Ecological transitions — But for whom? A perspective from the Pleistocene

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ARTICLE INFO

ABSTRACT

This paper deals with the so-called Middle Pleistocene revolution, that is, the transition between the Early and Middle Pleistocene between 1.2 and 0.5 million years ago. Our knowledge about biotic changes during this transition has been so far largely based on studies of large mammals. Here we address the issue whether all faunal groups were equally affected. Three datasets have been used: (a) European large mammals present in the Middle and Late Pleistocene, (b) European fossil bird species recorded from the Early, Middle and Late Pleistocene of Europe, and (c) present-day birds currently classified in subfamilies that contain at least one Palaearctic representative species. Each species was allocated to all those geographical areas, climates, habitats in which it is present today; migratory status was also recorded. These datasets serve to undertake a biochronological analysis of mammal and bird groups, thus establishing patterns and processes of extinction and survival at the genus and species levels. The end of the Middle Pleistocene appears to have been a significant boundary in respect of herbivorous mammals, which suffered considerable depletion. In contrast, most genera and species of European birds in the Middle Pleistocene survived into the Late Pleistocene, even to the present day. Furthermore, at least 58% of the Middle–Pleistocene bird species were already present in the Early Pleistocene record. The most successful survivors in the Palaearctic Pleistocene were species from genera that had been the most climatically-tolerant during the late Cenozoic, usually from speciose and widely-distributed genera. We conclude that major transitions in Earth history have leant largely on biochronology and the perceived turnovers of faunas. Boundaries have usually depended heavily on changes to specific taxa of organisms. In this paper we show that what may appear as epic boundaries are largely scale- and taxon-dependent. Their usefulness must therefore be open to question. Here we advocate an individualistic and taxon specific approach in understanding the major ecological changes that have marked the history organisms.

1. Introduction

The transition between the Early and Middle Pleistocene between 1.2 and 0.5 million years ago (Ma), sometimes known as the Middle–Pleistocene revolution, is recognised as a major event in Earth history. High amplitude 100 thousand year (ka) climate cycles replaced low-amplitude 41 ka cycles and there was a significant build-up of global ice volume after 940 ka (Head and Gibbard, 2005). Such drastic changes appear to have been accompanied by significant restructuring of the Palaearctic and other mammalian faunas (van den Bergh et al., 2001; Markova, 2005, 2007; O'Regan et al., 2005; Kahlke et al., 2007; Palombo, 2007; Arribas et al., 2009). During the Pleistocene the emergence of new species and the disappearance of others occurred at a similar rate although there has been the generalised view that there was an overall decline in species diversity through the Middle and Late Pleistocene (Stuart, 1991). Thus the Middle Pleistocene appears to be a long period of transition in the Palaearctic, between the relatively warm old world of the Pliocene and Early Pleistocene and the new ice world of the Late Pleistocene (Finlayson, 2009).

The Middle Pleistocene world clearly did not come to an abrupt end with the onset of the Late Pleistocene. New steppe-tundra mammals were replacing the established warm savannah ones during the Middle Pleistocene but the process continued into the Late Pleistocene up to MIS 3 (Stewart, 2005) and even later (Stuart et al., 2004). What does appear to have changed is the almost total halt of appearance of new species to replace the old ones (Stuart, 1991). Long evolutionary trajectories, such

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as the mammoth line (from *Mammuthus meridionalis* in wooded steppe through *Mammuthus trogontheri* in steppe to *Mammuthus primigenius* in steppe-tundra), came to an end (Lister and Sher, 2001). The Middle Pleistocene was not the end of an old world but it does seem to mark the beginning of its end. It is true that it probably affected the northern temperate and boreal regions (particularly the Palaearctic because of the geographical disconnection with the tropical south) worst of all. Our knowledge has been based largely on studies of large mammals. Here we ask the question whether all faunal groups were equally affected and aim to answer this question by comparing the European large mammal fauna with the avifauna of Europe and the wider Palaearctic.

2. Material and methods

We compiled three datasets using extensive sources in the published literature (see references):

(a) a list of the European large mammals present in the Middle and Late Pleistocene, a total of 55 species. Small mammals were left out because of difficulties in taxonomic revision and allocation;

(b) a dataset, based largely on Tyrberg (1998, 2008), Mlikovsky (2002) and references therein, listing all European fossil bird species so far recorded from the Early, Middle and Late Pleistocene of Europe, a total of 507 species; and

(c) a list all species of present-day birds currently classified in subfamilies that contain at least one Palaearctic representative species, a total of 5058 species. Each species was allocated to all those geographical areas, bioclimates, and habitats in which it is present today; migratory status was also recorded (Table 1).

These datasets constituted the basis for the analyses presented below.

