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High species richness in hemiboreal forests of the northern Russian Altai, southern Siberia

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Abstract

Questions: We discovered forests with very high local numbers of vascular plant species in southern Siberia. Are these the most species-rich forests of the Eurasian boreal and temperate zones, and which factors cause such high species richness?

Location: Altai Mountains in southern Siberia, Altai Republic, Russia.

Methods: We sampled vegetation and measured environmental variables across the Altai Mountains in plots of 100 m^2 and established series of nested plots of the size from 1 to 1000 m^2 at sites with the highest species richness. We compared the richest forests with other forests of the Altai and with literature records of species-rich vegetation types from elsewhere.

Results: The richest forests contained 45 vascular plant species per 1 m^2, 82 per 10 m^2, 114 per 100 m^2 and 149 per 1000 m^2. They are open hemiboreal forests dominated by *Pinus sylvestris*, with an admixture of *Betula pendula*, and sparse shrub and moss layers. About 95% of their vascular plant species are in the herb layer. All species are native. These forests occur in a forest-steppe landscape of the northern Altai, where the mean January temperature is between –12.5 and –10 °C, mean July temperature is 16–18 °C, and total annual precipitation is 560–610 mm. Soils are deep and mesic, with a pH of 6.2–6.4.

Conclusions: Hemiboreal forests of the northern Russian Altai are probably the most species-rich forests in boreal and temperate Eurasia. Such a high concentration of many species in small plots probably results from the incidental combination of several factors conducive to high species richness. These factors include the rich regional flora of the Altai Mountains, stability of the environment of this region since the Pleistocene, heterogeneity of the mountainous forest-steppe landscape with a combination of forested areas on north-facing slopes and steppes on south-facing ones, an open canopy that ameliorates microclimate conditions but does not exclude light-demanding species through strong shading, a macroclimate that is not too harsh, mesic soils with near-neutral pH, and limited competition within the herb layer.

Introduction

Plant communities with many species concentrated in small areas have always attracted and puzzled ecologists. It is generally accepted that the highest numbers of vascular plant species within areas from 100 m^2 to 1 ha are found in tropical rain forests (Whitmore et al. 1985; Gentry & Dodson 1987; Duivenvoorden 1994). In areas of 1–50 m^2, the greatest richness of vascular plants has been reported from temperate European dry and semi-dry grasslands on base-rich soils (van der Maarel & Titlyanova 1989; Kull & Zobel 1991; Klimeš et al. 2001; Vasilevich 2009) and

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mountain grasslands of Argentina (Cantero et al. 1999). Many species per plot of 100–1000 m^2 have also been reported from regions with a mediterranean-type climate, especially eastern Mediterranean shrublands (Naveh & Whittaker 1979; Bergmeier 1995; Chytrý et al. 2010a), South African fynbos (Naveh & Whittaker 1979; Schmiedel et al. 2010) and tropical savannas such as the Brazilian cerrado (Eiten 1978).

Boreal and temperate forests generally contain fewer vascular plant species per small area than tropical forests (Gentry & Dodson 1987) and usually also fewer species than grasslands occurring in the same region. This is probably why patterns of maximum species richness in boreal and temperate forests have not received much attention and remain poorly studied.

During our recent studies of vegetation diversity in southern Siberia (Ermakov et al. 2000; Chytrý et al. 2007, 2008), we discovered forests with a very rich herb layer in the northern part of the Altai Mountains, which probably contain remarkably more vascular plant species in small plots than any other forest in boreal and temperate Eurasia.

In this paper, we: (1) provide a basic description of the species-rich forests of the northern Altai; (2) compare their species numbers with other boreal and temperate forests in the world and in other types of forest and non-forest vegetation of the same region; (3) relate their species richness to environmental factors in a regional context; and (4) discuss possible explanations for their extraordinarily high species richness.

Methods

Study area

The study area is the Russian part of the Altai Mountains, in the Altai Republic, which is a federal state of the Russian Federation. Siliceous bedrock of Proterozoic to Devonian age predominates, with locally occurring beds of limestone (Nekhoroschev 1966; Chlachula 2001). In the northern Altai foothills mean annual precipitation locally exceeds 800 mm, but decreases in the lee of the mountain ranges in the south and southeast (Gidrometeoizdat 1966–1970; Polikarpov et al. 1986). Precipitation peaks in the summer. Temperatures are generally higher in the northern Altai foothills and decrease with increasing altitude towards the southeast. Most of the study area is covered with natural vegetation, which is influenced only weakly by humans, except in some areas where there is livestock grazing. Natural vegetation varies in response to the NW–SE climatic gradient. In the Biya River basin in the northern Altai foothills the relatively oceanic, warm and wet climate supports forests with *Abies sibirica, Betula pendula, Picea obovata, Pinus sibirica, P. sylvestris* and *Populus tremula*. In the Katun' River valley and adjacent mountain ranges north of the Seminskii Range, annual precipitation is 400–700 mm, which supports a forest-steppe landscape consisting of a mosaic of *Pinus sylvestris–Betula pendula* hemiboreal forests and meadow steppes. Further to the south, high-mountain areas are covered with shrubby tundra dominated by *Betula rotundifolia* and mountain forests of *Pinus sibirica*, whereas valleys are covered with a forest-steppe mosaic of *Larix sibirica* forests and low-productivity steppes dominated by tussock-forming short grasses. Intermountain valleys and plateaus in the southernmost part of the Russian Altai, with less than 250 mm of annual precipitation, are dominated by a patchy mosaic of steppe and tundra at drier and wetter sites, respectively, while forests are restricted to small patches of suitable habitats in river floodplains and on north-facing slopes (Kuminova 1960; Walter 1974; Pyak et al. 2008).

