Range shifts in Quaternary European aquatic Coleoptera

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ABSTRACT

Aim To undertake a quantitative review of the Quaternary fossil record of European water beetles to evaluate their geographical and temporal coverage, and to characterize the extent and typology of the shifts in their geographical ranges.

Location Europe.

Methods We compiled Quaternary water beetle records from public databases and published references. We included in the analyses species of ten families of aquatic Coleoptera, and recorded range shifts through the comparison of the location of fossil remains with the current distribution of the species. We explored the ecological representativeness of the fossil record, as well as the relationship between range shifts and the habitat type of the species.

Results Our final data set included over 9,000 records for 259 water beetle species. Aquatic beetle fossil remains have been documented exclusively north of 42° N, with most of the records from the British Isles and virtually none from Southern Europe or the Mediterranean Basin. Over 80% of the records were from the Late Glacial and the Holocene periods (the last 15 kyr), and overall approximately 20% of the species have been recorded outside their present range (23% excluding Holocene records). Most range shifts were southern or western extensions of presently widespread, northern species, with ten species displaying major range shifts through the Palaearctic. Lentic species were significantly more likely to have experienced major range shifts, even accounting for the general ecological bias of the fossil record towards lentic habitats.

Main conclusions Our results show that the Quaternary record of aquatic Coleoptera is geographically, temporally and ecologically skewed, necessitating caution when making general conclusions about range changes and ecological stability on the basis of such scattered evidence. Most central and northern European species for which there are fossil records seem to have conserved their ranges through the Late Pleistocene, with geographical shifts mostly restricted to species with current widespread north Palaearctic or Holarctic distributions. Major range shifts through the Palaearctic are taxonomically uneven, suggesting either an idiosyncratic behaviour of taxa depending on ecological or phylogenetic factors, or a sampling artefact produced by the limited availability of taxonomic expertise.

Keywords

Pleistocene, water beetles, range shifts, speciation, fossils, climate change, evolutionary stasis.

INTRODUCTION

The Quaternary period, spanning the last 2.6 million years (Myr), has been aptly described as a time of extraordinary oscillations in global climate (Williams *et al.*, 1998). Large terrestrial ice-caps started to develop in the Northern Hemisphere *ca.* 2.75 Myr (Maslin *et al.*, 1996; Jansen *et al.*, 2000) resulting in multiple glacial–interglacial cycles driven by variations in orbital insolation on Milankovitch time-scales (Hays *et al.*, 1976; Imbrie & Imbrie, 1979). Such repetitive climatic changes have for long been considered to lead to an increase in speciation due to their clear effect on geographic ranges of both plants and animals, with the consequent increased likelihood of isolating small populations in areas under new selective regimes. Pleistocene climatic changes and the dramatic changes in ecological conditions or repeated fragmentation of populations during the glacials and interglacials were viewed as the cause of the origin of most extant European species (Rand, 1948; Mayr, 1970).

Despite more than half century of research, the evolutionary role of the Quaternary climatic changes remains, however, controversial (e.g. Klicka & Zink, 1997; Bennett, 2004; Baker, 2008). While numerous phylogeographical studies attest to the intraspecific genetic and geographical consequences of climatic changes (e.g. Avise & Walker, 1998; Avise *et al.*, 1998; Johns & Avise, 1998; see Avise, 2000 and Hewitt, 2000 for reviews), there is less evidence for extinction and speciation events. Some molecular studies have illustrated examples of species that very probably did arise in the Pleistocene or Holocene, such as some mammals (Hosey, 1982; Capanna *et al.*, 1996; Lister, 2004), birds (Klicka *et al.*, 1999), fish (Seehausen, 2002) and insects (Freitag, 1979; Knowles, 2000, 2001; Knowles & Otte, 2000; Barraclough & Vogler, 2002; Carisio *et al.*, 2004; Ribera & Vogler, 2004; Turgeon *et al.*, 2005; Contreras-Díaz *et al.*,

2007; Previsic *et al.*, 2009). It is not known to what extent these are exceptions or a common situation, as in some other cases species underwent range fragmentation and re-expansion with each cycle, but this either did not result in genetic differentiation, or subsequent re-expansion and mixing of populations eliminated incipient speciation (see e.g. Angus, 1973, 1983 for examples with water beetles, and Bennett, 1997 for a review).

An important source of evidence to support the view of the Quaternary as a period of generalized range shifts producing evolutionary stasis has come in the last decades from Quaternary entomology (Coope, 1978; Coope, 2004). Due to the hardness of the external insect cuticle (and in particular that of Coleoptera), there are numerous remains of insects in Quaternary deposits, which retain enough morphological detail to be studied and identified with criteria similar to that used with the extant fauna (Coope, 1986; Buckland & Coope, 1991; Elias, 1994). It must be noted that these remains are not fossils in the classic sense, as they are not mineralised, although we use the term “fossils” through the text for simplicity. Work on these well-preserved beetle remains, mostly from northern and central Europe and North America, has demonstrated that there was little evolutionary change (speciation and extinction) during the Pleistocene, with general morphological stasis, sometimes to an extraordinary detail (Coope, 1979, 1994, 1995; Angus, 1983; Böcher, 1989, 1995; Elias, 1994; Ashworth, 1996; Bennett, 1997). Confronted with rapid climatic change, species did not seem to acquire novel traits but instead tracked areas where conditions matched their ecological requirements (Bennett, 1997; Dynesius & Jansson, 2000; Coope, 2004; Benton & Emerson, 2007). As a result, the geographical range of most species should be highly dynamic, and evolutionary inferences concerning the geography of species in the past will often not be reliable (Gaston, 1998; Knowles, 2001; Losos & Glor, 2003).

