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Phylogeographic patterns in widespread corvid birds

E. Haring [a,*], A. Gamauf [a], A. Kryukov [b]

[a] *Museum of Natural History Vienna, 1st Zoological Department, Burgring 7, A-1010 Vienna, Austria*
[b] *Institute of Biology and Soil Science, Russian Academy of Sciences, Vladivostok 690022, Russia*

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Abstract

Intraspecific genetic diversity and phylogeography of *Corvus corone* was investigated using the mitochondrial (mt) control region as a molecular marker. A split into two distinct mt lineages was observed. One represents individuals from a wide geographic range spanning from England to the Russian Far East (Kamchatka), while the other one was found in the Primorye and Khabarovsk regions (southern parts of Russian Far East) as well as Japan. For comparison, we investigated several widespread Palearctic corvid taxa with respect to their phylogeographic patterns. A deep split into two lineages was revealed in five cases: Besides *C. corone*, within *Corvus frugilegus*, *Pica pica*, and between the species pairs *Corvus monedula–Corvus dauuricus* and *Cyanopica cyanus–Cyanopica cooki*. Although these taxa display a variety of distribution patterns, from disjunct, para/allopatric to continuous, the genetic pattern and level of divergence between clades is very similar. This implies that the differentiation started in about the same time range. In contrast, no differentiation into highly divergent lineages was detected in *Corvus corax*, *Perisoreus infaustus*, and *Nucifraga caryocatactes*. We try to explain the two phylogeographic patterns in corvid birds with ecological factors accompanying the changing climatic conditions during the Pleistocene. The deep genetic splits within several widely distributed Palearctic corvids are discussed with respect to taxonomic questions.

Keywords: Corvidae; Phylogeography; West–East Palearctic differentiation; Pleistocene; Intraspecific variation

1. Introduction

The family Corvidae comprises 113 species grouped in 25 genera, which are rather different in appearance and size (Goodwin, 1986; Madge and Burn, 1993). Evolution of this group of birds as well as controversial views on the phylogenetic relationships among and within genera were addressed in several molecular studies (Helm-Bychowski and Cracraft, 1993; Espinosa de los Monteros and Cracraft, 1997; Cibois and Pasquet, 1999; Omland et al., 2000, 2006; Saunders and Edwards, 2000; Kryukov and Odati, 2000; Fok et al., 2002; Iwasa et al., 2002; Lee et al., 2003; Ericson et al., 2005; Feldman and Omland, 2005; Baker and Omland, 2006; Ekman and Ericson, 2006). In some of these papers paraphyly and the existence of genetically differentiated cryptic species were indicated by sequence analyses of mitochondrial (mt) DNA (control region, CR; *cytochrome b*, *cytb*) or microsatellite studies. For example, in the common raven *Corvus corax* two very distinct clades of mt haplotypes were detected (Omland et al., 2000). One clade, which is the sister group of the Chihuahuan raven *Corvus cryptoleucus*, consists of haplotypes from Californian populations whereas the other clade comprises populations distributed over the remaining Holarctic. Further examples are the phylogeographic subdivisions in *Cyanopica cyanus* and *Pica pica* revealed by sequence data of the mt CR and the *cytb* gene. For the azure-winged magpie *Cy. cyanus* it has been shown that the two geographically disjunctive forms represent clearly differentiated mt lineages (Fok et al., 2002; Kryukov et al., 2004). Morphometric analyses (Kryukov et al., 2004) corroborated the split into two distinct species, as proposed earlier by Fok et al. (2002): the western *Cyanopica cooki* (Iberian Peninsula) and the eastern *Cy. cyanus* (Eastern Palearctic). A similar mt haplotype pattern with

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[*] Corresponding author. Fax: +43 1 5235254.
E-mail address: elisabeth.haring@nhm-wien.ac.at (E. Haring).

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two clearly separated groups was found in the magpie *P. pica*, a species with a continuous distribution area spanning throughout the Palearctic and the western part of the Nearctic (Lee et al., 2003; Kryukov et al., 2004).

Another example is the carrion crow *Corvus corone* Linnaeus, 1758, where investigation of the *cytb* gene revealed two distinct haplogroups (Kryukov and Suzuki, 2000). One represented individuals from France to northern Sakhalin Island (comprising the three subspecies, *C. c. corone*, *C. c. cornix* and *C. c. orientalis*), whereas the other one included exclusively *C. c. orientalis* individuals from the south-eastern part of the distribution area (Russian Far East: Primorye region and Southern Sakhalin). The taxonomic subdivision of *C. corone* has been controversial. Parkin et al. (2003) and Stepanyan (2003) treated it as a superspecies with two semispecies, *C. corone* (*C. c. corone* and *C. c. orientalis*, both black coloured) and *C. cornix* (with a grey and black plumage, hybridizing with the former two). Knox et al. (2002) considered *C. orientalis* as a separate species. Most checklists, however, still treat *C. corone* as a single species with up to six subspecies (Mayr and Greenway, 1962; Cramp and Perrins, 1994; Dickinson, 2003), a classification we adopted in the present work.

Since in the study of Kryukov and Suzuki (2000) the western regions of the distribution range of *C. corone* were underrepresented, more data were needed to corroborate those findings. Therefore, in the present study we performed an extended analysis with a much larger sample size to cover a broader geographic range. Our aim was to find out whether the distinct position of the eastern clade within *C. c. orientalis* can be confirmed with another molecular marker and to test if the subspecies can be distinguished genetically.

Furthermore we asked, whether similar phylogeographic patterns might be also found in other corvid species. Therefore, we included several additional taxa with a similar wide-spread distribution in the Palearctic for comparison with the results obtained from *C. corone* as well as from *Cy. cyanus*/*Cy. cooki*, and *P. pica* (Kryukov et al., 2004): (1) The rook *Corvus frugilegus* Linnaeus, 1758: The range of this species covers almost the entire temperate southern Palearctic (from Scandinavia and north-western France to low Amur River and the Korean Peninsula). Two subspecies are currently accepted (Dickinson, 2003), *C. f. frugilegus* Linnaeus, 1758, and *C. f. pastinator* Gould, 1845. The ranges are separated by a presumably narrow gap zone in Central Siberia. Interactions and contacts of the two subspecies in Siberia have not been studied yet. (2) The common raven *Corvus corax* Linnaeus, 1758: This species is distributed all over the Holarctic. The "Holarctic clade" described by Omland et al. (2000, 2006) comprises eight to eleven subspecies (Mayr and Greenway, 1962; Dickinson, 2003). For comparison of intraspecific genetic diversities among corvid taxa we included *C. corax* with more representatives from the Palearctic range, especially from the Western Palearctic. (3) The closely related species pair, Eurasian jackdaw *Corvus monedula* Linnaeus, 1758, and Daurian jackdaw *Corvus dauuricus* Pallas, 1776: Their treatment as two distinct species has been controversial in the past (Meise, 1928; Rustamov, 1954; Ivanov and Stegman, 1964; Bährmann, 1968; Dickinson, 2003). The polytypic *C. monedula* occurs in the temperate and southern zone of the Western Palearctic, whereas the monotypic *C. dauuricus* is found in the east. (4) The Eurasian nuthatch *Nucifraga caryocatactes* Linnaeus, 1758: This species covers the Palearctic from Central Europe to Japan and Taiwan, with several isolated occurrences. It is subdivided into nine subspecies (Mayr and Greenway, 1962; Dickinson, 2003). (5) The Siberian jay *Perisoreus infaustus* Linnaeus, 1758: This species is distributed over the Northern Palearctic and comprises usually eight to ten subspecies (Mayr and Greenway, 1962; Dickinson, 2003), but some ornithologists even treated it as monotypic (Buturlin, 1916).

As a molecular marker we selected the mt CR, which is widely used for phylogeographic analyses and has been employed successfully in our previous study (Kryukov et al., 2004). We screened the species mentioned above for the presence/absence of phylogeographic patterns such as a split into two distinct lineages as found in *C. corone*, *P. pica*, and *Cyanopica.* For this purpose we investigated specimens from geographically widely separated origins.

2. Materials and methods

2.1. Samples, DNA extraction, PCR amplification, and sequencing

Liver and muscle samples stored in ethanol, skin samples from foot pads of museum specimens, as well as feathers were used for DNA extraction. Sequences of 179 individuals from ten species were included (Appendix A). Subspecific assignment was done according to Dickinson (2003). For *P. pica* subspecific taxonomy is partly ambiguous. Although several previously analysed specimens (Ppcpic4, Ppicpic5, Ppicbac5, Ppicbac6) may be assigned to *P. pica fennorum* (Ya. Red'kin, personal communication), we kept the taxonomic names that we used in our previous study (i.e., *P. p. pica*, *P. p. bactriana*) to avoid confusion and facilitate comparisons of individuals between studies. Besides that, according to our data, the classical subspecific division is not supported. DNA from feathers and museum material was extracted by incubation of tissues in a 10% Chelex (Bio-Rad) solution containing proteinase K (0.5 mg/ml) for 4 h at 56 °C (with agitation). Subsequently extractions were heated to 95 °C for 5 min and centrifuged for 1 min. The supernatant was purified using the QIAquick PCR Purification Kit (Qiagen) with a final volume of 30–70 µl elution buffer. DNA from muscle samples was extracted by overnight incubation at 50 °C in extraction buffer (10 mM Tris–HCl, pH 8.0, 10 mM EDTA, 50 mM NaCl, 40 mM dithiothreitol, 1% SDS, 0.5 mg/ml proteinase K). DNA was purified by two PCI (phenol/chloroform/isoamylalcohol, 25:24:1) and one CI (chloroform/

isoamylalcohol, 1:1) extractions followed by precipitation with 1/10 vol. 3 M NaAc, 3× vol. EtOH. The following primers were used for the amplification of the control region (CR): CR-Cor+ (ACCCTTCAAGTGCGTAGC AG) and Phe-Cor−(TTGACATCTTCAGTGTCATGC). These primers amplify a partial sequence of the CR (positions 693–1308 of the reference sequence of *C. c. cyanus*, AJ458536) as well as 21 bp of the adjacent *tRNA-Phe* gene (length of PCR fragment ~680 bp). To obtain the CR sequence from old samples with bad DNA quality overlapping PCR fragments were amplified using various primers: For the 5′-fragment CR-Cor3− (TAAAAATTGTTGTTT ATTTTG) or CR-Cor6− (GATGATTTGGACAATCT AGG) in combination with CR-Cor+, and for the 3′-fragment CR-Cor5+ (ACTAGGAATTATCACCRAAA), CR-Cor4+ (ATTTTTATCTTGTCATTTTA), or CR-Cor2+ (TCGTTTATTTTTATTTTGTAA) in combination with Phe-Cor−.

PCR was performed on a Master gradient thermocycler (Eppendorf) in 25 μl with 0.5 U Dynazyme DNA polymerase (Finnzyme OY), 1 μM of each primer and 0.2 mM of each dNTP (Boehringer Mannheim); annealing temperature: 58 °C; 35 reaction cycles. Control reactions of both DNA extraction and PCR amplification were performed. PCR products were extracted from agarose gels using the QIQquick Gel Extraction Kit (Qiagen) and cloned (TOPO TA Cloning Kit, Invitrogen). Sequencing of both strands was performed by MWG-Biotech (Germany). To detect whether amplified sequences contained more than one variant (e.g., nuclear pseudogenes) selected PCR products were directly sequenced in both directions on an automated LiCor sequencer. No double bands were detected in these amplifications.

2.2. Phylogenetic analysis

Editing and alignment of sequences were performed using the BioEdit software package version 5.0.9 (Hall, 1999). Neighbour-joining (NJ; Saitou and Nei, 1987) dendrograms were calculated with the software package PAUP (version 4.0b10; Swofford, 2002) using *p*-distances. Bootstrap analyses were performed with 1000 replicates. Bayesian trees were calculated using MrBayes 3.0 (Huelsenbeck and Ronquist, 2001) by MCMC sampling for 6 million generations (four simultaneous MC chains, sample frequency 100, burn-in 10,000). The substitution model HKY85 + I + G was determined with the ModelTest software (version 3.06; Posada and Crandall, 1998). As outgroup species for the comprehensive tree we used *Cyanocorax cyanomelas* and *Cyanocorax chrysops*. For calculation of other trees the taxon with the lowest average distance was chosen as outgroup. For these sub-trees new alignments were made from reduced data sets. The number of haplotypes (n_h), number of polymorphic sites (n_p), nucleotide diversity (π), and haplotype diversity (h) were calculated with ARLEQUIN 2.000 (Schneider et al., 2000). Average p-distances between and within clades and subclades were calculated with the software PHYLTEST (Kumar, 1996). The expected mismatch distribution of an expanding population was calculated with DNASP v.3.99.5 (Rozas et al., 2003) to fit the observed data with models of population expansion. We also calculated the raggedness index (r) of the mismatch distribution (Harpeding, 1994). The raggedness index takes high values when sequences are diverse and few individuals share the same haplotypes, which is expected in constant populations with multimodal mismatch distributions. Moreover, Tajima's D was calculated using DNASP v.3.99.5. Negative values of Tajima's D suggest recent demographic expansion. Significance ($\alpha = 0.05$) of both raggedness index and Tajima's D were evaluated by comparison to a distribution generated from 10,000 random simulations of the data.