Data sampling and analysis

We sampled all types of natural forest vegetation along an ca. 280-km long NW–SE transect, which followed a strong gradient of climatic continentality across the Altai Mountains (49° 57′–52° 21′ N, 85° 35′–88° 23′ E, 290–2490 m a.s.l.). The least continental area on this gradient was the precipitation-rich northern Altai foothills, where mesic forests dominate the landscape. The opposite end of the gradient was in the area with a cool and dry continental climate around the Chuya Basin in the southeast, where the landscape corresponds to mountain tundra-steppe. Sampling was done in August 2005 and July 2006. We used sample plots of 10 m × 10 m located in central parts of physiognomically and ecologically homogeneous forest stands. Sampling was stratified in order to capture the maximum diversity of vegetation types. Sites affected by recent disturbances, for example, early stages of post-fire succession or strongly grazed forests near settlements, were avoided. In total, we sampled 104 plots of forest vegetation.

In each plot, we recorded all vascular plant species and estimated their cover on the nine-degree Braun-Blanquet scale (van der Maarel 1979). In addition, the total cover of each layer was estimated as a percentage. In those sites where we recorded more than 85 species in a 10 m × 10 m plot, we established one series of square nested plots of increasing size, namely 1, 10, 100 and 1000 m^2, and recorded all species of vascular plants in each of them. Besides species that rooted in the plot, we also recorded species that were rooted outside but overlapped the plot with their above-ground parts.

In each plot of 10 m × 10 m, we measured the following variables:

Altitude was measured with a GPS receiver (Garmin 60CSx).

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Climatic variables (July and January mean temperature and summer and winter precipitation) were estimated from a climatic model prepared in the ArcGIS 8.2 geographic information system (www.esri.com). The model was based on the combination of Russian climate station data and altitudes from a digitized 1:200 000 topographic map. Temperature values for different altitudes were computed based on the adiabatic lapse rate of 0.65 °C per 100 m of altitude. Precipitation was computed from precipitation–altitude charts compiled for each of the aridity–humidity sectors of the Altai–Sayan region (Polikarpov et al. 1986). There were strong correlations between summer and winter precipitation ($r = 0.847$, $P < 0.001$) and January and July temperature ($r = 0.956$, $P < 0.001$).

Potential solar radiation above the herb layer was calculated from slope aspect (measured by compass), inclination (measured by clinometer) and latitude (measured by GPS). This accounted for shading by the canopy and adjacent topographic features, which were estimated from digital hemispheric photographs taken in a vertical direction at a height of 1.5 m above the ground at each site. Solar radiation calculations were performed using the Gap Light Analyser 2.0 software (www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm). Radiation was estimated as the mean daily sum of potential direct and diffuse radiation for the period 1 April to 31 October.

Heat index was calculated from slope inclination and aspect according to McCune & Keon (2002: Eq. 3 with aspect folded around the NE–SW line). The values of this index are high on steep SW-facing slopes, low on steep NE-facing slopes and medium on flat land, gentle slopes and steep SE- or NW-facing slopes.

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

Soil pH and *electrical conductivity* were measured from a mixed soil sample from four places within each plot. Samples were 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 using PH114 digital pH meter and CM113 conductivity meter (Snail Instruments, Beroun, Czech Republic). Conductivity caused by hydrogen ions was subtracted according to Sjörs (1950) to provide a measure of the amount of other ions in the soils solution, namely nutrient availability.

Relationships between the number of species and environmental variables were described using quantile regression, which is suitable for data with unequal variation in the response variable (Koenker & Bassett 1978; Cade & Noon 2003). In contrast to ordinary least squares regression, which fits the response through the mean values, quantile regression offers several alternative solutions differing in the quantile selected. As we were particularly interested in the maximum species richness and assumed that it was constrained by the limiting environmental factors, we selected the 0.9 quantile to fit the upper boundary of the examined relationship. Since the relationship between maximum species richness and environment is often non-linear, we chose a non-parametric version of quantile regression based on quadratic splines, which is available in the package *cobs* (P.T. Ng & M. Maechler; version 1.2-2; http://CRAN.R-project.org/package=cobs.) of the R program (R Development Core Team 2010, Vienna, Austria). To ease the interpretation of richness–environment relationships, we manually modified the number of knots, which control for the shape of the resulting relationship, to avoid a multimodal response (the maximum number of knots was set to six and was decreased where appropriate).

Throughout this paper, the term 'species' denotes vascular plant species unless stated otherwise, 'richness' denotes species richness, and 'temperate zone' is taken in a narrow sense, excluding the warm-temperate zone, i.e. areas with prevailing evergreen broad-leaved forests (Walter & Breckle 2002).

