

## Phylogeography and hybridization of corvid birds in the Palearctic Region

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Natural hybridization increases a lot phenotypic and genetic diversity and shapes intra-species patterns, which is a subject of phylogeography. We studied mitochondrial and complete genome variation in the bird family Corvidae, genera *Corvus*, *Pica*, *Cyanopica*, *Perisoreus* and *Nucifraga*. In the classic case of natural hybridization between carrion and hooded crows in Siberia, we found no decreased fitness of hybrids, but instead positive assortative mating which should restrict hybrid zone width. Several genetic markers were unable to discriminate between pure carrion and hooded crows. Mitochondrial DNA sequences revealed no difference between carrion and hooded crows, but instead two diverged haplogroups within the eastern part of the distribution range of the carrion crow. NGS resulted in a clear pattern of diversification of pure forms and hybrids (by using SNPs), and showed genomic regions of increased variability, the so-called "speciation islands". Comparing European and Siberian crow hybrid zones, differences in genome regions bearing genes of melanogenesis supposedly under divergent selection were found. Comparative phylogeographic analysis of 10 widely distributed Palearctic species revealed two kinds of patterns: one with a division into two haplogroups, western and eastern, and another one without such a division. These two phylogeographic patterns might be explained by different habitat preferences: mainly open fields for the first group and forests for the second one. One glacial refuge was assigned to the latter group, while west-east group species might have survived in several refuges. One of such species, the Eurasian magpie (*Pica pica*) has a gap in its range in Transbaikalia, which is currently shrinking before our eyes. The two subspecies divided by this gap differ in phenotype, mtDNA and vocalization. In their young contact zone, some hybridization occurs with small introgression limited by certain post-zygotic isolation.

Key words: phylogeography; hybrid zone; crow; magpie; speciation; genetic variation; DNA; isolation; divergence.

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## Филогеография и гибридизация врановых птиц Палеарктики

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Природная гибридизация значительно увеличивает фенотипическую и генотипическую изменчивость и формирует внутривидовую структуру, изучением которой занимается филогеография. Нами исследована изменчивость митохондриального и полного геномов птиц семейства врановые Corvidae, родов *Corvus*, *Pica*, *Cyanopica*, *Perisoreus* и *Nucifraga*. Анализируя классический случай естественной гибридизации между серой и черной воронами (*Corvus corone cornix* и *C. c. corone*) в Сибири, мы не обнаружили предполагаемого уменьшения приспособленности гибридов, однако установили ассортативность скрещиваний, которая должна ограничивать ширину гибридной зоны. В результате использования нескольких подходов и генетических маркеров не найдено различий между серой и черной воронами, но в процессе секвенирования митохондриального генома установлено наличие дифференциации на два гаплотипа в пределах ареала восточной черной вороны. При полногеномном секвенировании нами впервые обнаружена явная диверсификация чистых форм и гибридов по SNP и исследованы участки генома с повышенной дифференциацией – «островки видообразования». Сопоставление геномов птиц из европейской и сибирской гибридных зон выявило частично разные участки, ответственные за меланогенез, с признаками дивергентного отбора. Сравнительная филогеография десяти видов врановых, широко распространенных в Палеарктике, позволила выделить две категории ареалов: с дифференциацией на западные и восточные группы гаплотипов и без такого разделения. Это можно объяснить различными экологическими предпочтениями: к полукрытым биотопам у птиц первой группы и к лесам у второй. Представители второй группы пережили плейстоценовые оледенения в предполагаемом единственном лесном рефугиуме с последующим бутылочным горлышком, что объясняет их гомогенность, а виды первой группы могли сформироваться в нескольких местах. Один из таких видов – сорока *Pica pica* – имеет разрыв ареала в Забайкалье, который в настоящее время заполняется. Принадлежащие разным гаплогруппам популяции, различающиеся по фенотипам, мтДНК и вокализации, образуют зону

контакта с ограниченной гибридизацией, но в целом репродуктивно изолированы. Таким образом, современная динамика видовых ареалов формирует филогеографическую структуру видов.

Ключевые слова: филогеография; гибридные зоны; вороны; сороки; видообразование; генетическая изменчивость; изоляция; дивергенция.

