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Phylogeography of a widespread Palaearctic forest bird species: The White-backed Woodpecker (Aves, Picidae)

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Abstract

We use multilocus molecular data and species distribution modelling to investigate the phylogenetics and the phylogeography of the White-backed Woodpecker (*Dendrocopos leucotos*), a bird species widely distributed over the entire Palaearctic. Our phylogenetic results reveal three well-supported clades within *D. leucotos*: the Chinese endemic subspecies (*tangi*, *insularis*), the northerly distributed subspecies (*leucotos*, *uralensis*) and the four poorly genetically differentiated Japanese subspecies (*subcirris*, *stejnegeri*, *namiyei, owstoni*), and the south-western Palaearctic *lilfordi* subspecies. According to our results, the Amami Woodpecker, endemic to Amami Oshima Island (Ryukyu archipelago, Japan) sometimes treated as full species *Dendrocopos owstoni*, does not deserve a species-level status. Based on the mitochondrial phylogeographic results, the Japanese archipelago was recently colonized only once by *D. leucotos* from eastern Eurasia. Our results suggest a split between the *leucotos* and *lilfordi* lineages that dates back to mid-Pleistocene (around 0.6 Mya) with likely no gene flow between these two subspecies since then. Our results thus do not support a phylogeographic pattern in which Central Europe and Northern Europe were recolonized from one or several southern glacial refugia where *lilfordi* populations persisted through several Pleistocene glacial periods. Spatial variation in mitochondrial diversity across *leucotos/uralensis* populations and niche ecological modelling suggest a possible eastward population expansion from a unique glacial refugium likely located in Central Europe. Molecular species delimitation methods, gene flow analyses and differences in adult and juvenile plumage indicate that the *lilfordi* subspecies may warrant to be ranked as a valid phylogenetic species. Further studies are nevertheless needed in the Balkans, where *leucotos* and *lilfordi* came recently into contact to measure the effectiveness of reproductive barriers and gene flow.

KEYWORDS

biogeography, *Dendrocopos leucotos*, glacial refugia, Palaearctic, Pleistocene, species limits

1 | INTRODUCTION

The White-backed Woodpecker *Dendrocopos leucotos* (Bechstein, 1802) is a forest-dwelling bird widely distributed over the entire Palaearctic from Western Europe to eastern Russia, Mongolia, China and Japan (Figure 1). It is part of a large Palaearctic and Indo-Malayan radiation (genus *Dendrocopos*, 10 species; see Fuchs & Pons, 2015) of large pied woodpeckers (body size: 23–28 cm), with its closest relative being the Okinawa Woodpecker (*Dendrocopos noguchii*) (Fuchs & Pons, 2015; Winkler & Christie, 2020). The White-backed Woodpecker has a specialized ecological niche. Indeed, it is more dependent on old-growth deciduous or mixed forests with rotten wood especially standing trees, where it can forage on large wood-boring insect larvae, than other co-distributed *Dendrocopos* woodpeckers (Gorman, 2014; Winkler & Christie, 2020).

Nowadays, eleven or twelve morphological subspecies are generally recognized based on plumage and body size variations (Gill et al., 2020; Winkler & Christie, 2020). Four of them (*subcirris*, *stejnegeri*, *namiyei and owstoni*), endemic to the Japanese archipelago where they occur from sea-level to mountain forests, are distributed from northern Hokkaido up to the small islands in the southern Ryukyu archipelago. The Amami Woodpecker *Dendrocopos leucotos owstoni*, which differs from other subspecies by its darker plumage, is only found on Amami Oshima (Ryukyu archipelago) where it inhabits old mature evergreen broadleaved forests and has been treated as a full species in recent checklists (Gill et al., 2020; Winkler et al., 2020). Two other subspecies occur in central (*Dendrocopos leucotos tangi*) and southern (*Dendrocopos leucotos fohkiensis*) mainland China, and another subspecies (*Dendrocopos leucotos insularis*) is endemic to the island of Taiwan. In Eurasia, the nominate subspecies has a very wide and continuous range spreading from Northern and Central Europe to eastern Asia along with the poorly differentiated subspecies *Dendrocopos leucotos uralensis* (Winkler & Christie, 2020), which is distributed from the Ural Mountains to Lake Baikal. Finally, the southern subspecies *Dendrocopos leucotos lilfordi*, which has well-marked distinctive plumage characteristics (six black bars on rump and back versus none or partial in nominate), is larger than *Dendrocopos leucotos leucotos* with which it is in geographical contact in Central Europe (Croatia, Serbia, Slovenia). Unlike the nominate subspecies, *D. l. lilfordi* possesses a fragmented range restricted to old mountainous forests of the southern Palaearctic (Pyrenees, Apennines, Balkans, Asia Minor and Caucasia).

Quaternary (−2.58 million years ago to nowadays) climatic oscillations caused historical range contractions and expansions of organisms and were therefore important factors affecting the phylogeographical structure and the levels of genetic diversity of many taxa throughout the temperate Northern Hemisphere (Avise, 2000; Avise & Walker, 1998; Hewitt, 2000; Taberlet et al., 1998). Regarding the White-backed Woodpecker, several plausible phylogeographical hypotheses could explain its present-day geographical distribution and genetic structure across the Western Palaearctic. One scenario is that northern *leucotos* populations of the Western Palaearctic would originate from the *lilfordi* lineage which expanded from one or several southern Pleistocene glacial refugia when the climate became favourable to population expansion after the last glacial maximum (in Europe,

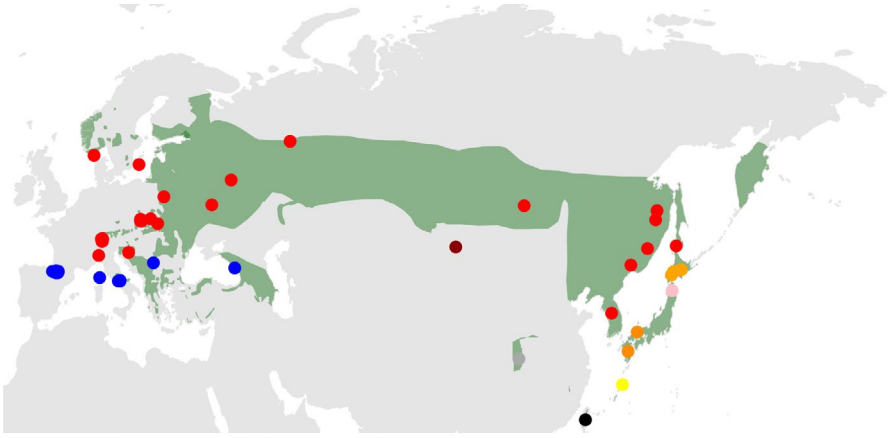

FIGURE 1 Distribution of the White-backed Woodpecker (BirdLife International & NatureServe, 2013) and sampling localities included in the present study. *Dendrocopos leucotos leucotos* northern group includes *leucotos* (red) and *uralensis* (brown). Japanese subspecies (light orange = *subcirris*; pink = *stejnegeri*; dark orange = *namiyei*; yellow = *owstoni*). Chinese subspecies group (black = *insularis*; grey = *tangi*). Southern group *lilfordi* (blue). Precise sampling localities and sample size are reported in the table S1. Several checklists and monographies considered that *D. leucotos* was occurring in Kamchatka, Russia (e.g. BirdLife International & Nature Serve, 2013; Vaurie, 1959; Winkler & Christie, 2020); a recent review of type specimens concluded that there is no evidence for the presence of *D. leucotos* in Kamchatka (Grangé & Red'kin 2019). Maps were made using R (R Core Team, 2013) libraries maps and mapdata (Becker & Wilks, 2013), maptools (Bivand & Lewin-Koh, 2014) and scales (Wickham, 2014)

around 20 kya). This scenario has been described for many organisms exhibiting varied dispersal abilities (Hewitt, 2000; Weiss & Ferrand, 2007). The Western Palaearctic contains at least four primary areas that acted as refugia for forest birds: the Iberian Peninsula, Central Italy, the Balkans and the Caucasia (e.g. Drovetski et al., 2018; Hewitt, 2004). Under this scenario, we expect low genetic divergence, the sharing of mitochondrial haplotypes between *leucotos* and *lilfordi* and higher genetic diversity in *lilfordi* populations because it would have successfully persisted through Pleistocene climatic oscillations in one or several southern European refugia (Hewitt, 1996, 2000). The second hypothesis relies upon an independent evolution of *leucotos* and *lilfordi* for a significant amount of time. Under this scenario, the Western Palaearctic was first colonized by an ancestral Asian lineage that nowadays only persists in small fragmented *lilfordi* populations found in southern European mountains, while the current northern and central European *leucotos* populations were more recently established from an unknown glacial refugium not located in southern Europe but likely in eastern Asia as suggested by Voous (1947). If this hypothesis is correct, an old separation and significant genetic divergence between the subspecies *lilfordi* and *leucotos* are expected. Linked to this scenario, we could also expect very little divergence across populations from the northern subspecies, which occupies a large and contiguous distribution (from South Korea to Norway); such a pattern was found for two other partly sympatric woodpecker species, the Three-Toed (*Picoides tridactylus*) and Great spotted (*Dendrocopos major*) Woodpecker (Perktaş & Quintero, 2013; Zink, et al., 2002).

In the present study, we aim to reconstruct the phylogenetic relationships of the White-backed Woodpecker subspecies using multilocus genetic data and we used the mitochondrial gene COI to discriminate between alternative phylogeographical hypotheses that may explain the present-day geographical distribution of the genetic variability within *D. leucotos*. We focused on the phylogeography of the two parapatric subspecies (*lilfordi* and *leucotos*) that occur in the Western Palaearctic for which efficient sampling was available to infer demographic history and genetic diversity within populations. Using species distribution modelling, we compared the phylogeographical scenario inferred from genetics with the areas where climatic conditions remained potentially favourable to the White-backed Woodpecker during the last 120,000 years. We also assessed the possibility that *D. l. lilfordi*, which currently does not occur in Corsica, historically inhabited this island using ecological niche modelling and genetic results we obtained from two museum specimens supposedly collected in Corsica at the end of the nineteenth century.

The taxonomic and conservation implications of our results are discussed taking into consideration that some of the currently defined subspecies of *D. leucotos* may represent full species as it was recently suggested for other Palaearctic Pied woodpecker species (e.g. *D. major*, Perktas & Quintero, 2013; *Dendrocoptes medius*, Kamp et al., 2019). This is particularly important as some populations attributable to these taxa strongly depend on old-growth deciduous or mixed forests, which are under threat due to forest management practices. This is for example the case for the Swedish *D. l. leucotos* population which is classified as critically endangered 'CR' on the Swedish national red list and *D. l. lilfordi* classified as vulnerable 'VU' in France and in Italy. In Spain, the latter subspecies is considered 'In danger of extinction' on the Spanish Catalogue of Threatened Species (Real Decreto 139/2011).

