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Site types revisited: comparison of traditional Russian and Finnish classification systems for European Boreal forests

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Abstract

Questions: Forest classifications are tools used in research, monitoring, and management. In Finland, the Cajanderian forest site type classification is based on the composition of understory vegetation with the assumption that it reflects in a predictable way the site's productive value. In Russia, the Sukachevian forest classification is similarly based on understory vegetation but also accounts for tree species, soil wetness, and paludification. Here we ask whether Cajander's and Sukachev's forest types are effectively the same in terms of species composition, site productivity, and biodiversity.

Location: Boreal forests on mineral soils in Finland and Russian part of Fennoscandia.

Methods: We use vegetation and soil survey data to compare the Cajanderian and the Sukachevian systems in terms of the understory community composition (that is supposed to define them), soil fertility and tree productivity (that they are expected to indicate), and biodiversity (that is of interest for conservation purposes). We create and employ class prediction models to divide Russian and Finnish sites into Cajander's and Sukachev's types, respectively, based on vegetation composition. We perform cross-comparisons between the two systems by NMDS ordination and statistical tests.

Results: Within both systems the site types formed similar, meaningful gradients in terms of the studied variables. Certain site types from the two systems were largely overlapping in community composition and arranged similarly along the fertility gradient and may thus be considered comparable.

Conclusions: The Cajanderian and the Sukachevian systems were both developed in the European boreal zone but differ in terms of the exact rules by which site types are determined. Our results show that analogous types between the systems can be identified. These findings aid in endeavors of technology and information transfer between Finnish and Russian forests for the purposes of basic or applied ecological research and forest management.

Keywords: Forest site type, forest type, Cajander, Sukachev, vegetation, soil fertility, plant species richness, forest typology

Introduction

Forest site type classifications are tools used in ecological and forestry research, forest resource monitoring, and forest management planning. Classification schemes can be built around the properties of the tree stand, other vegetation layers, and/or abiotic factors (Lahti, 1995; Skovsgaard and Vanclay, 2008). Classifications are supposed to group forest sites based on differences in tree productivity or other ecological values in a way that conveys to a sufficient degree the information that is needed in the relevant use cases. As forest ecosystems are dynamic and vary in multiple ways and at various scales, forest classification schemes are always artificial to some degree. However, they are still considered useful and necessary in real-life forest management contexts.

The forest site type classification used in Finland was developed by A.K. Cajander in the early 1900s (Cajander, 1949, 1909). It is widely used in forest inventories, management planning, and forest monitoring. In Russia, V.N. Sukachev developed his forest classification system around the same time as Cajander. It is used especially in the European part of Russia (Fomin et al., 2017). Both Cajander's and Sukachev's classification systems are vegetation-based: they build on the premise that the occurrence of plant species and the composition of forest understory vegetation reflect environmental factors. In particular, vegetation is assumed to reflect the specific combination of all the environmental factors that prevail on the site and contribute to site quality, and thus vegetation is thought to be a more informative indicator of site quality than any individual environmental factor (e.g. soil type) (Cajander, 1949; Sukachev, 1960).

The vegetation in a boreal forest comprises the tree stand, the shrub layer, the field layer (consisting of small tree and shrub seedlings, dwarf shrubs, herbs, and graminoids), and the ground layer (consisting of bryophytes and lichens) (Nilsson and Wardle, 2005). The focus of the Cajanderian classification is on the field and ground layer (henceforth referred to together as the understory), excluding the characteristics of the tree stand. The understory vegetation is assumed to indicate the biological value of the site regardless of the development stage or management history of the stand: the site type definitions account for the vegetation changes caused by succession and/or harvesting by describing not only characteristic climax communities but also characteristic seral stages. In Sukachev's classification, forest types are determined based on several factors in addition to the understory: the composition and structure of the tree stand, soil moisture, and site productivity (Fomin et al., 2017). It thus formally takes into account also temporally variable, secondary environmental factors (e.g. tree species, microclimate), whereas Cajander's classification assumes that comparatively permanent, primary environmental factors (e.g. basic properties of the soil, macroclimate) are manifested in the vegetation even as secondary factors change over time.

While Cajander's classification aims to predict stand productivity, Sukachev's classification is more refined in that it encompasses a larger number of types that are more uniform than Cajander's site types.

Sukachev considered Cajander's forest site types based solely on the understory to indicate site value for forestry purposes, but to be unreliable in indicating plant community composition, for which more detailed forest types are required (Sukachev, 1960). Excluding the dominant tree species or tree species composition as a source of variation is a central divergence of the Cajanderian classification from Sukachev's system (Lahti and Väisänen, 1987). The tree species composition of the stand influence the understory vegetation mainly via canopy coverage (amount of light), litter composition, and root-rhizosphere competition (Bäcklund et al., 2015). These influences can blur the distinction between Cajander's site types (Lahti and Väisänen, 1987; Tonteri et al., 1990a). While Sukachev considered the influence of tree species to be essential, he also considered Cajander's site types to roughly correspond with his classification if they were divided according to tree species (Sukachev, 1960). This would mean, conversely, that Sukachev's types grouped by the understory characterization would more or less correspond to Cajander's site types. This link between the two systems has been utilized in previous studies (Lukina et al., 2019b; Sukhanov et al., 2014), but has not been formally tested. More detailed information about the overlap between the two systems could facilitate transfer of information and forest management tools between Finland and Russia.

Both Cajander's and Sukachev's systems are approximately one hundred years old, and the forests that they were created to describe have since been subjected to multiple anthropogenic pressures that are known to modify forest vegetation (Hedwall et al., 2019). As ecosystems undergo rapid, anthropogenic changes, it is necessary to re-evaluate the functionality of classifications used to guide their management. Both Cajander and Sukachev considered that mature forests assigned into the same type ought to be comparatively uniform in species composition, environmental responses, and site quality, and that forests of the same type ought to require similar management under the same economic objectives and constraints (Fomin et al., 2017). Since the inception of these classifications, forest management objectives have diversified beyond economic ones to include multiple ecosystem services, resilience, and biodiversity (Barbati et al., 2014; Moen et al., 2014; Seidl et al., 2016). Thus, it is worthwhile to ask whether these existing, widely used classifications provide information that is useful also for the purposes of multifunctional forest management: for example, to examine how well they indicate not only stand productivity but also other ecosystem services and biodiversity.

In this study, we compare the Cajanderian and the Sukachevian classification systems in terms of i) understory community composition, ii) soil fertility and tree productivity, and iii) biodiversity. We hypothesize that certain types from the two systems are analogous and associated with similar value ranges for the variables describing the site. As the site types are defined based on understory vegetation with a focus on dominant or indicator species, sites of the same type are expected to be comparatively similar in species composition. The site type is also intended to indicate the productive value of the site, so sites of the same type are expected to be of similar biological productivity. The site types were not originally designed to indicate biodiversity values, but they have been found to do so for some species groups such as herbs or vascular plants (Nieppola, 1993; Similä et al., 2006). We thus expect species richness to differ less within than between site types.

Methods

Forest site types

In this study, we focus on the classification of forests on mineral soils. In the study area, most mineral soils are podzols, and brown soils are rare. The organic layer is most often mor humus, but also moder humus and, in brown soils, mull occur.

