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Diversity of forest vegetation across a strong gradient of climatic continentality: Western Sayan Mountains, southern Siberia

Milan Chytrý · Jiří Danihelka · Svatava Kubešová · Pavel Lustyk · Nikolai Ermakov · Michal Hájek · Petra Hájková · Martin Kočí · Zdenka Otýpková · Jan Roleček · Marcela Řezníčková · Petr Šmarda · Milan Valachovič · Denis Popov · Ivan Pišút

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Abstract Southern Siberian mountain ranges encompass strong climatic contrasts from the relatively oceanic northern foothills to strongly continental intermountain basins in the south. Landscape-scale climatic differences create vegetation patterns, which are analogous to the broad-scale vegetation zonation over large areas of northern Eurasia. In their southern, continental areas, these mountains harbour forest types which potentially resemble the full-glacial forests recently reconstructed for Central Europe. To identify forest vegetation–environment relationships in the southern Siberian mountain ranges, forest vegetation of the Western Sayan Mountains was sampled on a 280 km transect running from the northern foothills with oceanic climatic features to the continental Central Tuvinian Basin in the south. Based on the species composition, vegetation was classified into hemiboreal forests, occurring at drier and summer-warm sites with high-pH soil, and taiga, occurring at wetter, summer-cool sites with acidic soil. Hemiboreal forests included *Betula pendula-Pinus sylvestris* mesic forest, *Larix sibirica* dry forest and *Pinus sylvestris* dry forest. Taiga included *Abies sibirica-Betula pendula* wet forest, *Abies sibirica-Pinus sibirica* mesic forest and *Pinus sibirica-Picea obovata* continental forest. Hemiboreal forests were richer in vascular plant species, while taiga was richer in ground-dwelling cryptogams. Vegetation–environment relationships were analysed by indirect and direct ordination. Winter and summer temperatures and precipitation exerted a dominant influence on species composition. Soil pH was also an important correlate of species composition, but this factor itself was probably controlled by precipitation. At a more local scale, the main source of variation in species composition was topography, producing landscape patterns of contrasting plant communities on slopes of different aspects and valley bottoms. The response of tree species to major

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M. Chytrý (✉) · J. Danihelka · S. Kubešová · P. Lustyk · M. Hájek · P. Hájková · M. Kočí · Z. Otýpková · J. Roleček · M. Řezníčková · P. Šmarda
Department of Botany and Zoology, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic
e-mail: chytry@sci.muni.cz

J. Danihelka · M. Hájek · P. Hájková
Institute of Botany, Academy of Sciences of the Czech Republic, Poříčí 3a, 603 00 Brno, Czech Republic

S. Kubešová
Department of Botany, Moravian Museum, Hviezdoslavova 29a, 627 00 Brno, Czech Republic

N. Ermakov
Central Siberian Botanical Garden, Russian Academy of Sciences, Zolotodolinskaya 101, Novosibirsk 630090, Russia

M. Valachovič · I. Pišút
Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, 845 23 Bratislava, Slovakia

D. Popov
Institute of Cytology and Genetics, Russian Academy of Sciences, Lavrent'eva 10, Novosibirsk 630090, Russia

environmental factors was expressed with Huisman–Olff–Fresco models. *Larix sibirica* appeared to be most resistant to drought and winter frosts, *Pinus sibirica* was adapted to low temperatures both in winter and summer, and *Picea obovata* had an intermediate response to climate. *Betula pendula, Pinus sylvestris* and *Populus tremula* were associated with the warmest sites with intermediate precipitation, while *Abies sibirica* was the most moisture-demanding species, sensitive to deep winter frosts.

Keywords Classification · Hemiboreal forest · Ordination · Soil pH · Species response curve · Taiga · Vegetation–environment relationships

Introduction

Siberia harbours one of the world's largest areas of natural forest—the taiga. Although the major zonation patterns of Siberian taiga were recognized early (Alekhin 1951, Lavrenko and Sochava 1956, Walter 1974), patterns of floristic differentiation, species richness and vegetation–environment relationships at finer scales are still poorly known (Spribille and Chytrý 2002). The main reason for this lack of knowledge is the focus of traditional Russian vegetation science on dominant species, without detailed analysis of species composition (Sukachev and Dylis 1964). Only recently a more detailed picture of floristic diversity and its environmental correlates was provided by some synthetic phytosociological studies, which focused on the southern Siberian hemiboreal forests (Ermakov et al. 1991, 2000; Ermakov 2003), Mongolian forests (Hilbig 1995), and taiga of the Lake Baikal region (Anenkhonov and Chytrý 1998) and Yakutia (Ermakov et al. 2002). It appears from these studies that the diversity of the herb and moss layer of Siberian forests may vary considerably even though dominant tree species are the same across huge areas. Thus, variation in floristic diversity may deviate from the patterns of zonation of tree dominants, described in earlier studies. Due to the lack of focus on species composition in most previous studies, very little information is available on the patterns of plant species richness in Siberian forests at the habitat level.

Siberian forests are of great interest to conservationists, because in many areas, their huge tracts are still preserved in a natural state and are almost without human impact. Detailed surveys of vegetation and floristic diversity of these forests have only been done in rather restricted areas while there are many areas which are still waiting for their basic botanical reconnaissance. Siberian forests are also of great interest to ecologists for many reasons, of which we will mention just two. First, the tree species composition of some Siberian forests is very similar to the vanished forests that have been recently reconstructed based on fossil pollen and charcoal from the full-glacial period in eastern Central Europe (Willis et al. 2000, Jankovská et al. 2002). Given that the modern continental climate of southern Siberia is very close to the Central European climate during the Pleistocene glacial periods (Frenzel et al. 1992), Siberian forests are the closest modern analogy to the full-glacial forests of Central Europe. Exploration of their diversity may therefore contribute to a deeper understanding of palaeoecology and genesis of European biota. Second, Siberian tree species, in particular Siberian pine (*Pinus sibirica*) and Siberian larch (*Larix sibirica*), are adapted to growth at extremely cold and dry sites, the very climatic limit of forests. Any extension or constriction of their range at the expense or benefit of treeless vegetation can thus be considered as fingerprints of climate change, as in the case of their closely related species *Pinus cembra* and *Larix decidua* at the alpine timberline of the Alps (Tinner and Kaltenrieder 2005).

Within Siberia, the mountain ranges in the south, the Altai and the Sayans, are an appropriate model area for a study of vegetation–environment relationships because they are situated at the border of three biomes, taiga, steppe and alpine tundra (Alekhin 1951; Lavrenko and Sochava 1956; Walter 1974), and their heterogeneous topography creates considerable climatic contrasts between the relatively oceanic areas in the north and strongly continental areas in the south. Therefore it is possible to compare different vegetation types in contrasting environments and to study species responses across long environmental gradients. Vegetation change over a distance of a few dozen kilometres in these mountain ranges often corresponds to a change which could be only observed at a distance of several thousand km in lowland areas of Siberia. In addition, regional floras of these mountains are richer than elsewhere in

Siberia, with more than 1400 vascular plant species per 100,000 km^2 (Malyshev 1993). Many species of European flora reach their eastern distribution limits in these mountains (Meusel et al. 1965–1992), which makes the current vegetation patterns in this area very relevant for the interpretation of the history of European vegetation.

The aim of this article is to explore habitat-level floristic diversity and its environmental correlates in forests of the central part of the mountainous area of southern Siberia, the Western Sayan Mountains. This area was selected because (1) it includes a strong north–south gradient of climatic continentality with considerable change in floristic diversity; (2) it is very little influenced by humans and represents an area of great conservation value. Given the possible links between the modern Siberian vegetation and European palaeovegetation, we will pay particular attention to the climatic relationships of plant communities and individual species in this area.

Study area

The area is situated in southern Siberia (Russia) between the towns of Sayanogorsk and Ermakovskoe in the north and the Russian–Mongolian border in the south (50° 43′–53° 11′ N; 91° 08′–93° 28′ E). It includes the moutain range of the Western Sayan and areas adjacent to the Central Tuvinian Basin, namely the northern fringes of the Tannu-Ola Range, which runs along the Russian–Mongolian border. The Sayano-Shushenskii Biosphere Reserve is situated in the central part of the study area.

The Western Sayan Mountains are formed on a Palaeozoic platform, which was denudated and raised again in the Tertiary (Voskresenskii 1962; Olyunin 1975). The lower and middle sections of the mountains (altitudes of 350–1700 m) have a rugged topography with steep slopes and deep valleys. This area contains numerous rock outcrops, cliffs and talus slopes (Ermakov et al. 2006). It consists of various metamorphic rocks, in particular base-rich chloride slates. Igneous rocks and limestones occupy small areas. The high-mountain area (1700–2860 m) is characterized by different landforms including both ancient tablelands (peneplains) and areas with steep slopes, rugged ridges and deep valleys. Similar landforms are also typical of the Tannu-Ola Range. The Central Tuvinian Basin has flat or gently undulating landforms at altitudes of 550–1100 m (Mikhailov 1961; Olyunin 1975).

Due to its location in the centre of Eurasia, the macroclimate of the study area is strongly continental. Local climate, however, is considerably modified by its mountainous topography. The high-frontal ranges (up to altitudes of 2400–2860 m) of the Western Sayan intercept the humid westerly (Atlantic) air masses, which weaken the continental climatic features (Milkov 1977; Polikarpov et al. 1986). This area and the adjacent northern Altai thus become warmer and more humid than elsewhere in Siberia. At lower to middle altitudes, the temperature of the coldest month (January) ranges from −11°C to −22°C, while the temperature of the warmest month (July) is from +16°C to +19°C and annual precipitation varies from 500 mm to 900 mm (Gidrometeoizdat 1966–1970). The abundant winter precipitation forms snow cover of up to 1.5 m, protecting soil and ground vegetation from frost. At the north-facing, windward slopes of the main (Osevoi) ridge of the Western Sayan, annual precipitation is about 1600 mm. In contrast, southern part of the Western Sayan, Central Tuvinian Basin and the Tannu-Ola Range are in an area of rain shadow. Their climate is arid and continental, with annual precipitation below 400 mm, of which 88–95% falls during a short period from late July to September. January temperatures range from −27°C to −34°C and July temperatures from +16°C to +18°C. Winter frosts are even more extreme on the summits of the Tannu-Ola Range (Gidrometeoizdat 1966–1970). In winter the weather is affected by the northern Asian anticyclone, which results in cooling, the formation of stagnant cold air masses and the absence of stable snow cover.