3. Results

3.1. Mammals

Table 2 lists the mammalian genera and number of species per genus present in the European Middle Pleistocene. The number of Middle Pleistocene genera and species that appear to have become extinct by the onset of the Late Pleistocene (though not all concurrently) is 7 (20%) and 22 (40%) respectively. Information in Table 2 and subsequent analyses have been based on an extensive and critical literature review: Kurten (1968), Kurten and Anderson (1980), Currant (1989), Cerdeño (1990, 1998), Lister (1990), Kahlke (1991), Alberdi et al. (1995), Pasitschniak-Arts and Lariviere (1995), Petronio (1995), Sempere et al. (1996), Geist (1998), Lister et al. (1998), Currant and Jacobi (2001), Lebel et al. (2001), Schreve (2001a,b), Stuart and Lister (2001, 2007), Pérez et al. (2002), Baryshnikov et al. (2002), Drees (2003), Orlando et al. (2003), Burger et al. (2004), Genov (2004), Moigne et al. (2004), Breda and Marco Marchetti (2005), Lucchini et al. (2005), Crégut-Bonnoure (2005), Álvarez-Lao and García-García (2006), Dockner (2006), Eisenmann (2006), Glimmerveen et al. (2006), Pidancier et al. (2006), Rivals (2006), Sotnikova and Nikolskiy (2006), Gilmour et al. (2007), Martínez-Navarro et al. (2007), Pushkina (2007), Billia (2008a,b), Döppes et al. (2008), van der Made and Tong (2008), Rivals et al. (2009), Sommer et al. (2009), Turner (2009), Croitor and Brugal (2010), and Valli (2010).

Briefly, our analysis indicates the following.

3.1.1. Proboscidea

The species of *Mammuthus* in this period were *Mammuthus trogontheri* and *Mammuthus primigenius* with the former disappearing at the end of the Middle Pleistocene and the latter persisting into the Holocene. *Palaeoloxodon (Elephas) antiquus* was the only species in this genus in the Middle Pleistocene and became extinct before the end of the Pleistocene.

Table 1
Regions, bioclimates and habitats as defined in this paper.

Bioclimate	Region	Range Covered
Warm-wet	Neotropical	Most of South and Central America; south-eastern North America
Warm-wet	Congolese	Most of sub-Saharan Africa
Warm-wet	Madagascar	Madagascar and Comoro Islands
Warm-wet	Indo-Malayan	South-east Asia
Warm-wet	New Guinean	New Guinea and tropical Australia
Warm-wet	Atlantic	Macaronesia and other Atlantic Islands
Warm-wet	Caribbean	Caribbean
Warm-wet	Indian	South Asia and Indian Ocean Islands
Warm-wet	Pacific	Pacific Islands
Temperate-wet	West European	Temperate western Europe
Temperate-wet	Chinese	Temperate China
Temperate-wet	New Zealand	New Zealand
Cool-wet	North-west European	North-west Europe
Cool-wet	North-east Chinese	North-east China, south-east Siberia, Japan
Cool-wet	South Greenland	South Greenland
Cool-wet	North-east American	Eastern Canada and north-eastern United States
Warm-dry	Saharo-Arabian	Sahara, Arabia, parts of southern Central Asia, much of Iberia, parts of northern Mediterranean and Middle East
Warm-dry	Australian	Most of Australia
Warm-dry	Namibian	South-west Africa
Warm-dry	Sonoran	South-west United States
Warm-dry	Pampan	South-east South America
Temperate-dry	Steppic	North-east Europe through Central Asia to eastern Siberia
Temperate-dry	Steppic	Western North America
Cold-dry	Siberian	Arctic and Boreal Russia
Cold-dry	Alaskan	Arctic America
Cold-dry	Patagonian	Antarctic South America
Cold-dry	Greenland	Most of Greenland
Montane	North American	Rockies and Central American highlands
Montane	Andean	Andes
Montane	Himalayan	Himalayas and large ranges to the west
Montane	Ethiopian	Ethiopian highlands south along East Africa to South Africa

[1] Climate definitions: mean annual temperature — <0 cold; 0–10 cool; 10–20 temperate; >20 warm annual rainfall — <600 mm dry; >600 mm wet.
[2] Habitats allocated: forest, steppe, shrubland, treeless (grassland and steppe), tundra, desert, rocky, wetlands, and marine. (Climate definitions[1] and Habitats allocated[2] from Finlayson 2011).

Table 2
Genera and species of Middle Pleistocene (MP) European mammals and losses by the beginning of the Upper Pleistocene (UP) (*mammals endemic of Mediterranean islands have not been considered).

Genus*	Present MP	Extinct UP
Palaeoloxodon	1	1
Mammuthus	2	1
Equus	6	4
Dicerorhinus	3	1
Coelodonta	1	0
Elasmotherium	1	1
Sus	1	0
Hippopotamus	2	2
Cervus	1	0
Dama	2	2
Alces	1	0
Cervalces	3	3
Capreolus	2	0
Rangifer	1	0
Megaloceros	2	1
Bos	1	0
Bison	1	0
Ovibos	1	0
Rupicapra	1	0
Capra	0	0
Hemitragus	2	2
Saiga	1	0
Crocuta	1	0
Panthera	2	0
Felis	1	0
Lynx	2	0
Canis	1	0
Cuon	2	1
Vulpes	1	0
Alopex	1	0
Gulo	1	0
Meles	1	0
Ursus	3	1
Macaca	1	1
Homo	2	1
Species	55	22 (40% loss)
Genera	35	7 (20% loss)