Results

We found six forest sites with more than 85 vascular plant species per 100 m^2 in the Altai Mountains. At these six sites, the highest numbers we recorded were 45 species per 1 m^2, 82 per 10 m^2, 114 per 100 m^2 and 149 per 1000 m^2 (Table 1). The three richest sites were found on NW-facing slopes above the Uznezya Creek, a right-side tributary of the Katun' River, 1.2 km NNE to 2.6 km NE of the village of Uznezya, ca. 48 km south of the city of Gorno-Altaisk. Other forests with 94–95 species per 100 m^2 were found in a similar topographic situation, on N to NW-facing slopes above the Kuyum Creek, east of the village of Anos.

Table 1. Number of species in the six most species-rich forest vegetation plots in the Altai Mountains. The highest values for particular plot sizes are bolded. See App. S1 for full data on species composition, site location and selected environmental factors.

Plot no.	1	2	3	4	5	6
No. of vascular plant species per 1 m^2	43	**45**	38	25	10	25
No. of vascular plant species per 10 m^2	**82**	74	67	63	44	44
No. of vascular plant species per 100 m^2	**114**	107	102	95	94	88
No. of vascular plant species per 1000 m^2	**149**	126	139	122	108	138
No. of terricolous moss species per 100 m^2	5	7	**8**	6	7	7

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Another forest with 88 species per 100 m^2 was sampled on a SW-facing slope near the village of Kamlak (ca. 40 km SSW of Gorno-Altaisk). We recorded 11 additional forest plots with more than 60 species per 100 m^2 within a distance of up to 17 km from these sites, but not elsewhere in the Altai Mountains, except in an alluvial woodland near the village of Paspaul, ca. 50 km NE of Uznezya (Fig. 1).

In addition to vascular plants, each of the six richest plots contained five to eight species of terricolous mosses per 100 m^2. No terricolous liverworts or lichens were found in the plots. Epiphytic cryptogams were not sampled. The richest plot had a total of 119 species of vascular plants and terricolous mosses per 100 m^2.

On average, the species lists of the six richest plots contained 1.8 ± 0.6% tree, 2.8 ± 1.3% shrub and 95.4 ± 1.1% species in the herb layer (including 1.0 ± 0.6% juvenile trees or shrubs in the herb layer, 73.1 ± 2.8% dicot herbs, 9.8 ± 1.5% grasses, 3.0 ± 0.8% other graminoids such as *Carex* and *Luzula*, 6.2 ± 1.1% other monocots, 1.6 ± 0.9% ferns and 0.6 ± 0.5% horsetails).

All of the six forest sites with more than 85 vascular plant species per 100 m^2 had a relatively open canopy with ocular cover estimates of 30–55%, dominated by *Pinus sylvestris*, with admixed *Betula pendula* at some sites (Fig. 2). The shrub layer was sparse, with cover of up to 5% or was absent. Herb layer cover was between 85% and 90% in the plots on NW- to N-facing slopes and about 50% in the plot on a SW slope. Common species of the herb layer included the grasses *Brachypodium pinnatum* and *Calamagrostis arundinacea*, and the dicot herbs *Galium boreale, Rubus saxatilis* and *Viola mirabilis*. The tall ferns *Athyrium filix-femina* and *Pteridium aquilinum* attained a high level of cover at some sites. However, there were no strongly dominant species and a single herb-layer species never exceeded 25% cover, except *Athyrium filix-femina*, which attained a cover of 30% in one plot. A moss layer was present in all of these plots, but its total cover was always less than 5%. All the vascular plant species recorded in these forests were native to the Altai Mountains.

The six most species-rich forest sites were found on valley slopes in non-riverine and non-ecotonal situations, in homogeneous forested areas that were much larger than the sampled plots. They did not exhibit any visible signs of management, except occasional cattle grazing at some sites. They occurred at altitudes of 410–550 m, in an area with mean January temperature of –12.5 to –10 °C, mean July temperature of 16–18 °C and annual precipitation of 560–610 mm.

The data set of 104 plots from the broader area of the Altai Mountains showed that the upper limit of forest