The main vegetation types include steppe at the bottom of the Central Tuvinian Basin, forest-steppe and forest at middle altitudes and alpine tundra above the timberline. Forests occupy larger areas particularly on the northern side of the Western Sayan where precipitation and winter temperatures are comparatively high. In contrast, in the areas adjacent to the Central Tuvinian Basin, where both precipitation and winter temperatures are low, steppe ascends to higher altitudes while forest becomes restricted (Zhitlukhina 1988). In the forest-steppe landscapes, the pattern of treeless and forest patches is strongly determined by slope aspect, with steppe regularly occurring on south-facing slopes and forest on north-facing slopes. The timberline is located at altitudes of 1600–1750 m in the areas north of the main (Osevoi) ridge of the Western Sayan, but it ascends to higher altitudes (up to 2000 m) on drier southern ranges.

Methods

Data sampling

In order to obtain a data set representing the maximum variation of forest vegetation in the study area, we sampled forest vegetation on an approximately 280 km long north–south transect which followed the steep gradient of increasing climate continentality from the relatively oceanic northern edge of the Western Sayan to the continental areas adjacent to the Central Tuvinian Basin (Fig. 1). According to previous observations (Smagin et al. 1980; Polikarpov et al. 1986; Zhitlukhina 1988), this climatic gradient underlies the main gradient in vegetation diversity, so the sampling scheme basically corresponded to the gradsect method (Austin and Heyligers 1989). The transect followed the Yenisei river valley, flooded by the Sayano-Shushenskii water reservoir, which facilitated access to both low-altitude and high-altitude areas and to landforms of varied topography. The transect started on the Dzhoiskii ridge near the village of Sabinka in the north and ended at the Khonderei pass north of the village of Khandagaity in the south, situated in the Tannu-Ola Range. An additional and shorter N-S transect was sampled across the main ridge of the Western Sayan east of the Yenisei valley between the villages of Tanzybei and Aradan.

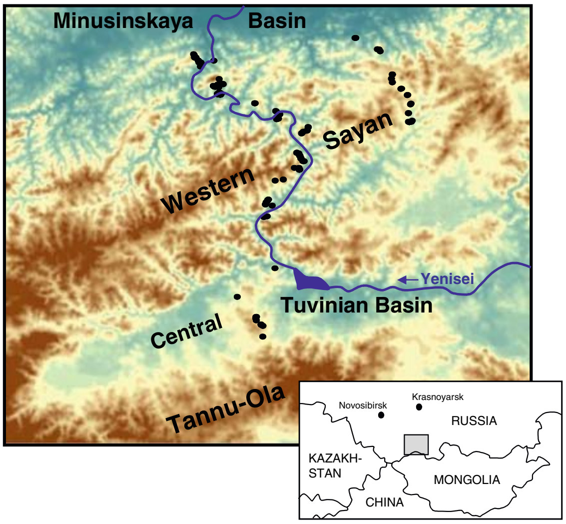

Fig. 1 Map of the study area with the sampled sites

Sampling units were vegetation plots of 10 × 10 m, randomly located in central parts of physiognomically and ecologically homogeneous vegetation stands. Sites affected by recent disturbances, e.g. early stages of post-fire succession, were avoided. Landscape sectors with different macroclimates, sharply separated by mountain ridges, were used as the basic sampling strata along the landscape transect. Within each stratum, we established a plot on each of the following landforms: north-facing slope, south-facing slope, ridge summit and valley bottom. If the same landform in a given stratum contained vegetation types of contrasting physiognomy or with different dominants (including different dominants of forest undergrowth), we placed one plot in each of these vegetation types. Replicated sampling of the same physiognomic vegetation type on the same landform and climatic sector was avoided. Sampling was done in July–August of 2003 and 2004. We sampled 129 plots in total.

In each plot, we recorded all species of vascular plants, ground-dwelling bryophytes and macrolichens, and estimated their cover on the nine-degree Braun-Blanquet scale (Westhoff and van der Maarel 1973). The taxonomy and nomenclature of vascular plants, bryophytes and lichens follow Cherepanov (1995), Ignatov and Afonina (1992) and Andreev et al. (1996), respectively.

In addition, we estimated percentage cover of the tree, shrub, herb and moss layers (the latter including lichens) and measured the height of the tree layer (with a Silva Clino Master clinometer), shrub layer and herb layer. Percentage cover of litter was estimated in each plot.

Along with vegetation variables, we measured the following variables, which we expected to have an effect on species composition:

Altitude was measured by a GPS receiver Garmin eTrex and checked against a topographic map of the scale 1 : 100 000.

Easting and northing were taken from geographic coordinates measured by GPS.

Slope inclination was measured in degrees with a Silva Clino Master clinometer.

Landform was assigned to one of these categories: convex ridge/steep slope, flat ridge, gentle slope, flat bottom, depression, moist depression.

Climatic variables (mean temperatures of July and January and mean sums of precipitation in the summer and winter half of the year) were estimated from a climatic model prepared in the geographic information system ArcGIS version 8.2 (www.esri.com). The model was based on a combination of data from Russian climate stations and altitudes from a digitized topographic map of the scale 1 : 200 000. Temperature values for different altitudes were computed based on the adiabatic lapse rate of 0.65°C per 100 m of altitude (Polikarpov et al. 1986). Precipitation values were computed on the basis of precipitation-altitude charts compiled by Polikarpov et al. (1986) for each of the aridity-humidity sectors recognized in the Altai–Sayan mountain system (Smagin et al. 1980; Polikarpov et al. 1986). Due to the high correlation between summer and winter precipitation ($r = 0.91$), only annual precipitation was used in calculations. However, July and January temperatures were weakly correlated ($r = 0.45$), therefore they were treated separately.

Potential solar radiation above the canopy (Above radiation) was calculated from the measured values of latitude, slope aspect and inclination, and accounted for shading by the surrounding topographic features. Potential solar radiation below the canopy (Transmitted radiation) was additionally accounted for shading by the forest canopy. Topographic and canopy shading was measured from hemispheric photographs taken in a vertical direction at a height of 1.5 m above ground at three sites within each plot. A Nikon CoolPix 4500 digital camera with a fish-eye lens was used. Calculations were done using Gap Light Analyzer software (Frazer et al. 1999) and averaged over the three photographs from each plot. Radiation was estimated as the daily sum of direct and diffuse radiation for 21 June.

Radiation and heat indices were calculated from slope inclination and aspect according to McCune and Keon (2002: Eq. 3). These two indices differ in that the radiation index attains maximal values on S-facing slopes and the heat index on SW-facing slopes.

Soil depth was measured in three places in each plot and averaged. Soils deeper than 30 cm were arbitrarily given the value of 30 cm.

Soil texture was assigned to one or more of the following categories: clayey, loamy, sandy, gravely, stony, scree, rock.

Soil pH and the conductivity of the soil solution were measured from a mixed soil sample taken in three places in each plot. It was taken from the mineral topsoil horizon at a depth of 5–10 cm or less if the soil was very shallow. Each sample was extracted in distilled water for 24 h (weight ratio of soil/water was 0.4) and measured by the digital pH-meter PH114 and conductivity meter CM113 (Snail Instruments, Beroun, Czech Republic). Conductivity caused by H^+ ions was subtracted according to Sjörs (1952).

Data analysis

The numerical classification of vegetation plots, based on their species composition, was performed with TWINSPAN (Hill 1979), using its modified version available in the JUICE program (Tichý 2002). TWINSPAN is a divisive classification method which usually performs well if the aim is to divide species composition data sets into a small number of groups. A disadvantage of this method is that it basically produces partitions with cluster numbers equal to 2, 4, 8, 16 etc., while partitions with other numbers of clusters are skipped even though they may be ecologically relevant. Therefore we used a modification of TWINSPAN which calculated, after each division, the mean Sørensen dissimilarity in species composition between all pairs of plots within each terminal cluster. Then, only the cluster with the highest mean internal dissimilarity (i.e. the most diverse cluster) was divided using the usual TWINSPAN divisive algorithm. In such a way, we received successive partitions with 2, 3, 4, 5 etc., clusters, and of these, we accepted the partition which was effectively interpretable in ecological terms, based on our field experience. Both TWINSPAN and Sørensen dissimilarity were calculated with pseudo-species based on three cover intervals: 0–5%, 5–25% and 25–100%.

TWINSPAN classification was summarized in a synoptic table of species by clusters. In the table, species were ordered according to their diagnostic value for individual clusters, expressed as fidelity. Fidelity was calculated using the phi coefficient of association (Sokal and Rohlf 1995; Chytrý et al. 2002), applied to the classified data set with cluster sizes equalized to 5% of the total data set size according to Tichý and Chytrý (2006). Species with $\Phi > 0.30$ were considered as diagnostic for individual clusters (vegetation types), but species whose occurrence concentration in the plots of a particular cluster was not significant at $P < 0.05$ (Fisher's exact test) were excluded. Within the table, species were ordered by decreasing fidelity to individual clusters i.e., by their decreasing diagnostic value. For species that did not meet these fidelity criteria, fidelity to two groups resulting from the first TWINSPAN division was calculated in the same way in order to obtain diagnostic species for a higher hierarchical level of classification. Fidelity was calculated and the table was edited in the JUICE program (Tichý 2002).