Unrooted parsimony haplotype networks (95% probability level) of the *C. corone* data set were constructed by the method of Templeton et al. (1992) with the software TCS version 1.21 (Clement et al., 2000) treating gaps as 5th character state.

Previously published CR sequences of *P. infaustus* from GenBank were compared to the sequences determined in this study: Accession Nos. AF131078 (Saunders and Edwards, 2000) and AF218935 (Uimaniemi et al., unpublished). The sequences determined in the course of the present study as well as those from our previous study are registered under the GenBank Accession Nos. in Appendix A.

3. Results

The alignment of CR sequences (long fragment) with a length of 690 sites included 169 individuals from 10 species of which 167 comprised the ingroup (Appendix A). The NJ tree shown in Fig. 1 illustrates the genetic differentiation within the taxa under study. Among the main clades there are five cases where a subdivision into differentiated subclades can be observed: (1) within each of the species *C. corone*, *C. frugilegus*, and *P. pica*, and (2) in the two species pairs *Cy. cyanus*/*Cy. cooki* and *C. monedula*/*C. dauuricus*, where the subdivision corresponds to the respective species assignments. These splits correspond to geographic divisions and we designated the subclades as "western" and "eastern" groups, although in *C. corone* and in *P. pica* the "western group" extends far to the east covering almost the entire Palearctic except its easternmost part (Lee et al., 2003; this study). In contrast, in *N. nucifraga*, *P. infaustus*, and *C. corax*, no similar intraspecific subdivision into two or more subclades was observed. Each of the species forms only one compact clade of closely related sequences.

Since the tree is intended to illustrate the raw data and to give an overview of the amount of genetic differentiation between clades, it does not include the sample codes. Instead we indicate whether a geographic grouping (west/east) was found within species or species pairs. Average distances within the respective clades/subclades, and between pairs

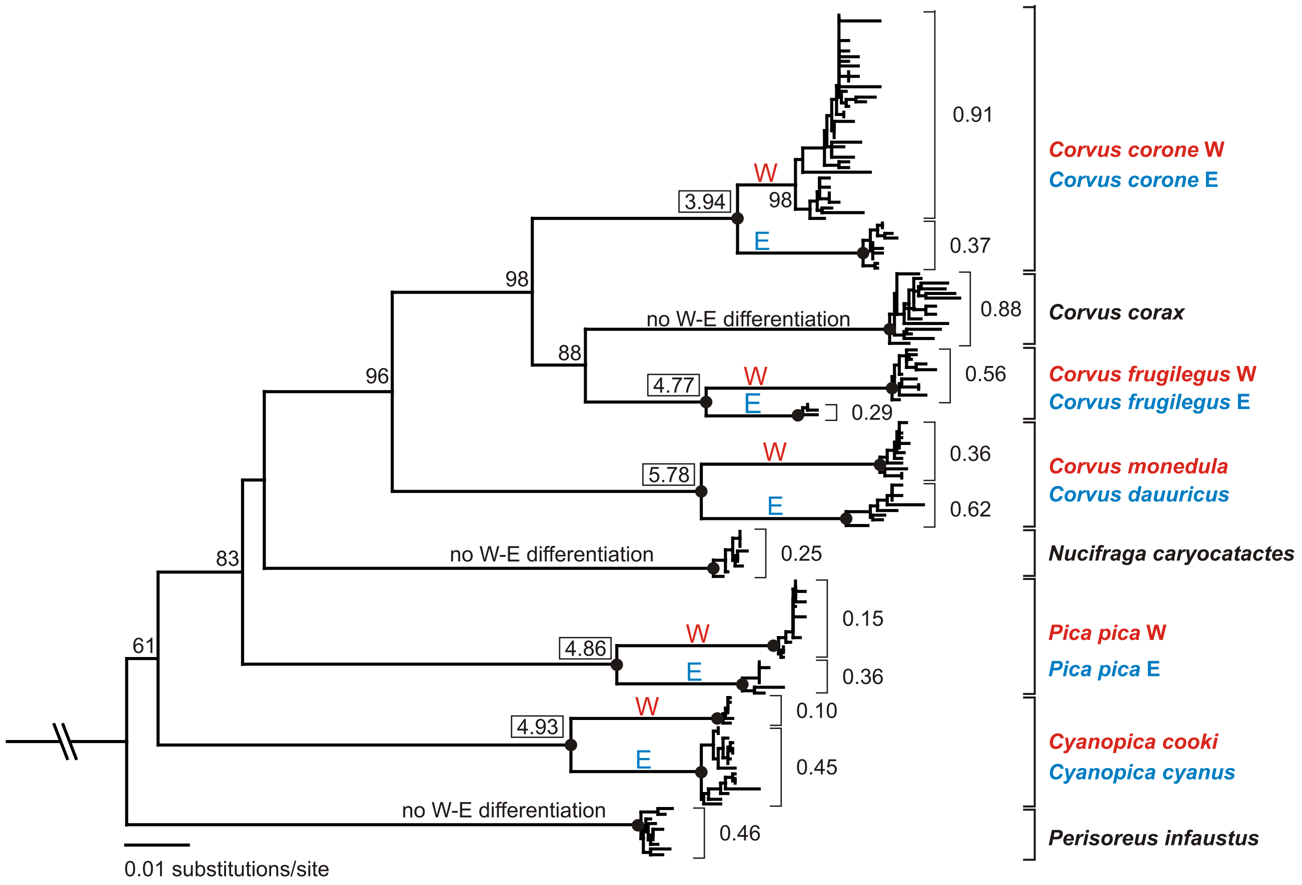

Fig. 1. NJ tree based on 169 CR sequences (167 ingroup) from widespread Eurasian corvid taxa to demonstrate the large-scale geographic patterns. West (red)–east (blue) differentiation found within species or between sibling species is indicated on branches (W,E). Average *p*-distances (%) within clades/subclades are given on the right and average distances (%) between eastern and western subclades are given at the nodes (framed). Nodes with bootstrap values of 100% are depicted as black dots. Bootstrap values (>50%) are indicated at the nodes (not for nodes within clades/subclades). Outgroup species: *Cyanocorax cyanomelas*, *Cyanocorax chrysops* (not shown).

of subclades are shown. Bootstrap support for clades and subclades was generally high (100%, except 98% for the western *C. corone* subclade). The posterior probability values obtained in the Bayesian analysis (same topology, not shown) were also high: 100% for all clades/subclades except the western *P. pica* clade (99%) and the western *C. corone* clade (collapsed).

In Figs. 2–4 we present more detailed species trees (NJ) based on alignments of reduced data sets together with distribution maps indicating the geographic origins of the samples. Ten specimens, of whom only the 5′-fragment could be amplified, were assigned to mt clades on the basis of this shorter sequence. The assignment of these individuals was straightforward and unambiguous, although in a comprehensive tree based on the 5′-fragment of all individuals (not shown) the deeper nodes are not clearly resolved.

3.1. Species with west–east differentiation

3.1.1. Corvus corone (Fig. 2)

The two subclades found in *C. corone* do not reflect current taxonomic (subspecific) differentiation. The eastern one contains 10 individuals from Far East, representing *C. c. orientalis*, whereas the other subclade comprises 41 individuals representing the subspecies *C. c. corone* (western Europe), *C. c. cornix* (eastern Europe to Central Siberia), *C. c. orientalis* (eastern Siberia), as well as two additional subspecies from the southern parts of the distribution range (*C. c. sardonius* and *C. c. capellanus*). Hybrids between *C. c. corone* and *C. c. cornix* and between *C. c. cornix* and *C. c. orientalis* are found in the western subclade. The western subclade is further subdivided into two clusters (nodes a and b in Fig. 2), although it has to be emphasized that clade a is very poorly supported. Cluster a comprises members of the five subspecies investigated, while cluster b contains eight *C. c. orientalis* individuals and one individual morphologically classified as a hybrid between *C. c. orientalis* and *C. c. cornix*, which was trapped in the Siberian hybrid zone. The geographic range of these individuals (origins indicated in the distribution map by white triangles) overlaps widely with that of the remaining members of the western subclade (black triangles) as well as with the eastern subclade (black dots). Thus, with the exception of the eastern subclade (Primorye and Khabarovsk regions, Russia; Japan) no further clear-cut geographic structuring of the *C. corone* clade is found.

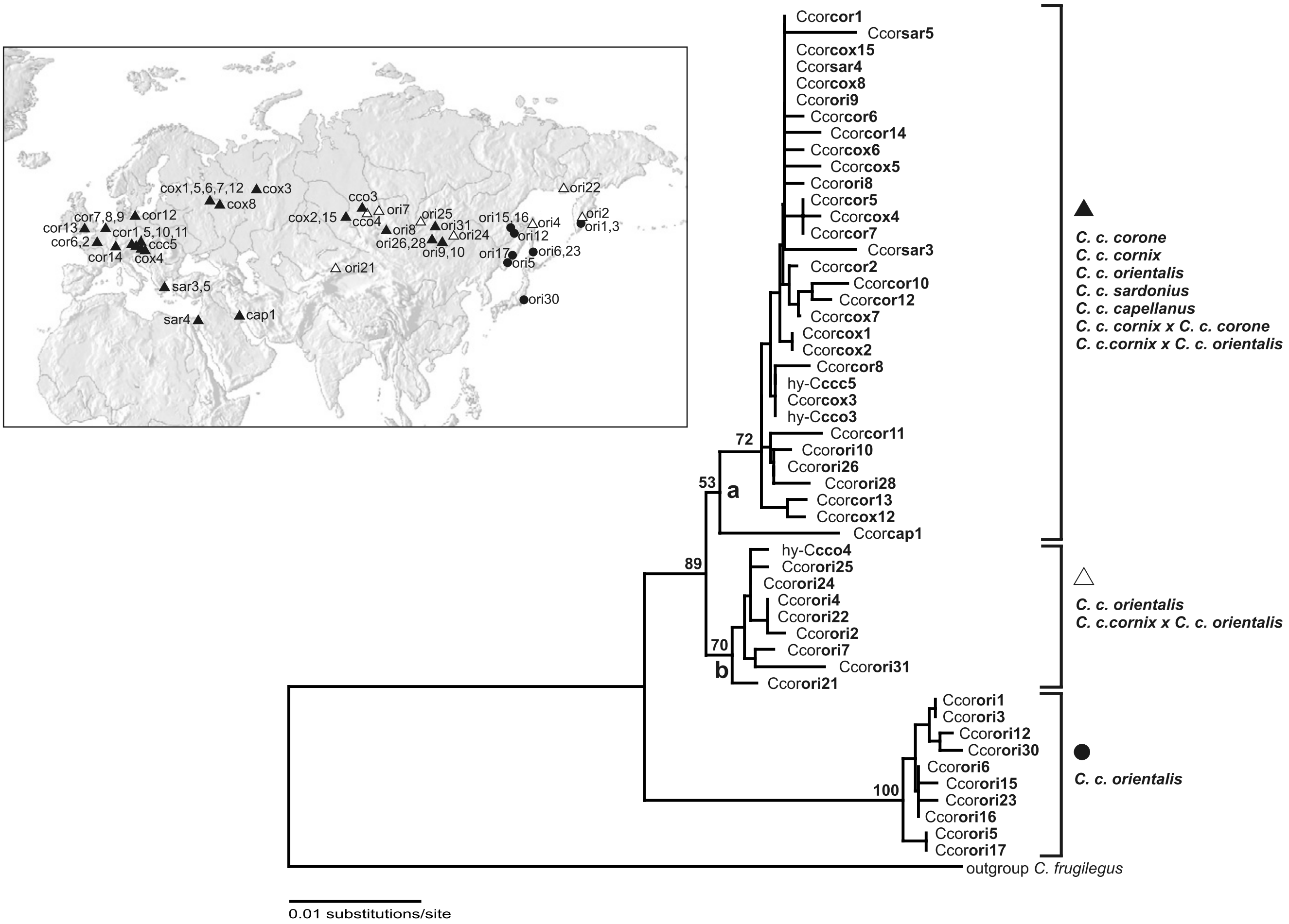

Fig. 2. NJ tree based on CR sequences of *C. corone* and geographic origin of samples. Labcodes of specimens in the tree correspond to those in Appendix A; in the map only the last three letters plus number are used. Nodes a and b are described in the text. Bootstrap values (>50%) are indicated at the nodes. Sample Ccorcor9 is present in the map only (small fragment sequenced only).

Moreover, the genetic differentiation is neither in accordance with taxonomy nor with the two conspicuous variants of plumage colour (black vs. grey–black): the western group includes both forms, while the eastern group comprises only black individuals.

For a better illustration of haplotype relationships we constructed parsimony networks (Fig. 5). Since the western and eastern group could not be connected under the 95% connection limit, (they are separated by 21 substitutions) two separate networks were calculated. The eastern subclade, composed of exclusively *C. c. orientalis* appears quite simple with four lineages originating from a central haplotype. In the network of the western group the most prominent split is that between two clusters corresponding to the subclades a and b observed in the NJ tree (Fig. 2). The samples of this group are linked to the main cluster by several connections of at least seven mutational steps. The main cluster comprises all subspecies analyzed except the individual of *C. c. capellanus*, which is found distantly from both clusters (9 and 10 steps, respectively). Within the main cluster there is no taxonomic (i.e., geographic) pattern. Interestingly, the central haplotype (with the highest outgroup weight in the network; 0.17) is composed of sequences of the three subspecies *C. c. cornix*, *C. c. orientalis*, and *C. c. sardonius*. The two other *C. c. sardonius* individuals are found more distantly (4 and 6 steps, respectively) from this haplotype.

