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RESEARCH PAPER

Habitats and population structure of rare orchids from the genus *Cypripedium* in Siberia

Ekaterina L. Zheleznaya[1]*, Andrei A. Zverev[2,3] & Nadezhda V. Stepantsova[4]

Ekaterina L. Zheleznaya[1]*
e-mail: zheleznaya@yandex.ru

Andrei A. Zverev[2,3]
e-mail: ibiss@rambler.ru

Nadezhda V. Stepantsova[4]
e-mail: s-nadia11@yandex.ru

[1] Peoples' Friendship University of Russia, Moscow, Russia

[2] Tomsk State University, Tomsk, Russia

[3] Central Siberian Botanical Garden SB RAS, Novosibirsk, Russia

[4] Irkutsk State University, Irkutsk, Russia

* corresponding author

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ABSTRACT

Cypripedium calceolus L., *C. macranthos* Sw. and *C. ventricosum* Sw. are rare Eurasian orchid species, whose habitats are poorly studied in Siberia. In this paper, we describe 55 sympatric and 10 separated populations of the three species, located in Russia within Republic of Buryatia, Irkutsk Region, Krasnoyarsk Territory, and Republic of Altai. *Cypripedium macranthos* plants dominated the most of the sympatric populations. Vegetation surveys were performed in all localities, and the collected data were analyzed using the IBIS software. We applied the phytoindication scales elaborated by Tsatsenkin and his colleagues for ecological indicator value analysis. The *Cypripedium* populations were characterized by high floristic diversity of their habitats; however, all of them were found in areas where both canopy density and ground cover were low. In the most of the separated populations, ontogenetic spectra of *Cypripedium* species corresponded to the base spectrum with a predominance of the adult vegetative and reproductive shoots.

Keywords: *Cypripedium*, types of plant communities, sympatric populations, separated populations, Tsatsenkin phytoindication scales, partial shoot, ontogenetic stages

РЕЗЮМЕ

Железная Е.Л., Зверев А.А., Степанцова Н.В. Фитоценотическая характеристика и структура ценопопуляций редких видов *Cypripedium* в Сибири. *Cypripedium calceolus* L., *C. macranthos* Sw. и *C. ventricosum* Sw. – редкие евразийские виды орхидей, местообитания которых в Сибири мало изучены. В данной работе мы описываем 55 симпатрических и 10 изолированных популяций этих видов, расположенных на территории Республики Бурятия, Иркутской области, Красноярского края и Республики Алтай. Растения *C. macranthos* доминировали в большинстве симпатрических популяций. Во всех местообитаниях были проведены геоботанические описания, а собранные данные проанализированы с помощью программного обеспечения IBIS. Проведена фитоиндикационная оценка местообитаний по экологическим шкалам И.А. Цаценкина и др. с помощью интегрированной ботанической информационной системы IBIS v.7.2. По результатам оценки местообитаний по полному флористическому составу они хорошо географически разделились, однако сомкнутость крон и общее проективное покрытие ярусов, так же, как и экологические характеристики в местообитаниях, оказались сходными. В большинстве изолированных популяций онтогенетические спектры соответствовали базовому спектру с преобладанием взрослых вегетативных и генеративных побегов.

Ключевые слова: *Cypripedium*, основные типы фитоценозов, симпатрические ценопопуляции, изолированные ценопопуляции, экологические шкалы Цаценкина, парциальный побег, онтогенетические состояния

Cypripedium calceolus L., *C. macranthos* Sw., and *C. ventricosum* Sw. are rare orchid species included in the Red Data Book of Russian Federation (Trutnev 2008) and several regional Red Data Books (Gaikova et al. 2010, Pronin 2013, Maneev et al. 2017, Stepanov 2022). In Russia, *C. calceolus* is distributed in the forest zone of the European part of the country, in the Urals, in Southern Siberia and in the Far East of Russia. *C. macranthos* occurs in European Russia (only few localities), the Urals, Southern Siberia, and also in the Far East of Russia (Vakhrameeva et al. 2008). *C. ventricosum* (an interspecific hybrid between *C. calceolus* and *C. macranthos*) occurs in areas where the parent species ranges overlap (Averyanov 1999). Populations of *C. calceolus* and *C. macranthos* can grow both isolated from each other, and in sympatric populations, which are especially common in the Urals, Southern Siberia, and in the Far East. The density of individual plants in the populations of these three rare species in different parts of their ranges varies from single individuals per 0.1 m² (such coenopopulation loci are found in each of the studied species) to 21 024 shoots in the population of *C. macranthos* within an area of 0.24 ha in Yakutia (Afanas'eva & Danilova 2011) or 600 000 shoots in a population of *C. calceolus* within an area of 107.7 ha in the Vladimir Region (Sergeev et al. 2013). The most numerous populations of *C. calceolus*, *C. macranthos*, and *C. ventricosum* are concentrated on soil rich in calcium, typical for rich fens, limestone slopes, and quarries (Vakhrameeva et al. 2008). In particular, this is due to the fact that *Cypripedium* is a phytocoenotic and ecotopic patient (stress tolerant) (Zaugolnova et al. 1992) intolerant to competition of other herbs when growing in swamps, screes, and overgrown quarries. In coniferous, mixed coniferous-broad-leaved, broad-leaved, small-leaved, and mixed coniferous-small-leaved forests, as well as in transitional mires, *Cypripedium*