The main purpose of evolutionary biology is still investigating the processes taking place in nature. Although we generally imagine the various forces creating the incredible diversity of organisms and the mechanisms maintaining this diversity, understanding speciation in all aspects is still a challenging matter. Even if we agree that the main mechanism of divergence might be geographic isolation, other factors are disputed heavily. Among them, natural hybridization and hybrid zones were named as “natural laboratories” (Hewitt, 1988) or “windows on the evolutionary process” (Harrison, 1990). Hybrid zones can tell us a lot about the level of isolation between populations and reality of the so-called species isolating mechanisms. If hybridization between formerly isolated diverged forms occurs, this may result in increased variation and thus complicates the pattern of intraspecies’ variation, which is studied by modern phylogeography. It deals with patterns and processes of distribution of genetic lineages throughout the species’ ranges or particular gene genealogies (Avice, 2000) and is still in many cases based on markers of mitochondrial genomes. Phylogeography is meant to explain the biogeographic history of populations and to shed light on the formation of the species.

Within the bird family Corvidae there are several species widely distributed in the Palearctic. It includes species very variable in shape, rather large in size, numerous and observable. Thus, they are convenient subjects for evolutionary studies. Crows (*Corvus corone*) are most prominent among corvids as the hybrid zone between carrion and hooded crows is a classical text-book case of natural hybridization occurred presumably by means of secondary contact in the Holocene (Mayr, 1942, 1963). This group represents the polytypic species *Corvus corone*, including the western carrion crow *C. c. corone*, eastern carrion crow *C. c. orientalis* and hooded crow *C. c. cornix* located between them (Fig. 1). The taxonomy of the forms included in this group is still a subject of hot debates and the taxa are treated as distinct species by some authors or *C. corone* is treated as a superspecies with several semispecies. The European hybrid zone is rather well studied, while the Siberian one was only discovered by starting our study.

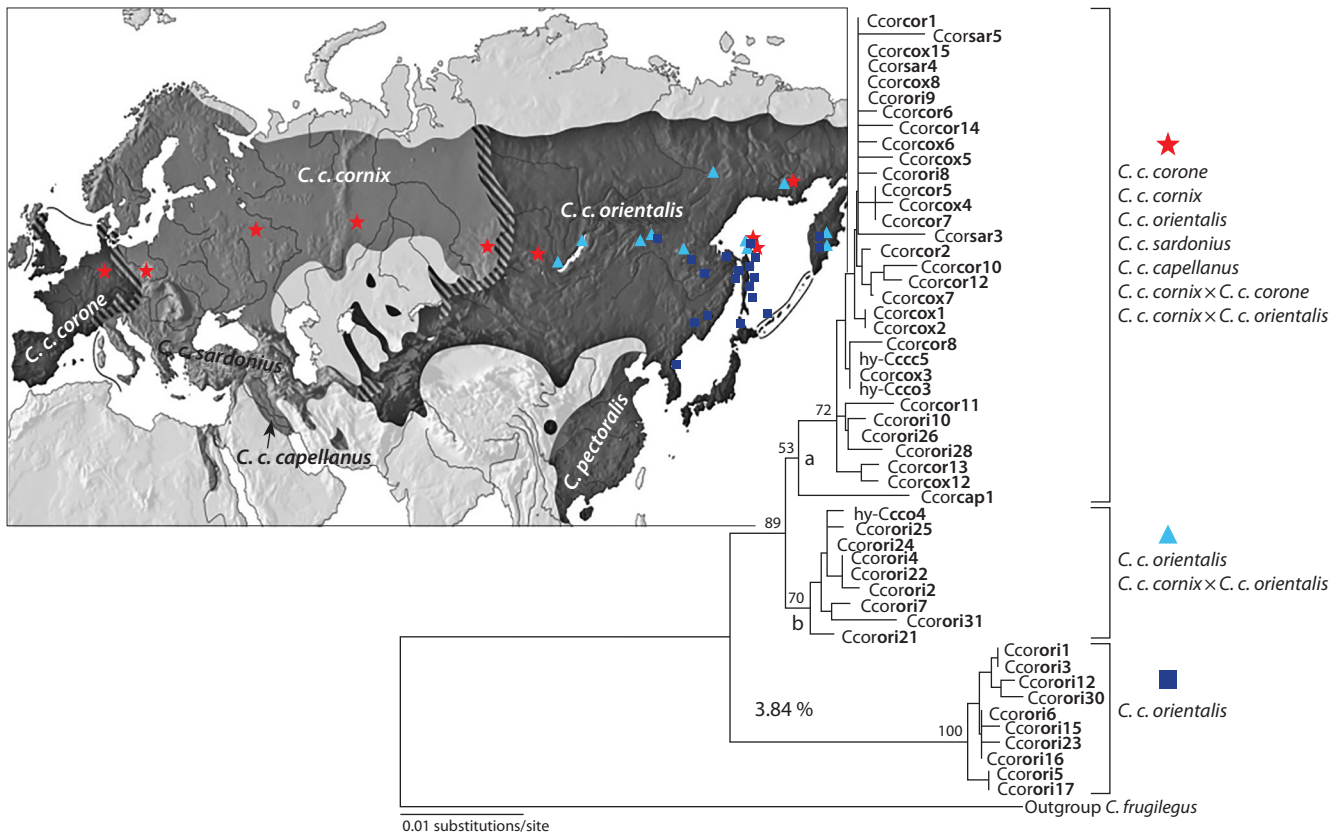
During field trips in 1984–1991 we conducted ecological observations in the region between Ob and Yenisey rivers, mainly along the Transsiberian railway. Here the hybrid zone was ~150 km in width (Kryukov, Blinov, 1989, 1994; Blinov, Kryukov, 1992; Blinov et al., 1993). There was a clinal variation of plumage phenotypes within the zone, with the portion of intermediates (presumably hybrids) reaching 33 % at maximum in the center of the zone and decreasing to its borders. Also, phenotypic variation increased towards the center of the zone, while its edges were rather homogeneous. No ecological preferences were found for both forms, and phenotypically different pairs nested side by side. Breeding success was the same over all kinds of mating pairs. The portion of intermediates was the same in the stages of nestlings, subadults and