For the western subclade of *C. corone* we performed a mismatch analysis to examine whether the observed data would fit with the model of population expansion. We carried out the analyses with subclades a and b separately (the single sample from Iraq, Ccorcap1, was excluded from the analysis since it is not clear whether it represents an additional clade). For both data sets the distribution of pairwise sequence differences yielded a multimodal distribution consistent with a stable population at equilibrium (not shown). However, the raggedness index (Harpeding, 1994) was not significant for subclade a ($P = 0.10$) and thus in accordance with the assumption of population expansion. Moreover, Tajima's D was significantly negative for subclade a ($D = -2.181$, $P < 0.01$). For subclade b, the raggedness index was significantly different from that expected under the population expansion model ($P = 0.05$) and Tajima's D was not significantly different from zero ($D = -1.128$, $P > 0.10$), results that are in favour for a stable population size. Summarizing, the data are in accordance with a population expansion model only with respect to subclade a.

3.1.2. *Corvus frugilegus* (Fig. 3a)

Although the sample number is comparatively low for *C. frugilegus* a clear differentiation into two subclades becomes apparent. This grouping corresponds in general to the division into the two subspecies *C. f. frugilegus* (west) and *C. f. pastinator* (east). The western group comprises

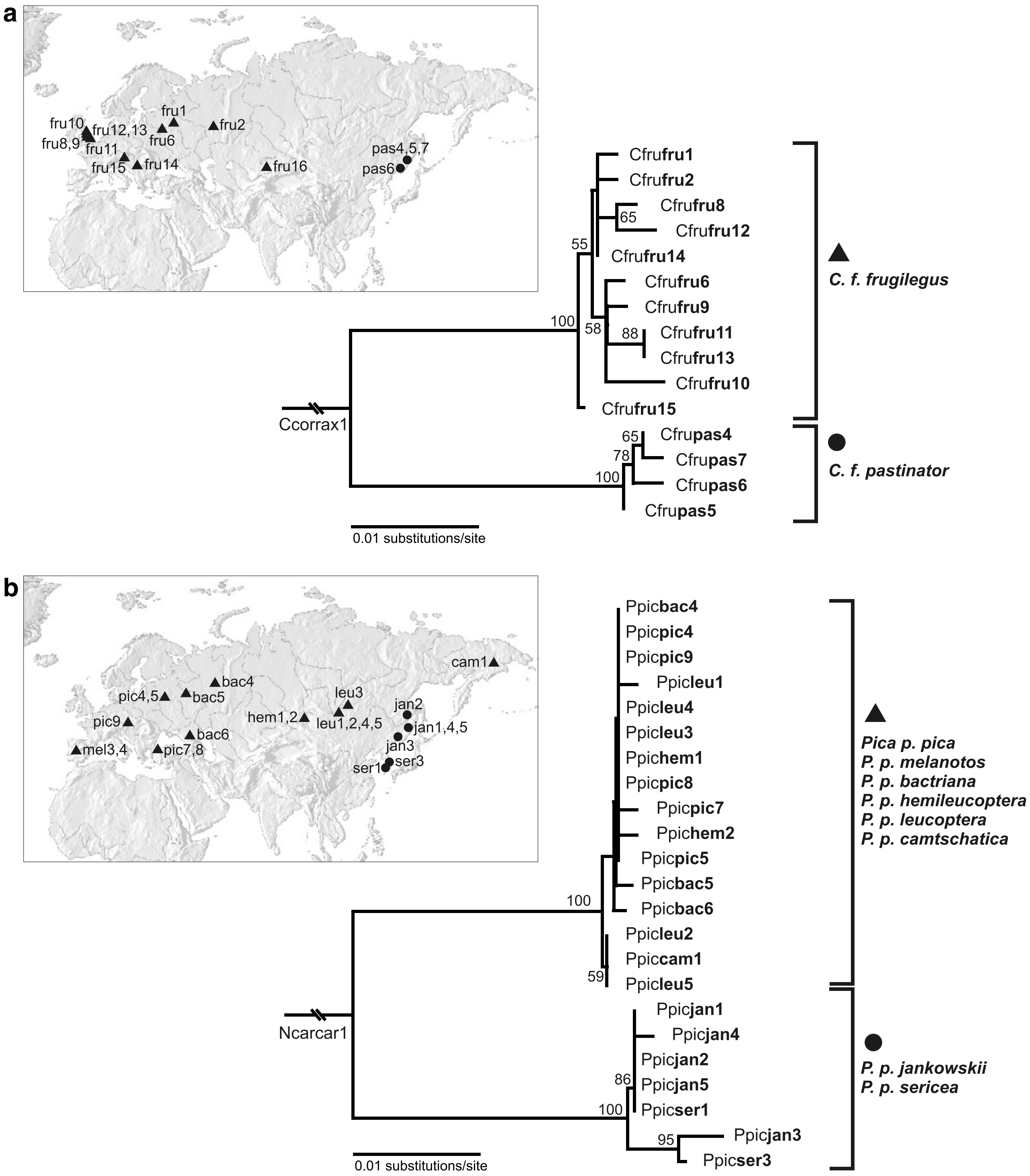

Fig. 3. NJ tree based on CR sequences of *C. frugilegus* (a), *P. pica* (b), *C. monedula*/*C. dauuricus* (c), and *Cy. cyanus*/*Cy. cooki* (d) and geographic origin of samples. Labcodes of specimens in the trees correspond to those in Appendix A; in the map only the last three letters plus number are used. Bootstrap values (>50%) are indicated at the nodes. Specimens assigned to clades on the basis of short sequences (not included in the tree): *C. frugilegus* (a): Cfrufru16 (western subclade); *P. pica* (b): Ppicmel3, Ppicmel4 (western subclade).

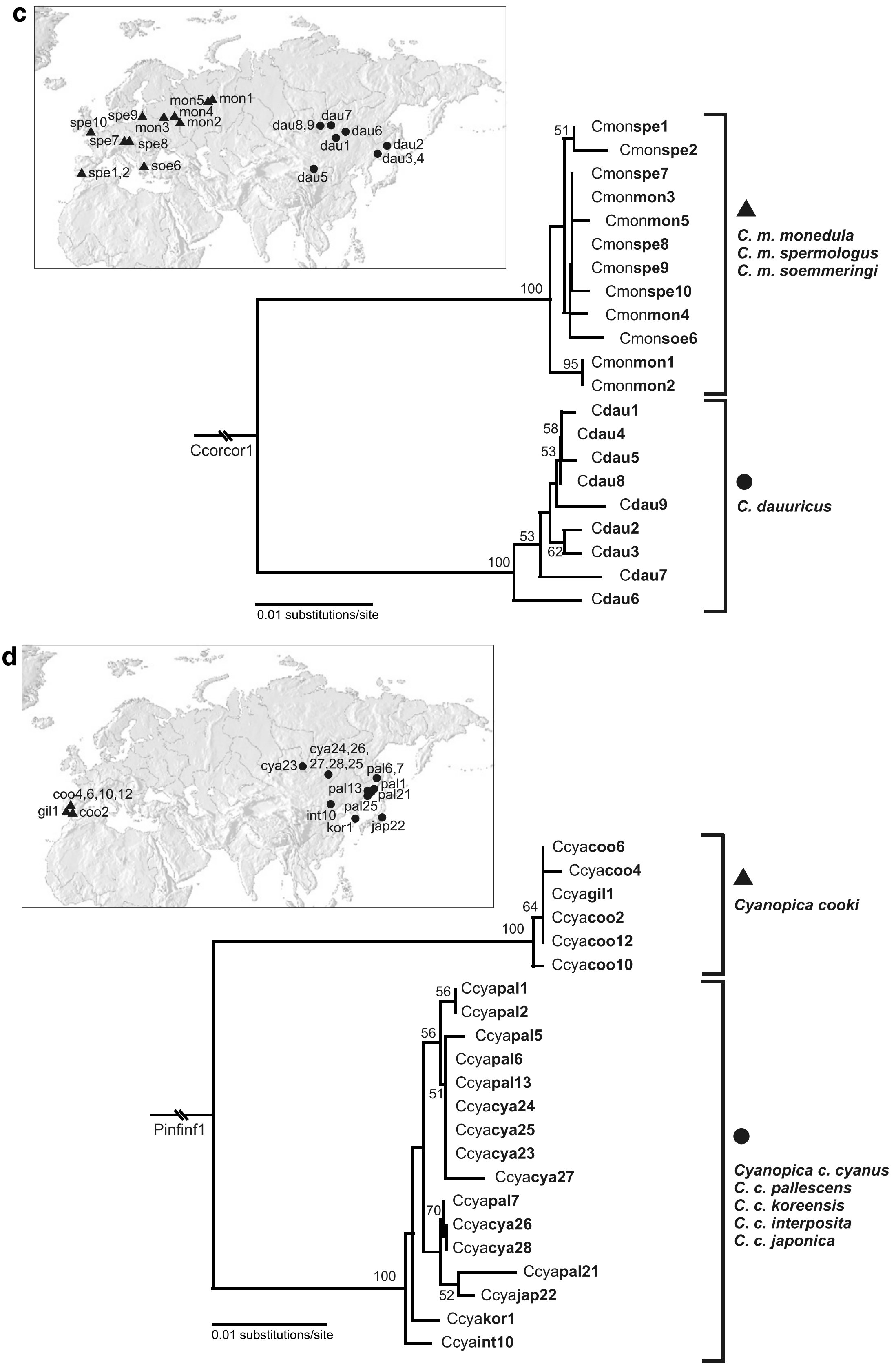

Fig. 3 (*continued*)

samples from England to western Russia: The four individuals of *C. f. pastinator* in the eastern subclade originate from Primorye region. Moreover, one individual was assigned to the western group based on the sequence of

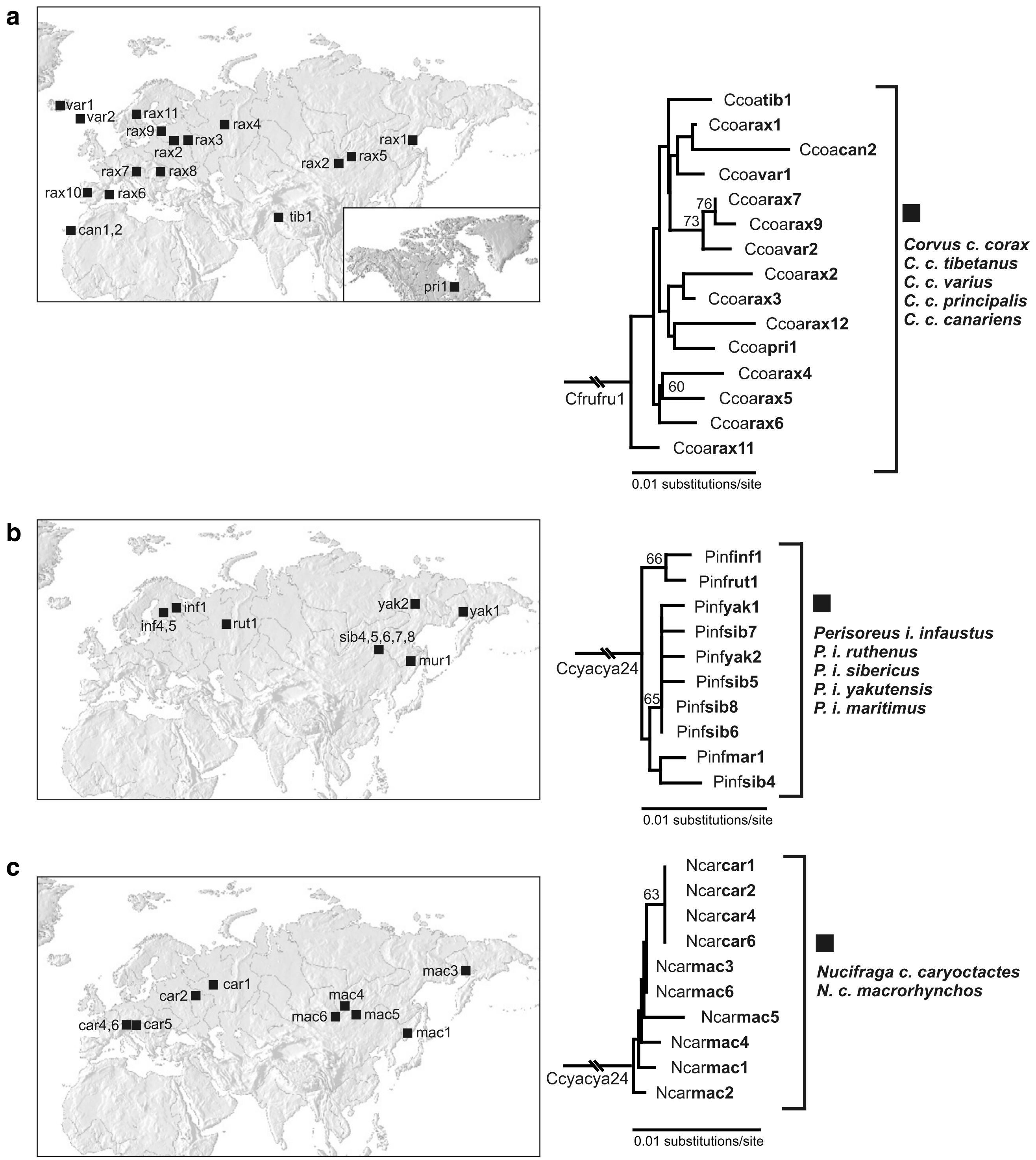

Fig. 4. NJ tree based on CR sequences of *C. corax* (a), *P. infaustus* (b), and *N. caryocatactes* (c) and geographic origin of samples. Labcodes of specimens in the tree correspond to those in Appendix A; in the map only the last three letters plus number are used. Bootstrap values (>50%) are indicated at the nodes. Specimens assigned to clades on the basis of short sequences: *C. corax* (a): Ccoarax8, Ccoarax10, Ccoacan1; *P. infaustus* (b): Pinfinf5, Pinfinf4, *N. caryocatactes* (c): Ncarcar5.

the small (5′) CR fragment: Cfrufru16 from Central Asia, Issyk-Kul, Kyrgyzstan.