In Cajander's system, six forest site types are arranged from fertile to poor sites as follows: herb-rich forests (HR), herb-rich heath forests (HRH), mesic heath forests (MH), sub-xeric heath forests (SXH), xeric heath forests (XH), and barren heath forests (BH) (Kalela, 1961). Herb-rich forests are found on brown soils and heath forests mainly on Podzol soils. Climatic variation from south to north unavoidably creates variation in vegetation within the site types, as do local topographic and soil conditions. Several sub-types thus exist within each forest site type. These are commonly referred to as forest types (cf. forest site types). The forest site types have been defined so that they describe the potential (tree) productivity of forest sites in relation to sites of other types consistently across vegetation zones from south to north, but the productivity of the sites of each type decreases towards the north. The forest site types are often called after their most common, primarily southern forest types with names based on characteristic species: herb-rich forests as *Oxalis-Maianthemum* type group, herb-rich heath forests as *Oxalis-Myrtillus* (*Vaccinium myrtillus*) type group, mesic heath forests as *Myrtillus* type group, sub-xeric heath forests as *Vaccinium* (*Vaccinium vitis-idaea*) type group , xeric heath forests as *Calluna* type group, and barren heath forests as *Cladina* type group. The characteristics of Cajander's forest site types are described in more detail in Appendix S1.

The focus of Cajander's classification is on placing forest sites along a single productivity gradient, whereas Sukachev's classification specifically describes three gradients: productivity, wetness, and paludification. Forest sites are classified first by dominant tree species (in the study area – pine (*Pinus* *sylvestris*) or spruce (*Picea abies*)), then into groups (e.g. green moss pine forest group includes *Vaccinium myrtillus* pine and *Vaccinium vitis-idaea* pine forest types), and finally into forest types. Sukachev's forest types for mineral soils from the richest to the poorest conditions are *Herbae* spruce/pine type (HE), *Oxalis* spruce/pine type (OX), *Vaccinium myrtillus* spruce/pine type (VM), *Vaccinium vitis-idaea* spruce/pine type (VV), and Lichen pine type (LI). A more detailed description of Sukachev's forest types is given in Appendix S2. We must note that Sukachev's site types were not originally intended to be used without information on the dominant tree species, but in order to test for their similarity with Cajander's site types we combined spruce and pine types (Table 1).

Specifically, we hypothesized certain site types along the productivity gradient to correspond between the two systems (Table 1). This correspondence is examined with an ordination analysis, cross-tabulation, and statistical tests.

Data collection

Vegetation, tree stand, and soil surveys were carried out on systematic sample plot networks in Finland in 2006 and in Russian Karelia in 2009-2010 (Figure 1). The surveys were conducted in Finland as part of the BioSoil Project carried out under the Forest Focus scheme (Regulation (EC) Nr. 2152/2003; Durrant et al., 2011; Galluzzi et al., 2019), and in Russian Karelia by the Russian Academy of Sciences following the same principle as part of cooperation under UN-ECE ICP Forests programme (http://icp-forests.net/). In Finland, the sample plots were circular and 400 m^2 in area. All plant and lichen species in the plot were recorded, and the percentage cover of each species was visually estimated on four 2 m^2 sampling quadrats per plot, following the sampling of the earlier vegetation survey carried out on the plots in 1985-86 (Tonteri et al., 2016). Vascular plant species observed within the sample plot but not in the sampling quadrats were recorded as 0.01% cover. In Russia, each sample plot consisted of four 100 m^2 sub-plots, where the cover of all plant and lichen species was visually estimated. Species cover values were averaged across the quadrats (Finland) or sub-plots (Russia) to produce an estimate for the sample plot. Some taxa that were challenging to identify to the species level were recorded at the genus level (e.g. the shrubs *Salix* spp., herbaceous *Hieracium* spp. and *Taraxacum* spp., and the bryophytes *Brachythecium* spp. and *Plagiomnium* spp.). Plots were classified into site types by field observers. Mineral soils and peatlands were separated using as criteria the existence of a peat layer or the dominance of peatland vegetation (e.g. *Sphagnum* spp.). Peatlands were excluded from data, as our focus is mineral soils. In both countries, most of the plots were of intermediate fertility (Mesic heath and Sub-xeric heath in the Cajanderian system; *Vaccinium myrtillus* type and *V. vitis-idaea* type in the Sukachevian system; Table 1).

The tree stand was described in terms of tree species composition, and mean height, diameter at breast height, number of living trees, and total basal area were assessed (Lukina et al., 2019b; Tonteri et al., 2016). An estimate of total volume (m^3ha^{-1}) was calculated based on these measurements. The age of the stand was estimated based on one or more core drill samples.

We selected carbon to nitrogen ratio (C:N), exchangeable calcium concentration (Ca, cmol(+)kg^{-1}), and pH in the organic layer as the soil variables to be examined as they have been found to be good indicators of soil fertility in boreal forests (Salemaa et al., 2008; Tamminen, 1993). Four samples of the organic layer were taken within the sample plots but outside the vegetation sampling quadrats. The samples were dried, ground, and passed through a sieve. The pH was measured in water. Total N and C were determined on a CHN analyzer (LECO). Exchangeable Ca (cmol(+)kg^{-1}) was determined with ICP-AES in 0.1 M $BaCl_2$ solution.

As data were not collected from recently harvested plots in Russian Karelia, plots where the tree stand was younger than 25 years were excluded from the Finnish data. In the end a total of 427 sample plots – 341 sample plots in Finland and 86 sample plots in Russian Karelia – were included in the study (Figure 1).

Analyses

We compared the Cajanderian and the Sukachevian classification systems in terms of the understory community composition, soil fertility and tree productivity, and measures of biodiversity in the understory. The sample plots were classified *in situ* during the surveys by trained field biologists, in Finland into Cajander's forest site types and in Russia into Sukachev's forest types. In the Cajanderian classification, determination of site type is based on the occurrence and abundance of indicator species, and sometimes even physiognomic characteristics of the vegetation (Hotanen et al., 2008; Kuusipalo, 1996; Lehto and Leikola, 1987). In the Sukachevian classification, the forest type is determined based on the structure and productivity of the tree layer, the landform, soil, and ground conditions, and the composition of ground vegetation (Kryshen et al., 2003; Kryshen, 2010). To perform a cross-tabulation of classifications between the two systems, we used AdaBoost class prediction models to produce predictions of Cajander's forest site type for the Russian plots and Sukachev's forest type for the Finnish plots based on the vegetation data. The models were built using the function 'boosting' available in the package 'adabag' for R (Alfaro et al., 2013). Model selection and the final models are described in more detail in Appendix S3. By employing class prediction models in addition to the country-specific *in-situ* classifications, we were able to assign types according to both Cajander and Sukachev for both Finnish and Russian sample plots.

We used global non-metric multidimensional scaling of plant species abundances to position the plots along the main compositional gradients, fitted with the function ‘metaMDS’ in package ‘vegan’ for R (Oksanen et al., 2019). We used square root transformation and Wisconsin double standardization on the data, Bray-Curtis index as the community dissimilarity measure, and two dimensions for the ordination. The ordination analysis was performed for the combined Finnish and Russian dataset. We used the result to visualize the forest site types in the ordination space, comparing the positioning of types in the two systems (using *in-situ* and modeled classifications together) and of pairs of hypothetically corresponding types (using only country-specific *in-situ* classifications).

