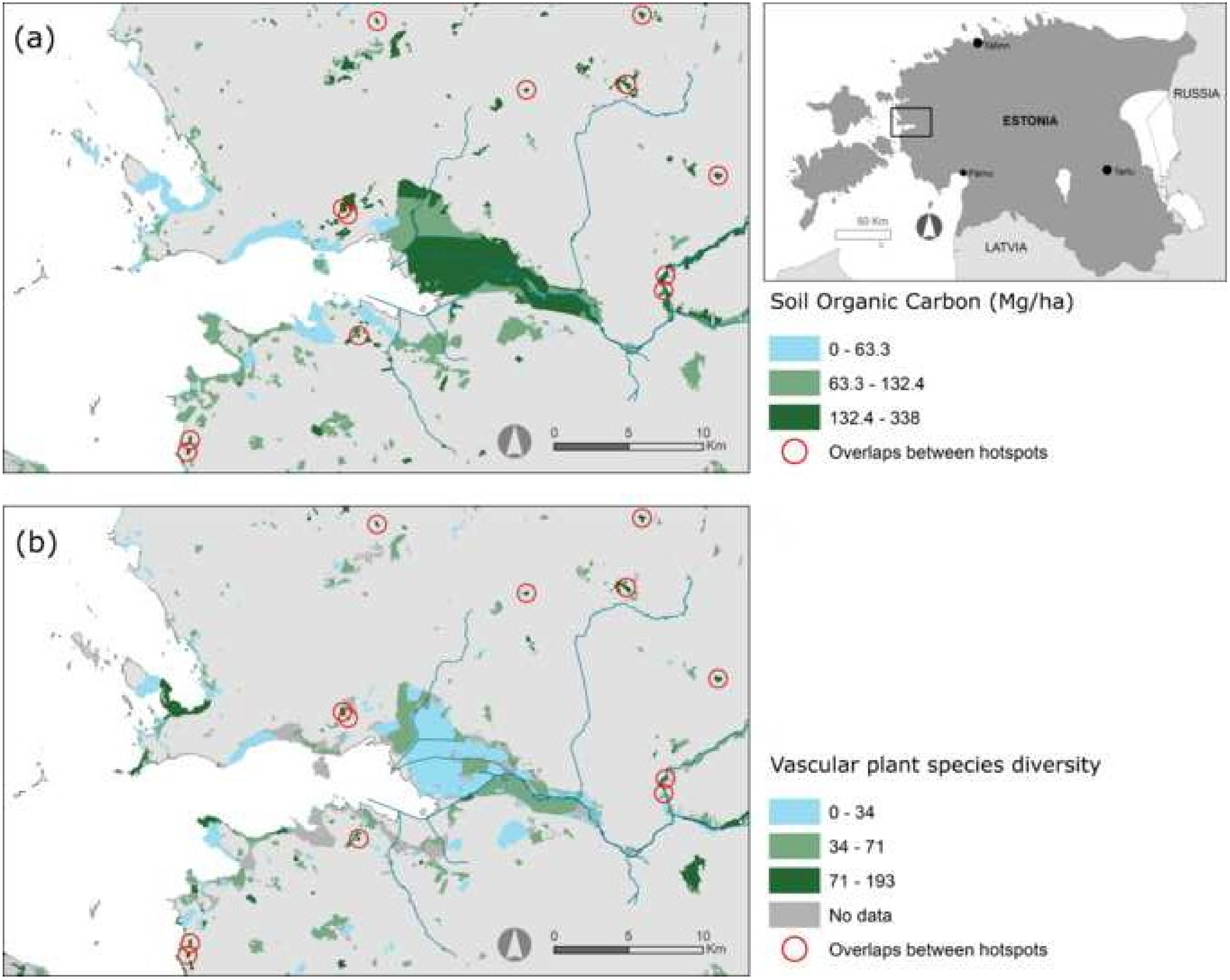
Click here to download high resolution image



Figure

Click here to download high resolution image




(a)
0
5
10
Km
ESTONIA
RUSSIA
LATVIA
Tallinn
Pärnu
Tartu
50 Km
0
Soil Organic Carbon (Mg/ha)
0 - 63.3
63.3 - 132.4
132.4 - 338
Overlaps between hotspots
(b)
0
5
10
Km
Vascular plant species diversity
0 - 34
34 - 71
71 - 193
No data
Overlaps between hotspots

Figure

Click here to download high resolution image