3.1.3. *Pica pica* (Fig. 3b)

The eastern subclade of *P. pica* is formed by seven individuals from the Russian Far East (Primorye and Khabarovsk regions) and Korea. It includes members of the subspecies *P. p. sericea* and *P. p. jankowskii.* The western subclade comprises 16 individuals representing the five subspecies *P. p. pica*, *P. p. leucoptera*, *P. p. hemileucoptera*, *P. p. bactriana*, and *P. p. camtschatica*. Two individuals from Spain (*P. p. melanotos*; Ppicmel3, Ppicmel4) belong to this subclade

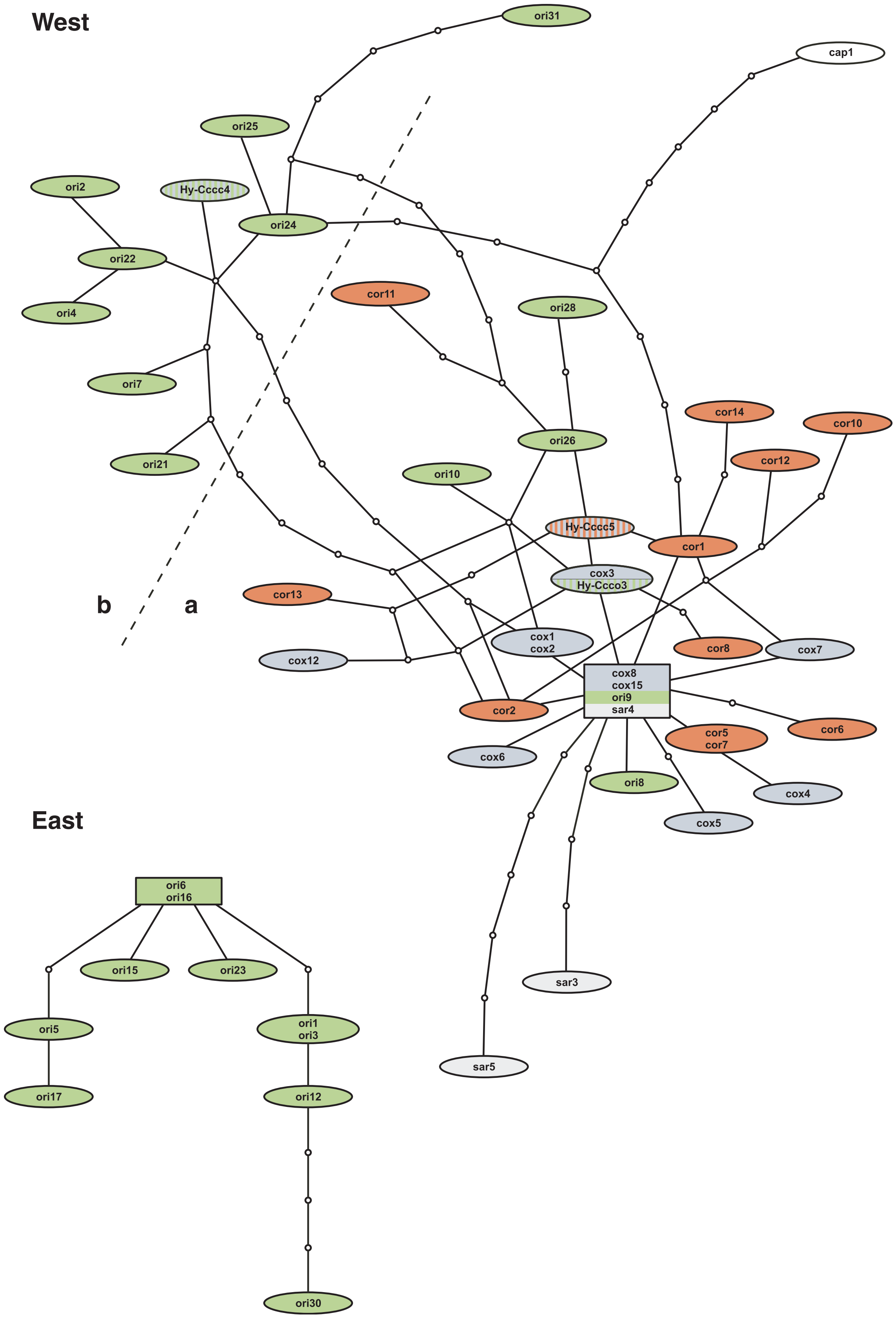

Fig. 5. Parsimony network of *C. corone*: The western and eastern subclades cannot be connected under the 95% limit. The dotted line indicates the split between subclades a and b of the western clade. Labcodes of specimens correspond to those in Appendix A (the last three letters indicating subspecies plus number). Subspecific assignment is also illustrated by different colours. The central haplotypes (with highest outgroup weight) are depicted as squares. Small circles indicate steps connecting the haplotypes.

according to the sequences of the 5′-fragment. Thus, this group spans a vast region extending from Spain, western Europe, Turkey, central Russia and Transbaikalia to Chukotka Peninsula in Northeast Asia. Within subclades no further clustering according to subspecific division is found.

3.1.4. Corvus monedula/Corvus dauuricus (Fig. 3c)

The 12 individuals belonging to the western subclade (from Spain to western Russia/Kirov region) represent three subspecies of *C. monedula* (*C. m. monedula*, *C. m. spermologus*, *C. m. soemmerringii*) and the nine individuals in the eastern subclade represent *C. dauuricus.* Their localities range from Baikal region to Russian Far East and Central China. Thus, the geographic extension of the eastern group is similar to that found within *Cyanopica*, while in *C. frugilegus P. pica*, and *C. corone* it seems to be more restricted to the east.

3.1.5. Cyanopica cyanus/Cyanopica cooki (Fig. 3d)

The six individuals of *Cy. c. cooki* and one individual of *Cy. c. gili* represent the western subclade. The sequence of *Cy. c. gili* is identical with that of three specimens of *Cy. c. cooki* with the exception of a 1-bp deletion. The other two sequences representing *Cy. c. cooki* differ by one substitution each. The eastern subclade is formed by 16 individuals of *Cy. cyanus* (subspecies *Cy. cy. pallescens*, *Cy. cy. cyanus*, *Cy. cy. koreensis*, *Cy. cy. interposita*, *Cy. cy. japonica*) covering a region from Lake Baikal to North China, Primorye Region, Russia, Korea, and Japan. There is no obvious pattern in the tree with respect to these subspecies. E.g, *Cy. cy. pallescens* is present in two clusters together with *Cy. cy. cyanus* and *Cy. cy. japonica*, respectively.

3.2. Species lacking west–east differentiation (Figs. 4a–c)

The *C. corax* (Fig. 4a) clade contains 15 individuals representing five subspecies: *C. c. corax*, *C. c. tibetanus*, *C. c. varius*, *C. c. principalis*, *C. c. canariensis* (after Dickinson, 2003) covering the whole Palearctic from Iceland to the Russian Far East, and in the south to the Canary Islands and to Tibet. The Nearctic region is represented by a sample from Canada. From two individuals of *C. c. corax* (Ccoarax8, Spain; Ccoarax10, Romania) and from one of *C. c. canariensis* (Ccoacan1, Fuerteventura) only the small CR fragment was obtained. These three sequences fall into the variation of the other *C. corax* sequences: Ccoarax8 clusters with Ccoapri1 from Canada, while Ccoarax10 is identical with Ccoavar2 from Faroe Islands (Denmark). The specimen Ccoacan1 differs by two substitutions from Ccoacan2 from which the complete fragment was isolated. The latter branches off in the middle of the *C. corax* clade, the next relative being Ccoarax1 from the Russian Far East.

The two other species *P. infaustus* (Fig. 4b) and *N. caryocatactes* (Fig. 4c) forming a single clade each both cover a wide geographic west-east range. Interestingly, within both species distances are very low (Table 1). Samples of *P. infaustus* originate from Finland to Northeast Siberia (Magadan region) representing five subspecies (*P. i. infaustus*, *P. i. ruthenus*, *P. i. sibericus*, *P. i. yakutensis*, *P. i. maritimus*). Two 5′-fragments of *P. i. infaustus* were obtained of samples from Finland (Pinfinf4, Pinfinf5). Pinfinf5 is identical to Pinfinf1 and Pinfinf4 differs in one position from this sequence. Previously published CR sequences of *P. infaustus* (Saunders and Edwards, 2000; Uimaniemi, GenBank direct submission) were compared

Table 1
Genetic diversity within and between clades/subclades in the 690-bp CR section

		C.cor	C.fru	P.pic	Cy.coo/Cy.cya	C.mon/C.dau	C.rax	P.inf	N.car
W	h	98.9	98.2	93.3	80.0	98.5	—	—	—
	π	1.000	0.772	0.350	0.157	0.643	—	—	—
	$n/n_{\mathrm{h}}/n_{\mathrm{p}}$	41/35/60	11/10/ 19	16/10/10	6/4/3	12/11/15	—	—	—
	p	0.9	0.6	0.2	0.1	0.4	—	—	—
	Range (p)	0–2.5	0–1.1	0–0.3	0–0.3	0–0.8	—	—	—
E	h	95.6	100.0	71.4	95.0	100.00	—	—	—
	π	0.507	0.366	0.410	0.523	0.707	—	—	—
	$n/n_{\mathrm{h}}/n_{\mathrm{p}}$	10/8/11	4/4/4	7/4/11	16/11/14	9/9/17	—	—	—
	p	0.4	0.3	0.4	0.5	0.6	—	—	—
	Range (p)	0–0.9	0–0.5	0–1.3	0–1.3	0–1.6	—	—	—
W vs. E	p	3.9	4.8	4.9	4.9	5.8	—	—	—
		3.2–4.6	4.1–5.2	4.4–5.5	4.6–5.6	5.4–6.4	—	—	—
Single group	h	—	—	—	—	—	100.0	97.8	84.4
	π	—	—	—	—	—	1.160	0.545	0.279
	$n/n_{\mathrm{h}}/n_{\mathrm{p}}$	—	—	—	—	—	15/15/36	10/9/13	10/6/7
	p	—	—	—	—	—	0.9	0.5	0.3
	Range (p)	—	—	—	—	—	0–1.3	0–1.0	0–0.3

Note. h, haplotype diversity (100×); π, nucleotide diversity (100×); n, number of sequences; n_{h}, number of haplotypes; n_{p}, number of polymorphic sites; p, average p-distances; range (p), range of distances. For the taxa with west–east pattern the values were calculated for western (W) and eastern (E) groups separately. Abbreviations of species: C.cor, *C. corone*; C.fru, *C. frugilegus*; P.pic, *P. pica*; *Cy.*coo, *Cy. cooki*; *Cy.*cya, *Cy. cyanus*; C.mon, *C. monedula*; C.dau, *C. dauuricus*; C.rax, *C. corax*; P.inf, *P. infaustus*; N.car, *N. caryocatactes*.

to the sequences determined in this study (over the 599 bp comparable section present in both data sets). For both sequences neither subspecies assignment nor the geographic origin were available, yet they proved to be very similar. One of them (AF218935) is identical with Pinfsib8 and Pinfsib6. The other one (AF131078) differed in one position from Pinfinf1 and Pinfrut1, respectively.

The samples of *N. caryocatactes* representing two subspecies (*N. c. caryocatactes*, *N. c. macrorhynchos*) originate from Central and northeastern Europe and southern Siberia as well as the Russian Far East. The 5′-sequence was obtained only from sample Ncarcar5 (Austria), it is identical to almost all other samples of *N. caryocatactes*, except Ncarmac5 and Ncarmac2 (one substitution to each).

3.3. Genetic diversity and differentiation

Genetic diversity and differentiation between groups were examined by calculating the average distances between and within clades and subclades, numbers of haplotypes, numbers of polymorphic sites, nucleotide diversities, and haplotype diversities (Table 1). The *p*-distances found between the pairs of western and eastern subclades in *C. corone*, *C. frugilegus*, *P. pica*, *Cy. cooki*/*Cy. cyanus* and *C. monedula*/*C. dauuricus* range from 3.9% to 5.8%. In these species average distances within subclades are in the same range as average distances found within the three species without west–east differentiation pattern (*C. corax*, *N. caryocatactes*, and *P. infaustus*). Considering the huge geographic ranges, distances within clades/subclades are quite low, e.g., 0.2% for the western group of *P. pica* spanning a range from the Iberian peninsula to Chukotka (NE Siberia). The highest average distance within clades/subclades (0.9%) is found in *C. corax* and in the western group of *C. corone.* Nucleotide diversity is in general also rather low (lowest in *Cy. cooki*, highest in *C. corax*), while haplotype diversity is quite high in all groups.

