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Endemic *Oxytropis* Species of the Section *Orobia* (Fabaceae) from Asian Russia: Genetic Diversity and Demographic Dynamics

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Abstract—Nucleotide polymorphism of the *psbA–trnH*, *trnL–trnF*, and *trnS–trnG* intergenic spacers of chloroplast DNA was analyzed to assess the genetic diversity and demographic dynamics of endemic *Oxytropis* species of the section *Orobia* in two speciation centers, Southern Siberia and northeast Asia. Of the 34 studied populations of endemic species, five were monomorphic. These populations were found only in the species from northeast Asia. Eighteen populations (52.9%) were characterized by high haplotype diversity (*h* from 0.600 to 1.000), and 24 populations (70.6%) were characterized by low nucleotide diversity (π from 0.0001 to 0.0029). The reconstruction of demographic histories of 16 endemic populations showed that only four populations were characterized by bimodal mismatch distribution, corresponding to the demographic equilibrium model, while in all other populations, mismatch distribution was unimodal, corresponding to the population expansion model. Two populations of endemic species, *O. leucantha* subsp. *tschukotcensis* and *O. popoviana* (in Magadan oblast and Buryatia, respectively), with the high level of genetic diversity in a state of population stability were identified. These populations are probably located on the territory of ancient refugia and are of particular interest from the point of view of the species gene pool conservation.

Keywords: Fabaceae, *Oxytropis*, *Orobia*, genetic diversity, demographic history, chloroplast DNA

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INTRODUCTION

The large polymorphic genus *Oxytropis* DC. (Fabaceae) in northeast Asia is characterized by active speciation, in particular, resulting from progressive ecological differentiation [1–3]. In Asian Russia, there are foci of species diversity of the genus, which are also centers of intensive speciation. These regions primary include mountains and mountain–steppe regions of Southern Siberia, as well as coastal and mountain regions of the northern part of the Russian Far East (northeast Asia) [2, 4]. Species diversification in Southern Siberia may be determined by relief heterogeneity, when high ecotope diversity and mosaic environmental conditions of mountain ecosystems lead to the appearance of closely spaced populations of *Oxytropis* species with different ecological demands, and also contribute to the isolation of individual habitats. Active speciation in northeast Asia may be associated with the peculiarities of the existence of *Oxytropis* species in harsh environment (sea coasts, highlands, pioneer stages of volcanic overgrowth), which leads to intensive development of new forms. At the same time, the appearance of new forms often takes place on the basis of polyploidization and introgressive hybridization and is accompanied by rapid adaptive radiation of young species [2, 3]. All these processes are also characteristic of *Oxytropis* species of the *Orobia* Bunge section, the largest and most complex in taxonomic terms.

The section *Orobia* includes about 110 species in Europe, Asia, and America; 58 taxa are distributed in Asian Russia, of which 37 species and subspecies are endemic [3]. Endemic species often exist in the form of small isolated populations and constitute the most vulnerable part of the regional flora. Many endemic species of the section *Orobia* are listed in regional Red Data Books [5–13] as vulnerable, rare or endangered plants, and two species, *O. nivea* Bunge and *O. todomoshiriensis* Miyabe et Miyake, are listed in the Red Data Book of the Russian Federation [14] (Table 1).

In addition, some widespread *Oxytropis* species of the section *Orobia* are actively eliminated due to their ornamental, medicinal [15–17] and fodder [18, 19] importance. Obviously, the population conservation and restoration of their sizes is needed not only for vulnerable, rare, and endangered endemics, but also for widespread species. One of the necessary conditions for the plant diversity conservation and maintenance is the study of the genetic processes in natural populations. These studies can provide a fundamental basis for the development of plant diversity conservation measures (for example, introducing rare and endangered species into culture), as well as the development of alternative sources of medicinal raw materials, and the reintroduction of these species into natural ecosystems.

In previous studies, endemic *Oxytropis* species from Baikal Siberia [20] and a number of species of the section *Orobia* were analyzed [21–24]. Nucleotide polymorphism was analyzed using the *psbA–trnH*, *trnL–trnF*, and *trnS–trnG* intergenic spacers of chloroplast DNA (cpDNA), which were found to be efficient for the assessment of genetic resources, population demographic history, and reconstruction of phylogenetic relationships. In the present study, large additional material for 32 endemic species and subspecies of the section *Orobia* (according to [3]), including *O. sylvatica*, which is listed as an endemic of Northern Asia in the Red Books of the Irkutsk oblast [8] and Zabaykalski krai [10] was examined.

The objective of this study was to analyze the genetic diversity and demographic dynamics of endemic *Oxytropis* species of the section *Orobia* from Asian Russia based on sequence variation of the cpDNA intergenic spacers *psbA–trnH* + *trnL–trnF* + *trnS–trnG*.

MATERIALS AND METHODS

Plant material used in the study consisted of 617 accessions from 112 natural locations of 42 species and subspecies of the genus *Oxytropis*, section *Orobia* (Table 1). The names of taxa and sections are given according to L.I. Malyshev [3], with the exception of *O. ruthenica* Vass. [25]. The storage locations of voucher accessions are listed in Table 1. The total range of the section *Orobia* in Asian Russia (Fig. 1) is given according to the data of D.V. Sandanov et al. [26], the ranges of the studied species of the section *Orobia* are given in [27]. Most endemic species are characterized by limited distribution range, which is associated with their narrow ecological confinement, including substrate specificity, requirements for insolation, moisture, etc. More than half of the species (18 out of 32) are narrow-local endemics, like *O. calcareorum*, *O. hidakamontana*, *O. kunashiriensis*, and *O. todomoshiriensis*. The last two species are found only in one or two locations. A number of endemic species have disjunctive ranges of varying size. For example, extensive ranges of *O. adamsiana*, *O. evenorum*, and *O. ochotensis* and small ranges of *O. arctica* subsp. *taimyrensis*, *O. campanulata*, *O. candicans*, and *O. tichomirovii*. For comparative analysis, the study included populations of 10 widespread species of the section *Orobia* (Table 1) collected during the study, the ranges of which extend beyond the study area. The sizes of the ranges of these species also vary from the widespread *O. sajanensis*, the range of which is limited to Eastern Siberia and Northern Mongolia, to the widespread *O. strobilacea*, the range of which covers Northeastern Kazakhstan, Southern Siberia, the Far East, Northern Mongolia, and the Chinese Altai. The northern limit of the range of this species is about 56° N.

The methods of DNA extraction, amplification, and sequencing of the *psbA–trnH*, *trnL–trnF*, and *trnS–trnG* intergenic spacers are described in our previous study [28]. Individual preparations of total DNA were extracted from plant leaves using CTAB buffer according to the method [29] with some modifications [30]. Amplification of *psbA–trnH, trnL–trnF* and *trnS–trnG* was performed using universal primers and recommended reaction conditions [31, 32]. Nucleotide sequences of forward and reverse chains were determined on an ABI 3500 genetic analyzer (Applied Biosystems, Unites States), edited using the Staden Package v. 1.5 software package [33], then aligned in the SeaView v. 4.7 software program [34], and combined in DnaSP v. 5.0 software [35]. The matrix of combined sequences of three cpDNA regions was used to calculate the number of haplotypes, haplotype (h) and nucleotide (π) diversity (for populations with five or more accessions), as well as the population stability indices, i.e., Tajima's D [36] and Fu's F_s [37] tests, and to analyze the mismatch distribution in the Arlequin v. 3.5 [38] and DnaSP [35] software programs.

Haplotype diversity was considered low at the values from 0.100 to 0.359; medium, at the values from 0.360 to 0.599; and high, at the values of 0.600 to 1.000. Nucleotide diversity was considered low at the values from 0.0001 to 0.0029; medium, at the values of 0.0030 to 0.0054; and high, at the values of 0.0055 to 0.0080.

The experiments were carried out using equipment from the Joint-Use Center "Biotechnology and Genetic Engineering," Federal Scientific Center of Biodiversity, Far Eastern Branch, Russian Academy of Sciences.