2 | MATERIALS AND METHODS

2.1 | Sampling

We obtained fresh (blood, feathers, muscle, $n = 62$) and dry (toe pads, $n = 8$) tissue samples from 70 individuals covering a large part of the White-backed Woodpecker distribution (Figure 1 and see Table S1 for details of exact localities). We further included 10 mitochondrial sequences that were available on GenBank (https://www.ncbi.nlm.nih.gov/) in the phylogeographical analyses (Accession Numbers in Table S1). Eight (*leucotos, lilfordi*, *subcirris*, *stejnegeri*, *namiyei, owstoni, insularis and tangi*) out of the eleven subspecies currently recognized (Winkler & Christie, 2020) were included in the present study. Two insular subspecies (*takahashii* and *quelpartensis*) morphologically very close to *Dendrocopos leucotos namiyei* and *Dendrocopos leucotos stejnegeri*, respectively (Vaurie, 1959; Short, 1982), and one mainland subspecies from south-east China (*fohkiensis*) were not available for this study. The two Korean subspecies whose validity is often questioned are much likely of recent origin (Winkler & Christie, 2020). *Dendrocopos leucotos fohkiensis* is distributed in southern China, and we sampled the other two subspecies that bound its distribution (*tangi* and *insularis*). Furthermore, the subspecies *fokhiensis* is morphologically intermediate between *tangi* and *insularis* (Cheng, 1956). We also sampled two *D. l. lilfordi* specimens, supposedly collected in Corsica during the nineteenth century, currently preserved at the Museum of Natural History of Bern, Switzerland.

2.2 | Phylogenetic analyses

2.2.1 | Published data corrections

During the course of this study, we realized that sequencing/editing errors, involving one base pair in each case,

were present in two published sequences (*D. l. leucotos* ZMUC 141307, GenBank Accession Numbers: KR049420, Myoglobin; *D. l. leucotos* BON-126, GenBank Accession Numbers: GU571366, COI). The sequences were corrected prior to the analyses.

2.2.2 | DNA extraction, amplification and sequencing

DNA was extracted from muscle, blood or feather calamus using the DNA Blood and Tissue (Qiagen, Valencia) Extraction Kit. DNA was extracted from historical specimens using the DNA Mini Kit (Qiagen, Valencia) following the manufacturer's protocol except that digestion volume was doubled (400 µl instead of 200 µl) and 30 µl of DTT was added to the digestion solution. Digestion of tissues was performed for 16 hr.

We amplified and sequenced three nuclear autosomal introns fibrinogen intron 5 (FGB), myoglobin intron 2 (MB) and transforming growth factor beta 2 (TGFb2) using standard amplification protocols with varied annealing temperature and primers previously published (Fuchs & Pons, 2015). We included 75 intron sequences in the phylogenetic analyses among which 39 were retrieved from GenBank (Table S1).

The mitochondrial cytochrome *c* oxidase subunit I (COI) was amplified and sequenced using primers COIext/FISH1R (Johnsen et al., 2010; Ward et al., 2009) following standard amplification protocols. We designed eight internal primers in order to amplify the COI from the historical specimens: primer details are given in Table 1. Our data set for *D. leucotos* comprised 82 COI sequences of which 10 were previously published in GenBank and Bold (see Table S1). We also included in the phylogenetic analyses 32 COI sequences among which 26 were retrieved from GenBank of related *Dendrocopos* species sensu Fuchs and Pons (2015), including a broad sampling of the widely distributed *D. major*, in order to have an independent comparison for intra- versus interspecific differentiation. Trees were rooted with sequences from *Picoides pubescens* and *Veniliornis mixtus* (e.g. Fuchs & Pons, 2015; Shakya et al., 2017). Detailed information on the sequences included in the analyses is reported in Table S1.

2.2.3 | Determining the phase of alleles

We used PHASE v2.1.1 (Stephens, Smith, Donnelly, 2001), as implemented in DNASP 5.0 (Librado & Rozas, 2009), to infer the alleles for each nuclear locus. Genetic diversity parameters including haplotype diversity (Hd), Watterson's theta (Θ) and nucleotide diversity (π) were estimated in DNAsp 5.0 (Librado & Rozas, 2009) for each lineage.

2.2.4 | Gene trees, species tree and molecular divergence time estimates

Nuclear gene tree reconstructions of the unique nuclear alleles were performed using Bayesian inference (BI), as implemented in MRBAYES 3.2 (Ronquist et al., 2012). We used the nst = mixed and rates = invgamma options such that model uncertainty is taken into account during the phylogenetic reconstruction. Four Metropolis-coupled Markov chain Monte Carlo (MCMC) chains (one cold and three heated) were run for $5*10^6$ iterations, with trees sampled every 10^3 iterations.

We estimated the time to most recent common ancestor (TMRCA) among the *Dendrocopos* unique mitochondrial haplotypes using BEAST 1.8.2 (Drummond et al., 2012), with a strict molecular clock model, a TIM + I substitution model selected using TOPALI (Milne et al., 2009) under the Bayesian information criterion, and a Yule tree prior. MCMC chains were run for 10^7 steps and were sampled every 10^3 steps. We used three substitution rates and their associated uncertainties to calibrate the trees. The first rate (0.016 substitutions per site per lineage per million year [s s^{-1} L^{-1} myr^{-1}]; 95% HPD: 0.014–0.019 s s^{-1} L^{-1} myr^{-1}) was based on the complete mtDNA genomes from honeycreepers (Passeriformes, Drepanididae) and calibration points based on the age of volcanic islands in the Hawaiian archipelago as proposed by Lerner et al. (2011). The second rate was the fourfold degenerated sites rate derived from complete mtDNA sequences of Adelie Penguins (*Pygoscelis adeliae*) (0.073 s/s/l/myr: 95% HPD: 0.025–0.123 s/s/l/myr; Subramanian et al. (2009)). The third rate was a body mass-corrected mitochondrial clock recently

TABLE 1 Information on the two external and the eight internal primers designed to amplify the COI from the historical specimens

Forward primer	Reverse primer
COIExt: ACGCTTTAACACTCAGCCATCTTACC	leuCOI55H: AATCCCCCGATTATGATGGG
leuCOI36L: TCACCGCCCATGCATTTGTG	leuco263H: ACTGTGGAGGAGGCTAGGAG
leuco260L: ATAAGCTTYTGACTTCTCCC	leuco403H: TCCTAGGATTGATGAGATGC
leuco385L: CTCAGTAGACCTAGCCATCTT	leuco526H: GTACCGGGAGTGATAGGAGT
leuco507L: CCTATTCGTCTGATCTGTCC	FISH1R: TAGACTTCTGGGTGGCCAAAGAATCA

proposed by Nabholz et al. (2016). We employed the equation, $10^{(-0.145*\log_{10}(\text{body}_{\text{mass}})+0.459)}/100$, corresponding to their calibration set 2, to calculate the body mass-corrected substitution rate for the COI third codon position in our data set. We assumed an average body mass for five of the six sampled *Dendrocopos* species of 82.6 g (Dunning, 2007; no body mass data were available for *D. noguchii* in Dunning (2007), Winkler et al. (2020) or on Vertnet). We used the mitochondrial topology to estimate the third codon position branch lengths using PAML v4.9 (Yang, 2007). The branch lengths were then converted to divergence times in R using scripts from Nabholz et al. (2016).

We reconstructed a species tree using the coalescent-based model implemented in *BEAST (Heled & Drummond, 2010). We selected the substitution model for each locus using TOPALI (Milne et al., 2009) under the Bayesian information criterion (COI: TrN + I, FGB: TrN, MB: JC + G, TGFb2: K80). Each locus had its own substitution rate matrix and clock model (all assigned to a strict clock model). The species tree analyses, as implemented in *BEAST require predefined species or species-level lineages. We defined nine species within our data set corresponding to the out-groups (*P. pubescens, V. mixtus*, *Dendrocopos major major/pinetorum/numidus*, *Dendrocopos syriacus*, *Dendrocopos darjellensis*, *D. noguchii*) and the three White-backed Woodpecker clades for which all loci were available (the Japanese endemic subspecies, *D. l. leucotos/uralensis* and *D. l. lilfordi*). We used a Yule process for the tree prior with a normal prior distribution for the COI substitution rate (0.016 s/s/l/myr; 95% HPD: 0.011–0.021 s/s/l/myr). We conducted two runs for $25*10^6$ iterations, with trees and parameters sampled every $5*10^3$ iterations and discarding the first $2.5*10^6$ iterations as the burn-in period. TRACER v1.6 (Rambaut & Drummond, 2009) was used to ensure that our effective sample size of the underlying posterior distribution was large enough (>200) for a meaningful estimation of parameters.

2.2.5 | Molecular species delimitation methods

We used a Bayesian implementation of the general mixed Yule-coalescent model (bGMYC 1.0; Reid & Carstens, 2012) to delimit species-level lineages using molecular data. This implementation is an extension of the GMYC model (Pons et al., 2006) that incorporates gene tree uncertainty by sampling over the posterior distribution of sampled gene trees. We obtained a posterior distribution of ultrametric gene trees from the 33 unique mitochondrial haplotypes using the strategy described above. We ran MCMC for 10^7 iterations with sampling of parameters and trees every 1,000 iterations. The first 10% of the samples were removed as the burn-in period. We analysed 100 trees sampled randomly from the posterior distribution and used the default setting in bGMYC. We ran the MCMC chains for $5*10^4$ iterations, with a burn-in of $4*10^4$ iterations, and sampled parameters every 100 iterations.

We also used the software BPPv3.4 (Flouri et al., 2018) to estimate the joint probability of the species tree and the speciation probability (model A11, Yang & Rannala, 2014), testing both algorithm 0 and algorithm 1, for the four-locus data set. We used invgamma priors on the population size parameters (θ) and the age of the root in the species tree (τ_0); the values for the invgamma distribution were determined by *MinimalistBPP* (https://brannala.github.io/bpps/#/). We allowed the loci to have different rates (locus rate = 1, Dirichlet distribution) and took into account the differences in heredity scalar (heredity = 2). We ran the rjMCMC analyses for $4*10^5$ generations with a burn-in period of $4*10^4$ and different starting seeds. Each analysis was run twice. We did not include the lineages *D. l. insularis/l. tangi* and *Dendrocopos major japonicus* as they were only represented by the mitochondrial locus.