4. Discussion

The comprehensive tree based on CR sequences (Fig. 1) should not be considered as a phylogenetic analysis of the genus *Corvus* or the family Corvidae. It is just intended to demonstrate the strong diversification of the mt gene pool in some of the selected taxa. In some cases the observed distances within species were higher than those usually found even between good species (Helbig et al., 1995; Klicka and Zink, 1997; Omland et al., 2000). In general, with the exception of *C. frugilegus* (where the two clades represent the two subspecies), subspecies were not differentiated at the mt sequence level. At most the subclades represent groups of subspecies. In some species subspecific division is not in accordance with the genetic grouping into western and eastern clades (i.e., in *C. corone* and *P. pica*). Within several subclades (or clades in the case of *P. infaustus*, and *N. nucifraga*) sequence diversity is rather low, suggesting genetic bottlenecks by population decline during glacial periods or by rapid postglacial population expansions from small refuge areas. Although in some of our examples the number of specimens investigated for each species is low, their geographic distribution covers a wide area (maximum west–east range). Nevertheless, it is possible that in some taxa of our analysis displaying only one clade, shallow genetic sub-structuring might also exist, reflecting differentiation at a rather recent time level. While this would deserve further investigation, the present study was aimed to detect deeper splits and thus our results provide only first hints concerning the level of diversity within clades/subclades.

4.1. Genetic patterns and ecological factors

Before we discuss the results of the various species in detail we will try to interpret the genetic patterns with regard to phylogeographic considerations and ecological factors. Two kinds of patterns become apparent: In five cases we find two clearly separated mt lineages representing groups within species (*C. corone*, *C. frugilegus*, *P. pica*) or two closely related species (*C. monedula*/*C. dauuricus* and *Cy. cyanus*/*Cy. cooki*, which were formerly treated as conspecific). On the other hand, *C. corax*, *P. infaustus*, and *N. nucifraga* do not show such geographic differentiation. We designated the two genetic patterns as "west–east pattern" and "single-group pattern", respectively. Examples for a similar west–east differentiation in the Palerctic are found in several other bird groups (e.g., *Pernis apivorus*–*P. ptilorhyncus*, Gamauf and Haring, 2004; *Milvus* [*m.*] *migrans*–*M.* [*m.*] *lineatus*, Johnson et al., 2005; *Buteo buteo*–*B. japonicus*, Kruckenhauser et al., 2004; *Circus aeruginosus*–*C. spilonotus*, Fefelov, 2001; *Dendrocopos major*, Zink et al., 2002; *Parus montanus*, Salzburger et al., 2002).

The west–east pattern corresponds to category I of the five phylogeographic patterns described by Avise (2000): spatially circumscribed haplogroups separated by large genetic gaps. Avise (2000) considered long term intrinsic barriers to genetic exchange as a likely explanation for such a pattern. In the case of the species analyzed it is plausible to assume repeated expansions and restrictions of distribution ranges in the course of oscillations of cold and warm periods during the Pleistocene. Separated refuge areas (western and eastern) during cold periods led to accumulation of diversity. Given the present distribution patterns, secondary contact and even merging of distribution ranges allowing a certain degree of gene flow may have occurred during warm periods. In the system of Avise (2000) the single-group pattern corresponds to category IV, i.e., a shallow gene tree with sympatric lineages, which is expected for species with high gene flow among populations or populations that have not been sundered by long-term biogeographic barriers.

Of course, one has to keep in mind that the mt data reflect only the history of the maternal lineage. Differences in sex specific migration behaviour, such as in the case of ducks (Kulikova et al., 2004), might cause different genetic patterns of nuclear and mt markers. Although the taxa investigated show some sex and age specific differences in migration behaviour, both sexes presumably migrate together and may contribute similarly to gene flow. Thus, it is conceivable that the mt data represent on the whole the history of those taxa. Yet, the next important step in the investigation of these phylogenetic splits should be the application of nuclear markers.

The similar magnitude of between-group distances found between the subclades in the various species with west–east pattern implies that first, similar mechanisms might have accounted for the present genetic gaps, and second, that the processes occurred at similar time levels. However, applying a molecular clock and calculating divergence times is presently not possible. As pointed out in Kryukov et al. (2004) concerning *P. pica* and *Cy. cyanus*/*Cy. cooki*, one problem is that the variation in evolutionary rates makes comparisons between species unreliable. E.g., in *Pica* and *Cyanopica* CR and *cytb* seem to evolve at similar rates, although *cytb* is in general thought to be less variable than the CR. Nonetheless, tradition has played an important role in the establishment of a generally applied substitution rate for *cytb* of 2% per my. Yet, this is a questionable approach and most attempts to estimate divergence times found in the literature suffer from the same problem: the lack of a reliable calibration point (discussed in detail in Garcia-Moreno, 2004 and Kryukov et al., 2004). Nevertheless, despite the fact that the calculation of divergence times without a proper calibration point is illegitimate for the west–east differentiation found in this study, the distances between subclades suggest that the splits occurred in the remote past. Assuming the glacial cycles as the cause for the genetic splits the divergence could have started in the early Pleistocene.

The question arises whether the two phylogeographic patterns can be explained by different ecological requirements. Most parts of the present distribution ranges of the taxa investigated (with the exception of *C. corax*) did not provide suitable habitats during the cold phases of the Pleistocene. In Table 2 we summarize habitat preferences together with distribution as well as migratory and breeding behaviour of the taxa investigated. Common to the taxa displaying the west-east pattern is their preference of rather open habitats where they feed in low vegetation. They occur in more temperate zones avoiding extreme climates and dense forests. In contrast, two of the taxa with single-group pattern, *N. caryocatactes* and *P. infaustus*, prefer forest habitats and are adapted to cooler climates and higher altitudes and/or latitudes. *N. caryocatactes* is specialized on nut-eating and evolved a special behaviour for storing food enabling the species to use food depots during the winter time. *P. infaustus* uses various kinds of animal food and seeds. *C. corax* is a generalist concerning habitat as well as climate, avoiding only the interior of large dense forests. Concerning food this species is a generalist too being able to prey on medium sized vertebrates (e.g., birds, hares) or scavenge on large mammals. With respect to sociality the taxa with west–east pattern show similar social behaviour outside the breeding season. With the exception of *C. corone* and partly *P. pica*, they are even social during reproduction, breeding mostly in colonies. The taxa with single-group pattern are single breeder and territorial (*C. corax* only during the breeding time). Concerning migratory behaviour there is no clear pattern. Several taxa with west–east pattern usually migrate while *Pica* and *Cyanopica* are mainly resident. Among the taxa with single-group, *N. caryocatactes* and *P. infaustus* are normally resident year round, only under extreme climatic conditions eruptive migration (*N. c. macrorhynchos*) in large flocks sporadically occurs. *C. corax* is more flexible being migratory only under the extreme climatic conditions in the northernmost parts of the distribution range (food shortage and snow-rich climate). In summary, it seems that the two genetic patters are mainly associated with different habitat requirements and to some extent with social and breeding behaviour, the latter factors may in fact be connected with habitat.

Which regions could have provided moderate climates with suitable habitats during the cold periods of the Pleistocene? The eastern groups (*C. corone*-east, *C. frugilegus*-east, *C. dauuricus*, *Cy. cyanus*, *P. pica*-east) are currently distributed in the south-eastern parts of the Russian Far East (e.g., Primorye region) and, in some cases, their ranges extend westwards into the Baikal region and southwards into China. It can be assumed that for these groups south-eastern China served as a major refuge area providing open steppe habitats (Kahlke, 1994). In the west, the picture is not so clear (see below concerning *C. corone*). As possible refuge areas the Mediterranean region (Iberia, Apennine Peninsula, Balkans; mild climate) as well as the region from the Caspian basin to Lake Balhash and Tarim basin (cooler climate and forest steppe) could be assumed. During Pleistocene cold periods, the high mountain ranges in the southern part of Central Asia, e.g., Sajan, Altai, Tienshan, Himalaya and their foothills (4000–7500 m ASL), stretching several hundred up to 3000 km in west-east direction and up to 2500 km north-south, represented insurmountable barriers between western and eastern refugia.

Concerning the taxa with single group pattern the low genetic diversity in *N. caryocatactes* and *P. infaustus* suggest that these species underwent severe bottlenecks, but survival of relic populations did not occur in more than one isolated glacial refuge. During the last glacial maximum the only larger and continuous region of coniferous forest extended from Central to Eastern Siberia (Central Siberian Mountains to Baikal and Amur regions) (Kahlke, 1994) or, according to Nazarenko (1982), was even more restricted to the Altai mountains. Thus, it can be assumed that the two species survived in that region. In the West Palearctic, on the other hand, regions with suitable habitats were scarce and restricted to the very south. Most probably they were not accessible because of the large glaciated

Table 2
Ecological characteristics of the corvid species investigated summarized after Rustamov (1954), Goodwin (1986), Madge and Burn (1993), and Glutz von Blotzheim and Bauer (1993)

Taxon	Migratory behaviour	Distribution	Habitat	Feeding behaviour	Food	Breeding
P. pica	Resident	Holarctic, whole Europe and NW Africa to Kamchatka, Russian Far East, S China, parts of N America	Semi-open, semi-arid habitats, anthropogenic landscapes; avoids densely forested and treeless regions, extremely rocky habitats and wetlands	Single or in small family groups, foraging on ground	Various invertebrates, seeds, fruits, berries, small vertebrates, carrion	Solitary nester to small loose colony
Cy. cyanus	Resident	Transbaikalia to Russian Far East and NE China, Japan	Open cultivated grass country with groups of trees, hedgerows, river banks	Foraging in small to medium-sized flocks (often family parties) in trees and on ground	Invertebrates, esp. beetles, seeds, fruits	Loose small to medium-sized colonies
Cy. cooki	Resident	Iberia; lower and middle latitudes	Open forests, groves of olive, cork, oak, etc.	See *Cy. cyanus*	See *Cy. cyanus*	See *Cy. cyanus*
C. frugilegus	Migratory to resident	Palearctic; boreal, temperate, middle latitude to lowlands, absent in warmer regions, up to 2000 m ASL	Open grassland, croplands with groups of tall trees, avenues etc, extreme climates, dense woodland, wetlands, extreme dry and rocky surfaces are avoided	Foraging in small to very large flocks on ground	Earthworms, beetles, other invertebrates, cereal grain and other plants	Highly social, small to very large breeding colonies
C. monedula	Resident to migratory	Middle and upper middle latitudes of W Palearctic to W Siberia, boreal, temperate and Mediterranean lowlands	Open habitat like pasture, meadows, cropland; avoids extreme heat, ice, snow	In small to medium sized flocks on ground	Invertebrates, fruit, seeds, carrion	Small colonies
C. dauuricus	Resident to migratory	E Parearctic, C Siberia to Russian Far East, W China and Japan	Open, hilly country with cultivated areas pastures with scattered trees, river valleys, mountains up to 2000 m ASL; avoids dense forests	In small flocks on ground	Invertebrates, fruit, seeds, carrion	Loose colonies
C. corone	Resident to migratory	Palearctic; subarctic and boreal to temperate zones	Semi-arid steppe habitats, open farmland, scattered trees, copses, small woodlands, tolerates forest edges, up to 2000 m ASL	Foraging solitary to medium sized flocks on ground	Invertebrates and cereal grain, small vertebrates, eggs, carrion, scraps	Single pairs, territorial
C. corax	Resident to dispersive	Holarctic, from arctic to the tropics; sea level to 5800 m ASL	Generalist, excluding only the interior of large dense forests, shrubby terrain, wetland and intensively used farmland	Single or in small to medium-sized flocks, mainly on ground	Small to medium-sized vertebrates killed or scavenged, invertebrates, plants (cereals, fruits)	Single pairs, territorial
N. caryocatactes	Resident to dispersive, eruptive migration	Palearctic, from lowland up to tree line	Cool continental coniferous forests	Mainly on trees, ground	Mostly seeds and nuts, invertebrates	Single pairs, territorial
P. infaustus	Resident, movements in NE Siberia	N Palearctic, higher altitudes from Scandinavia through East Siberia up to 2200 m ASL	Dense stands of coniferous forest	Mainly on trees, ground	Mostly invertebrates, seeds, berries, small vertebrates, carrion	Single pairs, territorial

regions and extensive tundra. The comparatively high genetic diversity found in *C. corax* suggests that this species did not pass through severe bottlenecks. As a generalist it could even have remained more widely distributed.

In the following we discuss the results of each species separately with respect to their distribution, phylogeography and ecology and in connection to the current literature.