There is no doubt that Quaternary remains of insects provide an inestimable tool for taxonomists, ecologists and biogeographers, as they bridge the gap between studies of living animals and their direct ancestors (Coope, 2004). Nevertheless, the value of the available fossil data to extract general conclusions about the role of Quaternary climatic changes on speciation or species distributions lies in its degree of geographical and temporal completeness, as well as ecological representativeness. The apparent stasis in Coleoptera, with little recognizable influence of extinction or speciation, may be a reflection of the geographical bias of fossil data toward higher latitudes (Ribera & Vogler, 2004). Despite the numerous examples of evolutionary stasis and range shifts (Elias, 1994), there has been no quantitative evaluation of the extent of these patterns in the context of the overall Quaternary beetle fauna. It is necessary to evaluate the representativeness of the Quaternary fossil record to recognize its limitations when drawing general conclusions of wide temporal and geographical extent.

Here we do a quantitative analysis of the fossil record of European water beetles to evaluate their geographical and temporal coverage, and to characterize the extent and the way in which species shifted their ranges. The western European water beetle fauna is a suitable model to study problems related to the completeness of the insect fossil record, as water beetles are a rich and well-known insect group in both Europe and the Mediterranean Basin, exhibiting a high level of endemism but also with species widely distributed across the Palaearctic region (Ribera *et al.*, 2003; Löbl & Smetana, 2003, 2004). Aquatic Coleoptera are well represented in the Quaternary fossil record (Buckland & Coope, 1991; Elias, 1994; Buckland & Buckland, 2006), and include species from a phylogenetically heterogeneous set of families of two suborders of Coleoptera, representing several independent invasions of the aquatic medium (Beutel & Leschen, 2005; Hunt *et al.*, 2007). They are also functionally diverse, with different

degrees of dependency on the aquatic habitat, diet and other autecological characteristics.

METHODS

Data on water beetle fossils were compiled from the BugsCEP database (Buckland & Buckland, 2006), completed or updated with additional references. BugsCEP is a free research software which includes a comprehensible database of Coleopteran habitat, ecology, distribution and Quaternary fossil records (www.bugscep.com). At the moment of our compilation (January 2009) it included published palaeontomological beetle data for Europe with information for over 5,000 beetle taxa from more than 600 sites and 3,500 bibliographic references. In all, the database included over 90,000 fossil records, although an important part corresponds to specimens unidentified at the species level.

We included in the analyses species from families Gyrinidae, Haliplidae, Noteridae, Dytiscidae, Helophoridae, Hydrochidae, Hydrophilidae, Hydraenidae, Elmidae and Dryopidae. Terrestrial species of Helophoridae and Hydrophilidae were excluded. We first assessed the geographical representativeness of the water beetle data by randomly selecting 1,000 subsets of an equivalent number of localities from the overall data set, measuring the average, maximum and minimum latitude and longitude, and comparing them with those obtained from the actual data.

Range shifts were identified by comparing the location of fossil records with the current distributional range of the species, assessed through world and Palaearctic catalogues (Hansen, 1999; Nilsson, 2001, 2003, 2004; Löbl & Smetana, 2003, 2004)

with more detailed information from specialised literature to determine the precise range when the fossil record was close to the edge of the current distribution. To assess the relative fossil coverage for different European areas, we compiled species numbers of aquatic Coleoptera for 12 regions of Western Europe (data from Ribera *et al.*, 2003, updated; see Appendix S1 in Supporting Information). We explored possible ecological bias in the fossil record, as well as the relationship between range shifts and the habitat type of the species. The main habitat type of the studied species was defined according to the general water flow regime, and three categories were distinguished: (1) lotic (strictly running water); (2) both running and standing water; and (3) lentic (strictly standing water) (see Ribera & Vogler, 2000 for details on habitat choice criteria). Water flow is the most important habitat characteristic determining the composition of the assemblages of aquatic Coleoptera, and species tend to be restricted to either standing water bodies or to running water, both in the larval and in the more dispersive adult stage (Ribera & Vogler, 2000; Ribera, 2008 and references therein).

During the last glacial maximum sea level was ca. 120 m below current values (Lambeck & Chappell, 2001; Sossian & Rosenthal, 2009), and as a consequence Ireland and Great Britain were connected to the European continent through a wide land corridor (Lambeck, 1995). The Holocene raise in sea level resulted in the isolation of Ireland and Great Britain as islands. This process alone is expected to result in a reduction in the number of species due to the reduction in area and the increase of isolation (Munroe, 1948; MacArthur & Wilson, 1967; Rosenzweig, 1995), independently of range shifts due to change in environmental conditions. To try to disentangle the effect of insularisation from range shifts due to climatic change we estimated the species richness for 12 countries of Western Europe plus the five largest western European islands, using the data in Ribera *et al.* (2003) updated whenever

necessary. Two different scenarios could be compared: i) current conditions and ii) Early Holocene. Following Ribera *et al.*, (2003), we used three geographical parameters to predict species numbers using linear regression: total area size (Area), southernmost latitude of a geographic area (sLat) and the extent of the land connection to adjacent areas (“Connectivity”, Con). These three parameters were shown to be strongly correlated with species richness of water beetles across 15 European islands and mainland areas (>800 species, $r^2 > 0.9$, $p < 0.00001$; Ribera *et al.*, 2003). Area, connectivity and number of species were log-transformed and multiple regression models were constructed using the software SPSS version 17.0.

In the first scenario (present), islands were considered to have a connectivity of zero (although an arbitrary value of 1 km was assigned to avoid log 0 values), while in the second scenario (early Holocene) we estimated the length of the land-bridge connecting the British Isles and continental Europe. This bridge seems to have remained, although with a decreasing width as the deglaciation progressed, until around 7,000 years BP (Lambeck, 1995; Peltier *et al.*, 2002). The British Isles were essentially ice free by 15-13 kyr BP (Ballantyne, 1997; Shennan *et al.*, 2002) and the sea level at this period was around 50 - 40 m below present (Lambeck, 1995; Shennan *et al.*, 2002; Sossian & Rosenthal, 2009). Thus, Britain and Ireland were considered as peninsulas with a connectivity value of 430 and 40 km, respectively, as estimated from the emerged land-bridges according to a sea level of around -50 m below the current shoreline.