adults. Thus, progeny of any kinds of crossings had the same fitness. In total, no selection against hybrids was observed. While checking the content of mating pairs, we noted that any kind of homogeneous and heterogeneous pairs could be met. At the same time, statistically significant positive assortative mating was discovered and proved in the center of the zone (Kryukov, Blinov, 1989; Blinov, Kryukov, 1992). It means that black-colored carrion crows mated preferentially with black-colored ones, while black-grey hooded individuals, with hooded ones. The same was confirmed for the European zone (Saino, Villa, 1992). This phenomenon was assumed to restrict the hybridization process and thus the widening of the zone.

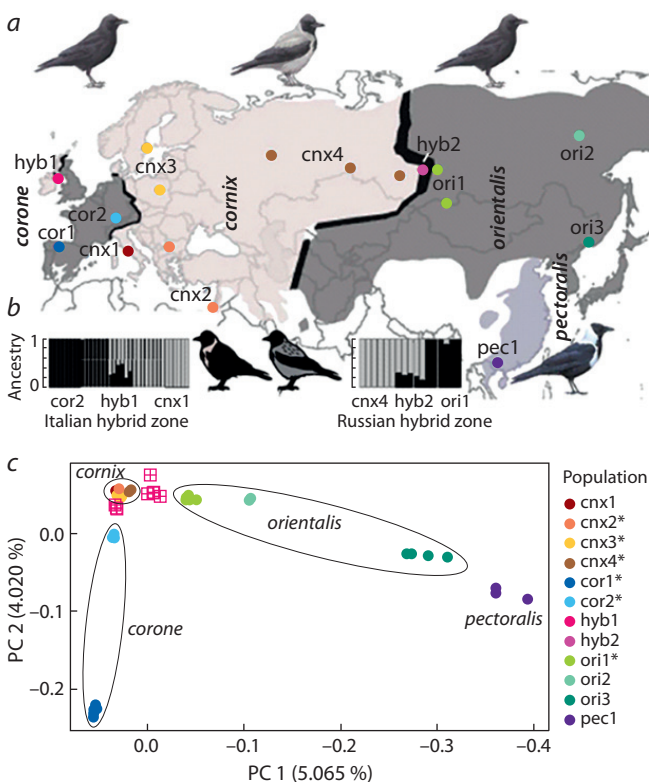
Single phenotypic hybrids may be met even far away from the zone borders, in both allopatric initial ranges. Throughout the years we tried to use several kinds of genetic markers in order to trace the detailed structure of the zone. But no difference between *C. c. corone* and *C. c. cornix* was found at the level of karyotypes: both taxa have 80 chromosomes with identical morphology (Roslik, Kryukov, 2001). In RFLP analysis and allozymes, no difference between parental forms was found either, but several new variants of albumine, esterase and transferrine were revealed in some hybrid specimens (Kryukov et al., 1992). Genomic analyses using hypervariable DNA fingerprinting (with a minisatellite probe from bacteriophage M13) revealed no specific markers (Uphyrkina et al., 1995). Also, an RAPD-PCR analysis showed that variability in carrion and hooded crows is less than in the hybrids (Spiridonova, Kryukov, 2004).