4.2. Taxa displaying the west–east pattern

4.2.1. Corvus corone

According to a widely accepted opinion *C. corone* represents a single species with a continuous distribution subdivided in up to six subspecies (Mayr and Greenway, 1962) which were included in our analysis with the exception of *C. c. sharpii.* The tree with its division into two subclades, one of them being further divided into two subclades, is neither concordant with the affiliation of individuals to subspecies nor with their most visible characteristic, the plumage colour, i.e., *C. c. corone* and *C. c. orientalis* (black) vs. *C. c. cornix, C. c. sardonius*, and *C. c. capellanus* (grey–black) (see Fig. 2). The eastern subclade represents birds from the Russian Far East and Japan which are all black. Since the distribution of *C. c. orientalis* extends in the south up to China and Kashmir (Cramp and Perrins, 1994), it can be assumed that this haplogroup is also present in those regions. Nevertheless this remains to be investigated. Considering the western subclade the geographic origins of the samples suggest that there might have been more than one refuge: One subclade (a), which is formed by the majority of the individuals, ranges from England to Central Siberia (Dauria), the second subclade (b) comprises individuals from more eastern regions, namely from Kyrgyzstan and Baikal region to the northeast of Russia (Kamchatka). The sample from Iraq (Ccorcap1) cannot be assigned clearly to one of these two groups, it might even represent a third lineage. Certainly, this subdivision of the western clade can be explained by incomplete lineage sorting, but the geographic affiliations can be taken as a subtle hint that the lineages may have evolved in isolated refuges. Considering the huge geographic range of subclade (a), a population expansion of this group after the last glaciation appears plausible. The mismatch distribution analysis supports this assumption. While for subclade (b) the analysis points into the direction of a stable population, this might also be due to the small samples size.

Within the western clade, the most striking result is its composition of black populations in the west and east, while there is a black–grey form in the centre. The hybrid zone between *C. c. cornix* and *C. c. orientalis* extends between Ob’ and Yenissey Rivers in western Siberia and is about 150 km in width (Kryukov and Blinov, 1989; Blinov and Kryukov, 1992). The European hybrid zone (width between 30 and 100 km) between *C. c. corone* and *C. c. cornix* was first described in detail by Meise (1928). It extends from the Ligurian Apennines through the southern edge of the Alps and through central Europe north to Jutland as well as to southern Scotland (Mayr, 1942, 1963). Several studies showed that this zone was remarkably stable during the last century or moved only rather slowly and locally (Cook, 1975; Picozzi, 1976; Oeser, 1986; Brtek, 1987; Saino and Vila, 1992; Haas and Brodin, 2005). Aspects of interactions between *C. c. corone* and *C. c. cornix* as well as taxonomic problems were recently considered in detail (Parkin et al., 2003). It was assumed that the hybrid zone between *C. c. corone* and *C. c. cornix* represents a secondary contact zone between previously isolated populations (Meise, 1928; Mayr, 1959). The mt CR data do not corroborate this assumption since the two subspecies are not differentiated with this marker and thus there is no indication of prior isolation. The lack of a clear concordance between mt haplotype and plumage colour suggests that there is substantial gene flow between *C. c. corone* and *C. c. cornix*. This is in accordance with observations from the hybrid zone were phenotypically intermediate colour morphs (from *cornix*-like grey–black pattern to almost black) are found quite frequently (Aubrecht, 1979 and citations therein). The question arises why the hybrid zones as recognized by phenotypes remain stable and rather narrow. Kryukov and Blinov (1989) and later Saino and Vila (1992) found that pair composition within the hybrid zones in Siberia and Italy, respectively, was non-random. Saino and Vila (1992) interpreted their data assuming that assortative mating was partly the outcome of differential habitat selection by the phenotypes. Since the parental populations are adapted to different environments each of them is thought to be competitively superior to the other in its own range. They assumed that “the hybrid zone could be considered as the narrow belt, where ecological features are such that hybrids are not at a selective disadvantage with respect to the crows in parental populations” (Saino and Vila, 1992). While Rolando (1993) and Parkin et al. (2003) reported reduced fitness of hybrids, Kryukov and Blinov (1989) found no evidence for selection against hybrids. In any case, the stability of the hybrid zone could also be due to the fact that possible habitats are occupied throughout the distribution range, and therefore drastic shifts of breeding areas are impeded. It is reasonable to assume that the crow hybrid zones are maintained by a balance between dispersion, ecological preferences, and a certain level of assortative mating. Consequently, the actual hybrid zone may be much wider than we can detect from the plumage phenotypes. This would explain the lack of geographic pattern in the mt haplotypes.

There are three possible explanations for the present distribution of plumage colours: (1) The grey–black form arose rather recently in the centre of an otherwise black species with low genetic diversity. In addition, the grey–black plumage colour might have been linked with a gene advantageous in more dry habitats (e.g., assuming that this form originated in an Aralo-Caspian refuge). Subsequently this plumage type spread over a huge range rather fast. In this case no genetic differentiation would be detectable at the mt level. (2) The grey–black form (including *C. c. cornix*, *C. c. sardonius* and *C. c. capellanus*) originated from a rather small ancestral population within a separate (southern) glacial refuge. Initially this group might have possessed a different mt haplotype. But in the course of a postglacial expansion it came into contact and hybridized with the black *C. c. corone* in the West and *C. c. orientalis* in the East. This subsequently resulted in a replacement of mt genes in the grey–black taxon. A similar situation was found in two sibling bat species of the genus *Myotis* (Berthier et al., 2006) as well as in lacertids of the genus *Podarcis* (Podnar et al., 2005). Considering the haplotype distribution (Fig. 5) especially of the representatives of the grey–black taxa with distinct haplotypes (especially that of *C. c. capellanus*), explanation (2) appears not likely. The fact that the most distinct haplotypes in subclade a belong to grey-black taxa and that the western clade is vaguely divided into two groups (a, b) suggests (a) third scenario: (3) The black *C. c. orientalis* represented by subclade (b) survived the last glaciation in a separate SE Asian refuge. Subclade (a) represents a second refuge area, where forms (the grey–black and the black one) coexisted facilitating extensive hybridization already in the course of the glaciation period. Alternatively, *C. c. corone* could be the result of postglacial hybridisation of male *C. c. orientalis* (black) with females of the grey–black taxon in the course of expansion of distribution ranges. To test these hypotheses, analysis of nuclear markers are necessary to find out whether there is a nuclear differentiation contrasting with mt haplotypes. Nevertheless, even then it remains a matter of speculation whether mt haplotypes were lost by hybridisation and /or drift. Certainly, larger samples and additional populations of all subspecies (especially the southernmost populations) should be analyzed.

With respect to taxonomy the present data provide a rather clear picture: The present data do not support the recent proposal to treat the European carrion crow and hooded crow as distinct species (*C. corone*, *C. cornix*; Parkin et al., 2003). One might ask whether the two mt clades represent two distinct species. In this case the western species would comprise black as well as black–grey forms, while the eastern one would only represent the most eastern black populations. However, such a split is not justified without corroboration by morphological, behavioural and other data (e.g., vocalization) and detailed analysis of the contact zone between the two haplogroups.

4.2.2. *Corvus monedula*

In the past, the two species *C. monedula*–*C. dauuricus* which have a parapatric distribution were treated as distinct species of a new genus *Coloeus* (Hartert, 1903; Vaurie, 1959; Blake and Vaurie in Mayr and Greenway, 1962), while other authors assigned them to the genus *Corvus* (Rustamov, 1954; Ivanov and Stegman, 1964; Bährmann, 1968). The reciprocal monophyly for *C. monedula* and *C. dauuricus* found in our trees and the comparatively high distance between the two subclades may corroborate their treatment as two distinct species as proposed previously (Vaurie, 1954; Nechaev, 1975; Dickinson, 2003). According to Panov (1989) however, the species hybridize in the Altai mountain range, South Siberia and Mongolia with about 9% of the sampled individuals being hybrids. Nechaev (1975) gives a detailed description of hybrids from those regions. To assess further the degree of gene flow investigation of more individuals from regions in South Siberia, where hybridization could occur, is necessary.

4.2.3. *Corvus frugilegus*

The division of *C. frugilegus* into two distinct groups represented by the mt subclades corresponds in general to the distinction of two parapatric subspecies, *C. f. frugilegus* and *C. f. pastinator*. Again, a decision whether the western and eastern groups represent two distinct species is not possible on mere *p*-distances. Therefore, it is necessary to investigate more individuals from regions where the two groups come into contact (presumably western Altai region) and to apply nuclear markers to assess the degree of gene flow. In our present sample only one overwintering specimen from Issyk-Kul (Cfrufru16) is of interest in this context. It is found in the western clade which is in accordance to its geographic origin.

4.2.4. *Pica pica*

Although *P. pica* has a continuous distribution range from Western Europe to the Russian Far East and South China, with isolates in Kamchatka and Arabia, there is a clear division into two mt groups. Besides this genetic gap, no differentiation of the various subspecies is observed. The same distinction was found by Lee et al. (2003) who investigated portions of the mitochondrial genes for *16S rRNA, tRNA-Leu* and *NADH dehydrogenase (nd1)*. Moreover, in that study, individuals from localities representing the western subclade of our study are more closely related to a clade comprising two North American species, *Pica hudsonia* and *Pica nuttalli*. This result does not contradict, but fits well into the hypothesis of repeated expansions/shrinking of distribution ranges of the populations representing the western haplogroup. Given the wide present day distribution of the western group of very closely related haplotypes (from Spain to Chukotka) it seems that this species can colonize huge areas rather fast. In this context it is interesting that the "western" clade included a sample from the extreme east of the Palearctic (Ppiccam1). Although, *P. pica* is extremely sedentary (only in Siberia in colder years "northern" birds move further to the south) it is conceivable that this expansion accompanied the postglacial expansion of suitable habitat. It can be assumed that the two North American species are descendants of an ancient expansion of birds carrying the "western" haplotypes eastwards to North America. Isolation of those populations in the New World during the following glacial period could have initiated the subsequent divergence leading to present day *P. hudsonia* and *P. nuttalli*. The present range of the eastern clade may be rather limited extending not further to the north than e.g., Khabarovsk region, Russian Far East. Concerning possible hybridization between the western and eastern group, the data available so far allow no final conclusions. Since in our sample there is a gap of collection sites between Baikal region and Khabarovsk region, the border of the geographic ranges of the two groups cannot be localized, but it might be located in Mongolia (Eck, 1997). Where the two haplogroups meet, or whether high mountain ranges or the lack of suitable habitat may act as barriers impeding an expansion of the eastern haplogroup, is still unclear. Furthermore, it remains to be investigated whether the two subclades are characterized by distinct morphological features. Cramp and Perrins (1994) and Ebels (2003) reported that there are differences in vocalisation between *P. p. pica* and *P. p. sericea* supporting our findings.

4.2.5. *Cyanopica*

The wide geographic gap between the western and eastern range of the azure-winged magpie *Cy. cyanus*, spanning about nine thousand kilometres, was the classical example of a species with disjunctive distribution range. The main part of the range stretches from Lake Baikal and central China to the Japanese islands, while a much smaller region is inhabited by populations in Spain and Portugal. The treatment of *Cy. cyanus* as two distinct species, *Cy. cyanus* and *Cy. cooki*, differing by details of colouration and morphometric measurements as well as mt haplotypes (Fok et al., 2002; Kryukov et al., 2004) was discussed in detail previously (Kryukov et al., 2004). Genetic differentiation and the Pleistocene fossil records from Gibraltar/Spain (Cooper, 2000) preclude the possibility of an introduction of the azure-winged magpie into Western Europe in historic times. Another example of such an extreme biogeographic pattern can be found in the genus *Sitta*, with the Corsican nuthatch being closely related to the Chinese nuthatch, with no intermediate in between (Pasquet, 1998). In contrast to species like *P. pica* and *C. corone* which seem to have extreme expansion capacities, this is obviously not the case in *Cyanopica*. Following the assumption of a recurring refuge area in eastern China the range of the eastern *Cy. cyanus* has expanded considerably, e.g., in recent time in the Baikal region (I. Fefelov, personal communication). In contrast, the European *Cy. cooki* remained restricted to comparatively small areas in southern Spain and Portugal. The rather fragmented distribution of *Cy. cooki* may be explained by dry climate as well as habitat destruction due to agricultural interferences. Moreover, it was considered as a pest for agriculture, and therefore its nests were often destroyed (Dos Santos, 1968).

4.3. Taxa displaying the single-group pattern

4.3.1. *Perisoreus infaustus*

Although only a small number of samples of *P. infaustus* could be analyzed, they represent a wide geographic range. Besides the lack of a deep split into two subclades the species is characterized by low intraspecific distances. A geographic pattern at the level of very low genetic distances was described by Uimaniemi (2004) in an extensive study of Fennoscandian and Siberian populations of *P. infaustus* (based on two variable parts of the mt CR). She found three different mtDNA lineages (Fennoscandia, Siberia, Yenisey region), which were supposed to have evolved in separate Pleistocene refugia. This contradicts the assumption of Nazarenko (1982) who postulated an Altai Mountain forest refuge for *P. infaustus* where it survived the last glacial maximum, and from where it spread to east and as well to west in the Holocene. The latter opinion corresponds with our assumptions, since that region is adjacent to the region we mentioned above (Central to Eastern Siberia). Compared to the other species, the differentiation within *P. infaustus* appears not very pronounced and thus does not imply a long term (or repeated) isolation. The differentiation between the Fennoscandian and Siberian populations is reflected also in our tree: Samples Pinfinf1 and Pinfrut1 form the Fennoscandian group and the samples Pinfyak1 to Pinfsib8 form the Siberian group, although bootstrap support is below 50% for both groups. The mean genetic distance (approximately 2%) found by Uimaniemi (2004) between these two groups is twice as high as the maximal divergence within *P. infaustus* in our tree. However, this might be caused by different variability of the CR sections analyzed and the fact that the third branch in the study of Uimaniemi (2004) comprising samples from Yenisey Region is not represented in our study. For a more detailed phylogeographic study of this species samples from western Siberia would be essential.