RESULTS

Nucleotide sequences of each of the *psbA–trnH*, *trnL–trnF*, and *trnS–trnG* regions of cpDNA were obtained for 253 new *Oxytropis* accessions of the section *Orobia*. The length of the combined matrix after alignment constituted 2465 sites, of which 99 had gaps in the alignment or missing data, 2323 were monomorphic, and 43 were variable. Among the latter, 33 nucleotide substitutions were parsimony informative

Table 1. The studied populations of 42 *Oxytropis* species and subspecies of the section *Orobia*, growing location, sample size, population codes and haplotypes

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
Endemic species				
O. adamsiana (Trautv.) Jurtzev, 2*n* = 32, 48 [3]				
1 Central Taimyr Peninsula, Byrranga Mountains and Foothills, Ledyanaya Bay, Lake Taimyr (1) MW*	74.48824°, 99.6955°	ADAM1	U37	[23]
2. Southwestern Taimyr, Putorana Plateau, vicinity of the Lake Ayan (3) MW*	68.99894°, 94.49041°	ADAM2	U37	[23]
3. Southeastern Taimyr, Fomich River. Northern bank of Besstochnoe Lake (1) MW*	71.67283°, 108.30425°	ADAM3	U38	[23]
4. Southeastern Taimyr, Kotuy River vicinity of the mouth of Medvezhya River (1) MHA*	71.59456°, 102.66325°	ADAM4	U39 (=H11)	[23], ([55])
5. Buryatia, vicinity of the settlement of Uakit, left bank of the Uakit River (10) NSK*, UUDE*	55.56461°, 113.60958°	ADAM5	U40–U47	[23]
O. ajanensis subsp. *semiglobosa*** (Jurtzev) N.S. Pavlova, 2*n* = 16 [3]				
1. Central Chukotka, right bank of the Kuvet River, Volchok Stream (1) LE*	68.76065°, 177.98252°	AJAN1	H35	[55]
2. Magadan oblast, vicinity of the Atargan Spit (9) MAG*	59.54362°, 151.50457°	**AJAN2**	**B1**	**p/s**
*O. ammophila*** Turcz., 2*n* = 16 [56]				
1. Krasnoyarsk krai, Krasnoyarsk, Akademgorodok (1)	55.98333°, 92.74406°	AMM	H14	[55]
O. arctica subsp. *taimyrensis* Jurtzev (=*O. karga* Saposhn. ex Polozh.), 2*n* = 64 [3]				
1. Southeastern Taimyr, north of the Anabar Plateau, Eriechka River (1) MW*	71.22725°, 103.284453°	**ATAIM1**	**B2**	**p/s**
2. Eastern Taimyr, vicinity of the confluence of Bolshaya Lesnaya Rassokha and Novaya rivers (1) MW*	72.62114°, 101.28875°	**ATAIM2**	**B3**	
3. Southwestern Taimyr, Putorana Plateau, Ayan Lake in the mouth of Amnundakta River (1) MW*	69.06297°, 94.16686°	**ATAIM3**	**B4**	
4. Southwestern Taimyr, Putorana Plateau, vicinity of Ayan Lake, canyon of Gulemi River (1) MW*	68.95331°, 94.13617°	**ATAIM4**	**B5**	
*O. calcareorum*** N.S. Pavlova, 2*n* = 32 [57]				
1. Sakhalin Island, south of the East Sakhalin Ridge, Vaida (9) VLA*	49.88538°, 143.45667°	**CAL**	**B6** (=H16), **B7–B9**	**p/s** ([55])
O. campanulata Vass., 2*n* = 32, 32 + B [3], 2*n* = 16 [56]				
1. Krasnoyarsk krai, vicinity of the settlement Zamyatino (1) KRAS*	56.19333°, 92.85365°	CAM1	H17	[55]
2. Altai, vicinity of Barnaul (9) VGBI*	53.26053°, 83.68011°	**CAM2**	**B10–B17**	**p/s**
*O. candicans*** (Pall.) DC., 2*n* = 16 [3]				
1. Krasnoyarsk krai, vicinity of the settlement of Pogorelka (1) KRAS*	56.34971°, 92.98437°	CAN	H20	[55]
*O. czekanowskii*** Jurtzev, 2*n*, no data				
1. Southeastern Taimyr, Anabar Plateau, Afanasyevskie lakes (1) MHA*, MW*	71.62900°, 106.34550°	CZEK1	H21	[55]

Table 1. (Contd.)

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
2. Southeastern Taimyr, Fomich River at the mouth of the Talygyr-Yuryakh River (1) MW*	71.67456°, 108.37317°	**CZEK2**	**B2**	**p/s**
3. Southeastern Taimyr, Anabar Plateau, Eriechka River (1) MW*	71.28881°, 103.23794°	**CZEK3**	**B18**	
4. Southwestern Taimyr, Putorana Plateau, vicinity of Ayan Lake (2) MW*	69.06089°, 94.18775°	**CZEK4**	**B5, B19**	
*O. darpirensis*** Jurtzev et Khokhr., 2*n*, no data				
1. Republic of Sakha (Yakutia), vicinity of Lake Darpir near the mouth of the Belyak stream (8) MAG*	64.18142°, 148.04129°	**DAR1**	**B20**	**p/s**
2. Magadan oblast, Omulevka River basin, mouth of the Harkindya River (8) MAG*	64.29319°, 148.59421°	**DAR2**	**B20**	
3. Magadan oblast, Uochat River valley (8) MAG*	63.89886°, 148.43036°	**DAR3**	**B20, B21**	
4. Magadan oblast, Upper course of Taskan River, Veselyi stream (1) MAG*	63.55620°, 149.39584°	**DAR4**	**B21**	
O. erecta Kom., 2*n* = 48 [3]				
1. Kamchatka krai, Avacha Bay (16) MW*	52.98920°, 158.84728°	EKAZ	H16, H17, H18	[22]
2. Kamchatka krai, Sopka Ploskaya volcano (1) MW*	56.05140°, 160.28545°	EKAP	H19	[22]
3. Kamchatka krai, Avachinskaya Sopka, vicinity of Petropavlovsk-Kamchatsky (1) MW*	53.21607°, 158.66132°	EKAA	H17	[22]
4. Kamchatka krai, Lake Tolmacheva (1) MW*	52.61761°, 157.71090°	EKAT	H20	[22]
O. evenorum Jurtzev et A. Khokhr., 2*n* = 48, 96 [3], 2*n* = 32 [58]				
1. Kamchatka krai, vicinity of the settlement of Esso, Gargachan Pass (3)	55.87080°, 158.66225°	KAM	H7	[21]
2. Magadan oblast, vicinity of Magadan, upper course of the Medvezhka River (3)	59.70552°, 150.68691°	MEDV	H8, H9	[21]
3. Magadan oblast, Nedorazumeniya Island, coast of the Sea of Okhotsk (1)	59.58750°, 150.40515°	EVE	H8	[21]
4. Magadan oblast, upper course of the Ola River (11) UUH*	60.62826°, 151.28889°	OLA	H10–H13	[21]
5. Magadan oblast, Olskoe Plateau (13) UUH*	60.62886°, 151.25697°	OPL	H13–H16	[21]
6. Magadan oblast, Atargan Cape (8) UUH*	59.53871°, 151.50345°	ATA	H15, H17–H20	[21]
7. Magadan oblast, Armansky Pass (10) UUH*	59.70555°, 150.68643°	ARM	H8, H21	[21]
O. hidakamontana Miyabe et Tatew., 2*n* = 16 [3], 2*n* = 64 [57]				
1. Kuril Islands, Shikotan Island, Shikotan (2)	43.86958°, 146.85635°	HID	H24	[55]
O. ircutensis M. Pop., 2*n* = 32 [3]				
1. Buryatia, vicinity of the settlement of Arshan, bank of the Kyngarga River (9) UUH*	51.91568°, 102.42701°	**IRCUT**	**B22–B25**	**p/s**
*O. itoana*** Tatew. (=*O. rishiriensis* Matsum. = *O. rishiriensis* Matsum. subsp. *itoana* (Tatew.) Worosch.), 2*n*, no data				
1. Kuril Islands, Iturup Island, Osennyaya Bay (1) MHA*	45.10248°, 147.697931°	ITO	H32	[55]
O. kunashiriensis Kitam., 2*n*, no data				
1. Kuril Islands, Kunashir Island, Cape Lovtsova (2)	44.451820°, 146.569906°	KUN	H39	[22]

Table 1. (Contd.)

