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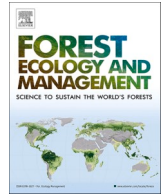**Title:** Abundance and diversity of edible wild plants in managed boreal forests

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Abundance and diversity of edible wild plants in managed boreal forests

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ABSTRACT

Boreal forests are rich in non-timber forest products from plants: wild berries and herbs used commercially or by households as food, medicine, decoration, or raw material. Approximately two hundred wild plant species have been documented for their nutritional uses in Finland, and many of these species occur in forests. However, the provisioning of edible plants by managed forests has received little attention, despite the fact that forest vegetation is altered by forest management practices. In this study, we use nation-wide forest vegetation and tree stand data consisting of a total of 1,778 sample plots to quantify the richness and abundance of edible wild plants in Finnish forests. Responses of edible species richness, abundance, and composition to stand characteristics such as site type, tree species composition, stand density, and management history are analyzed with regression models, NMDS ordination, and diagnostic species analysis, for forests on mineral soils and on peatlands separately. A total of 68 edible wild plant species occur in our dataset, with their occurrence and abundance varying between species and between sites. Our results indicate that habitat characteristics, namely site fertility and stand density, are the strongest determinants of overall edible plant provisioning. The richness of edible species as well as their total abundance were lower in less fertile site types and in denser stands. Recent timber harvesting and plantation as opposed to natural regeneration had a negative effect on edible species abundance in mineral soil forests. Several edible plant species confined to the richest site types accounted for the increase in species richness, while different forest management practices had generally none or a negligible number of diagnostic species. We conclude that a large and diverse set of edible wild plants occurs in Finnish forests, and the effects of stand characteristics and management on overall edible plant richness and abundance may be muddled by opposite species-level responses. Edible plant provisioning should be further analyzed at the level of smaller species groups or individual species to reveal the opportunities to support it in managed forests.

1. Introduction

Non-timber forest products (NTFPs) refer to products other than wood harvested from forests for human consumption as food, medicine, or decorative or raw material. Edible NTFPs, or wild foods, include mushrooms, berries, herbs, lichens, and parts of trees such as shoots and sap (Turner et al., 2011). The harvesting of NTFPs has a long history, and still today many people rely on or complement their diets with forest-based wild foods (Duchesne and Wetzel, 2002; Shanley et al., 2014). Exact estimates of their economic value are challenging to make, but overall NTFPs are believed to make significant contributions to livelihoods both in household use and as a source of income (Wahlén, 2017). Furthermore, they can be associated with important cultural and recreational values (Shanley et al., 2014). They therefore warrant consideration as a part of forests' value to humans.

Novel interests in the potential of edible wild plants to contribute to dietary improvements, rural development, and people's connectedness to nature have emerged in recent years (Łuczaj et al., 2012; Pinela et al., 2017; Turner et al., 2011). However, many open questions remain with regards to the compatibility of edible plant provisioning and forestry (Duchesne and Wetzel, 2002). Forest management for timber production is habitat-altering in several ways: it modifies stand structure and

composition and thereby canopy openness and light availability via tree species selection, thinning, and harvesting, and impacts soil conditions via litter composition, soil disturbance, drainage, and fertilization. The occurrence, abundance, and diversity of edible forest plants may be affected by these changes, either negatively or positively. Edible plant species are diverse and can vary widely in their habitat preferences, succession patterns, and resistance and resilience to disturbances. Forest management choices can also affect the yield of the edible part of the plant; for example, nitrogen fertilization has been found to decrease the yield of bilberry (*Vaccinium myrtillus*) independent of effects on plant cover (Granath and Strengbom, 2017).

Multifunctional forest management, i.e. management that supports the simultaneous provisioning of multiple forest ecosystem services and the maintenance of forest biodiversity, is of large and widely recognized importance throughout the world, as is the crucial role of forest research in supporting it (Gamfeldt et al., 2013; Mori et al., 2017). Multifunctional forest management requires that the ecological structures and processes that underlie ecosystem services as well as their responses to management interventions are understood. A key part of this is knowledge on the occurrence patterns of forest species and the community-structuring effects of management practices (Thompson et al., 2011). Much of the research on reconciling NTFP provision with timber production has been focused on tropical contexts (Guariguata et al., 2010; Lawrence, 2003). However, the interest in wild foods is growing also in northern regions. For example, in British Columbia, Canada, Clason et al. (2008) studied the effects of thinning and fertilization treatments on edible and berry-producing herbs and shrubs, and found their total cover to be higher in thinned and fertilized stands than unthinned and old-growth stands. Their results suggest potential for promoting the provisioning of these NTFPs especially in young managed stands. Besides NTFP provisioning, understory and shrub layer vegetation plays a major role in fundamental ecosystem functions in northern forests (Nilsson and Wardle, 2005), making the understanding of its interactions with forest management of high importance.

In boreal Finland, approximately 200 wild vascular plant species are edible (Rikkinen, 2018). At least one third of them are adapted to grow primarily or secondarily in forests (Hämet-Ahti et al., 1986). Depending on the species, different parts of the plant – leaves, flowers, fruit, seeds, or roots – can be edible, and can be used as ingredients in various kinds of foods or drinks. In most cases the collection of wild plants for food falls under the so-called everyman's rights. Historically, the nutritional use of many wild plants in Finland has been characterized by the necessary improvement of people's subsistence in the northern low-productivity climate, emergency use during famines or depression, and connections to traditional medicine (Rautio et al., 2014), and the use of edible wild plants declined with the advance of modernized agriculture, trade, and urbanization. However, a re-emergence of interest in wild foods has taken place since the late 20th century, influenced in recent years e.g. by evidence of their health-promoting properties (Hohtola, 2010).

Finnish forests have been subjected to multiple human uses and impacts for centuries. In the 20th century the management of Finnish forests became dominated by rotation forestry that aims at efficient timber production for the needs of the forest industry (Kotilainen and Rytteri, 2011). The disturbance and successional dynamics of managed production forests differ substantially from those in natural conditions (Kuuluvainen, 2009, 2002), causing changes in forest ecosystems and landscapes that directly affect species occurrence (Tikkanen et al., 2006) and thereby potentially the abundance of edible plant species. Reflecting global trends, the stated goals of Finnish forest management have diversified beyond timber production in recent years to include biodiversity conservation, climate change mitigation, and maintenance of other ecosystem services (Äijälä et al., 2014; National Forest Strategy 2025, 2015). The relationship of forest management and non-timber benefits has become a central topic of research (Pohjanmies et al., 2017), including some NTFPs. For example, several studies have

examined the impact of stand management practices on bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*) yields and identified management practices that reconcile berry production with traditional forestry goals (Kilpeläinen et al., 2018; Miina et al., 2016, 2009; Turtiainen et al., 2013). In addition to bilberry and cowberry, also the availability of mushrooms (Tahvanainen et al., 2016) and non-timber products from trees (shoots, leaves, bark, resin, and sap) (Kurttila et al., 2018) in managed forests have been studied, with conclusions suggesting that modifications to conventional management regimes are required to support their provisioning.

Besides the most common wild berries, the harvesting of other edible forest plants is not regularly monitored in Finland (Peltola, 2014) and the variation in their supply has not been studied as extensively. Yet, forestry activities and other human impacts are known to alter forest vegetation (Hedwall et al., 2019, 2013; Tonteri et al., 2016; Vanha-Majamaa et al., 2017). In this study, we compile a list of edible wild plant species from literature and use extensive plant survey data to quantify their richness and abundance in Finnish forests. Combining these data with stand inventory data, we evaluate the responses of edible species richness and abundance to stand characteristics to initiate an exploration of the opportunities to reconcile their production with commercial forestry. In addition, we analyze the edible plant species community composition to explore which species are associated with what kinds of forests and which typically occur together. We anticipate that edible plants represent a diverse subset of forest plants and that their richness, abundance, and composition is affected by stand characteristics that have been previously shown to affect forest vegetation. Specifically, we hypothesize 1) that due to a sampling effect, edible plant richness is higher in more fertile sites that are in general more species-rich (Heikkinen and Mäkipää, 2010; Widenfalk and Weslien, 2009), and 2) that edible plant abundance is higher in open stands due to higher light availability and higher coverage of light-favoring species, but lower in recently harvested stands due to the negative effects of harvesting and soil disturbance on species like bilberry (Hedwall et al., 2013; Tonteri et al., 2016). In addition, we hypothesize 3) that edible species composition differs between stands of varying fertility, young and old stands, recently harvested and unharvested stands, and drained and undrained stands (Hart and Chen, 2008; Kaarlejärvi et al., 2020; Maanavilja et al., 2014; Salemaa et al., 2008).

2. Methods

2.1. Study area and data

Finland is the most forested country in the world (FAO, 2015). Finnish forests are part of the boreal zone, with comparatively low vascular plant species diversity. Forest stands are typically dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and/or birch (*Betula pendula* or *B. pubescens*), and the understory by a handful of dwarf shrubs but a rich bryophyte and lichen flora (Esseen et al., 1997; Salemaa et al., 2008). Forests grow both on mineral soils (herb-rich forests and heath forests) and on peatlands, with differences in growth conditions, vegetation, and management (Korhonen et al., 2017; Tomppo, 1999).

We used tree stand and vegetation data collected in Finland in 1985–1986 in connection with the Finnish National Forest Inventory (Mäkipää and Heikkinen, 2003). The inventory was carried out on a systematic sampling network that spanned the entire country and covered all types of forestry land on mineral soils and peatlands. The sampling network consisted of sample plot clusters. In southern Finland, the clusters were located evenly along a 16 km × 16 km grid, and each cluster consisted of four sample plots spaced 400 m apart. In northern Finland, the clusters were located along a 24 km × 32 km grid, and each cluster contained three sample plots spaced 600 m apart. The sample plots were circular with a 9.77 m radius (area 0.03 ha).

In the inventory, the sample plots were described in terms of site

type, soil type, drainage status, and age and development stage of the tree strata. Recent harvesting, stand management, and soil management actions were identified and their timing estimated. The tree basal area (m^2 ha^{-1}) was measured for Scots pine, Norway spruce, and deciduous trees collectively. The canopy cover of each tree species was assessed, including tree saplings that were part of the shrub layer (<1.5 m in height) or field layer (<0.5 m in height). We calculated total canopy cover by combining the cover values from the different layers using the Jennings-Fischer formula (Chytrý et al., 2020; Jennings et al., 2009) that accounts for partial overlap of vegetation layers.

Field and ground layer vegetation was surveyed in four to six rectangular, systematically positioned, 2 m^2 sampling quadrats per sample plot. The cover of all vascular plants and ground-dwelling bryophytes and lichens was visually estimated within the quadrats with a percentage cover scale, with the following class centres: 0.1, 0.2, 0.5, 1, 2, 3, 5, 7, between 10 and 90 with an interval of 5, 93, 95, 97, 98, 99, 100; 31 classes in all. The cover values were averaged across the quadrats to produce an estimate for the sample plot. In addition, all vascular plants observed in the plot but not in the sampling quadrats were recorded and included in the dataset with a cover of 0.1%. The cover of all species in the shrub layer was assessed for the entire sample plot. We calculated cover values for taxa occurring in both shrub and field layers with the Jennings-Fischer formula.

