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Phylogeography and taxonomic status of the *Formica picea* complex (Hymenoptera: Formicidae)

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Abstract. The black bog ant *Formica picea* complex is widespread from the Atlantic to the Pacific coasts of Eurasia. This complex was earlier believed to consist of one or two species (*F. picea* and *F. candida*). However, molecular analysis suggested that it includes three cryptic species. One is *F. picea* from Europe, another, *F. candida*, is currently known exclusively from Kyrgyzstan, while the third one, temporarily designated here as *Formica* sp., inhabits the easternmost part of Eurasia from China to Kamchatka. It is unknown how *F. picea* and *Formica* sp. are distributed in Siberia and whether their ranges intersect. Here we studied a sample of this complex from Siberia using mtDNA and found that their ranges overlap. The distribution of *Formica* sp. extends from the south of West Siberia, including Altai, to China, and the Russian Far East. No phylogeographic structure was detected, suggesting their recent dispersal from a single source. *F. picea* was found as far as East Siberia, but was relatively rare. While the European and West Siberian populations were genetically closely related, the specimens from Zabaykalsky Krai differed, suggesting a putative East Siberian refugium. We also determined that ecologically *F. picea* inhabits peat bogs in lowland areas and grassy communities above the tree line in the European mountains; in Altai, it is found in mountain steppes, while in Transbaikalia, in waterlogged areas along riverbanks. *Formica* sp. thrives in dry steppes and low riverbanks, but avoids bogs. Thus, *F. picea* and *Formica* sp. differ genetically, and have different distribution ranges, as well as habitat preferences. This supports the opinion that *Formica* sp. should be recognized as a distinct species.

Key words: *Formica picea*; *Formica candida*; cryptic species; Northern Eurasia; Siberia

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Филогеография и таксономический статус видового комплекса *Formica picea* (Hymenoptera: Formicidae)

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Аннотация. Комплекс *Formica picea*, или черный болотный муравей, широко распространен по всему северу Евразии, от Испании и Ирландии до побережья Тихого океана и Тибета, примерно между 35 и 66.5° северной широты. Ранее считалось, что он состоит из одного или двух видов (*F. picea* и *F. candida*). Однако молекулярный анализ показал, что в него входят три криптических вида. Один из них – *F. picea* из Европы, другой – *F. candida*, известный исключительно из Киргизии, а третий, временно обозначенный как *Formica* sp., обитает на востоке Евразии: от Китая до Камчатки. До сих пор было неизвестно, каково распределение *F. picea* и *Formica* sp. в Сибири, пересекаются ли их ареалы. Мы изучили образцы этого комплекса из Сибири с использованием митохондриальной ДНК и обнаружили, что их ареалы перекрываются. Ареал *Formica* sp. охватывает юг Западной Сибири, включая Алтай, на восток – до Тихоокеанского побережья. Филогеографической структуры не обнаружено, что указывает на недавнее расселение из одного источника. Мы нашли мало образцов *F. picea* в Сибири, это свидетельствует, что здесь этот вид встречается редко. Самая восточная находка вида была сделана в Забайкальском крае. *F. picea* обитает на торфяных болотах в пределах равнин и травяных сообществах выше линии леса в европейских горах; на Алтае – в горных степях, а в Забайкалье – на влажных участках у речных берегов. *Formica* sp. предпочитает сухие степи и низкие берега рек, но избегает болот. Таким образом, оказалось, что *F. picea* и *Formica* sp. отличаются генетически, имеют разные ареалы и биотопические предпочтения по местообитаниям. Это свидетельствует в пользу того, что *Formica* sp. можно считать отдельным видом.

Ключевые слова: *Formica picea*; *Formica candida*; виды-двойники; Северная Евразия; Сибирь

Introduction

The *Formica picea* Nylander, 1846 species complex, i. e. black bog ant, is widespread in the Palearctic, from Spain and Ireland to the Pacific coast and Tibet, and between approximately 35 and 66.5° N latitude (Ruzsky, 1905; Pleshanov, 1966; Dlussky, 1967; Dmitrienko, Petrenko, 1976; Kupyanskaya, 1990; Berman et al., 2007; Antonov, Pleshanov, 2008; Radchenko, 2016; Seifert, 2018) (Fig. 1). For a long time, *F. picea* was considered a single species with high geographic variation (Dlussky, 1967). Bolton (1995) proposed that the name *F. candida* Smith, 1878 takes precedence over *F. picea*. Not all specialists adopted this suggestion, leading to confusing parallel usage of both names in the literature.

Seifert (2004) suggested that *F. picea* and *F. candida* are two distinct species, based on their pubescence and certain morphometric parameters. Seifert (2004) also designated a neotype of *F. candida* collected from Kyrgyzstan due to the loss of the original type specimen. However, Zakharov et al. (2019) disagreed with Seifert's conclusions, pointing out the smooth gradient of morphological variation from Europe to the Far East.

There were several molecular studies that included members of the *F. picea*/*F. candida* complex (Goropashnaya, 2003; Goropashnaya et al., 2012; Antonov, Bukin, 2016; Chen, Zhou, 2017; Schär et al., 2018). However, none of these aimed to explore the differences between the two taxa, instead simply using one or the other name. Moreover, some authors used the mitochondrial *cytb* gene, and others, *cox1/COI*, so their results could not be directly compared.