4.3.2. *Nucifraga caryocatactes*

Considering the huge geographic range of the samples of *N. caryocatactes*, the genetic diversity within this species as revealed by the CR sequences is surprisingly low. However, it should be noted that of the nine currently described subspecies (Dickinson, 2003) we included only two. Especially representatives of the more southern regions of the species' distribution (e.g., southern slopes of the Himalayas) were not available. The low diversity within the North Palearctic sample could be explained by the assumption of a rapid postglacial expansion of a population that had experienced a severe bottleneck. Also this species, in contrast to other corvids studied here, is known as an eruptive long distance migrant in case of food (nut) shortage. Thus we can suppose considerable gene flow which should counteract differentiation of populations. Since *N. cary-*

ocatactes and *P. infaustus* have similar habitat requirements we assume that they may have survived the cold periods in the same area. This is in accordance with the assumption of an Altai forest refuge proposed by Nazarenko (1982).

4.3.3. *Corvus corax*

The lack of geographic pattern within the *C. corax* sample (covering a west–east range from Iceland and Canary Islands through Europe and Asia to Canada), combined with high diversity could be explained by high current gene flow. Omland et al. (2000) revealed two genetically differentiated groups in *C. corax* based on the mt CR and the *cytb* gene as well as on microsatellites: the geographically widespread "Holarctic clade", occurring from France, through Russia and Alaska to the eastern USA (Maine), and the "California clade", which is restricted to the western USA. The California clade is more closely related to the Chihuahuan raven *C. cryptoleucus* (Southwest USA, northern Mexico), thus rendering *C. corax* paraphyletic. The results were interpreted in the way that *C. corax* may have been formerly divided into two allopatric groups that are now in the process of re-emerging. This seems a plausible explanation for the situation in North America assuming that—similarly as it has apparently happened in *P. pica*—waves of expansion could have easily reached North America over the Beringian route. But in contrast to *P. pica*, where the Nearctic species *P. hudsonia* and *P. nuttalli* are geographically and genetically distinct from the Palearctic *P. pica* clade, the situation with *C. corax* is different because the Palearctic populations are nested in a big clade together with the Nearctic populations. The Holarctic clade has been investigated in more detail by Omland et al. (2006). The results indicated low haplotype sharing between the two hemispheres suggesting low levels of maternal gene flow. The present study was more tightly focussed on the Palearctic range of *C. corax* including samples from 16 localities. We found no pattern in the geographic distribution of the various haplotypes, and especially there is no west–east differentiation. The intraspecific diversity is quite high (Table 1) suggesting that the species underwent no bottlenecks during the (last) glaciations.

5. Conclusions

Expansions and restrictions of animal distribution ranges during and between glaciations strongly depended on secondary effects of climate changes on vegetation and food resources. We examined the patterns of mt diversity in several widely distributed Palearctic corvids and related them to ecological factors. Presently, the taxa investigated show a variety of distribution patterns, from disjunct (e.g., *Cy. cyanus*/*Cy. cooki*) or para/allopatric (e.g., *C. monedula*/*C. dauuricus*) to continuous (e.g., *P. pica*). The genetic patterns found in these taxa can be divided in two types. We discovered deep genetic splits within some taxa (west–east pattern), while others are genetically strikingly similar over huge geographic ranges (single-group pattern). These two phylogeographic patterns may be explained by different habitat preferences, the most prominent being the preference for either open to semi open habitats vs. (mainly coniferous) forest dominated habitats.

Remarkably, the intraspecific variation of plumage colouration is rather different in the taxa investigated. It is not surprising that those taxa with striking plumage characters distinguishing between geographic groups are more prone to taxonomic splits. For example, the former *C. monedula* was split into the two species *C. monedula* and *C. dauuricus* (Dickinson, 2003), and the same is the case for *C. corone*/*C. cornix* (Knox et al., 2002; Parkin et al., 2003). In contrast, the other taxa possessing no such pronounced differences in external traits remained unaffected from taxonomic changes or were split into different species only as a consequence of genetic data (*Cy. cyanus*/*Cy. cooki*; Fok et al., 2002). The data presented here bring up new questions for each of the taxa investigated. These should be analyzed in detail using different characters, such as molecular (e.g., nuclear) and morphological (e.g., morphometric) traits, as well as vocalizations.

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Appendix A

Specimens included in the analysis

Species/subspecies	Labcode	Tissue	Geographic origin	Source/voucher number	Accession No.
Corvus corone					
C. c. corone	Ccorcor1	Mu/Li	Austria, Gars/Kamp	N. Schuller	EU070774
	Ccorcor2	Mu/Li	France, Paris	E. Pasquet MNHN 3356	EU070775
	Ccorcor5	Fe	Austria, Unterwolfern	NMW 82.612	EU070776
	Ccorcor6	Mu/Li	France, Paris	E. Pasquet MNHN 3354	EU070777
	Ccorcor7	Fe	Netherlands, Leiden	A. Gamauf	EU070778
	Ccorcor8	Fe	Netherlands, Leiden	A. Gamauf	EU070779
	Ccorcor9*	Fe	Netherlands, Leiden	A. Gamauf	EU070773
	Ccorcor10	Fe	Austria, Öblarn	B. Däubl	EU070780
	Ccorcor11	Fe	Austria, Öblarn	B. Däubl	EU070781
	Ccorcor12	Fe	Germany, Rostock	E. Haring	EU070782
	Ccorcor13	Fe	Great Britain, Glastonburry	B. Däubl	EU070783
	Ccorcor14	Fe	France, Strasbourg	B. Däubl	EU070784
C. c. cornix	Ccorcox1	Mu/Li	Russia, Moscow	AK 0101	EU070785
	Ccorcox2	Mu/Li	Russia, Novosibirsk	AK 327	EU070786
	Ccorcox3	Mu/Li	Russia, Kirov	V. Sotnikov/AK 0164	EU070787
	Ccorcox4	Mu/Li	Austria, Schönherrn	M. Ulreich	EU070788
	Ccorcox5	Mu/Li	Russia, Moscow	Ya. Red'kin/AK 0304	EU070789
	Ccorcox6	Mu/Li	Russia, Moscow	Ya. Red'kin/AK 0308	EU070790
	Ccorcox7	Mu/Li	Russia, Moscow	Ya. Red'kin/AK 0312	EU070791
	Ccorcox8	Mu/Li	Russia, Ivanovo reg.	Ya. Red'kin/AK 0213	EU070792
	Ccorcox12	Mu/Li	Russia, Moscow	AK 715	EU070793
	Ccorcox15	Mu/Li	Russia, Novosibirsk	AK 303	EU070794
C. c. orientalis	Ccorori1	Mu/Li	Russia, Kamchatka, Pinachevo	AK 154	EU070795
	Ccorori2	Mu/Li	Russia, Kamchatka, Pinachevo	AK 155	EU070796
	Ccorori3	Mu/Li	Russia, Kamchatka, Pinachevo	AK 156	EU070797
	Ccorori4	Mu/Li	Russia, N Sakhalin, Oha	I. Kartavtseva/AK 732	EU070798
	Ccorori5	Mu/Li	Russia, Primorye reg.	AK 602	EU070799
	Ccorori6	Mu/Li	Russia, S Sakhalin	N. Pavlov/AK 811	EU070800
	Ccorori7	Mu/Li	Russia, Krasnojarsk	AK 325	EU070801
	Ccorori8	Mu/Li	Russia, S-Central Siberia, Tuva	Ya. Red'kin/AK 0103	EU070802
	Ccorori9	Fe	Russia, S Siberia, Dauuria, Chongeo-Nur	A. Gamauf	EU070803
	Ccorori10	Fe	Russia, S Siberia, Dauuria, Chongeo-Nur	A. Gamauf	EU070804
	Ccorori12	Mu/Li	Russia, Khabarovsk reg., Solnechny	AK 0288	EU070805
	Ccorori15	Mu/Li	Russia, Khabarovsk reg., Evoron Lake	N. Terentjev/AK 0244	EU070806
	Ccorori16	Mu/Li	Russia, Khabarovsk reg., Evoron Lake	N. Terentjev/AK 0245	EU070807
	Ccorori17	Mu/Li	Russia, Primorye reg.	AK 601	EU070808
	Ccorori21	Bl	Kyrgyzstan, Issyk-Kul Lake	J. Martens, MAR1852	EU070809
	Ccorori22	Mu/Li	Russia, Magadan reg., Ola settl.	N. Dokuchajev/AK 0417	EU070810
	Ccorori23	Mu/Li	Russia, S Sakhalin, Korsakov distr.	I. Ganitsky, ZMMU RYA1050	EU070811
	Ccorori24	Mu/Li	Russia, Chita reg., Kawykutschi-Gasimurskije	Weigl	EU070812
	Ccorori25	Fe	Russia, Baikal Lake, Olkhon Island	B. Däubl	EU070813
	Ccorori26	Fe	Russia, Chita reg., Kira	B. Däubl	EU070814
	Ccorori28	Fe	Russia, Chita reg., Kira	B. Däubl	EU070815
	Ccorori30	Mu/Li	Japan, Tokyo, Confu-Shi Jindaiji	W. Morass/W. Neuner, TLF	EU070816
	Ccorori31	Mu/Li	Russia, Buriatia, W Chorinsk	S. Weigl	EU070817
C. c. capellanus	Ccorcap1	Pa	Iraq, N-Amara	ZFMK 65.1203	EU070818
C.s c. sardonius	Ccorsar3	Fe	Greece, Ag. Ioannis, Pilion	B. Däubl	EU070819
	Ccorsar4	Pa	Israel, Atlit/Haifa	NMW 76.681	EU070820
	Ccorsar5	Fe	Greece, Volos	E. Haring	EU070821
Hybrid *C. c. corone* x *C. c. cornix*	hy-Cccc5	Fe	Austria, Hadersdorf	E. Haring	EU070822
Hybrid *C. c. cornix* x *C. c. orientalis*	hy-Ccco3	DNA	Russia, W Siberia, Kemerovo reg.	AK 307	EU070823
	hy-Ccco4	DNA	Russia, W Siberia, Kemerovo reg.	AK 312	EU070824

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Appendix A (*continued*)

Species/subspecies	Labcode	Tissue	Geographic origin	Source/voucher number	Accession No.
Corvus corax					
C. c. corax	Ccoarax1	Mu/Li	Russia, Okhotsk sea, Ayan	AK 0276	EU070825
	Ccoarax2	Mu/Li	Russia, Smolensk reg.	Ya. Red'kin, ZMMU LVE55	EU070826
	Ccoarax3	Mu/Li	Russia, Moscow reg.	Ya. Red'kin, ZMMU LVE59	EU070827
	Ccoarax4	Mu/Li	Russia, Kirov reg.	V. Sotnikov, ZMMU SVD2400	EU070828
	Ccoarax5	Mu/Li	Russia, Chita reg.	Weigl	EU070829
	Ccoarax6	Fe	Spain, Mallorca	P. Sziemer	EU070830
	Ccoarax7	Pa	Austria, Steyr	NMW 87.417	EU070831
	Ccoarax8*	Pa	Romania, Rastolita	NMW 76.484	EU070764
	Ccoarax9	Fe	Estonia, SW Tartu	A. Gamauf	EU070832
	Ccoarax10*	Pa	Spain, Linares de Riofrio	Phyl. Mus. Jena 7556	EU070765
	Ccoarax11	Pa	Sweden, Östersund	Phyl. Mus. Jena 7558	EU070833
	Ccoarax12	Mu/Li	Russia, Buriatia, Beloozersk	S. Weigl	EU070834
C. c. principalis	Ccoapri1	Pa	Canada, Ontario, Moosonee	NMW 73.200	EU070835
C. c. varius	Ccoavar1	Pa	Iceland, Kjos	NMW 88.372	EU070836
	Ccoavar2	Pa	Denmark, Faroe Islands, Nólsoy	ZFMK 53.7	EU070837
C. c. canariensis	Ccoacan1*	Pa	Spain, Canary Islands, Fuertoventura, Oliva	NMW 63.837	EU070766
	Ccoacan2	Fe	Canary Islands, Fuertoventura	R. Barone	EU070838
C. c. tibetanus	Ccoatib1	Pa	China, Khalatse, Ladak	ZFMK F.VII.3.g8.β	EU070839
Corvus frugilegus					
C. f. frugilegus	Cfrufru1	Mu/Li	Russia, Iwanovo reg.	A. Bogdanov/AK 0102	EU070840
	Cfrufru2	Mu/Li	Russia, Kirov reg.	V. Sotnikov, ZMMU/AK 0166	EU070841
	Cfrufru6	Mu/Li	Russia, Smolensk reg.	Ya. Red'kin, ZMMU/AK 0217	EU070842
	Cfrufru8	Fe	Great Britain, Barnard Castle	E. Haring	EU070843
	Cfrufru9	Fe	Great Britain, Barnard Castle	E. Haring	EU070844
	Cfrufru10	Fe	Great Britain, Alnwick	E. Haring	EU070845
	Cfrufru11	Fe	Great Britain, Leeds	E. Haring	EU070846
	Cfrufru12	Fe	Great Britain, Easby Abbey	E. Haring	EU070847
	Cfrufru13	Fe	Great Britain, Richmond	E. Haring	EU070848
	Cfrufru14	Fe	Serbia, Beograd	E. Haring	EU070849
	Cfrufru15	Mu/Li	Austria, Graz	A. Koller	EU070850
	Cfrufru16*	Pa	Kyrgyzstan, Issyk-Kul Lake	NMW 63.816	EU070767
C. f. pastinator	Cfrupas4	Mu/Li	Russia, Primorye reg., Gaivoron	A. Tsvetkov, ZMMU EAK037	EU070851
	Cfrupas5	Mu/Li	Russia, Primorye reg., Gaivoron	A. Tsvetkov, ZMMU EAK036	EU070852
	Cfrupas6	Mu/Li	Russia, Primorye reg., Lipovtsy	AK 911	EU070853
	Cfrupas7	Mu/Li	Russia, Primorye reg., Gaivoron	Ya. Red'kin, ZMMU/AK 0331	EU070854
Corvus monedula					
C. m. spermologus	Cmonspe1	Fe	Spain, N Burgillos, NE Sevilla	A. Gamauf	EU070855
	Cmonspe2	Fe	Spain, N Burgillos, NE Sevilla	A. Gamauf	EU070856
	Cmonspe7	Fe	Austria, Schloß Hubertendorf	NMW 94222	EU070857
	Cmonspe8	Fe	Austria, Schloßhof	R. Kaltenegger	EU070858
	Cmonspe9	Fe	Lithuania	E. Haring	EU070859
	Cmonspe10	Fe	Great Britain, Stonehenge	B. Däubl	EU070860
C. m. monedula	Cmonmon1	Mu/Li	Russia, Kirov reg.	V. Sotnikov, ZMMU SVD2405	EU070861
	Cmonmon2	Mu/Li	Russia, Moscow	Ya. Red'kin, ZMMU/AK 0303	EU070862
	Cmonmon3	Mu/Li	Russia, Smolensk reg.	D. Gluhov, ZMMU SKY007	EU070863
	Cmonmon4	Mu/Li	Russia, Ivanovo reg.	Ya. Red'kin, ZMMU/AK 0220	EU070864
	Cmonmon5	Mu/Li	Russia, Kirov reg.	V. Sotnikov, ZMMU/AK 0222	EU070865
C. m. soemmeringii	Cmonsoe6	Fe	Greece, Poliracho, Kozani	B. Däubl	EU070866
Corvus dauuricus					
	Cdau1	Mu/Li	Russia, Dauuria, Koonkoor	A. Gamauf	EU070867
	Cdau2	Mu/Li	Russia, Primorye reg.	AK 917	EU070868
	Cdau3	Mu/Li	Russia, Primorye reg., Gaivoron	Ya. Red'kin/AK 0338	EU070869
	Cdau4	Mu/Li	Russia, Primorye reg., Gaivoron	Ya. Red'kin/AK 0341	EU070870
	Cdau5	Pa	China, Gan'su, mountain Hoi-Syan	M. Berezowsky, ZMMU 90686	EU070871