3.1.2. Perissodactyla

Six horses are recorded in the Middle Pleistocene: *Equus altidens*, *Equus suessenbornensis*, *Equus(ferus) mosbachensis*, *Equus taubachensis*, *Equus caballus* and *Equus hydruntinus*. Of these, only the latter two are recorded from the Late Pleistocene. Three rhinoceroses of the genus *Dicerorhinus (Stephanorhinus)* occur in the Middle Pleistocene – *Dicerorhinus hundsheimensis*, *Dicerorhinus hemitoechus* and *Dicerorhinus kirchbergensis (mercki)* – of which the latter two are present in the Late Pleistocene. Of the other rhinoceroces, the only species in the genus *Coelodonta* remains until the early Holocene whilst *Elasmotherium* persisted in Eastern Europe until the end of the Middle Pleistocene.

3.1.3. Artiodactyla

Of the wild boar lineage the subspecies *Sus scrofa priscus* became extinct during MIS 13–15 whilst the subspecies *attila*, *majori*, *vittatus* and *meridionalis* persisted to the present. The two European Middle Pleistocene hippopotamuses *Hippopotamus amphibius* and *Hippopotamus antiquus* were effectively extinguished by the end of the Middle Pleistocene, only a few *H. amphibius* reaching the beginning of the Late Pleistocene.

Seven deer (Cervidae) genera are present in the European Middle Pleistocene: *Cervus* is represented by the red deer *Cervus elaphus* that persists to the present day, with the subspecies *acoronatus* disappearing at the end of the Middle Pleistocene. The fallow deers, *Dama,* represented by *Dama dama* and *Dama clactoniana* in the Middle Pleistocene are effectively gone by the start of the Late Pleistocene. *Alces* persists to the present although a small subspecies may have disappeared at the end of the Middle Pleistocene (MIS 6). The three species of Middle Pleistocene

Cervalces (*Cervalces carnutorum*, *Cervalces gallicus* and *Cervalces latifrons*) disappear at the end of this period although the precise status of these as possible chronospecies remains unclear. The two species of roe deer, the western *Cervalces capreolus* and the eastern *Cervalces pygargus*, and the Reindeer *Rangifer tarandus* persisted to the present. Finally, of the two giant deer, *Megaloceros, Megaloceros savini* (belonging to the oldest – "*Megaloceros verticornis*" – lineage) disappeared at the end of the Middle Pleistocene whilst *Megaloceros giganteus* persisted into the early Holocene.

Amongst the Bovidae, the only species of the genus *Bos* (*Bos primigenius*) persisted into the Holocene whilst *Bison* (represented by the Middle Pleistocene *Bison priscus*) persisted into the Late Pleistocene. The Middle Pleistocene *Ovibos pallantis* persisted to the Late Pleistocene. The present-day musk ox, *Ovibos moschatus,* is probably a descendant of this lineage. The lineage *Rupicapra* persisted to the present and diverged in the Late Pleistocene into two species, *Rupicapra rupicapra* and *Rupicapra pyrenaica.* The genus *Capra,* on the other hand, appears to have arrived in Europe from the east at the start of the Late Pleistocene as *Capra caucasica prepyrenaica* from which *Capra ibex* and *Capra pyrenaica* evolved? Two Middle Pleistocene *Hemitragus* (*Hemitragus bonali* and *Hemitragus cedrensis*) appear not to survive beyond the Middle Pleistocene although *cedrensis* is cited from the Late Pleistocene. Finally, *Saiga tatarica* persisted to the present.

3.1.4. Carnivora

In contrast to the 18 species of herbivore that disappeared at the end of the Middle Pleistocene, only one carnivore appears to have done so (Table 2). The spotted hyaena *Crocuta crocuta* (subspecies *crocuta*, *intermedia*, *spelaea*), lion *Panthera leo* (subspecies *spelaea*), leopard *Panthera pardus,* wild cat *Felis silvestris,* lynxes *Lynx pardina* and *Lynx lynx,* wolf *Canis lupus,* cuon lineage *Cuon priscus-alpinus,* red fox *Vulpes vulpes,* arctic fox *Alopex lagopus,* wolverine *Gulo schlosseri-gulo* lineage, and European badgers *Meles meles atavus, Meles meles meles,* all persisted into the Holocene. The only carnivore species to disappear at the end of the Middle Pleistocene is *Ursus deningeri*, with *Ursus spelaeus* persisting to the Late Pleistocene and *Ursus arctos* to the Holocene.

3.1.5. Primates

Two species became extinct in Europe at the end of the Middle Pleistocene: the barbary macaque *Macaca sylvanus* and Heidelberg man *Homo heidelbergensis*. The macaque persisted in North Africa and a Heidelberg lineage is assumed to have evolved into the Neanderthal *Homo neanderthalensis* which emerged at the end of the Middle Pleistocene and persisted until the latter stages of the Pleistocene.