A recent study on the *F. picea* complex showed that it included one more species, in addition to *F. picea* and *F. candida* (Zhigulskaya et al., 2022). While *F. picea* turned out to be restricted to Europe, as well as to one location from Tibet, ants from all east Eurasian locations (lowland China and the Far

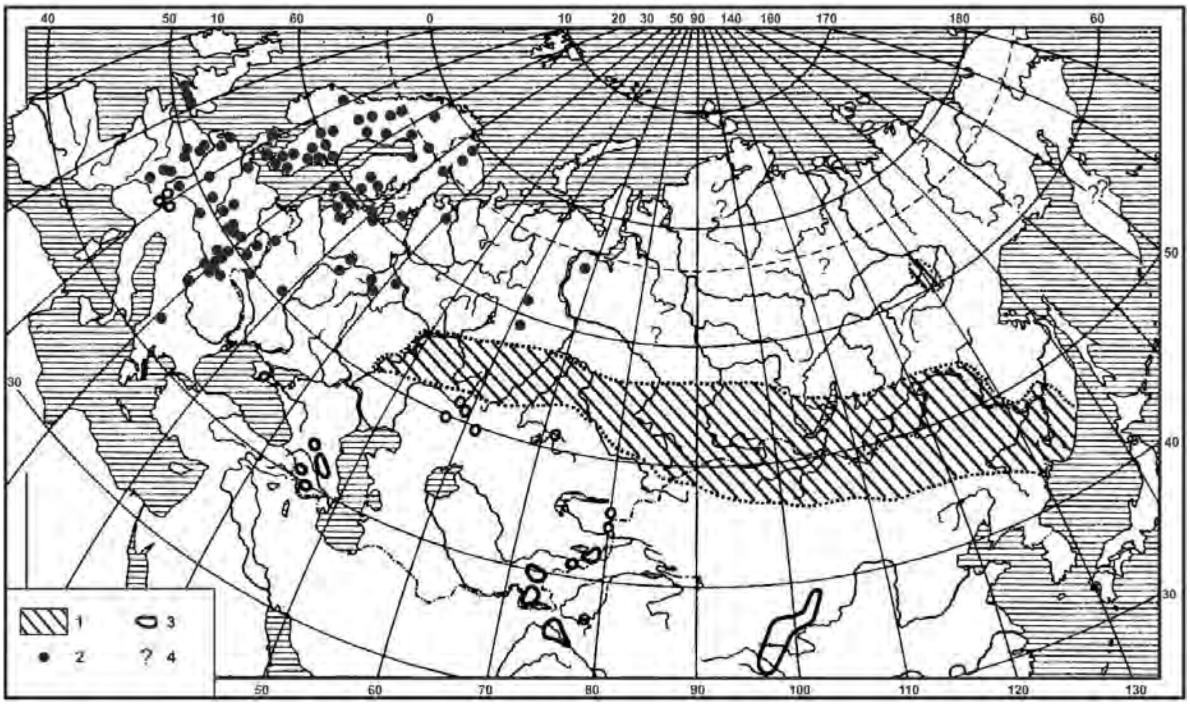

Fig. 1. Geographical distribution and ecology of the *F. picea* complex.

Characteristic habitats: 1 – diverse habitats; 2 – peat bogs; 3 – mountain meadows; 4 – no details provided (scheme from (Dlussky, 1967)).

East of Russia) were highly genetically divergent from other known *Formica* species. Geographic and genetic differences suggest that it should be regarded as a distinct species, although the formal description was not yet performed. Thus, this new taxon is hereafter referred to as *Formica* sp. There seem to be no obvious morphological distinctions for *Formica* sp. that could clearly differentiate it from *F. picea* and *F. candida*, supporting the observations of Zakharov and Dlussky (Zakharov et al., 2019) on high levels of intrapopulation and geographic variation for this complex.

Siberia currently remains a blank spot in this respect: it is unknown how far *F. picea* goes eastwards from the Urals, and how far west can *Formica* sp. be found. In this study we collected an extensive sample from different parts of Siberia in order to determine the ranges of both taxa, as well as to infer phylogeographic patterns. In order to search for putative ecological differences between *F. picea* and *Formica* sp., we also documented habitat preferences, which had been previously well described for European *F. picea* (Dlussky, 1967; Zakharov, 2015; Radchenko, 2016; Seifert, 2018; Zakharov et al., 2019).

Materials and methods

We surveyed a wide range of habitat types, from steppes to bogs, in both lowland and mountainous landscapes of Siberia and the Russian Far East (see the Table, Figs. 2, 3). Ants were collected into 96 % ethanol in a series of 6–10 specimens from nests, as well as from forage plants. The collection material is stored in the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia).

Ants of the *F. picea* complex were taken for genetic analysis from 85 locations (Fig. 2): for 47, obtained by us in this study, for the rest, they were taken from our previous study (Zhigulskaya et al., 2022) and from GenBank.