RESULTS

Our final data set included a total of 9,326 available records (Appendix S2) for 259 water beetle species (see Appendix S3). A number of records were previously removed because lack (over 7,500) or ambiguous (ca. 3,000) species identification (mostly closely related species complexes). Dytiscidae was the family with more species represented as fossils, followed by Hydrophilidae, Helophoridae and Hydraenidae (Table 1).

With the sole exception of one species (*Hydraena coopei* Angus), known only from fossil remains (Angus, 1997), all fossil identified at species level were matched with extant species. All species with known Quaternary fossils currently have wide geographical distributions in the Palaearctic or Northern Holarctic, with the single exception of the lotic *Rhithrodytes crux* (Fabricius), known from the Alpes Maritimes in France and NW Italy (Bameul, 1989) and found as fossil in the same area (Ponel *et al.*, 2001).

Geographical coverage

Of the 603 sites with beetle data (excluding some archaeological records from artificial settings and other exclusively anthropogenic samples), a total of 403 sites had records of unambiguously identified water beetles. Water beetle sites encompass most of the latitudinal and longitudinal ranges of the overall Coleoptera data set, although the randomization test shown that they are slightly skewed towards the South and the West (Table 2). All 403 sites with remains of aquatic Coleoptera were located north of 42° N (north of the Pyrenees, Fig. 1), with 91.8% of the sites (encompassing 91.2% of the records) north of latitude 50° N. Localities north of 52°N (the southern limit of the ice sheets in the LGM; Dawson, 1992) included 56.6% of the records, and the British Isles encompassed 80.8% of the records (and 70.6% of the sites). This pattern was similar for

the overall set of coleopteran fossil records, with over 90% of sites situated north of Latitude 50° N. With the exception of a few records in south France and north Italy, there are no fossils records for water beetles in Southern Europe or the Mediterranean Basin (Fig. 1).

The percentage of species of the current fauna that is represented in the Quaternary fossil record (irrespective of the geographical provenance and the age of the fossils) is inversely correlated with the current total species richness ($r = -0.97$; Fig. 2). For the southern areas the proportion of species with fossil record is a highly biased sample of the extant fauna, with only the species with the widest geographical distributions represented (see below).

Temporal coverage

The oldest Quaternary water beetle records go back to the early stages of the Middle-Pleistocene (Coope, 2006; Parfitt *et al.*, 2005). However, 58.3% are from the Holocene, 36.6% from the Late-Pleistocene, and only 5.1 % have been associated to the Middle-Pleistocene. Most Late-Pleistocene fossils correspond actually to the Late-glacial period, with over 82.4% of the complete data set in the last 15 kyr (Fig. 3). This pattern is similar for the overall data set of Quaternary beetle fossils in the BugsCEP database, with 83.5% of all records from the Holocene and Late-glacial, 12.2% from Late-Pleistocene and 4.25% from the Middle Pleistocene. There are only a few records from Late Pliocene/Early Pleistocene deposits for some unambiguously identified species in sites from England (Lesne, 1920, 1926) and Greenland (Böcher, 1989, 1995; Bennike & Böcher, 1990).

Distributional changes

Of the 259 species studied, 50 (19.3%) have Quaternary remains found outside their current distributional range (Tables 1 and 3). All of them are species with current wide (mostly trans-continental) distributions in the Palaearctic or Holarctic regions (Table 3). The Holocene fauna could be considered in many senses very similar to the extant fauna, and thus the inclusion of very recent, Holocene records could bias the proportions of species experiencing range shift. When Holocene records were excluded the database was reduced to 3,769 records of 198 species. Of these, 45 experienced range shifts (i.e. only four had exclusive Holocene range shifts), so the percentage of species found outside their current distributional range increased from 19.3 to 22.7%.

Nineteen (38%) of the 50 species that experienced range shifts (including Holocene) correspond to records from the British Isles and/or Iceland and the Faroes of species currently found in adjacent areas in continental Europe in a latitudinal range encompassing the fossil record. They may be interpreted as potential island extinctions (see Methods).

Fourteen species (5.4% of those for which there are fossil records and 28% of the species recorded outside their present range) have fossil records south of their current range, the North Palaearctic or Holarctic regions (Table 3, Fig. 4). In four species (1.5%, 8%) outsider records represent a western longitudinal extension of their current ranges, and for other three species fossil records are northern extensions of species currently distributed in the Southwest of the Palaearctic region (Table 3).

Finally, ten species (3.8% of those for which there are fossil records and 20% of the species recorded outside their present range) have fossil records far outside their current distribution, since at present they do not occur in Western Europe (Tables 3, 4, Fig. 4). They are all from deposits previous to the Holocene. The present range of these species comprises some regions of Eastern Europe, Asia and, for some of them, North

America. With the exception of *Hygrotus unguicularis* (Crotch) (= *Coelambus mongolicus* Jakovlev) and *Agabus coxalis* Sharp (Dytiscidae), all belong to the family Helophoridae (genus *Helophorus*) (Tables 3, 4). In the case of *A. coxalis*, there is one subspecies of uncertain taxonomic status in the Caucasus (*A. coxalis schmidtii* Zaitzev, Nilsson, 2001), which, if related to the Ukraine populations, would greatly reduce the extent of the range shift.

There are 22 species recorded from deposits older than the LGM in sites that were covered by ice sheets during the LGM (Table 5). Although they are currently found in the same regions as they are recorded as fossils, they could not have lived there during the glacial maximum, so they should have experienced at least two range shifts: outside the glaciated areas during the LGM, and back during the Holocene.