The inventories were conducted in a total of over 3,000 sample plots. We applied several data selection criteria to improve the consistency and representativeness of the data set. First, in the inventories, if the sample plot was located over more than one forest type or forestry stand (i.e. a parcel of forest that is homogenous in structure and type and used as the operational unit in forest management), it was divided according to the stand borders. Thus, also the vegetation sampling quadrats from one sample plot could be divided between stands representing different growth conditions. In this study, we used only sample plots that were within a single stand, so that all plots were described by the same minimum number of sampling quadrats (i.e. four). Second, we included only plots classified as forest land (where tree growth is $\geq$ 1 m^3 ha^{-1} $year^{-1}$). After these restrictions, the sample size of some habitat types (barren heath forests, fjell forests, *Sphagnum fuscum* pine bogs) was very small (less than five) so those plots were excluded. Three sample plots that were found as outliers in the ordination analysis (analyses described below) were also excluded. The final dataset contained 1,778 sample plots, of which 1,271 were on mineral soils and 507 on peatlands. Because of the restrictions imposed by the data selection, the original sample plot cluster structure was weakened with many clusters represented by only one sample plot. Sample plot cluster was still tested as a random effect in the statistical models (described below) but was found non-significant and was ultimately excluded.

2.2. Edible plant species

A list of edible wild plant species, i.e. species used as food or food supplement and thus known or assumed to be nutritious and/or safe to consume (Turner et al., 2011), was compiled from literature describing the traditional or more recent use of wild plants as food in Finland (Appendix A). Plants with edible parts include several trees (e.g. *Betula* spp., *Picea abies*, *Sorbus aucuparia*), but to focus on edible plant species not directly targeted in stand management, including in tending and thinning of young stands, we excluded tree species. We also excluded species that are red-listed Finnish Environment Institute (SYKE) et al. (2019), occurring only as casual, or that have been shown to be toxic despite historic nutritional use. We note that some forest and peatland plants are collected and used for cosmetics and medical products (e.g. *Rhododendron tomentosum* and *Drosera* spp.), but we focus here on edible plants only. Taxa were included at the genus level if they are challenging to identify in the field to the species level and if all species of the genus are edible (e.g. *Taraxacum* spp.). This produced a list of 173 taxa. Out of these species, 69 have cultural, human-modified, or semi-natural

habitats as their primary habitat, 30 have herb-rich or heath forests on mineral soils as their primary habitat, and 7 have mires as their primary habitat (Finnish Environment Institute (SYKE) et al., 2019).

Out of the 173 compiled taxa, 68 were observed in the dataset (Appendix A). Here, 31 species have cultural habitats, 20 species have herb-rich or heath forests, and 7 species have mires as their primary habitat (Appendix A). The compiled list includes plants with virtually every part described as edible (e.g. *Taraxacum* spp.) as well as ones with the usage as food limited to berries (e.g. *Vaccinium microcarpum* and *V. uliginosum*) or flowers (e.g. *Calluna vulgaris*) (Appendix A). Henceforth we will refer to the compiled list collectively as edible plants.

We used three measures of edible plant provisioning: edible species richness (i.e. total number of edible plant species), richness of edible species with percentage cover $\geq$ 1% (to focus on species with established presence on the site), and total abundance (i.e. summed percentage cover of edible species).

2.3. Analyses

We constructed multiple regression models of edible species richness and abundance as functions of stand characteristics. A Poisson distribution with log-link was assumed for edible species richness and richness of edible plant species with $\geq$ 1% cover. Total abundance was logit transformed (x' = log(x/(1-x)), where x = total abundance/1000) to correct for skewness and the transformed values were modeled with standard linear regression. Models were created separately for forests on mineral soils (n = 1271) and forests on peatlands (n = 507).

As explanatory variables, we used stand properties: geographical location (latitude and longitude), altitude (m above sea level), vegetation zone (Ahti et al., 1968), site type (Pohjanmies et al., 2020), soil type, regeneration method, drainage status, recent harvesting history (harvesting within the past 10 years), soil management, stand development stage, stand age (years), basal area (m^2 ha^{-1}), canopy cover, and basal area of different tree species (m^2 ha^{-1}) (Appendix B). Site types were coded for mineral soils and peatlands as parallel fertility classes 1–5 with class 1 as the most fertile (Appendix B: Table S2). Before constructing the models, we calculated correlations between all possible explanatory variables. For numeric variables, we used Pearson's correlation. Correlation between two categorical variables was calculated with Cramér's V, and correlation between one numeric and one categorical variable was calculated as the correlation between observed and predicted values, i.e. the true values and mean values within categories. Variables that were highly correlated were not used in the same model.

Model construction was carried out in a stepwise fashion. Initial models were created with the explanatory variables that were most strongly correlated with the response variables, i.e. that were the best predictors of the response variable. On mineral soils: For species richness and richness of species with $\geq$ 1% cover, models were initialized with site type and basal area of different tree species as explanatory variables. For total abundance, the initial model was created with site type and stand age as explanatory variables. On peatlands: For species richness, models were initialized with site type and basal area of spruce as explanatory variables. For richness of species with $\geq$ 1% cover, models were initialized with site type and basal area of deciduous trees as explanatory variables. For total abundance, the initial model was created with site type and stand age as explanatory variables. In addition, vegetation zone was a required variable in all models due to earlier research showing the strong covariation between latitude and forest vegetation composition (Tonteri et al., 1990). Variables were then tested and added into the models hierarchically and model improvement was assessed based on Akaike information criterion (AIC). Interaction effect between vegetation zone and site type was also tested. As more variables were added to the models, the differences in AIC between models could become very small. To select the final models as ones with best predictive ability, between four and seven models with the lowest AIC and with all significant effects (p-value < 0.05) were further assessed with

four-fold cross-validation, where the data was split into 75% training sets and 25% test sets. Mean squared prediction errors were calculated for the test sets and the final models were selected based on the lowest mean error. Final model performance was evaluated with pseudo-R^2, calculated as 1 - (Residual Deviance/Null Deviance), for the Poisson regression models, and adjusted R^2 for the standard linear regression models. All models were fitted in R v. 3.6.0.

To facilitate the interpretation of the results of the regression analysis, we analysed and visualised the relationship of species composition and the same explanatory variables as used in the regression models, and additionally edible species richness and abundance with NMDS-ordination using vegan package (Oksanen et al., 2019). We calculated the distances based on Sørensen similarity index from Wisconsin-transformed species community data; we omitted species with a frequency of ≤ 2 as they can heavily influence NMDS-ordination (Poos and Jackson, 2012) but their occurrence can be coincidental. We settled with a three-dimensional solution, where the stress was reduced to 0.148 for forests on mineral soils and to 0.153 for forests on peatlands. The correlation of explanatory variables (n = 17) and the NMDS-ordination was tested with env_fit-function and the alpha level was Bonferroni adjusted to 0.003. Ordination graphs with the explanatory variables with the best

fit based on squared correlation coefficient ($r^2 > 0.25$) with NMDS-ordination space are presented in the results. We used ordisurf-function with default settings to calculate and draw smooth surfaces for continuous variables.

In addition, we used Juice program (Tichý, 2002) to define diagnostic species based on phi coefficient (Chytrý et al., 2002) and constancy ratio (Dengler, 2003) for classes of categorical explanatory variables that were found significant in the regression models. Both values were calculated on presence-absence data. The strength of the phi coefficient is that it accounts for unequal sample sizes. To obtain robust diagnostic species, we set the threshold for phi-value for 0.2 and constancy ratio to 1.5, meaning that the relative abundance of the species in the class (or classes) in question must be 1.5 times higher as in any other class of the explanatory variable. Finally, we tested the statistical significance of the diagnostic species with Fisher's exact test and accepted only those that obtained p-values < 0.05.
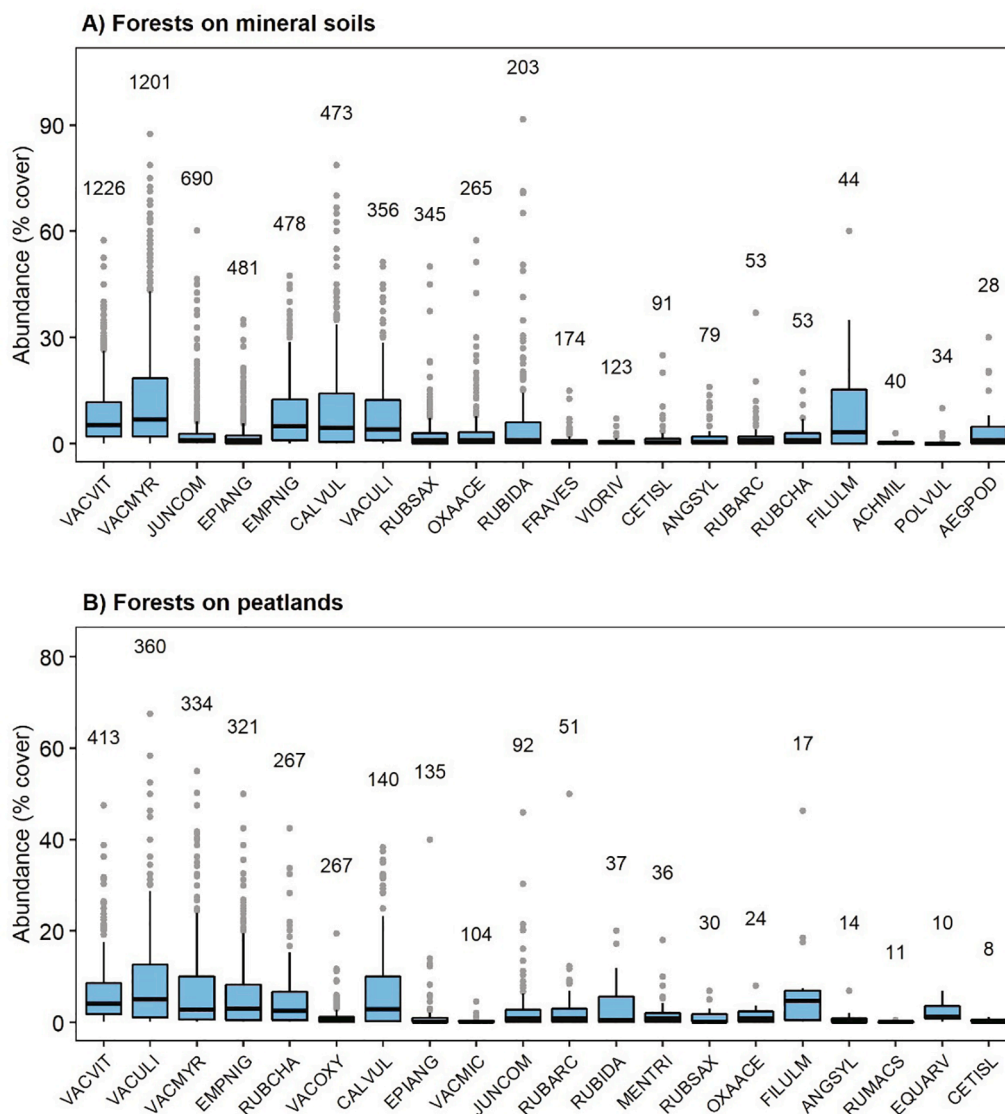
Fig. 1. Box-and-whiskers plots showing the distributions of the non-zero percent cover values of the twenty most common species in the data set. The number above the plotted values shows the number of observations of the species in the dataset (i.e. number of non-zero percent cover values). Abbreviations for species names are explained in Appendix A.