populations are dominated by adult vegetative and generative plants (Tatarenko 1996, Ishmuratova et al. 2003, Bychenko 2010, Barabantsova & Berdnikova 2017, Fardeeva et al. 2020, 2022). Tatarenko (1996) gives a basic spectrum of 0 % : 8 % : 44 % : 48 % (j : im : v : g) for populations of *C. calceolus* and *C. macranthos*. It indicates the predominance of vegetative reproduction, as there are no juvenile plants, and the immature ones may also have vegetative origin. However, Fardeeva et al. (2022) identified three types of basic age spectra for *C. calceolus*: 1) centered (3 : 11 : 47 : 40), the most common in the European part of the Russia; 2) bimodal (15 : 26 : 33 : 26), predominantly found in western regions; 3) right-sided (0 : 3 : 13 : 82 : 2) (j : im : v : g : s) which manifests in the continental climate of the eastern regions of European Russia. In *C. calceolus*, the predominance of juvenile (up to 58 %) and/or immature (up to 52 %) plants was observed only in populations on river valley slopes with sparse moss and grass cover (Puchnina 1999), in peatmoss pine forests (Ishmuratova et al. 2003, Fardeeva et al. 2022), or in swampy habitats and limestone outcrops (Teteryuk 2003). This indicates a fairly active seed renewal along with the vegetative reproduction, provided there is no competition from other plants and the luminosity is optimal. Our goals were to find out the types of phytocoenoses with sympatric populations and to evaluate the interaction of different species therein.

The objectives of our study included: 1. To identify the main types of plant communities with populations of *C. calceolus*, *C. macranthos*, and *C. ventricosum*; 2. To assess the habitats of these species using the phytoindication scales; 3. To compare numbers, ontogenetic structure, and average density of all counting units in sympatric and isolated populations of the studied species in the established temporary plots within different community types.

MATERIAL AND METHODS

The studies were carried out in 2009 and 2011 in the south of the Krasnoyarsk Territory, in 2010, 2013 and 2014 in the Irkutsk Region and in the Republic of Buryatia, and in 2012 in the Altai Republic. Most of the research was carried out in the Altaiskiy, Barguzinskiy and Baikalo-Lenskiy Nature Reserves, and in the Shushenskiy Bor National Park (Table 1). In total, 55 sympatric and 10 isolated populations were studied.

For each study area, several (3–10) 10×10 m temporary plots were set. We made a complete vegetation relevé in each plot, following the Braun-Blanquet (1964) recommmendations. Mediate ecological assessment of habitats was carried out using phytoindication scales of Tsatsenkin et al. (1978) in the integrated botanical information system IBIS v.7.2 (Zverev 2020). The geobotanical plots were ordinated by DCA (Hill & Lewicki 1979). *Cypripedium* habitats were compared by DCA ordogram for the complete floristic composition (including forest layers), and by evaluating distribution of ecological optima in the axes of soil moisture and nutrient content factors according to the Tsatsenkin scales. The figures were compiled in PAST 4.13 software (Hammer et al. 2001).

To study the ontogenetic and spatial structure of populations, temporary study plots were established within phytocoenoses using a tape measure, pegs and GPS. The sizes of the plots varied depending on the area occupied by the population.

In population-ontogenetic studies of rhizomatous species *C. calceolus*, *C. macranthos*, and *C. ventricosum*, an aboveground shoot or ramet serves as a phytocoenotic counting unit (Zaugolnova et al. 1988).

Ontogenetic stages were identified according to generally accepted methods (Rabotnov 1950, Uranov 1975, Gatzuk et al. 1980, Zaugolnova et al. 1988, Tatarenko 1996, Bychenko 2004, Zheleznaya 2009). Following the latter, the ontogeny of an individual plant is divided into 4 periods and 9 stages: I. Latent period (seed); II. Pre-reproductive period (seedling, juvenile (j), immature (im), mature vegetative (v)); III. Reproductive period (young, mature and old reproductive (g)); IV. Post-reproductive period (senescent (s)). The senile period is rarely specified for orchids, because plants often die off after the last flowering. It is also difficult to distinguish a senile plant from a young vegetative plant with reduced vitality visually when observing only its aboveground part (Vakhrameeva et al. 2008).