Ecological bias

Most of the water beetle species with fossil data are typical of lentic water bodies (59.9%) or both lentic and lotic (21.4%), with only 18.7% typical of lotic environments. The current Western European fauna includes 41% of lotic and 38% of lentic species (21% can be found in both habitats or could not be characterized, Ribera *et al.*, 2003; see Appendix S1). Similarly, most of the species found outside their current ranges inhabit either lentic or both lotic and lentic water bodies (72% and 10%, respectively), while only nine (18%) are strictly lotic species (Table 3). The fossil record is thus highly skewed towards lentic species (two-way contingency test, $p < 0.0001$; Table 6), even when only the central and northern species are considered (i.e. removing Iberian, Italian and other exclusive Mediterranean species; $p < 0.0001$). Among the species with fossil remains there was no association between habitat and range shift ($p = 0.16$; Table 6), even when island extinctions were not considered ($p = 0.10$). However, all species

with major range shifts were lentic, representing a significant association with respect to all fossil species ($p = 0.03$; Table 6). Finally, six of the eighteen potential island extinctions (33.3%) correspond to strictly lotic species, a proportion higher than that of the overall fossil record (18.6%) but still not significantly different from a random sample of the British fauna ($p = 0.15$; Table 6).

DISCUSSION

Representativeness of the Quaternary fossil record of European aquatic

Coleoptera

There is no evidence in the beetle fossil record to support the idea that the repeated climatic changes during the Quaternary resulted in increased speciation, extinction or morphological and ecological changes (Coope, 1979; Elias 1994). However, our results show that the fossil record of Quaternary European water beetles is geographically, temporally and ecologically uneven, which affects the generality of this conclusion.

Geographical bias

Known Quaternary aquatic beetle fossils are mostly located at higher latitudes, and particularly concentrated in the British Isles. Crucially, for large parts of Europe and the Mediterranean Basin there are no known remains. This is the case of the Iberian, Italian, Balkan and Anatolian peninsulas and North Africa, the areas with the highest richness of endemics (Myers, 2000; Balletto & Casale, 1991; Greuter, 1991; Taberlet *et al.*, 1998; Ribera *et al.*, 2003) and the less affected by the glaciations. At the Last Glacial Maximum (23–18 kyr BP) the European ice sheet extended north of 52° N and permafrost north of 47° N (Dawson, 1992), while the Mediterranean peninsulas had a

more temperate climate and vegetation (e.g. Huntley, 1988; Bennett *et al.*, 1991; Hewitt, 2000).

Temporal bias

The temporal extent of the Quaternary aquatic beetle record is markedly biased towards the recent. Most of the fossil records are from the last 15,000 years, with a poor representation of the early Late Pleistocene and the Middle Pleistocene, and a virtual absence of Early Pleistocene fossils, which actually represents more than half of the Quaternary period (Fig. 3). This pattern is similar for the overall Coleoptera fossil record, and probably related to the limitations in the preservation of the fossil remains, but also because good Early Pleistocene sites are very rare. There is an important paleontological gap between the exoskeletal remains preserved in the unconsolidated Pleistocene sediments and the mineral replacements and trace fossils preserved in bedrock from the Tertiary back to the Palaeozoic. Sites containing fossil insect remains more than 1 million years old are extremely rare (Elias, 2007a,b), and almost exclusively from Arctic and sub-Arctic regions (Elias *et al.*, 2006, 2007a), since the long-term preservation of chitinous exoskeletons is greatly facilitated by permanently frozen ground or permafrost. Repeated glaciations at lower latitudes obliterated nearly all organic terrestrial deposits during the Pleistocene (Elias *et al.*, 2006).

The lack of fossil data for large parts of the Quaternary (specially for the first half) represents a serious limitation to drawing general conclusions about the role of Quaternary climatic cycles on speciation events, since the available information covers in its vast majority only the last glacial cycle. Some molecular studies place the diversification events at the first periods of the Quaternary (e.g. Ribera & Vogler, 2004; Carisio *et al.*, 2004).

Ecological bias

An additional bias in the fossil record emerged from the ecological characteristics of the species. Most of the species recorded as fossils inhabit standing water bodies, despite the fact that the proportion of lotic species is higher in the extant European fauna (Ribera *et al.*, 2003). Fossil beetle assemblages have been recovered from a wide variety of sedimentary environments, but they are especially frequent in anoxic water-lain sediments that concentrate the remains in layers of organic detritus (Coope, 2004). Sediments of lentic environments such as lakes and ponds (but also bogs, fens or mires) have yielded abundant, diverse assemblages of fossil beetles, especially in deposits from the littoral zone and where a stream enters a lake or pond (Elias, 2007b). Although fluvial sediments also yield fossil beetles, they are scarcer, and the most productive type of fluvial deposit is an accumulation of organic detritus, laid down in secondary channel bends, backflows, and pools between riffles (Elias, 2007b). This ecological bias can also be related with the observed geographical bias in the fossil data: the fossil record is geographically concentrated in higher latitudes, with a higher proportion of lentic species (Ribera *et al.*, 2003). However, even when these differences were taken into account the proportion of lentic species among the fossil remains was significantly higher than a random representative sample.

What can we conclude from Quaternary range shifts?

Notwithstanding the limitations noted above, we can extract valuable information from the data set of fossil water beetles concerning the role of climatic changes in altering the distributions of species during the late Quaternary. This knowledge is of high value for biogeographical research, with important implications for ongoing and future global

climate change. The fossil data compiled here show that for ca. 80% of the species their fossil remains have been found within their current distributional ranges. This percentage was only slightly smaller (ca. 77%) when the Holocene records were excluded from the database. This is, however, not necessarily indicative that these species did not change their ranges during the Quaternary. To determine distributional ranges, and how they change with time, the record of absences may be as important as that of presences (Lobo, 2008). Due to the incompleteness of the Quaternary fossil record it is less reliable to determine absences, and thus cycles of contraction-expansion will not be detected unless the current range is in the “contracted” phase. Considering we are in a warm interglacial, this would favour the identification of range shifts of northern species (as was the case) against more temperate southern species, which may be close to their maximum historical ranges. When a fossil is found in an area currently occupied by the same species it is not possible to know if there was continuous presence of populations in the area or if there were successive local extinctions and recolonisations – unless the area was covered by ice sheets during the glacials. Some of these species have been recorded as fossils from periods prior to the LGM, so they should have become locally extinct or changed their ranges tracking suitable climatic conditions during the last glacial, with subsequent recolonisation during the Holocene (see e.g. Coope, 1978 for other examples in terrestrial Coleoptera).