3.2. Birds

Table 3 lists the avian genera and number of species per genus present in the European Middle Pleistocene. The number of Middle Pleistocene genera and species that appear to have become extinct by the onset of the Late Pleistocene (though not all concurrently) is 3 (1.55%) and 22 (5.88%) respectively. The information at Table 3 and subsequent analyses have been based on a critical literature review following the syntheses provided by Tyrberg (1998, 2008) and Mlikovsky (2002) and references within these monographs. The following subdivision is based on the recent phylogenetic analysis by Hackett et al. (2008). Cluster allocations follow these authors.

3.2.1. Struthioniformes (Cluster Q)

There is only one species of ostrich present in the Middle Pleistocene, the present-day *Struthio camelus*, which survives to the present day in parts of the western Palaearctic (Cramp, 1977).

3.2.2. Anseriformes and Galliformes (Cluster P)

Of the 24 genera present in the Middle Pleistocene only one (the quail *Palaeocryptonyx*) goes extinct at the end of the Middle Pleistocene.

Table 3
Genera and species of Middle Pleistocene (MP) European birds and losses by the beginning of the Upper Pleistocene (UP).

Genus	Present MP	Extinct UP
Struthio	1	0
Cygnus	3	0
Anser	7	2
Branta	3	0
Tadorna	2	0
Anas	7	0
Marmaronetta	1	0
Netta	1	0
Aythya	4	0
Somateria	1	0
Clangula	1	0
Melanitta	2	0
Bucephala	1	0
Mergus	4	1
Oxyura	1	0
Bonasa	1	0
Lagopus	2	0
Tetrao	4	1
Tetraogallus	2	0
Alectoris	4	1
Ammoperdix	1	0
Francolinus	1	0
Perdix	1	0
Palaeocryptonyx	1	1
Coturnix	1	0
Tachybaptus	1	0
Podiceps	4	0
Pterocles	3	0
Syrrhaptes	1	0
Columba	3	0
Streptopelia	1	0
Caprimulgus	3	1
Apus	4	1
Tetrax	1	0
Neotis	1	0
Otis	2	1
Clamator	1	0
Cuculus	1	0
Rallus	1	0
Porzana	3	0
Crex	1	0
Gallinula	2	1
Porphyrio	1	0
Fulica	1	0
Grus	5	1
Anthropoides	1	0
Gavia	2	0
Calonectris	1	0
Hydrobates	1	0
Oceanodroma	1	0
Ciconia	2	0
Pelargosteon	1	1
Pelecanus	1	0
Botaurus	1	0
Ixobrychus	1	0
Nycticorax	1	0
Bubulcus	1	0
Ardeola	1	0
Egretta	1	0
Casmerodius	1	0
Ardea	2	0
Plegadis	1	0
Geronticus	1	0
Platalea	1	0
Phalacrocorax	2	0
Anhinga	1	0
Haematopus	1	0
Himantopus	1	0
Recurvirostra	1	0
Burhinus	1	0
Glareola	1	0
Charadrius	3	0
Pluvialis	2	0
Vanellus	1	0
Calidris	3	0

Table 3 (*continued*)

Genus	Present MP	Extinct UP
Philomachus	2	1
Lymnocryptes	1	0
Gallinago	2	0
Scolopax	1	0
Limosa	2	0
Numenius	3	0
Tringa	6	0
Xenus	1	0
Actitis	1	0
Arenaria	1	0
Phalaropus	1	0
Stercorarius	2	0
Larus	6	0
Rissa	1	0
Sterna	2	0
Chlidonias	2	0
Uria	1	0
Alca	1	0
Pinguinus	1	0
Alle	1	0
Fratercula	1	0
Pernis	1	0
Milvus	2	0
Haliaeetus	2	1
Gypaetus	2	1
Neophron	1	0
Gyps	1	0
Aegypius	1	0
Circaetus	1	0
Circus	4	0
Accipiter	2	0
Buteo	2	0
Aquila	5	0
Hieraaetus	2	0
Buthierax	1	1
Pandion	1	0
Tyto	1	0
Otus	1	0
Bubo	3	1
Ketupa	1	0
Surnia	2	1
Glaucidium	1	0
Athene	1	0
Strix	3	0
Asio	3	0
Aegolius	1	0
Upupa	2	1
Jynx	1	0
Picus	2	0
Dryocopus	1	0
Dendrocopos	4	0
Picoides	1	0
Merops	1	0
Coracias	1	0
Falco	9	0
Lanius	5	0
Garrulus	1	0
Perisoreus	1	0
Cyanopica	1	0
Pica	1	0
Nucifraga	1	0
Pyrrhocorax	2	0
Corvus	8	2
Melanocorypha	3	0
Calandrella	3	0
Galerida	2	0
Lullula	1	0
Alauda	1	0
Eremophila	1	0
Riparia	1	0
Hirundo	3	0
Delichon	1	0
Prinia	1	0
Acrocephalus	2	0
Hippolais	1	0
Sylvia	6	0
Pycnonotus	2	0

Table 3 (continued)