Climate data were taken from the AISORI database (Veselov et al. 2022).

RESULTS

Climatic parameters

Since the studied populations of *Cypripedium* were located more than 2000 km from each other (Fig. 1) (Zheleznaya 2015), it was assumed that the structure of populations and morphometric parameters of plants are influenced by climatic features and phytocoenotic environment. The following were chosen as the main climatic parameters: duration of the period with air temperatures above 10°C, degree days 10°C, and total annual precipitation. Maximum duration of the period with air temperatures above 10°C and degree days 10°C were observed in the Minusinsk Basin and along the Teletskoye Lake shores, respectively. The minimal values of these factors were registered in the Khamar-Daban Mts and in the Barguzinskiy Nature Reserve. The highest annual precipitation was observed on the Khamar-Daban Ridge slopes and near the Teletskoye Lake, whereas the lowest took place in the Minusinsk Basin and the Baikalskiy Range foothills (Table 1).

Types of phytocoenoses and environmental factors

Populations of *Cypripedium* in different geographical areas are confined to 16 types of forest phytocoenoses (Table 2). Both sympatric and isolated populations of *Cypripedium* occur in primary forests as well as in secondary ones. Primary forests are represented by Scots pine, spruce, larch, mixed fir-pine-spruce, and Scots pine-Siberian stone pine forests. Secondary forests comprise mainly birch ones but also mixed spruce-birch, pine-birch, and pine-poplar forests (Table 2) (Tyulina 1967, 1976, Smagin et al. 1980). The table of relevés made in plots with *Cypripedium* species is attached (Appendix 1).

Figures 2 and 3 show mediate ecological assessment of habitats according to the phytoindication scales of Tsatsen-