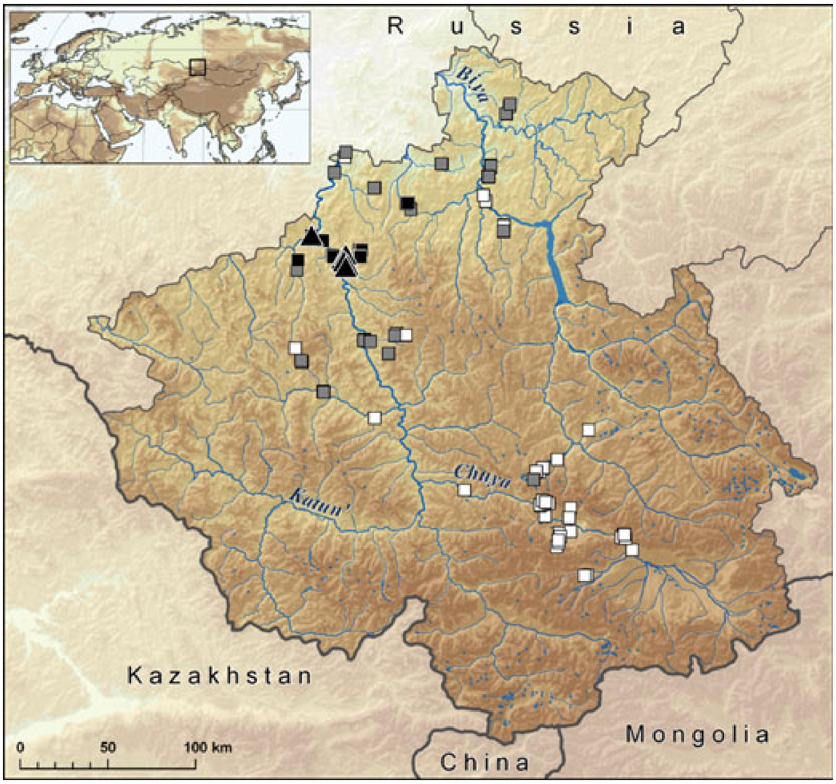

Fig. 1. Number of vascular plant species in forest vegetation plots of 100 m^2 in the Altai Mountains: white squares: ≤40 species, grey squares: 40–60 species, black squares: 60–85 species; black triangles: >85 species.

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Fig. 2. Species-rich hemiboreal forests of the northern Altai: (a) *Pinus sylvestris–Betula pendula* forest on a north-facing slope in the Kuyum Creek valley near the village of Anos; (b) species-rich herb layer with *Athyrium filix-femina* in a *Pinus sylvestris–Betula pendula* forest in the Uznezya Creek valley near the village of Uznezya; (c) *Pinus sylvestris* forest on a SW-facing slope near the village of Kamlak; (d) expositional forest steppe near the village of Kamlak.

species richness tended to peak in areas with altitudes of about 500 m, mean January temperature of about –13 °C and annual precipitation of about 600 mm (Fig. 3a–c). There was no interpretable relationship between species richness of the Altai forests and the heat load index, i.e. their location on SW- vs NE-facing slopes (Fig. 3d). Maximum species richness tended to have a unimodal relationship with canopy openness: it was highest in forests with a tree layer cover of between 30% and 50% and potential transmitted solar radiation of about 10 $\mathrm{mol{\cdot}m^{-2}{\cdot}d^{-1}}$ (Fig. 3e–f). The richest forests occurred on soils deeper than 20 cm (Fig. 3g). Maximum species richness increased within the range of soil pH(H_2O) from 4.2 to ca. 6.0 and levelled off at higher values: the richest forests had soil pH between 6.2 and 6.4 (Fig. 3h). Richness peaked at conductivity of about 100 $\mathrm{\mu S{\cdot}cm^{-1}}$ (Fig. 3i). There was also a thin (≤ 2 cm) layer of litter in the richest forests, which covered 30–60% of the soil surface. When we analysed relationships between the number of species within particular growth forms and the above-mentioned environmental variables, the patterns for graminoids and non-graminoid herbs were very similar to the patterns for the whole community presented in Fig. 3, whereas patterns for trees and other woody plants hardly showed any distinct trends (not shown).