The sequencing of the mitochondrial *cytochrome b* (*cytb*) gene revealed no difference between carrion and hooded crows (so this marker is inappropriate for further detailed study of the hybrid zone), but unexpectedly we discovered a clear difference within the eastern carrion crows in a geographic context (see Fig. 1). While homogeneous over the most part of the distribution, from West Europe to Kamchatka, haplotypes in the South Far East differed considerably (Kryukov, Suzuki, 2000). Further analysis of the mitochondrial CR revealed a more detailed pattern, with three haplogroups, the most derived being the group occupying the extreme southeastern part of the range: the Russian Far East, Korea and Japan (Haring et al., 2007). Interestingly, in East Siberia, Kamchatka, and North Sakhalin, a haplogroup slightly differentiated from the western group was found, reflecting probably additional refugia. Then, in the distinct species, *Corvus pectoralis* from China, we found the same haplotype as in southeasternmost populations of *C. corone* (Haring et al., 2012). This may imply mitochondrial capture from one species to another due to suspected ancient hybridization.

Crows became a subject for geneticists from other countries as well. Haas et al. (2009) found no difference between carrion and hooded crows in their study of *MC1R* gene, the candidate for melanogenesis, and most microsatellite loci. The same result was obtained in sequencing analyses of 25 nuclear intronic loci, but different expression profiles between carrion



**Fig. 1.** Distribution of *Corvus corone* s. l. with hybrid zones shaded and collecting localities; and NJ tree based on mitochondrial Control Region sequences (modified after Haring et al., 2007).

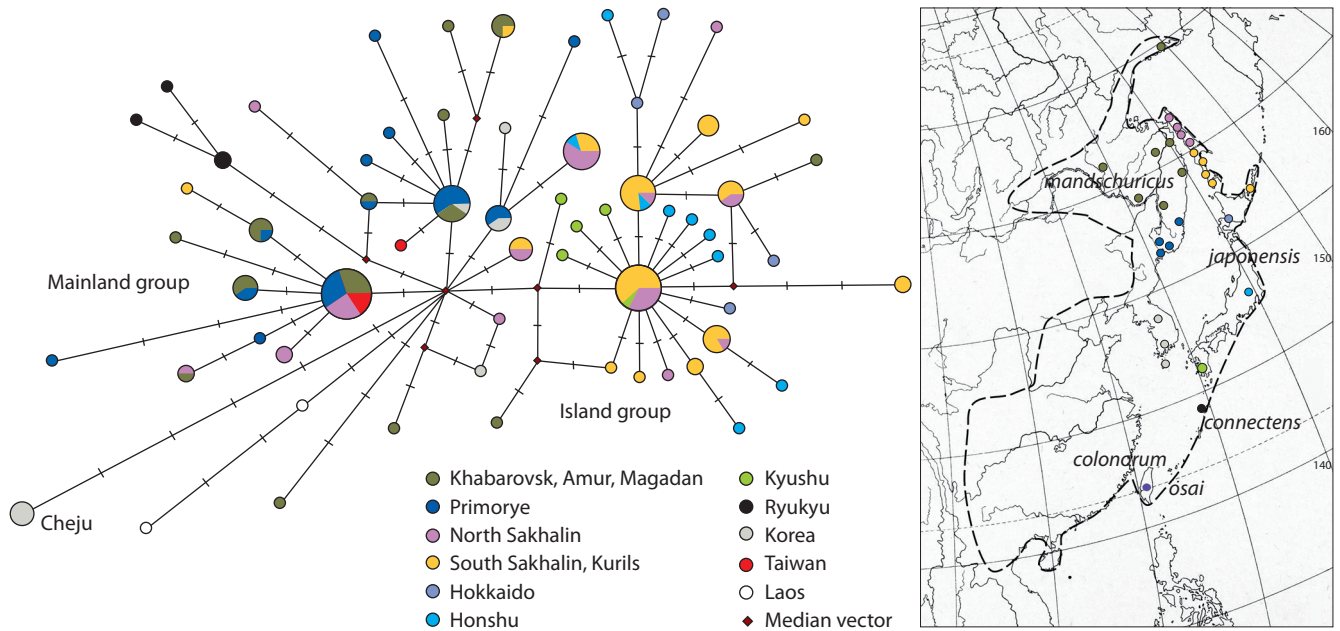


**Fig. 2.** a, The ranges of *Corvus corone* complex and collecting localities; b, Phenotypic content of the hybrid zones and adjacent populations; c, PCA-analysis by 16.6 million SNPs (modified after Vijay et al., 2016).

and hooded crows were found in some of 1301 core genes analyzed (Wolf et al., 2010). In total, all these data support the view that the three forms are very closely related and have diverged recently, only thousands of years ago. From a taxonomic view, this supports their subspecies status: *Corvus corone corone*, *C. c. orientalis* and *C. c. cornix*.