DNA was extracted from individual worker ants preserved in ethanol using commercial silica columns (BioSilica, Novosibirsk, Russia), following the method outlined in (Shekhovtsov et al., 2020). We amplified a segment of the mitochondrial cytochrome c oxidase subunit 1 (*cox1*) gene with the universal primers LCO1490m (5′-TACTC-AACAA-ATCAC-AAAGA-TATTG-G-3′; modified from (Folmer et al., 1994)) and HCO2198 (5′-TAAAC-TTCAG-GGTGA-CCAAA-AAATC-A-3′) (Folmer et al., 1994). Additionally, we amplified a portion of the cytochrome b (*cytb*) gene using primers Fcbl-F (5′-ACCCT-CACCT-GTAAA-TATTT-CTT-3′) and Fcbl-R (5′-GGAAT-AGATC-GTAAA-ATTGC-AT-3′) (Zhigulskaya et al., 2022). PCR was conducted with the Biomaster HS-Taq PCR Mix (Biolabmix, Novosibirsk, Russia).

The DNA fragments obtained were visualized through agarose gel electrophoresis. Unincorporated primers and nucleotide phosphates were eliminated using shrimp alkaline phosphatase and *Escherichia coli* exonuclease I mixture (New England Biolabs, Ipswich, MA, USA). Sanger sequencing was conducted on a 3130xl DNA Analyzer (Applied Biosystems, Framingham, MA, USA) at the SB RAS Genomics Core Facility (ICBFM SB RAS, Novosibirsk, Russia) using both forward and reverse primers. The resulting sequences were submitted to GenBank with accession numbers PQ807734–PQ807780 (*cox1*) and PQ810811–PQ810857 (*cytb*). Sequences from other researchers were also incorporated into this study (refer to the Table for GenBank accessions). This dataset includes the

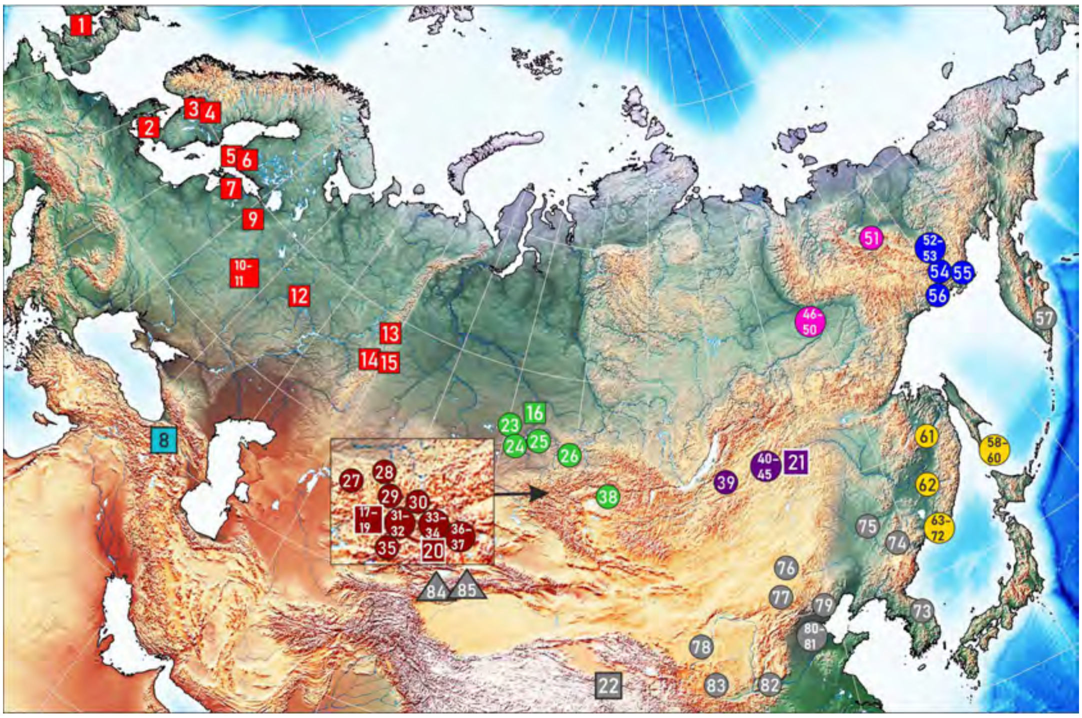

Fig. 2. *F. picea* complex specimens used in this study.

Location numbers refer to the Table. Rectangles: *F. picea*; circles: *Formica* sp.; triangles: *F. candida*.