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
O. kusnetzovii Kryl. et Steinb., 2*n* = 32, 48 [3]				
1. Khakassia, the settlement of Priiskovy, Verka River (1) KRAS*	54.63820°, 88.72302°	KUSN	H26	[55]
O. leucantha subsp. *subarctica* Jurtzev, 2*n* = 48, 96 [3]				
1. Southeastern Taimyr, vicinity of the settlement of Khatanga (1) MW*	71.96753°, 102.43335°	**LSUBAR**	**B26**	**p/s**
O. leucantha subsp. *tschukotcensis* Jurtzev, 2*n* = 48, 64, 96 [3]				
1. Chukotka, Rudnaya Sopka, Sredniy Penvelveem River (7) MAG*	66.85869°, 168.62474°	**LEU1**	**B27–B32**	**p/s**
2. Magadan oblast, vicinity of Lake Urultun (11)	63.80838°, 148.23867°	**LEU2**	**B33–B39**	
3. Magadan oblast, vicinity of the settlement of Burkandia and Lake Malyk, Missurio Stream (12) MAG*	63.46700°, 147.80216°	**LEU3**	**B40–B43**	
4. Magadan oblast, vicinity of Lake Malyk (11) MAG*	63.50987°, 147.83722°	**LEU4**	**B35, B36, B43–B50**	
5. Chukotka, interfluve of the Rytgylveem and Spokoynaya rivers (1) MAG*	62.81164°, 175.43947°	**LEU5**	**B51**	
6. Chukotka, Velikaya River, headwaters of Burny Stream (1) MAG*	63.40874°, 173.91426°	**LEU6**	**B51**	
O. litoralis Kom., 2*n*, no data				
1. Kamchatka krai, northeastern part of the Kamchatka Peninsula (1) VLA*	56.183024°, 162.685323°	LKAM	H10	[22]
2. Kamchatka krai, vicinity of Krutoberegovo, Lake Nerpichye (1) VLA*	56.329578°, 162.752581°	LKAN	H10	[22]
*O. nivea**** Bunge, 2*n*, no data				
1. Altai, Chikhachev Ridge, Lake Dlynnoe (1) NSK*	50.22603°, 89.27478°	**NIV**	**B52**	**p/s**
O. ochotensis Bunge, 2*n* = 64 [3]				
1. Kamchatka krai, Klyuchevskaya Sopka volcano (10)	56.03389°, 160.18849°	OKAK	H1–H3	[22]
2. Kamchatka krai, Sopka Ploskaya volcano (14) VLA*	55.95479°, 160.40705°	OKAP	H1, H2	[22]
3. Kamchatka krai, Avachinsky volcano (14) VLA*	53.20745°, 158.79925°	OKAA	H4–H7	[22]
4. Kamchatka krai, vicinity of Ust-Kamchatsk, slope of Uvalnaya Mountain (1) VLA*	56.24313°, 162.79575°	OKAU	H8	[22]
5. Kamchatka krai, middle course of Raduga River (1) VLA*	56.65913°, 161.89511°	OKAR	H9	[22]
6. Kamchatka krai, mountains of Kamchatka Cape, headwaters of River Uglovaya (1) VLA*	56.16866°, 162.84108°	OKAM	H10	[22]
7. Magadan oblast, vicinity of the settlement of Orotuk (10) MAG*	62.16069°, 148.82526°	OMAO	H11	[22]
8. Magadan oblast, vicinity of the settlement of Burkandya (3) MAG*	63.41688°, 147.64938°	OMAB	H12, H13	[22]
9. Magadan oblast, vicinity of the settlement of Shturmovoy (1) MAG*	62.74906°, 149.87879°	OMAS	H14	[22]
10. Magadan oblast, vicinity of the settlement of Madaun, Lebedinaya Mountain (1) MAG*	60.62673°, 150.95026°	OMAM	H15	[22]

Table 1. (Contd.)

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
O. popoviana** Peschkova, 2_n_ = 16 [59], 2_n_ = 32 [60]				
1. Buryatia, vicinity of the settlement of Baraty (9) UUH*	51.28442°, 106.35136°	**POP1**	**B53–B56**	**p/s**
2. Buryatia, vicinity of the settlement of Yagodnoe (8) UUH*	51.37951°, 106.47345°	**POP2**	**B53, B57**	
O. retusa** Matsum., 2_n_ = 16 [3]				
1. Kuril Islands, Paramushir Island, Shelekhov Bay (2)	50.36799°, 155.63203°	RET1	H30, H31	[55]
2. Kuril Islands, Matua Island (2)	48.08200°, 153.25402°	**RET2**	**B58**	**p/s**
O. ruthenica Vass., 2_n_ = 16 [3]				
1. Primorsky krai, Russky Island, Cape Tobizina (17) VBGI*	42.94547°, 131.87088°	RRUT	H21	[22]
2. Primorsky krai, Russky Island, Cape Vyatlina (17) VLA*	42.97027°, 131.90563°	RRUV	H21–H23	[22]
3. Primorsky krai, Popov Island, Pogranichnaya Bay (14) VBGI*	42.94917°, 131.73245°	RPOP	H23, H24	[22]
4. Primorsky krai, Putyatin Island, western coast (19) VBGI*	42.85023°, 132.43753°	RPUZ	H25–H29	[22]
5. Primorsky krai, Putyatin Island, eastern coast (13) VBGI*	42.87255°, 132.41589°	RPUV	H27, H30	[22]
6. Primorsky krai, vicinity of the settlement of Amgu (6) VBGI*	45.84587°, 137.65308°	RAMG	H31, H32	[22]
7. Primorsky krai, vicinity of the settlement of Wrangel, Cape Kamensky (13)	42.76308°, 133.05125°	RVRA	H32–H38	[22]
O. sachalinensis** Miyabe et Tatew., 2_n_ = 16 [3]				
1. Sakhalin Island, Schmidt Peninsula, Taliki River (1)	54.27862°, 142.80762°	SACH	H34	[55]
O. sordida subsp. _arctolenensis_ Jurtzev, 2_n_, no data				
1. Southeastern Taimyr, Anabar Plateau, lower course of Eriechka River (1) MW*	71.28831°, 103.23975°	**SARCT**	**B59**	**p/s**
O. sordida subsp. _schamurinii_ Jurtzev, 2_n_ = 96 [3]				
1. Chukotka, Wrangel Island, Somnitelnaya Bay (2) MAG*	70.97850°, 179.58535°	SSCHA	H22, H23	[21]
O. suprajenissejensis** Kuvajev et Sonnikova, 2_n_, no data				
1. Krasnoyarsk krai, Western Sayan, Sayano-Shushensky Nature Reserve (1) KRAS*	52.04916°, 91.96597°	SUPR1	H42	[55]
2. Krasnoyarsk krai, Sayan Reservoir valley (1) KRAS*	52.55235°, 91.71194°	SUPR2	H42	[55]
O. sylvatica** (Pall.) DC., 2_n_ = 16, 32 [3]				
1. Buryatia, vicinity of the settlement of Udinsk (12) UUH*	52.117079°, 109.133596°	**SYLVAT**	**B60–B62** (=S1–S3), **B63–B65**	**p/s** ([20])
O. tichomirovii** Jurtzev, 2_n_ = 16 [3]				
1. Eastern Taimyr, Tarelka Mountain, upper course of Nizhnyaya Zhdanikha River (1) MW*	71.93409°, 103.95653°	**TICH**	**B66**	**p/s**
O. todomoshiriensis*** Miyabe et Miyake, 2_n_ > 64 [3]				
1. Southern Sakhalin, Moneron Island (1) LE*	46.24855°, 141.25276°	TODOM	H43	[55]
O. vassilczenkoi Jurtzev, 2_n_ = 32 [3]				

Table 1. (Contd.)