In any case, the overall conclusion is that most Quaternary fossil remains of aquatic beetles from central and Northern Europe are of species currently present in the same area. Even with the caution that there may be undetected shifts, this is in disagreement with the view that the present-day range of a species is not informative, and that evolutionary inferences concerning the geography of species in the recent past will often not be reliable (Gaston, 1998; Knowles, 2001; Losos & Glor, 2003).

The percentage of the current North European fauna represented as Quaternary fossils is remarkably high, with values of ca. 70-80% of the species (Fig. 2). As already noted, most of these fossil remains are very recent (mid to late Holocene), but the fact that there are no known fossil remains of any of the species with current restricted distributions in the Mediterranean region can nevertheless be taken as a strong evidence that these species were never present in central and northern Europe, at least during the last glacial cycle (with the unavoidable caveat of the potential incompleteness of the fossil record). This, together with the general stability of ranges shown above, outlines a scenario in which the northern areas would have a stable pool of widely distributed, mostly lentic species (i.e. with good dispersal abilities, Ribera 2008) which experience limited latitudinal or, to a lesser extent, longitudinal range shifts in response to climatic change. Although not included in our review, some recent work on the Arctic regions of North America and Siberia allows extension of this scenario to the whole Holarctic (e.g. Elias, 2000; Zinovjev, 2006; Kuzmina *et al.* 2008), and (although with still incomplete data) to the whole Pleistocene (Elias *et al.*, 2006). The existence of two partly non-overlapping species pools (Mediterranean species with ranges never extending to northern Europe, and northern species with limited southern expansions during the glacials) is in agreement with increasing evidence from molecular studies of the role of the Mediterranean peninsulas as a source of endemism, not of re-colonization of the areas affected by glaciations (Bilton *et al.* 1998; Petit *et al.*, 2003; Ribera & Vogler, 2004; Hofreiter & Stewart, 2009).

A considerable proportion of the species that shifted ranges would be compatible with the result of island extinctions. As noted above, the Holocene raise in sea level resulted in the isolation of Ireland and Great Britain as islands, and this process alone is expected to result in a reduction in the number of species due to the reduction in area

and the increase of isolation (Munroe, 1948; MacArthur & Wilson, 1967; Rosenzweig, 1995), perhaps as the result of local extinction without the possibility of recolonisation due to the opening of the Channel (e.g. *Gyrinus colymbus* during the medieval Little Ice Age, Girling, 1984, Table 3). Results of regression models were in agreement with this hypothesis. The total species number in the seventeen regions considered was predicted with good accuracy based on the three geographical parameters (Table 7) for the two different scenarios, present ($R^2 = 0.76$) and the beginning of the Holocene ($R^2 = 0.87$). When Britain and Ireland were considered islands, their number of species was consistently underestimated, while when they were considered peninsulas (situation at the beginning of the Holocene) their species richness was overestimated (194 species in Ireland against the current 181, and 274 species in Britain against the current 253; Table 6). Although this can only be considered a suggestion based on indirect evidence, it may be hypothesized that the current number of species for both islands might be an intermediate situation from the early Holocene as peninsulas towards the equilibrium as islands.

The possibility that some of the species considered to be potential “island extinctions” could have become extinct due to ecological reasons must also be considered (e.g. species restricted to more continental areas, such as *Helophorus aquaticus* (Linnaeus) or *H. discrepans* Rey; (RBA, unpublished observations). Similarly, human activities could also be related to the extinction of some of these missing island species. A very important factor in the extinction of island populations seems to have been the arrival of humans and their impact upon island ecosystems (Patton, 2000). The extirpation of species in Great Britain and Ireland as consequence of human activities has been widely reported, with around 40 and 15 pre-Linnaean extinctions recorded amongst British and Irish Holocene Coleoptera, respectively (see

Whitehouse, 2006 and references therein). Although most of these extirpations concern saproxylophagous species and are attributed to forest clearance in the Neolithic, the effects of deforestation undoubtedly resulted in changes of sedimentation in many rivers and other water bodies, altering communities of water and riparian beetles. This could be the case of some of the extinctions of Elmidae, which are known to be sensitive to anthropogenic alterations (Osborne, 1998; Smith, 2001; see also Baker *et al.*, 1993 for an example in North America).

Some of the species found as fossils in the British Isles and other parts of Europe are currently distributed at a considerable distance from their Pleistocene sites, and thereby they can be unequivocally attributed to range shifts. For most of them these range movements correspond to relatively limited expansions south or west of their current ranges, but ten species can be said to have suffered major shift ranges (i.e. at a continental scale) during the Pleistocene climate changes. Elias (1994) summarizes evidence for changing distribution patterns through the last glacial/interglacial cycle for many European and North American insect taxa. Such movements of species in response to Quaternary climatic oscillations involved range changes in all directions (Coope, 1990, 2004). At least in the case of the water beetle fauna, these large shifts seem to be highly taxonomically biased, as eight of the ten species belong to a single family, Helophoridae. This taxonomic bias could be related to the difficulty in identifying species within other water beetle groups or to ecological traits that enhanced large range shifts in species of this family. In this sense, it is worth noting that species of the families Helophoridae and some species of Hydraenidae (which display important range changes, although at lower geographical scales) have terrestrial larvae (Jäch & Balke, 2008), which through some unknown process may be related to their higher dispersal ability.

As noted above, the Quaternary fossil “species pool” consists almost exclusively of taxa with large geographical ranges, with an over-representation of lentic species.