Community dissimilarity between Cajander’s and Sukachev’s types was tested with permutational multivariate ANOVA across pairs of site types (function ‘adonis’ in package ‘vegan’ for R; (Oksanen et al., 2019). Specifically, we tested each Cajander’s forest site type against all Sukachev’s site types with the expectation that hypothetically corresponding types have the smallest differences. Bray-Curtis index was used as the measure of community dissimilarity and the dependent variable, and forest site type/forest type as the explanatory variable. Effect size was measured as the coefficient of determination (R^2) calculated by the test function. In the community dissimilarity tests we used only country-specific *in-situ* classifications.

Pairwise comparisons of biodiversity, soil, and tree productivity variables were performed using the non-parametric Wilcoxon-Mann-Whitney test, given the differences in sample sizes between the site types (Table 1). As measures of biodiversity we used total species richness in the understory, species richness of plant groups (dwarf shrubs, graminoids, herbs, bryophytes, lichens), and number of rare species (defined as species with only one or two occurrences in the data set). Soil conditions were described as carbon-nitrogen (C:N) ratio, exchangeable Ca, and soil pH. Tree productivity was measured as the ratio of stand age to stand total volume. To estimate effect sizes, rank-biserial correlations were calculated as

$$r = {}^{(2 \times W_1)}/_{(n_1 \times n_2)} - 1$$

where W_1 is the test statistic (the sum of wins and ties for group 1), and n_1 and n_2 are the sizes of group 1 and group 2. Rank-biserial correlation can range from minus one to plus one so that a value of zero indicates no effect. Group 1 was always Cajander’s forest site type and group 2 Sukachev’s forest type, meaning that a negative r indicates smaller values for Cajander’s than Sukachev’s type, and a positive r vice versa. The Wilcoxon-Mann-Whitney tests were performed in R. In all pairwise comparisons we used only country-specific *in-situ* classifications.

Results

Characteristics of the sample plots

The sample plots in Finland and in Russia were similar in terms of the distribution of dominant tree species, stand age, and stand volume (Figure 2). In both countries, majority of sampled stands were dominated by pine (*Pinus sylvestris*) or spruce (*Picea abies*), less than 100 years old, and less than 300 m^3 in total volume (Figure 2).

A total of 381 taxa were recorded in the studied forests. Out of these, three occurred in nearly all (95%) of the plots: the moss *Pleurozium schreberi* and the dwarf shrubs *Vaccinium vitis-idaea* and *Vaccinium myrtillus*. A further four species occurred in more than 75% of the plots: the mosses *Hylocomium splendens*, *Dicranum scoparium*, and *Dicranum polysetum*, and the grass *Avenella flexuosa*. A total of only 15 species occurred in more than half of the plots. By contrast, a total of 100 taxa were observed in one plot only. There were 168 taxa that were observed only in Finland and 25 taxa that were observed only in Russia. The species observed only in one of the two countries were mostly rare (observed on only one or a few plots), but among the species observed only in Finland were also some common species such as *Anemone nemorosa*, *Hypericum maculatum*, and *Viola palustris* (each found on 19 plots in Finland). The most common species found uniquely in Russia was *Rosa acicularis* (found on seven plots in Russia). In both Finland and Russia, more fertile forest site types as well as types with more observations had higher total species richness and higher numbers of unique species (Appendix S4: Table 1).

Correspondence of types between the two systems

Classification of Finnish plots into Sukachev's forest types and Russian plots into Cajander's forest site types led to a similar distribution of types as in the original respective datasets, with the majority of sites being classified into types of intermediate fertility in both countries (Appendix S3: Table 2, 3). Comparing assigned types across the two systems, the site types matched according to the hypothesized correspondence in 61.8% of the plots (Table 2). The greatest overlap among the hypothesized site type pairs was between MH and VM: 99.0% of MH plots were classified as VM type, and 60.6% of VM plots as MH. The smallest overlap was between HRH and OX: only 5.2% of HRH plots were classified as OX, while most of them (86.2%) were classified as VM. The largest variation was within VM: while 60.6% of the plots of this type were classified as MH, the types for the remaining 39.4% varied from HR to SXH.

The arrangement of the site types in the ordination space followed the fertility sequence, from the least fertile xeric heath forests to the most productive herb-rich forests (Cajanderian classification) and, analogously, from the Lichen type to the *Herbae* type (Sukachevian classification) (Figure 3). Upon visual inspection, the most distinctive difference between the systems is the positioning of Cajander's HRH type, which fall partially over Sukachev's VM, OX, and HE types (Figure 3). The Finnish plots showed a greater spread in the ordination space than the Russian plots (Figure 3). This indicates greater variation in species composition, which was shown also by the higher number of species included in the Finnish data (Appendix S4: Table 1); however, this is likely affected by the higher number of sample plots in Finland. The prevalence of dominant tree species followed the same fertility gradient, with birch and spruce being more common as the dominant species in the more fertile types and pine more common in the less fertile types (Appendix S4: Figure 1).

Pairwise community dissimilarities

Pairs of Cajander's forest site type and Sukachev's forest type that were hypothesized to correspond were largely overlapping in the ordination space (Figure 4). Yet, based on the multivariate ANOVA, community dissimilarity was statistically significant between almost all pairs of site types (Table 3). No significant dissimilarity was found only between HR and HE. Then again, the effect sizes for pairs hypothesized to correspond were quite small (R^2 ranging from 0.03 to 0.13; Table 3).

Pairwise comparisons of site productivity and species richness

Variables describing soil fertility varied logically between the site types along the fertility gradient: C:N ratio was lower and exchangeable Ca and pH of organic layer were higher in the more fertile site types (Figure 5). C:N ratio was in general higher in the Russian plots than the Finnish plots, and this was true also within site type pairs hypothesized to be analogous (Figure 5A). The difference in C:N was statistically significant between HR and HE, SXH and VV, and MH and VM, with the first two having a high rank-biserial correlation ($r < -0.7$; Table 4). Exchangeable Ca concentration showed the opposite pattern, being generally lower in Russian plots than Finnish plots regardless of the site type (Figure 5B). However, when differences between site types hypothesized to be analogous were statistically significant, they were small in effect (rank-biserial correlation -0.25 – 0.17; Table 5). In organic layer pH, more substantial statistically significant differences were observed: rank-biserial correlation ranging from -0.57 between MH and VM to -0.98 between XH and LI (Table 6).

Similar to the soil variables, tree productivity, measured as the ratio of stand age to stand volume, was higher in the more fertile site types (Figure 5D). Tree productivity was higher in the Finnish plots than in the Russian plots with a statistically significant difference between HRH and OX, MH and VM, and SXH and VV. Out of these, the effectively largest difference was between HRH and OX (r = 0.59; Table 7).

Plots of more fertile types had higher total species richness (Figure 6A) as well as higher richness of vascular plants and bryophytes (Figure 6B-C) and more rare species (Figure 6D). Lichen species richness was higher in less fertile site types (Figure 6D). Total species richness and bryophyte species richness were higher with a statistically significant difference in Sukachev's forest types than corresponding Cajander's site types in the case of OX and HRH, and VM and MH. In addition, vascular species richness was significantly higher in OX than in HRH. For OX and HRH, all of these differences were also large in effect (r = -0.80, r = -0.72, and r = -0.69 for total, vascular, and bryophyte species richness, respectively; Tables 8-10). Lichen species richness was significantly higher in VM and VV than in MH and SXH, respectively, with the difference between VV and SXH being large in effect (r = -0.65; Table 11). There were no statistically significant differences in the numbers of rare species between the hypothesized site type pairs (Figure 6E), but there were between other pairs (Table 12).