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
1. Magadan oblast, vicinity of the settlement of Tal-Yuryakh, Arkagala River valley (14) MAG*	65.096498°, 160.104725°	VAS1	U48–U52	[23]
2. Magadan oblast, Pravye Imlyaki River valley (1) MAG*	65.096498°, 160.104725°	VAS2	U51 (=H46)	[23], ([55])
3. Chukotka, floodplain of the Yarkoveem River (9) MAG*	66.93205°, 167.00095°	VAS3	U51, U53–U57	[23]
4. Kamchatka krai (mainland), Vetveisky Range, Seinav Mountain (13) VLA*	61.00551°, 166.04596°	VAS4	U58–U65	[23]
Widespread species				
O. alpina Bunge, 2*n* = 16, 32 [3]				
1. Altai, Tarkhata River valley (1) MHA*	49.77161°, 88.44811°	ALP1	H12	[55]
2. Altai, Ukok Plateau, right bank of Zhumaly River (7) NSK*	50.29831°, 96.41817°	**ALP2**	**B67–B70**	**p/s**
O. altaica (Pall.) Pers., 2*n* = 16 [3]				
1. Tuva, Academician Obruchev Range, upper course of Uluch-O River (1) KRAS*	52.27694°, 94.72392°	**ALT1**	**B71**	**p/s**
2. Altai, Chikhacheva Ridge, Yarly-Amry River (2) MW*	50.33603°, 87.75967°	**ALT2**	**B72**	
O. ambigua (Pall.) DC., 2*n* = 32 [3]				
1. Altai, North Chuisky Ridge, Aktru River valley (1) MHA*	50.07566°, 87.76436°	AMB	H13	[55]
O. argentata (Pall.) Pers., 2*n* = 16 [3]				
1. Altai Mountains, vicinity of the settlement of Balykcha, Chulyshman River valley (1) MHA*	50.46097°, 89.80448°	ARG	H15	[55]
O. maydelliana Trautv., 2*n* = 96 [3]				
1. Kamchatka krai (mainland), lower course of Penzhina River (11) VLA*	62.52045°, 166.03990°	**MAYD1**	**B73–B76**	**p/s**
2. Kamchatka krai (mainland), vicinity of Manil, Kamenny Ridge (11) VLA*	62.61783°, 165.43117°	**MAYD2**	**B77, B78**	
3. Chukotka, Rudnaya Mountain, Sredniy Penvelveem River (6) MAG*	67.36339°, 169.45861°	**MAYD3**	**B79, B80**	
4. Chukotka, vicinity of Lake Tytyl (northern part) (8) MAG*	67.38228°, 169.45964°	**MAYD4**	**B79, B81**	
5. Chukotka, southern bank of Lake Tytyl (8) MAG*	67.28477°, 169.32884°	**MAYD5**	**B79**	
6. Chukotka, vicinity of Anadyr airport (the settlement of Ugolnye Kopi) (10) MAG*	64.69954°, 177.78900°	**MAYD6**	**B82**	
7. Chukotka, left bank of Kurupka River (5) MAG*	64.66430°, 174.20883°	**MAYD7**	**B83**	
8. Chukotka, the pass between Getlyanen and Marich rivers (7) MAG*	65.08189°, 172.68447°	**MAYD8**	**B83, B84**	
9. Eastern part of the Chukotka Peninsula, Lake Koolen (1) LE*	65.95014°, 171.12440°	MAYD9	H27	[55]
O. recognita Bunge, 2*n* = 32 [3]				
1. Altai, left bank of Dzhazator River (10) NSK*	49.63292°, 87.87214°	**RECOG1**	**B85–B89**	**p/s**
2. Altai, Ukok Plateau (8) NSK*	49.49742°, 88.13044°	**RECOG2**	**B87, B90–B96**	
O. sajanensis Jurtzev, 2*n*, no data				

Table 1. (Contd.)

Species, chromosome number [source], growing location (number of accessions)	Coordinates N, E	Population code	Haplotype	Source
1. Buryatia, vicinity of the settlement of Mondy (9) UUH*	51.68250°, 100.93895°	**SAJAN**	**B23, B25, B97–B99**	**p/s**
O. sordida (Willd.) Pers., $2n = 48, 64$ [3]				
1. Buryatia, vicinity of the settlement of Ina (8) UUH*	53.73205°, 110.24701°	SORD1	H1–H5	[21]
2. Southeastern Taimyr, middle course of Poligai River (1) MW*	72.48247°, 109.72975°	**SORD2**	**B100**	**p/s**
3. Southeastern Taimyr, Anabar Plateau, mouth of Kotuikan River (1) MW*	70.57503°, 103.55227°	**SORD3**	**B101**	
O. strobilacea Bunge, $2n = 16, 32, 48, 64$ [3]				
1. Buryatia, vicinity of the settlement of Zaigraevo (5) UUH*	51.87514°, 108.24616°	STR1	U1–U3	[23]
2. Buryatia, vicinity of the settlement of Komsomolskoe (10) UUH*	52.47898°, 111.08677°	STR2	U1–U7	[23]
3. Buryatia, vicinity of the settlement of Maisk (15) UUH*	54.61287°, 110.77431°	STR3	U8–U18	[23]
4. Buryatia, Dzherginsky State Nature Reserve, Ukshaki tract (5) UUH*	55.20353°, 111.44875°	STR4	U19–U23	[23]
5. Buryatia, vicinity of the settlement of Tory (6) UUH*	51.76222°, 102.95333°	STR5	U24–U26	[23]
6. Buryatia, vicinity of the settlement of Mondy, bank of Aerkhan River (3) UUH*	51.69750°, 100.86746°	STR6	U27–U29	[23]
7. Buryatia, vicinity of the settlement of Zun-Murino (11) UUH*	51.74499°, 102.86646°	STR7	U26, U27, U30–U36	[23]
O. sulphurea (Fisch. ex DC.) Ledeb., $2n = 32$ [60]				
1. Kazakhstan, Rassypnoy Belok Ridge (1) NSK*	50.16142°, 83.78697°	**SULPH**	**B102**	**p/s**

The populations analyzed in the present study (p/s) are shown in bold. * Herbarium acronym: KRAS, Herbarium of the Krasnoyarsk State Pedagogical University, Krasnoyarsk; LE, Herbarium of Higher Plants of the Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg; MAG, Herbarium of the Institute of Biological Problems of the North, Far Eastern Branch, Russian Academy of Sciences, Magadan; MHA, Herbarium of the Main Botanical Garden, Russian Academy of Sciences, Moscow; MW, Herbarium of the Moscow State University, Moscow; NS, Herbarium named after I.M. Krasnoborov, Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, Novosibirsk; NSK, Herbarium named after M.G. Popov, Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences, Novosibirsk; UUDE, Scientific Herbarium of the Buryat State University, Ulan-Ude; UUH, Herbarium of the Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude; VBGI, Herbarium of the Botanical Garden-Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok; VLA, Bioresource collection of the Federal Scientific Center of Biodiversity, Far Eastern Branch, Russian Academy of Sciences (registration number 2797657), Vladivostok; ** the species is listed in regional Red Data Books; *** the species is listed in the Red Data Book of the Russian Federation.

and 10 were single. Nucleotide substitutions, indel variations, and the length of mononucleotide (poly-T and poly-A motifs) and dinucleotide (AT motif) repeats revealed 102 haplotypes (B1–B102, Table 1). The haplotype sequences were deposited in the international GenBank database (http://www.ncbi.nlm.nih.gov) under the accession numbers PV138255–PV138265 and PV165627–PV165717 (*psbA–trnH*); PV185528–PV185629 (*trnL–trnF*); PV216598–PV216699 (*trnS–trnG*).