The matrix of species × vegetation plots with square-root transformed percentage covers was subsequently subjected to detrended correspondence analysis (DCA; Hill and Gauch 1980), using the CANOCO 4.5 package (ter Braak and Šmilauer 2002). DCA is an indirect ordination method, which extracts the main variation in species composition independently of environmental variables. To quantify and test the effect of individual environmental variables on species composition, we performed Monte Carlo tests (999 permutations) in a series of canonical correspondence analyses (CCA), each containing all vegetation plots and a single environmental variable (ter Braak and Šmilauer 2002). This test produced F values to measure the magnitude of the covariance between each variable and species composition and the corresponding significance level. Variables with a significant effect on species composition at $P < 0.05$ were then passively projected onto the ordination plot of DCA to help to interpret gradients in species composition.

For the seven most important tree species of the study area, responses to the main environmental variables were fitted using the Huisman-Olff-Fresco models (HOF; Huisman et al. 1993). HOF is a hierarchical set of five species response models with increasing complexity: model I—flat with no response, II—monotonously increasing or decreasing, III—monotonously increasing or decreasing with a 'plateau', IV—symmetric unimodal and V—asymmetric unimodal response. Four parameters of these models were estimated using a non-linear maximum likelihood estimation procedure (Oksanen and Minchin 2002), available in Jari Oksanen's 'gravy' library (http://cc.oulu.fi/%7Ejarioksa/softhelp/softalist.html) for the R program (http://www.r-project.org). This routine was run externally from the JUICE program (Tichý 2002) using a procedure developed by David Zelený and Lubomír Tichý and available at http://sci.muni.cz/botany/zeleny/hof.php.

Results

Main forest types

In the first division of TWINSPAN classification (Fig. 2), hemiboreal forests were separated from taiga forests. The former tend to occur in areas with less precipitation, higher summer temperatures and on soils with higher pH (Fig. 3), and to be richer in species of herb layer but poorer in ground-dwelling cryptogams (Fig. 4). Hemiboreal forests and taiga were each further divided into three sub-groups, hereafter named according to the main tree species ordered by their decreasing importance (Table 1, Fig. 5):

1. *Betula pendula-Pinus sylvestris* mesic hemiboreal forest (Table 1, cluster 1) is found on the relatively warm northern foothills and frontal ranges of the Western Sayan, especially on the Dzhoiskii Range SW of Sayanogorsk, and occasionally also in the Yenisei valley in the central part of the Western Sayan. It occurs on steep or gentle slopes of different aspects. Tree layer cover is mostly between 40 and 60%. Dominant trees are *Betula pendula* and *Pinus sylvestris*, the former being probably supported by past forest fires or cutting. *Larix sibirica* is admixed especially in the central part of the Western Sayan and *Populus tremula* in formerly disturbed stands in the area of northern foothills. The shrub layer is developed in most stands, but it rarely exceeds 25% cover. The herb layer is well developed (60–80%) and species-rich, consisting of herbs and graminoids, many of which are also typical of meadow steppe and have a Eurasian temperate distribution. It is often

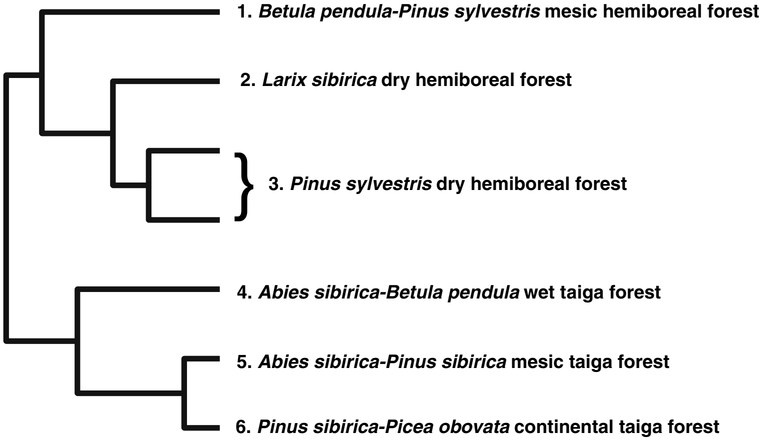

Fig. 2 TWINSPAN classification of the Western Sayan forests into six clusters

dominated by *Carex pediformis* s. lat. The moss layer is sparsely developed (cover about 1%) and species-poor.

2. *Larix sibirica* dry hemiboreal forest (Table 1, cluster 2) occurs in winter-cool areas in the southern part of the Western Sayan and on the Tannu-Ola Range, which are dry or have variable moisture during the growing season. It is found on both steep and gentle slopes of different aspects. The tree layer mostly attains covers of 25–50% and is dominated by *Larix sibirica*, in places with an admixture of *Pinus sibirica*. In these areas with a distinctive continental climate, *Pinus sylvestris* is absent and *Betula pendula* is very rare. The shrub layer is often sparse, but rather dense stands of *Rhododendron dauricum* can develop in places with shallow soil. The herb layer usually has a cover of 60–80%, but it is poorer in species than the other two types of hemiboreal forests in the study area. It consists of species adapted to spring and early summer moisture shortage and strong winter frosts, combined with poor plant protection by shallow snow cover. Many of these species have a central Asian distribution. In many stands the herb layer is dominated by *Iris ruthenica*, and in places also by *Calamagrostis pavlovii* or *Carex pediformis* s. lat. The moss layer can be very sparse, but in places pleurocarpous moss *Rhytidium rugosum* can form extensive carpets covering most of the ground surface.

3. *Pinus sylvestris* dry hemiboreal forest (Table 1, cluster 3) consists of two clusters suggested by TWINSPAN, which were merged because of unclear ecological differences between them (Fig. 2). This forest is found in the northern and central Western Sayan. It tends to occur on steep south-facing slopes with rock outcrops. Although the macroclimate in this area is less continental than in more southern areas, where the previous forest type is found, continental features are strenghtened by topoclimatic effects on steep slopes. The tree layer is open, mostly with a cover of 20–40%, dominated by *Pinus sylvestris* and containing an admixture of *Betula pendula*, *Larix sibirica* or *Pinus sibirica*. The shrub layer is usually well developed, with a cover of 20–30% and dominance of *Caragana arborescens* or *Rhododendron dauricum*. The herb layer usually has a cover 20–50% and contains a number of drought and frost adapted species, many of them with central Asian distribution. The dominant species of the herb layer are the same as in the previous community (*Calamagrostis pavlovii, Carex pediformis* s. lat. and *Iris ruthenica*). The moss layer has variable cover and its most frequent dominant species is *Rhytidium rugosum.*

4. *Abies sibirica-Betula pendula* wet taiga forest (Table 1, cluster 4) is found in the relatively warm and precipitation-rich areas of the northern and central Western Sayan, where it is confined to the wet places on lower slopes and the bottoms of stream valleys. In winter these habitats are protected by thick snow cover, while in summer they are well supplied with water. Soils in such places are the most productive within the study area. The tree layer, with a cover of 20–60%, is dominated by *Abies sibirica*, in places also by *Betula pendula*, whose dominance may partly be due to former disturbance. *Pinus sibirica* and *Picea obovata* are often admixed in the canopy and *Sorbus sibirica* in the subcanopy layer. The shrub

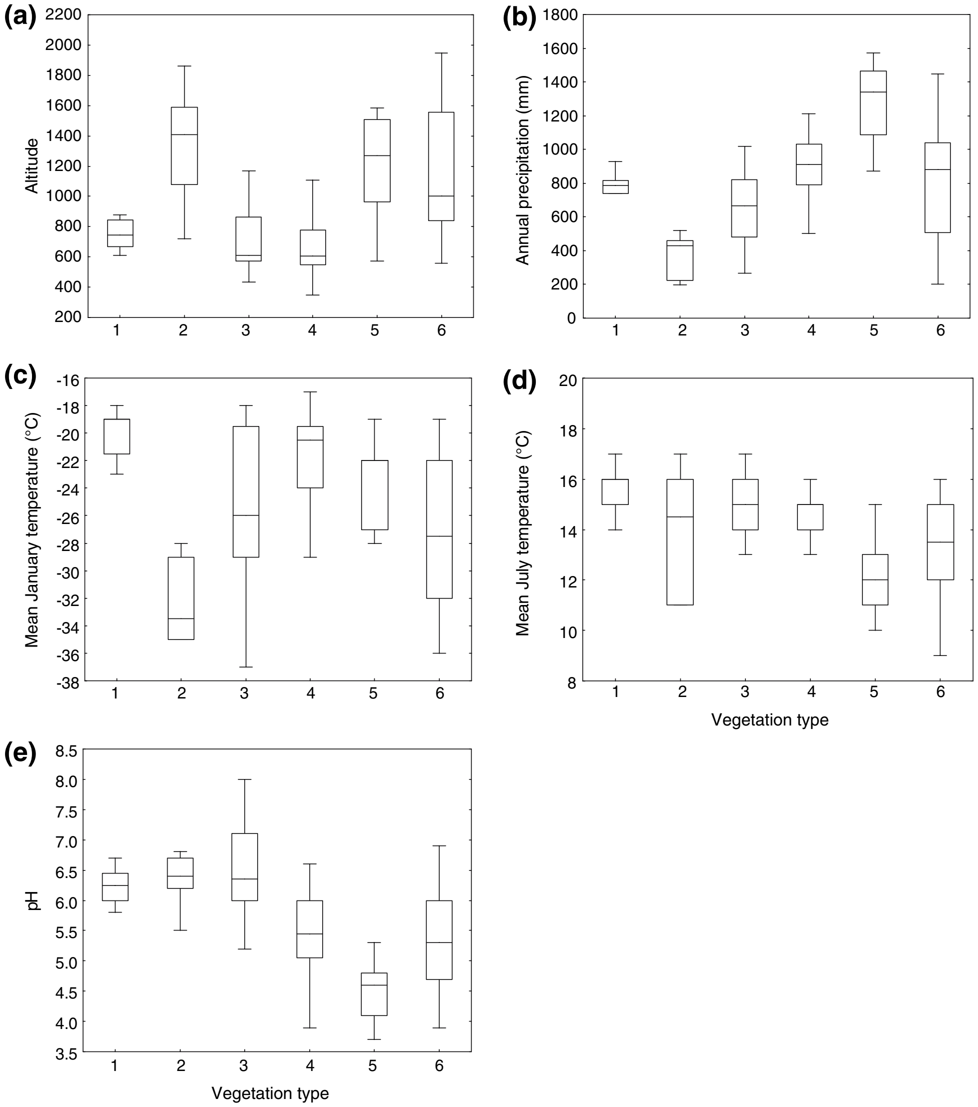

Fig. 3 Relationships of the six main forest types to altitude, climate and soil pH. Boxes represent median and quartiles; whiskers indicate 5% and 95% quantiles. See Fig. 2 for the names of vegetation types

