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The role of birds in Late Pleistocene Eurosiberian-Mediterranean boundary reconstructions in Western Europe

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A B S T R A C T

Birds have been considered good climate indicators in Pleistocene environmental reconstructions, due to their current distribution and specific ecological requirements. They have been analyzed as associations and in some cases also as indicator species for the climate during the Late Pleistocene, which is a stage that shows strong climatic fluctuations. In this work we present an analysis of the relative abundances of thirty-three of these indicator species of Aves in Late Pleistocene Western European sites, in order to characterize the avian associations and bird species behavior, and also shed light on the corresponding ecosystems of the different geographical areas of Europe during this stage. Our analysis reveals four main groups of sites, which correspond mainly to the current biome distribution. Nevertheless, the position of some sites in the analysis is markedly different, revealing a drift southward of the Eurosiberian-Mediterranean boundary during the Late Pleistocene. The results also allow us to analyze the behavior of the various species, whose distributions seem to be controlled by the predominant vegetation in each area more than by the temperature. The different associations of each area suggest that Central Europe was forested or at least point to the presence of forest patches in this area at the end of the Pleistocene. They also reveal the need for avian association analysis instead of the use of isolated bird species to produce landscape and climate reconstructions.

1. Introduction

To characterize the different faunal associations and ecosystems during the last cold stage and decipher the effect of climatic changes, analyses and reconstructions based on the fossil record from this time period have been developed using different methodologies. Small vertebrates (López-García et al., 2013), large mammals (Álvarez-Lao, 2014), and the distribution of plant remains (Hardy, 2010) are some recent examples, among many others.

Birds have been used as climate indicators because they are currently a diverse vertebrate group (Gill, 2007) and are usually associated with particular habitats. Furthermore, they are commonly recorded and well-preserved in sites of Pleistocene age (Mlíkovski, 2002; Tyrberg, 2007; Núñez-Lahuerta et al., 2016a, b).

Many analyses of the Pleistocene climate and ecosystems have been performed on the basis of avian assemblages: *e.g.*.Demarcq and Mourer-Chauviré (1976) developed a method of calculating thermal indices, which was subsequently applied by Bochenski (2000) and Lorenc (2007) to Polish Vistulian sites; Tyrberg (1991) analyzed the glacial relict distribution of some taxa in the Western Palearctic, and more recently the avian faunas of the Last Interglacial (Tyrberg, 2007); Sánchez-Marco (1996, 1999, 2004, 2007) described the paleoenvironments of the Iberian and European Pleistocene using the bird record; Finlayson (2011) undertook an analysis of the response of bird assemblages to climate change; Tomek and colleagues (2012) studied the avian association of Biśnik (Poland) in order to ascertain the changes in landscape over the last 300,000 years; Holm and Svenning (2014) analyzed the responses of birds to climate changes over the last 180,000 years, using a data matrix with their presence/absence at all European sites; Stewart and Jacobi (2015) also analyzed the responses of birds to climate changes, but using the data from a cold stage site in England. Recently, Lagerholm and colleagues (2017) modeled the distribution of ptarmigans and analyzed ancient DNA in order to shed light on the responses of cold-adapted species to climate warming.

The Quaternary is a period characterized by major climatic fluctuations. These are best known for the Late Pleistocene owing to the overwhelming amount of data recorded in recent decades from

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ice cores, pollen, marine sediments, etc.(Valsecchi et al., 2012; Sanchez-Goñi et al., 2013). The Weichselian (equivalent to the Wisconsinan, Würmian and Devensian) refers to the last glacial cycle. This is a cold stage which covers almost the whole Late Pleistocene, beginning in Marine Isotope Stage (MIS) 5dand ending in the Younger Dryas Stadial (*i.e.* from 120ka to 10000BP; Hughes et al., 2013). During this period the global ice cover reached a relative maximum, called the Last Glacial Maximum (LGM), about 21ka ago.

The main objective of this work is to study the bird distribution in Western Europe during the Late Pleistocene. To this end, a methodology that has already provided good results for large mammals (statistical analysis of the number of identified specimens; Álvarez-Lao, Álvarez-Lao, 2014; Sauqué et al., 2016) is applied to the avian record. Applied to the Late Pleistocene record, this methodology will reveal whether the bird distribution corresponds to the different paleogeographic provinces in Western Europe, as happens for example with ungulates in relation to the Eurosiberian and Mediterranean regions (Sauqué et al., 2016), and as was pointed out by the work of Sánchez-Marco (2004, 2007). We then analyze the role of the bird species that have classically been considered good climate indicators. Finally, the aim is to compare the results obtained with those from previously published analyses.

2. Material and methods

2.1. Abbreviations

bDb: birds Data base; NISP: number of identified specimens;MNI: minimum number of individuals; CA: correspondence analysis; DCA: detrended correspondence analysis; LGM: Last Glacial Maximum, around 21ka.