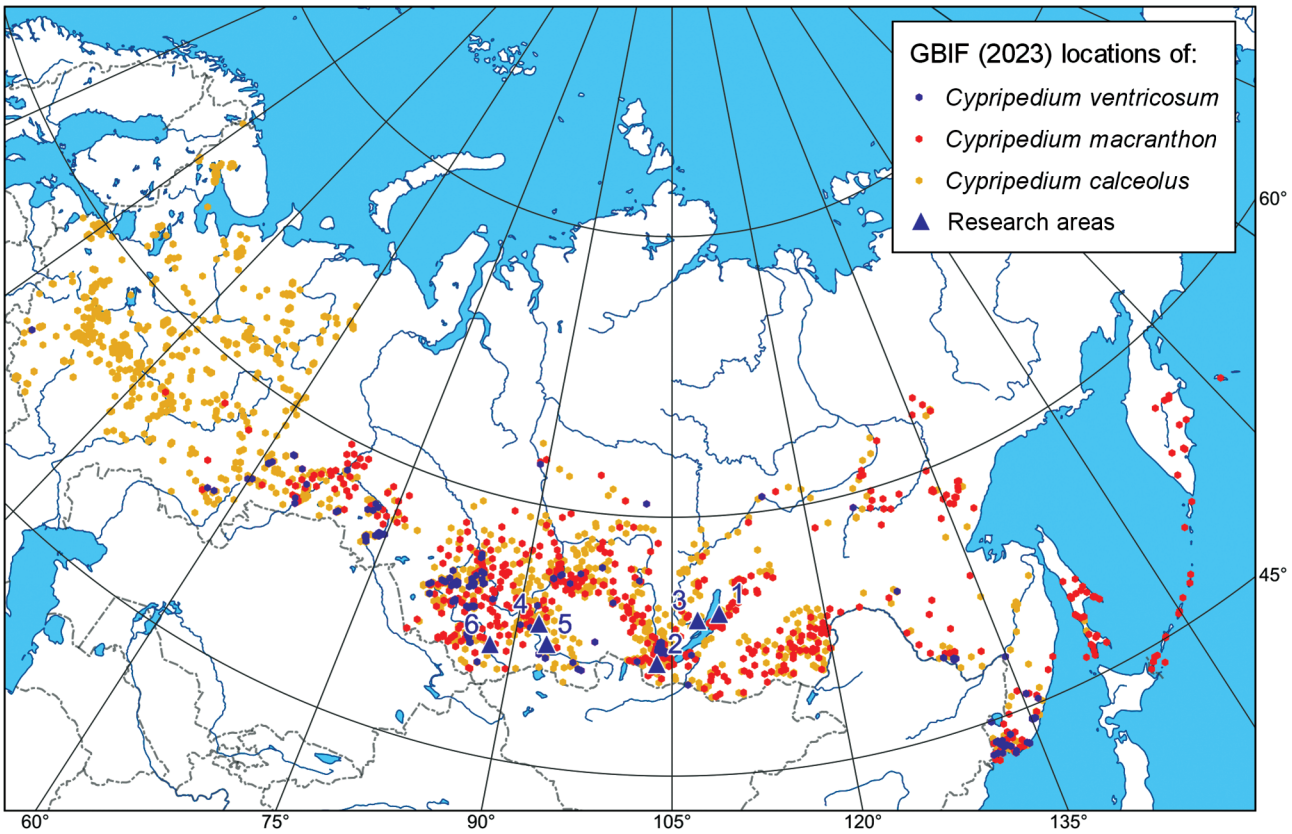

Figure 1 Distribution of *Cypripedium calceolus* L., *C. macranthos* Sw. and *C. ventricosum* Sw. study sites and overall distribution of studied species in Russia according to GBIF data (2023). Study sites: 1 –Barguzinskiy Nature Reserve; 2 – Khamar-Daban Mts; 3 –Baikalo-Lenskiy Nature Reserve; 4. Shushenskiy Bor National Park; 5 – Usinsk Basin; 6 – Altaiskiy Nature Reserve (Zheleznaya 2015)

kin et al. (1978) using the IBIS v.7.2 system (Zverev 2020) with the ordination of geobotanical plots.

Structure and population size of *Cypripedium* species

The characters of sympatric populations of *Cypripedium* in Siberia are given in Table 3. The most numerous populations of *Cypripedium*, also occupying the maximal areas, were observed in the Shushenskiy Bor National Park. In the Baikalskiy Ridge foothills, population clumps with small numbers of individuals are scattered over a large area. The average population density is 0.04–6.00 shoots/ m². *C. macranthos* dominates all the sympatric populations, except for those from the Khamar-Daban Mts. (Table 3).

The *C. ventricosum* plants were first discovered in the area of the Baikalo-Lenskiy Nature Reserve and its vicinities in 2013–2014 (Stepantsova & Zheleznaya 2016).

The number of reproductive shoots of *Cypripedium* can change greatly from year to year. For example, that of *C. macranthos* in the pine forest with *Rhytidium* on the Lena River bank of Baikalo-Lenskiy Nature Reserve in 2014 was half of that in 2013. But these years the analogous numbers did not change for *C. calceolus* and *C. ventricosum* for these locality (Zheleznaya 2015). These three species of *Cypripedium* cannot be reliably distinguished from each other in the non-flowering state. Therefore, according to the abundance of juvenile (j) plants, only the intensity of

Table 1. Climatic characteristics of the study sites (Veselov et al. 2022).

Study site	Duration of the period with temperatures above 10°C, days	Degree days 10°C, C°	Annual precipitation, mm
Krasnoyarsk Krai,Shushenskiy Bor National Park, Minusinsk Basin ('Minusinskaya kotlovina')	132	2173	345
Altai Republic, Altaiskiy Nature Reserve, Teletskoye Lake	128	1999	917
Irkutsk Region, Khamar-Daban Mts, Slyudyanka River in low-mountain area)	76	956	1365
Irkutsk Region, Baikalo-Lenskiy Nature Reserve, foothills of the Baikalsky Ridge	96	1465	346
Krasnoyarsk Krai, Usinsk Basin ('Usinskaya kotlovina')	107	1560	392
Republic of Buryatia, Barguzinskiy Nature Reserve, Barguzinsky Ridge	74	1067	429

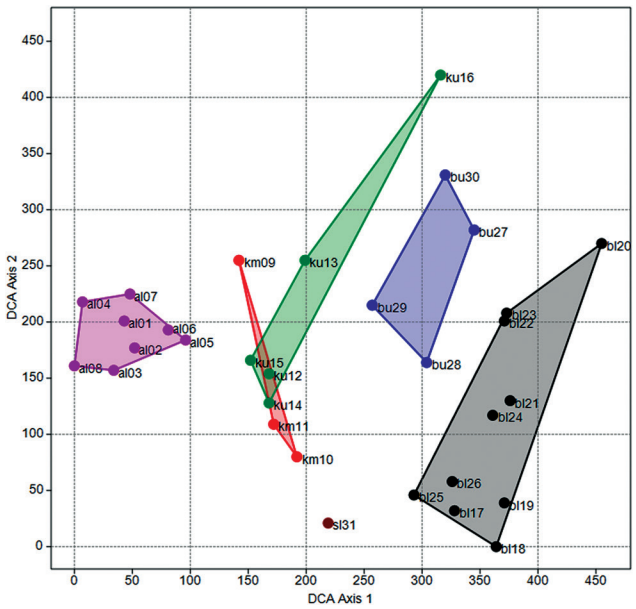

Figure 2 DCA ordogram for the complete floristic composition of the *Cypripedium* species habitats (the taxa weights are expressed as percentages)