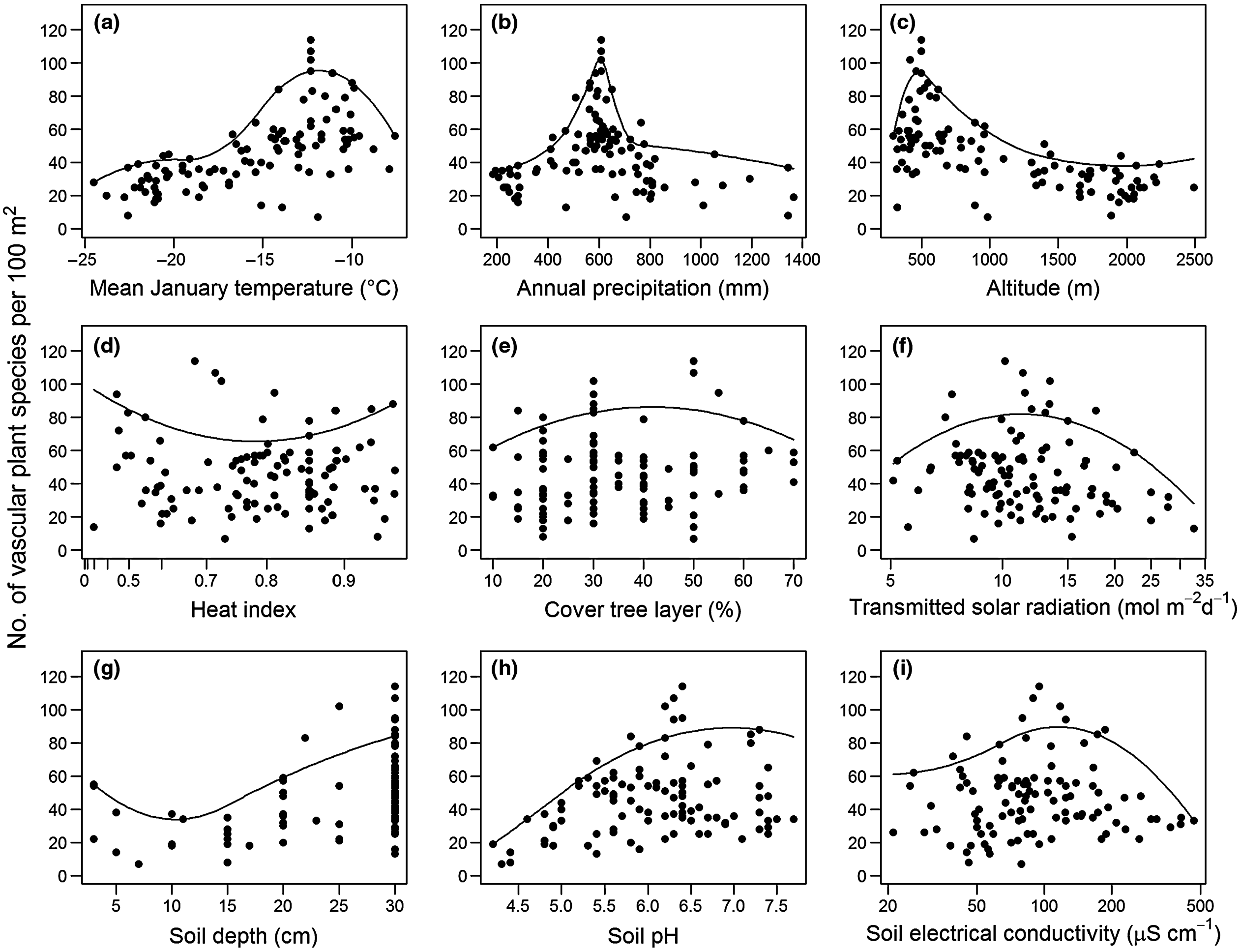

Fig. 3. Number of vascular plant species recorded in forest vegetation plots of 100 m^2 across the Altai Mountains plotted against environmental variables. Non-parametric regression curves are fitted using quantile regression with quadratic splines and the 0.9 quantile. Note the cubic transformation of the horizontal axis in (d) and its logarithmic transformation in (f) and (i).

Discussion

Are the Altai forests the most species-rich among the world's boreal and temperate forests?

Over the range of plot sizes we used for sampling (1–1000 m^2), the number of vascular plant species encountered in the *Pinus sylvestris–Betula pendula* forests of the northern Altai is probably the highest reported so far from boreal and temperate Eurasia. However, these forests are much poorer than the richest tropical rain forests, which have been reported to contain 233 vascular plant species per 100 m^2 (Whitmore et al. 1985) and 313 per 1000 m^2 (Duivenvoorden 1994). Some subtropical or warm-temperate forests are also richer: for example, the richest forest vegetation plot of 400 m^2 included in the National Vegetation Database of Taiwan (Chiou et al. 2009) contains 164 species of vascular plants (C.-F. Li, personal communication). However, unlike in the Altaian and other boreal to temperate forests, where over 90% of the species can be herbaceous, a considerable proportion of species richness of tropical and subtropical forests is made up of woody species, lianas and epiphytes (Gentry & Dodson 1987).

The Altaian species-rich hemiboreal forests described in this paper would probably be even slightly richer if vernal geophytes were recorded. The geophytes *Anemonoides altaica*, *A. caerulea*, *Corydalis bracteata*, *Dentaria sibirica* and *Erythronium sibiricum* regularly occur in these forests and form a distinct layer with a cover of 30–60% in spring (Ermakov et al. 2000), but these were already invisible at the time of sampling. Also, some species with tiny shoots may be overlooked in species-rich vegetation (Klimeš et al. 2001), especially in larger plots, although we spent 4–5 h sampling the species-rich plots.

In Fig. 4 we summarize selected records of high species richness from Eurasian and North American boreal, temperate and Mediterranean forests, which we compiled

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from literature, a vegetation plot database of Siberian forests (N. Ermakov, unpublished data) and the Czech National Phytosociological Database (Chytrý & Rafajová 2003; code EU-CZ-001 according to Dengler et al. 2011). We report the highest values for particular plot sizes and regions if they are higher than or close to the values we recorded in the Altai forests. Naveh & Whittaker (1979) reported 138 species per 1000 m^2 from a grazed Mediterranean woodland in Israel. Solomeshch et al. (1989) found 94 species per 625 m^2 in a *Betula pendula–Pinus sylvestris–Larix sibirica* hemiboreal forest of the Southern Urals. Krestov et al. (2006) reported 98 species per 400 m^2 in an *Abies holophylla–Tilia amurensis* forest in the Vladivostok region in the Russian Far East. Ermakov (unpublished data) sampled forests in different parts of Siberia and recorded a maximum of 88 species in plots of 200 m^2 in *Betula pendula* and *Betula pendula–Larix sibirica* hemiboreal forests in the West Siberian Plain and Minusinsk Basin, respectively. Chytrý et al. (2007) found 69 species per 100 m^2 in a *Pinus sylvestris* hemiboreal forest of the Western Sayan, a mountain range adjacent to the Altai in the east.