The crow hybrid zones were studied in a more general aspect as a model to understand the genetic aspects of speciation via the genome landscapes approach, specifically, to reveal a connection between gene flow across the hybrid zones and diversification visualized clearly by feather coloration (very different in carrion and hooded crows). It was found that genes associated with melanogenesis pathways and hormone regulation are expressed differently in carrion and hooded crows and are located in a very small genomic region of the so-called “speciation islands”. It was suspected that in this genomic region there is an inversion. These genes were supposed to be responsible for maintaining plumage differentiation of the crossing forms in spite of ongoing, though restricted, gene flow (Poelstra et al., 2014).

Because the “speciation islands” are subject to divergent selection, they would cross the hybrid zones slower than neutral alleles. So the next genome-wide study was aimed to compare the processes in both European and Siberian hybrid zones. 124 complete genomes were analyzed and genomic regions with increased variability were found. In a PCA analysis by SNPs, we for the first time found clear differences between hooded and both carrion crow clusters, while hybrids appear in between them (Fig. 2). While comparing allopatric



**Fig. 3.** Phylogenetic network based on *cytb* gene of mtDNA of *Corvus macrorhynchos*, and collecting localities (after Kryukov et al., 2012).

populations and hybrid zones by  $F_{st}$  in a “sliding window” method, several genomic regions of increased diversity were discovered. These local peaks of genomic differentiation in the Siberian hybrid zone were rather low compared with those of the European zone, which corresponds to their widths. The main such peaks were located at the 18th chromosome in the case of the European zone and 21st for the Siberian one. Accordingly, the candidate genes of the metabolic pathway of melanogenesis that were supposed to be involved in selection against gene flow were only partly shared among both zones, suggesting their independence (Vijay et al., 2016).

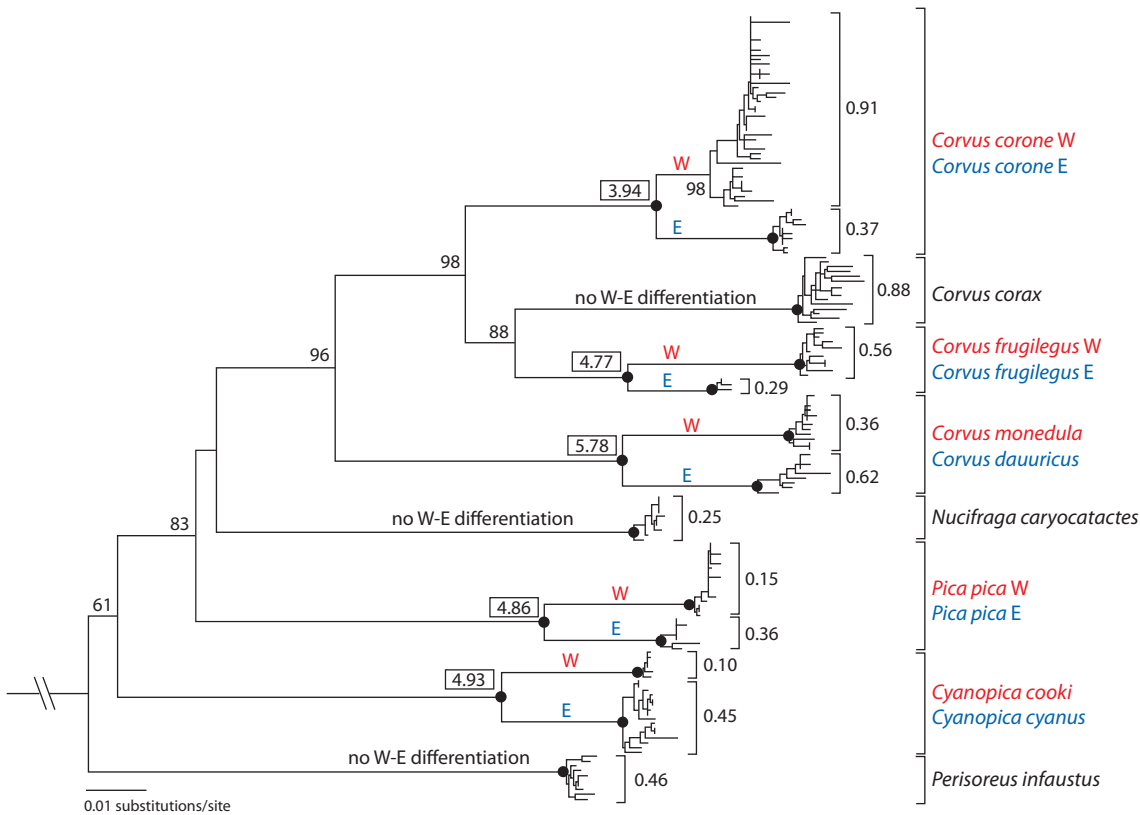
Another crow species, black-colored, with a massive bill, is the jungle crow (*Corvus macrorhynchos*), which inhabits Eastern Asia. We studied patterns of its genetic variation by using sequences of the mitochondrial *cytochrome b* gene. *C. macrorhynchos* demonstrates a high level of sequence variation with a tendency to geographic differentiation throughout its range. The haplotype network shows two haplogroups (Fig. 3). The island group comprises the populations of Sakhalin, Hokkaido, Honshu and Kyushu, while the mainland group includes the populations from Primorye, Khabarovsk, Amur, Magadan regions and Laos. Haplotypes of Taiwan and Ryukyu Islands proved to be closer to the mainland group. The population of Cheju Island (Korea) contains only one haplotype which is quite distant. This pattern allowed us to develop a phylogeographic hypothesis regarding the two ways of settling of the Japanese island from the mainland: one from Sakhalin and Hokkaido until Kyushu, and the other from the South via Taiwan or, less likely, from the Korean Peninsula. Interestingly, the lowest level of nucleotide diversity was found within the marginal north-west population in the western part of Amur region. *C. macrorhynchos* experienced population growth in the recent past and is still expanding its range, at least in the north and north-west of the range (Kryukov et al., 2012).