We used the MCMC method implemented in IMa2 (Hey, 2010) to fit the data to a model that included both isolation and migration to enable us to estimate the level of historical gene flow between the two primary *D. leucotos* lineages: (a) *D. l. lilfordi* and (b) the clade comprising *D. l. leucotos/uralensis* and all endemic Japanese subspecies. We defined inheritance scales to reflect the difference in inheritance modes among the loci: 0.25 for the mtDNA locus and 1.0 for the two autosomal loci (TGFb2 had to be excluded because of its low number of variable sites, 1). We used an HKY model of nucleotide substitution for all loci. We used a geometric heating scheme (h1 = 0.9, h2 = 0.3) coupled with 100 chains. For each data set, upper bounds for the prior for the final run were adjusted based on preliminary runs with large uniform priors. Parameters and genealogies were sampled every 100 steps until we had sampled 10^5 genealogies. The fit of 25 demographic models involving different combinations of population sizes and migration rates was then determined using likelihood ratio tests under the L-mode setting in IMa2 (Hey & Nielsen, 2007). To assess convergence, we monitored the extent of autocorrelation and parameter trend lines throughout the run and we also compared the results between four independent runs. Incorporating a genetically structured population like the *D. leucotos*/Japanese subspecies clade violates one of the assumptions of the isolation-with-migration model (Hey & Nielsen, 2004, 2007). We tested the impact of adding the Japanese endemic subspecies (and hence structure) on gene flow estimates by performing additional runs without them. We expect that the impact will be minimal because empirical and simulation data suggest that the associated bias in parameter estimation introduced by the presence of hidden population structure is limited (Strasburg & Rieseberg, 2010).

2.3 | Genetic structure across the Western Palaearctic

2.3.1 | Selection on the mitochondrial loci

We used the McDonald–Kreitman test (MK) (McDonald & Kreitman, 1991), as implemented in DnaSP v. 5.10.01 (Librado & Rozas, 2009) to test whether selection was acting on the mitochondrial protein-coding gene (COI) used to infer phylogeny and population genetics. MK tests were performed between *leucotos* and *lilfordi*, the only subspecies for which sample sizes were large enough.

2.3.2 | Diversity indices, genetic distance and network

Standard diversity indices for *leucotos/uralensis* ($N = 44$) and *lilfordi* ($N = 23$) were calculated using Arlequin 3.5 (Excoffier & Lisher, 2010). Subspecies from Japan and China were not included due to small sample size. We used Arlequin 3.5 to perform Fu's *Fs* and Tajima' *D* tests (1,000 replicates) to detect signatures of population expansion. Fu's *Fs* and Tajima' *D* were initially developed to test for selection, but in the absence of the latter, significant negative values are indicative of population expansion. We calculated D_{xy} (average number of nucleotide substitution per site between taxa pairs using DNAsp (Librado & Rozas, 2009). We generated a median-joining network including all subspecies to visualize relationships among haplotypes with NETWORK 10 (Bandelt et al., 1999).

2.4 | Ecological niche modelling

Species occurrence data were downloaded using the rgbif package (Chamberlin et al., 2020; Chamberlain & Boettiger, 2017) using the *Coordinate = TRUE* and *Basis Of Record = 'PRESERVED_SPECIMEN'* filters. These occurrences were complemented by occurrence data derived from the individuals used for the genetic analyses. After checking for georeferencing errors and removing duplicates, the total number of observations was 370 for *D. l. leucotos/uralensis*, 58 for *D. l. lilfordi* and 42 for the Japanese subspecies. We did not perform species distribution modelling for the *D. l. insularis/tangi* lineage because too few data were available for meaningful species distribution modelling.

We used climatic layers from the WorldClim database (Hijmans et al., 2005; 2.5 min resolution) and restricted the study area to the following coordinates (latitude extent: 25–70; longitude extent: −11 to 172), corresponding to the extent of the distribution of *D. leucotos*. Among these 19 BioClim climatic variables, nine variables were retained for the analyses. These variables were selected using *raster.cor.matrix*, as implemented in the ENMtools package (Warren et al., 2017) and a correlation threshold of 0.8. Retained variables included annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), annual precipitation (BIO12), precipitation of the driest month (BIO14), precipitation seasonality (BIO15) and precipitation of the coldest quarter of the year (BIO19).

We built species distribution models for each of the three lineages using the maximum entropy algorithm implemented in Maxent ver. 3.3.3 (Phillips et al., 2006). For each lineage, we used 20% of the observations for testing (on randomly sampled 1,000 background points) and 80% for model training. We used the area under the receiver operating characteristic curve (AUC) to determine whether the predictions generated by Maxent for current conditions were better than random. The AUC is a commonly used measurement for comparison of model performance (Elith et al., 2006). The AUC ranges from 0 to 1, with greater scores indicating better discrimination ability; an AUC greater than 0.5 indicates that the model discriminates better than random.

Niche models for each lineage were then projected on palaeoclimatic layers from three time periods: the last interglacial (about 130,000 years ago; Otto-Bliesner et al., 2006), the last glacial maximum (21,000 years ago) and the mid-Holocene (8,326–4,200 years ago) (Fordham et al., 2017). Layers were downloaded from http://www.paleoclim.org/ (Brown et al., 2018).

We tested for differentiation in niche models using the niche.equivalency.test function, as implemented in the phyloclim (Heibl & Calenge, 2018) package. We performed 99 replicates on the occurrence data for each lineage. We did pairwise comparisons for the three primary linages: *lilfordi* versus *leucotos*, *lilfordi* versus Japanese subspecies and *leucotos* versus Japanese subspecies.

3 | RESULTS

3.1 | Multilocus phylogenetic relationships

3.1.1 | Gene trees

We performed the phylogenetic analyses on the 33 COI unique haplotypes from our data set using BEAST 1.8.2 (Figure 2). Seventeen unique haplotypes were identified for *D. leucotos*. The analyses identified a clade with the Okinawa Woodpecker (*D. noguchii*) being sister (PP: 1; Figure 2) to a monophyletic *D. leucotos* (PP: 0.96). *Dendrocopos l. insularis/D. l. tangi* (PP: 1) was the first lineage to split within the *D. leucotos* complex, but this relationship was not strongly supported (PP: 0.73).

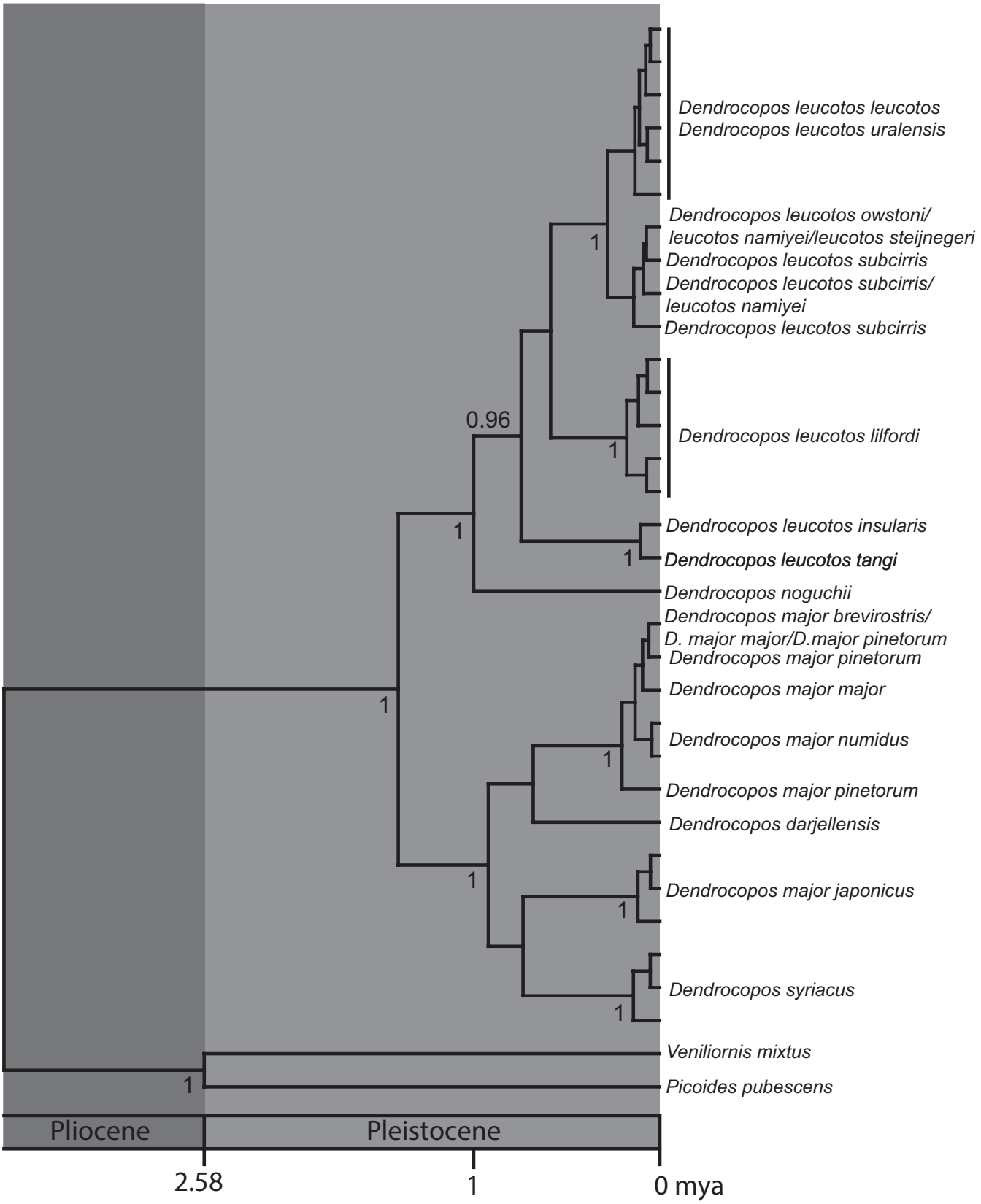

FIGURE 2 Fifty per cent majority-rule consensus tree obtained from the Bayesian analyses of the mitochondrial markers (COI) using BEAST 1.8.2. Only unique haplotypes were included in the matrix. Values close to nodes represent Bayesian posterior probabilities (PP). *Veniliornis mixtus* and *Picoides pubescens* were used as out-group