Discussion

Overall, the results of this study show that there are similarities as well as differences between the Cajanderian and Sukachevian classifications, both in terms of the understory community composition and the characteristics of the sites. Both Cajanderian and Sukachevian classifications found major vegetational gradients in boreal forests and ecological gradients that caused them. The results support to some extent the hypothesized correspondence of types between the two systems.

Visual inspection of the sample plots' location in the ordination space when grouped by site type suggests similar arrangement for Cajander's forest site types and Sukachev's forest types: both follow a fertility gradient, as is expected based on the original design of both classification systems. Visually, each pair of corresponding types is overlapping in the ordination space. However, based on the PERMANOVA, there were statistically significant differences in community composition between all pairs of site types, including the corresponding types except for the most fertile ones (herb-rich forests and *Herbae* type). Then again, in terms of effect size, the differences were the smallest between the corresponding site types. This suggests that if a correspondence of site types in the two systems is sought, the hypothesized pairing is likely the most accurate one.

That said, the cross-tabulation of Cajander's forest site types and Sukachev's forest types showed variable degrees of agreement between the two systems. In total, 61.8 % of the sample plots were classified into Cajander's and Sukachev's types that matched according to the hypothesized pairing. In particular, Cajander's herb-rich heath forests and sub-xeric heath forests tended to be classified as Sukachev's *Vaccinium myrtillus* type, and Sukachev's Lichen type as Cajander's sub-xeric heath forests. The results suggest that especially Cajander's HRH type does not have a clearly corresponding type in the Sukachevian system but is positioned somewhere in between Sukachev's HE/OX and VM types. These discrepancies likely reflect the differences between the classification systems: the Cajanderian system pays more attention to indicator species, while the Sukachevian system pays more attention to dominant species (for example, *Vaccinium myrtillus*). In addition, Sukachev's VM type may appear so extensive (largely covering Cajander's HRH and SXH types) because it is originally intended to be further divided by tree species. The result of a 61.8 % match is also affected by the classification process itself. The small sample sizes of the rarest site types (especially Cajander's HR and XH, and Sukachev's HE, OX, and LI) meant a small amount of data for training the classification models. This too may have contributed to the extent of Sukachev's VM type as predicted for the Finnish data. While the error rate of the models was reasonably low according to the cross-validation procedure, their ability to classify new data may still be limited, especially in a case such as vegetation data that is highly affected by sampling effort. Finally, it can be challenging to identify the types consistently even *in situ*. For example, compositional overlap among Cajander's site types has been found to be high and borderline cases can be difficult to classify (Tonteri et al., 1990b, 1990a).

Variables describing site productivity also followed the fertility gradient. Organic layer C:N ratio, exchangeable Ca content, and pH are measures of soil productivity: C:N ratio is lower and exchangeable Ca and pH are higher in more fertile sites. The order of the site types followed this pattern. Interestingly, C:N ratio and pH were higher in Russian than Finnish plots. This may result from several factors (climate, frequency of forest fires, management, stand age) that are not possible to entangle based on the dataset. Then again, tree productivity (the ratio of stand age to volume) was higher in Finnish than in Russian plots. These results likely reflect differences in fire or management history (Perring et al., 2018) – for example, intensive management of stands in Finland has promoted tree growth. The differences between the countries in C:N ratio, soil pH, and tree productivity displayed themselves as statistically significant, high-effect differences between site types that were expected to be similar. Still, even if the absolute values differ, the gradients formed by the site types are the same. Such a result could be expected also, for example, if plots of the same Cajanderian forest site type from northern and southern Finland were compared, as the purpose of the system is to organize forests by their productivity within vegetation zones not necessarily in absolute terms but in comparative terms (Hotanen et al., 2008).

The observed differences among site types in terms of plant species richness also suggest that within both classification systems, site type can be a plausible indicator of biodiversity. In both systems, total species richness and vascular plant and bryophyte species richness were higher in more fertile site types, and lichen species richness was higher in less fertile site types. Previous work in Finland has shown that forest site type is a good indicator for vascular plant diversity (Similä et al., 2006). Salemaa et al. (2008) found plant species composition and especially the number of herb species to correlate well with site index (a measure of tree productivity). In several cases, species richness was higher in Sukachev's forest type than the corresponding Cajander's site type. For bryophytes and lichens, the higher richness may be due to differences in the data collection, as these species were recorded from a larger area in Russian than Finnish sample plots. However, it is also possible that the higher bryophyte and lichen richness in Russian plots is affected by management history, as intensive forest management has led to decreases in abundance and even local extinctions of these taxa in Finnish forests (Tonteri et al., 2016; Vanha-Majamaa et al., 2017).

In summary, our results suggest that both Cajander's and Sukachev's site type classifications logically arrange the variation within the focal forests with respect to multiple characteristics – community composition, soil fertility, tree productivity, and biodiversity in the understory – and do so in a similar way. The correspondence between certain types in the Cajanderian and Sukachevian system, as assumed by previous work (Lukina et al., 2019b; Sukhanov et al., 2014), appears to be true at least similarly to the correspondence between Cajander's forest site types in different vegetation zones within Finland. We must note, though, that the unequal sample sizes between the two countries and between site types in our data require that the results are interpreted with caution. More reliable statistical analyses would require more equal sample sizes. The correspondence between Cajander's and Sukachev's types in both extremes of the fertility gradient is especially uncertain.

Our results also illustrate that within both systems there is overlap between the site types in terms of species composition and soil properties. In Finland, the Cajanderian classification has not gone without criticism from the beginning (Keltikangas, 1959; Oksanen, 1990). For example, it has been criticized for underestimating the impact of tree species (Kuusipalo, 1985) and for the overlap between the site types

(Lahti and Väisänen, 1987). In Russia, several classifications more or less similar to Sukachev's have been developed (Rysin, 1975). In addition to fundamental criticisms of Cajander's and Sukachev's vegetation classification approach, the applicability of the systems in modern forests has been questioned. The original descriptions of Cajander's and Sukachev's forest types were based on the understory species composition of mature, unmanaged forests. However, those have become rare in Finland (Kuuluvainen and Gauthier, 2018) as well as in Karelia and adjacent territories (Shorohova et al., 2019). Cajander eventually defined his classification to include variation caused by stand succession as well as management, and it has indeed been shown that the successional stage and the disturbance history of the stand influence the composition of the understory (Fedorchuk et al., 2005; Genikova et al., 2019, 2012; Uotila et al., 2005; Uotila and Kouki, 2005). In addition, forest management practices other than harvesting (e.g. fertilization; Genikova and Kharitonov, 2018; Strengbom and Nordin, 2008) and other anthropogenic environmental changes (Hedwall et al., 2019) can influence the understory vegetation. These factors may explain some of the overlap between site types observed also in our study. Accounting for the tree species composition of the stand (as originally intended by Sukachev) may group forest sites into types with more distinct understory community compositions than the classifications used in this study. Besides vegetation, tree species also influence soil properties (Lukina et al., 2019a; Tamminen, 2000). That said, the expected patterns of community composition, soil fertility, tree productivity, and biodiversity were still found.