Representatives of the *F. picea* complex with available *cox1/cytb* sequences

No.	Loc.	Coord.	Altitude	*cox1*	*cytb*
	Formica picea				
1	United Kingdom: Cors Goch Nature Reserve	N53.308 E–4.253	78	–	AY786145 (as *F. candida*)
2	Denmark	N55.830 E12.560	30	LT977411	–
3	Sweden: Varmland	N59.426 E13.271	50	–	JX170886
4	Sweden: Trajmossen, Brattforsheden	N59.695 E13.889	170	–	AY786144 (as *F. candida*)
5	Finland: Nylandia, Raasepori, Harpar Stortraesket	N59.975 E23.436	4	MZ607401*	–
6	Finland: Helsinki, Vihti	N60.417 E24.317	39	–	AY786146* (as *F. candida*)
7	Estonia: Torma	N58.813 E26.738	86	–	AY786147 (as *F. candida*)
8	Armenia: Aragats Mountains	N40.432 E44.236	2728	ON220876	ON228281
9	Russia: Novgorod oblast	N58.517 E31.267	36	–	AY786148 (as *F. candida*)
10	Russia: Moscow oblast, Odintsovo district	N55.733 E36.850	184	ON220886-87	ON228278-79
11	Russia: Moscow oblast	N55.751 E37.617	148	–	AY786149 (as *F. candida*)
12	Russia: Novgorod oblast, Kerzhenskiy Natural Reserve, swamp	N56.467 E44.500	ca. 120	ON220875	ON228280
13	Russia: Perm Krai, Kachkanar	N58.700 E59.483	307	–	AY786152 (as *F. candida*)
14	Russia: Revda, Sverdlovsk oblast	N56.800 E59.917	260	–	AY786151 (as *F. candida*)
15	Russia: Yekaterinburg	N56.833 E60.583	369	–	AY786150 (as *F. candida*)
16	**Russia: Tomsk oblast, Melnikovo village, swamp**	**N56.550 E84.067**	**90**	**PQ810826**	**PQ807749**
17	**Russia: Altai Republic, Abay village, swamp**	**N50.419 E85.066**	**1068**	**PQ810820**	**PQ807743**
18	**Russia: Altai Republic, Amur village, residual hills, stony steppe**	**N50.402 E85.107**	**1100**	**PQ810821**	**PQ807744**
19	**Russia: Altai Republic, Amur village, residual hills, stony steppe**	**N50.402 E85.107**	**1100**	**PQ810835**	**PQ807758**
20	**Russia: Altai Republic, Kosh-Agach village, steppe**	**N49.992 E88.664**	**2275**	**PQ810842**	**PQ807765**
21	**Russia: Zabaikalsky Krai, Gazimursky Zavod village, Kotikha River floodplain, swamp with rare trees**	**N51.545 E118.342**	**770**	**PQ810811**	**PQ807734**
22	China: Quinghai, Tibet	N35.000 E96.000	ca. 4500	–	AY786157 (as *F. candida*)
	***Formica* sp.**				
23	**Russia: Novosibirsk oblast, Kabinetnoye village, halophytic meadow**	**N55.117 E81.233**	**140**	**PQ810851**	**PQ807774**
24	**Russia: Novosibirsk oblast, Ordynsky district, steppe meadow**	**N54.320 E81.850**	**116**	**PQ810852**	**PQ807775**
25	Russia: Novosibirsk oblast, Iskitim district, steppe	N54.450 E83.470	230	ON220885	–
26	**Russia: Republic of Khakassia, Lake Shira, steppe**	**N54.534 E90.199**	**350**	**PQ810857**	**PQ807780**
27	**Russia: Altai Krai, Tigirek village, meadow with shrubs**	**N51.146 E83.010**	**500**	**PQ810831**	**PQ807754**
28	**Russia: Altai Republic, Ilyinka village, meadow by the river**	**N51.517 E85.033**	**690**	**PQ810843**	**PQ807766**
29	**Russia: Altai Republic, Yabogan village, steppe**	**N50.940 E85.021**	**1090**	**PQ810834**	**PQ807757**
30	Russia: Altai Republic, Ongudai village, stony steppe	N50.733 E86.133	810	ON220880	ON228273
31	**Russia: Altai Republic, Abay village, steppe near the swamp**	**N50.419 E85.066**	**1070**	**PQ810830**	**PQ807753**
32	**Russia: Altai Republic, Ust-Koksa village, stony steppe**	**N50.270 E85.615**	**1080**	**PQ810841**	**PQ807764**
33	**Russia: Altai Republic, Kurai village, steppe**	**N50.224 E87.932**	**1500**	**PQ810822**	**PQ807745**
34	**Russia: Altai Republic, Kurai village, steppe**	**N50.224 E87.932**	**1500**	**PQ810823**	**PQ807746**
35	**Russia: Altai Republic, Amur village, meadow near the lake**	**N50.223 E84.898**	**1980**	**PQ810840**	**PQ807763**
36	**Russia: Altai Republic, Kosh-Agach village, solonchak**	**N49.992 E88.664**	**1800**	**PQ810824**	**PQ807747**
37	**Russia: Altai Republic, Kosh-Agach village, solonchak**	**N49.992 E88.664**	**1800**	**PQ810825**	**PQ807748**

Table (continued)