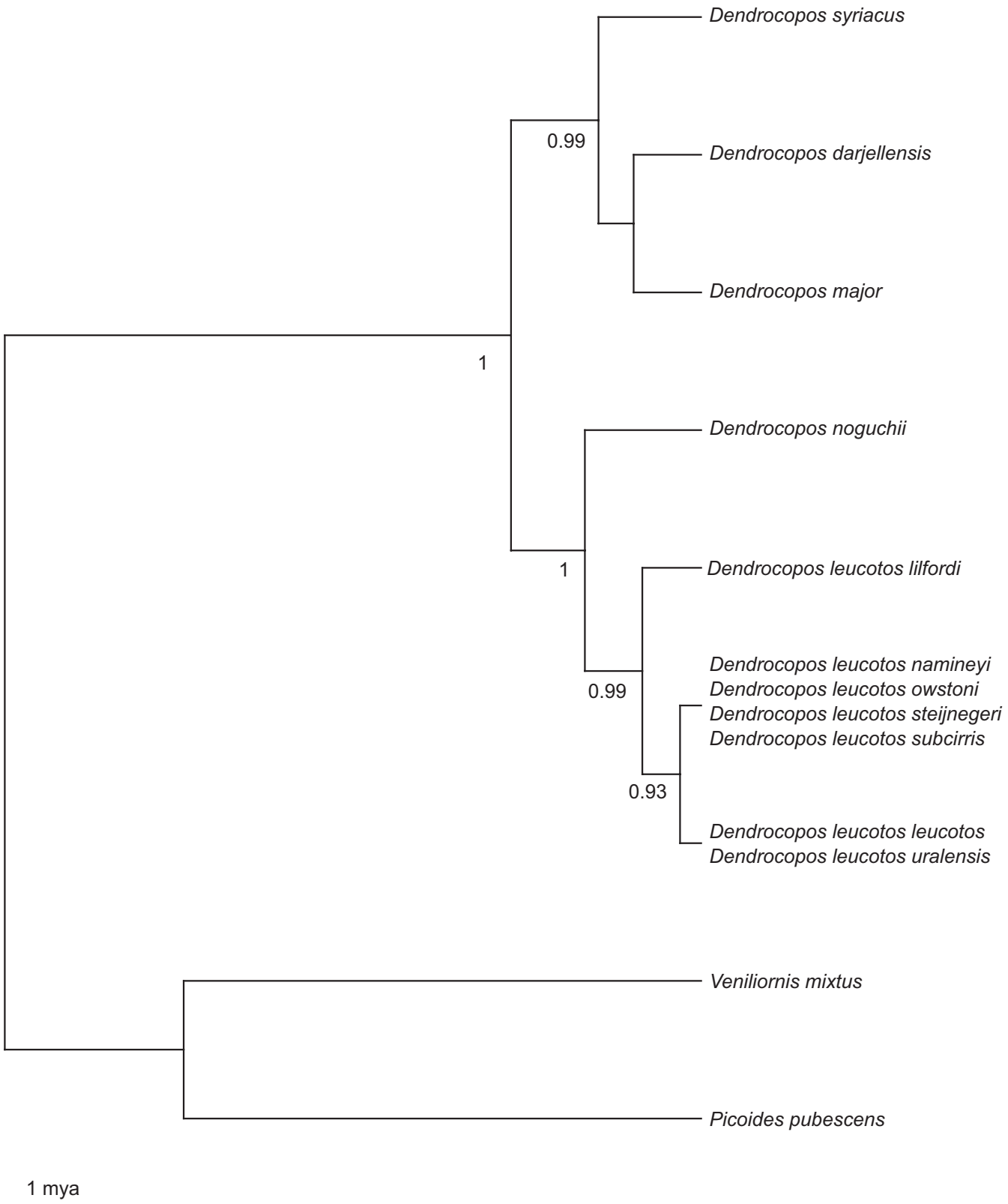

FIGURE 3 Species tree based on the phased nuclear alleles obtained with *BEAST. Values close to nodes represent Bayesian posterior probabilities (PP). PP values < 0 .90 not shown. *Veniliornis mixtus* and *Picoides pubescens* were used as out-group. Chinese subspecies (*tangi*, *insularis*) could not be included in the data set

Dendrocopos l. lilfordi individuals formed a strongly supported clade (PP: 1). The White-backed subspecies found in Japan (*ownstoni*, *steijnegeri*, *subcirris, nameyi*) and *D. l. leucotos/uralensis* formed a clade (PP: 1) that was sister to *D. l. lilfordi*. In addition, *D. major* was not monophyletic with populations from the Western Palaearctic

(Austria, France, Morocco, Netherlands, Norway, Russia, Sweden, Tunisia; *D. m. major*, *Dendrocopos major pinetorum*, *Dendrocopos major numidus*) being more closely related to *D. darjellensis*, whereas the eastern populations of *D. major* (*D. m. japonicus,* Russia, South Korea, Japan) were more closely related to *D. syriacus*, although the support for its non-monophyly was quite weak (PP: 0.78).

We failed to obtain nuclear DNA from the subspecies *D. l. insularis* and *D. l. tangi*. The nuclear gene trees were very poorly resolved (FGB, TGFb2) or polytomized (MB) (Figures S1–S3). In most cases, species were not monophyletic or undisputed species were found to share alleles (e.g. *D. major*, *D. syriacus* and *Dendrocopos leucotos subcirris* in FGB), suggesting that incomplete lineage sorting is still present in *Dendrocopos* at these loci. Concerning *D. leucotos*, the number of alleles found in the nuclear loci was two (TGFb2), five (MB) and six (FGB). For the three nuclear loci, *D. l. lilfordi* had only one allele that was shared with individuals from the northern lineage (MB, TGFb2) or private (FGB). Genetic diversity summary statistics for the three nuclear introns are reported in Table S2.

3.1.2 | Species tree

The subspecies *D. l. insularis* and *D. l. tangi* could not be included in the species tree analyses (Figure 3) since no nuclear data were obtained. The topology resulting from the *BEAST analyses indicated that the Japanese subspecies are related to *D. l. leucotos* and *D. l. uralensis* (PP: 0.93) and that all lineages mentioned above are sister to *D. l. lilfordi* (PP: 0.99).

3.1.3 | Molecular species delimitation methods

The bGMYC molecular species delimitation method recovered four species in the sampled members of the genus *Dendrocopos*. Even well-accepted species were lumped (*D. syriacus w*ith *D. m. japonicus* ($p = 0.08$), *D. darjellensis* with *D. m. major/pinetorum/numidus* ($p = 0.09$), although in several cases the *p*-values were close to significance threshold ($p = 0.05$). Within *D. leucotos*, the *p*-values were 0.07–0.09 for the species status of *D. l. insularis*/*D. l. tangi* versus *D. l. leucotos*/*D. l. lilfordi* and 0.11 for *D. l. leucotos* versus *D. l. lilfordi*.

The analyses performed with BPP indicated that the nine species model received the highest posterior probability (PP: 0.998 in both algorithms 0 and 1). Noticeably, *D. l. leucotos/uralensis*, the Japanese subspecies clade and *D. l. lilfordi* all received speciation probabilities of 1.0. The species tree topology was very similar to the *Beast results, with the single difference involving the relationships of *D. syriacus*, *D. major* (Western) and *D. darjellensis*.

3.2 | Divergence time estimates

Molecular divergence time analyses, performed with the Fringillidae COI rate, a strict clock model and a TIM + I model, indicated that *D. leucotos* diverged from *D. noguchii* about 1.1 Mya (95% HPD: 0.7–1.5 Mya), that *D. l. insularis/D. l. tangi* splitted from the remaining *D. leucotos* subspecies clade 0.8 Mya (95% HPD: 0.5–1.1 Mya) and that *D. l. lilfordi* splitted from the northern taxa about 0.6 Mya (95% HPD: 0.4–0.9 Mya). These splits were simultaneous with the splits between *D. darjellensis* and the Western Palearctic *D. major* (0.7 Mya, 95% HPD: 0.4–1.0 Mya) and between *D. syriacus* and *D. m. japonicus* (0.8 Mya, 95% HPD: 0.5–1.1 Mya). Very similar estimates were obtained using the fourfold degenerated rate (e.g. *D. leucotos*/*D. noguchii* 0.9 Mya, 95% HPD: 0.3–1.7 Mya; *D. l. leucotos-uralensis*/*D. l. lilfordi* 0.5 Mya, 95% HPD: 0.15–0.9 Mya). Estimates obtained using the body mass-corrected rate were about three times older: *D. leucotos* diverged from *D. noguchii* about 3.6 Mya (95%: 2.8–4.4 Mya), *D. l. insularis/D. l. tangi* from the *D. l. leucotos*/*D. l. lilfordi* clade 2.4 Mya (95%: 1.9–2.9 Mya) and the two latter subspecies diverging from each other about 1.9 Mya (95%: 1.6–2.4 Mya).

Within *D. leucotos*, divergence times obtained in the species tree analyses (calibrated using the Lerner et al., 2011 rates) were similar to the one obtained using the mitochondrial DNA alone: *D. l. lilfordi* splitted from the northern taxa about 0.6 Mya (95% HPD: 0.2–1.0 Mya).

The *D. major*/*D. leucotos* clade started to diversify about 1.1–2.1 Mya (mtDNA only: Lerner et al. (2011) rate, 95% HPD: 1.1–2.0 Mya, fourfold rate: 95% HPD: 0.5–2.6 Mya; species tree: 95% HPD: 1.3–2.9 Mya).

3.3 | Population genetics

3.3.1 | Mitochondrial genetic diversity and genetic distance

Hd and π were much higher in *lilfordi* populations than in *leucotos/uralensis* populations (see Table 2). The MK tests did not detect any significant evidence of selection in the mitochondrial DNA (COI) gene when comparing *leucotos/uralensis* with *lilfordi* (Fisher's exact test, $p = 0.49$). Tajima's *D* and Fu's tests suggested strong evidence of population expansion for the *leucotos/uralensis* lineage (Table 2). By contrast, we did not detect any sign of population expansion for *lilfordi*. These results thus suggest a different historical demography for these two subspecies. The D_{xy} distance between *lifordi* and *leucotos* was 2.1% which compares to the distances between *D. noguchii* and *D. leucotos* sensu lato (3.3%), between *D. major*

(W Palaearctic) and *D. darjellensis* (1.9%), and between *D. major* (E Palaearctic) and *D. syriacus* (2.6%). The D_{xy} value for the *D. l. insularis/tangi* versus the remaining *D. leucotos* subspecies was 1.8%.

3.3.2 | Median-joining network

The median-joining network was based on 80 COI sequences and included the two Chinese subspecies (Figure 4). Seventeen haplotypes clustered in four sub-networks corresponding to the four main clades highlighted in the COI phylogenetic analyses (Figure 2). The Japanese subspecies sub-network was closely related to the Eurasian *leucotos* sub-network (two mutation steps). The most common Japanese haplotype was shared by *owstoni*, *subcirris*, *stejnegeri* and *namiyei* highlighting both their close genetic proximity and their recent origin. All Japanese subspecies form a monophyletic group. The northern *leucotos* sub-network displayed a star-like shape with a common central haplotype having a wide geographical distribution at the centre of the network and derived haplotypes weakly differentiated radiating from the ancestral haplotype. Such a pattern is commonly observed in the case of recent population expansion, also suggested for *leucotos* by the Fu's *Fs* and Tajima significant tests (Table 2). It is remarkable that the most common *leucotos* haplotype has a very wide geographical distribution ranging from Western Europe to eastern Russia. It is also worth noting the high haplotype diversity found in Poland ($n = 4$) compared with Scandinavia ($n = 2$), other European countries ($n = 1$) and especially Russia and Mongolia which cover huge areas ($n = 1$). Only two individuals were available for Chinese subspecies (*insularis*, *tangi*) which group together in the same sub-network and are at the same time well differentiated from both *leucotos* and *lilfordi* sub-networks. The most common *lilfordi* haplotype was shared between White-backed Woodpeckers coming from the Pyrenees and the Balkans (Figure 4). All individuals from central Italy ($n = 5$) hold the same haplotype that diverges from the most common *lilfordi* haplotype by one mutation step, while the only Caucasian White-backed Woodpecker included in the network was more distant (three mutation steps). Both White-backed Woodpeckers supposedly collected in Corsica

TABLE 2 Number of individuals (Ni), haplotypes (Nh), polymorphic sites (Np), haplotype diversity (Hd), nucleotide diversity (π), Tajima's *D* and Fu's statistics obtained for the northern *leucotos* group (*leucotos* and *uralensis*) and the southern *lilfordi* group using the mitochondrial gene COI (647bp)

	leucotos/uralensis	*lilfordi*
Ni	44	23
Nh	6	5
Np	5	6
Hd	0.29	0.64
π	0.0005	0.002
Tajima's *D*	−1.82	−1.08
p-value	**0.02**	0.14
Fu's Fs	−5.19	−0.81
p-value	**0.0001**	0.28

Note: In bold, significant values supporting population expansion.