Widespread lentic species are likely to respond in a different manner to climatic changes than lotic, southern species, generally with smaller ranges (Ribera *et al.*, 2003; Ribera, 2008). Unfortunately, the lack of fossil records in Mediterranean areas and the low proportion of strictly lotic species among the fossil remains make difficult to know the effects of Quaternary climatic changes on their diversification and extinction. The only southern species of Aquatic Coleoptera with a restricted range found as Quaternary fossil was *Rhithrodytes crux*, in a site within its current range (Ponel *et al.*, 2001). *Ochthebius figueri* Garrido *et al.* (found in British Pleistocene deposits; Angus, 1993) was believed to be an Iberian endemic, but it has been recorded from Morocco (Ribera, 2000; Jäch, 2004) and it belongs to a group of species in the subgenus *Asiobates* known to have current scattered, presumably relict distributions (such as e.g. *Asiobates cantabricus* Balfour-Browne, known only from the types in a single locality in the NW of Spain but recently recorded from NE Turkey; Jäch, 1990; Kasapoğlu & Erman, 2002).

Species typical of lentic water bodies have been predicted to have better dispersal abilities, and more dynamic geographical ranges, than lotic species (Ribera & Vogler, 2000; Ribera, 2008). In agreement with these predictions, all species considered to have suffered major shifts were typical of standing water bodies, and the proportion of lotic species among the “island extinctions” was also higher than random. For the latter differences were not significant though, probably due to the low number of lotic species known as fossils in the British Isles. In addition to that, it must be considered that the reference species pool (that of central and northern Europe) is already impoverished in narrow-ranged lotic species, and thus the running water species found as fossils are strongly biased towards those with the larger geographical ranges and, presumably, the better dispersal abilities.

Concluding remarks

The extent to which the results of our work are applicable to other species-rich Mediterranean groups of beetles, or insects in general, remains to be investigated, although they suggest that caution needs to be exercised when analysing distributional data of the Quaternary beetle fossil record. Quaternary beetle research has progressed in a variety of ways during the last decade (Elias, 2006), but the sampling unavoidable deficiencies of the fossil data make it difficult to draw general conclusions about the origins of the Palaearctic fauna as a whole, and extrapolating from what we know of widespread, northern taxa may be misleading. In this sense, our results may go some way towards explaining the discrepancy between the fossil record and several recent invertebrate molecular phylogenetic studies that suggest speciation in southern peninsulas as a consequence of Quaternary climatic changes (e.g. Ribera & Vogler, 2004; Previsic *et al.*, 2009).

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BIOSKETCH

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Table 1. Number of species per family used in the analysis, number of species that have been found outside their current range (with the percentage in parenthesis) and those assigned to potential “island extinctions”.

FAMILY	Total species	Species outside current range	Island extinction
GYRINIDAE	12	4 (33.3%)	3
NOTERIDAE	2	0 (0%)	0
HALIPLIDAE	12	0 (0%)	0
DYTISCIDAE	111	15 (13.5%)	4
HYDROCHIDAE	7	1 (14.3%)	0
HELOPHORIDAE	29	14 (48.3%)	4
HYDROPHILIDAE	34	4 (11.8%)	2
HYDRAENIDAE	31	6 (19.4%)	1
DRYOPIDAE	5	1 (20%)	1
ELMIDAE	16	5 (31.3%)	4
	259	50 (19.3%)	19

Table 2. Analysis of the geographical representativeness of the water beetles data set, with the 95% confidence intervals for the 1000 random subsets of sites from the overall dataset.

Variable	95% confidence interval (random sampling)	Water beetles dataset
Average Latitude	54.36 - 54.88	54.21
Average Longitude	-0.17 - -0.03	-0.58
Maximum Latitude	80 - 82.45	74.5
Minimum Latitude	42.54 - 43.4	42.54
Maximum Longitude	30.07 - 30.48	24.65
Minimum Longitude	-68 - -53.83	-53.83

Table 3. Species found as fossils outside their current distribution. HT Habitat type (0 lotic, 2 lentic, 1 both). Codes for the areas: AU Austria, GB Great Britain (including Channel Islands), DE Denmark, FA Faroe Islands, FR France, GE Germany, GL Greenland, IC Iceland, IR Ireland, NL Netherlands, PL Poland, SW Sweden, SZ Switzerland, UK Ukraine. ¹Record by Foster & Carr (2008); ²doubtful island extinction (see Discussion).

SPECIES	DISTRIBUTION	Outsider fossils	Distributional change	H T
GYRINIDAE				
<i>Gyrinus caspius</i> Méné.	Wide Palaearctic	GB	Island extinction	2
<i>Gyrinus colymbus</i> Er.	Wide Palaearctic	GB	Island extinction	2
<i>Gyrinus opacus</i> Sahl.	N Holarctic	DE FR PL	Southern extension	2
<i>Orectochilus villosus</i> (Müll.)	Wide Palaearctic	GB IR	Island extinction	0
DYTISCIDAE				
<i>Agabus arcticus</i> (Payk.)	N Holarctic	DE FR GE PL	Southern extension	2
<i>Agabus coxalis</i> Sharp	E Palaearctic, Caucasus	UK	Western extension/ Large range shift	2
<i>Agabus serricornis</i> (Payk.)	N Palaearctic	GB	Southern extension	2
<i>Bidessus grossepunctatus</i> Vorbringer	Wide Palaearctic	GB	Island extinction ¹	2
<i>Colymbetes dolabratus</i> (Payk.)	N Holarctic	DE FR GB GE GL	Southern extension	2
<i>Colymbetes paykulli</i> Er.	Wide Palaearctic	GB IR	Longitudinal (W) extension	2
<i>Colymbetes striatus</i> (L.)	Wide Palaearctic	GB	Island extinction ²	2
<i>Ilybius angustior</i> Gyll.	Wide Palaearctic	GB	Longitudinal (W) extension	2
<i>Ilybius vittiger</i> (Gyll.)	N Holarctic	GB	Southern extension	2
<i>Hydroporus gyllenhalii</i> Schiödte	W Palaearctic	FA	Island extinction	2
<i>Hydroporus lapponum</i> (Gyll.)	N Holarctic	GB	Southern extension	2
<i>Hydroporus nigellus</i> LeC.	Wide Palaearctic	GB	Island extinction	2
<i>Hydroporus notabilis</i> LeC.	N Holarctic	IR GB	Southern extension	1
<i>Hygrotus unguicularis</i> Crotch	E Palaearctic	GB	Large range shift	2
<i>Oreodytes alpinus</i> (Payk.)	N Palaearctic	DE GB	Southern extension	2
HELOPHORIDAE				
<i>Helophorus glacialis</i> Villa	W Palaearctic	GB IR	Island extinction	2
<i>Helophorus aspericollis</i> Angus	E Palaearctic	GB UK	Large range shift	2
<i>Helophorus sibiricus</i> (Mots.)	N Holarctic	DE FR GB IR NL SZ UK	Southern extension	2
<i>Helophorus aquaticus</i> (L.)	Wide Palaearctic	GB	Island extinction ²	2
<i>Helophorus discrepans</i> Rey	W Palaearctic	GB	Island extinction ²	2
<i>Helophorus oblongus</i> LeC.	N Holarctic	FR GB UK	Large range shift	2
<i>Helophorus splendidus</i> Sahl.	E Palaearctic	GB GE	Large range shift	2
<i>Helophorus lapponicus</i> Thoms.	Wide Palaearctic	GB	Southern extension	2