No.	Loc.	Coord.	Altitude	*cox1*	*cytb*
38	**Russia: Republic of Tuva, Lake Dus-Khol, desertified steppe**	**N50.384 E94.870**	**990**	**PQ810836**	**PQ807759**
39	Russia: Buryatia Republic, Kizhinga village, steppe	N51.846 E109.913	700	ON220883-84	ON228270, ON228274
40	**Russia: Zabaikalsky Krai, Gazimur River, mixed-grass meadow**	**N51.764 E118.425**	**655**	**PQ810832**	**PQ807755**
41	**Russia: Zabaikalsky Krai, Gazimur River, mixed-grass meadow**	**N51.764 E118.425**	**655**	**PQ810833**	**PQ807756**
42	**Russia: Zabaikalsky Krai, Mount Kozlikha, meadow on a slope near a stream**	**N51.760 E118.713**	**730**	**PQ810837**	**PQ807760**
43	**Russia: Zabaikalsky Krai, Talovka River, swampy meadow**	**N51.450 E118.791**	**815**	**PQ810853**	**PQ807776**
44	**Russia: Zabaikalsky Krai, Uktycha River, steppe slope**	**N51.545 E118.342**	**750**	**PQ810854**	**PQ807777**
45	**Russia: Zabaikalsky Krai, Solonechnaya River, steppe meadow**	**N51.440 E118.907**	**750**	**PQ810855**	**PQ807778**
46	**Russia: Republic of Yakutia, Yakutsk, hygromesophytic meadow**	**N62.087 E129.289**	**260**	**PQ810845**	**PQ807768**
47	**Russia: Republic of Yakutia, Yakutsk, xerophytic meadow**	**N62.055 E129.644**	**100**	**PQ810846**	**PQ807769**
48	**Russia: Republic of Yakutia, Yakutsk, solonchak meadow**	**N62.021 E129.627**	**250**	**PQ810847**	**PQ807770**
49	**Russia: Republic of Yakutia, Yakutsk, lake Ytyk-Kyuel, meadow near the shore**	**N62.017 E129.618**	**100**	**PQ810848**	**PQ807771**
50	**Russia: Republic of Yakutia, Yakutsk, xerophytic meadow**	**N62.017 E129.618**	**100**	**PQ810849**	**PQ807772**
51	**Russia: Republic of Yakutia, Khayirdakh River, bank with *Chosenia***	**N66.263 E144.268**	**606**	**PQ810850**	**PQ807773**
52	Russia: Magadan oblast, Yagodnoye village, bank of Sokhatina River	N62.517 E149.617	465	ON220878	ON228277
53	Russia: Magadan oblast, Yagodnoye village, bank of Debin River	N62.750 E150.467	403	ON220879	ON228271
54	**Russia: Magadan oblast, Madaun village, gravel high floodplain**	**N60.615 E150.696**	**520**	**PQ810839**	**PQ807762**
55	**Russia: Magadan oblast, Klepka village, gravel high floodplain**	**N59.754 E151.491**	**78**	**PQ810838**	**PQ807761**
56	Russia: Magadan oblast, Arman village, gravel high floodplain	N59.667 E150.117	1	ON220872	ON228275
57	Russia: Kamchatka oblast	N53.190 E158.480	60	LT977377 (as *F. candida*)	–
58	**Russia: Sakhalin, Aniva, dry meadow**	**N46.019 E143.413**	**< than 10**	**PQ810812**	**PQ807735**
59	**Russia: Sakhalin, Aniva, dry meadow**	**N46.019 E143.413**	**< than 10**	**PQ810829**	**PQ807752**
60	**Russia: Sakhalin, Aniva, dry meadow**	**N46.019 E143.413**	**< than 10**	**PQ810819**	**PQ807742**
61	**Russia: Komsomolsk-on-Amur, Silinka River, floodplain with poplars**	**N50.550 E137.000**	**30**	**PQ810856**	**PQ807779**
62	**Russia: Khabarovsk Krai, sandy area on forest road**	**N66.263 E134.330**	**74**	**PQ810844**	**PQ807767**
63	Russia: Primorsky Krai, Lazo town, Lazovka river's bank	N43.380 E133.898	220	ON220881	ON228276
64	**Russia: Primorsky Krai, Kievka River, sandy seaside meadow**	**N42.855 E133.675**	**2–3**	**PQ810817**	**PQ807740**
65	**Russia: Primorsky Krai, Kievka River, sandy seaside meadow**	**N42.855 E133.675**	**2–3**	**PQ810818**	**PQ807741**
66	**Russia: Primorsky Krai, Kievka River, sandy seaside meadow**	**N42.855 E133.675**	**2–3**	**PQ810828**	**PQ807751**
67	**Russia: Primorsky Krai, Gryaznaya River, overgrown sand and gravel shoal**	**N43.361 E131.556**	**130–135**	**PQ810814**	**PQ807737**

Table (end)

No.	Loc.	Coord.	Altitude	*cox1*	*cytb*
68	**Russia: Primorsky Krai, Gryaznaya River, overgrown sand and gravel shoal**	**N43.361 E131.556**	**130–135**	**PQ810816**	**PQ807739**
69	Russia: Primorsky Krai, Sinii Utes town, gravel area	N43.062 E131.356	40–45	ON220882	ON228272
70	**Russia: Primorsky Krai, Andreyevka village, wasteland**	**N42.649 E131.140**	**7**	**PQ810813**	**PQ807736**
71	**Russia: Primorsky Krai, Andreyevka village, wasteland**	**N42.649 E131.140**	**7**	**PQ810815**	**PQ807738**
72	**Russia: Primorsky Krai, Andreyevka village, wasteland**	**N42.649 E131.140**	**7**	**PQ810827**	**PQ807750**
73	South Korea	–	–	MT800217 (as *F. candida*)	–
74	China: Yanbian, Jilin	N43.133 E129.183	750	KX665026-27 (as *F. candida*)	–
75	China: Harbin	N45.750 E126.633	140	KX665031-32 (as *F. candida*)	–
76	China: Xilin Gol League, Inner Mongolia	N43.930 E116.090	1040	KX665022, KX665024 (as *F. candida*)	–
77	China: Ulanqab, Inner Mongolia	N40.994 E113.132	1370	KX665023, KX665025 (as *F. candida*)	–
78	China: Helan Mountains, Inner Mongolia	N38.900 E105.967	3260	KX665019-21 (as *F. candida*)	–
79	China: Hebei, Qinglong	N40.407 E118.950	245	KX665028 (as *F. candida*)	–
80	China: Hebei, Xiaowutai Mountain	N39.941 E115.043	2840	KX665029-30 (as *F. candida*)	–
81	China: Hebei	–	–	HQ619704, HQ619710 (as *F. candida*)	HQ651081, HQ651074 (as *F. candida*)
82	China: Zhong-Tiao Mountains	N35.116 E111.772	520	KX665033 (as *F. candida*)	–
83	China: Liupan Mountains, Ningxia	N35.657 E106.205	1300	KX665034 (as *F. candida*)	–
		Formica candida			
84	Kyrgyzstan: Alai Valley	N39.703 E73.457	3200	–	AY786154*, AY78615, JX170887
85	Kyrgyzstan: Tian-Shan	–	–	–	AY786155–AY786156