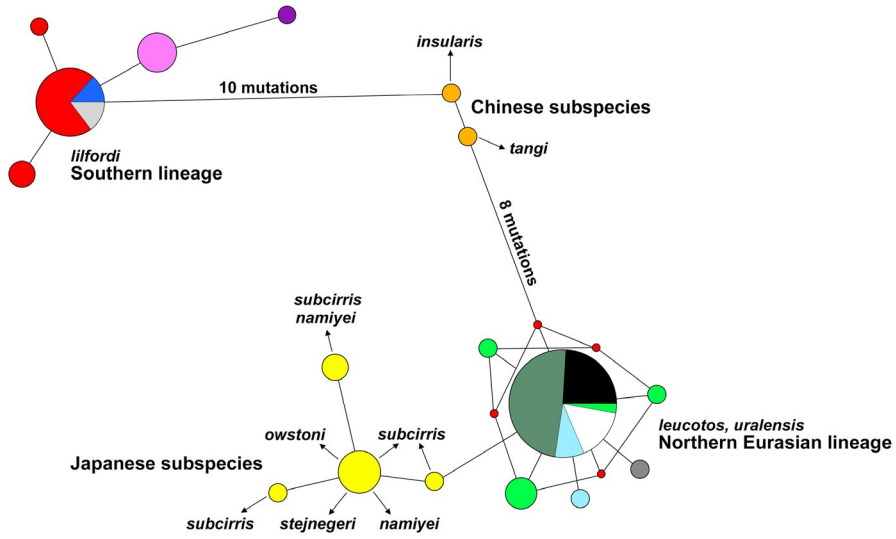

FIGURE 4 Median-joining network showing COI haplotypes relationships among *Dendrocopos leucotos* subspecies. The size of each circle is proportional to haplotype frequency. Red = Pyrenees; grey = Corsica? (see text); dark blue = Balkans, Serbia; pink = Abruzzi, Italy; violet = Caucasia, southern Russia; light green = Poland; Green = Western and Central Europe; black = Russia (west to far east); white = Mongolia; grey = South Korea; light blue = Scandinavia. Small red dots are unsampled haplotypes

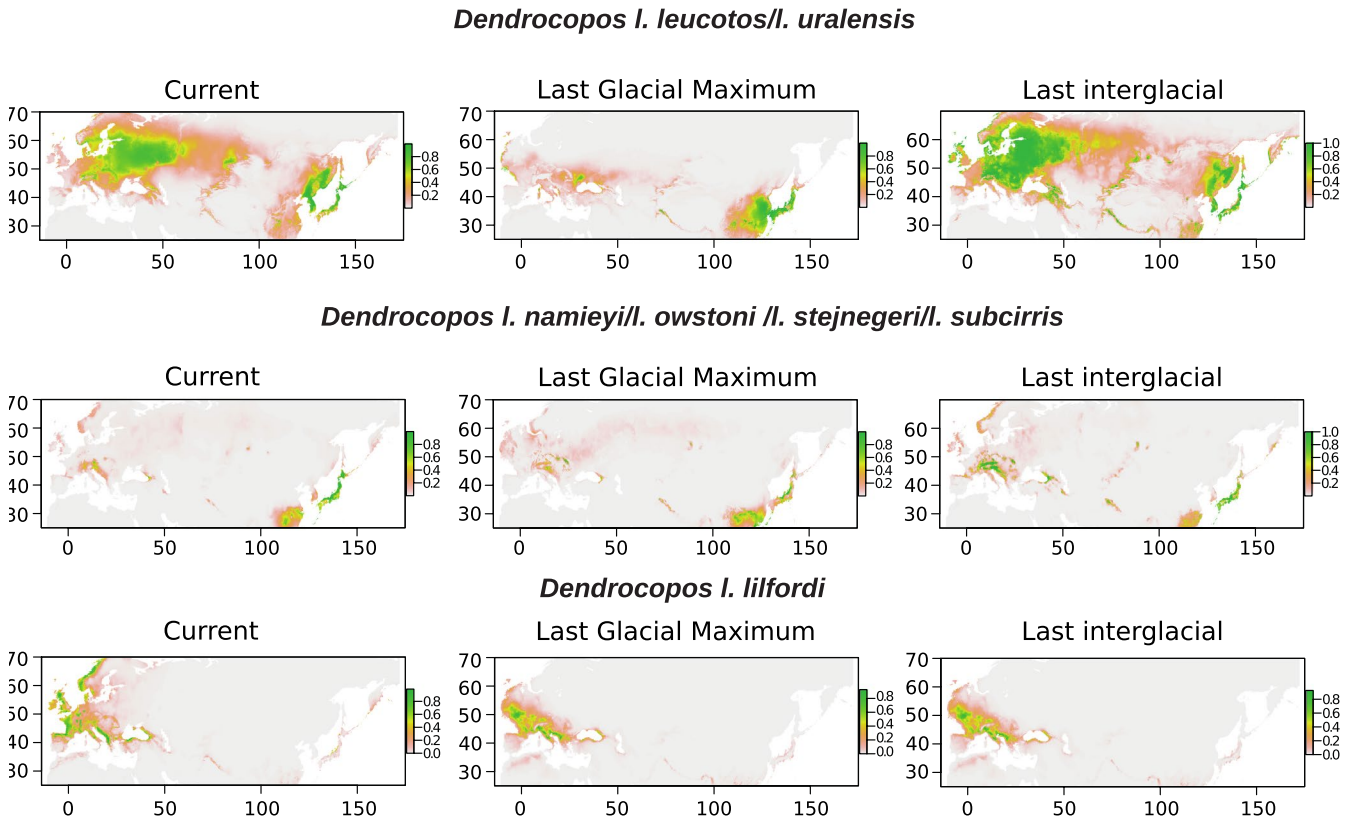

FIGURE 5 Predicted geographic distributions for *leucotos/uralensis,* the *japanese subspecies clade* and *lilfordi* subspecies of the White-backed Woodpecker. Nine climatic variables were used to build species distribution models: annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), annual precipitation (BIO12), precipitation of the driest month (BIO14), precipitation seasonality (BIO15) and precipitation of the coldest quarter of the year (BIO19). The niche models for current conditions were projected on palaeoclimatic layers from the last interglacial (about 130,000 years ago) and the last glacial maximum (21,000 years ago)

hold the most common haplotype found in the Balkans and Pyrenees.

3.3.3 | Gene flow among *D. leucotos* lineages

The results from the isolation-with-migration analyses were slightly different across runs; unrejected models that differed across runs implied the putative existence of differences in population sizes (a) between the two defined extant populations (*lilfordi* versus *leucotos/uralensis/owstoni/namiyei/subcirris/steijnegeri*) or (b) between the extant *leucotos/uralensis/owstoni/namiyei/subcirris/steijnegeri* and the ancestral population. Models that were always rejected across runs implied equal population sizes for the two extant populations and the ancestral population. Models that were never rejected included the full model, the models implying different population sizes among populations and models assuming equal population size between *D. l. lilfordi* and the ancestral population.

The common feature across all analyses was that the historical migration rate between the two extant populations was estimated to be 0 in all models that were not rejected by the likelihood ratio tests. Hence, the isolation-with-migration analyses strongly indicated that there is no historical gene flow between *lilfordi* and *leucotos/uralensis/owstoni/namiyei/subcirris/steijnegeri* and that alleles shared in the nuclear DNA are due to incomplete lineage sorting.

3.4 | Ecological niche modelling

For the three lineages, the AUC value was higher than 0.92 (*leucotos* = 0.93, *lilfordi* = 0.97, Japanese subspecies = 0.99); values higher than 0.76 are considered to correspond to a useful predictive model (Phillips & Dudík, 2008).

Models projected on current bioclimatic data were good representations of the current knowledge regarding the distribution of the species. One exception involves the climatic suitability for *D. l. lilfordi*, where the current distribution is much more restricted when compared to its potential distribution based on bioclimatic data (see below).

For the Japanese lineage, the highest predicted suitability is along the Japanese archipelago with other suitable areas

in the Korean peninsula and south-eastern China (Figure 5). The predicted range of the lineage may have been stable in the Japanese archipelago during the last 120,000 years (Figure 5), with other continuously putatively stable areas being south-eastern China and Central Europe.

For the *D. l. leucotos/uralensis* lineage, the highest predicted suitability is Central and Eastern Europe west of the Ural Mountains, around Lake Baikal, north-eastern China, the Korean peninsula and the isolated Kamchatka Peninsula (Figure 5). Suitable climatic conditions were highly restricted for this lineage at the last glacial maximum (Figure 5), with two areas having high suitability, Central Europe around the Carpathians Mountains and south-eastern China and Japan. Projections of the niche model on palaeoclimatic layers indicate a distribution extent very similar to current conditions for the last interglacial and mid-Holocene periods (Figure 5, Figure S4).

For *D. l. lilfordi*, the current distribution is only a fraction of the potential distribution of the lineage based on the bioclimatic data (Figure 5). Indeed, in addition to regions currently occupied by the lineage, vast areas of Western Europe (France, Great Britain and Scandinavia) are climatically potentially suitable for this lineage. The potential suitable distribution of this lineage has been relatively stable since the last interglacial (Figure 5), with the four south-western Palearctic refugia (Iberia, Italy, Balkans and Caucasia) being suitable throughout. Noticeably, Corsica had suitable, yet limited to the centre of the island, climatic conditions for *D. l. lilfordi* throughout the last 120,000 years (Figure S4).

The *niche.equivalency.test* was highly significant for the three pairwise comparisons, suggesting that the three lineages occupy different niches *leucotos/uralensis* versus *lilfordi*: Schoener's $D = 0.13$, $p < .0001$; Japanese subspecies versus *lilfordi*: Schoener's $D = 0.17$, $p < .0001$; Japanese subspecies versus *leucotos/uralensis*: Schoener's $D = 0.20$, $p < .0001$.