In this study, we examined two traditional boreal forest classification systems that are still widely used in Finland and Russia. Forest classifications are, however, still actively developed. With the widespread use of concentrated clear-cutting in the second half of the 20th century, classification of secondary forests became a problem, which is solved in dynamic classifications. Simultaneously with the Sukachevian and Cajanderian systems, a dynamic (genetic) classification of the forests of the Far East in Russia was developed by Ivashkevich (1916), developed later by Kolesnikov (1974) and other forest researchers. A dynamic typology that reflects the current state of the forests of Eastern Fennoscandia is also being developed (Kryshen', 2010). Its essence lies in associations for each stage of succession that have been identified based on the types of forests' growing conditions as identified by Sukachev, indicating the dynamic series for forests on mineral soils (Kryshen et al., 2018).

International nature conservation, monitoring, and management efforts have created needs for harmonized vegetation classifications of varying specificity. For example, in Europe a shared system of vegetation classification has been developed as part of the EUNIS habitat classification (Davies et al., 2004). Another example is the EuroVegChecklist, which is based on specifically on floristic composition unlike the broader EUNIS (Mucina et al., 2016). Shared needs for knowledge transfer exist also within the European boreal zone, and the results of our study suggest that it may be possible to use existing forest classification systems somewhat interchangeably to facilitate these endeavors. Whether the correspondence between the site types is good enough will depend on the exact purpose. Detailed, site-specific understanding is likely required in any case for responsible and effective forest management choices: “Sound planning in forestry is site-specific but arranged generally according to the forest site types” (Paal et al., 2010). New demands placed on forests have given rise also to new demands for the information provided by forest classifications. Recently emerged paradigms of forest ecology and natural resource management, such as ecosystem management and resilience thinking, emphasize the complexity, dynamism, and unpredictability of ecosystems (Messier et al., 2015). Traditional forest classifications combined with ecosystem-level understanding and site-specific knowledge may serve as a basis for modern, multifunctional forest management.

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Author contributions

P.M., M.S. and A.K. conceived of the research idea; A.K., E.T., N.G., S.M., H.I., T.T., and M.S. led the data collection and data management; T.P. performed statistical analyses with contributions from J.O. and M.S.; T.P. wrote the paper with contributions from J.-P.H., A.K., and N.G.; all authors discussed the results and commented on the manuscript.

Data availability

The data used in this study are stored in the internal databases of Natural Resources Institute Finland (Luke), and the Center for Forest Ecology and Productivity and Karelian Research Centre, Russian Academy of Sciences. The authors will provide all data upon request.

Supporting information

Appendix S1. Description of Cajander's forest site types

Appendix S2. Description of Sukachev's forest types

Appendix S3. Site type classification models

Appendix S4. Supplementary results

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Tables

Table 1. Hypothesized correspondence between Cajander's forest site types and Sukachev's forest types. Types on the same row are hypothesized to be analogous between the two systems. The column '*n*' shows the number of plots classified into the site type in our dataset.

Cajander's forest site type (Finland)			**Sukachev's forest type (Russian Karelia)**		
Name	**Abbreviation**	***n***	**Name**	**Abbreviation**	***n***
Herb-rich forest	HR	10	*Herbae*	HE	4
Herb-rich heath forest	HRH	50	*Oxalis*	OX	6
Mesic heath forest	MH	165	*Vaccinium myrtillus*	VM	46
Sub-xeric heath forest	SXH	102	*Vaccinium vitis-idaea*	VV	23
Xeric heath forest	XH	14	Lichen	LI	7

Table 2. Cross-tabulation of Cajander's site type (rows) and Sukachev's forest type (columns). The column and row labeled 'Match (%)' shows the percentage of plots classified into site types that matched according to the hypothesized correspondence (Table 1). For example, 47.1% of herb-rich forest plots (HR) were classified as *Herbae* type (HE), and 61.5% of *Herbae* type plots were classified as herb-rich forest.

Type	**HE**	**OX**	**VM**	**VV**	**LI**	**Match (%)**
HR	8	7	2	0	0	47.1
HRH	5	3	50	0	0	5.2
MH	0	0	194	2	0	99.0
SXH	0	0	74	57	8	41.0
XH	0	0	0	15	2	11.8
Match (%)	61.5	30.0	60.6	77.0	20.0	61.8

Table 3. Pairwise community dissimilarity. Shown are the coefficients of determination (R^2). Statistically significant values (p-value < 0.05) are shown with grey background shading.

	HE	OX	VM	VV	LI
HR	0.08	▨ 0.11	▨ 0.22	▨ 0.39	▨ 0.29
HRH	▨ 0.03	▨ 0.04	▨ 0.12	▨ 0.21	▨ 0.10

MH	0.04	0.06	0.03	0.06	0.05
SXH	0.09	0.14	0.13	0.04	0.07
XH	0.35	0.42	0.22	0.11	0.13

Table 4. Pairwise comparisons of soil C:N ratio. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-1.00	-0.84	-0.82	-1.00	-1.00
HRH	-1.00	-0.45	-0.68	-1.00	-1.00
MH	-0.34	0.22	-0.27	-0.85	-0.89
SXH	0.22	0.56	0.00	-0.73	-0.77
XH	0.57	0.77	0.22	-0.59	-0.43

Table 5. Pairwise comparisons of exchangeable Ca. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-0.25	-0.40	-0.14	-0.17	-0.14
HRH	0.00	-0.17	0.35	0.46	0.52
MH	-0.28	-0.40	0.11	0.34	0.41
SXH	-0.56	-0.57	-0.17	0.17	0.18
XH	-0.79	-0.86	-0.57	-0.31	-0.49

Table 6. Pairwise comparisons of organic layer pH. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-0.55	-0.63	-0.33	-0.28	-0.26
HRH	-0.59	-0.54	-0.02	0.07	-0.03
MH	-0.94	-0.84	-0.57	-0.49	-0.74

SXH	-0.95	-0.92	-0.75	-0.67	-0.90
XH	-1.00	-0.95	-0.83	-0.75	-0.98

Table 7. Pairwise comparisons of tree productivity. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	0.70	0.73	0.79	0.94	1.00
HRH	0.68	0.59	0.69	0.84	0.88
MH	0.24	0.20	0.27	0.49	0.66
SXH	0.03	0.03	0.06	0.30	0.48
XH	-0.29	-0.33	-0.40	-0.24	-0.06

Table 8. Pairwise comparisons of total species richness. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-0.05	-0.37	0.80	0.96	1.00
HRH	-0.47	-0.80	0.52	0.89	0.95
MH	-0.89	-0.96	-0.29	0.37	0.41
SXH	-0.98	-1.00	-0.52	0.16	0.18
XH	-1.00	-1.00	-0.83	-0.42	-0.45

Table 9. Pairwise comparisons of vascular plant species richness. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	0.25	-0.10	0.93	1.00	1.00
HRH	-0.36	-0.72	0.73	0.96	1.00
MH	-0.87	-0.96	-0.03	0.60	0.76
SXH	-0.98	-1.00	-0.34	0.32	0.43

XH	-1.00	-1.00	-0.83	-0.41	-0.46

Table 10. Pairwise comparisons of bryophyte species richness. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-0.63	-0.73	-0.23	0.40	0.27
HRH	-0.62	-0.69	-0.22	0.37	0.24
MH	-0.77	-0.82	-0.44	0.18	0.14
SXH	-0.87	-0.90	-0.57	0.06	0.02
XH	-0.98	-0.99	-0.76	-0.20	-0.11

Table 11. Pairwise comparisons of lichen species richness. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	-0.25	-0.17	-0.76	-1.00	-1.00
HRH	-0.11	-0.05	-0.68	-1.00	-1.00
MH	0.18	0.19	-0.46	-0.96	-0.95
SXH	0.67	0.64	0.14	-0.65	-0.57
XH	0.98	0.95	0.60	-0.27	-0.14

Table 12. Pairwise comparisons of number of rare species. Shown are the rank-biserial correlations. The values have grey background shading for pairs where a statistically significant difference (p-value < 0.05) was observed.