Note. Loc. – location numbers referring to Fig. 2; altitude provided in m above sea level. Asterisks denote type of material/locations. Specimens sequenced in this study are indicated in boldface.

cytb sequence for the *F. candida* neotype (AY786154). The haplotype network was constructed using the median joining algorithm in Pop ART v. 1.7 (Leigh, Bryant, 2015).

Results

Out of the 47 ant specimens sequenced in this study for *cox1* and *cytb*, 6 belonged to *F. picea*, and 41, to *Formica* sp. We did not detect haplotypes of *F. candida* (Seifert, 2004) in any of the sampling points, despite the extensive survey area. *F. picea* and *Formica* sp. significantly differed at the DNA level (Fig. 4).

For *F. picea*, a notable geographic split was evident: samples from Europe and West Siberia formed a tight cluster, while samples from Armenia and Transbaikalia diverged from them (Fig. 4). For *Formica* sp., the larger sample size resulted in a more informative network. However, no regions with a specific set of haplotypes were identified. Genetic diversity was substantial, especially for three samples (from different regions) that differed markedly from other haplotypes.

F. picea was found in five locations east of the Urals: in the Altai mountains, in the lowlands of West Siberia, as well as in East Siberia. The West Siberian location (Melnikovo, Tomsk oblast) was in a fen with a tall birch. The nest (with no external structures) was located in a sedge hummock with a fern; nest entry was in moss.

In the Altai mountains, we found nests of *F. picea*: three in Central Altai near the Abay (locations No. 17 in the Table and Fig. 2) and Amur (locations No. 18–19 in the Table and

Fig. 3. Habitats of *Formica* sp. and *F. picea*.

a – Central Altai, near Abay village, lowland swamp (*F. picea*); *b* – the same area; meadows on the site of drained swamps (co-occurrence of *Formica* sp. and *F. picea*); *c* – the same area; stony steppes on rocky outcrops (*F. picea*); *d* – Central Altai, near Ust-Kan village, steppe (*Formica* sp); *e* – Magadan oblast, Nalednyy River (tributary of the Ola River) (*Formica* sp.); *f* – Zabaikalsky Krai, floodplain of the Talovka River (*Formica* sp.); *g* – Sakha Republic (Yakutia), Momsky District, Khairdakh River (*Formica* sp.); *h* – Magadan oblast, upper reaches of the Kolyma River, steppe (*Formica* sp.); *i* – Magadan oblast, an island in the upper reaches of the Kolyma River near the eastern end of the Big Ananchag Range (*Formica* sp.); *j* – same area; nest exits of *Formica* sp.; *k* – Zabaikalsky Krai, floodplain of the Kotikha River (*F. picea*); *i* – Novosibirsk oblast, Kabinetnoye village, halophytic meadow (*Formica* sp.); *m* – Southeast Altai, near Kosh-Agach village, Tabozhok town, stony steppe (*F. picea*). For more details, see the Table.

Fig. 2) villages (ca. 1100 m a. s. l.), and one in the Southeast Altai (locations No. 20 in the Table and Fig. 2), near the Kosh-Agach village (2275 m a. s. l.). Near the Abay village, a single nest was detected in a damp area on the edge of a bog, where it transitioned into a steppe meadow, 150–200 m away from a small lake. The nest had a ground part in the form of a small dome made of thin blades of grass, no more than 10 cm high and about 15 cm in diameter. Two other nests were found on southern steppe slopes, with no external structures and exits located under the rocks.

In East Siberia, *F. picea* was detected in Zabaykalsky Krai, east of the Gazimursky Zavod town (locations No. 21 in the Table and Fig. 2), at 770 m a. s. l., within the forest belt. The nest was found on a swampy floodplain of the Kotikha River (a third-order tributary of the Gazimur River), with saplings of alder, birch, and larch. The nest, without visible external structures, was located under a layer of litter composed of fallen leaves and dry grass.

Specimens of *Formica* sp. were detected in 61 locations (Fig. 2). Their habitats included floodplain (including long-term and deeply flooded sandy-pebble spits) and non-floodplain terraces of different heights on rivers of various sizes, meadows of diverse composition and projective cover, sparse forests, steppes (from mixed grass to desert), foothills and highlands of Altai. This ant was found to avoid forests with closed canopies, as well as wetlands.