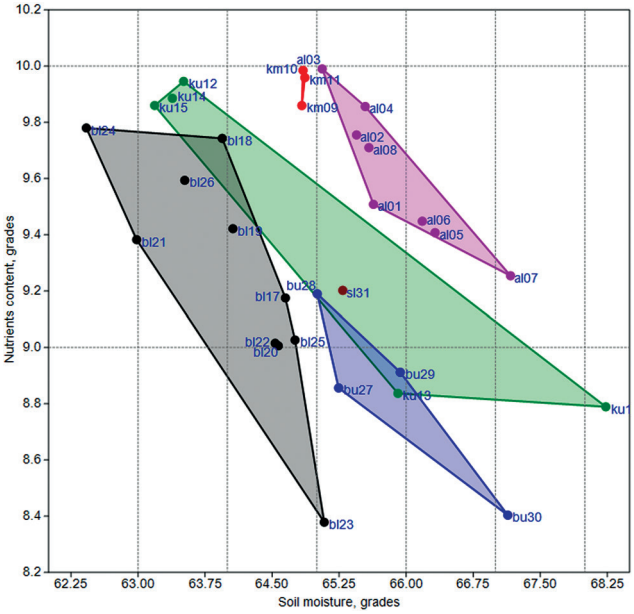

Figure 3 Distribution of indicator value optima of *Cypripedium* habitats in the axes of soil moisture and nutrient content (fertility – salinization), based upon the Tsatsenkin et al. (1978) phytoindication scales

Table 2. Main types of plant communities with *Cypripedium* species populations.

Forest type	Locality and locality names	Locality coordinates and altitude above sea level
1. Secondary birch forest with *Betula pendula Pteridium aquilinum* and herbs	Altaiskiy Nature Reserve (al01, 02, 03, 04)	51.36150°N 87.84369°E, 557 m; 51.42050°N 87.80564°E, 735 m; 51.42169°N 87.80578°E, 765 m; 51.35144°N 87.76117°E, 441 m
2. Pine (*Pinus sylvestris*) forest with *Pteridium aquilinum* and mixed herbs	Altaiskiy Nature Reserve (al05, 06)	51.77725°N 87.62275°E, 564 m
3. Pine (*Pinus sylvestris*) forest with *Carex* and mixed herbs	Altaiskiy Nature Reserve (al07)	51.34886°N 87.85800°E, 472 m
4. Secondary birch (*Betula pendula*) forest with mixed herbs	Altaiskiy Nature Reserve (al08)	51.41025°N 87.79561°E, 456 m
5. Secondary pine-birch (*Pinus sylvestris* and *Betula pendula*) forest with mixed herbs	Shushenskiy Bor National Park (km09, 11)	53.28756°N 92.02694°E, 288 m; 53.27019N 92.01447°E, 288 m
6. Secondary birch (*Betula pendula*) forest with mixed herbs	Shushenskiy Bor National Park (km10)	53.27056°N 91.94836°E, 282 m
7. Secondary birch (*Betula pendula*) forest with mixed herbs and steppe plants	Usinsk Basin (ku12, 14, 15)	52.14269°N 92.85967°E, 698 m; 52.15272°N 92.79159°E, 620 m ; 52.14302°N 92.78142°E, 620 m
8. Larch (*Larix sibirica*) forest with *Carex* and mixed herbs	Usinsk Basin (ku13)	52.14089°N 92.82659°E, 672 m
9. Secondary spruce-birch (*Picea obovata* and *Betula pendula*) forest with mixed herbs	Usinsk Basin (ku16)	52.14211°N 92.81253°E, 610 m
10. Pine (*Pinus sylvestris*) forest with *Rhytidium*	Baikalo-Lenskiy Nature Reserve (bl17, 18, 19, 21, 22, 23, 24, 25, 26)	53.80547°N 107.03192°E, 744 m; 53.83417°N 107.02933°E, 710 m; 53.83294°N 107.02558°E, 715 m; 53.88397°N 107.18681°E, 737 m; 53.88428°N 107.18661°E, 746 m; 53.88333°N 107.18186°E, 796 m; 53.88211°N 107.18386°E, 677 m; 53.88311°N 107.18253E, 766 m; 53.88281°N 107.18331°E, 733 m
11. Spruce (*Picea obovata*) forest with *Rhytidium*	Baikalo-Lenskiy Nature Reserve (bl20)	53.83642°N 107.04161°E, 645 m
12. Fir-pine-spruce (*Abies sibirica*, *Pinus sylvestris* and *Picea obovata*) mixed herb forest	Barguzinskiy Nature Reserve (bu27)	54.33025°N 109.57781°E, 546 m
13. Pine-stone pine (*Pinus sylvestris* and *P. sibirica*) forest with mixed herbs	Barguzinskiy Nature Reserve (bu28)	54.30991°N 110.56396°E, 611 m
14. Pine (*Pinus sylvestris*) forest with *Pteridium aquilinum* and mixed herbs	Barguzinskiy Nature Reserve (bu29)	54.30378°N 110.56298°E, 616 m
15. Fir-spruce (*Abies sibirica* and *Picea obovata*) forest with mixed herbs	Barguzinskiy Nature Reserve (bu30)	54.30397°N 110.57987°E, 641 m
16. Secondary pine-poplar (*Pinus sylvestris* and *Populus suaveolens*) forest with mixed herbs	Khamar-Daban Mts., Slyudyanka River floodplain (sl31)	51.63119°N 103.67656°E, 582 m