Appendix A (*continued*)

Species/subspecies	Labcode	Tissue	Geographic origin	Source/voucher number	Accession No.
	Cdau6	Mu/Li	Russia, Chita reg., Batakan	S. Weigl	EU070872
	Cdau7	Mu/Li	Russia, Buriatia, Charamodun	S. Weigl	EU070873
	Cdau8	Fe	Russia, Baikal Lake, Olkhon Island	B. Däubl	EU070874
	Cdau9	Fe	Russia, Baikal Lake, Olkhon Island	B. Däubl	EU070875
Cyanopica cooki					
Cy. c. cooki	Ccyacoo2	Fe	Spain, N Burgillos, NE Sevilla	A. Gamauf	AY701134
	Ccyacoo4	DNA	Spain, Badajoz	J.G. Martinez/C. de la Cruz	AY701133
	Ccyacoo6	DNA	Spain, Badajoz	J.G. Martinez/C. de la Cruz	AY701132
	Ccyacoo10	DNA	Spain, Badajoz	J.G. Martinez/C. de la Cruz	AY701135
	Ccyacoo12	DNA	Spain, Badajoz	J.G. Martinez/C. de la Cruz	AY701131
Cy. c. gili	Ccyagil1	Fe	Portugal, Algarve, Alvor	W. Scheres, B. Wylie, D. Radford/AK 0328	AY701136
Cyanopica cyanus					
Cy. y. cyanus	Ccyacya23	Fe	Russia, Irkutsk City	I. Fefelov	AY701137
	Ccyacya24	Mu/Li	Russia, Chita reg., Olowjannaja	S. Weigl	AY701138
	Ccyacya26	Mu/Li	Russia, Chita reg., Olowjannaja	S. Weigl	AY701140
	Ccyacya27	Mu/Li	Russia, Chita reg., Olowjannaja	S. Weigl	AY701141
	Ccyacya28	Mu/Li	Russia, Chita reg., Olowjannaja	S. Weigl	AY701142
	Ccyacya25	Mu/Li	Russia, Chita reg., Olowjannaja	S. Weigl	AY701139
Cy. cy. pallescens	Ccyapal1	Fe	Russia, Primorye reg., Nadezhdinskaya	A. Kryukov	AY701143
	Ccyapal2	Mu/Li	Russia, Primorye reg., western part	AK 916	AY701144
	Ccyapal5	Mu/Li	Russia, Primorye reg., western part	AK 914	AY701145
	Ccyapal6	Mu/Li	Russia, Khabarovsk reg., Kutusovska	AK 0260	AY701146
	Ccyapal7	Mu/Li	Russia, Khabarovsk reg., Kutusovska	AK 0261	AY701147
	Ccyapal13	Mu/Li	Russia, Primorye reg., Gaivoron	V. Sotnikov, ZMMU CBH247	AY701148
	Ccyapal21	Mu/Li	Russia, Primorye reg., Arsenjev	Ya. Red'kin, ZMMU RYA309	AY701149
Cy. cy. koreensis	Ccyakor1	Mu/Li	South Korea, Chungnam prov.	H. Park, CGRB 0251	AY701150
Cy. cy. interposita	Ccyaint10	Fe	China, Beijing	A. Gamauf	AY701152
Cy. cy. japonica	Ccyajap22	Mu/Li	Japan, near Tokyo, Kawaguchi	T. Hiraoka/AK 0203	AY701151
Perisoreus infaustus					
P. i. infaustus	Pinfinf1	Mu/Li	Russia, Karelia	A. Tsvetkov, ZMMU/AK 0315	EU070876
	Pinfinf4*	Pa	Finnland	NMW 310.88	EU070768
	Pinfinf5*	Pa	Finnland	NMW 310.87	EU070769
P. i. ruthenus	Pinfrut1	Li	Russia, Kirov reg.	V. Sotnikov, ZMMU SVD 2404	EU070877
P. i. sibericus	Pinfsib4	Mu	Russia, Chita reg., WSW Urjupino	S. Weigl	EU070878
	Pinfsib5	Mu	Russia, Chita reg., WSW Urjupino	S. Weigl	EU070879
	Pinfsib6	Mu	Russia, Chita reg., WSW Urjupino	S. Weigl	EU070880
	Pinfsib7	Mu	Russia, Chita reg., WSW Urjupino	S. Weigl	EU070881
	Pinfsib8	Mu	Russia, Chita reg., WSW Urjupino	S. Weigl	EU070882
P. i. yakutensis	Pinfyak1	Li	Russia, Magadan reg., Omolon	N. Dokuchajev/AK 011	EU070783
	Pinfyak2	Li	Russia, Yakutia, Indigirka	S. Rupasov, ZMMU 115754	EU070784
P. i. maritimus	Pinfmar1	Li	Russia, Khabarovsk reg., Mulpa river	I. Tiunov/AK 0142	EU070785
Nucifraga caryocatactes					
N. c. caryocatactes	Ncarcar1	Li	Russia, Kirov reg.	V. Sotnikov, ZMMU/AK 0171	EU070786
	Ncarcar2	Li	Russia, Ivanovo reg.	V. But'ev/AK 0110	EU070787
	Ncarcar4	Ba	Austria, Tyrol	NMW 82.498	EU070788
	Ncarcar5*	Ba	Austria, Gaflenz	NMW 85.398	EU070770
	Ncarcar6	Mu	Austria, Wattental	TLF 2005-035	EU070889
N. c. macrorhynchos	Ncarmac1	Li	Russia, Primorye reg., Arsenyev	A. Tsvetkov, ZMMU RYA427	EU070890
	Ncarmac2	Li	Russia, Primorye reg., Arsenyev	Ya. Red'kin, ZMMU RYA550	EU070891
	Ncarmac3	Li	Russia, Magadan reg., Omolon	N. Dokuchajev/AK 009	EU070892
	Ncarmac4	Fe	Russia, Baikal Lake, Listvjanka	A. Gamauf	EU070893
	Ncarmac5	Mu	Russia, Buryatia	S. Weigl	EU070894
	Ncarmac6	Mu	Russia, Buyatia, Samarta	S. Weigl	EU070895

(*continued on next page*)

Appendix A (*continued*)

Species/subspecies	Labcode	Tissue	Geographic origin	Source/voucher number	Accession No.
Pica pica					
P. p. pica	Ppicpic4	Li	Russia, Smolensk reg.	D. Gluhov, ZMMU/AK 0113	AY701156
	Ppicpic5	Li	Russia, Smolensk reg.	D. Gluhov, ZMMU LVE65	AY701157
	Ppicpic7	Fe	Turkey, Büyük Camlica, Istanbul-Üsküdar	R. Kothbauer	AY701166
	Ppicpic8	Fe	Turkey, Büyük Camlica, Istanbul-Üsküdar	R. Kothbauer	AY701165
	Ppicpic9	Mu	Austria, Gars/Kamp	N. Teufelbauer	EU070896
P. p. melanotos	Ppicmel3*	Pa	Spain, Linares de Riofrio	Phyl. Mus. Jena 7086	EU070771
	Ppicmel4*	Pa	Spain, Linares de Riofrio	Phyl. Mus. Jena 7087	EU070772
P. p. bactriana	Ppicbac4	Li	Russia, Kirov reg.	V. Sotnikov, ZMMU/AK 0168	AY701153
	Ppicbac5	Mu	Russia, Ivanovo reg.	Ya. Red'kin, ZMMU/AK 0223	AY701154
	Ppicbac6	Li	Russia, N Caucasus, Kislovodsk	Ya. Red'kin, ZMMU/AK 0112	AY701155
P. p. hemileucoptera	Ppichem1	Li	Russia, S Siberia, Tuva, Muhur-Aksy	A. Tsvetkov, ZMMU/AK 136	AY701163
	Ppichem2	Li	Russia, S Siberia, Tuva, Muhur-Aksy	A. Tsvetkov, ZMMU/AK 138	AY701164
P. p. leucoptera	Ppicleu1	Mu	Russia, Buryatia, Ulan-Ude	S. Weigl	AY701158
	Ppicleu2	Mu	Russia, Buryatia, Ulan-Ude	S. Weigl	AY701159
	Ppicleu3	Mu	Russia, Buryatia, Schartal	S. Weigl	AY701160
	Ppicleu4	Mu	Russia, Buryatia, Ulan-Ude	S. Weigl	AY701161
	Ppicleu5	Mu	Russia, Buryatia, Ulan-Ude	S. Weigl	AY701162
P. p. jankowskii	Ppicjan1	Li	Russia, Primorye reg., Nadezhdinskaya	AK 712	AY701167
	Ppicjan2	Li, Mu	Russia, Khabarovsk reg., Solnechny	AK 0281	AY701168
	Ppicjan3	Li	Russia, Primorye reg., Gaivoron	A. Tsvetkov, ZMMU EAK041	AY701169
	Ppicjan4	Li	Russia, Primorye reg., Nadezhdinskaya	AK 713	AY701170
	Ppicjan5	Li	Russia, Primorye reg., Nadezhdinskaya	AK 714	AY701171
P. p. sericea	Ppicser1	Li	South Korea, Chuncheon city	Jong Teak Kim, CGRB 0244	AY701172
	Ppicser3	Li	South Korea, Chungnam prov.	H. Park, CGRB 0250	AY701173
P. p. camtschatica	Ppiccam1	Li	E Russia, Anadyr' river, Markovo settl.	A. Shestakov, ZMMU/AK 0736	EU070897
Outgroup					
Cyanocorax cyanomelas					
	Ccme1	Pa	Brazil, Karumba, Mato Grosso	NMW 81.697	EU070899
Cyanocorax chrysops chrysops					
	Cchrchr1	Pa	Argentina, Colonia Mado, Misiones	NMW 84.144	EU070898

Abbreviations: Mu/Li, muscle/liver sample; Bl, blood; Fe, feather; Pa, tissue from foot pad; AK, Alexei Kryukov, tissue collection number; NMW, Museum of Natural History Vienna (Austria); CGRB, Conservation Genome Resource Bank for Korean Wildlife (Korea); MNHN, Museum of Natural History Paris (France); Phyl. Mus. Jena, Phyletisches Museum Jena, University of Jena (Germany); TLF, Tiroler Landesmuseum Ferdinandeum, Innsbruck (Austria); ZFMK, Alexander Koenig Research Institute and Zoological Museum, Bonn (Germany); ZMMU, Zoological Museum Moscow State University (Russia). * indicates samples from which only the small CR fragment could be obtained. Hybrids were recognized by plumage phenotype.

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