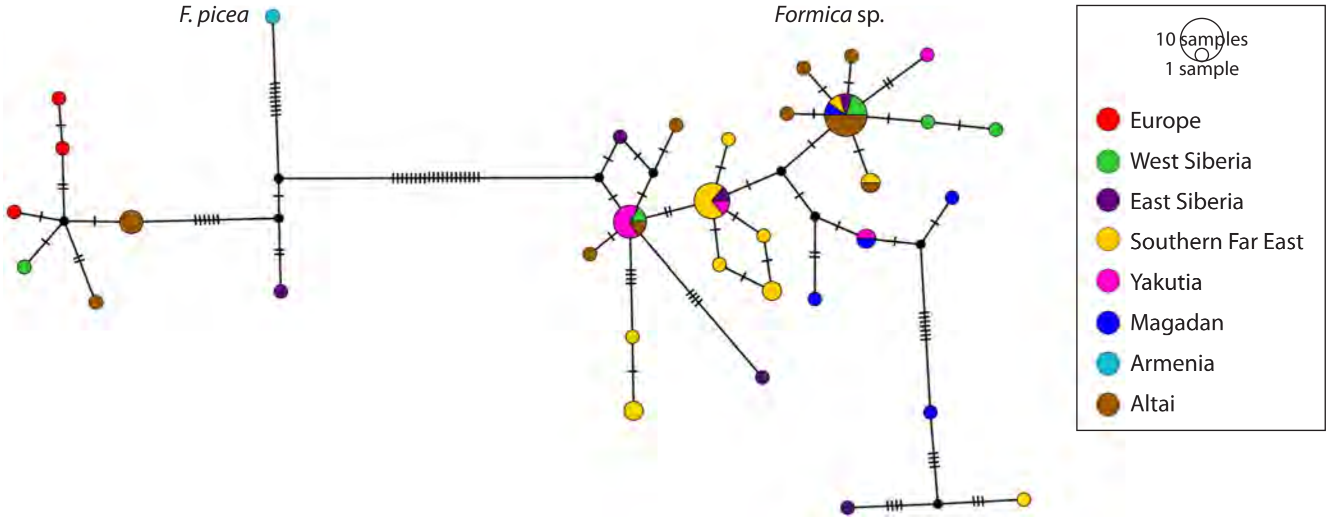

Fig. 4. Haplotype network for the combined *cox1*+*cytb* sequences.
Dashes represent the number of nucleotide substitutions.

Discussion

Genetic patterns

As in the previous study (Zhigulskaya et al., 2022), *F. picea* and *Formica* sp. were significantly different on mtDNA levels, with no intermediate haplotypes found (Fig. 4). Expectedly, we found no haplotypes of *F. candida* sensu Seifert (2004), which is probably limited to certain regions of Kyrgyzstan.

Throughout the distribution of *Formica* sp., from the Altai mountains to the Pacific coast and eastern China, there is a pretty high genetic variation, but with no obvious genetic structure (Fig. 4). This probably indicates recent colonization of this region without a bottleneck event and high dispersal abilities of the species. Unfortunately, there are no *cox1* data on *Formica* sp. from China, a region with a milder climate that could serve as a refugium/ancestral region of *Formica* sp.

Noteworthy, three haplotypes differed by 8–15 nucleotide substitutions from the main cluster (Fig. 4). However, all three were from different and geographically remote regions. This might imply that the history of the species is complex, with high dispersal rate and multiple colonization waves.

Although the data on the *cox1* gene in *F. picea* remain limited, several interesting insights can be gleaned from the haplotype network (Fig. 4). Most haplotypes form a tight cluster, indicating close genetic relationships. This cluster comprises specimens from the Altai and West Siberia, suggesting recent (likely Holocene) dispersal into these regions. The Armenian haplotype is distantly related to this group, as expected given the geographic distance and mountain barriers. Notably, the East Siberian haplotype is also distinct from the European cluster. Intriguingly, this pattern may indicate that East Siberian populations of *F. picea* belong to a different genetic lineage relative to the European/West Siberian group, and that an East Siberian refugium for the species may have existed. Of course, drawing firm conclusions based on a single specimen would be premature; thus, we intend to examine additional specimens from the region in future studies.

Geographic distribution

There are a lot of studies on the distribution and habitat preferences of the *F. picea/F. candida* complex. In various parts of its range, these ants are known to inhabit diverse habitats: fens, meadows, steppes, as well as sparse forests on plains, floodplains, and in highlands. In the south taiga zone of Siberia, black bog ants are found in swamps, in wet mixed forests, in pine woods (Omelchenko, Zhigulskaya, 1998; Dlussky, 2001; Gridina, 2003). They are ubiquitous in Central Yakutia and the Baikal Region, from boggy larch forests, dry pine-larch forests, and steppe-like and steppe biotopes to bare rock formations, with nest densities reaching up to 30 nests per 100 square meters (Pleshanov, 1966; Dmitrienko, Petrenko, 1976).

However, they are particularly ecologically versatile and abundant in the mountain-steppe landscapes of Tuva, Southeast and Central Altai, as well as in the steppes of Transbaikalia, where they dominate almost all habitats, from solonetzes and solonchaks to dry steppes on sandy and stony soils (Zhigulskaya, 1968, 2009, 2011; Chesnokova, Omelchenko, 2011).

In Northeast Asia, the complex is associated primarily with river valleys; high abundance is observed in sparse *Populus* and *Chosenia* groves and on gravel-sandy spits in floodplains. Much less frequently, and only as isolated nests, *Formica* sp. can be found in mesoxeromorphic sparse forests (in Yakutia, specifically in pine forests), in steppe habitats, or southern slopes with sphagnum-moss bogs (Berman et al., 2007).