3. Results

3.1. Richness and abundance of edible plant species

Majority of the examined species were both rare (occurring in few sample plots) and scarce (low in abundance when present). The most common species were *Vaccinium vitis-idaea* (observed on 96% and 81% of the plots on mineral soils and on peatlands, respectively) and *V. myrtillus* (on 94% and 66% of the plots on mineral soils and on peatlands, respectively). An additional nine species were observed on more than 10% of the plots on both mineral soils and peatlands (Fig. 1). Based on the diagnostic species analysis, *Juniperus communis, Rubus saxatilis, Oxalis acetosella, Fragaria vesca,* and *Viola riviniana* were strong characters, i.e. clearly associated and relatively frequent, of forests on mineral soils, and *Vaccinium oxycoccos, Rubus chamaemorus, Vaccinium uliginosum, Vaccinium microcarpum* and *Menyanthes trifoliata* of forests on peatlands. A few species (*Vaccinium vitis-idaea*, *V. myrtillus*, *V. uliginosum, Empetrum nigrum,* and *Calluna vulgaris*) were common on both mineral soil and peatland plots.

Total edible species richness and abundance across the sample plots were skewed towards low values (Fig. 2). On plots on mineral soils, the mean number of edible plant species was 5.4 (SD = 2.1, SE = 0.06), mean number of species with $\geq 1\%$ cover was 3.5 (SD = 1.4, SE = 0.04), and mean total abundance was 35.8% (SD = 23.0%, SE = 0.64%). The correlation between total plant species richness and edible species richness on mineral soils was 0.63 (p-value < 0.001). On plots on peatlands, the mean number of edible plant species was 5.4 (SD = 1.8, SE = 0.08), mean number of species with $\geq 1\%$ cover was 3.3 (SD = 1.6, SE = 0.07), and mean total abundance was 27.6% (SD = 19.9%, SE = 0.88%). The correlation between total plant species richness and edible species richness was 0.57 (p-value < 0.001). All sample plots had at least one edible plant species present, as the smallest observed value of species richness was 1 and of total abundance 0.1%. The highest observed number of edible species on a plot was 18 on mineral soils and 14 on peatlands, and the highest total abundances were 135% on mineral soils

and 118% on peatlands (Fig. 2). As the cover of each species is evaluated separately and species can grow in layers and interlace in the understorey, the total abundance within a sampling plot can sum up to over 100%.

3.2. Impacts of stand characteristics

3.2.1. Mineral soils

On mineral soils, statistically significant associations (p-value greater than 0.05) were observed between all response variables and site type, basal area of tree species, and east coordinate (longitude) of the sample plot. Compared with the most fertile site type 1 (herb-rich forests), the less productive the site type the lower was the edible species richness (Table 1). Likewise, total abundance of edible plants was lower in the other site types compared with herb-rich forests, but the effect did not become stronger in less fertile types. Basal area of all tree species had a negative association with edible species richness, and basal area of spruce and deciduous species had a negative association with edible species abundance. Longitude had a positive association with all response variables.

In addition to site type, basal area, and longitude, vegetation zone and harvesting history had a statistically significant association with richness of edible species with $\geq 1\%$ cover and with total edible plant abundance. The effect of harvesting was negative and stronger for final felling (i.e. clear-cut harvest) than other types of harvesting, as compared with no harvesting. Richness of edible species with $\geq 1\%$ cover was higher in northern boreal zone and total edible plant abundance was higher in middle and northern boreal zone than the reference (hemiboreal zone).

Finally, statistically significant associations were found also between total edible plant abundance and stand age, soil type, and regeneration method. The association with stand age was positive, with higher stand age indicating higher total abundance. Stands that had been naturally regenerated had higher abundance than planted stands. Stands where the soil type was coarse (sand or gravel) or coarse moraine had lower
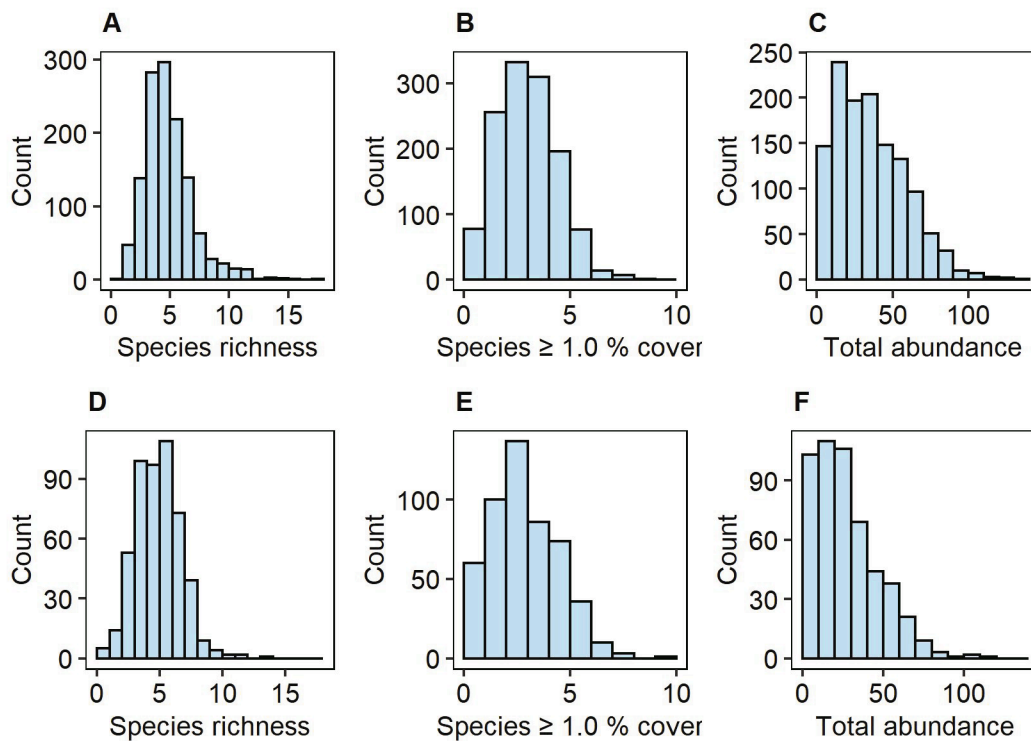
Fig. 2. Distributions of edible species richness (number of species observed in the sample plot), richness of edible species with $\geq 1\%$ cover, and total abundance (total percent cover) values. Panels A-C: plots on mineral soils; panels D-F: plots on peatlands.

Table 1
Estimates of regression parameters, calculated effect sizes, and coefficient of determination (R^2) for edible species richness and abundance on mineral soils. Statistically significant effects are shown in bold. Significance levels of the estimated parameters: *** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; . $0.05 < p < 0.1$. Note that for total edible abundance the effects are for the odds ratio (x/(1-x), where x = total abundance / 1000).

	Edible species richness			Richness of edible species with $\geq$ 1% cover			Total edible plant abundance		
	Parameter		Effect	Parameter		Effect	Parameter		Effect
Intercept	**2.167**	***	**8.73**	**1.065**	***	**2.90**	**−4.026**	***	**0.02**
Site type 2 (ref. 1)	**−0.161**	*	**0.85**	−0.194	.	0.82	**−0.686**	***	**0.50**
Site type 3	**−0.633**	***	**0.53**	**−0.493**	***	**0.61**	**−0.601**	***	**0.55**
Site type 4	**−0.669**	***	**0.51**	**−0.506**	***	**0.60**	**−0.640**	***	**0.53**
Site type 5	**−0.792**	***	**0.45**	**−0.611**	***	**0.54**	**−0.583**	**	**0.56**
Veg. zone southern boreal (ref. hemiboreal)	−0.073		0.93	0.014		1.01	0.123		1.13
Veg. zone middle boreal	−0.090		0.91	0.124		1.13	**0.411**	**	**1.51**
Veg. zone northern boreal	−0.107		0.90	**0.220**	*	**1.25**	**0.489**	***	**1.63**
BA pine	**−0.005**	**	**1.00**	−0.003		1.00			
BA spruce	**−0.014**	***	**0.99**	**−0.018**	***	**0.98**	**−0.025**	***	**0.98**
BA deciduous	**−0.013**	***	**0.99**	**−0.013**	**	**0.99**	**−0.027**	***	**0.97**
Longitude	**0.011**	*	**1.01**	**0.028**	***	**1.03**	**0.037**	***	**1.04**
Stand age							**0.003**	***	**1.00**
Harvest 'Other' (ref. No harvest)				−0.089	*	0.99	**−0.229**	***	**0.80**
Harvest Final felling				−0.154	*	0.86	**−0.453**	***	**0.64**
Soil type Coarse moraine (ref. Rocky)							**−0.290**	*	**0.75**
Soil type Fine moraine							−0.118		0.89
Soil type Coarse							**−0.485**	***	**0.62**
Soil type Fine							−0.235	.	0.79
Regeneration Natural (ref. Plantation)							**0.216**	***	**1.24**
R^2	0.328			0.254			0.251		
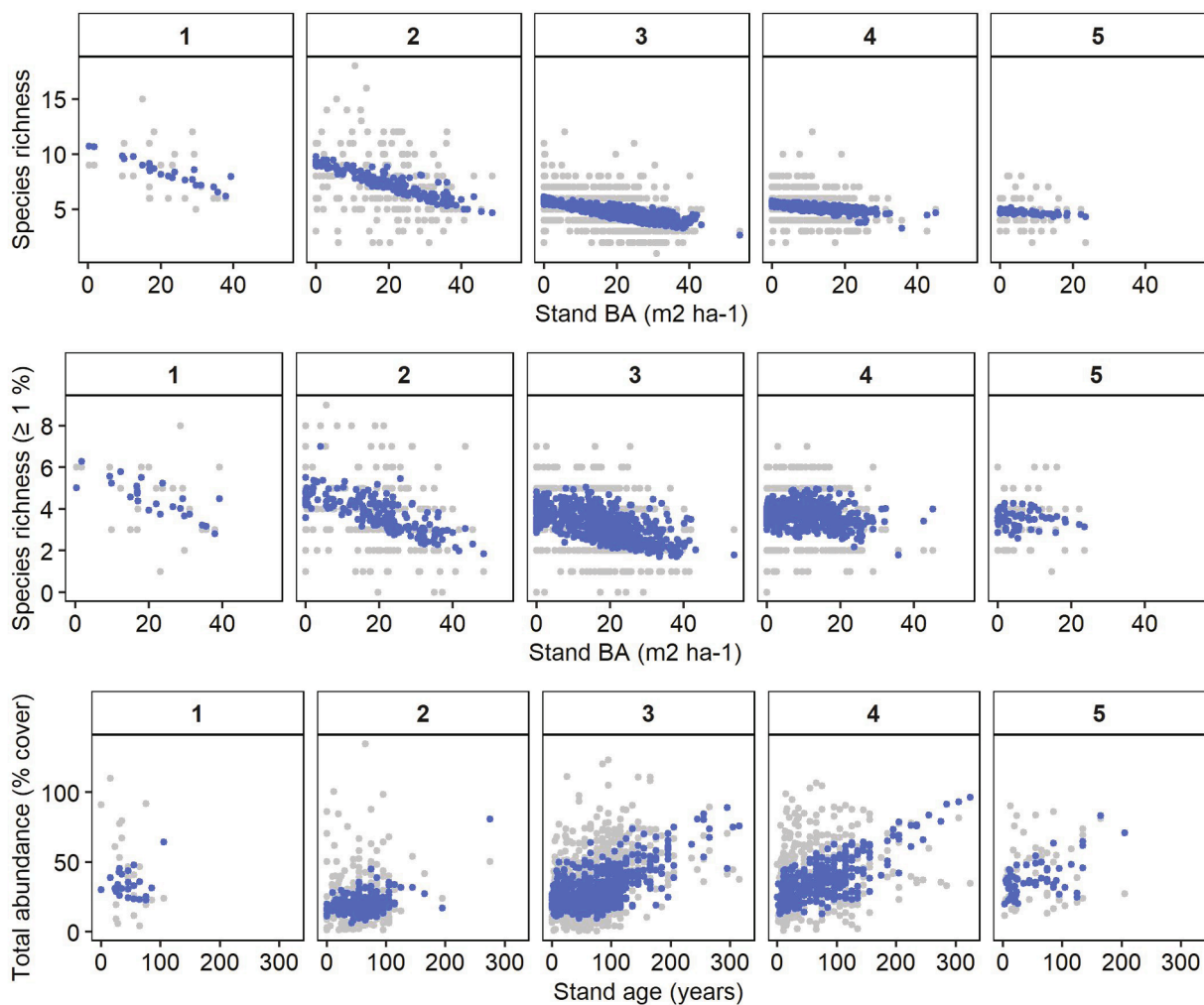
Fig. 3. Edible species richness and abundance on plots on mineral soils by site type (panels) and stand basal area (BA) or age (x-axis). Shown are the true observed values (in grey) and the model predictions (in blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundance than the reference rocky.