4 | DISCUSSION

4.1 | Phylogenetic relationships among morphological subspecies

Our phylogenetic results support the existence of three well-supported monophyletic groups within *D. leucotos* and confirm that *D. noguchii* is the sister species of *D. leucotos* (Fuchs & Pons, 2015; Winkler et al., 2005). Relationships among the three primary lineages are not well-resolved most probably because of the relatively short sequences data upon which our phylogenetic analyses were based. Nevertheless, our results suggest that the Chinese subspecies (*tangi*, *insularis*) were the first to branch off around 0.8 Mya. A similar phylogenetic pattern was found for the Great Spotted Woodpecker *D. major* for which the lineage distributed in China was also the first to split around 0.8 Mya (Perktaş & Quintero, 2013); we nevertheless highlight that caution should be taken when comparing the divergence times between the two studies because different molecular clocks were used. The second split dated back to about 0.5–0.6 Mya separated the northern *leucotos* group including two subspecies not genetically differentiated (*leucotos*, *uralensis*) and the four Japanese subspecies (*namiyei*, *subcirris*, *stejnegeri* and *owstoni*) from the southern *lilfordi* subspecies. Within the northern group, the Japanese subspecies formed a clade with respect to the continental White-Backed Woodpeckers. The Amami Woodpecker sometimes treated as a full species (*D. owstoni*; Winkler et al., 2020) is not genetically differentiated from other Japanese subspecies with which it shares the most common haplotype found across the Japanese archipelago. Significant differences in plumage and morphology highlighted for this insular taxon, only found in Amami Oshima Island (northern Ryukyu archipelago), do not reflect an old divergent evolutionary history. They may result from a rapid evolution or phenotypic plasticity related to humid subtropical insular environment and/or drift.

One further surprising result is the paraphyly of the Great Spotted Woodpecker. Indeed, our mitochondrial results support a topology where the western subspecies of *D. major* are more closely related to *D. darjellensis* than to the eastern *D. m. japonicus* subspecies which is sister to *D. syriacus*. This hypothesis was not highlighted in previous studies due to limited geographic (Fuchs & Pons, 2015) and/or taxonomic (Perktaş & Quintero, 2013; Zink, Drovetski, et al., 2002) sampling. Additional studies based on a multilocus approach and including individuals from the Chinese and himalayensis populations are necessary to validate this result and test further hypotheses regarding species limits and/or introgression of mitochondrial DNA across species.

4.2 | Biogeographic history

Our molecular data clearly suggest that the Japanese archipelago was recently colonized from eastern Eurasia by *D. leucotos* only once. The four subspecies are only little genetically differentiated: all morphological subspecies share a common haplotype and the three derived haplotypes differ from this ancestral haplotype by only one to three mutations. The Ryukyu archipelago, which lies off the southern shore of Hokkaido, was likely colonized independently by *D. l. owstoni* and *D. noguchii* which are not sister relatives. More samples from the eastern range of *D. leucotos* and especially from China would be crucial to understand the biogeographic history of this species in Asia in more details. On the mainland, the Eurasian *leucotos* group holds a common haplotype over an extremely wide geographical range,

from Western Europe (Norway) up to eastern Asia (South Korea). Within this group, the genetic variation is very low and not geographically structured, a conclusion also reached by Ellegren et al. (1999) based on the sampling of Polish and Scandinavian populations. The star-like network and significant tests of population expansion clearly suggest that all present-day populations recently and rapidly expanded from a unique glacial refugium. However, surprisingly, most of the haplotype diversity is found in Europe and specifically in Poland, which holds four of the six haplotypes found in the Eurasian *leucotos* group. In contrast, in Russia and Mongolia, where twelve White-backed Woodpeckers were sampled over a large area, only one haplotype was detected. Such a geographical distribution of the genetic variability within the *leucotos* group is hardly compatible with the most common phylogeographical pattern generally invoked for forest bird species, that is a colonization of the Western Palaearctic from an Eastern Palaearctic refugium, which was ice-free during the last glacial maximum, while most of Europe was still covered by ice (Adams, 1997; Hewitt, 1996; Hughes et al., 2013; Pentzold et al., 2013; Pons et al., 2015; Schmitt & Varga, 2012; Voous, 1947; Zink, Drovetski, et al., 2002). Our mitochondrial data could support the persistence of a *leucotos* population in Central Europe in a so-called cryptic glacial refugium, possibly located around the Carpathians (see below), from which the subspecies expanded eastward across Siberia after the last glacial maximum. Consistent with mitochondrial data, climatic niche modelling suggests that suitable climatic conditions might have persisted in Central Europe during the last glacial maximum (Figure 5). In further support of this hypothesis, a postglacial eastward range expansion from Central Europe to Siberia has also been suggested for the Adder (*Vipera berus*) (Schmitt & Varga, 2012) and the Willow Tit (*Poecile montanus*) (Pavlova et al., 2006). The classical view of glacial stages where trees were restricted to localized refugial areas in southern Europe and the Mediterranean basin was challenged by palaeobotanical evidence (Birks & Willis, 2008) and tree megafossils (Kullman, 2002). These authors suggest that during the glacial periods tree ranges were more extensive than previously believed and that many local areas of small tree populations in Central Europe persisted in cryptic refugia. In a study devoted to the phylogeography of the bank vole *Clethrionomys glareolus*, a European rodent species strongly associated with forest habitat, Deffontaine et al. (2005) stated that the endemic Mediterranean phylogroups did not contribute to the postglacial recolonization of much of the Palaearctic species range. Instead, the major part of this region was apparently recolonized by bank voles that survived in a glacial refugium possibly around the Carpathian Mountains, which were covered by small patches of mixed forests of coniferous and deciduous trees during the last glacial maximum (see also Provan & Benett, 2008, for a review on the existence of a Carpathian cryptic refugia for mammals, reptiles and amphibians). More studies based on larger samples especially from the eastern range of the species' distribution would be welcomed to confirm the eastward range expansion of *leucotos* from a European cryptic refugium.

By contrast with the wide and continuous range of *D. l. leucotos*, *D. l. lilfordi* occupies a fragmented geographical range, restricted to the mountainous regions of the south-western Palaearctic. In line with its scattered geographical distribution, our mitochondrial results suggest a completely different historical demography for this southern subspecies. *Dendrocopos l. lilfordi* holds a much higher genetic diversity than *D. l. leucotos* and unlike the latter its populations did not show any sign of recent expansion. Although based on small sample sizes in the Apennines ($n = 5$) and Caucasia ($n = 1$), the geographical distribution of *lilfordi* haplotypes suggests a strong structure of the genetic variability among allopatric populations. Each mountainous population (Pyrenees, Abruzzi, Caucasia) holds its private haplotypes and does not share any haplotype with their counterparts. The only exception to this pattern are the Balkans which hold the most common Pyrenean haplotype, suggesting possible past gene flow between both regions and a more extended geographical distribution of *lilfordi* in the past than nowadays as predicted by our climatic niche modelling results (Figure 5). Tomialojć (2000) also suggested that the White-backed Woodpecker, being the most dependent woodpecker species on decaying deciduous timbers, failed to survive in lowlands of Western Europe because of woodland management since the medieval times.

4.3 | Western Palaearctic phylogeographical pattern

The Pleistocene has played a major role in the differentiation at the intraspecific and interspecific level of many temperate palaearctic organisms including forest and woodland birds (e.g. Brito, 2005; Drovetski et al., 2018; Hewitt, 2004; Kvist et al., 2004; Pons et al., 2011, 2015; Schmitt, 2007). Our genetic results support a mid-Pleistocene divergence between *lilfordi* and *leucotos*. The two subspecies possess different phylogeographic structures and demographic histories. In contrast to *lilfordi,* whose allopatric small populations are genetically slightly differentiated and persisted through the Pleistocene climatic oscillations in Southern Europe, our results suggest no geographical structure and recent spatial expansion of the *leucotos* lineage from a unique refuge, as suggested by the negative values of Tajima's *D* and Fu's *Fs* statistics. In Europe, the White-backed Woodpecker has a two-clade genetic structure corresponding to *D. l. leucotos* found in central and northern regions and *D. l. lilfordi* restricted to southern mountainous areas. Both subspecies are

presently in geographical contact in the northern Balkans following the recent southward range expansion of *D. l. leucotos* (Hans Winkler, unpublished data). Our results do not support a phylogeographical pattern in which Central and Northern Europe would have been recolonized from one or several southern glacial refugia where *lilfordi* populations persisted during the Quaternary. Pentzold et al. (2013) found a similar two-clade genetic structure for the European populations of the Coal tit (*Periparus ater*) and Pons et al. (2015) for the Eurasian Treecreeper (*Certhia familiaris*). In both species, an old lineage mostly restricted to Southern Europe co-exists with a much more widely distributed lineage whose range extends from Western Europe up to eastern Asia. To explain such a pattern, the authors propose a double colonization of Europe from the eastern Asian range because the northern subspecies (*Periparus ater ater* and *Certhia familiaris familiaris/macrodactyla,* respectively; see Pentzold et al., 2013; Pons et al., 2015) were closely related to eastern subspecies. This is probably not the case for the White-backed Woodpecker for which both Chinese subspecies are the first to branch off while *lilfordi* and *leucotos* are sister taxa. Duriez et al. (2007) highlighted a similar phylogenetic structure in the Western Capercaillie (*Tetrao urogallus*) which has a sister Asian species (*Tetrao parvirostris*) and includes two divergent European lineages (the '*aquitanus*' lineage with a southern scattered mountainous distribution and the '*urogallus*' lineage with a much wider Eurasian range). Moreover, it is worth noting that *D. leucotos* shares a concordant phylogeographic pattern with its main preys, saproxylic beetles, especially Cerambycidae, which are also associated with old-growth deciduous or mixed forests where rotten trees are available (e.g. Drag et al., 2015). Interestingly, a shared phylogeographic between predator and preys is also known for other woodpecker species and their respective preys (e.g. Three-toed woodpecker and bark beetles; Sallé et al., 2007; Zink et al., 2002).

4.4 | Presence of the White-backed Woodpecker in Corsica?

In the present study, we also included two White-backed Woodpeckers specimens, putatively collected in Corsica. These two specimens were probably collected during the second half of the nineteenth century when the White-backed Woodpecker was possibly still found in Corsica according to some authors (Chappuis, 1976; Grangé, 2015a; Moltoni & Brichetti, 1977; but see Thibault & Bonaccorsi, 1999, for an opposite opinion). In addition, the vocalizations of the White-backed Woodpecker were recorded once in Corsica in the middle of the twentieth century by Chappuis (1976), but a possible confusion with the Great Spotted Woodpecker cannot be fully excluded (Grangé, 2015a). The two putative Corsican specimens included in this study hold the most common *lilfordi* haplotype distributed in the Pyrenees and the Balkans. If the putative presence of the White-backed woodpecker in Corsica resulted from an ancient colonization event, one would have expected that both specimens hold a slightly divergent haplotype from the most ancestral haplotype as it is observed in the Abruzzi and the Caucasia (see Figure 4), but this is not the case. The second hypothesis of a more recent colonization from the nearby Italian Peninsula, possibly during the last glacial maximum when the sea level was lower than today, can also be rejected because the putative Corsican specimens do not show the Abruzzi haplotype. The hypothesis that Corsica was colonized by what can possibly be an older and more widespread Pyrenean/Balkans lineage cannot be ruled out by our data set. Our mitochondrial data neither strongly argue for the Corsican origin of these two museum specimens nor can definitively reject it. Interestingly, the species distribution modelling suggests that Corsica had potentially suitable habitats for *lilfordi* throughout the last 120,000 years (Figure S4). The absence of *D. leucotos* sensu lato fossils in Corsica and the fact that *D. major* is known from two Pleistocene sites in Corsica (Grangé, 2015a) would argue for the hypothesis that *D. leucotos* never colonized Corsica. Yet, *D. leucotos* is usually much scarcer than *D. major* and the fact that the latter, although present, was only found in two localities suggests that the probability of finding *D. leucotos* fossils is very low. As a consequence, the problem remains currently unresolved and only genome-wide data may help to solve it.