Table 3. Some characters of the *Cypripedium* sympatric populations in Siberia.

Locality, it's ecological peculiarities and observation year	Accounting area, m²	Number of reproductive shoots C.m.:C.c.:C.v.	Average density of shoots/m²	Number of populations C.m.:C.c.:C.v.	Average distance between populations, m	Relative number of j plants, %
Shushenskiy Bor National Park, the swamp edge (2009)	216–56620	3206:428:552	0.05–0.29	9:9:9	100–4300	6.1
Usinsk Basin, dry slopes, 20-25° (2009)	40–1253	121:107:1	0.31–1.10	2:2:1	2000	6.7
Altaiskiy Nature Reserve, Teletskoye Lake shore, wet slopes, 20-25° (2012)	1–7800	143:85:26	0.06	5:3:5	1400–6000	8.0
Khamar-Daban Mts, Slyudyanka River floodplain (2013)	10000	71:134:5	0.04	1:1:1	-	1.1
Baikalo-Lenskiy Nature Reserve, limestone slopes, 15-40° (2013)	0.25–200	171:25:28	0.6–6.0	5:4:8	14–245	3.2

seed reproduction in the populations of these species as a whole can be estimated (Table 2). The relative abundance of juvenile plants in the studied populations was 1.1–8.0 %. Adult vegetative shoots dominated among the non-flowering shoots of *Cypripedium* in most of the studied populations (Zheleznaya 2015).

Separated populations of *C. calceolus* were studied in the Barguzinskiy Nature Reserve on the Barguzinskiy Range western slope ("Birikanskie Shcheki") and in the Usinsk Basin (Table 4). The most numerous *C. calceolus* population (246 shoots) grew in the secondary birch forest with steppe plant species in the Usinsk Basin. The average density in populations was 0.001–13.0 shoots/m².

Separated populations of *C. macranthos* were studied in the Barguzinskiy Nature Reserve on the western macroslope of the Barguzinskiy Ridge and in the Altaiskiy Nature Reserve along the Teletskoye Lake shores (Table 5). The most numerous *C. macranthos* population (527 shoots) grew in the pine-stone pine (with *Pinus sylvestris* and *P. sibirica*) forest with mixed herbs in the Barguzinskiy Nature Reserve. The average density in populations was 0.1–5.6 shoots/m².

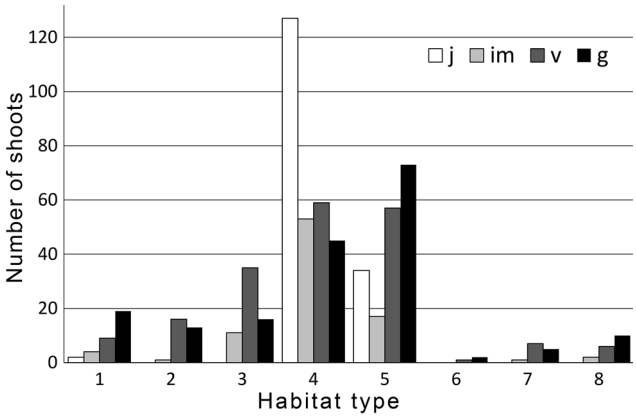

Figure 4 Ontogenetic spectra of *Cypripedium macranthos* and *C. calceolus* populations in different habitat types (1–8) in 2010 (Zheleznaya 2015). Abbreviations: j – juvenile, im – immature, v – adult vegetative, g – generative. Habitat types: 1–5 – *Cypripedium macranthos* in the pine-stone pine (*Pinus sylvestris* and *P. sibirica*) forest with mixed herbs (1), in the pine (*Pinus sylvestris*) forest with *Pteridium aquilinum* and mixed herbs (2–4), in the fir-pine-spruce mixed-herb forest (*Abies sibirica*, *Pinus sylvestris* and *Picea obovata*). 6–8 – *Cypripedium calceolus* in the pine (*Pinus sylvestris*) forest with *Rubus saxatilis* and *Pteridium aquilinum* (6), in the pine-stonepine (*Pinus sylvestris* and *P. sibirica*) forest with mixed herbs (7), in the fir-spruce (*Abies sibirica*, *Pinus sylvestris* and *Picea obovata*) forest with mixed herbs

Table 4. Size and area of separated *Cypripedium calceolus* populations in the Usinsk Basin and Barguzinskiy Nature Reserve.