The fit of the models was relatively weak (coefficient of determination ranging from 0.251 to 0.328; Table 1). In particular, the models were not able to predict the lowest and highest values (Fig. 3).

3.2.2. Peatlands

The effects of stand characteristics on edible species richness and abundance were less clear on peatland plots than on mineral soils. An effect of site type was observed only on edible species richness: species richness was significantly lower in site type 3, 4, and 5 than the reference type 1, but no significant difference was found between types 1 and 2 (Table 2). Basal area of spruce had a negative association, and altitude had a positive association with edible species richness and richness of edible species with ≥ 1% cover. The latter was negatively affected also by the basal area of deciduous species, and positively by stand age. Total edible plant abundance was found to be significantly affected only by stand age and longitude, both effects positive. In addition, total edible plant abundance was, on average, significantly higher in the northern boreal zone than the reference (southern boreal). Overall, the models fit the data quite poorly (coefficients of determination ranging from 0.118 to 0.180; Table 2). Similarly to the models constructed for mineral soils, these models failed to predict the low and high extremes of the observations (Fig. 4).

3.3. Species composition

For both the forests on mineral soils and peatlands, the correlation of all the explanatory variables with the NMDS-ordination space, except for harvest and longitude for peatlands, were found to be statistically significant even after Bonferroni correction (p-values < 0.003). However, most of the variables had very low fits. The explanatory variables that had the best fit with the NMDS-ordination space ($r^2 > 0.25$) for forests on mineral soils were edible species richness ($r^2 = 0.66$, p-value < 0.001), site type ($r^2 = 0.33$, p-value < 0.001), latitude ($r^2 = 0.37$, p-value < 0.001), and basal area of spruce ($r^2 = 0.32$, p-value < 0.001), and for peatlands basal area of spruce (r2 = 0.33, p-value < 0.001), edible species richness ($r^2 = 0.28$, p-value < 0.001), and site type ($r^2 = 0.25$, p-value < 0.001). The r^2 values sum up to over 100% due to intercorrelations among explanatory variables.

Compared with the explanatory variables selected for the regression models, the results were similar but not identical: harvesting method, longitude and basal area of pine and deciduous trees, which were found statistically significant for edible species richness of mineral soils and/or peatlands, had very low fits with the NMDS-ordination space. Besides site type, categorical variables had very low fits and only a few species reached the criteria for being diagnostic (Table 3 and 4). Nevertheless, as an example can be mentioned *Epilobium angustifolium* and *Rubus*

idaeus, which were diagnostic for both final felling and regeneration by plantation on mineral soils (Table 3), and on peatlands *E. angustifolium* was also diagnostic for the same variables, while *Vaccinium microcarpum* was diagnostic for sites with no harvest (Table 4).

3.3.1. Mineral soils

Based on the diagnostic species analysis and NMDS-ordination, edible species richness appeared to be influenced by differences in species composition between the site types on mineral soils. The NMDS ordination illustrates that site types were mainly separated along the NMDS axis 1. (Fig. 5). However, the turnover was relatively gradual and between adjacent site types along the site type series, none or only a few diagnostic species were identified, except for the herb-rich forests and herb-rich heath forests (Table 3). The most striking difference in species composition was between types 1 & 2 combined (herb-rich forests and herb-rich heath forests) against the other, less productive heath site types, which was reflected in a great number of diagnostic species associated with the former two types, e.g. *Rubus saxatilis*, *Oxalis acetosella*, *Rubus idaeus* and *Fragaria vesca* (Table 3). Type 1 (herb-rich forests) had clearly the highest number of diagnostic species, such as *Aegopodium podagraria*, *Viola canina*, *Equisetum arvense* and *Anthriscus sylvestris,* which practically did not occur in other types (Table 3). On the other hand, types 2 (herb-rich heath forests) and 3 (mesic heath forests) hosted a wider amplitude of species, which was reflected in a large hull area (Fig. 5). *Calluna vulgaris* and *Empetrum nigrum* were diagnostic for the two least fertile types, and *Cetraria islandica* for xeric heath forests (Table 3).

As detected by the regression models, high edible species richness was clearly associated with the two most fertile site types, and among others, the same species as listed above as diagnostics of forests of those types accounted for the increased species richness in the NMDS-ordination space for mineral soils (Fig. 6).

Basal area of spruce showed quite a different trend in the NMDS-ordination than edible species richness. *Vaccinium myrtillus*, *Oxalis acetosella*, *Ribes* spp., *Rubus saxatilis* and *Polygonum vulgare* appeared to be associated with high basal area of spruce, while e.g. *Cirsium arvense*, *Empetrum nigrum*, and *Cetraria islandica* were associated with low basal area of spruce (Fig. 7).

The species composition changed along the latitudinal gradient and the main trend was similar to that of edible species richness, even though based on the regression models vegetation zone (which is strongly correlated with latitude) was not found to strongly explain species richness patterns. *Vaccinium oxycoccos*, *Rubus chamaemorus* and *Arctous alpina*, among others, appeared to be associated with northerly latitudes, while *Ribes spicatum*, *Oxalis acetosella,* and *Aegopodium podagraria* with southerly latitudes (Fig. 8). For peatlands, the fit of latitude was very low and is therefore not presented in the results.

Table 2
Estimates of regression parameters, calculated effect sizes, and coefficient of determination (R^2) for edible species richness and abundance on peatlands. Statistically significant effects are shown in bold. Significance levels of the estimated parameters: *** p < 0.001; ** 0.001 < p < 0.01; * 0.01 < p < 0.05; . 0.05 < p < 0.1. Note that for total edible abundance the effects are for the odds ratio (x/(1-x)), where x = total abundance / 1000.