The genetic variability parameters in 53 populations of 20 species of the section *Orobia* (34 populations of 14 endemic species and 19 populations of six widespread species) are presented in Table 2, where the species are distributed taking into account their growth in one of the centers of active speciation, i.e., northeast Asia and Southern Siberia. Monomorphic populations were found only in the species of northeast Asia, namely, five populations of endemic species and three populations of widespread species *O. maydelliana* (Table 2). Among 34 populations of endemic species of the section *Orobia* from Asian Russia, 18 populations are characterized by high haplotype diversity (52.9%), and 24 populations (70.6%), by low nucleotide diversity. Among 19 populations of widespread species, 11 populations (57.9%) are char-

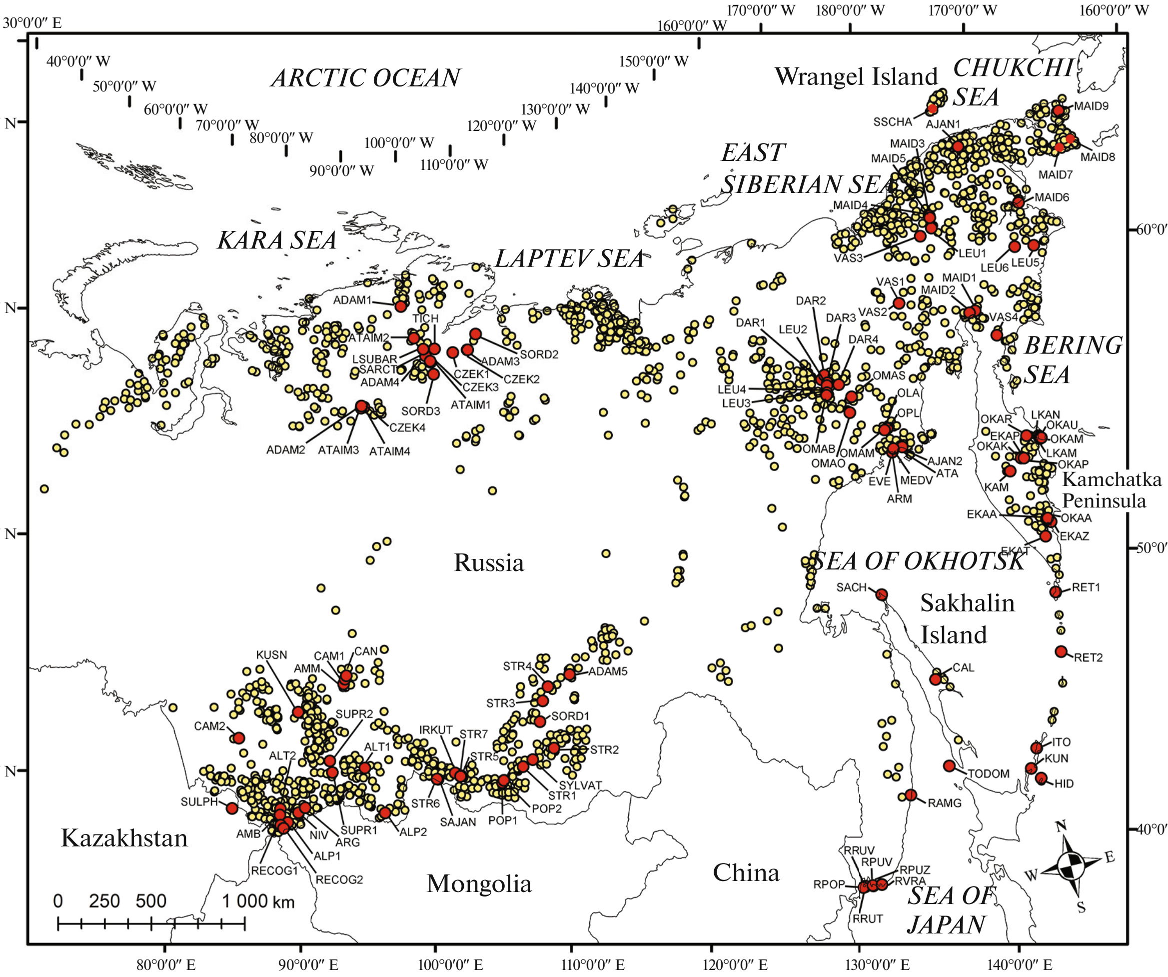

Fig. 1. Studied populations (red dots) of *Oxytropis* species of the *Orobia* section (see Table 1). Yellow dots indicate known populations of the representatives of the section according to D.V. Sandanov et al. [26].

acterized by high haplotype diversity, and 13 populations (68.4%) are characterized by low nucleotide diversity.

High levels of both genetic diversity indices were found in two populations from Southern Siberia, SYLVAT of *O. sylvatica* (endemic) and RECOG1 of *O. recognita* (widespread species); low levels of both indices were found in three populations of two endemic species, RRUV and RPUV of *O. ruthenica* from Russky Island (northeast Asia) and POP2 of *O. popoviana* (Southern Siberia), and two populations of widespread species, MAYD2 and MAYD3 of *O. maydelliana*. The combination of high haplotype diversity and low nucleotide diversity was found in 12 populations (including 11 from northeast Asia) of endemics (35.3%) and in eight populations of widespread species from Southern Siberia (42.1%).

The results of neutrality tests are presented in Table 3. The interpretation of the neutrality test results for zero, negative, and positive values is given according to [36, 37, 39–41]. The Tajima's *D* values of zero were found in 18 populations of endemics and six populations of widespread species *O. maydelliana* from northeast Asia. This means that the observed variability is close to the expected one, and the populations are evolving under conditions of "mutation–drift" equilibrium. Negative test values were determined for 10 populations of endemics (six populations from northeast Asia and four populations from southern Siberia) and eight populations of widespread species, indicating the presence of a large number of rare alleles and population expansion in size after a recent decline. Positive test values were found for six populations of endemics (four populations from northeast Asia and two populations from southern Siberia) and five populations of widespread species. All Tajima's *D* tests were statistically insignificant ($P > 0.05$), except for STR3 population of *O. strobilacea* (Table 3).

Negative values of Fu's F_s test were determined for 14 populations of endemic species (10 populations from northeast Asia and four populations from southern Siberia) and nine populations of widespread spe-

Table 2. Genetic diversity in the populations of *Oxytropis* species of the section *Orobia* from two speciation centers inferred from the cpDNA data

Species	Population code	Genetic diversity	
		haplotype (SD)	nucleotide (SD)
Endemic species			
Northeast Asia			
O. ajanensis subsp. *semiglobosa*	**AJAN2**	**0.000 (0.000)**	**0.0000 (0.0000)**
O. calcareorum	**CAL**	**0.583 (0.183)**	**0.0006 (0.0005)**
O. darpirensis	**DAR1**	**0.000 (0.000)**	**0.0000 (0.0000)**
	DAR2	**0.000 (0.000)**	**0.0000 (0.0000)**
	DAR3	**0.536 (0.123)**	**0.0004 (0.0004)**
O. erecta	EKAZ	0.425 (0.133)	0.0009 (0.0006)
O. evenorum	OLA	0.800 (0.075)	0.0010 (0.0007)
	OPL	0.679 (0.088)	0.0004 (0.0003)
	ATA	0.857 (0.108)	0.0015 (0.0010)
	ARM	0.356 (0.159)	0.0001 (0.0002)
O. leucantha subsp. *tschukotcensis*	**LEU1**	**0.952 (0.095)**	**0.0011 (0.0007)**
	LEU2	**0.891 (0.074)**	**0.0011 (0.0007)**
	LEU3	**0.697 (0.090)**	**0.0012 (0.0008)**
	LEU4	**0.982 (0.046)**	**0.0052 (0.0029)**
O. ochotensis	OKAK	0.378 (0.181)	0.0009 (0.0006)
	OKAP	0.385 (0.132)	0.0006 (0.0005)
	OKAA	0.495 (0.151)	0.0008 (0.0006)
	OMAO	0.000 (0.000)	0.0000 (0.0000)
O. ruthenica	RRUT	0.000 (0.000)	0.0000 (0.0000)
	RRUV	0.228 (0.129)	0.0002 (0.0002)
	RPOP	0.363 (0.130)	0.0002 (0.0002)
	RPUZ	0.637 (0.104)	0.0011 (0.0007)
	RPUV	0.154 (0.126)	0.0004 (0.0003)
	RAMG	0.600 (0.129)	0.0002 (0.0002)
	RVRA	0.872 (0.067)	0.0016 (0.0010)
O. vassilczenkoi	VAS1	0.769 (0.083)	0.0005 (0.0004)
	VAS3	0.917 (0.073)	0.0013 (0.0009)
	VAS4	0.897 (0.067)	0.0017 (0.0010)
Southern Siberia			
O. adamsiana	ADAM5	0.956 (0.059)	0.0047 (0.0027)
O. campanulata	**CAM2**	**0.972 (0.064)**	**0.0048 (0.0027)**
O. ircutensis	**IRCUT**	**0.694 (0.147)**	**0.0003 (0.0003)**
O. popoviana	**POP1**	**0.778 (0.110)**	**0.0030 (0.0018)**
	POP2	**0.250 (0.180)**	**0.0001 (0.0001)**
O. sylvatica	**SYLVAT**	**0.939 (0.048)**	**0.0059 (0.0032)**

Table 2. (Contd.)