layer has variable cover and is usually dominated by *Duschekia fruticosa*. The herb layer is dense (cover of 50–90%) and species-rich, dominated by tall ferns *Athyrium filix-femina, Diplazium sibiricum, Dryopteris expansa* and *Matteuccia struthiopteris* and tall grass *Calamagrostis obtusata*. The lower sub-layer of the herb layer is often formed of *Carex pediformis* s. lat. Most species in this forest type have Eurasian temperate or boreal distribution. The moss layer has a variable cover, most often between 20 and 50%, and is dominated by *Hylocomium splendens* and *Rhytidiadelphus triquetrus.*

5. *Abies sibirica-Pinus sibirica* mesic taiga forest (Table 1, cluster 5) occurs in the same area as the previous forest type, but at higher altitudes, where it is confined to north-facing slopes, which receive high precipitation but are relatively cool. In spite of this, soils on these slopes are less wet than in the previous type, which occurs on wet footslopes and valley bottoms. The tree layer usually has a cover of 20–50% and is dominated by *Abies sibirica* or *Pinus sibirica*; they form mixed stands, often with an admixture of *Picea obovata*. The shrub layer, often with *Lonicera altaica*, usually has a cover of less than

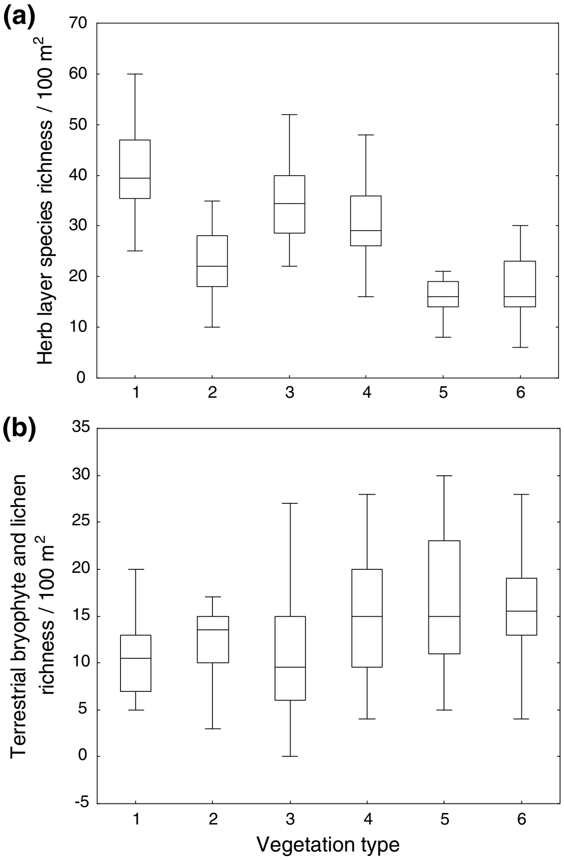

Fig. 4 Species richness per 100 m^2 of vascular plants in the herb layer (**a**) and ground-dwelling bryophytes and macrolichens (**b**) per 100 m^2 in the six main forest types. Boxes represent median and quartiles; whiskers indicate 5% and 95% quantiles. See Fig. 2 for the names of vegetation types

15%. The herb layer is species-poor, with a cover of 30–70%, dominated by *Vaccinium myrtillus* or *Bergenia crassifolia*, the latter being common in places with stony soil. Most species have boreal distribution ranges. The moss layer is usually very well developed, with a cover of 50–90%, and dominated by mesophilous or moisture-demanding mosses such as *Dicranum scoparium, Hylocomium splendens, Pleurozium schreberi, Polytrichum commune* and *Sphagnum* spp.

6. *Pinus sibirica-Picea obovata* continental taiga forest (Table 1, cluster 6) occurs throughout the study area in sites which are cooler and drier than those supporting taiga types with *Abies sibirica*, on slopes of different inclination and aspect. In the Tannu-Ola Range these forests occur near the timberline at altitudes of 1650–1950 m, while in the Western Sayan they can be found from altitudes of around 600 m up to the timberline. The tree layer, usually with 20–40% cover, is dominated by *Pinus sibirica* with a constant admixture of *Picea obovata*. In some places, *Larix sibirica* also occurs in the tree layer. The shrub layer is usually sparse, with a cover of less than 30%, and often dominated by *Rhododendron dauricum*. The herb layer has a cover of 30–60% and is usually dominated by *Vaccinium vitis-idaea*, which is adapted to a more continental climate than *V. myrtillus*, or by *Bergenia crassifolia*, which is especially common on stony soils. The moss layer has a cover of 30–90% and is dominated by *Hylocomium splendens, Pleurozium schreberi* and *Sphagnum* spp. Macrolichens of the genus *Cladonia* frequently occur in this forest type.

Gradients in species composition

Detrended correspondence analysis (DCA) revealed two strong gradients in species composition along the first two axes (Fig. 6; axis 1 eigenvalue 0.565, gradient length 4.365; axis 2 eigenvalue 0.426, gradient length 4.268; total inertia 12.069). The eigenvalue of the third axis was considerably lower (0.263).

Of the measured environmental variables, species composition is mainly influenced by pH and climatic variables (Table 2). The effect of some topographic variables, substrate types and incident radiation was significant but less important.

The passive projection of significant environmental variables onto the DCA ordination diagram (Fig. 7) suggests that the main gradient in species composition (axis 1) is correlated with soil pH, which is itself negatively correlated with precipitation. The second most important gradient (axis 2) is correlated with temperature, especially with a decreasing January temperature towards the southern, more continental part of the study area.

The passive projection of vegetation structure variables onto the same ordination diagram (Fig. 8) suggests that the shrub layer is richest in species at warm sites with high pH soils. The herb layer is richest at the same sites, but it is most productive at wet and warm sites. The moss layer is most dense and species-rich at cool and acidic sites at higher altitudes.

Tree species responses to environmental variables

Species response curves fitted using HOF models (Fig. 9) describe the relationships between the main tree species of the Western Sayan and the most important environmental variables. *Abies sibirica* is the most oceanic tree species, occurring in precipitation-rich areas with relatively warm winters, but summers can be relatively cool. Such areas are mostly found at lower and middle altitudes in the northern part of the study area. *Betula pendula, Pinus sylvestris* and *Populus tremula* have more continental affinities: they are found in relatively warm areas at lower altitudes with medium precipitation. *Picea*

Table 1 Synoptic table of species percentage occurrence (constancy) in six main forest types of the Western Sayan resulting from the TWINSPAN classification. 1. *Betula pendula-Pinus sylvestris* mesic hemiboreal forest, 2. *Larix sibirica* dry hemiboreal forest, 3. *Pinus sylvestris* dry hemiboreal forest, 4. *Abies sibirica-Betula pendula* wet taiga forest, 5. *Abies sibirica-Pinus sibirica* mesic taiga forest, 6. *Pinus sibirica-Picea obovata* continental taiga forest. Diagnostic species of individual forest types are determined using the phi coefficient of association (dark shading: $\Phi > 0.40$, light shading: $\Phi > 0.30$). Species with less than three occurrences in a particular forest type or species whose occurrence concentration probability in that forest type does not differ from random at $P < 0.05$ are excluded from the lists of diagnostic species even if their $\Phi > 0.30$. Species without diagnostic value occurring in > 10% of plots of the data set are shown at the end of the table. Vegetation layer abbreviations: T, tree layer (species names in bold); S, shrub layer; H, herb layer; M, moss layer

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
***Betula pendula-Pinus sylvestris* mesic hemiboreal forest**							
Sanguisorba officinalis	H	69	.	5	4	.	.
Brachypodium pinnatum	H	50	.	.	4	.	3
Vicia unijuga	H	50	.	5	.	.	3
Bupleurum longifolium [1]	H	38	.	.	4	.	.
Heracleum dissectum	H	56	.	5	7	.	3
Crepis sibirica	H	69	.	5	21	.	.
Calamagrostis arundinacea	H	69	.	.	21	.	6
Rubus saxatilis	H	88	14	35	7	.	3
Pulmonaria mollis	H	88	.	15	46	.	.
Lathyrus frolovii	H	50	.	.	14	.	3
Lathyrus gmelinii	H	56	.	.	21	.	3
Artemisia integrifolia	H	19	.	.	.	.	.
Alchemilla sp.	H	19	.	.	.	.	.
Pleurospermum uralense	H	50	.	.	18	.	3
Viola uniflora	H	75	21	10	11	6	6
Ptarmica impatiens	H	25	.	.	4	.	.
Viola hirta	H	25	.	.	4	.	.
Pteridium aquilinum	H	50	.	15	7	.	6
Trollius asiaticus	H	50	14	.	4	6	6
Lupinaster pentaphyllus	H	56	14	15	4	.	9
Ranunculus monophyllus	H	19	.	.	.	.	3
Melica nutans	H	38	.	.	18	.	3
Primula macrocalyx	H	25	.	5	4	.	.
Brachythecium starkei	M	25	.	5	4	.	.
***Larix sibirica* dry hemiboreal forest**							
Carex amgunensis	H	.	50	.	.	.	.
Larix sibirica	T+S	50	100	40	4	.	35
Lathyrus humilis	H	31	71	20	7	.	6
Geranium pseudosibiricum	H	25	57	10	.	.	6
***Pinus sylvestris* dry hemiboreal forest**							
Caragana pygmaea	S	.	.	50	.	.	.
Tephroseris integrifolia	H	.	.	35	.	.	.