	Edible species richness			Richness of edible species with ≥ 1% cover			Total edible plant abundance		
	Parameter		Effect	Parameter		Effect	Parameter		Effect
Intercept	**1.861**	***	**6.43**	**1.111**	***	**3.04**	**−6.333**	***	**0.00**
Site type 2 (ref. 1)	−0.222		0.80	−0.203		0.82	−0.250		0.78
Site type 3	**−0.376**	**	**0.69**	−0.251		0.78	−0.027		0.97
Site type 4	**−0.288**	*	**0.75**	−0.089		0.91	0.359		1.43
Site type 5	**−0.301**	*	**0.74**	−0.244		0.78	0.288		1.33
Veg. zone middle boreal (ref. southern boreal)	−0.002		1.00	0.026		1.03	0.045		1.05
Veg. zone northern boreal	0.019		1.02	0.091		1.09	**0.541**	**	**1.72**
BA spruce	**−0.010**	*	**0.99**	**−0.013**	*	**0.99**			
BA deciduous				**−0.022**	**	**0.98**			
Altitude	**0.001**	**	**1.00**	**0.002**	***	**1.00**			
Stand age				**0.002**	*	**1.00**	**0.006**	***	**1.01**
Longitude							**0.069**	***	**1.07**
R^2	0.118			0.180			0.136		
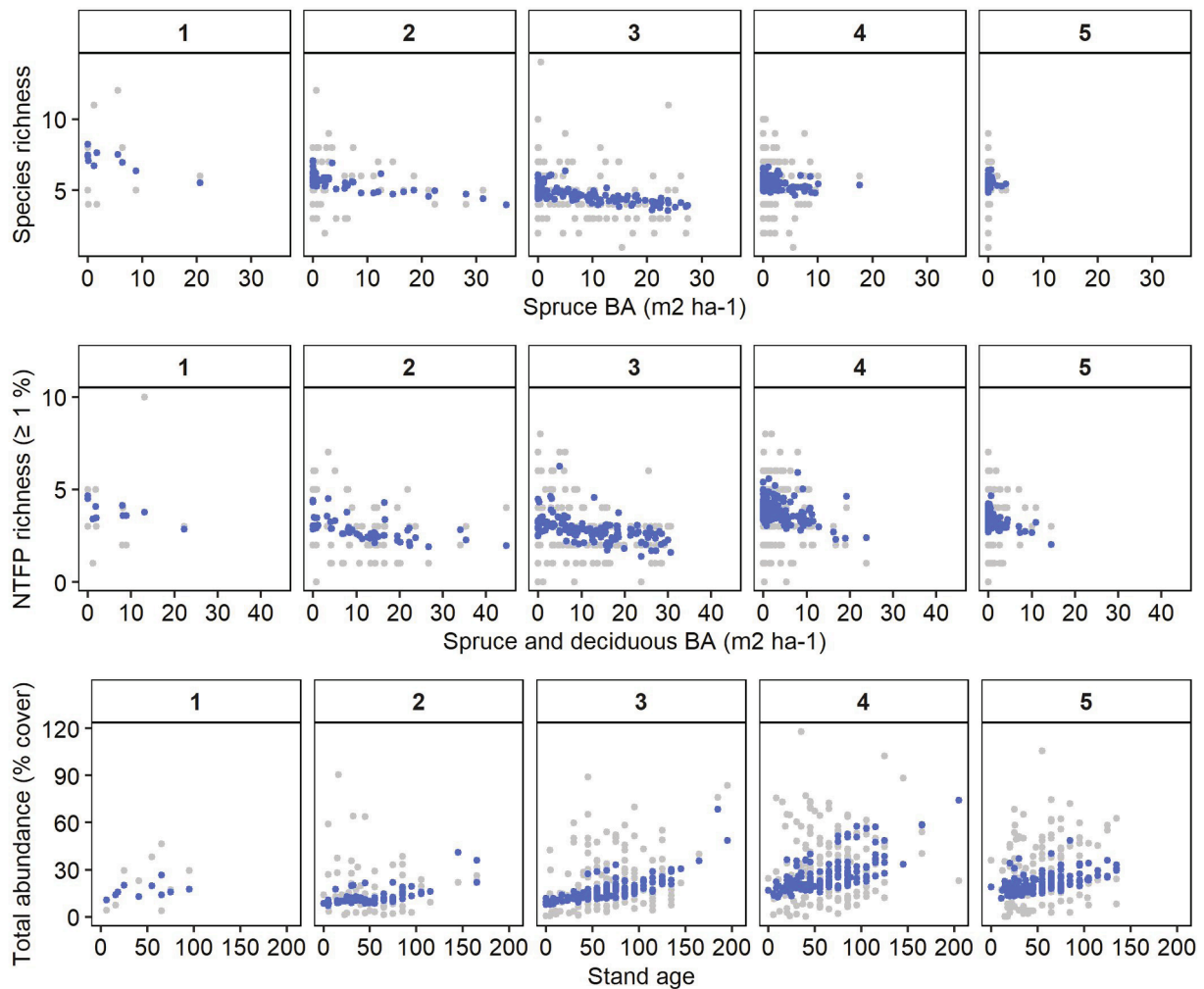
Fig. 4. Edible species richness and abundance in plots on peatlands by site type (panels) and basal area (BA) of spruce, spruce and deciduous species, or stand age (x-axis). Shown are the true observed values (in grey) and the model predictions (in blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3.2. Peatlands

Compared with forests on mineral soils, the species composition of peatland site types was overlapping more in the NMDS-ordination space, showing that species composition did not differ as greatly between the site types (Fig. 9). Nevertheless, several indicator species were identified for types 1 and 2, such as *Oxalis acetosella*, *Angelica sylvestris* and *Viola riviniana*. For instance, *Rubus saxatilis* and *Filipendula ulmaria* were diagnostic only for type 1, and *Rubus arcticus* and *Phragmites australis* for type 2. *Vaccinium uliginosum* and *Empetrum nigrum* were diagnostic for the two least fertile types, 4 and 5 (Table 4). Again, types 2 and 3 had the largest hulls, hosting the widest amplitude of species (Fig. 9).

For peatlands, the trend in edible species richness appeared to be non-linear (Fig. 10) and had considerably poorer fit with the NMDS-ordination space compared with mineral soils. Based on the ordination, it appeared that diagnostic species of both fertile (e.g. *Viola riviniana* and *Rubus arcticus*) and poor site types (e.g. *Vaccinium uliginosum* and *Empetrum nigrum*) could, however, be associated with relatively high species richness in peatlands (Fig. 10). However, the variation in edible species richness was generally quite low for peatlands.

Of all the explanatory variables, basal area of spruce had the best fit with the NMDS-ordination for peatlands and the relationship appeared linear in relation to the NMDS-axes (Fig. 11). For example, *Vaccinium myrtillus*, *Oxalis acetocella* and *Rubus saxatilis*, of which the two latter were also diagnostic species of site type 1 (*Oxalis acetosella* also for type 2) (Table 4), appeared to be associated with high basal area of spruce,

while *Vaccinium oxycoccos*, *Vaccinium uliginosum* and *Empetrum nigrum*, which were also diagnostic species of types 4 and 5, but also *Menyanthes trifoliata* and *Cetraria islandica*, were all associated with low basal area of spruce..

4. Discussion

In this study, we perform to our knowledge the first investigation of associations between stand characteristics and the provisioning of a comprehensive catalogue of edible plants in Finnish forests. We found that a high number of edible plant species occur in Finnish forests, and their combined species richness and total abundance are influenced by factors such as site fertility and stand density. The most important factors driving the differences in species composition between plots were similar to those of species richness, and several edible plant species were unique to certain site types. Edible species abundance was driven by additional factors which were not connected with variation in the species composition.

Out of the 173 edible plant taxa compiled from literature, 68 were observed in the extensive forest vegetation survey data used in this study. Most of the species were rare, and only 11 species occurred on more than 10% of the plots (whether plots on mineral soils or peatlands). Species found to be relatively frequent in forests on mineral soils and in peatland forests were typical forest and peatland species, respectively (Hämet-Ahti et al., 1986), while a few dominant dwarf

Table 3

Relative frequencies (%) of edible plant species in the forests on mineral soils by categorical explanatory variables. The species are ordered by their total frequency across the dataset. Diagnostic species with phi-value ≥ 0.2 are highlighted with orange (constancy ratio ≥ 2) or pale orange (constancy ratio ≥ 1.5). Species that had a frequency of only one per class were not considered diagnostic even if the criteria were met. 'Harvest' refers to harvesting history and 'Regen.' to regeneration method.

	Total freq.	Site type					Vegetation zone				Harvest			Regen.		Soil type				
		1	2	3	4	5	HB	SB	MB	NB	No harvest	Final felling	Other	Natural	Plantation	Fine	Coarse	Fine moraine	Coarse moraine	Rocky
No. of plots	1271	24	186	619	387	55	40	581	409	241	786	111	374	1001	270	164	95	389	579	44
Vaccinium vitis-idaea	1226	42	88	99	100	100	93	94	99	100	97	97	96	97	94	87	95	98	98	95
Vaccinium myrtillus	1201	54	87	98	97	78	90	93	94	98	95	89	94	95	92	82	85	98	97	95
Juniperus communis	690	33	46	61	54	20	55	57	56	45	57	42	53	54	56	45	55	59	54	55
Epilobium angustifolium	481	29	39	35	44	24	25	37	47	25	28	74	47	25	85	42	22	41	38	27
Empetrum nigrum	478			32	63	67	18	8	51	89	39	28	37	39	33	23	68	37	36	45
Calluna vulgaris	473		4	25	66	95	28	27	49	43	36	32	41	37	39	20	64	46	31	55
Vaccinium uliginosum	356		3	27	42	38	10	4	40	68	29	26	26	29	24	20	31	29	28	34
Rubus saxatilis	345	79	72	26	7		18	47	15	2	26	30	28	27	28	39	12	27	29	
Oxalis acetosella	265	71	74	17	1		38	36	10		19	25	23	23	14	37	4	15	24	2
Rubus idaeus	203	67	45	11	9	2	28	29	6		12	42	17	12	30	28	5	14	15	16
Fragaria vesca	174	54	56	8	1		30	25	4		14	19	12	14	13	30	5	10	14	
Viola riviniana	123	50	39	5	2		35	16	4	1	9	12	10	10	9	20	3	6	11	
Cetraria islandica	91		1	3	13	38	8	4	10	10	9	5	5	8	3	2	21	9	5	14
Angelica sylvestris	79	46	28	2	1		8	10	4		7	6	5	6	7	18	2	3	6	2
Rubus arcticus	53	8	12	4	2			4	7	1	4	11	3	4	6	9	1	3	4	
Rubus chamaemorus	53			6	4			1	5	11	5	3	3	4	4	3	3	2	6	5
Filipendula ulmaria	44	46	17	1			8	6	1	1	3	4	3	3	3	14		1	3	5
Achillea millefolium	40	21	14	1	1		5	6	1		4	1	3	3	4	12	2	2	2	
Polypodium vulgare	34	4	6	3	1		5	6			2	1	5	3	1	2		2	4	5
Aegopodium podagraria	28	33	9	1			3	4	1		3	4	1	2	2	7		1	3	2
Equisetum arvense	27	25	8	1	1		5	3	1	1	2	3	3	2	3	8	1	1	2	
Viola canina	27	13	4	2	1		10	4	1	1	2	4	3	1	4	3	6	2	1	
Alchemilla species	27	29	10	1			3	4	1	1	2	1	3	2	1	8		1	2	
Anthriscus sylvestris	23	25	8	1				3	1		2	2	2	1	3	9		1	1	
Rumex acetosa	22	8	6	1	1		3	2	2		1	7	1	1	3	5		1	1	2
Rumex acetosella	21		2	2	2			2	1	1	1	11	1	1	5	3	2	1	2	
Ribes alpinum	20	8	7	1			5	3			1	1	2	2	1	1		2	2	
Cornus suecica	20		2	2	1				2	5	2		1	1	2	2		1	3	
Vaccinium microcarpum	20			1	2	4		1	1	5	2	2	1	2	1	2	1	1	2	
Taraxacum species	18	4	6	1		2	5	2	1	1	1	2	2	1	2	2		1	2	
Urtica dioica	16	17	5	1	1		5	2			1	1	2	1	1	5		1	1	2
Vicia sepium	15	4	6	1			3	2			1		1	1	1	4	1	1	1	
Prunella vulgaris	14	13	4	1			3	2	1		1	1	1	1	1	5		1	1	
Vaccinium oxycoccos	13		1	2	4				2	2	1	1	1	1	1	1	2	1	1	
Stellaria media	11	4	4	1			5	1	1		1	2	2	1	1	2		1	1	2
Anthoxanthum odoratum	10		3	1			3	1	1	1	1		1	1	1	2		1	1	
Ribes spicatum	9	17	3					1	1		1	2	1	1	1	1		1	1	
Leucanthemum vulgare	8	4	2	1	1			1	1		1	1	1	1	2	2			1	
Arctostaphylos alpinus	8			1	1	2				3	1			1				1	1	
Pimpinella saxifraga	7		3	1			3	1	1		1		1	1	1	2		1	1	
Trifolium repens	6		2	1			3	1	1		1	1		1	1	2			1	
Trifolium pratense	6	8	2					1			1		1	1	1	3			1	
Ribes nigrum	5	4	1	1	1			1			1		1	1	1	1		1		
Trifolium medium	3		2				5	1			1			1		1	1	1		
Elytrigia repens	3		1	1				1			1	1		1	1	1			1	
Cirsium arvense	3	4	1		1			1			1		1	1	1	1			1	
Corylus avellana	2		1	1			5				1		1	1		1			1	
Trifolium hybridum	2	4	1					1			1		1	1		1			1	
Angelica archangelica	2	4	1						1	1	1			1		1			1	
Rosa majalis	2	4	1					1	1		1	1		1		1			1	
Plantago major	2		1					1			1		1	1		1			1	
Lamium purpureum	2			1				1			1			1				1		2
Lamium album	2		1				3	1			1		1	1	1	1				
Campanula glomerata	2		1	1				1			1	1			1				1	
Chenopodium album	1		1				3					1		1					1	
Hierochloe hirta	1	4						1					1		1	1				
Plantago lanceolata	1		1				3				1			1		1				
Capsella bursa-pastoris	1		1					1				1		1		1				
Scirpus sylvaticus	1		1					1			1				1	1				
Cardamine pratensis	1		1						1		1			1		1				
Silene vulgaris	1		1					1			1			1					1	
Argentina anserina	1		1					1			1				1	1				
Artemisia vulgaris	1			1				1				1			1			1		
Hierochloe australis	1		1					1			1			1		1				
Phragmites australis	1		1					1				1			1				1	

shrub species were common on both mineral soil and peatland plots. On average, edible species richness was similar on mineral soils and peatlands, but their total abundance was higher on mineral soils.