Species	Population code	Genetic diversity	
		haplotype (SD)	nucleotide (SD)
Widespread species			
Northeast Asia			
O. maydelliana	**MAYD1**	**0.491 (0.175)**	**0.0004 (0.0003)**
	MAYD2	**0.182 (0.144)**	**0.0001 (0.0001)**
	MAYD3	**0.333 (0.215)**	**0.0002 (0.0002)**
	MAYD4	**0.536 (0.123)**	**0.0004 (0.0004)**
	MAYD5	**0.000 (0.000)**	**0.0000 (0.0000)**
	MAYD6	**0.000 (0.000)**	**0.0000 (0.0000)**
	MAYD7	**0.000 (0.000)**	**0.0000 (0.0000)**
	MAYD8	**0.571 (0.119)**	**0.0002 (0.0002)**
Southern Siberia			
O. alpina	**ALP2**	**0.809 (0.130)**	**0.0009 (0.0007)**
O. recognita	**RECOG1**	**0.822 (0.097)**	**0.0059 (0.0033)**
	RECOG2	**1.000 (0.062)**	**0.0020 (0.0013)**
O. sajanensis	**SAJAN**	**0.806 (0.120)**	**0.0014 (0.0010)**
O. sordida	**SORD**	**0.786 (0.151)**	**0.0008 (0.0006)**
O. strobilacea	STR1	0.800 (0.164)	0.0009 (0.0007)
	STR2	0.867 (0.107)	0.0016 (0.0010)
	STR3	0.952 (0.040)	0.0032 (0.0018)
	STR4	1.000 (0.127)	0.0042 (0.0027)
	STR5	0.600 (0.215)	0.0013 (0.0009)
	STR7	0.964 (0.051)	0.0025 (0.0015)

SD, standard deviation. For population codes and sources, see Table 1. Data on genetic diversity of populations obtained in this study are shown in bold.

cies; positive values were found for 15 populations of endemic species (13 populations from northeast Asia and two populations from southern Siberia) and seven populations of widespread species (Table 3). Only two populations of endemic *O. leucantha* subsp. *tschukotcensis* and *O. ircutensis* (LEU1 and IRCUT, respectively) and one population of widespread species *O. recognita* (RECOG2) showed statistically significant ($P < 0.05$) negative values of Fu's F_s test, indicating a population expansion and an increase in size.

To reconstruct the population demographic histories, mismatch distribution analysis (used as a test for changes in population size) between haplotypes was carried out in 16 populations of endemics (Fig. 2a) and 13 populations of widespread species (Fig. 2b), since there were no nucleotide substitutions in the remaining populations. The bimodal pattern of the observed distributions, corresponding to the model of demographic equilibrium, i.e., long-term population stability (constant population size), was revealed in four populations (LEU4, OKAA, RRUV, POP1) of endemic species and three populations (MAYD4, RECOG1, SAYAN) of widespread species. In all other populations, the curves of the observed mismatch distributions coincided with or were close to the distribution expected in the model of rapid range expansion and were unimodal, indicating a population expansion (Fig. 2). The mismatch distribution patterns in IRCUT and RECOG2 populations were consistent with statistically significantly negative values of Fu's F_s test of neutrality, and in STR3 population, with the statistically significantly negative value of Tajima's D test (Table 3), indicating past expansion events in these populations.

The population expansion of nine populations of endemic species and nine populations of widespread species, the graphs of which showed a unimodal distribution is indirectly supported by negative values of one or both neutrality tests, despite their statistical insignificance (Table 3). The exceptions are three populations (EKAZ, SYLVAT and STR1), for which, despite the unimodal curve, which suggests population

Table 3. Neutrality/demography tests in the populations of *Oxytropis* species of the section *Orobia* populations in two speciation centers inferred from the cpDNA data

Species	Population code	Neutrality tests	
		Tajima's D	Fu's F_s
Endemic species			
Northeast Asia			
O. ajanensis subsp. *semiglobosa*	AJAN2	0.00000*	–
O. calcareorum	CAL	0.00000*	–0.20823*
O. darpirensis	DAR1	0.00000*	–
	DAR2	0.00000*	–
	DAR3	0.00000*	2.08349*
O. erecta	EKAZ	0.64998*	2.97993*
O. evenorum	OLA	–0.10001*	1.31278*
	OPL	–1.14915*	–0.51433*
	ATA	0.00000*	0.10080*
	ARM	0.00000*	0.41670*
O. leucantha subsp. *tschukotcensis*	LEU1	0.00000*	–2.61289**
	LEU2	0.00000*	–1.93713*
	LEU3	0.00000*	1.99626*
	LEU4	0.92078*	–1.63185*
O. ochotensis	OKAK	0.00000*	2.25165*
	OKAP	0.00000*	3.63909*
	OKAA	1.07960*	1.22076*
	OMAO	0.00000*	–
O. ruthenica	RRUT	0.00000*	–
	RRUV	–1.04864*	–0.12611*
	RPOP	0.00000*	0.64281*
	RPUZ	–0.77799*	1.47547*
	RPUV	–1.14915*	2.66362*
	RAMG	1.44510*	0.79518*
	RVRA	0.00000*	–0.39877*
O. vassilczenkoi	VAS1	0.00000*	–1.04897*
	VAS3	0.00000*	–0.99401*
	VAS4	–0.90920*	–1.19946*
Southern Siberia			
O. adamsiana	ADAM5	1.30268*	–0.02226*
O. campanulata	CAM2	–0.58325*	–0.74490*
O. ircutensis	IRCUT	–1.08823*	–1.41744**
O. popoviana	POP1	–1.14944*	3.77552*
	POP2	–1.05482*	–0.18197*
O. sylvatica	SYLVAT	0.15307*	1.69031*

Table 3. (Contd.)

Species	Population code	Neutrality tests	
		Tajima's D	Fu's F_s
Widespread species			
Northeast Asia			
O. maydelliana	MAYD1	0.00000*	–0.62653*
	MAYD2	0.00000*	–0.40988*
	MAYD3	–0.93302*	–0.00275*
	MAYD4	1.44880*	2.08349*
	MAYD5	0.00000*	–
	MAYD6	0.00000*	–
	MAYD7	0.00000*	–
	MAYD8	0.00000*	0.85642*
Southern Siberia			
O. alpina	ALP2	–1.00623*	0.12551*
O. recognita	RECOG1	0.02595*	5.00515*
	RECOG2	–1.05482*	–3.95661**
O. sajanensis	SAJAN	0.19590*	0.38785*
O. sordida	SORD	–1.31009*	–1.35883*
O. strobilacea	STR1	0.24314*	0.80363*
	STR2	–0.65748*	–1.40218*
	STR3	–1.49051**	–1.74962*
	STR4	–1.04849*	–0.31199*
	STR5	–0.93302*	1.81381*
	STR7	1.18560*	–2.19056*

"–," F_S is not calculated if there is only one allele in the sample; * P value >0.05; ** P value <0.05.

expansion, both neutrality tests were positive and statistically insignificant. It seems likely that local partial expansion could have occurred in these populations after some size decline.

DISCUSSION

Comparative analysis of genetic diversity in populations of species of the section *Orobia* in two speciation centers showed (Table 2) that monomorphic populations were found only in northeast Asia, both among endemics and widespread species. Haplotype diversity was high in most Siberian populations and only in half of the populations of northeast Asian endemic species. Nucleotide diversity was low in populations of all northeast Asian species, with the exception of one population of *O. leucantha* subsp. *tschukotcensis*, while for most Siberian endemics, medium and high nucleotide diversity levels were observed. A similar pattern was found in populations of endemic *Oxytropis* species from other sections represented in these two regions (Table 4). In particular, monomorphic populations were found only in northeast Asia, and all populations of this region were characterized by the low level of nucleotide diversity; haplotype diversity was high in only half of the populations of northeast Asian endemics (53.3%), but in most Siberian populations (78.6%). Three populations from southern Siberia (two populations of *O. glandulosa* and one population of *O. peschkovae*) were characterized by medium and high levels of nucleotide diversity.