Table 1 continued

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
Veronica incana	H	12	.	60	.	.	.
Aster alpinus	H	.	7	50	.	.	.
Schizonepeta multifida	H	6	.	45	.	.	.
Galium paniculatum	H	.	.	25	.	.	.
Viola dissecta	H	.	7	40	.	.	.
Sedum hybridum	H	.	.	30	.	.	3
Vicia amoena	H	.	.	20	.	.	.
Helictotrichon altaicum	H	.	.	20	.	.	.
Bupleurum scorzonerifolium	H	.	7	35	.	.	.
Poa sect. *Stenopoa*[2]	H	31	.	70	4	.	9
Galium verum	H	12	14	60	.	.	6
Kitagawia baicalensis	H	.	7	45	4	.	6
Orostachys spinosa	H	.	.	15	.	.	.
Pulsatilla turczaninovii	H	.	.	15	.	.	.
Pulsatilla patens s. lat.[3]	H	.	.	15	.	.	.
Adenophora stenanthina	H	.	.	15	.	.	.
Thymus serpyllum s. lat.[4]	H	.	.	15	.	.	.
Androsace septentrionalis	H	.	.	15	.	.	.
Polygala comosa	H	.	.	15	.	.	.
Tortula sinensis	M	.	.	15	.	.	.
Weissia condensa	M	.	.	15	.	.	.
Polygala sibirica	H	.	.	15	.	.	.
Dianthus versicolor	H	.	.	15	.	.	.
Potentilla acaulis	H	.	.	15	.	.	.
Campanula glomerata	H	19	7	55	.	.	6
Thalictrum foetidum	H	.	29	50	.	.	.
Phlomoides tuberosa	H	31	.	50	.	.	.
Cirsium serratuloides	H	12	7	45	4	.	3
Hedwigia ciliata	M	6	.	35	4	.	6
Neottianthe cucullata	H	6	21	45	.	.	.
Anemone sylvestris	H	.	7	25	.	.	.
Cotoneaster melanocarpus	S	38	21	65	.	.	3
Caragana arborescens	S	25	36	70	7	.	6
Artemisia gmelinii	H	6	7	30	.	.	.
***Abies sibirica-Betula pendula* wet taiga forest**							
Phegopteris connectilis	H	.	.	.	43	.	3
Paris quadrifolia	H	12	.	.	54	.	.
Athyrium filix-femina	H	19	.	.	68	12	.
Circaea alpina	H	12	.	.	64	12	3
Diplazium sibiricum	H	6	.	.	50	6	3
Matteuccia struthiopteris	H	.	.	.	21	.	.
Impatiens noli-tangere	H	.	.	.	21	.	.
Cinna latifolia	H	.	.	.	21	.	.
Urtica dioica	H	.	.	.	29	.	3
Oxalis acetosella	H	.	.	.	64	29	3
Plagiochila porelloides	M	.	7	15	71	12	9
Lactuca sibirica	H	.	.	.	18	.	.
Equisetum pratense	H	12	.	.	61	12	9
Ribes spicatum	S	6	.	5	36	.	.
Sambucus sibirica	S	6	.	.	29	.	.
Rhizomatopteris sudetica	H	.	.	.	14	.	.
Myosotis krylovii	H	.	.	.	14	.	.

Table 1 continued

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
Aconitum septentrionale	H	50	21	.	79	.	9
Dryopteris expansa	H	.	.	.	71	59	12
Ribes nigrum	S	.	.	.	39	12	9
Milium effusum	H	19	.	.	46	6	6
Cardamine macrophylla	H	.	.	.	25	.	9
***Abies sibirica-Pinus sibirica* mesic taiga forest**							
Barbilophozia lycopodioides	M	.	.	.	4	53	.
Anthoxanthum alpinum	H	.	.	.	.	41	.
Rumex alpestris	H	.	.	.	.	24	.
Listera cordata	H	.	.	.	.	24	.
Athyrium distentifolium	H	.	.	.	.	24	.
Sphagnum russowii	M	.	.	.	.	24	.
Polytrichum commune	M	.	.	.	7	47	6
Cladonia cenotea	M	.	.	.	.	18	.
Cladonia uncialis	M	.	.	.	.	18	.
Vaccinium myrtillus	H	25	7	5	7	82	24
Abies sibirica	T+S	12	.	.	79	100	18
Rhododendron aureum	H	.	.	.	.	35	15
Orthocaulis attenuatus	M	.	.	.	4	24	3
***Pinus sibirica-Picea obovata* continental taiga forest**							
Empetrum nigrum	H	.	.	.	.	.	24
Equisetum scirpoides	H	.	.	.	.	.	21
Cladonia cornuta	M	.	.	.	.	.	15
Luzula parviflora	H	.	.	.	.	.	12
Cladonia arbuscula	M	.	.	5	4	18	44
Cladonia stellaris	M	.	.	5	.	6	29
Vaccinium vitis-idaea	H	6	43	15	18	65	94
Hemiboreal forests							
Iris ruthenica	H	62	93	80	.	.	9
Aconitum barbatum	H	44	50	55	.	.	3
Achillea millefolium s. lat. [5]	H	31	14	30	.	.	.
Artemisia tanacetifolia	H	12	43	25	.	.	.
Polygonatum odoratum	H	38	.	35	.	.	.
Saussurea controversa	H	19	36	10	.	.	.
Veratrum nigrum	H	6	14	35	.	.	.
Gentiana macrophylla	H	19	21	15	.	.	.
Agrimonia pilosa	H	25	.	20	.	.	.
Bupleurum multinerve	H	6	21	10	.	.	.
Carex obtusata	H	6	14	25	.	.	.
Rosa acicularis	H	44	21	45	.	.	6
Fragaria vesca	H	19	7	15	.	.	.
Achnatherum sibiricum	H	12	7	15	.	.	.
Artemisia santolinifolia	H	.	7	20	.	.	.
Origanum vulgare	H	19	.	10	.	.	.
Silene nutans	H	25	.	10	.	.	.
Geranium transbaicalicum	H	6	14	10	.	.	.
Thesium repens	H	.	14	15	.	.	.
Spiraea media	S	44	7	60	7	.	6

Table 1 continued

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
Taiga forests							
Lycopodium annotinum	H	.	.	.	43	35	24
Carex iljinii	H	.	.	.	14	53	32
Linnaea borealis	H	6	7	.	46	82	59
Trientalis europaea	H	6	.	.	57	65	26
Lonicera altaica	S	.	14	.	57	65	56
Sorbus sibirica	H	.	.	5	39	53	38
Ledum palustre	H	.	.	.	.	24	32
Tetraphis pellucida	M	.	.	.	21	29	9
Mylia taylori	M	.	.	.	14	35	9
Gymnocarpium dryopteris	H	6	.	5	57	65	26
Calamagrostis langsdorffii	H	.	7	.	43	59	12
Sphagnum girgensohnii	M	.	.	.	.	24	18
Blepharostoma trichophyllum	M	.	.	.	11	12	12
Bergenia crassifolia	H	.	.	5	4	47	41
Calamagrostis obtusata	H	25	.	5	71	53	50
Cladonia digitata	M	.	.	.	4	6	18
Vaccinium uliginosum	H	.	.	.	.	12	18
Sphagnum capillifolium	M	.	.	.	.	12	18
Rhizomnium punctatum	M	.	.	.	21	12	.
Other species with percentage occurrence in the total data set > 10%							
Hylocomium splendens	M	56	57	20	86	76	88
Pleurozium schreberi	M	38	43	35	61	94	91
Pinus sibirica	T+S	31	64	40	54	76	91
Pinus sibirica	H	12	64	40	43	82	71
Carex pediformis s. lat. [6]	H	94	50	75	54	.	29
Spiraea chamaedrifolia	S	31	57	75	79	6	26
Ptilium crista-castrensis	M	31	36	10	39	65	71
Cruciata krylovii	H	94	29	40	82	.	15
Galium boreale	H	94	86	60	36	.	18
Betula pendula	T+S	81	14	45	57	18	29
Stellaria bungeana	H	25	21	25	75	29	44
Rhytidiadelphus triquetrus	M	50	29	20	79	29	26
Maianthemum bifolium	H	88	14	.	68	47	21
Calamagrostis pavlovii	H	44	86	55	7	.	50
Thalictrum minus	H	88	43	40	61	6	9
Rhododendron dauricum	S	6	43	50	7	35	59
Cerastium pauciflorum	H	62	50	.	64	6	24
Poa sibirica	H	19	71	40	21	6	47
Picea obovata	T+S	19	14	15	39	47	50
Sanionia uncinata	M	62	14	20	46	35	21
Brachythecium salebrosum	M	75	50	25	46	18	6
Rhytidium rugosum	M	12	86	80	.	.	29
Dicranum fuscescens	M	25	36	.	14	35	59
Rhodobryum roseum	M	25	43	30	57	6	15
Abies sibirica	H	6	.	10	61	71	12
Sorbus sibirica	T+S	25	.	5	57	41	24
Ptilidium pulcherrimum	M	38	14	20	14	41	38
Dicranum scoparium	M	38	7	10	25	53	26
Thuidium philibertii	M	19	14	15	54	.	24
Pinus sylvestris	T+S	62	.	65	.	6	21