On mineral soils, edible species richness and abundance were lower in less fertile site types and in denser stands, as hypothesized. These patterns are likely explained, first, by the higher overall species richness in fertile site types (herb-rich forests and herb-rich heath forests) than medium- and low-fertility types (Hämet-Ahti et al., 1986; Heikkinen and

Table 4

Relative frequencies (%) of edible plant species in the forests on peatlands by categorical explanatory variables. The species are ordered by their total frequency across the dataset. Diagnostic species with phi-value ≥ 0.2 are highlighted with orange (constancy ratio ≥ 2) or pale orange (constancy ratio ≥ 1.5). Species that had a frequency of only one per class were not considered diagnostic even if the criteria were met. 'Harvest' refers to harvesting history and 'Regen.' to regeneration method.

	Total freq.	Site type					Vegetation zone			Harvest			Regen.		Soil type	
		1	2	3	4	5	SB	MB	NB	No harvest	Final felling	Other	Natural	Plantation	Organic	Other
No. of plots	507	10	55	131	165	146	166	304	37	351	14	142	475	32	385	122
Vaccinium vitis-idaea	413	80	80	90	92	62	87	79	81	80	93	84	82	69	78	93
Vaccinium uliginosum	360	30	40	44	87	92	52	80	86	72	43	70	72	63	76	57
Vaccinium myrtillus	334	70	51	82	78	44	78	59	70	64	79	68	67	53	61	80
Empetrum nigrum	321	40	18	38	76	90	48	70	81	66	43	60	64	50	69	45
Vaccinium oxycoccos	267	30	29	24	59	82	40	58	68	53	50	52	54	31	62	25
Rubus chamaemorus	267		25	45	58	67	44	54	81	54	43	51	53	47	61	28
Calluna vulgaris	140	30	5	6	35	47	22	32	16	29	14	26	27	41	26	31
Epilobium angustifolium	135	60	45	36	24	12	31	24	24	21	57	37	24	72	28	24
Vaccinium microcarpum	104	30	4	6	15	45	10	25	30	25	7	11	21	13	24	10
Juniperus communis	92	60	38	28	14	3	15	19	22	17	7	21	18	19	16	25
Rubus arcticus	51	10	44	13	4	1	8	11	16	10	14	10	9	22	8	18
Rubus idaeus	37	30	24	13	2		18	2		6	14	10	7	13	7	8
Menyanthes trifoliata	36	10	15	8	6	4	5	7	22	7	7	7	7	3	9	1
Rubus saxatilis	30	50	18	9	2		12	3	5	6	7	6	6	3	4	11
Oxalis acetosella	24	20	24	7			9	3		5	7	4	5	3	3	9
Filipendula ulmaria	17	40	22		1		6	1	8	3	7	4	3	13	3	4
Angelica sylvestris	14	20	15	3			4	2	5	3		1	3	6	3	2
Rumex acetosa	11		9	3	1		2	2	3	2		4	1	16	2	2
Equisetum arvense	10		5	5	1		3	2		2		1	2	3	2	3
Cetraria islandica	8				1	4	1	2		2		1	1	3	2	
Phragmites australis	7		9	1	1		4	1		1		3	1		1	2
Fragaria vesca	7	20	5	2			3	1		2		1	1		1	4
Cornus suecica	7			2	2	1	1	1	5	1		1	1	3	1	4
Achillea millefolium	6		5	2			1	1		1		1	1	6	1	1
Viola riviniana	4	10	5				1	1		1		1	1			3
Aegopodium podagraria	4	10	5				1	1		1		1	1		1	2
Prunella vulgaris	3	20		1			1	1		1		1	1		1	2
Cirsium arvense	2		2	1				1		1			1	3	1	
Ribes alpinum	2			1	1		1					1	1		1	1
Urtica dioica	2			1	1		1			1		1	1	3	1	
Viola canina	2	10	2				1			1			1	3		2
Rosa majalis	1		2				1			1			1			1
Ribes nigrum	1		2					1				1	1			1
Polemonium acutiflorum	1	10						1		1			1		1	
Hierochloe hirta	1			1				1		1			1		1	
Glyceria fluitans	1		2				1			1			1		1	
Anthriscus sylvestris	1		2				1			1			1		1	
Stellaria media	1		2				1			1			1			1
Anthoxanthum odoratum	1		2				1			1				3		1
Trifolium repens	1		2				1			1				3		1
Taraxacum species	1	10						1		1			1		1	
Lamium purpureum	1			1			1			1			1		1	
Cardamine pratensis	1		2				1					1	1		1	
Scirpus sylvaticus	1	10					1					1		3	1	
Rumex acetosella	1			1				1				1	1			1

Mäkipää, 2010; Tonteri, 1994). Second, a high proportion of the edible species primarily occurs in cultural and semi-natural habitats, which recently felled, young, or semi-open stands may resemble. Additionally, species like *Epilobium angustifolium* can occur in high abundance in early successional heath forests (Uotila et al., 2005), and dominant dwarf shrubs like bilberry and cowberry are favored by semi-shade conditions or moderate or high canopy openness (Miina et al., 2009; Turtiainen et al., 2013). Based on the NMDS-ordination, only the basal area of spruce was strongly correlated with changes in species composition but not the basal area of deciduous trees or pine. This may be because compared with pine, spruce can form a dense canopy, resulting in stronger impact on the understory (Tonteri et al. 1990). Similarly to forests on mineral soils, edible species richness was lower in less fertile sites also in peatland forests, but there site fertility was not found to have an effect on total abundance. Edible species richness was negatively affected by basal area of spruce and/or deciduous trees, but not by basal area of pine.

Overall, the fit of the models was rather poor, and especially in the models constructed for the peatland data the number of explanatory variables found to be statistically significant was low. This suggests that some important environmental variables may have been missing from the analyses. For example, dispersal limitations (Gendreau-Berthiaume et al., 2015), legacy effects of past disturbances (Perring et al., 2018), and small-scale climate and soil conditions (Bell et al., 2016; Salemaa et al., 2008) can play large roles in the structuring of understory vegetation in boreal forests, of which the edible species are a subset. Another explanation may be that the set of species analyzed respond to the explanatory variables in differing ways, muddling the overall impact on their total richness and abundance. Edible plant species are diverse, including generalist and specialist species as well as different growth forms such as shrubs, dwarf shrubs, herbs, and grasses, and they therefore vary in their habitat requirements and responses to stand

Fig. 5. NMDS-ordination of forest on mineral soils based on Sørensen distance measure. Site types (fertility class) are displayed with hulls of different colour and sites within the hulls with points of corresponding colours. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r^2, 33% of the variation in the NMDS-ordination space can be explained by site type.

Fig. 6. NMDS-ordination of forests on mineral soils with edible species richness plotted as a smooth surface. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r^2, 66% of the variation in the NMDS-ordination space can be explained by edible species richness.

succession and disturbances (Tonteri et al., 2016; Uotila et al., 2005). For example, peatland drainage is one of the most significant factors explaining the distribution of boreal red-listed peatland plant species (Saarimaa et al., 2019; Tolvanen et al., 2020), but drainage was not found significant in our study. Depending on whether the plant species grow principally on undrained mires or in forests on mineral soils, they are expected to respond either negatively or positively to drainage. This may lessen the impact of drainage in the models in the present study.

Vegetation zone, which was a required variable in the models, was surprisingly not found to have a statistically significant association with edible species richness, either on mineral soils or on peatlands. However, for forests on mineral soils, latitude was found to correlate well with changes in species composition in NMDS-ordination, which is in congruence with the results of Tonteri et al. (1990). On the other hand, a statistically significant difference in total edible plant abundance was observed between southernmost and northernmost vegetation zones, with abundance being on average higher in the north than the south.

This indicates that certain edible species are increasingly abundant towards the north, which is likely the case for some common species such as *Vaccinium vitis-idaea*, *V. myrtillus*, *V. uliginosum*, *Empetrum nigrum*, *Rubus chamaemorus*, and *Calluna vulgaris* (Reinikainen et al., 2000). As a conclusion, in forests on mineral soils, species turnover takes place along the latitudinal gradient but does not affect the edible species richness per se, while the edible species composition and richness of peatlands remain relatively constant along the latitudinal gradient.