	HE	OX	VM	VV	LI
HR	0.23	0.15	0.65	0.72	0.66
HRH	-0.27	-0.32	0.23	0.35	0.22
MH	-0.61	-0.58	-0.07	0.07	-0.12
SXH	-0.61	-0.58	-0.08	0.05	-0.13
XH	-0.70	-0.64	-0.15	-0.02	-0.21

Figure legends

Figure 1. Map of the sample plot locations in Finland and Russian Karelia. In Finland, the shape of the points marking the plot locations show the different vegetation zones.

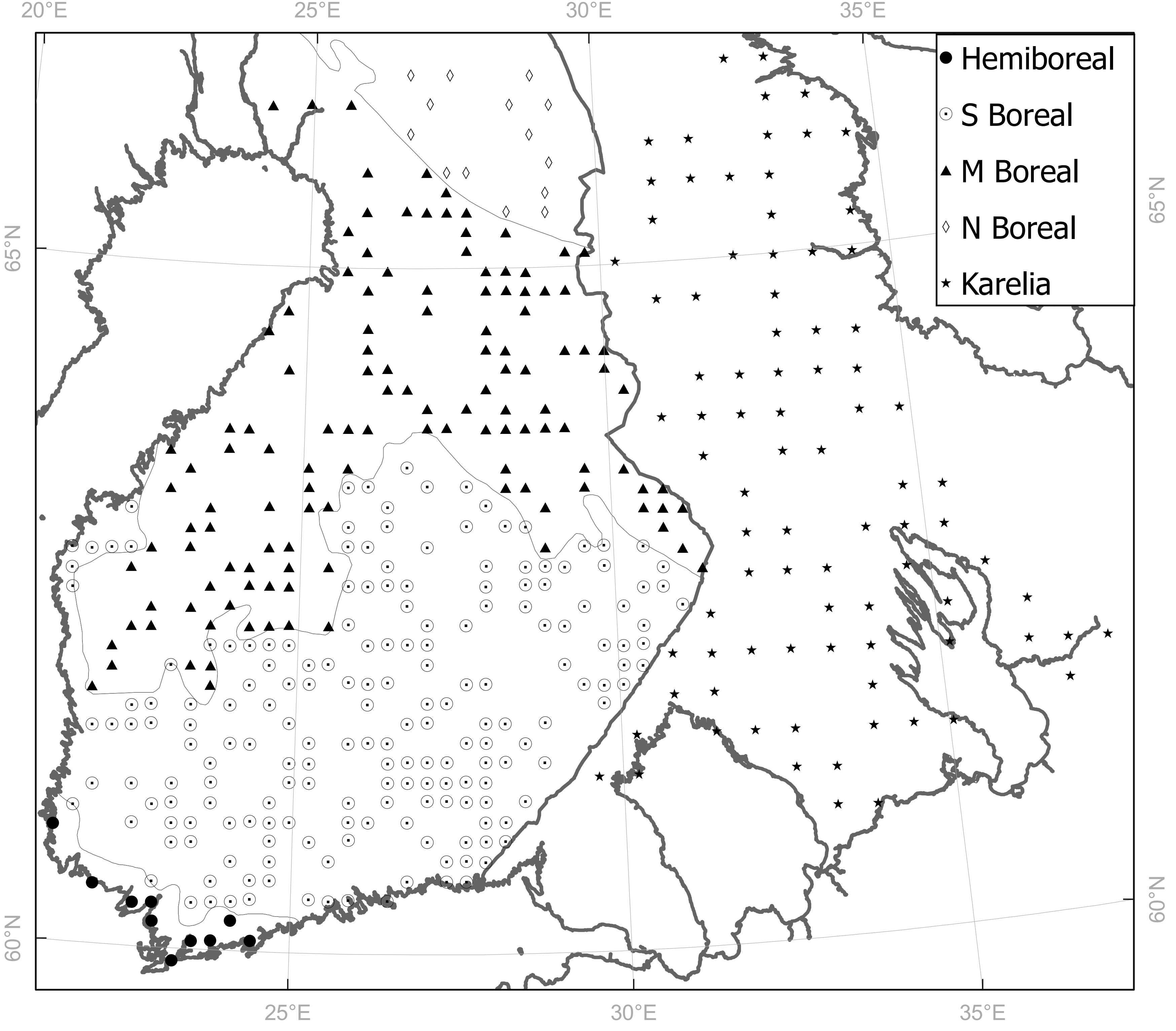
Figure 2. Distributions of stands by dominant tree species, stand age, and stand volume in the Finnish and Russian datasets.

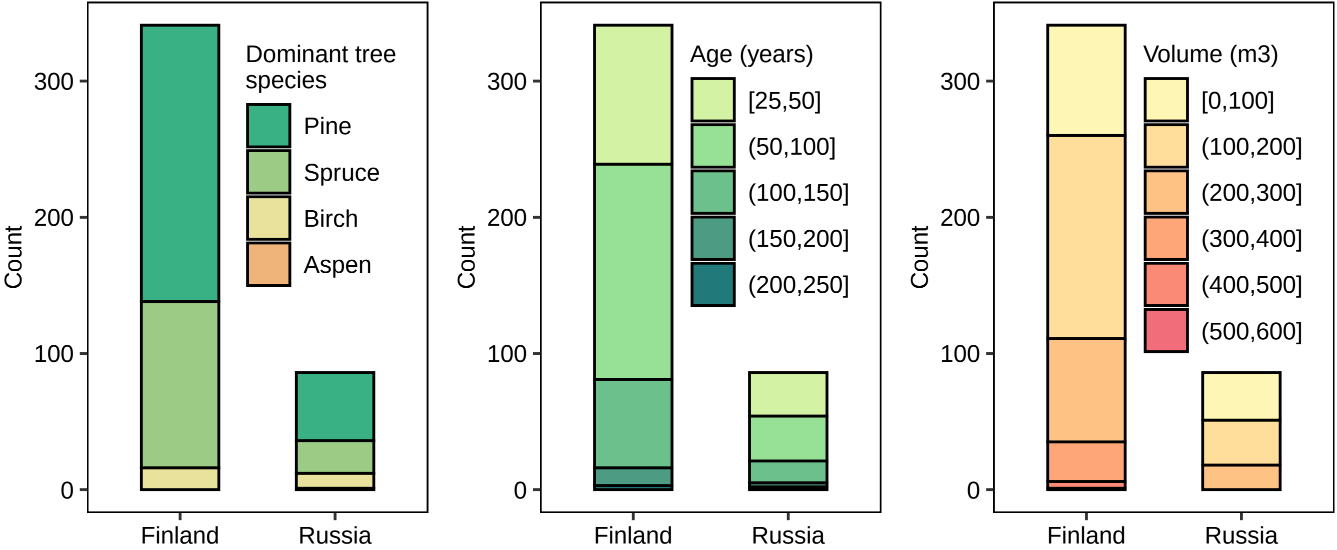
Figure 3. NMDS ordination of the combined vegetation data from Finland and Russia. The dashed lines mark the site types, according to Cajander's classification in (A) and Sukachev's classification in (B). The shape of the symbol shows from which country the data point is, and the color shows the site type.