European temperate forests are not richer. The Czech National Phytosociological Database (Chytrý & Rafajová 2003) contains ca. 16 000 records of species composition of forest vegetation from plots of known size in the Czech Republic. These data can be considered representative of the European temperate forests, but there was a maximum of 80, 82 and 84 species of vascular plant species recorded in forest plots of 100, 200 and 400 m^2, respectively (Fig. 4).

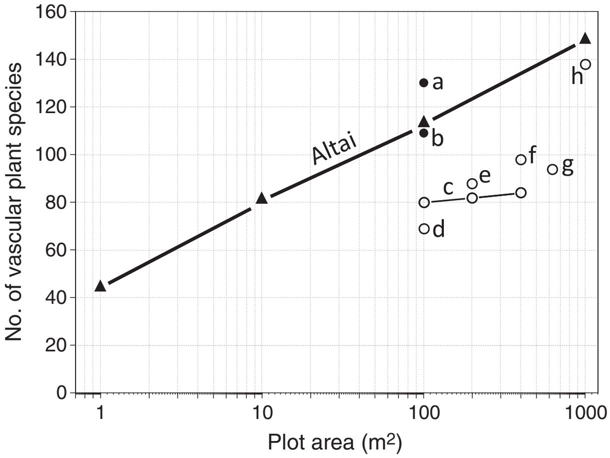

Fig. 4. Number of vascular plant species in the richest plots of different sizes recorded in the northern Altai forests (solid triangles and line) and selected records of high species richness in forests and woodlands from other boreal, temperate and Mediterranean regions of Eurasia (open circles) and North America (solid circles): (a) riparian forest in the Southern Appalachians (Brown & Peet 2003); (b) *Quercus* woodland in Oklahoma (Palmer et al. 2003); (c) deciduous forests in the Czech Republic (data from the Czech National Phytosociological Database); (d) *Pinus sylvestris* hemiboreal forest in the Western Sayan Mountains (Chytrý et al. 2007); (e) *Betula pendula* hemiboreal forests in the Western Siberian Plain and Minusinskaya Basin (N. Ermakov, unpublished data); (f) *Abies–Tilia* forest in the Russian Far East (Gumarova et al. in Krestov et al. 2006); (g) hemiboreal forest in the Southern Ural Mountains (Solomeshch et al. 1989); (h) grazed Mediterranean woodland in Israel (Naveh & Whittaker 1979). Note the logarithmic scale on the horizontal axis.

The richest forests in the southeastern USA probably contain more species in small plots than the richest Eurasian temperate forests (Fig. 4). Palmer et al. (2003) reported ca. 109 species per 100 m^2 from a *Quercus* woodland in NE Oklahoma. Brown & Peet (2003) presented data with ca. 130 species per 100 m^2 from a southern Appalachian riparian forest, which is more than the 114 species that we found in a plot of the same size in the Altai, but ca. 43 of the species they found were non-native. Fridley et al. (2005) reported 179 species per 1000 m^2 from the same area, but without indication of vegetation type.

Although the North American data indicate that there may be forests with greater species richness than those in the northern Altai, especially in the southeastern USA, we found no indication of the existence of richer or nearly-as-rich forests in boreal and temperate Eurasia. Moreover, unlike the southeastern US forests, the high species richness of the Altai forests is exclusively due to species that are native to this region. We believe that publication of our data will stimulate vegetation scientists to search for other boreal or temperate forests that might contain more species of vascular plants than those in the Altai.

Species richness of hemiboreal forests vs grasslands

The species-rich forests of the Altai Mountains are classified as hemiboreal (or subtaiga) forests, i.e. zonal forests occurring in a latitudinal belt between taiga in the north and steppe in the south (Hämet-Ahti 1981; Ermakov 2010). In general they are drier than taiga forests, have soils with a higher pH, and contain more herbs and fewer dwarf shrubs and bryophytes of boreal distribution in terms of both species number and biomass (Ermakov et al. 2000; Chytrý et al. 2007, 2008). In the western and central part of southern Siberia, hemiboreal forests are dominated by *Betula pendula, Larix sibirica, Pinus sylvestris* or *Populus tremula*, i.e. trees with relatively open canopies that permit high insolation of the herb layer. Broad-leaved tree species that form dense canopies are absent in the continental climate of southern Siberia, except for *Tilia sibirica*, but this species does not occur in the Altai (Meusel et al. 1978).

The most species-rich forests that we documented in the northern Altai had an open canopy, which permitted occurrence in their herb layer of many light-demanding species characteristic of tall-grass steppes (‘meadow steppes’ in Russian literature) and mesic to wet meadows.

Indeed, the high species richness of these forests was related to their rich herb layer, whereas there were very few species of tree and shrub and no lianas or vascular epiphytes. In this respect, species composition of these forests partly resembles that of semi-dry grasslands.