One of the main motivations of this study was to explore the relationships between forest management and the provisioning of edible plants. Forest management was described by direct variables (recent harvesting history, stand regeneration method, soil management, and drainage), and is also indirectly linked to tree stand variables (e.g. basal area and development stage). With respect to variables directly describing forest management activities, statistically significant associations were observed between harvesting history and richness of species with $\geq 1\%$ cover, and total abundance in forests on mineral soils. The

Fig. 7. NMDS-ordination of forests on mineral soils with basal area of spruce plotted as a smooth surface. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r^2, 32% of the variation in the NMDS-ordination space can be explained by basal area of spruce.
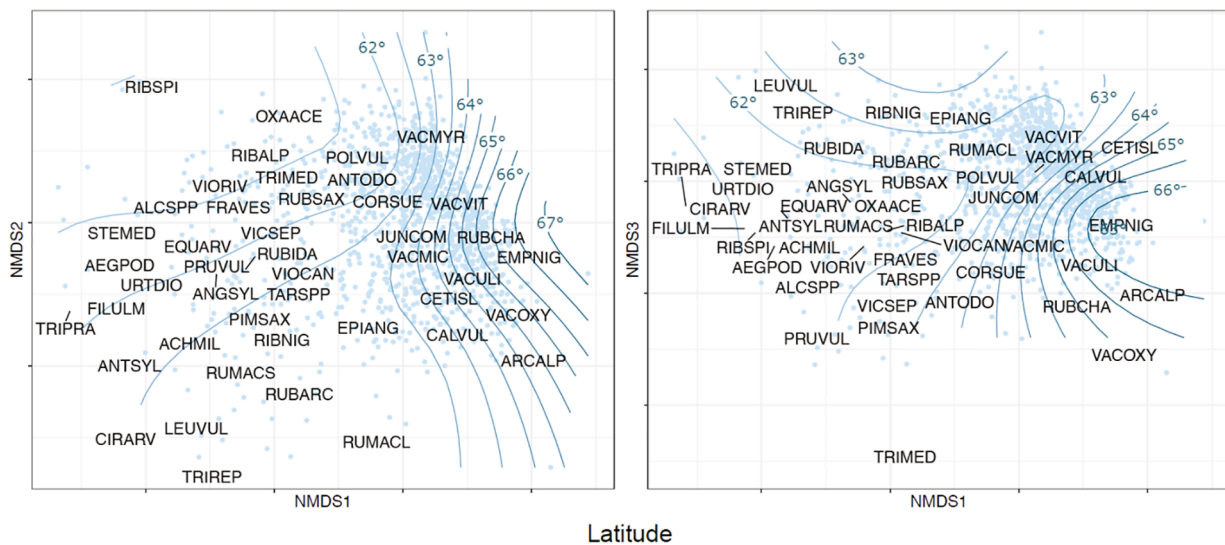
Fig. 8. NMDS-ordination of forests on mineral soils with latitude plotted as a smooth surface. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r^2, 36% of the variation in the NMDS-ordination space can be explained by latitude.

effects were negative: these measures were lower in stands where some harvesting had taken place in the past 10 years than when no harvesting had taken place, and even lower if the stand had been clear cut in the past 10 years. Total edible plant abundance was also found to be lower in planted than naturally regenerated forest stands. The negative effect of clear-cut harvesting and plantation on total abundance was expected and is likely explained by the negative impacts of these disturbances on typically abundant species such as bilberry (Hedwall et al., 2013; Tonteri et al., 2016). Contrary to our hypotheses, none of the aforementioned variables had a good fit with the NMDS-ordination space, suggesting that the patterns in edible species richness and abundance were not strongly related to changes in species composition. However, a small number of diagnostic species were identified also for these variables, implying that forest management activities induced at least some species-specific responses. Not surprisingly, final felling and regeneration by plantation promoted *Epilobium angustifolium* and *Rubus idaeus*, which both are pioneer species. On peatlands, none of the variables describing management history were found to have statistically significant effects on edible plant provisioning. Regarding all of these results,

we must note that the management activities included in the analyses were represented by unevenly sized categories in the dataset. In addition, as these categories were defined on site during the stand inventories rather than based on confirmed information on stand history, there may be inconsistencies in the data. Furthermore, the categories are rough and may hide variation that impacts vegetation, as responses of local species pools to disturbances can be rapid and depend on local environmental conditions in various ways (Kaarlejärvi et al., 2020).

Overall, the results of this study may still be considered to indicate some degree of association between forest management activities and edible plant provisioning. Stand density (basal area) was found to negatively influence edible plant provisioning; however so was harvesting on mineral soil sites. As the effect of intermediate harvesting (e. g. thinning) on edible species richness and abundance was smaller than the effect of final felling, there may be potential to support edible species richness and abundance by, for example, carefully conducted continuous cover forestry that maintains an uneven-aged, comparatively open stand and utilizes natural regeneration (cf. Vanha-Majamaa et al., 2017). However, we caution that here too the effects are likely species-
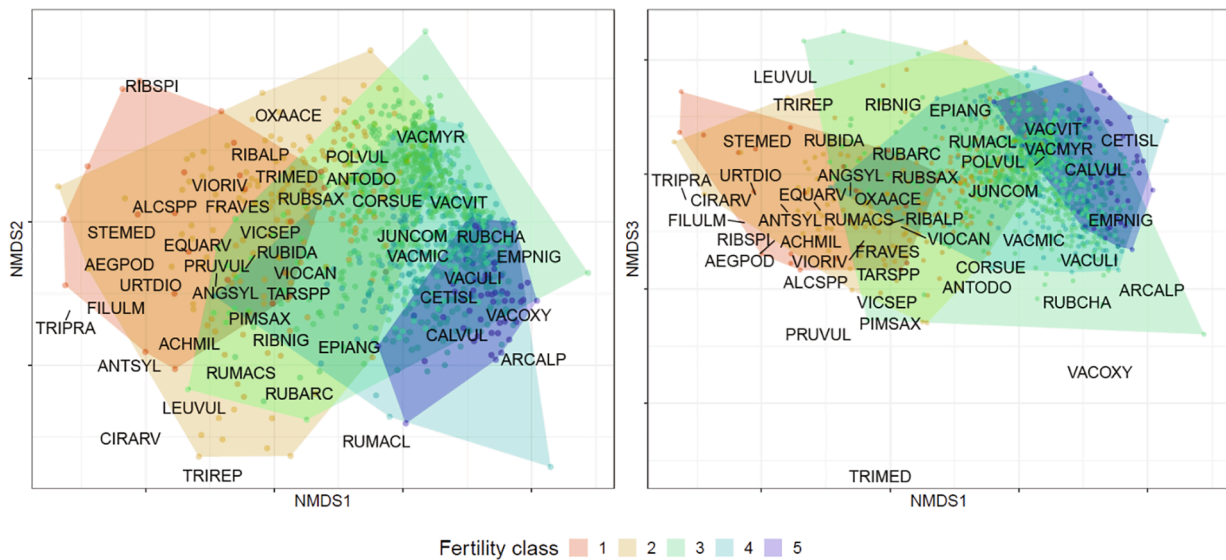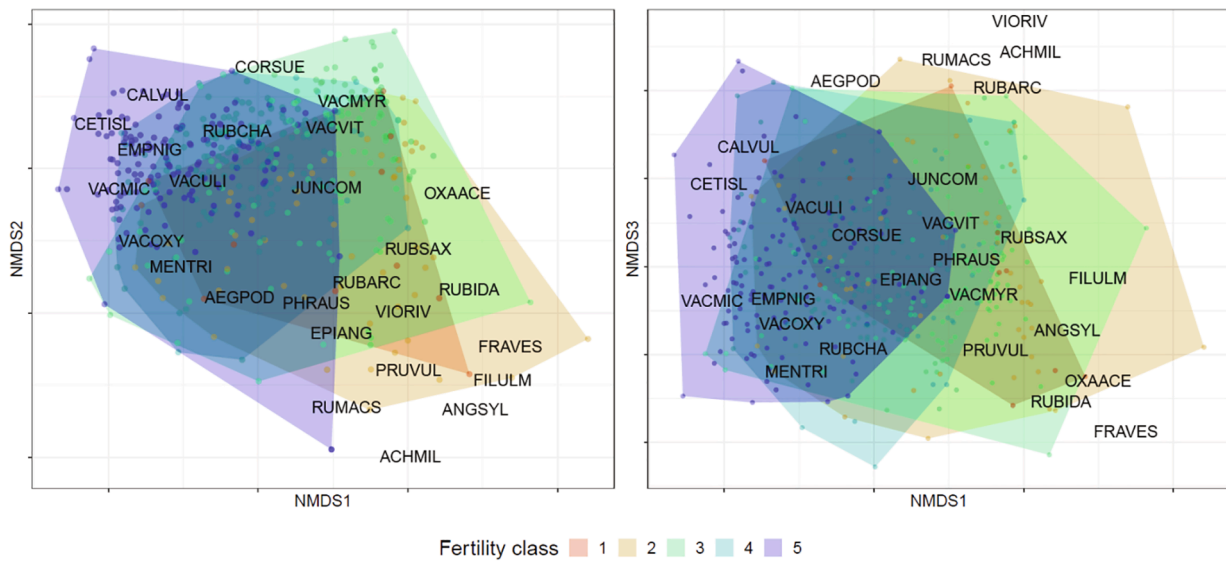
Fig. 9. NMDS-ordination of forests on peatlands based on Sørensen distance measure. The site types (fertility class 1–5) are displayed with hulls of different colour and sites within the hulls with points of corresponding colours. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r², 25% of the variation in the NMDS-ordination space can be explained by site type.
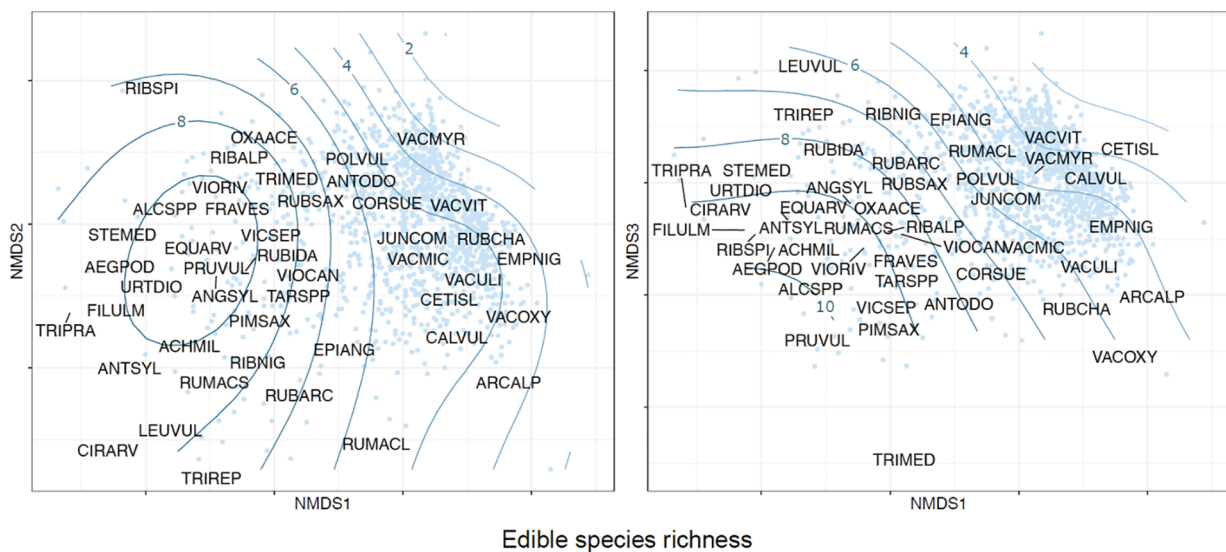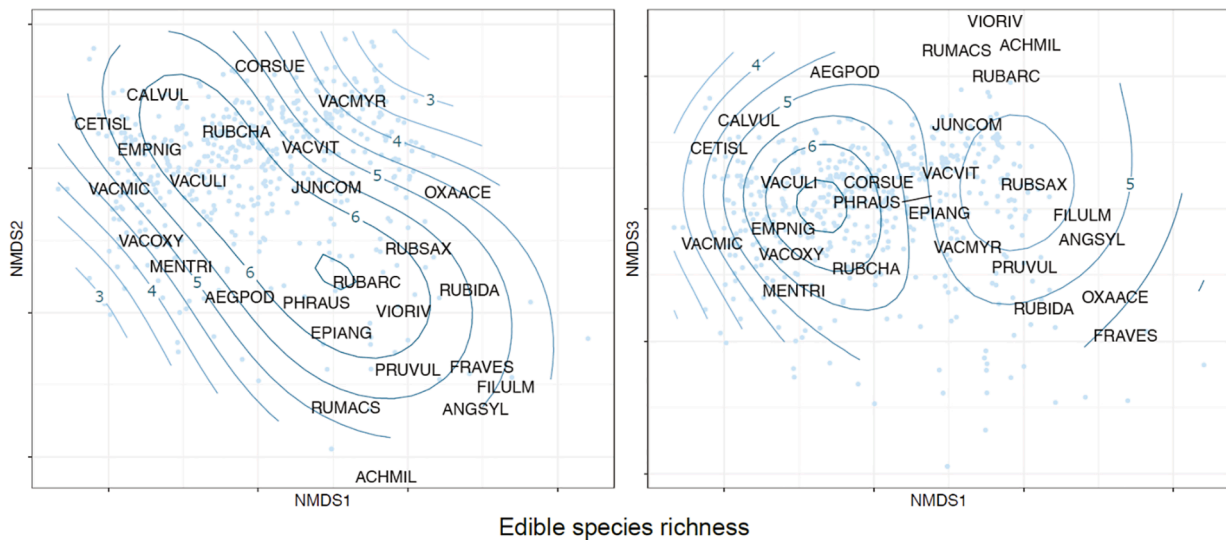