High values of nucleotide diversity in populations of Southern Siberia (Tables 2, 4) indicate a more ancient age of Siberian species. For instance, in relict species with long evolutionary history, during which mutations accumulated, the high level of nucleotide diversity was revealed [42, 43]. In addition, populations of Siberian species are located relatively close to the center of origin of the section *Orobia*, as well as to the center of origin of the genus *Oxytropis*, situated in

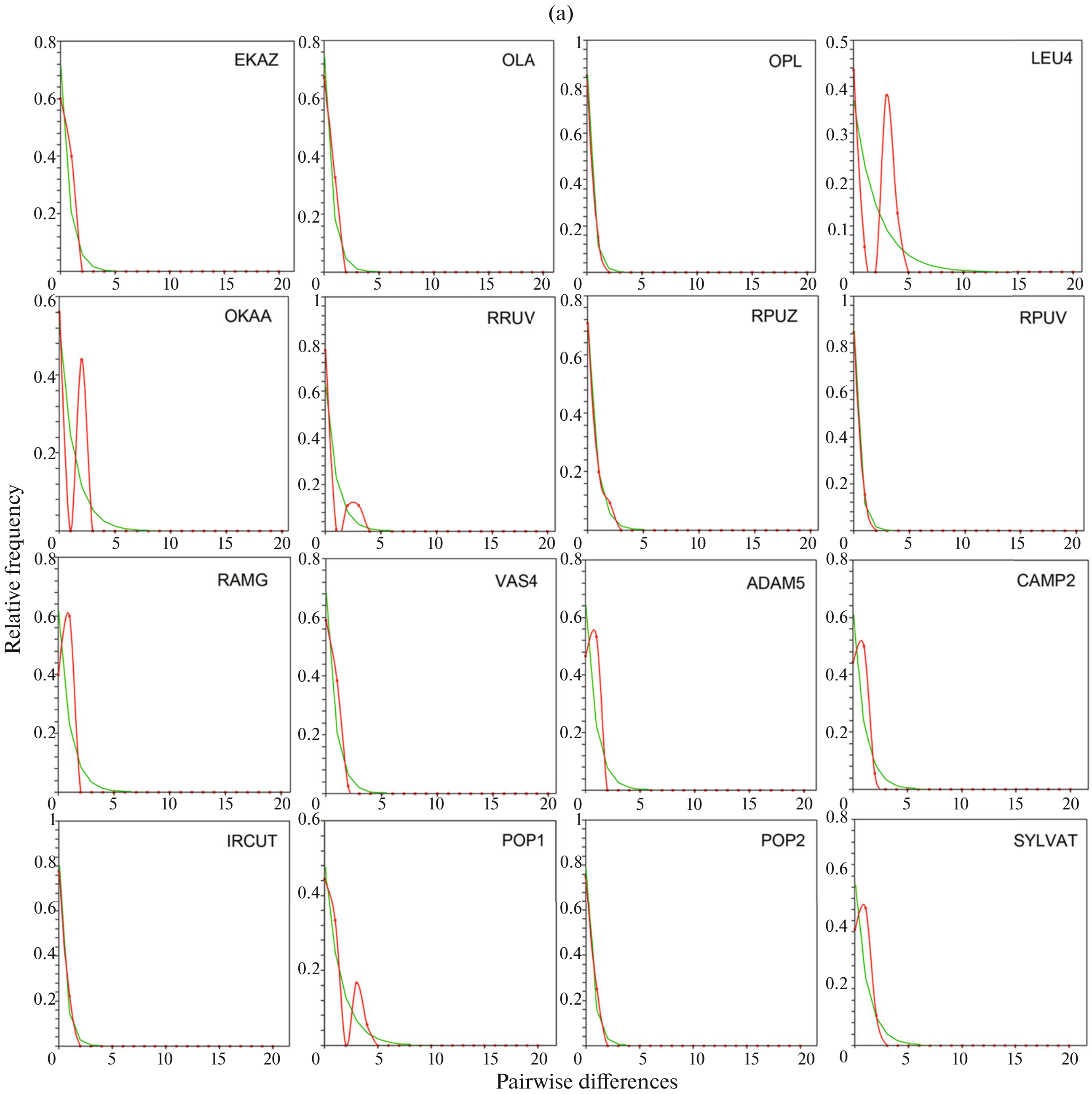

Fig. 2. Mismatch distribution between the haplotypes of cpDNA intergenic spacers in populations of *Oxytropis* species of the *Orobia* section. (a) Endemic species; (b) widespread species. For population codes, see Table 1.

Southern Siberia, the territory of the Altai-Sayan floristic province [4]. At the same time, the south of Siberia is the center where the processes of speciation based on polyploidization and hybridization are actively going on. Among the five examined Siberian endemics, three species (*O. adamsiana*, *O. campanulate*, and *O. ircutensis*) are polyploids, and two species (*O. popoviana* and *O. sylvatica*) have chromosome races with $2n = 16$ and 32 (Table 1). Many *Oxytropis* species of this region, including endemic ones, are characterized by high genetic diversity [24, 44–46] (Table 4). Polyploidization is also characteristic of species from northeast Asia. In general, the data on chromosome numbers are known for 33 taxa out of 42 species and subspecies of the section *Orobia* examined in the present study (Table 1). Among these, only 9 taxa were found to be diploids; and among 24 polyploids, the presence of chromosome races was identified in 11 taxa.

There are data on the genetic variability of *Oxytropis* species growing in the north China, in Inner Mon-

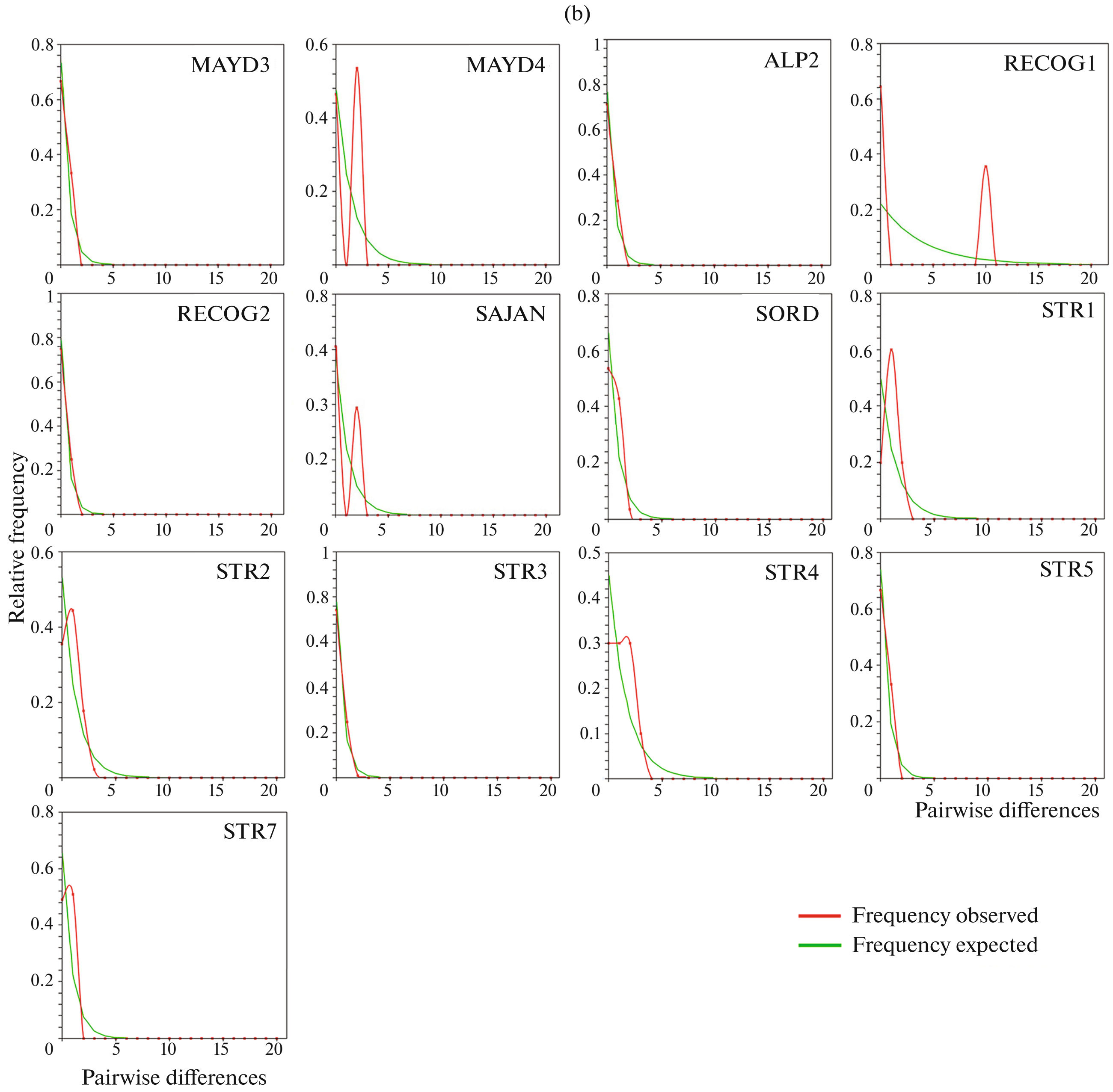

Fig. 2. (Contd.)