4.5 | Taxonomic conclusions

The current taxonomy applied to the White-backed Woodpecker does not correctly reflect the species evolutionary history. According to our genetic results, four lineages emerge: (a)—the Chinese species group includes at least two morphological subspecies. Based on its geographic distribution and morphology (Cheng, 1956), the subspecies *fokhiensis,* which could not be sampled, very likely belongs to this group. This lineage split from other White-backed woodpeckers around 0.8 Mya (mid-Pleistocene); (b)—the *leucotos* group currently includes two morphological subspecies (*leucotos* and *uralensis*) which are not genetically distinguishable in the present study; (c)—the Japanese subspecies group includes four morphological subspecies which are of recent origin and sister to the *leucotos* group. Our results do not support the species rank which is sometimes assigned to the insular *owstoni* (Winkler et al., 2020); (d)—the *lilfordi* group includes only one morphological subspecies which split from the *leucotos* group around 0.5-0.6 Mya.

The molecular species delimitation methods and the gene flow analyses (support for no historical gene flow) in line with the differences in ecology (Grangé, 2015b), adult plumage (rump mostly black, back barred black, red below more extensive than in *leucotos*) and juvenile plumage (undertail coverts not reddish and females without red on crown) (Grangé, unpublished results) suggest that the subspecies *lilfordi* may be elevated to the species rank. We also highlight that further studies are needed in the Balkans, where *leucotos* and *lilfordi* are geographically intertwined (Hans Winkler, unpublished data) to assess whether both subspecies are ecologically segregated, *lilfordi* exhibiting habitat preferences for mountainous forests over most of its distribution range, or syntopic and able to form mixed pairs. Given that the present work would support the species status for *lilfordi*, a species status is automatically deserved, under the phylogenetic species concept, to the *D. l. insularis*/*D. l. tangi* lineage, *D. insularis* (Gould, 1863) by priority. The inclusion of *Dendrocopos leucotos fokhiensis* will be needed to confirm the hypothesis that it is part of this group, as suggested according to morphology (Cheng, 1956).

4.6 | Conservation issues

The White-backed Woodpecker is currently assigned to the 'Least Concern' category in the world IUCN Red List of threatened species. Our mitochondrial results nevertheless stress the important conservation role of Białowieża Forest, the last remnant of primeval forest in lowlands of Europe and of the Carpathians forests, in sheltering the most genetically diversified population of *leucotos* while Eastern Palaearctic populations seem to be more uniform. Following the present study which emphasizes the genetic distinctiveness of *lilfordi* and knowing its fragmented range and relatively small breeding populations at the Western edge, for example 400–550 pairs for the French Pyrenean population and around 100 pairs on the Spanish side of the Pyrenees (Grangé, unpublished results, Campión & Senosiain, 2004; Carcamo, 2016), it all appears that the conservation status of this subspecies, as well as that of the Chinese subspecies, should be evaluated independently from other members of the northern Eurasian *leucotos* group. Most *lilfordi* populations are restricted to old-growth deciduous forests located in mountains in which dead trees and fallen timbers are abundant (Winkler & Christie, 2020). Yet, a large part of these habitats is subject to major threats due to intense logging activities. According to our ecological niche modelling, the current distribution of *lilfordi* is only a small part of its potential geographic distribution that could potentially include lowlands of western France and Great Britain if forested habitats were favourable to its ecological requirements in old forests and decaying deciduous timbers. In line with this, in Spain, there is a slow westward geographic expansion of the species that occupies new beech forests (Campión, unpublished results). This is probably due to the abandonment of charcoal manufacturing in the mid-20th century and the consequent ecological improvement of these forests, intensively exploited since the Middle Ages.

The conservation of *lilfordi* populations which are currently at risk in mountains of south-western Europe is thus directly dependent on the preservation of large areas of mature deciduous forests.

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REFERENCES

Adams, J. M. (1997). *Global land environments since the last interglacial*. Oak Ridge National Laboratory. http://www.esd.ornl.gov/ern/qen/nerc.html

Avise, J. C. (2000). *Phylogeography: The history and formation of species*. Harvard University.

Avise, J. C., & Walker, D. E. (1998). Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*, 457–463.

Bandelt, H. J., Forster, P., & Rohl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*, 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Becker, R. A., & Wilks, A. R. (2013). *mapdata: Extra Map Databases. R version by Brownrigg R. (2013) R package version 2.2-2*. http://CRAN.R-project.org/package=mapdata

BirdLife International and NatureServe (2013). *Bird species distribution maps of the world*. NatureServe, BirdLife International.

Birks, H. J. B., & Willis, K. J. (2008). Alpines, trees, and refugia in Europe. *Plant Ecology and Diversity*, *1*, 147–160. https://doi.org/10.1080/17550870802349146

Bivand, R., & Lewin-Koh, N. (2014). *maptools: Tools for reading and handling spatial objects. R package version 0.8-29*. http://CRAN.R-project.org/package=maptools

Brito, P. H. (2005). The influence of Pleistocene glacial refugia on tawny owl genetic diversity and phylogeography in western Europe. *Molecular Ecology*, *14*, 3077–3094. https://doi.org/10.1111/j.1365-294X.2005.02663.x

Brown, J., Hill, D., Dolan, A., Carnaval, A. C., & Haywood, A. M. (2018). PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. *Scientific Data*, *5*, 1–9. https://doi.org/10.1038/sdata.2018.254

Campión, D., & Senosiain, A. (2004). Pico dorsiblanco, *Dendrocopos leucotos*. In A. Madroño, C. González & J. C. Atienza (Eds.), *Libro Rojo de las Aves de España* (pp. 307–309). Dirección General para la Biodiversidad-SEO/BirdLife.

Carcamo, S. (2016). Distribution du Pic de Lilford *Dendrocopos leucotos lilfordi* à l'ouest des Pyrénées espagnoles. *Le Casseur D'os*, *16*, 96–104.

Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., & Ram, K. (2020). *rgbif: Interface to the global biodiversity information facility API_. R package version 2.2.0*. https://CRAN.R-project.org/package=rgbif

Chamberlain, S., & Boettiger, C. (2017). R Python, and Ruby clients for GBIF species occurrence data. *PeerJ PrePrints*. https://doi.org/10.7287/peerj.preprints.3304v1

Chappuis, C. (1976). Origine et évolution des vocalisations de certains oiseaux de Corse et des Baléares. *Alauda*, *44*, 475–495.

Cheng, T. (1956). A new form of White-backed Woodpecker (*Dendrocopos leucotos tangi* susp. Nov.) from Szechwan (China). *Acta Zoologica Sinica*, *8*, 133–142.

Deffontaine, V., Libois, R., Kotlik, P., Summer, R., Searle, J. B., & Michaux, J. R. (2005). Beyond the Mediterranean peninsulas: Evidence of central refugia for a temperate forest mammal species, the bank vole (*Clethrionomys glareolus*). *Molecular Ecology*, *14*, 1727–1739.

Drag, L., Hauck, D., Bérces, S., Michalcewicz, J., Šerić Jelaska, L., Aurenhammer, S., & Cizek, L. (2015). Genetic differentiation of populations of the Rosalia longicorn, *Rosalia alpina* (Coleoptera: Cerambycidae) in Central and South-east Europe. *Biological Journal of the Linnean Society*, *116*, 911–925.

Drovetski, S. V., Fadeev, I. V., Raković, M., Lopes, R. J., Boano, G., Pavia, M., Koblik, E. A., Lohman, Y. V., Red'kin, Y. A., Aghayan, S. A., Reis, S., Drovetskaya, S. S., & Voelker, G. (2018). A test of the European Pleistocene refugial paradigm, using a Western Palaearctic endemic bird species. *Proceedings of the Royal Society B*, *285*, 20181606. https://doi.org/10.1098/rspb.2018.1606

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Dunning, J. B. (2007). *CRC handbook of avian body masses* (2nd ed.). CRC Press.

Duriez, O., Sachet, J. M., Ménoni, E., Pidancier, N., Miquel, C., & Taberlet, P. (2007). Phylogeography of the capercaillie in Eurasia: What is the conservation status in the Pyrenees and Cantabrian Mounts? *Conservation Genetics*, *8*, 513–526. https://doi.org/10.1007/s10592-006-9165-2

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., … E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Ellegren, H., Carlson, A., & Stenberg, I. (1999). Genetic Structure and Variability of White-Backed Woodpecker (*Dendrocopos Leucotos*) Populations in Northern Europe. *Hereditas*, *130*, 291–299. https://doi.org/10.1111/j.1601-5223.1999.00291.x

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10*, 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Flouri, T., Jiao, X., Rannala, B., & Yang, Z. (2018). Species tree inference with BPP using genomic sequences and the multispecies coalescent. *Molecular Biology and Evolution*, *35*, 2585–2593. https://doi.org/10.1093/molbev/msy147

Fordham, D. A., Saltré, F., Haythorne, S., Wigley, T. M. L., Otto Bliesner, B. L., Chan, K. C., & Brook, B. W. (2017). PaleoView: A tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography*, *40*, 1348–1358. https://doi.org/10.1111/ecog.03031

Fuchs, J., & Pons, J. M. (2015). A new classification of the Pied Woodpeckers assemblage (Dendropicini, Picidae) based on a comprehensive multi-locus phylogeny. *Molecular Phylogenetics and Evolution*, *88*, 28–37. https://doi.org/10.1016/j.ympev.2015.03.016

Gill, F., Donsker, D., & Rasmussen, P. (Eds). (2020). *IOC World Bird List (v10.1)*. https://doi.org/10.14344/IOC.ML.10.1

Gorman, G. (2014). *Woodpeckers of the world: The complete guide*. Christopher Helm.

Grangé, J.-L. (2015a). Le pic à dos blanc *Dendrocopos leucotos* sl. en Corse, entre mythe et réalité. *Bulletin de la Société Des Sciences Historiques et Naturelles de la Corse*, *750–751*, 183–199.

Grangé, J.-L. (2015b). Breeding biology of the Lilford Woodpecker *Dendrocopos leucotos lilfordi* in the Western Pyrenees (SW

France). *Denisia 36, Zugleich Kataloge des Oberösterreichischen Landesmuseums Neue Serie*, *164*, 99–111.

Grangé, J. L., & Red'kin, Y. (2019). White-backed Woodpecker does not occur in Kamchatka, Russia. *Dutch Birding*, *41*, 103–106.