Fig. 10. NMDS-ordination of forests on peatlands with edible species richness plotted as a smooth surface. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r², 28% of the variation in the NMDS-ordination space can be explained by edible species richness.

specific, and with respect to our results this is purely speculative as our analyses did not explicitly include mature uneven-aged stands. What can be said, then again, is that the highest edible species richness was found in the most fertile site types both on mineral soils and peatlands. Herb-rich forests in particular are of high conservation value, and their protection is already encouraged (e.g. as part of the METSO programme in Finland). Protecting these species-rich habitats also preserves their high edible species richness.

It ought to be noted that our analyses involve some necessary simplifications that limit the interpretation of the results. First, we measured the cover of each plant species and used it as a measure of edible plant provisioning regardless of the part of the plant that is actually edible. This may be misleading especially with respect to berry or flower production (Clason et al., 2008). For example, *Rubus arcticus* (which in our dataset was among the 20 most common species in both mineral soils and peatlands) is known to vary greatly in annual yield (Kostamo et al., 2018). Further, some species are edible when they are

young and thus comparatively low in cover (e.g. young shoots of *Equisetum arvense* or young leaves of *Urtica dioica*). That said, abundance is still a likely indicator of the provisioning of edible parts in general (e.g. bilberry cover is a strong predictor of bilberry yield; Miina et al., 2009).

Second, the representativeness of the dataset is limited. Herb-rich forests (i.e. the highest fertility site type of forests on mineral soils) are greatly variable in vegetation, but only 2% of mineral soil plots were herb-rich forests; thus, the study may not adequately assess the abundance and diversity of edible plants in these forests. Similarly, only 2% of peatland plots were of the highest fertility type. Located primarily in production forests, the plots were also skewed towards low values in stand age: 78% and 86% of plots were <100 years old, and 2% and 0.2% more than 200 years old, on mineral soils and peatlands, respectively. Old-growth forests were thus underrepresented. Some edible plant species are also known to be favored by management practices that have been ceased (e.g. *Pimpinella saxifraga* and *Campanula glomerata* favored by slash-and-burn cultivation) or that have become rare in forests (e.g.
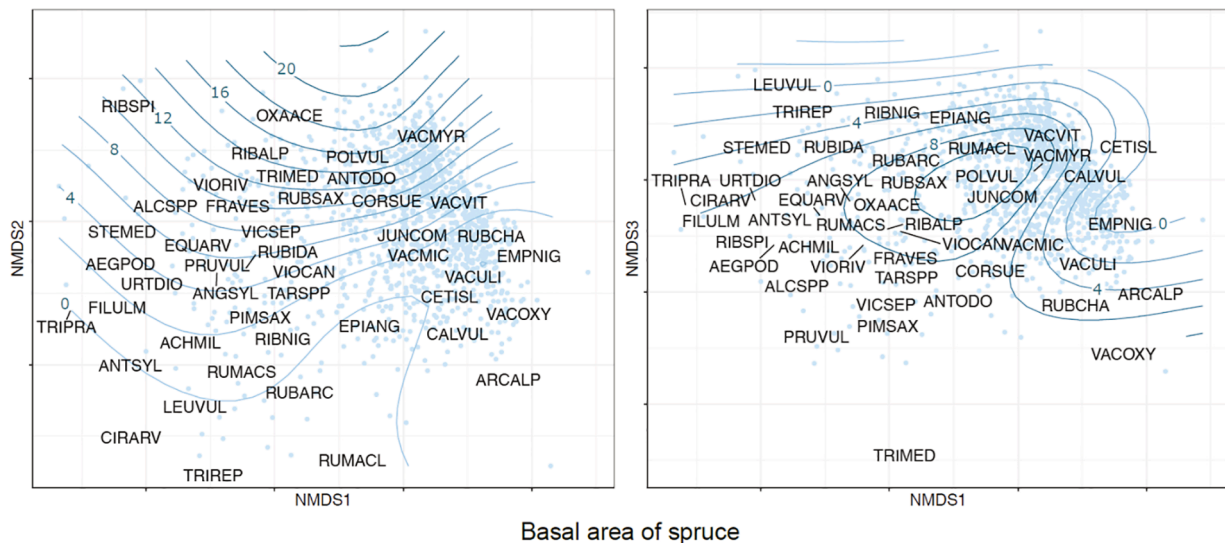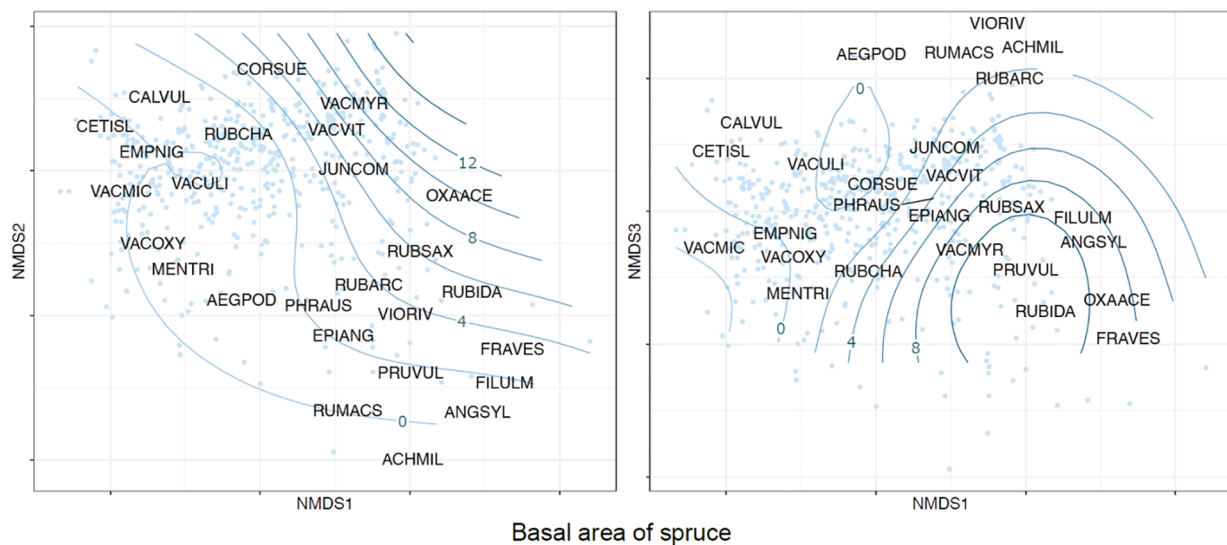
Fig. 11. NMDS-ordination of forests on peatlands with basal area of spruce plotted as a smooth surface. Species with a frequency of ≤ 2 were omitted from the ordination. Based on r^2, 52% of the variation in the NMDS-ordination space can be explained by basal area of spruce.

*Fragaria vesca, Filipendula ulmaria* and *Leucanthemum vulgare* which are favored by forest grazing) (Kontula et al., 2018).

In this study, we examined the total richness and abundance of all edible wild plant species occurring in Finland. Our focus was thereby on the supply of edible plants, not on the demand for them. A minority of the species are currently utilized commercially (Evira, 2016), and this is likely due to more factors than just availability. Globally, several factors in addition to habitat loss or degradation have contributed to the decline of wild food use, such as enhanced livelihoods, modernized agriculture, and urbanization (Łuczaj et al., 2012; Schulp et al., 2014; Shanley et al., 2014; Turner et al., 2011). In the EU, few data are available on the prevalence of collecting vascular plant NTFPs (Schulp et al., 2014) or the demand for these species as wild foods. That said, in Finland the opportunity for their utilization exists, as the collection of wild berries and most herbs is covered by the so-called everyman's rights. Collection of some species has restrictions; for example, *Angelica archangelica* is rare and protected in the southern part of Finland. Collection of leaves from woody-stemmed plants, such as *Vaccinium myrtillus* and *V. vitis-idaea*, requires landowner's permission; however, collecting their berries does not. In a recent survey study, Lovrić et al. (2020) found that a large share of Europeans collects NTFPs but not commercially, and hypothesized that a primary motivation for NTFP collection in Western Europe is recreation. If appreciation for nature-based recreation increases, it may contribute to an interest in edible wild plants as well in addition to their commercial uses.

To conclude, our results indicate that habitat characteristics, namely site fertility and stand density, are the strongest determinants of overall edible plant provisioning, and several edible plant species confined to the richest site types accounted for the increase in species richness. Regarding occurrence, however, we were unable to detect species-specific responses in some of the poorly represented classes of different management practices, and changes in abundance were not analyzed for individual species. Beyond the patterns detected in this study, the determinants of edible plant provisioning likely vary in identity, direction, and strength between species and species groups. It is therefore recommendable to further analyze the responses of edible plants to stand structure and forest management at the level of smaller species groups or individual species.

CRediT authorship contribution statement

Tähti Pohjanmies: Conceptualization, Methodology, Formal

analysis, Writing - original draft, Visualization. **Anni Jašková:** Methodology, Formal analysis, Writing - original draft, Visualization. **Juha-Pekka Hotanen:** Writing - review & editing. **Outi Manninen:** Writing - review & editing. **Maija Salemaa:** Writing - review & editing. **Anne Tolvanen:** Writing - review & editing. **Päivi Merilä:** Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A and B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119151.

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