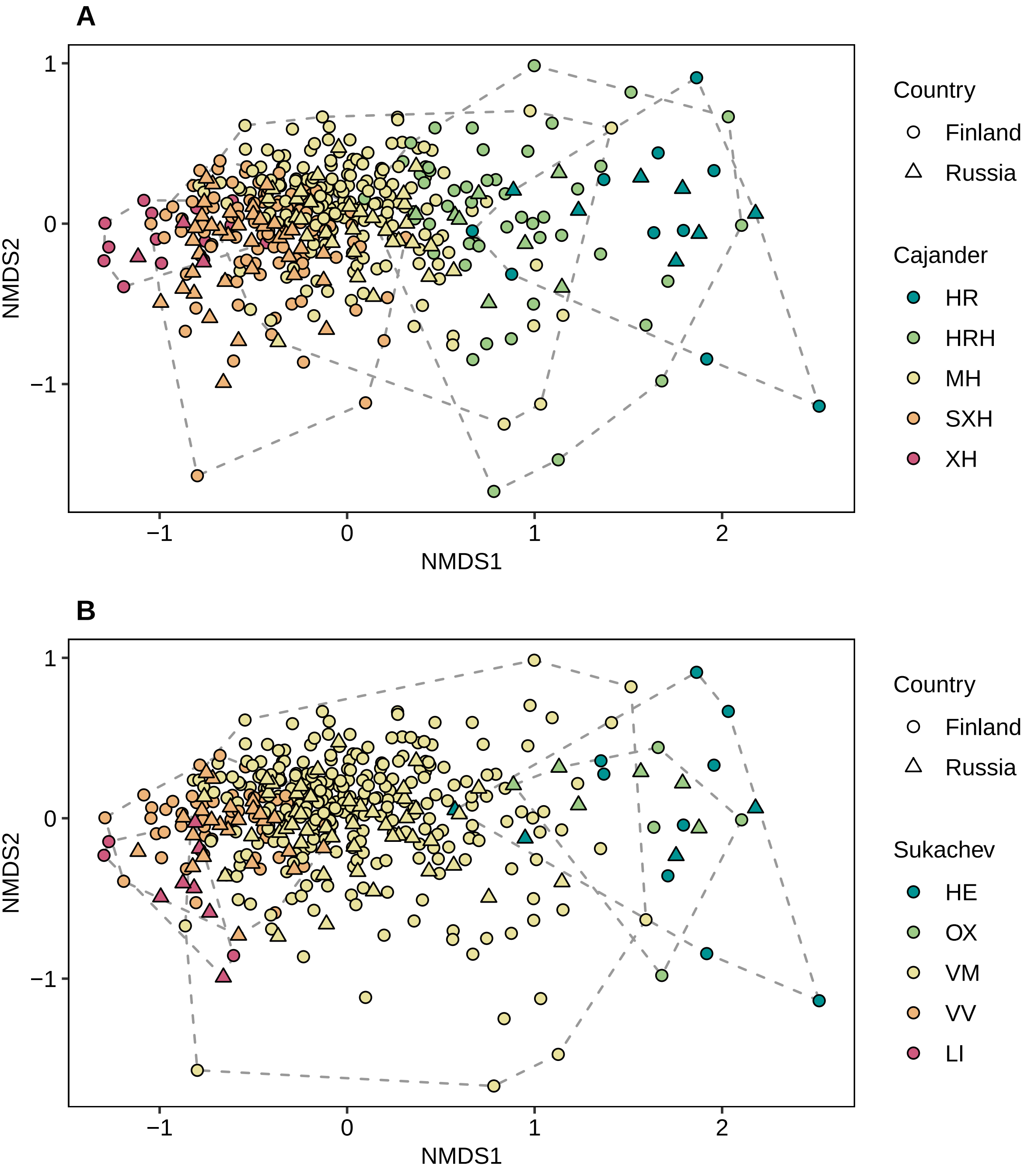
Figure 4. NMDS ordination of the combined vegetation data from Finland and Russia. In each panel A-E a Cajander's forest site type (orange dots) and the hypothetically corresponding Sukachev's forest type (blue triangle) is shown. The dashed lines mark the site types, and the grey dots show the rest of the sample plots.

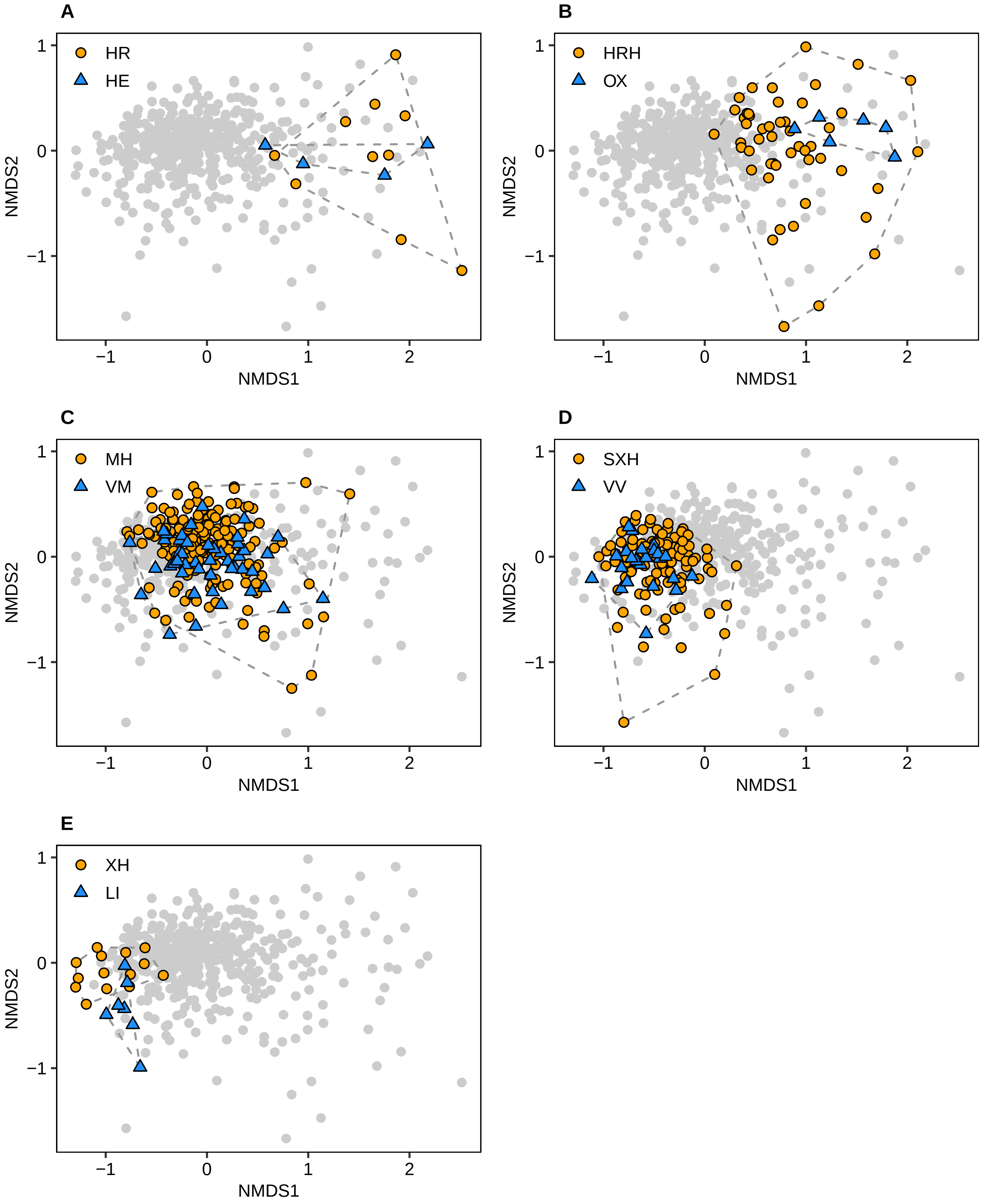
Figure 5. Box (median value and first and third quartiles) and whiskers (variability outside quartiles) plots showing the values of the variables describing site productivity in different site types: organic layer C:N ratio (panel A), exchangeable calcium (panel B), pH (panel C), and the ratio of stand volume and stand age (panel D) in the different site types. The boxes are colored according to the hypothesized correspondence between Cajander's and Sukachev's site types. Significance levels in tests of differences between pairs of site types: *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, ns $0.05 < p < 1$.