Temperate semi-dry grasslands on base-rich soils, including tall-grass steppes, are among the most species-rich plant communities in the world, especially in plots smaller than 100 m^2. For example, there are records of 67 vascular plant species per 1 m^2, 88 per 4 m^2, 105 per 16 m^2 and 133 per 100 m^2 from the semi-dry meadows in the White Carpathians, Czech Republic (Klimeš et al. 2001; Z. Otýpková & M. Chytrý, unpublished data). Alekhin (Russian sources from the 1930s, cited in Vasilevich 2009) reported 77 species per 1 m^2 and 110 species per 100 m^2 in steppes of the Central Chernozem Nature Reserve near the city of Kursk in southwest Russia. Semeniuk & Gudyna (Russian sources from the 1980s, cited in van der Maarel & Titlyanova 1989) recorded 88 species per 1 m^2 and 130 species per 100 m^2 in the same region. We recorded 109 species per 100 m^2 in a tall-grass steppe of the Southern Urals in Russia (J. Danihelka, unpublished data).

Although there are many published records of grassland species number per 1 m^2 that are higher than those reported from the Altai forests (with a probable maximum of 89 species recorded in a mountain grassland of Argentina; Cantero et al. 1999), the literature contains few records of higher richness per 10 or 100 m^2 except for those from the White Carpathian meadows. We sampled steppe vegetation in 92 plots of 100 m^2 across the Russian Altai, but the highest number of vascular plants species that we recorded was 90, which was 14 species fewer than in the richest forest plot of the same size in the northern Altai. The sites with the richest grasslands of the Altai were concentrated in the same area as the richest forests.

The lower maximum values of species richness of grasslands than of forests in the northern Altai suggest that the herb layer of hemiboreal forests may be a suitable habitat for many species because the open tree canopy does not exclude light-demanding species and, at the same time, it moderates extremes of the continental macroclimate of the wider area, thus supporting species characteristic of both woodlands and mesic to wet meadows. This observation is consistent with the fact that species richness within the Altai forests decreases if their canopy is very open (less than 20% cover), because of the retreat of mesophilous species.

Why do Altaian hemiboreal forests contain so many species?

Local species richness of plant communities is controlled by regional factors such as landscape context and the history of plant evolution and migration (Ricklefs & Schluter 1993; Zobel 1997), as well as by local factors such as abiotic site conditions and interspecific interactions (Grime 1973, 1979; Huston 1979). We suggest that exceptionally rich communities can only develop if several limiting factors that act as constraints on species richness simultaneously attain values that support or do not restrict high species richness. Here we discuss possible causes of the high richness of the Altai hemiboreal forests, starting with regional and proceeding to local factors.

1 *Floristic richness of the Altai region*. Large-scale species richness of the Siberian flora, which is the result of speciation and extinction over evolutionary history, generally increases from the north to the south and in mountainous areas. In the Altai Mountains, there are more than 2000 species of vascular plants per 1000 km^2, which is more than elsewhere in Siberia (Malyshev 1993; Mutke & Barthlott 2005). The high richness of the Altai flora is partly caused by its transitional character between Euro-Siberian and Central Asian floristic regions, but most species of the northern Altaian hemiboreal forests have European–southern Siberian distribution ranges (Nimis et al. 1994; Ermakov 2010). However, a rich regional flora is probably a necessary but not sufficient condition for development of communities with very high local species richness, because there are areas with richer regional floras but without records of higher local species richness.

2 *Long-term stability of the environment*. High-altitude landscapes in the central part of the Altai Mountains, including inter-mountain basins, were covered with glaciers in the Pleistocene, but the foothill areas (including those where the species-rich forests occur) were not glaciated (Chlachula 2001). Compared to other Eurasian regions, there seems to have been very limited environmental change in the Altai region since the Pleistocene. Macroclimatic differences between the Last Glacial Maximum and the present are less pronounced in this area than elsewhere in northern Eurasia (Tarasov et al. 1999; Kim et al. 2008). Fossil pollen data from the Altai indicate that vegetation change at the Pleistocene–Holocene transition was mainly quantitative (changing proportions of individual pollen types; Blyakharchuk et al. 2004), but did not include the significant change in species composition that was typical of other regions. Simulated palaeo-vegetation maps, based on palaeoclimatic models and plant functional types, also suggest considerable stability in the Altai region over the last 40 000 yrs (Allen et al. 2010). The area still contains mollusc assemblages that were typical of the full-glacial environments across large areas of Eurasia but became extinct in other regions that experienced considerable climate change, namely in Europe (Horsák et al. 2010). The changes in composition of mammal assemblages in the Altai have also been small since the Pleistocene (Agadjanian & Serdyuk 2005; Řičánková 2008). In

contrast to areas that experienced great changes during the Pleistocene–Holocene transition and/or later, areas with long periods of relative environmental stability may have accumulated more species, because fewer species went extinct. These processes of plant immigrations and extinctions acted on larger scales than the small vegetation plots that are the focus of this study, but it is possible that not only species pool size but also small-scale species richness is positively related to the habitat age at a millennial scale (Pärtel & Zobel 1999).