Genus	Present MP	Extinct UP
Phylloscopus	2	0
Remiz	1	0
Aegithalos	1	0
Parus	7	0
Onychognathus	1	0
Sturnus	1	0
Cercotrichas	1	0
Erithacus	1	0
Luscinia	3	0
Phoenicurus	2	0
Cercomela	1	0
Saxicola	2	0
Oenanthe	2	0
Monticola	2	0
Ficedula	2	0
Muscicapa	1	0
Turdus	6	0
Cinclus	1	0
Troglodytes	1	0
Certhia	1	0
Sitta	1	0
Tichodroma	1	0
Bombycilla	1	0
Regulus	1	0
Turdoides	1	0
Prunella	2	0
Passer	5	1
Petronia	1	0
Montifringilla	1	0
Anthus	6	0
Motacilla	4	0
Fringilla	2	0
Serinus	2	0
Carduelis	5	0
Loxia	2	0
Carpodacus	2	0
Pinicola	1	0
Pyrrhula	1	0
Coccothraustes	1	0
Plectrophenax	1	0
Emberiza	4	0
Species	374	22 (5.88% loss)
Genera	193	3 (1.55% loss)

The remaining genera survived to the present day. Only 6 of 56 species (10.71%) became extinct at the end of the Middle Pleistocene.

3.2.3. Columbiformes, Phoenicopteriformes, Podicepiformes (Cluster N)
All 6 genera and 13 species present in the Middle Pleistocene have survived to the present day.

3.2.4. Caprimulgiformes and Apodiformes (Clusters K and L)
The two genera present in the Middle Pleistocene have survived to the present day. Of the 7 species present in the Middle Pleistocene, 2 (28.56%) became extinct at the end of this period.

3.2.5. Gruiformes and Cuculiformes (Clusters J and I)
All 13 genera present in the Middle Pleistocene have survived to the present day. Three of 21 species (14.29%) became extinct at the end of the Middle Pleistocene.

3.2.6. Pelecaniiformes, Procellariiformes and Gaviiformes (Cluster H)
Of 20 Middle Pleistocene genera and 24 species only one species (and correspondingly genus — the stork *Pelargosteon tothi*) became extinct at the end of the Middle Pleistocene. All remaining genera and species are present today.

3.2.7. Charadriiformes (Cluster G)
All 30 Middle Pleistocene genera of waders, gulls and auks, groups well equipped to deal with Arctic conditions, continued into the Late Pleistocene and only one species became extinct.

3.2.8. Accipitriformes and Strigiformes (Cluster E)
Of the 25 genera of Middle Pleistocene raptors and owls, only one genus (*Buthierax*) became extinct at the end of this period. Only 5 of 45 species (11.11%) became extinct at this time.

3.2.9. Coraciiformes and Piciformes (Cluster C)
All 8 genera and 12 of the 13 Middle Pleistocene species remained to the present day. The species loss at the end of the Middle Pleistocene was therefore 7.69%.

3.2.10. Falconidae (Cluster B)
All 9 Middle Pleistocene species of falcons in the genus *Falco* survived to the present day.

3.2.11. Passeriformes (Cluster A)
All 63 Middle Pleistocene genera of passerines have survived to today. Only 3 of 132 species (2.27%) became extinct at the end of the Middle Pleistocene.

3.3. Present-day Palaearctic birds

It is clear from the results presented above that most genera and species of birds present in Europe in the Middle Pleistocene survived into the Late Pleistocene and most are still with us today. This observation is in stark contrast with the Middle–Late Pleistocene depletion of mammals, particularly herbivores. In this section we present results of an analysis of the biogeographical and ecological characteristics of present-day Palaearctic birds aimed at establishing those characteristics that made them good survivors.

3.3.1. Are present-day Palaearctic birds derived from speciose genera?
926 (45.02%) of the 2057 bird genera present in the world today belong to subfamilies that have at least one Palaearctic representative. 267 (28.83%) of these genera have at least one Palaearctic representative. Palaearctic genera are thus an impoverished subset of all bird genera (12.98%). A comparison of the average number of species per genus in the subset of 926 genera against the Palaearctic genera reveals that the Palaearctic species are derived from genera which have significantly more species than the remainder (Table 4). The distinction applies equally when non-passerines and passerines are analysed separately.

3.3.2. Are present-day Palaearctic birds derived from widely distributed genera?
Geographical extent was calculated for all 926 genera from Table 4. Fig. 1 shows that the genera that include Palaearctic species are amongst the most widespread of the 926 genera analysed. The comparison is equally valid when non-passerines and passerines are compared. Present-day Palaearctic species are therefore derived from geographically widespread genera.

3.3.3. Are present-day Palaearctic birds derived from the most climatically tolerant genera?
Climatic tolerance was calculated for all 926 genera from Table 4. Fig. 2 shows that the genera that include Palaearctic species are

Table 4
Number of bird species per genus amongst genera in subfamilies with Palaearctic representatives.