Table 1 continued

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
Lilium pilosiusculum	H	31	50	20	25	6	12
Dicranum polysetum	M	.	7	10	14	24	50
Cladonia coniocraea	M	25	7	5	36	24	24
Polytrichum juniperinum	M	6	14	20	25	29	24
Eurhynchium pulchellum	M	19	7	30	18	12	26
Pyrola rotundifolia s. lat. [7]	H	19	36	10	18	.	29
Barbilophozia barbata	M	6	21	15	21	12	29
Cladonia pyxidata	M	6	29	20	4	24	29
Geranium albiflorum	H	50	21	.	21	29	6
Cimicifuga foetida	H	38	14	35	14	.	12
Atragene sibirica	H	19	50	15	11	.	21
Pohlia nutans	M	12	29	5	4	35	26
Senecio nemorensis	H	12	7	20	36	.	15
Ptilidium ciliare	M	.	29	10	18	6	29
Plagiomnium cuspidatum	M	31	14	10	36	6	3
Cladonia rangiferina	M	.	.	10	11	18	38
Betula pendula	H	6	.	25	21	18	18
Oncophorus wahlenbergii	M	19	50	5	21	6	9
Hypnum cupressiforme	M	50	21	25	.	6	12
Rubus matsumuranus	S	19	.	15	39	.	12
Aconitum volubile	H	50	36	15	14	.	3
Plagiomnium confertidens	M	25	29	5	39	.	.
Duschekia fruticosa	T+S	.	.	5	21	24	26
Abietinella abietina	M	6	36	45	.	.	12
Cladonia fimbriata	M	12	29	20	7	6	18
Polytrichum strictum	M	6	.	.	.	41	29
Veratrum lobelianum	H	25	7	.	18	41	3
Polypodium sibiricum	H	6	7	35	14	6	9
Polemonium coeruleum	H	38	36	.	14	.	6
Populus tremula	T+S	31	.	20	21	.	6
Dicranum fragilifolium	M	6	21	.	11	12	24
Adoxa moschatellina	H	25	7	.	43	.	.
Padus avium	H	38	.	10	32	.	.
Pinus sylvestris	H	25	.	45	.	6	9
Plagiomnium drummondii	M	25	.	.	39	6	.
Dianthus superbus	H	19	36	25	.	.	9
Vicia nervata	H	12	36	30	4	.	6
Angelica sylvestris	H	38	.	.	29	.	6
Vicia cracca	H	31	36	15	.	.	6
Ceratodon purpureus	M	6	43	25	4	.	6
Padus avium	T+S	31	.	.	36	.	.
Cladonia furcata	M	.	14	20	.	18	18
Anemonoides altaica	H	6	.	.	25	6	15
Picea obovata	H	6	.	5	14	12	18
Paeonia anomala	H	12	21	5	18	.	9
Aegopodium alpestre	H	31	.	.	25	.	6
Populus tremula	H	31	.	10	14	.	9
Aulacomnium palustre	M	.	7	.	.	12	29
Cladonia pleurota	M	.	7	10	4	12	21
Goodyera repens	H	.	14	5	7	12	18
Hieracium umbellatum	H	31	.	25	4	.	3
Cladonia rangiformis	M	6	36	5	.	.	15

Table 1 continued

Group no.		1	2	3	4	5	6
No. of plots		16	14	20	28	17	34
Viola mauritii	H	6	.	30	4	.	12
Viola rupestris	H	25	14	15	4	.	6
Dicranum spadiceum	M	.	7	5	.	24	18
Cacalia hastata	H	25	7	.	25	.	.
Ranunculus propinquus s. lat. [8]	H	25	29	.	11	.	3
Aquilegia sibirica	H	31	14	5	4	.	9
Chamaenerion angustifolium	H	19	14	5	4	18	3
Caragana frutex	S	19	.	25	.	.	9
Euphorbia alpina	H	19	7	20	4	12	.
Orthodicranum montanum	M	6	.	.	11	18	12
Plagiomnium affine s. lat. [9]	M	12	21	.	18	.	.
Euphorbia discolor	H	.	.	25	4	.	12
Larix sibirica	H	6	21	25	.	.	3
Solidago dahurica	H	.	.	25	7	18	.
Cladonia gracilis	M	.	.	5	4	24	12
Bistorta major	H	31	.	5	.	24	.
Peltigera leucophlebia	M	.	21	5	.	.	18
Cirriphyllum piliferum	M	12	.	.	29	.	.

[1] *Bupleurum longifolium* is represented in the study area by subsp. *aureum*

[2] *Poa* sect. *Stenopoa* includes mainly *P. krylovii*, *P. reverdattoi*, *P. transbaicalica* and *P. urssulensis*

[3] *Pulsatilla patens* s. lat. probably includes *P. flavescens* and *P. multifida*

[4] *Thymus serpyllum* s. lat. includes *T. krylovii* and probably some other *Thymus* species

[5] *Achillea millefolium* s. lat. includes mainly *A. asiatica*

[6] *Carex pediformis* s. lat. includes *C. macroura*, *C. pediformis* and *C. rhizina*

[7] *Pyrola rotundifolia* s. lat. includes *P. incarnata* and *P. rotundifolia*

[8] *Ranunculus propinquus* s. lat. includes *R. grandifolius, R. japonicus* and *R. propinquus*, as well as *R. taigensis* (Timokhina in Malyshev and Peshkova 1993: 197)

[9] *Plagiomnium affine* s. lat. includes *P. ellipticum, P. medium, P. rostratum* and *P. vesicarium*

obovata is found in cooler areas, but it does not show any response to precipitation. The most continental trees of the study area are *Larix sibirica* and *Pinus sibirica*. The former is found in areas which are very dry and very cold in winter, but it does not have any specific response to summer temperatures. In contrast, the latter does not respond to precipitation but is associated with higher altitudes, which are cold both in winter and summer; it often forms the timberline.

Discussion

Forest types of the study area in a broader context

The main differentiation of forest vegetation of the Western Sayan into hemiboreal forests and taiga is consistent with previous studies from southern Siberia and northern Mongolia (Zhitlukhina 1988; Ermakov et al. 1991, 2000; Hilbig 1995; Ermakov 2003; Dulamsuren et al. 2005a). Hemiboreal forests (sensu Hämet-Ahti 1981), also called sub-taiga forests in Russian literature (Sochava 1979), form distinctive vegetation zone at the south of the Eurasian coniferous forest biome. At its southern edge this zone borders on the steppe zone in Siberia. Hemiboreal forests occur in warmer and drier habitats than the taiga and lack moisture demanding dark-coniferous trees such as *Abies sibirica, Picea obovata* and *Pinus sibirica*. Instead, they are dominated by light-coniferous or small-leaved trees, which are represented in the study area by *Larix sibirica, Pinus sylvestris, Betula pendula* and *Populus tremula.* Yet these trees are not restricted to the hemiboreal forests; they can dominate the taiga as well. The main distinctive

Fig. 5 Examples of stand structure of the six main forest types of the Western Sayan. **1**. *Betula pendula-Pinus sylvestris* mesic hemiboreal forest, **2**. *Larix sibirica* dry hemiboreal forest, **3**. *Pinus sylvestris* dry hemiboreal forest, **4**. *Abies sibirica-Betula pendula* wet taiga forest, **5**. *Abies sibirica-Pinus sibirica* mesic taiga forest, **6**. *Pinus sibirica-Picea obovata* continental taiga forest

feature of the hemiboreal forests in contrast to taiga is their well developed herb layer, which is rich in species of temperate distribution, while many vascular plants of boreal distribution are lacking. The moss layer also lacks many species of boreal distribution and unlike its occurrence in the taiga, it is usually rather sparse (Ermakov 1995; Ermakov et al. 2000).

Within the hemiboreal forests of the study area, type 1 (*Betula pendula-Pinus sylvestris* forest) is related to the birch-pine forests of southwestern Siberia, occurring in the lowlands and on the northern, moderately oceanic foothills of the southern Siberian mountains (Ermakov et al. 2000). Forests of this type host a number of thermophilous, both xerophilous and mesophilous Euro-Siberian temperate species (e.g. *Angelica sylvestris, Brachypodium pinnatum*, *Calamagrostis arundinacea* and *Pulmonaria mollis*; Nimis et al. 1994). In phytosociological classification, they form the class of *Brachypodio pinnati-Betuletea* (Ermakov et al. 1991, 2000). Types 2 and 3 include

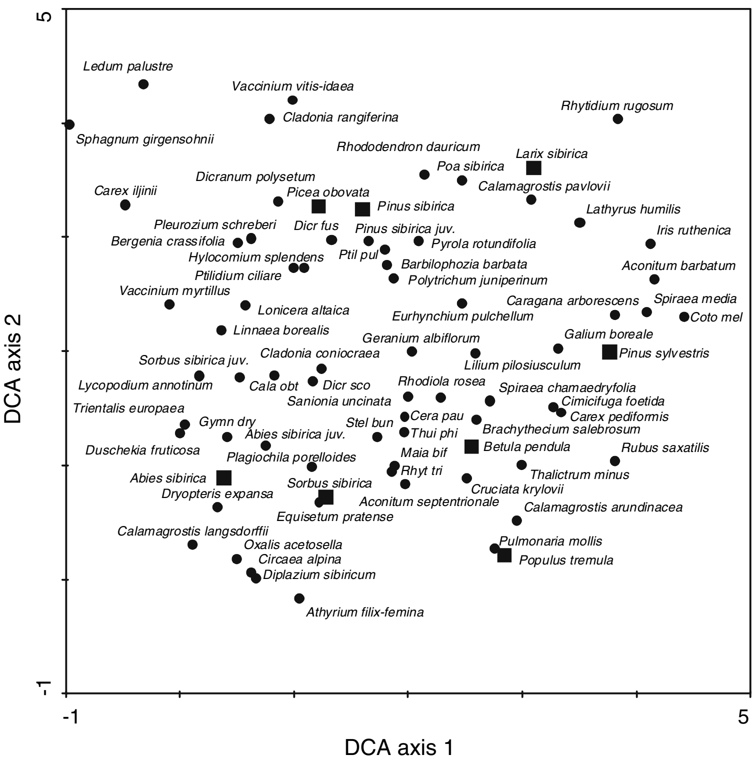

Fig. 6 Species scatter diagram of DCA ordination of forest vegetation plots from the Western Sayan. Trees are indicated by square symbols. *Cala obt*, *Calamagrostis obtusata*; *Cera pau*, *Cerastium pauciflorum*; *Coto mel*, *Cotoneaster melanocarpus*; *Dicr fus*, *Dicranum fuscescens*; *Dicr sco*, *Dicranum scoparium*; *Gymn dry*, *Gymnocarpium dryopteris*; *Maia bif*, *Maianthemum bifolium*; *Ptil pul*, *Ptilidium pulcherrimum*; *Rhyt tri*, *Rhytidiadelphus triquetrus*; *Stel bun*, *Stellaria bungeana*; *Thui phi*, *Thuidium philibertii*