The azure-winged magpie (*Cyanopica cyanus*) represents the well-known case of a widely distinct, disjunctive range. It

is distributed on the Iberian Peninsula in the west and on the Eastern Asia. Both groups of subspecies, western and eastern, differ from each other by color and size. Usually these isolates were treated as Tertiary relics, assuming the subdivision of a former continuous range during the Pleistocene. However there was a hypothesis that Portuguese or Spanish sailors might have brought these nice birds from Asia (China or less probably Japan) in the Medieval and released them in Europe. In such a case, the genetic affinity between the European and Asian populations would be lower than that between the Chinese and Japanese populations.

We performed analyses of the mitochondrial CR and the *cytb* gene from seven subspecies throughout the *C. cyanus* range (Kryukov et al., 2004). The results of the phylogenetic analyses reveal a clear pattern concerning the grouping of haplotypes derived from the eastern and western isolates of the azure-winged magpie. All kinds of trees, NJ, ML and MP, represent the similar subdivision for two clades, with the p-distance between them about 5.3 % for CR and 6.3 % for *cytb*. Within the clades, differentiation is very low (0.2–0.5 %). Applying the widely used value of 2 % divergence per myr (Klicka, Zink, 1997) to our *cytb* data set results in considerably high divergence times, e. g. >3 mya between Asian *C. c. cyanus* and European *C. c. cooki*. According to that rate, the phenotypic and genotypic differentiation of the azure-winged magpie had already started in the Pliocene, whereas repeated glacial expansions and restrictions of distribution ranges during the Pleistocene might have completed the process and enforced the differences.

Our multivariate morphometric analysis showed a clear differentiation between the Iberian azure-winged magpie and the Asian ones, which proved to be different in several measurements and in the space of two main canonical roots. The morphological data are in accordance with the genetic results (Fok et al., 2002; Kryukov et al., 2004), where sequence divergence between the western and eastern isolates was found to be



**Fig. 4.** Comparative phylogeography of 10 corvid species: ML tree based on CR of mtDNA (after Haring et al., 2007).

much higher than that among the Asian populations. Both data sets clearly reject the hypothesis of a recent introduction of azure-winged magpies into Europe. Since the morphological characters mainly represent the nuclear genome, this analysis can be regarded as an important complement to the genetic investigations, which altogether corroborate the suggested subdivision into the two species: *Cyanopica cyanus* Pallas, 1776 and *Cyanopica cooki* Bonaparte, 1850.

In addition to the above results, we obtained some more data from several corvid bird species by sequencing mitochondrial CR. Besides *Corvus corone* and *Cyanopica cyanus*, we found deep splits into two lineages within each of the following species: *Corvus frugilegus*, *Pica pica* and between the species pair *Corvus monedula* – *Corvus dauuricus* (formerly treated as conspecific). Each of them is divided into two haplogroups corresponding to the western and eastern parts of their range. In contrast to the taxa with the west-east pattern, no differentiation into clearly divergent lineages was detected in three other taxa: the raven (*Corvus corax*), the Siberian jay (*Perisoreus infaustus*) and the nutcracker (*Nucifraga caryocatactes*) (Fig. 4).