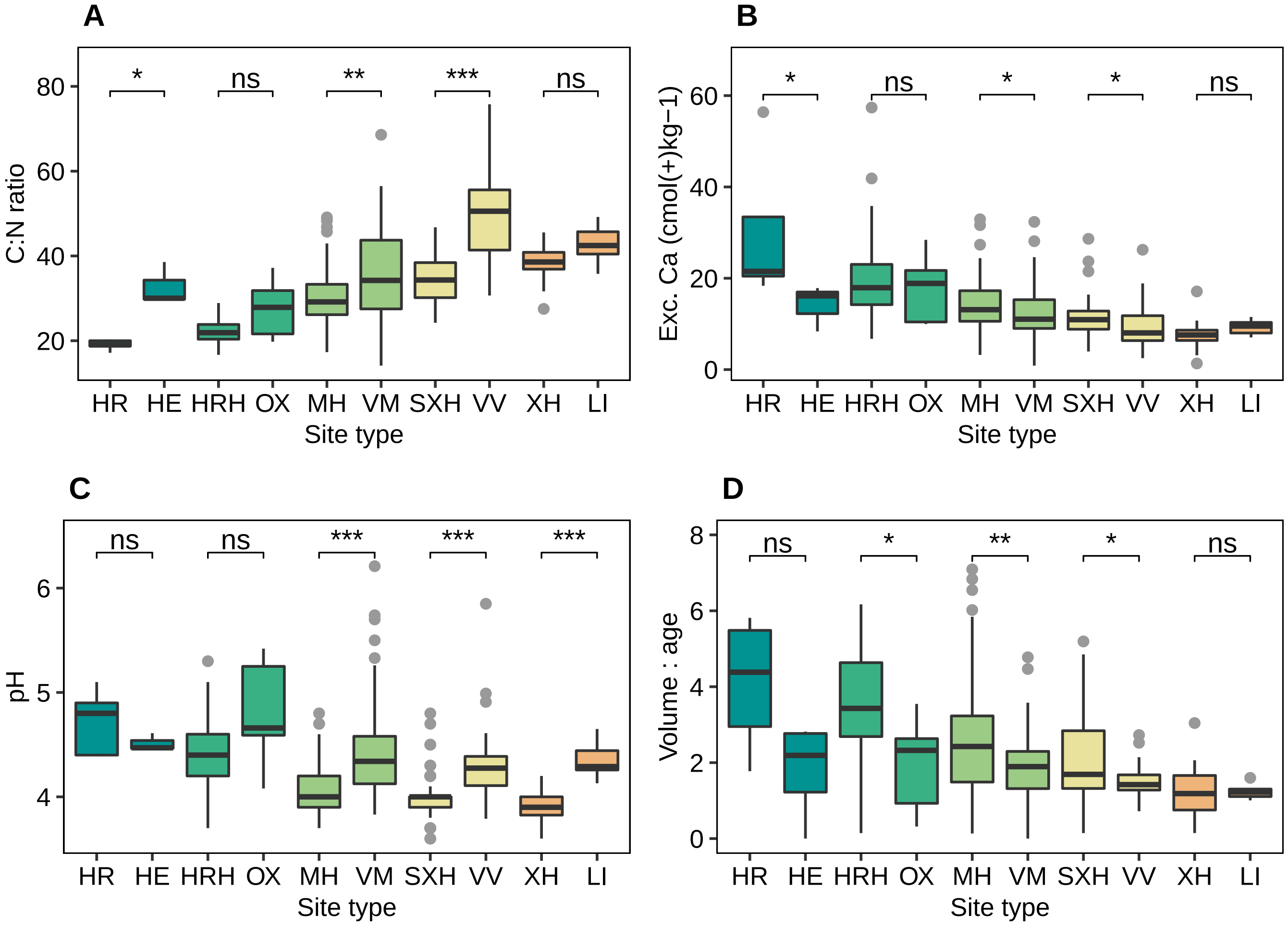
Figure 6. Box (median value and first and third quartiles) and whiskers (variability outside quartiles) plots showing the values of understory diversity in different site types: total species richness (panel A), richness of vascular plant species (panel B), bryophytes (panel C), and lichens (panel D), and number of rare species (panel E). The boxes are colored according to the hypothesized correspondence between Cajander's and Sukachev's site types. Significance levels in tests of differences between pairs of site types: *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, ns $0.05 < p < 1$.


20°E
25°E
30°E
35°E
65°N
60°N
25°E
30°E
35°E
65°N
60°N
● Hemiboreal
⊙ S Boreal
▲ M Boreal
◊ N Boreal
★ Karelia


Count
300
200
100
0
Finland
Russia
Dominant tree species
Pine
Spruce
Birch
Aspen
Age (years)
[25,50]
(50,100]
(100,150]
(150,200]
(200,250]
Volume (m3)
[0,100]
(100,200]
(200,300]
(300,400]
(400,500]
(500,600]


A
NMDS2
NMDS1
1
0
−1
−1
0
1
2
Country
Finland
Russia
Cajander
HR
HRH
MH
SXH
XH
B
NMDS2
NMDS1
1
0
−1
−1
0
1
2
Country
Finland
Russia
Sukachev
HE
OX
VM
VV
LI


A
HR
HE
B
HRH
OX
C
MH
VM
D
SXH
VV
E
XH
LI
NMDS1
NMDS2
−1
0
1
2


A
C:N ratio
80
60
40
20
* ns ** *** ns
HR HE HRH OX MH VM SXH VV XH LI
Site type
B
Exc. Ca (cmol(+)kg−1)
60
40
20
0
* ns * * ns
HR HE HRH OX MH VM SXH VV XH LI
Site type
C
pH
6
5
4
ns ns *** *** ***
HR HE HRH OX MH VM SXH VV XH LI
Site type
D
Volume : age
8
6
4
2
0
ns * ** * ns
HR HE HRH OX MH VM SXH VV XH LI
Site type