Locality / Phytocoenosis	Number of shoots	Area, m²	Average density of shoots per m²
Usinsk Basin			
Secondary spruce-birch forest with mixed herbs (ku16)	10	0.2	-
Secondary birch forest with mixed herbs and steppe plants (ku12)	75	21.6	3.50
Secondary birch forest with mixed herbs and steppe plants (ku14, 15)	246	≈250000	0.001
Larch forest with *Carex* and mixed herbs (ku13)	83	46.0	1.80
Barguzinskiy Nature Reserve			
Pine forest with *Pteridium aquilinum* and mixed herbs (bu29)	3	0.06	-
Fir-pine-spruce mixed herb forest (bu27)	18	10	1.8
Pine-stone pine (with *Pinus sylvestris* and *P. sibirica*) forest with mixed herbs (bu28)	13	1	13.0

Table 5. Size and area of separated *Cypripedium macranthos* populations in the Barguzinskiy and Altaiskiy Nature Reserves.

Locality/Phytocoenosis	Number of shoots	Area, m²	Average density of shoots per m²
Barguzinskiy Nature Reserve			
Pine forest with *Pteridium aquilinum* and mixed herbs (bu29)	64	604	0.1
Pine-stone pine herbs (with *Pinus sylvestris* and *P. sibirica*) forest with mixed herbs (bu28)	527	134.5	3.9
Altaiskiy Nature Reserve			
Pine forest with *Pteridium aquilinum* and mixed herbs (al05, 06)	136	762	5.6

In most separated *Cypripedium* populations, adult vegetative and reproductive shoots predominated, which corresponds to the basic spectra of these species (Fig. 4, Tatarenko 1996). However, juvenile individuals reached the largest abundance (44.7 %) in one of the *C. macranthos* populations in the Barguzinskiy Nature Reserve (Fig. 4–4). This is probably due to favorable weather conditions for their development, combined with optimal illumination and growth on limestone outcrops. There were no juvenile plants in the few *C. calceolus* populations in both regions

DISCUSSION

The habitats of *Cypripedium* species are geographically well-divided, according to the floristic composition survey results (Fig. 2). The ordograms from the Usinsk Basin and Shushenskiy Bor National Park are partially overlapping only. They are geographically much closer to each other than to those from the other study areas (Fig. 1, 2). The Tsatsenkin phytoindication scales, created purposefully for Siberia, evaluate only the soil moisture and fertility factors. In addition, we can use the data for *C. calceolus* only, while *C. ventricosum* and *C. macranthos* are not included in the scales. Habitats from different geographical areas partly overlap (Fig. 3), and completely separate polygons can be observed only for the populations from Altaiskiy Nature Reserve and Shushenskiy Bor National Park. The average representation of indicator taxa in relevés is about 86 % for the Tsatsenkin scales. The driest habitats can be noted in the Baikalo-Lenskiy Nature Reserve. The maximum range of habitat soil moisture is in the Usinsk Basin. Maximum soil richness is noted in both the Baikalo-Lenskiy Nature Reserve and the Usinsk Basin. Polygon appearance confirms the ecological plasticity of *C. calceolus*, *C. macranthos* and *C. ventricosum*, as these species form sympatric populations in most habitats. According to Tsatsenkin et al. (1978), the values of soil moisture fluctuate from 62.4 to 67.2 and those of nutrient content and soil salinity from 8.4 to 10 points (Fig. 4). These values correspond to the observed ecological amplitude of *C. calceolus*.

The density of the tree layer is low (0.3–0.5) in all habitats. The shrub layer cover is 30 % or less, up to its complete absence, and the grass layer is more or less open (with the total cover 5–60 %) in most of the studied phytocoenoses where the *Cypripedium* populations are found. Periodic spring ground fires destroy the undergrowth, resulting in increasing illumination which contributes to the active vegetative growth of *Cypripedium*, as it has also been reported for other regions (Smirnov 1969, Dementieva 1985).

The predominance of *C. macranthos* is characteristic for sympatric populations of the studied species in the central part of their ranges in Siberia (Zolotuhin & Zolotukhina 2015, Plikina et al. 2020). This is in contrast to habitats located westwards from the Urals, predominated by *C. calceolus* (Mamaev et al. 2004, Lesina 2015).