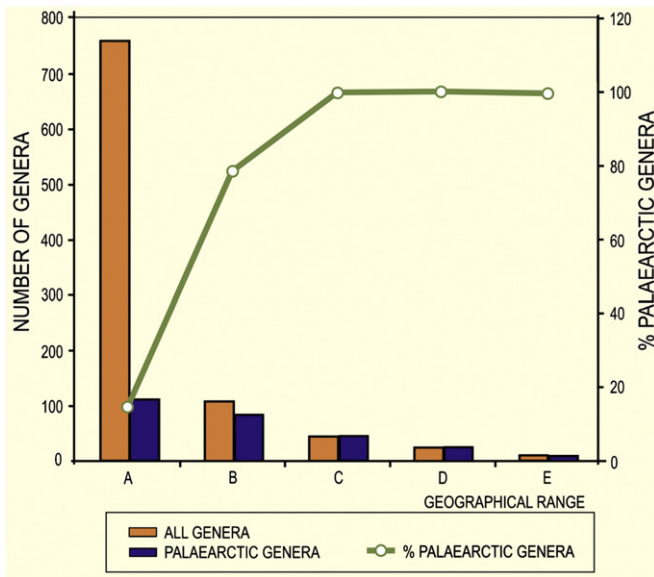|	Palaearctic genera	All genera
Mean number of Species	10.05243	5.462203
Standard deviation	12.72486	8.695459
Sample size (N)	267	926
95% confidence limits minimum	8.526087	4.902132
95% confidence limits maximum	11.57878	6.022274

Fig. 1. Distribution of all genera and Palaearctic genera by range occupation. A–E correspond to range categories in Table 1 (A = 0–20%, B = 21–40%, C = 41–60%, D = 61–80%, E = 81–100%).

Fig. 3. Distribution of all genera and Palaearctic genera by climate categorization: warm humid (WRMHUM), warm dry (WRMDRY), temperate humid (TMPHUM), temperate dry (TMPDRY), cold humid (CLDHUM), cold dry (CLDDRY), and montane (MON).

amongst the most climatically generalised and tolerant of the 926 genera analysed. Present-day Palaearctic species are therefore derived from the most climatically tolerant genera. Analysis of the climate types occupied by species in genera that includes Palaearctic species and those that do not (Fig. 3) reveals a predominance of temperate and cool climate genera with Palaearctic representatives and a relative scarcity of warm-wet species. The comparisons are equally valid when non-passerines and passerines are compared.

3.3.4. Are present-day Palaearctic birds derived from genera with particular habitat occupation characteristics?

An analysis of the habitats occupied, derived from Table 1, reveals that the genera which include Palaearctic species are overwhelmingly
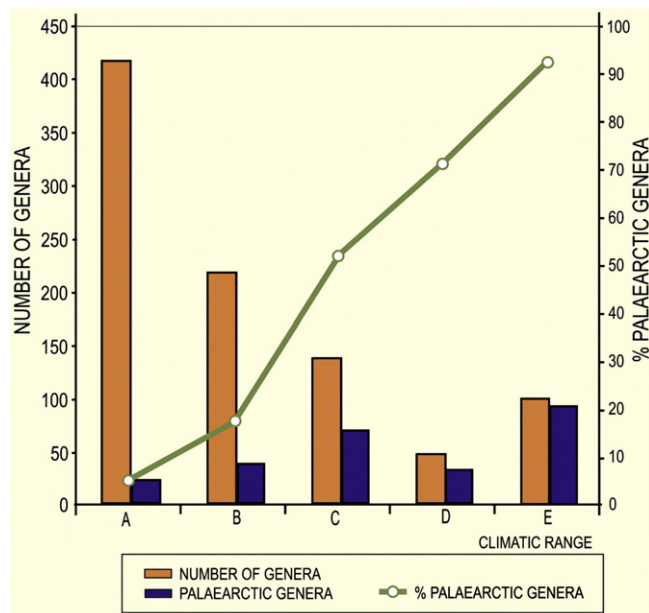
those of open, treeless, habitats (Fig. 4). This contrasts with the genera that do not include Palaearctic species that are predominantly occupiers of forest and associated tree formations. The comparisons are equally valid when non-passerines and passerines are compared.

3.3.5. Are present-day Palaearctic birds derived from genera with migratory habits?

It is clear from Fig. 5 that the genera that include Palaearctic species include a much greater proportion of migrants than the genera with no