It is notable that in each of these species distances between the western and eastern groups are similar, 4–5.8 %, which implies nearly the same timing of diversification events. Sequence diversity is rather low within each subclade and in the three single-group species. To explain these two types of phylogeographic pattern, one has to take into account ecological conditions which may have accompanied the climatic changes during the Pleistocene. We noted that all species of the first group preferably nest in semi-open habitats and forest edges, while the second group (single-group species) live mainly in

forests. The raven (*C. corax*) is an ubiquitous. We arrived at the conclusion that a prominent factor influencing the pattern of genetic differentiation seems to be the preference for either open to semi-open habitats (the west-east pattern) or forest dominated habitats (the single group pattern). Separated refuge areas (western and eastern) during cold periods led to accumulation of diversity. There could be several such open field refuges, but only one, namely, Altai-Sayan main forest refuge is known for LGM (Nazarenko, 1982; Anijalg et al., 2018) in which *P. infaustus* and *N. caryocatactes* might have survived (and probably suffered severe bottlenecks), followed by rapid spreading after the end of the Pleistocene. It seems that the two genetic patterns mentioned are mainly associated with different habitat requirements and to some extent with social and breeding behaviour. The comparatively high genetic diversity found in *C. corax* suggests that this species did not pass through severe bottlenecks as others. As a generalist, it could even have remained more widely distributed. Thus, comparative phylogeography helps get a general view on the interaction between macroecological features and patterns of the genetic variation.

One of the most common corvid species, the Eurasian magpie (*Pica pica* Linnaeus, 1758), is widely distributed throughout most Holarctic, with several isolated occurrences in Kamchatka, South Africa, North America and Saudi (Fig. 5). In the centre of the range, in Transbaikalia, there is a gap. Analyses of sequences of the mtDNA revealed deep genetic splits into four main lineages: (1) group West (European-Siberian), (2) group East (southern Far East), (3) *P. p. mauritanica* (North Africa) and (4) *P. p. hudsonia*

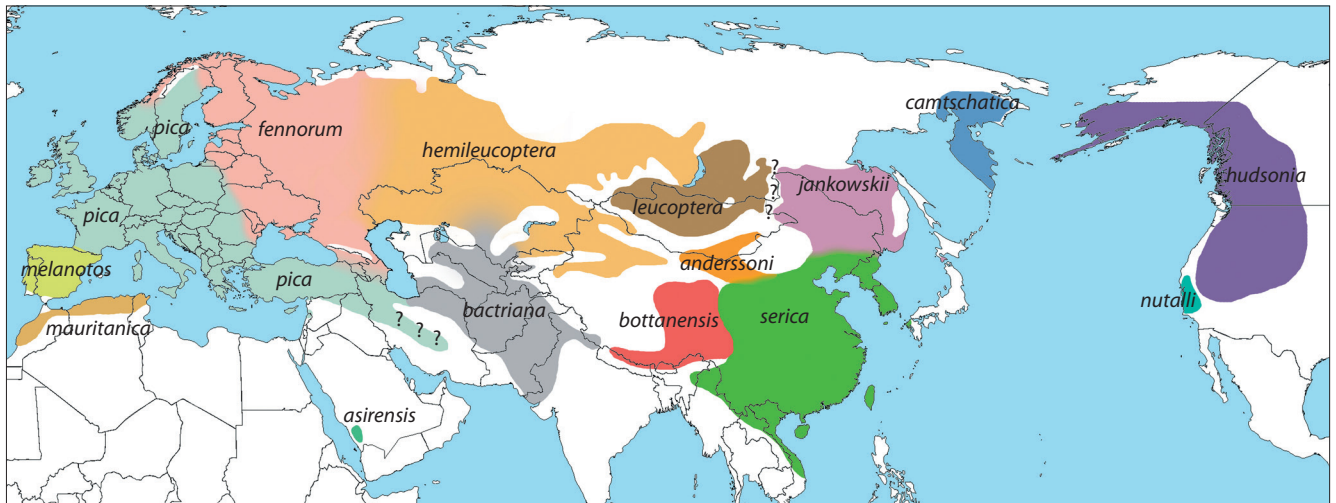


Fig. 5. Distribution of magpie *Pica pica* and its subspecies (after Kryukov et al., 2017).