It is also worth mentioning that the sympatric *Cypripedium* populations of the Khamar-Daban Mts. (the Southern Baikal Region) experience significant anthropogenic pressure. About 130 shoots of *C. macranthos*, more than 15 of *C. ventricosum*, and 3 of *C. calceolus*, taken from natural local populations, grow in a flower bed in one of the private farmsteads of the village of Slyudyanka. About 50 plants of *C. macranthos* and *C. calceolus* from this habitat were taken for introduction in Irkutsk (Gorbunov et al. 2012). The population of *C. macranthos* suffered the most serious damage of all the three species. The present-day predominance of *C. calceolus* in the sympatric populations of *Cypripedium* in this area is probably associated with this factor (Zheleznaya 2015).

The nearly complete absence of hybrid plants in the Usinsk Basin, despite the coexistence of *C. calceolus* and *C. macranthos*, may be due to the smaller "overlapping" of their flowering periods compared to other localities.

It is peculiar that the sympatric populations of *C. macranthos* and *C. ventricosum* lacking *C. calceolus*, as well as separate monospecific groups of *C. ventricosum* plants, are found in the Altaiskiy Nature Reserve. Hybrid plants could have been formed as a result of the long distance transport of the *C. calceolus* pollen by pollinators.

In Shushenskiy Bor National Park (2009) and the Baikalo-Lenskiy Nature Reserve (2013), a huge disproportion was observed in the sympatric populations of *Cypripedium*. The number of *C. macranthos* individuals exceeded that of *C. calceolus* more than 7 times, while the number of hybrid (*C. ventricosum*) individuals was almost the same as that of *C. calceolus* (Zheleznaya 2015).

The especially large coenopopulation of all the three *Cypripedium* species, found in 2014 in a sparse pine forest with mixed herbs on the Lena River right bank, was typical by the shoot development among the fallen pine branches, the latter apparently effectively retaining snow in spring. This can promote the growth of *C. calceolus* and *C. ventricosum*, more dependent on moisture compared to *C. macranthos* which can grow on dry limestone slopes. Soil moisture acts as a limiting factor in the driest habitats of the Baikalo-Lenskiy Nature Reserve.

The predominance of adult vegetative shoots is typical for populations of *Cypripedium* species in different parts of their ranges (Tatarenko 1996), since the individuals can produce renewal buds and rhizome is branching already starting from the immature stage (and sometimes even in the juvenile stage). *Cypripedium calceolus* generative plants grow most actively, forming clones with up to 28 shoots (own observations in the garden). A part of shoots of such clones usually does not flower every year. If the rhizome breaks when exposed to animals or rots, vegetative propagation occurs. This may explain the potential immortality of such clones. In any case, a number of researchers have noted an age of more than 100 years for *C. calceolus* (Kull 1988, Brzosko et al. 2002). The number of juvenile plants is very low. Seed reproduction in most of *Cypripedium* populations occurs infrequently. But this is offset by high life expectancy. Since 2014, more adult vegetative shoots were found in sympatric populations of *Cypripedium* in the Baikalo-Lenskiy Nature Reserve, compared to 2013. It can be assumed that this part of reproductive plants passed into a temporarily non-flowering state. It is possible that some reproductive plants of *C. macranthos* also passed into the state of secondary dormancy in 2014. Under unfavorable conditions or a disturbance of the energy balance of an individual caused by abundant flowering and fruiting,

orchids may stay dormant, without above-ground shoots (Vakhrameeva et al. 2008, Kull 2002), which is also called 'secondary dormancy' in Russian literature (Rabotnov 1950). However, separated monospecific populations of *C. macranthos* grew nearby the sympatric populations of *Cypripedium*, and the number of their reproductive shoots was much (sometimes by 10 times) higher.

Cypripedium macranthos had the maximum rates of fruit formation in sympatric populations in Shushenskiy Bor National Park (2011). It successfully competes with *C. calceolus* for pollinators. *C. ventricosum* had the minimal rates, because it can form fruits only being cross-pollinated with one of the parental taxa (Zheleznaya 2015).

CONCLUSION

Cypripedium populations in different geographical areas were found in 16 types of forest phytocoenoses, in both primary and secondary forests. According to the results of the habitat floristic investigation, the habitats are well-separated geographically. Soil moisture and fertility amplitudes are overlapping a bit for different habitats. The studied species are characterized by high ecological plasticity. Canopy density and total cover of the ground layers look similar for all habitats. *Cypripedium macranthos* plants dominated the most of the sympatric populations. In the most of the separated populations, the ontogenetic spectra corresponded to the base spectrum with a predominance of the adult vegetative and reproductive shoots. The population renewal occurs mainly by seed reproduction. But the latter is rarely observed in most of the studied populations, the fact which is compensated by a high life expectancy.

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