Fig. 2. Distribution of all genera and Palaearctic genera by climatic occupation. A–E correspond to climate categories in Table 1 (A = 0–20%, B = 21–40%, C = 41–60%, D = 61–80%, E = 81–100%).
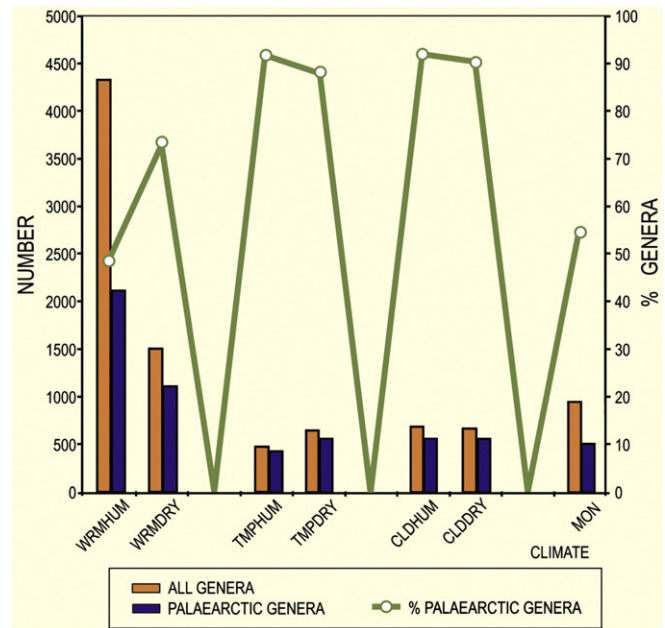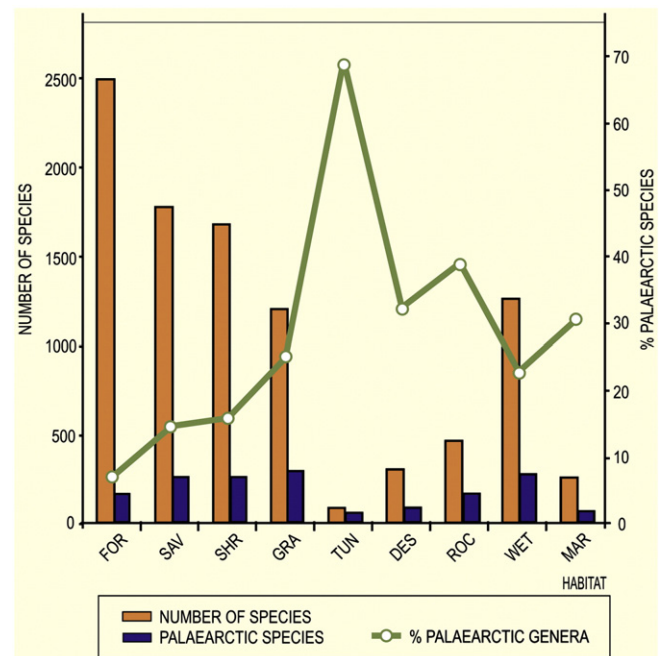

Fig. 4. Distribution of all genera and Palaearctic genera by migration habitat: forest (FOR), savannah (SAV), shrubland (SHR), grassland (GRA), tundra (TUN), desert (DES), rocky (ROC), wetland (WET), and marine (MAR).
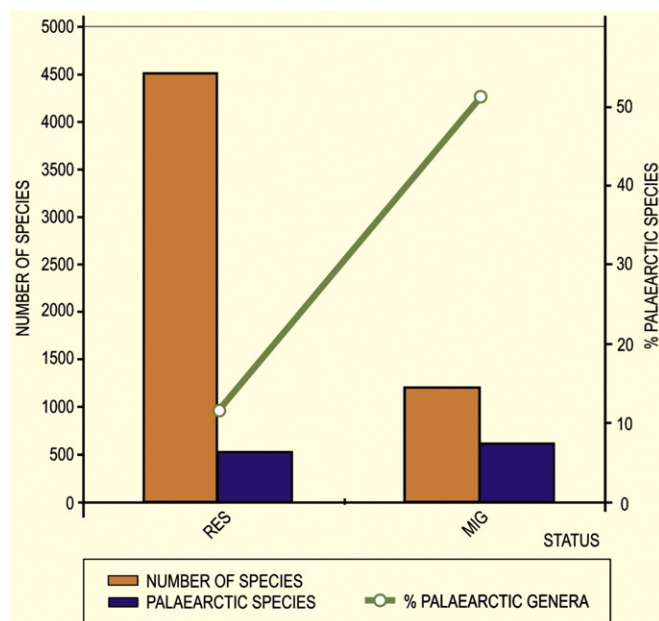
Fig. 5. Distribution of all genera and Palaearctic genera by migration strategy resident (RES) and migratory (MIG).

Palaearctic representatives which are overwhelmingly sedentary. The comparisons are equally valid when non-passerines and passerines are examined.

4. Discussion

4.1. Generalising macro-faunal turnover and change across taxa

It is clear from the results presented in this paper that the answer to the question posed – Ecological Transitions, but for whom? – depends on the taxon being studied, the chronological period under consideration and the region being explored. Whilst a case might be made that the end of the Middle Pleistocene was a significant boundary in respect of herbivorous mammals, the same cannot be argued in respect of carnivores or birds. This is an important conclusion since it raises doubts over theories that aim to generalise from an examination of specific taxa. A case in point is the turnover pulse hypothesis (Vrba, 1993) which links faunal turnover to major climatic events. It is perhaps not surprising to find that this hypothesis owes a great deal of its basis to the study of African bovids as we have seen that mammalian herbivores seem to respond more directly to macro-climatic events than do the other groups studied. The turnover-pulse's large scale corollary – the theory of punctuated equilibria (Gould and Eldredge, 1977) – would therefore also be heavily taxon-dependent.