Since the black bog ant turned out to include several cryptic taxa, this raises a question if they have different habitat preferences. Here we obtained certain data on this point, which are, of course, far from exhaustive. For *F. picea*, we currently know that it is found from West Europe to West Siberia. We also have single findings from Transbaikalia (this study) and Tibet (AY786157), implying the presence of this taxon between Siberia and Tibet. *F. picea* appears to be rare in Asia, since we found only six locations of this species compared to 41 for *Formica* sp. Of these, only two were not from the mountains: a location in Tomsk oblast and one from mid-altitude highlands of Transbaikalia. Based on our findings, we can suggest that *F. picea* appears to be associated with fens, but not peatlands. The latter is probably due to the fact that peatlands in Siberia are still insufficiently studied by myrmecologists.

Formica sp., on the other hand, appears to be found even more widely than previously thought (Zhigulskaya et al., 2022). In this study it was recorded across a vast area, from West Siberia to the Pacific Ocean, and from 66.5°N in Yakutia (Khayyrdakh River) roughly to 35°N in the southern part of the Korean Peninsula (Fig. 2), as well as from sea level up to approximately 3500 m a. s. l., across a broad range of habitats (except for forests with closed canopy). Furthermore, unlike *F. picea*, *Formica* sp. has not been found in bogs in Europe, Siberia, or Altai. Conversely, only *Formica* sp. is known from river floodplains, and from these areas, it can spread to xeromorphic slopes and sections of low floodplain terraces.

The versatility of *Formica* sp. to moisture is striking: it can colonize both long-term flooded habitats on floodplains (that is, for about a month of the 4.5-month active period in the Subarctic) and dry zonal steppes. Notably, in the Altai Mountains, *Formica* sp. nests were found in both types of habitats.

In this study, we found that the distributions of *Formica* sp. and *F. picea* significantly overlap, probably from the Urals to Transbaikalia (Fig. 2), and we expect this overlap to expand when new data on bog ants are obtained. However, the ecological preferences of these two taxa seem to differ, which can be prospectively formulated as follows: *Formica* sp. avoids fens, while *F. picea* does not like low floodplains.

In this connection, the cases of syntopic occurrences of both taxa in the Central Altai are of particular note. Here, these two nests were found a few dozens of meters apart on the floodplain of the Abay River. The nest of *F. picea* was at the edge of a wet swampy depression about 1.5 m deep, while that of *Formica* sp. was on a dry steppe meadow that was formed in a dried fen. In the same location, about 3 km apart, we found a *F. picea* nest on a southern slope of the residual hills with rock outcrops, occupied by steppes.

We can suggest that in the Altai, *F. picea* inhabits meadows, and can move into both wet habitats and moderately dry steppes on southern slopes, as well as mountain steppes above the forest edge. However, it is unclear why this species can use both very wet and very dry habitats (Bönner, 1915; Skwarra, 1929; Stitz et al., 1939; Seifert, 2004, 2018).

To this, we can put forward the hypothesis that the generalist *F. picea* has to constrict itself to the habitats where it can compete with other ant species (Dlussky, 1967). "Apparently, while spreading westward, *F. picea* (a eurytopic forest-steppe species of Mongolian origin) was displaced by species of the *F. rufibarbis* group into bogs. In these bogs, the *F. rufibarbis* species are virtually absent, whereas *F. picea* can survive, owing to its eurytopy and plasticity in nest construction. In the mountains, this species inhabits higher altitudes than other species of the *F. rufibarbis* group (except for *F. subpilosa pamirica* and *litoralis* in Central Asia, which exclusively occupy river thalwegs, rocky screes, and sands). *F. picea* cannot compete with *F. fusca* and its closely related species, as it is virtually absent in forests; instead, it is associated with more or less open habitats (meadows, steppified areas, sparse forests, river floodplains, and bogs)" (translated from: Dlussky, 1967, p. 63).

If this idea is correct, *Formica* sp. outcompetes *F. picea* on the vast floodplains and xeromorphic habitats of Asian Russia. So, *F. picea* is outcompeted both in Siberia and in Europe by different local ant species.

Conclusions

We can summarize the following important points inferred from our study: only *F. picea* is found in Europe, whereas both *F. picea* and *Formica* sp. are found in North Asia. We failed to detect *F. candida* on this vast territory, and we can surmise that in the current understanding proposed by Seifert (2004), it is a Central Asian taxon. In the south of West and East Siberia, the ranges of *F. picea* and *Formica* sp. overlap, but they have different ecological preferences. *F. picea* is probably constrained to fens on the plains, and to subalpine meadows in the mountains. *Formica* sp. is broadly tolerant to humidity but is not found in fens. The cases of syntopic distribution of these ants, which we described in Altai, are apparently associated with transient successional processes. The relative rarity of *F. picea* in our collections possibly reflects the insufficient study of raised bogs in Asia, the typical habitats of the species in Europe. Differences in the distribution and habitat preference of *F. picea* and *Formica* sp. are probably the result of competition, according to G.M. Dlussky (1967).

F. picea and *Formica* sp. differ genetically and have different distribution ranges, as well as habitat preferences. This supports the opinion that *Formica* sp. should be recognized as a distinct species.

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