2.2. Matrix construction

In order to analyze the different avian assemblages, data on the NISP (number of identified specimens) of Late Pleistocene European sites have been included in a matrix (our bDb). As the studied sites present a high diversity (Tyrberg, 2007), only the taxa described in previous works as interesting due to their climate-related behavior are included in the analysis (Sánchez-Marco, 2004; Holm and Svenning, 2014). The fossil remains of small passerines have not been added to the bDb. Those taxa identified only at a single site and taxa in open nomenclature have not been added either. The species used in the present study are: *Cygnus olor, Cygnus cygnus, Anser erythropus, Branta bernicla, Branta leucopsis, Aythya marila, Melanitta fusca, Melanitta nigra, Somateria mollisima, Clangula hyemalis, Bucephala clangula, Mergus merganser, Mergellus albellus, Gyps fulvus, Aegypius monachus, Circus macrourus, Buteo lagopus, Buteo rufinus, Haliaeetus albicilla, Falco rusticulus, Falco vespertinus, Lagopus lagopus, Lagopus muta, Tetrao urogallus, Tetrao tetrix, Bonasa bonasia, Tetrax tetrax, Gallinago media, Bubo scandiacus, Surnia ulula, Aegolius funereus, Pyrrhocorax pyrrhocorax* and *Pyrrhocorax graculus.*

As the analyzed time range is so wide (from 120ka to 10000BP), in some cases different layers of the same site are grouped as one (*e.g.* Castiglione and Ermittia) provided that all the layers belong to the Late Pleistocene. The small number of sites with the necessary information available prevents us from distinguishing between the different stages of the Late Pleistocene.

The sites are grouped according to the current distribution of ecological regions in Western Europe. The selected regions, applied with aim of analyzing the Eurosiberian-Mediterranean boundary, are as follows: Mediterranean scrubland and forests, Atlantic sites, and Central European sites, the latter two categories belonging to the Eurosiberian area (Fig. 1). We employ data on the Biogeographical Regions provided by the European Topic Centre on Biological Diversity (available here: http://bd.eionet.europa.eu/activities/Natura_2000/chapter1).

Álvarez-Lao (2014) compared a variety of European sites with a NISP higher than 100 and at least three different taxa. As the available avian information from the sites is not as high as for the mammal record, the original criterion of NISP>100 used in previous works (Álvarez-Lao, Álvarez-Lao, 2014; Sauqué et al., 2016) proved too high in this case. For this reason, sites with NISP>50 were added to the bDb. Although the number of Late Pleistocene sites in Europe with bird information is high (Tyrberg, 2007), sites with the NISP available are more limited. There are extensive works that only include the minimum number of individuals (MNI), and some works only include the faunal lists. Fifty-two sites that fulfilled these terms were added to the matrix (Fig. 1, Table 1): Casa da Moura (Domingues-Figueiredo, 2010), Furninha (Brugal et al., 2012), Lapa da Rainha (Domingues-Figueiredo, 2010), Gruta Nova da Columbeira (Domingues-Figueiredo, 2010), El Castillo (Sánchez-Marco, 2005), Valdegoba (Sánchez-Marco, 2005), Labeko (Elorza, 2000), Ermittia (Elorza, 1993), Praileaitz (Moreno-García, 2017), Erralla (Eastham, 1985), Aitzbitarte (Sánchez-Marco, 2011), Berroberria (Sánchez-Marco, 2005), Cau d'en Borras (Sánchez-Marco, 2005), Gorham (Cooper, 1999), Vanguard (Cooper, 1999), Devil's Tower (Cooper, 1999), Bourrouilla (Eastham, 1988), La Vache (Laroulandie, 2000), Morin (Gourichon, 1993), Combe Saunière (Laroulandie, 2000), Taï (Louchart and Soave, 2002), Pierre-Châtel (Desbrosse and Moruer-Chauviré, 1972), Coscia (Louchart, 2002), Castiglione (Louchart, 2002), Lazaret (Roger, 2004), Fate (Roger, 2004), Arene Candide (Cassoli, 1980), Fumane (Peresani et al., 2011), Ortucchio (Alhaique and Recchi, 2001), Polesini (Radmilli, 1974), Ingarano (Bedetti and Pavia, 2007), Santuario della Madonna (Gala and Tagliacozzo, 2010), Romanelli (Cassoli and Tagliacozzo, 1997), Vindija (Malez, 1988), Luegloch (Fladerer and Reiner, 1996), Dolní Věstonice (Wertz et al., 2016), Pavlov (Bochenski et al., 2009), Přemostí (Wertz et al., 2016), Oblazowa (Nadachowski et al., 1993), Mumotwa (Bochenski, 1981), Koziarnia (Bochenski, 1974), Nietoperzowa (Bochenski, 1974), Biśnik (Tomek et al., 2012), Krucza Skala (Bochenski and Tomek, 2004), Deszczowa (Cyrek et al., 2000), Komarowa (Tomek and Bochenski, 2005), Zamkowa Dolna (Bochenski, 1974), Raj (Bochenski, 1974), Kalman Lambrecht (Jánossy, 1986), Pilisszántó (Jánossy, 1986), Curata (Gal, 2003), Devetashka (Boev, 1999). . The NISP data are converted to percentages.

2.3. Statistical analysis

The matrix was analyzed with PAST v.2.14 software (Hammer et al., 2001) by means of a correspondence analysis, which is a recognized method of discovering geographical groupings, patterns and environmental gradients (Greenacre, 1984). It projects a multivariate database onto two dimensions, allowing the grouping patterns to be visualized in a plot. Correspondence analysis (CA) presents some problems: the tendency to compress the end of the ordinate axis squeezes together both samples and data, and the arch effect means that the environmental gradient is not linked with the first axis. For this reason, we have used a detrended correspondence analysis (DCA) (Sauqué et al., 2016), which is also a highly useful tool in the analysis of ecological databases (Hill and Gauch, 1980). To avoid the problems associated with the CA, the DCA rescales itself, and thus removes the compression of the data. Then it performs the detrending and bending of the arch, to link it to the axis.

The "column labels" tool of the DCA in the PAST software was used to establish the relative position of the species with respect to

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