3 *Heterogeneity of the surrounding landscape*. The Altai species-rich forests occur in a topographically heterogeneous landscape of mountain valleys, which harbour contrasting habitats on the valley bottoms, lower and upper slopes and south- and north-facing slopes. However, unlike the species-poorer forests of the Altai, which also often occur in similar topographical situations, the species-rich forests are located in the forest-steppe zone. In the areas with ca. 500–600 mm of annual precipitation, the Altai landscape is covered by 'expositional forest-steppe' (Fig. 2d), that is, a landscape mosaic in which the occurrence of patches of steppe or forest consistently depends on slope aspect (= exposition), with south-facing slopes covered by steppe and north-facing slopes by forest (Sedel'nikov et al. 2008). In areas with higher or lower precipitation, the landscapes are dominated by either forest or steppe, respectively, and they become more uniform. This is consistent with the concept of 'effective heterogeneity' (Sarr et al. 2005), which predicts that landscape topographical variability creates stronger gradients of soil moisture in semi-arid to subhumid landscapes than in either arid or humid landscapes. Thus, if we compared landscapes of identical topographic heterogeneity across a precipitation gradient, biological heterogeneity (β-diversity) would be greater under intermediate precipitation regimes and would decline under wetter or drier conditions (Sarr et al. 2005). Heterogeneity of the northern Altai landscape may have positively affected high species richness of forest patches in at least two ways. First, during periods of climatic change in the past, sensitive species may have easily escaped to patches of different vegetation on nearby slopes and returned to their original sites after climate change was reversed. This may have reduced species extinctions on the landscape scale. Second, landscape mosaics may support the spatial mass effect, i.e. species dispersal from vegetation patches where the species find optimal conditions to nearby patches of different vegetation that enable species persistence but not population growth (Shmida & Ellner 1984; Leibold et al. 2004). Indeed, the rich forests of the Altai contain some species typical of steppes or alluvial grasslands, which are represented in the forest herb layer by scattered and isolated individuals, sometimes sterile or with stunted growth.

4 *Local abiotic factors*. The Altai species-rich forests are characterized by a combination of moderate environmental conditions that are suitable for many herb-layer species. First, like other forests of southern Siberia, they have a relatively open canopy, which supports simultaneous occurrence of forest species with species of open grassland. It has been shown that after invasion of these forests by broad-leaved trees, which reduce light penetration through the canopy, herb-layer species richness decreases considerably (Chytrý et al. 2010b). Second, these forests occur in an area that is among the warmest parts of the Altai Mountains. In addition, winter precipitation is sufficient to develop a continuous snow cover, which protects the herb layer from winter frosts. Thus the harsh continental climate typical of other parts of the Altai Mountains, as well as other regions of Siberia, is moderated here. Third, most of the richest forests were found on north- to northeast-facing slopes with deep soils, i.e. in mesic conditions. It is probable that these soils are wetter in spring after snowmelt and drier in summer. Such conditions support formation of a peculiar mixture of species that includes not only mesophilous species but also drought-adapted steppe species and species of wet meadows. Fourth, the Altai species-rich forests occur on soils of near-neutral pH, which are suitable for most species of the southern Siberian forest flora. Generally, southern Siberian forests are species-rich on soils with pH > 5, while species numbers decline if pH is below that value (Chytrý et al. 2007). Although within-plot heterogeneity might contribute to local richness, all plots were selected to be as homogeneous as possible. In any case, the species-rich plots were visually no more heterogeneous than plots used for sampling of the species-poorer forests elsewhere in the Altai Mountains.

5 *Limited competition in the herb layer*. The herb layer of the Altaian species-rich forests contains no strongly dominating species. With a single exception in a single plot, there were no species with cover higher than 25% in the herb layers of the richest forest plots. This suggests limited competition in the herb layer. Grime (1973, 1979) observed a unimodal relationship between species richness and plant community biomass, asserting that at high biomass levels competition intensifies, which leads to exclusion of competitively weak species and floristic impoverishment of the community. We did not measure biomass in the Altaian hemiboreal forests, however, herb-layer biomass in similar hemiboreal forests of the Southern Urals never exceeded 250 $g{\cdot}m^{-2}$ (Chytrý et al. 2010b), which was probably not sufficient to reach the declining phase of the species richness–biomass curve. This declining phase usually starts at biomass values higher than 400 $g{\cdot}m^{-2}$ according to the grassland studies (Moore & Keddy 1989; Zobel & Liira 1997; Crawley et al. 2005; Hejcman et al. 2010). Possible explanations for the upper limit on the forest herb-layer biomass,

which may decrease the intensity of competition within the herb layer, include canopy shading (Axmanová et al. 2012), competition for water and nutrients from the tree layer, and disturbances (Huston 1979, 1994). The richest forests that we sampled may have been occasionally grazed by domestic livestock, especially cattle, but they did not show any evidence of intensive or frequent grazing. However, their herb layer may have been occasionally disturbed by strong summer droughts or winter frosts, which occur in this continental region.

We do not know the relative importance of the five above-mentioned explanations of the high local species richness of the hemiboreal forests in the northern Altai Mountains. Nor do we know whether all of them are valid, and on the other hand we may have missed other plausible explanations. However, we believe that the high species richness of these forests is a result of the incidental combination of all of these factors: a rich regional flora, long-term environmental stability, heterogeneity of the mountainous forest-steppe landscape, an open tree layer that ameliorates microclimate but does not exclude light-demanding species through strong shading, a not-too-harsh macroclimate, mesic soil with pH > 5 and limited competition in the herb layer.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data from the six most species-rich sites in the Altai Mountains.

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