<i>Helophorus pallidus</i> Gebl.	N Palaearctic	GB	Southern extension	2
<i>Helophorus orientalis</i> Mots.	N Holarctic	GB UK	Large range shift	2
<i>Helophorus mongoliensis</i> Angus	E Palaearctic	GB	Large range shift	2
<i>Helophorus praenanus</i> (Lom.)	E Palaearctic	GB UK	Large range shift	2
<i>Helophorus browni</i> McCorkle	N Holarctic	UK	Large range shift	2
<i>Helophorus khnzoriani</i> Angus	E. Palaearctic	GL SW	Large range shift	2
HYDROCHIDAE				
<i>Hydrochus flavipennis</i> Küster	W Palaearctic	GB	Northern extension	1
HYDROPHILIDAE				
<i>Chaetarthria seminulum</i> (Hbst.)	Wide Palaearctic	IR	Island extinction	2
<i>Hydrobius arcticus</i> Kuw.	N Palaearctic	GB	Southern extension	2
<i>Laccobius decorus</i> Gyll.	Wide Palaearctic	GB	Longitudinal (W) extension	2
<i>Coelostoma orbiculare</i> (F.)	Wide Palaearctic	FA IR	Island extinction	2
HYDRAENIDAE				
<i>Ochthebius figueroi</i> Garrido G.	SW Palaearctic	GB	Northern extension	1
<i>Ochthebius kaninensis</i> Popp.	N Palaearctic	GB	Southern extension	0
<i>Ochthebius foveolatus</i> Germ.	W Palaearctic	GB SZ	Island extinction	0
<i>Ochthebius lenensis</i> Popp.	N Palaearctic	DE GE	Southern extension	2
<i>Ochthebius pedicularius</i> Kuw.	W Palaearctic	GB	Longitudinal (W) extension	0
<i>Hydraena britteni</i> Joy	W Palaearctic	IC	Island extinction	1
ELMIDAE				
<i>Dupophilus brevis</i> Muls. & Rey	SW Palaearctic	GB	Northern extension	0
<i>Esolus parallelepipedus</i> (P. Müller)	Wide Palaearctic	GB	Island extinction	0
<i>Esolus pygmaeus</i> (P. Müller)	Wide Palaearctic	GB	Island extinction	0
<i>Limnius opacus</i> P. Müller	Wide Palaearctic	GB	Island extinction	0
<i>Stenelmis consobrina</i> Dufour	Wide Palaearctic	GB	Island extinction	0
DRYOPIDAE				
<i>Dryops griseus</i> (Er.)	W Palaearctic	GB	Island extinction	1

Table 4. Species which have suffered major range shifts. Extant distribution and fossil sites where they have been found are indicated.

Species	Extant distribution	Fossil sites
<i>Helophorus aspericollis</i>	Siberia, Mongolia and Far East	Britain (e.g. Gibbard <i>et al.</i> , 1982; Briggs <i>et al.</i> 1985) Ukraine (Angus, 1973)
<i>Helophorus browni</i>	Siberia, Mongolia, China, Canada and Alaska	Ukraine (Angus, 1973)
<i>Helophorus khnzoriani</i>	Altai, Tuva	Sweden (Lundqvist, 1978), Greenland (Böcher, 1995)
<i>Helophorus mongoliensis</i>	Siberia, Mongolia, China, Canada and Alaska	Britain (Angus, 1973; Briggs <i>et al.</i> , 1985)
<i>Helophorus oblongus</i>	Northern Asia (mainly Siberia) and North America	France (Ponel, 1994, 1995; Ponel <i>et al.</i> , 2003; Buckland, 2007) Britain (Rose <i>et al.</i> , 1980; Briggs <i>et al.</i> , 1985) Ukraine (Angus, 1973)
<i>Helophorus orientalis</i>	Western Russia to the Far East and North America	Britain (Morgan, 1969; Angus, 1970; Briggs <i>et al.</i> , 1985; Coope <i>et al.</i> , 1997) Ukraine (Angus, 1973)
<i>Helophorus praenanus</i>	Siberia, Mongolia and Far East	Britain (e.g. Gibbard <i>et al.</i> , 1982; Briggs <i>et al.</i> , 1985; Coope, 2000) Ukraine (Angus, 1973)

<i>Helophorus splendidus</i>	Northern Asia (mainly Siberia) and North America	Britain (Coope & Brophy, 1972; Simpkins, 1974; Coope, 1977a; Coope <i>et al.</i> , 1997; Maddy <i>et al.</i> , 1998) Germany (Walkling & Coope, 1996)
<i>Hygrotus unguicularis</i>	Western Russia to China and North America	Britain (Coope, 1977b)
<i>Agabus coxalis</i>	East Palaearctic, Caucasus	Ukraine (RBA, unpublished data)

Table 5. Species recorded from deposits older than the Last Glacial Maximum in sites that were covered by ice sheets during the LGM. HT Habitat type (0 lotic, 2 lentic, 1 both). Codes for the countries: GB United Kingdom (including Channel Islands), GE Germany, GL Greenland, IC Iceland, IR Ireland, SV Sweden.