Heibl, C., & Calenge, C. (2018). *phyloclim: Integrating Phylogenetics and Climatic Niche Modeling. R package version 0.9.5*. https://CRAN.R-project.org/package=phyloclim

Heled, J., & Drummond, A. J. (2010). Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, *27*, 570–580.

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*, 247–276.

Hewitt, G. M. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, *405*, 907–913.

Hewitt, G. M. (2004). Genetic consequences of climatic oscillation in the Quaterny. *Philosophical Transactions of the Royal Society B; Biological Sciences*, *359*, 183–195.

Hey, J. (2010). Isolation with migration models for more than two populations. *Molecular Biology and Evolution*, *27*, 905–920.

Hey, J., & Nielsen, R. (2004). Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics*, *167*, 747–760.

Hey, J., & Nielsen, R. (2007). Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 2785–2790. https://doi.org/10.1073/pnas.0611164104

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hughes, P. D., Gibbard, P. L., & Ehlers, J. (2013). Timing of glaciation during the last glacial cycle: Evaluating the concept of a global 'Last Glacial Maximum'(LGM). *Earth-Science Reviews*, *125*, 171–198. https://doi.org/10.1016/j.earscirev.2013.07.003

Johnsen, A., Rindal, E., Ericson, P. G. P., Zuccon, D., Kerr, K. C. R., Stoeckle, M. Y., & Lifjeld, D. (2010). DNA barcoding of Scandinavian birds reveals divergent lineages in trans-Atlantic species. *Journal of Ornithology*, *151*, 565–578. https://doi.org/10.1007/s10336-009-0490-3

Kamp, L., Pasinelli, G., Milanesi, P., Drovetski, S. V., Kosiński, Z., Kossenko, S., Robles, H., & Schweizer, M. (2019). Significant Asia-Europe divergence in the middle spotted woodpecker (Aves: Picidae). *Zoologica Scripta*, *48*, 17–32. https://doi.org/10.1111/zsc.12320

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, *90*, 68–77. https://doi.org/10.1046/j.0022-0477.2001.00630.x

Kvist, L., Viiri, K., Dias, P. C., Rytkönen, S., & Orell, M. (2004). Glacial history and colonization of Europe by the blue tit *Parus caeruleus*. *Journal of Avian Biology*, *35*, 352–359.

Lerner, H. R. L., Meyer, M., James, H. F., Hofreiter, M., & Fleischer, R. C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. *Current Biology*, *21*, 1838–1844. https://doi.org/10.1016/j.cub.2011.09.039

Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*, 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

McDonald, J. H., & Kreitman, M. (1991). Adaptive protein evolution at the Adh locus in *Drosophila*. *Nature*, *351*, 652–654. https://doi.org/10.1038/351652a0

Milne, I., Lindner, D., Bayer, M., Husmeier, D., McGuire, G., Marshall, D. F., & Wright, F. (2009). *TOPALi* v2: A rich graphical interface for evolutionary analyses of multiple alignments on HPC clusters and multi-core desktops. *Bioinformatics*, *25*, 126–127. https://doi.org/10.1093/bioinformatics/btn575

Moltoni, E., & Brichetti, P. (1977). Osservazioni ornitologiche in Corsica alla fine del maggio 1977. *Rivista Italiana di Ornitologia*, *47*, 149–205.

Nabholz, B., Lanfear, R., & Fuchs, J. (2016). Body mass-corrected molecular rate for bird mitochondrial DNA. *Molecular Ecology*, *25*, 4438–4449. https://doi.org/10.1111/mec.13780

Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H., & Hu, A. (2006). Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science*, *311*, 1751–1753. https://doi.org/10.1126/science.1120808

Pavlova, A., Rohwer, S., Drovetski, S. V., & Zink, R. M. (2006). Different post-Pleistocene histories of Eurasian parids. *Journal of Heredity*, *97*, 389–402. https://doi.org/10.1093/jhered/esl011

Pentzold, S., Tritsch, C., Martens, J., Tietze, D. T., Giacalone, G., Valvo, M. L., Nazarenko, A. A., Kvist, L., & Päckert, M. (2013). Where is the line? Phylogeography and secondary contact of western Palearctic coal tits (*Periparus ater*: Aves, Passeriformes, Paridae). *Zoologischer Anzeiger*, *252*, 367–382. https://doi.org/10.1016/j.jcz.2012.10.003

Perktaş, U., & Quintero, E. (2013). A wide geographical survey of mitochondrial DNA variation in the great spotted woodpecker complex, Dendrocopos major (Aves: Picidae). *Biological Journal of the Linnean Society*, *108*, 173–188.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–239. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., Kamoun, S., Sumlin, W. D., & Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, *55*, 595–609. https://doi.org/10.1080/10635150600852011

Pons, J.-M., Olioso, G., Cruaud, C., & Fuchs, J. (2011). Phylogeography of the Eurasian green woodpecker (*Picus viridis*). *Journal of Biogeography*, *38*, 311–325. https://doi.org/10.1111/j.1365-2699.2010.02401.x

Pons, J.-M., Thibault, J.-C., Fournier, J., Olioso, G., Rakovic, M., Tellini Florenzano, G., & Fuchs, J. (2015). Genetic variation among Corsican and continental populations of the Eurasian treecreeper (Aves: *Certhia familiaris*) reveals the existence of a palaeoendemic mitochondrial lineage. *Biological Journal of the Linnean Society*, *115*, 134–153.

Provan, J., & Benett, K. D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology and Evolution*, *23*, 564–571. https://doi.org/10.1016/j.tree.2008.06.010

R Core Team (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Rambaut, A., & Drummond, A. J. (2009). *Tracer version 1.6*. http://beast.bio.ed.ac.uk

Reid, N. M., & Carstens, B. C. (2012). Phylogenetic estimation error can decrease the accuracy of species delimitation: A Bayesian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology*, *12*, 196. https://doi.org/10.1186/1471-2148-12-196

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., … Huelsenbeck, J.P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542.

Sallé, A., Arthofer, W., Lieutier, F., Stauffer, C., & Kerdelhué, C. (2007). Phylogeography of a host-specific insect: Genetic structure of Ips typographus in Europe does not reflect past fragmentation of its host. *Biological Journal of the Linnean Society*, *90*, 239–246.

Schmitt, T. (2007). Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology*, *4*, 11. https://doi.org/10.1186/1742-9994-4-11

Schmitt, T., & Varga, Z. (2012). Extra-Mediterranean refugia: The rule and not the exception? *Frontiers in Zoology*, *9*, 22. https://doi.org/10.1186/1742-9994-9-22

Shakya, S. B., Fuchs, J., Pons, J.-M., & Sheldon, F. H. (2017). Tapping the woodpecker tree for evolutionary insight. *Molecular Phylogenetics and Evolution*, *116*, 182–191. https://doi.org/10.1016/j.ympev.2017.09.005

Short, L. L. (1982). *Woodpeckers of the World*, Greenville, Delaware: Delaware Museum of Natural History.

Stephens, M., Smith, N. J., & Donnelly, P. (2001). A new statistical method for haplotype reconstruction from population data. *Am. J. Hum. Genet*, *68*, 978–989.

Strasburg, J. L., & Rieseberg, L. H. (2010). How robust are ''Isolation with Migration'' analyses to violations of the IM Model? A simulation study. *Molecular Biology and Evolution*, *27*, 297–310. https://doi.org/10.1093/molbev/msp233

Subramanian, S., Denver, D. R., Millar, C. D., Heupink, T., Aschrafi, A., Emslie, S. D., Baroni, C., & Lambert, D. M. (2009). High mitogenomic evolutionary rates and time dependency. *Trends in Genetics*, *25*, 482–486. https://doi.org/10.1016/j.tig.2009.09.005

Taberlet, P., Fumagalli, L., Wust-Saucy, A. G., & Cosson, J. F. (1998). Comparative phylogeography and post glacial colonization. *Molecular Ecology*, *7*, 453–464.

Thibault, J.-C., & Bonaccorsi, G. (1999). *The Birds of Corsica. An annotated check-list. No 17*. British Ornithologists Union, Tring.

Tomialojć, L. (2000). An East-West gradient in the breeding distribution and species richness of the European woodland avifauna. *Acta Ornithologica*, *35*, 3–17.

Vaurie, C. (1959). *Systematic notes on Palearctic birds*. American Museum Novitates no 35 Picidae: The Genus Dendrocopos (Part, 1), 1946,1–29.

Voous, K. H. (1947). On the history of the distribution of the Genus *Dendrocopos*. *Limosa*, *20*, 1–142.

Ward, R. D., Hanner, R., & Hebert, P. D. N. (2009). The campaign to DNA barcode all fishes, FISH-BOL. *Journal of Fish Biology*, *74*, 329–356. https://doi.org/10.1111/j.1095-8649.2008.02080.x

Warren, D., Matzke, N., Cardillo, M., & Dinnage, R. (2017). *ENMTools: Analysis of niche evolution using niche and distribution models. R package version 0.2*.

Weiss, S., & Ferrand, N. (2007). *Phylogeography of the Southern Europe Refugia – Evolutionary perspectives on the origins and conservation of European biodiversity* (p. 390). Springer.

Wickham, H. (2014). *scales: Scale functions for graphics. R package version 0.2.4*. http://CRAN.Rproject.org/package=scales

Winkler, H., & Christie, D. A. (2020). White-backed Woodpecker (*Dendrocopos leucotos*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie & E. de Juana (Eds.), *Handbook of the birds of the World Alive*. Lynx Edicions.

Winkler, H., Christie, D. A., Kirwan, G. M., & Sharpe, C. J. (2020). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie & E. de Juana (Eds.), *Okinawa Woodpecker (*Dendrocopos noguchii*)*. Handbook of the Birds of the World Alive. Lynx Edicions.

Winkler, H., Kotaka, N., Gamauf, A., Nittinger, F., & Haring, E. (2005). On the phylogenetic position of the Okinawa woodpecker (*Sapheopipo noguchii*). *Journal of Ornithology*, *146*, 103–110. https://doi.org/10.1007/s10336-004-0063-4

Yang, Z. (2007). PAML 4: Phylogenetic Analysis by Maximum Likelihood. *Molecular Biology and. Evolution*, *24*, 1586–1591. https://doi.org/10.1093/molbev/msm088

Yang, Z., & Rannala, B. (2014). Unguided species delimitation using DNA sequence data from multiple loci. *Molecular Biology and. Evolution*, *31*, 3125–3135. https://doi.org/10.1093/molbev/msu279

Zink, R. M., Drovetski, S. V., & Rohwer, S. (2002). Phylogeographic patterns in the great spotted woodpecker *Dendrocopos major* across Eurasia. *Journal of Avian Biology*, *33*, 175–178.

Zink, R. M., Rohwer, S., Drovetski, S., Blackwell-Rago, R. C., & Farrell, S. L. (2002). Holarctic phylogeography and species limits of three-toed woodpeckers. *The Condor*, *104*, 167–170. https://doi.org/10.1093/condor/104.1.167

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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