dry hemiboreal forests. The former type (*Larix sibirica* forest) occurs in the southern part of the study area i.e. in the lee of the main range of the Western Sayan, where the macroclimate is very dry and winter-cold. These forests are related to larch forests distributed in the continental interior parts of the southern Siberian and northern Mongolian mountain ranges (Hilbig 1995; Ermakov et al. 2000). In contrast, the latter type (*Pinus sylvestris* forest) is found on dry south-facing slopes in the more oceanic northern parts of the Western Sayan. Species adapted to drought and frost prevail over mesophilous species in the hemiboreal forests of types 2 and 3. A number of species in these forests have a central Asian distribution and many of them also grow in dry steppes or dry types of alpine tundra (e.g. *Calamagrostis pavlovii, Carex amgunensis, Kitagawia baicalensis* and *Poa sibirica*). In phytosociological classification these forests are assigned to a separate class of southern Siberian and Mongolian drought and cold adapted forests, called *Irido ruthenicae-Laricetea sibiricae* (Zhitlukhina 1988; Ermakov 1995) or *Rhytidio rugosi-Laricetea sibiricae* (Korotkov and Ermakov 1999; Ermakov et al. 2000). Thus the Western Sayan is an area where these two major types of hemiboreal forests meet, each of them occupying habitats with environmental features corresponding to those which prevail in the central part of their geographic range.

The taiga of the Western Sayan is mainly dominated by dark-coniferous species *Abies sibirica, Pinus sibirica* and, in places, *Picea obovata*. Type 4 (*Abies sibirica-Betula pendula* forest), the most thermophilous and species-rich taiga type in the study area, is closely related to the *Abies sibirica* forests of humid areas in the northern Altai Mountains, which contain a number of species typical of mesic European broad-leaved forests e.g., *Asarum europaeum, Brachypodium sylvaticum* and *Viburnum opulus* (Ermakov 1998, 2003). The continuous European ranges of these species reach their eastern limits in the southern Urals. The northern fringes of the Altai, Western Sayan and their respective foothills is the only area where they occur in Siberia (Meusel et al. 1965–1992), isolated from their continuous ranges. They are considered as relicts of the pre-Pleistocene broad-leaved forests (Ermakov 1998, 2003). In phytosociological classification, forests containing several of these species and lacking most species of boreal distribution were assigned to the

Table 2 Environmental variables with significant gross effect on species composition of forest vegetation (canonical correspondence analysis with Monte Carlo permutation test; $P < 0.05$)

Environmental variable	*F*-value
pH	0.38
Altitude	0.33
Annual precipitation	0.32
January temperature	0.32
Northing	0.31
July temperature	0.26
Inclination	0.21
Landform: flat bottom	0.18
Landform: ridge top or steep slope	0.18
Bare ground	0.18
Soil depth	0.17
Litter cover	0.17
Above radiation	0.17
Transmitted radiation	0.17
Easting	0.16
Topographic radiation	0.16
Landform: gentle slope	0.16
Substrate type: scree	0.15
Substrate type: sand	0.15
Substrate type: rock	0.14
Heat Index	0.13

Variables are ranked by decreasing value of the *F* statistic, which measures the relative strength of the effect of each variable. Variables with non-significant effect include Substrate type: loam, Substrate type: stones, Conductivity, Substrate type: gravel, Substrate type: clay

phytosociological class of European broad-leaved forests, *Querco-Fagetea*, and the southern Siberian endemic alliance *Milio effusi-Abietion sibiricae* (Ermakov 1998, 2003). Although some species typical of the European broad-leaved forests (e.g. *Milium effusum* and *Paris quadrifolia*) do occur in the *Abies sibirica-Betula pendula* forests of the Western Sayan, most sites sampled in this study contained several taiga species as well (e.g. *Gymnocarpium dryopteris, Linnaea borealis, Lycopodium annotinum, Trientalis europaea* and a number of bryophytes), which suggest their closer affinity to the taiga. Thus in phytosociological classification, they would belong to the class of boreal coniferous forests (*Vaccinio-Piceetea*). Very similar vegetation is found in humid valleys around the eastern shore of Lake Baikal (alliance *Aconito rubicundi-Abietion sibiricae*; Chytrý et al. 1995; Anenkhonov and Chytrý 1998). Types 5 and 6 (*Abies sibirica-Pinus sibirica* forests and *Pinus sibirica-Picea obovata* forests) are dark-coniferous boreal forests clearly corresponding to the class *Vaccinio-Piceetea*, the former being typical of warmer and the latter of cooler habitats.

Vegetation–environment relationships

Climatic variables and soil pH were identified as the most important determinants for the species composition of forest vegetation in the Western Sayan. The overriding effect of macroclimate partly results from the large geographic extent of the present study and the fact that sampling followed a steep north–south gradient of increasing climatic continentality. Precipitation and temperature are weakly correlated in the study area, because the former is largely conditioned by its position on either the windward or leeward side of the main mountain ranges, while the latter is mainly determined by altitude. Altitude is more strongly correlated with summer temperatures than winter temperatures, because at the same altitudes winter temperatures tend to be lower in the continental southern areas than in the more oceanic north (Polikarpov et al. 1986). Weak correlations between climatic variables make it possible to explore the separate effects of each of them. Precipitation appears to be the main factor responsible for the differentiation of hemiboreal forests (in drier areas) from taiga (in wetter areas). Within each of these main forest types, sub-types are differentiated especially according to temperature, particularly winter temperature (Figs. 3 and 7).

Soil pH is negatively correlated with precipitation in the study area (Chytrý et al. 2007), which suggests the control of soil pH through calcium leaching. Alongside precipitation and moisture availability, pH can be an important factor responsible for the floristic differentiation of hemiboreal forests and taiga. The distinction between wet/acidic and dry/base-rich sites can be amplified by positive feedback loops. Abundant soil moisture supports the growth of bryophytes, which decrease soil pH (Vitt 2000). Coniferous trees growing at humid sites also tend to produce more biomass and to accumulate more litter, which contributes to soil acidification by releasing organic acids (Ovington 1953; Finzi et al. 1998; Fisher and

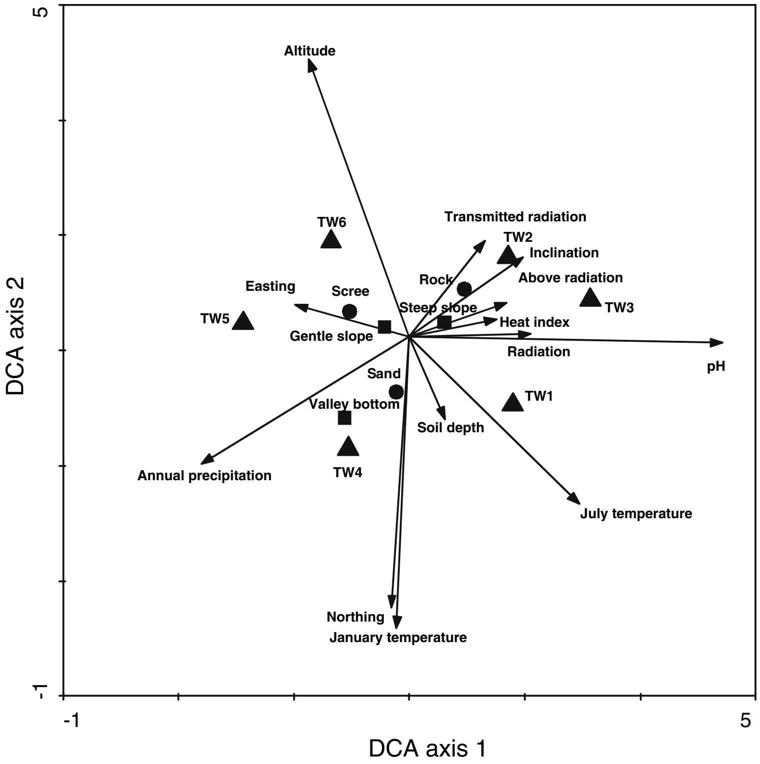

Fig. 7 Passive projection of environmental variables onto the DCA diagram from Fig. 6. Values of individual variables increase in the directions of the arrows. For categorical variables centroids are shown of those vegetation plots in which the particular category is present. Triangles indicate centroids of the subsets of vegetation plots assigned to one of the six clusters in TWINSPAN classification (labelled by TW + cluster number; see Fig. 2 for cluster names). Environmental variables that are not significantly associated with species compositions (see Table 2) are not shown