SPECIES	HT	Found before LGM
DYTISCIDAE		
<i>Hydroporus palustris</i> (L.)	1	GB IR
<i>Hydroporus morio</i> Aubé	2	GL
<i>Hydroporus memnonius</i> Nic.	1	GB IR
<i>Hydroporus melanarius</i> Sturm	1	GB
<i>Hydroporus longicornis</i> Sharp	0	GB
<i>Nebrioporus depressus/elegans</i> (F.)/(Panz.)	1	GB
<i>Agabus bipustulatus</i> (L.)	1	GB GL IC IR SV
<i>Ilybius wasastjernae</i> (Sahl.)	2	GB
<i>Agabus affinis</i> (Payk.)	2	GB
<i>Agabus congener</i> (Thun.)	2	IR
<i>Agabus confinis</i> (Gyll.)	2	SV
<i>Ilybius guttiger</i> (Gyll.)	2	GB
<i>Rhantus grapii</i> (Gyll.)	2	GB
GYRINIDAE		
<i>Gyrinus marinus</i> Gyll.	1	SV
HYDRAENIDAE		
<i>Hydraena riparia</i> Kug.	1	SV
HELOPHORIDAE		
<i>Helophorus grandis</i> Ill.	2	GB
<i>Helophorus aequalis</i> Thoms.	2	IR
<i>Helophorus khnzoriani</i> Angus	2	SV
<i>Helophorus minutus</i> F.	2	GE
HYDROPHILIDAE		
<i>Hydrobius fuscipes</i> (L.)	2	GB GE
<i>Enochrus fuscipennis</i> (Thoms.)	2	GB
<i>Cymbiodyta marginellus</i> (F.)	2	GE
ELMIDAE		
<i>Normandia nitens</i> (P. Müller)	0	SV

Table 6. Chi-squared test on the contingency tables of the number of species of aquatic Coleoptera found as fossils for association between habitat type (lotic, lentic, both). df: degrees of freedom of the contrast.

Contrast	χ^2	df	<i>P</i>
Current European species			
All species	80.43	2	<0.0001
Excluding Mediterranean species	27.20	2	<0.0001
Species found outside current range			
All	3.7	2	0.16
Excluding "island extinctions"	4.55	2	0.10
Large range shifts	6.98	2	<0.05
British species	3.78	2	0.15

Table 7. Number of species and geographical variables used in the analysis. Area (km²); sLat: southernmost latitude (degrees); Con: length of the connection with mainland (“connectivity”) (km); S: total number of species.

Region	Predictable variables					Predicted S (Holocene)	Predicted S (Present)
	Area	Total S	sLat	Con (Present)	Con (Holocene)		
Corsica	8680	192	41.30	0	0.00	121.64	141.54
Ireland	81638	180	51.50	0	170.00	194.10	96.91
Sardinia	24090	237	39.00	0	0.00	144.20	200.06
Sicily	25708	235	36.50	0	0.00	176.66	243.80
Mallorca	3640	141	39.30	0	0.00	145.44	141.66
Britain	230977	248	50.00	0	430.00	274.398	129.51
Holland	41526	272	51.30	330	330	237.319	188.00
Iberia	583254	469	36.00	400	400	831.49	948.67
Norway	385252	219	58.00	510	510	147.89	176.64
Sweden	449964	273	55.00	510	510	188.45	226.91
Denmark	43098	245	54.50	73	330	182.60	122.20
Germany	357021	358	47.50	875	875	402.01	409.87
Italy	251536	478	38.00	580	580	789.57	743.23
France	551695	460	42.50	940	940	611.57	647.29
Finland	338000	243	60.00	1140	1140	155.27	165.40
Iceland	103000	11	64.50	0	0	17.50	38.23
Faroe Islands	1400	12	61.40	0	0	24.31	23.12

Figure captions

Figure 1. Location of the sites with fossils of Coleoptera (asterisks) and water beetles (black dots) in Western Europe. Insert, detail of the British Isles. In grey, maximum extend of the ice sheets during the Last Glacial Maximum (from Ehlers & Gibbard, 2004).

Figure 2. Fossil *versus* present water beetle fauna for some European regions. a) Number of present species and number of species recorded as fossils (wherever). Numbers into bars indicate the percentage of the present fauna of each country recorded as fossils. b) Relationship between the number of present species and the percentage of these species recorded as fossils. AU, Austria; GB, United Kingdom; DE, Denmark; FI, Finland; FR, France; GE, Germany; IP, Iberian Peninsula; IR, Ireland; IT, Italy; NL, Netherlands; NR, Norway; SV, Sweden.

Figure 3. Distribution of the fossil record of water beetles along the Quaternary timescale. Numbers above bars are the percentage of the total dataset.

Figure 4. Some examples of range shift in the European water beetle fauna. a) Island extinction (*Helophorus glacialis*); b) Northern extension of a Southern species (*Dupophilus brevis*); c) Southern extension of a Northern species (*Ilybius vittiger*); d) Longitudinal extension (to the West) (*Lacobiuss decoratus*); e) Large range shift (*Helophorus orientalis*). Gray area represents the current distributional range of the species and the black stars are the sites where have been found as fossils outside their present ranges.

Figure 1

Figure 2

Figure 3

Figure 4