golia, on the territory close to the center of origin of the genus *Oxytropis*, obtained on the basis of five intergenic spacers of cpDNA [47]. For instance, in populations of the narrow-local endemic species *O. neimonggolica* C.W. Chang & Y.Z. Zhao, the haplotype diversity varied from 0.607 to 0.679; in *O. diversifolia* E. Peter, from 0.750 to 1.000; in *O. leptophylla* (Pall.) DC., from 0.389 to 0.694, and the level of nucleotide diversity was low in all three species (from 0.00011 to 0.00218) [47]. According to the SLAF-seq (Specific-Locus Amplified Fragment Sequencing) analysis, 17 *Oxytropis* species from Northern China [48], growing to the south of the populations examined in our studies (south of 40° N), were also characterized by the low level of nucleotide diversity (from 0.000057 to 0.000121), compared to the variation range of this index in most populations from the center of origin of the section *Orobia* (0.0013–0.0059 (Table 2)).

Concerning endemic species of the section *Orobia* from northeast Asia (Table 2), it is obvious that the presence of monomorphic populations, the low level of nucleotide diversity in all populations, and the low level of haplotype diversity in half of the populations studied are the result of mutual influence of a number

Table 4. Genetic diversity in populations of endemic *Oxytropis* species from Asian Russia inferred from the cpDNA data

Section, species (number of examined populations), source	Number of populations[1] (of them monomorphic)/ individuals/haplotypes	Diversity[1]	
		haplotype	nucleotide
Northeast Asia (7 species, 15 populations)			
Section *Arctobia* Bunge			
O. exserta Jurtz. (3) [49]	1(0)/7/3	0.524	0.0020
O. kamtschatica Hult. (2) [49]	1(1)/5/1	0.000	0.0000
O. pumilio (Pall.) Ledeb. (4) [49]	1(0)/9/4	0.583	0.0005
Section *Gloeocephala* Bunge			
O. vasskovskyi Jurtz. (5) [61]	4(0)/35/12	0.524; 0.692; 0.822; 1.000	0.0003–0.0008
O. anadyrensis Vass. (4) [50]	2(1)/24/3	0.000; 0.143	0.0000; 0.0001
O. trautvetteri Meinsh. (1) [50]	1(1)/10/1	0.000	0.0000
Section *Verticillares* DC.			
O. chankaensis Jurtz. (5) [62]	5(0)/63/7	0.604–0.758	0.0004–0.0005
Southern Siberia (6 species, 14 populations)			
Section *Polyadena* Bunge			
O. glandulosa Turcz. (4) [44]	4(0)/49/11	0.133; 0.356; 0.703; 0.911	0.0002 0.0006 0.0036 0.0059
Section *Verticillares* DC.			
O. bargusinensis Peschkova (2) [20]	2(0)/30/16	0.762; 0.895	0.0018; 0.0022
O. interposita Sipl. (1) [20]	1(0)/14/5	0.769	0.0015
O. tompudae M. Pop. (1) [20, 46]	1(0)/6/6	0.893	0.0026
Section *Xerobia* Bunge			
O. peschkovae M. Popov (2) [45]	2(0)/20/11	0.345; 0.972	0.0016; 0.0082
O. triphylla (Pall.) Pers. (7) [45]	4(0)/34/21	0.800–1.000	0.0018–0.0025

[1] Genetic diversity data are presented for populations with 5 or more accessions.

of factors, among which the key role is probably played by the evolutionary history of the species on the territory that experienced intensive glaciation in the Pleistocene, as it was shown previously for the *Oxytropis* species of the sections *Arctobia* [49] and *Gloeocephala* [50].

The combination of high haplotype and low nucleotide diversity found in one third of endemic populations (35.3%) and almost half of the populations of widespread species (42.1%) suggests rapid population growth from an ancient population with small effective size [51]. It should be noted that these data are consistent with the results of a study of the demographic histories of five populations of endemic species (OLA and OPL of *O. evenorum*, RRUZ of *O. ruthenica*, VAS4 of *O. vassilczenkoi*, and IRCUT of *O. ircutensis*) and eight populations of widespread species (Table 2), the diagrams of which are unimodal, indicating population expansion (Fig. 2).

Mismatch distribution analysis performed in 29 populations showed (Fig. 2) that seven of these populations were in a state of demographic equilibrium, or population stability. Among the latter, there were populations with the high level of haplotype diversity (LEU4 and POP1 of the endemic species *O. leucantha* subsp. *tschukotcensis* and *O. popoviana*, respectively; RECOG1 and SAYAN of widespread species *O. recognita* and *O. sajanensis*, respectively), as well as with the low level of haplotype diversity (island population RRUV of *O. ruthenica*). Statistically insignificant results from neutrality tests for these populations suggest the absence of the effect of demographic expansion on genetic diversity. Both populations of endemics (LEU4 and POP1) have, in addition to high haplotype (0.982 and 0.778, respectively), an increased level of nucleotide polymorphism (0.0052 and 0.0030, respectively). The analysis showed that this was not associated with the fluctuations in the range size or the population growth, but was rather associated with the population isolation and location on the territory of ancient refugia, in Magadan oblast and Buryatia, for O. *leucantha* subsp. *tschukotcensis* and *O. popoviana*, respectively. It is known that these territories were not covered by continuous ice sheets during the last glacial period, either in Buryatia [52] or in northeast Asia [53]. Therefore, these populations are of particular interest as reserves of genetic variability for the corresponding species.

The demographic histories of the other 22 populations studied (Fig. 2, Table 3) are indicative of past expansion. Most endemic *Oxytropis* species are characterized by narrow ecological confinement to strictly defined environmental conditions. That is why, in the case of endemics, it is more likely to have undergone only demographic expansion, whereas populations of widespread species may have undergone both demographic and spatial expansion with the high level of gene flow between neighboring populations. Statistically significant negative values of Fu's F_s test in two populations of endemic species (LEU1 and IRCUT) and a population of a widespread species (RECOG2) suggest a deviation from neutrality, and the high haplotype diversity detected may be associated with steady population growth.

Similar demographic dynamics pattern was found in most of the studied populations of *O. bargusinensis* Peschk., *O. gracillima* Bunge, *O. lanata* (Pall.) DC., *O. oxyphylla* (Pall.) DC., *O. selengensis* Bunge of the section *Verticillares* from Baikal Siberia and the adjacent territory of Mongolia [20, 54], which were characterized by demographic expansion. Only four out of 14 studied populations of these species were in a state of population stability and were characterized by high genetic diversity indices, which was indicative of their probable location in the isolated refugia, like the above-mentioned LEU1, IRCUT, and RECOG2 populations of the species of the section *Orobia*.

Thus, the study of genetic diversity and demographic histories of populations of endemic *Oxytropis* species of the section *Orobia* from two major speciation centers of Asian Russia (Southern Siberia and northeastern Asia) showed that evolutionary changes at the intraspecific level occurred in both regions. The demographic dynamics of most populations, both of endemic and widespread species, reflect the processes of general expansion. Species from Southern Siberia are characterized by the higher level of genetic diversity compared to northeastern Asia. Two populations of endemic species *O. leucantha* subsp. *tschukotcensis* and *O. popoviana* (in Magadan oblast and Buryatia, respectively) characterized by the high level of genetic diversity and were in the state of population stability were identified. These populations are probably located on the territory of ancient refugia and are of particular interest from the point of view of the species gene pool conservation.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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