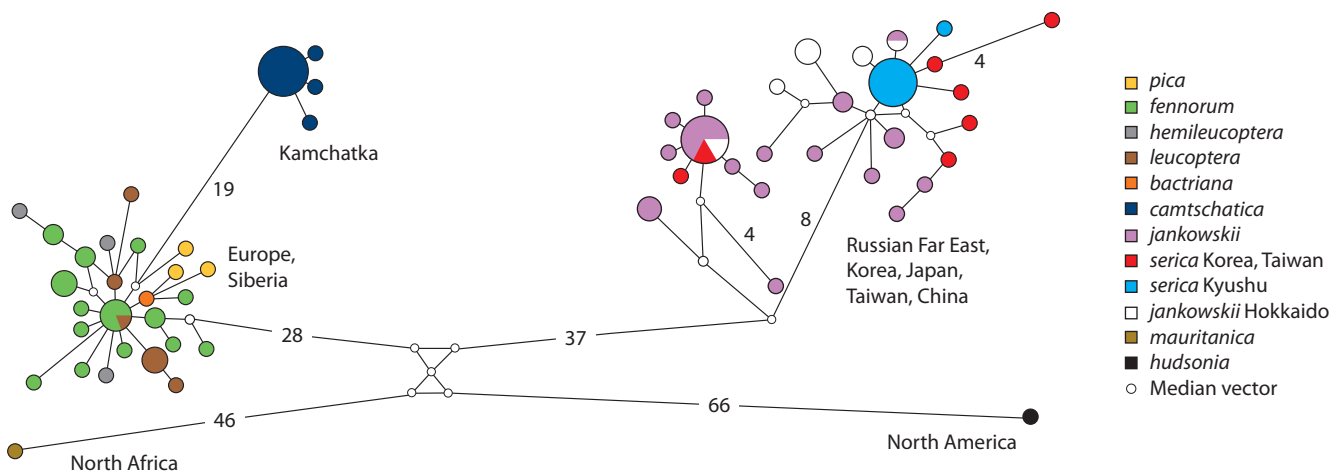


Fig. 6. Phylogenetic median-joining network for *Pica pica* based on CR of mtDNA (after Kryukov et al., 2017).

(North America) (Kryukov et al., 2017). These lineages show a geographic pattern corresponding to the subspecies or groups of subspecies with distinct phenotypic features.

In the phylogenetic network, the western subspecies group differs from the eastern one by more than 66 substitutions (Fig. 6). Differentiation within the widely-distributed group West is rather small, implying recent expansion. We detected a separate lineage in Kamchatka with clear affinity to this Euro-Siberian group. The Kamchatka lineage is homogeneous too, implying a recent bottleneck. Group East consists of two subclades without clear geographic pattern, presumably due to admixing of populations which diverged in Pleistocene refuges. The homogeneity of the Kyushu population supports historical reports on the species' introduction from Korea. The high variation in the recently established Hokkaido population can be explained by an ongoing ship-assisted invasion from the variable populations of the Far Eastern mainland. Bioacoustic data reflect phylogeographic patterns, i. e. the split into mt lineages, and differentiate groups of subspecies. Overall, our data support a scenario of divergence in geographic isolation. Furthermore, we report for the first time the fast spreading of *P. p. jankowskii* towards the west along the

upper Amur River, and a slower shifting of *P. p. leucoptera* in the opposite direction, thus yielding a new contact zone in Transbaikalia. Here the density of the Argun' river population, bearing admixture of the both mitochondrial haplogroups, is very low, but we found a few mixed pairs and phenotypical intermediates. Breeding success was dramatically decreased and in many nests only unfertilized eggs were found. This may imply sterility of F1 hybrids. This case may serve as a sample of a reproductive isolation in the zone of the secondary contact of the forms diverged by phenotypes, DNA and vocalization when they were isolated geographically.

Here I shortly overlooked several cases of intra-species genetic variation of corvid birds widely distributed in the Palearctic. The degree of their divergence depends on historical and biogeographic factors. Most species demonstrate an allopatric mode of speciation. Pleistocene cyclic glaciations and interglacial periods have greatly influenced the species distribution ranges and interaction of forms, some of them were shaped due to repeated isolation in Pleistocene refugia. In the case when distribution ranges came to the secondary contacts after spreading, successful introgression within the narrow

hybrid zones occurs (*Corvus c. cornix* with *C. c. corone* and *C. c. orientalis*), or semisympatry with reproductive isolation (*Pica p. leucoptera* and *P. p. jankowskii*). Timing of the initial divergence and secondary contacts is hard to determine and is always disputable, mainly due to the lack of reliable calibration by fossil records in birds. Intra-species taxonomy, traditionally based on morphology, often does not correspond with DNA sequence data. However, mtDNA sequences still represent a useful tool for phylogeographic aims, even when using short DNA regions, provided that sampling covers the main part of the species distribution range.

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