4.2. Comparing mammalian and avian response to Pleistocene environmental change in the Palaearctic

Mammalian herbivores were more heavily dependent on biological change (e.g. in dentition) than were carnivores or birds. Range and habitat changes were also operative provided the rate of change did not exceed the capacity for adaptation. Thus we observe adaptations to the changing world of grasslands and savannahs amongst mammalian herbivores in the Miocene, Pliocene and Early Pleistocene. As the frequency of change intensified in the Middle and Late Pleistocene the ability to respond in this manner appears to be significantly reduced and extinction dominated over speciation. In the Late Pleistocene Palaearctic we observe significant range reduction amongst warm-temperate herbivores of forested and wooded environments and concomitant range expansions of steppe-tundra herbivores (Finlayson and Carrión, 2007; Carrión et al., 2008). Once the ice receded it was the turn of the steppe-tundra species to survive in reduced geographical areas. The present-day mammalian herbivore communities of the Palaearctic are thus impoverished versions of those of earlier times.

We may contrast this situation with the almost complete survival of Palaearctic bird taxa during the Pleistocene at a time when speciation rates were heavily reduced (Klicka and Zink, 1997). In this respect, it is important to note that the Middle Pleistocene avifauna of Europe is, in itself, almost a carbon-copy of the Early Pleistocene avifauna. In our analysis we found that 219 (58.56%) of the 374 Middle Pleistocene species (from Table 3) were already present in the Early Pleistocene; when we consider problems of preservation of fossil material and reduced number of older sites this proportion is significant. It is even more dramatic when we note that all Middle Pleistocene genera were already present in the Early Pleistocene and the majority date back to the Miocene–Pliocene (Mlikovsky, 2002).

The mid-late Tertiary situation was probably, in itself, an impoverishment of earlier times. If we take the Coraciiformes, a group of mainly warm, tropical, species now poorly represented by a handful of Palaearctic species as a case study we realise the extent of the impoverishment, which appears to have occurred at a much earlier date amongst birds than in mammals. The group includes seven orders of birds of which three are represented in the western Palaearctic and are of interest to us here. They are the hoopoes, woodpeckers and coraciiforms (in our case bee-eaters, rollers and kingfishers). Only six of the 22 extant families, 11 of 120 genera, and 18 of 669 species are represented in the western Palaearctic today.

This impoverished situation was not always so. The Eocene and Oligocene of Europe, with its tropical and paratropical forests (Janis, 1993), was home to a great diversity of birds from these orders and families (Blondel and Mourer Chauviré, 1988), some of which were abundant (Mayr, 2005). They included mousebirds (Coliidae, currently confined to sub-Saharan Africa), trogons (Trogonidae, today mainly tropical American but also tropical African and Asian), cuckoo-rollers (Leptosomidae, currently confined to Madagascar), motmots and todies (Momotidae and Todidae, currently New World tropical species; but see Mayr (2005) for taxonomic attribution), kingfishers (Alcedinidae), early forms of rollers (Coraciidae), hoopoes (Messelirrisoridae; Mayr, 2000), woodpeckers (Mayr, 2006) and forms ancestral to woodpeckers, jacamars and puffbirds (Galbulidae and Bucconidae, today of tropical America). To these we must add the ground hornbills (Bucerotidae) that have been reported from two Late Miocene western Palaearctic localities (Morocco: Brunet, 1971; Bulgaria: Boev and Kovachev, 2007). This means that all seven orders, and many families, once lived in what is today the western Palaearctic. Only a few managed to survive the drastic climate changes of the Late Tertiary. The warm-humid climate, forest, forms fared worst.

It is therefore hugely important to note the predominance of non-forest avian genera and species within the Palaearctic today. It is the product of a long term process that has affected orders, families, genera and species at different temporal scales throughout the Tertiary. The survivors at the beginning of the Pleistocene, and certainly by the Middle Pleistocene, were already the resilient forms that had managed to break away from their tropical prisons as these were becoming restricted to low latitudes.

Thus, as we have observed in this paper, the successful survivors in the Palaearctic Pleistocene were species from genera that had been the most climatically-tolerant, usually from speciose and widely-distributed genera. Although not specifically covered by this paper, we note that many of the genera with Palaearctic species have a predominance of non-Palaearctic species. In most cases the Palaearctic species are a small subset, often a single species, of the entire genus, which tends to be tropical. We interpret this as the adaptation of one or several species to the changing world of the Palaearctic in the Late Tertiary at a time when most species were being forced into low-latitude refugia.

4.3. Bird migration as a response to living in a cool and arid high latitude world

A number of theories have been proposed for the origins of bird migration. The dominant perspectives adopt a present-day position. Migrants are either low latitude species that have spread northwards to exploit temporary superabundances of seasonal foods or they are high latitude species that have been forced south by harsh winters. Our results suggest that migration is a deep time phenomenon which probably has its roots amongst Tertiary birds living in high latitude tropical and sub-tropical forests which would have had to perform short-term movements to avoid seasonal changes in photoperiod. As the rigours of the Late Tertiary and Quaternary worlds enhanced the winter seasonal deficit at high latitudes so these species were required to travel longer distances each time. In the specific case of trans-Saharan migration, this phenomenon would have continued to distend the breeding and winter ranges of many species even into the Holocene when the Sahara expanded significantly. The rapid manner, in which many birds can alter migratory behaviour, often in a few generations (Berthold and Helbig, 1992), indicates that migratory flexibility has been a major part of the avian package that has permitted their survival in the harsh Quaternary of the Palaearctic.

Acknowledgements

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