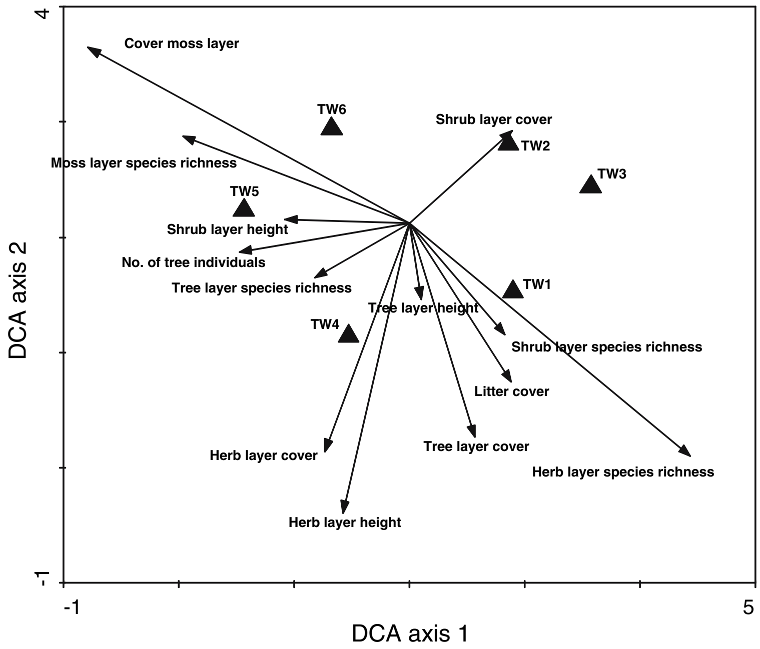

Fig. 8 Passive projection of vegetation structure variables onto the DCA diagram from Fig. 6. Values of individual variables increase in the directions of the arrows. Triangles indicate centroids of the subsets of vegetation plots assigned to one of the six clusters in TWINSPAN classification (labelled by TW + cluster number; see Fig. 2 for cluster names)

Binkley 2000). These processes seem to amplify the floristic differentiation between hemiboreal forests and taiga, the former harbouring more calcicoles and the latter containing predominantly calcifuges.

Hemiboreal forests of the Western Sayan contain more species of vascular plants but less species of ground-dwelling cryptogams than the taiga. The local species richness of vascular plant flora in the study

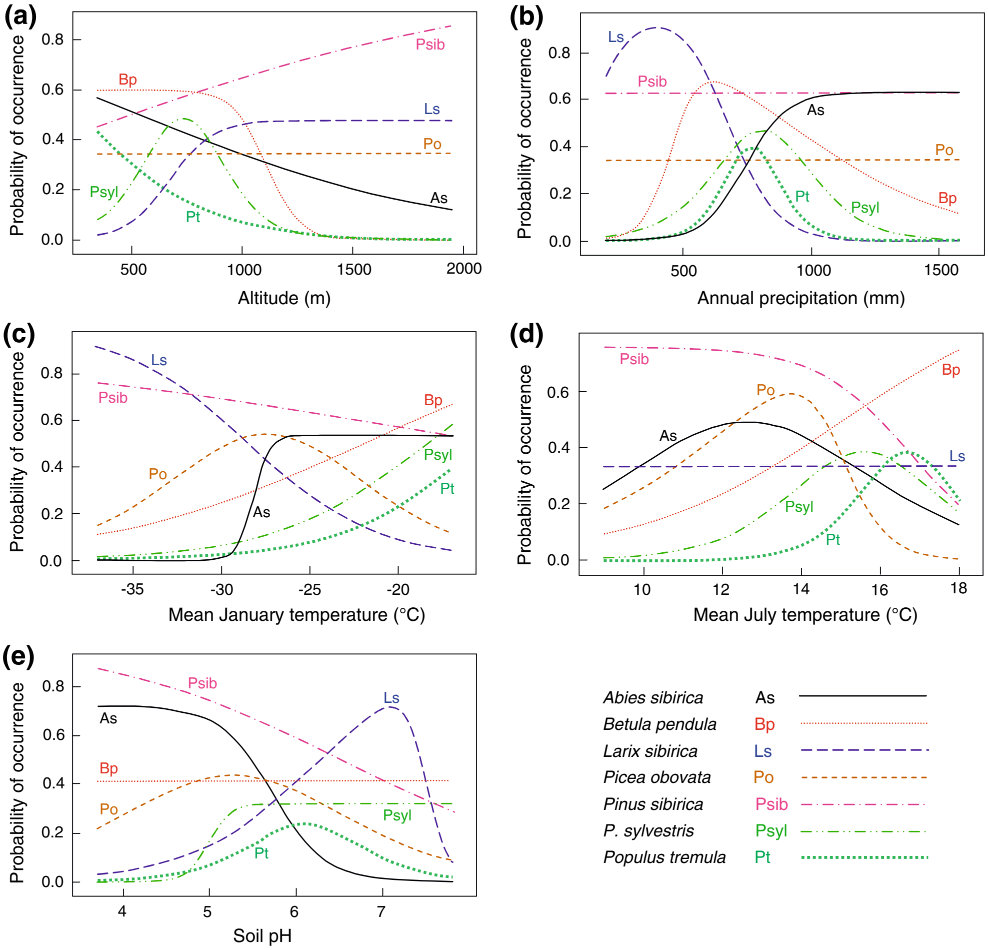

Fig. 9 Probability of occurrence of the main tree species of the Western Sayan on the gradients of altitude, climatic variables and pH, modelled with the Huisman–Olff–Fresco models. Only species occurrences in the tree layer were considered for modelling

area is highest at relatively warm sites with a high-pH soil (Chytrý et al. 2007). Of the forest communities, such environments support the *Betula pendula-Pinus sylvestris* mesic hemiboreal forests. The rich species pool of these forests includes several species which also commonly occur in moderately dry meadow steppes, but it also contains many species confined to the forest undergrowth. Ermakov et al. (2000) suggested that this species pool could be a relict of the Late Pliocene southern Siberian forest-steppe. In contrast, taiga forests in wetter, cooler and more acidic habitats are poorer in vascular plants, but richer in bryophytes and lichens.

Besides climate and pH, the other environmental variables measured in this study appeared to have a much weaker or even non-significant effect on species composition. Relatively important is slope aspect and related variables such as topographically derived radiation and heat indices. Soil variables other than pH appeared to be dependent on these topographic variables and their effect on vegetation was parallel to the effect of topography. Steep south-facing slopes tend to support hemiboreal forests, especially the dry ones (types 2 and 3), while taiga is more often found on north-facing slopes or valley bottoms (Fig. 7). However, the relationships between slope aspect and vegetation are more complex in the study area. In the relatively warm and precipitation-rich areas in the north, north-facing slopes are often occupied by the *Abies sibirica-Pinus sibirica* taiga (type 5) and south facing slopes by *Pinus sylvestris* hemiboreal forest (type 3). In the central part of the Western Sayan, various types of taiga are confined to north-facing slopes, while the south-facing slopes support the *Larix sibirica* hemiboreal forest (type 2) or mountain steppes. In the areas adjacent to the dry Central Tuvinian Basin, steppe predominates on south-facing slopes while north-facing slopes are occupied by the *Larix sibirica* hemiboreal forest (type 2).

The characteristic landscape pattern with treeless south-facing and forested north-facing slopes (called 'expositional forest-steppe' in Russian literature) predominates across large areas south of the main Western Sayan range. Based on his studies in Mongolia, Hilbig (1995, 2003) suggested that this pattern resulted from past human impact and large-scale deforestation of the previously forested landscape. However, the central part of the Western Sayan Mountains, e.g. the Yenisei valley, is a poorly accessible area with no permanent settlements and there is almost no direct human impact upon vegetation, except for some restricted sites. Still, the pattern of expositional forest-steppe is well developed there. This observation is consistent with the views of other authors (Gunin et al. 1999; Dulamsuren et al. 2005a, b) who argued that the expositional forest-steppe of northern Mongolia (and southern Siberia) is a natural landscape pattern caused by climate, although in populated areas grazing may have increased the proportion of steppe at the expense of forest.

Climatic responses of the main tree species

The responses of the main tree species to climatic variables identified in the Western Sayan (Fig. 9) correspond the reconstructed responses of these species to climate change in the Pleistocene and early Holocene. The resistance of *Larix sibirica* to drought and winter frosts and of *Pinus sibirica* to low temperatures in both summer and winter is consistent with the fossil record, which indicates that these species were widespread in the full-glacial landscapes of eastern Central Europe, such as the Western Carpathians (Jankovská et al. 2002), Great Hungarian Plain and the adjacent hilly landscapes (Rybníčková and Rybníček 1992; Willis et al. 2000). Central European populations of these trees evolved in separate species (or subspecies in some taxonomic treatments), *Larix decidua* and *Pinus cembra.* In early Holocene, populations of these species retreated from the lowlands to their present habitats at the timberline in the central Alps and central Carpathians (Ellenberg 1996). There is evidence (Tinner and Kaltenrieder 2005) that their response to climatic change at the timberline was rapid and reflected ecological tolerance of their sibling species in southern Siberia: *Larix* was supported by periods of dry climate while *Pinus cembra* only spread after the climate became more humid.

Other tree species which are present in the full-glacial fossil record from eastern Central Europe, namely *Betula pendula, Picea* (European *P. abies* is closely related to Siberian *P. obovata*) and *Pinus sylvestris*, appear to be more thermophilous and moisture demanding than *Larix sibirica* and *Pinus sibirica* in the Western Sayan. This suggests that the full-glacial landscape of eastern Central Europe provided both more extreme habitats covered with steppe, tundra or *Larix decidua* or *Pinus cembra* woodlands, and less extreme habitats, e.g. in river floodplains or in warmer and wetter valleys, which supported *Betula, Picea* and *Pinus sylvestris*. Another explanation may be that at least during some periods of the full glacial, climate was not as harsh as in the present southern foothills of the Western Sayan. In contrast, the full-glacial climate of eastern Central Europe seems to be cooler and drier than currently found in the northern part of the Western Sayan, where *Abies sibirica* taiga is widespread. Fir is absent or present only as solitary pollen grains in the full-glacial fossil record from Central Europe, which corresponds to its higher moisture requirements and sensitivity to very cold winter temperatures as revealed from its distribution in the Western Sayan (Fig. 9). These ecological requirements enabled fir to spread over Central Europe only after climatic amelioration in the Late Glacial and especially in the humid mid Holocene (Berglund et al. 1996).

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