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# A review of Quaternary range shifts in 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 10 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 9000 records for 259 water beetle species. Fossil remains of aquatic beetles 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 currently widespread, northern species, with 10 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 extrapolating general conclusions about range changes and ecological stability to other areas or periods 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

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

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## 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 c. 2.75 Ma, with subsequent multiple glacial–interglacial cycles driven by variations in orbital insolation on Milankovitch time-scales. Such repetitive climatic changes have long been considered to lead to an increase in speciation due to their clear effect on geographical ranges of both plants and animals, with the consequent increased likelihood of isolating small populations in areas under new selective regimes (Dynesius & Jansson, 2000). Pleistocene climatic changes and the dramatic changes in ecological conditions or repeated fragmentation of populations during the glacials and inter-glacials 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 controversial (e.g. Bennett, 2004; Baker, 2008). While numerous phylogeographical studies attest to the intra-specific genetic and geographical consequences of climatic changes (see Avise, 2000 and Hewitt, 2000 for reviews), there is limited evidence for extinction and/or speciation events. Some molecular studies have illustrated examples of species that very probably did arise in the Pleistocene or Holocene, such as some mammals (Capanna *et al.*, 1996; Lister, 2004), birds (Klicka *et al.*, 1999), fish (Seehausen, 2002) and insects (Barracough & Vogler, 2002; Carisio *et al.*, 2004; Ribera & Vogler, 2004; Turgeon *et al.*, 2005; Contreras-Díaz *et al.*, 2007; Previšić *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 subsequent 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, 2004). Due to the hardness of the external insect cuticle (and in particular that of Coleoptera), remains of insects were frequently preserved in Quaternary deposits. These often retain enough morphological detail to be studied and identified with criteria similar to those used with the extant fauna (Elias, 1994). Work on these well-preserved beetle remains, mostly from northern and central Europe and North America, has demonstrated that there was little extinction during the Pleistocene. Moreover, an extraordinary degree of morphological stasis is apparent when fossil specimens are compared with current specimens, suggesting that there has also been little evolutionary change, as fossil communities make sense in terms of the modern ecologies of the beetles (e.g. Angus, 1983; Coope, 1994, 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 present-day range of a species will often differ greatly from the range when it first arose and, according to several authors, the evolutionary inferences concerning the geography of species in the past will often not be reliable (Gaston, 1998; Losos & Glor, 2003).

There is no doubt that Quaternary remains of insects provide a valuable tool for taxonomists, ecologists and biogeographers, as they bridge the gap between studies of living animals and their ancestors (Coope, 2004). Nevertheless, the value of the available fossil data for extracting 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 evolutionary stasis in Coleoptera during the Quaternary, with little evidence 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 morphological 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 undertake 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 have shifted their ranges. The western European water beetle fauna is a suitable model for studying 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 Palearctic region (Löbl & Smetana, 2003, 2004; Ribera *et al.*, 2003). Aquatic Coleoptera are well represented in the Quaternary fossil record (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, completed or updated with additional references. BugsCEP is a free research tool that includes a comprehensive database of Coleopteran habitat, ecology, distribution and Quaternary fossil records (Buckland & Buckland, 2006). At the time of our compilation (January 2009) it included published fossil beetle data for Europe with information on over 5000 beetle taxa from more than 600 sites and 3500 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, from the overall data set, 1000 subsets with the same number of sites as those having water beetle fossils, measuring the average, maximum and minimum latitude and longitude, and comparing them with those obtained from the observed subset of sites with water beetle fossils.

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; Löbl & Smetana, 2003, 2004) with more detailed information from specialized 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 characteristics 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 (LGM) sea level was c. 120 m below current values (Lambeck & Chappell, 2001), and as a consequence Ireland and Great Britain were connected to the European continent through a wide land corridor (Lambeck, 1995). Post-glacial rise 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 in isolation (Rosenzweig, 1995), independently of range shifts due to change in environmental conditions. As a way to explore the potential effect of insularization independently 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: (1) current conditions, and (2) the late glacial period (13–10 kyr BP). 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 geographical 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 zero values), while in the second scenario (late glacial) 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 7000 yr BP (Lambeck, 1995). The British Isles were essentially ice free by 15–13 kyr BP and the sea level at this period was around 50–40 m below present (Lambeck, 1995). 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

After culling available records lacking species-level identifications (over 7500) or having ambiguous designations (mostly closely related species complexes; c. 3000), our final data set included a total of 9326 records (Appendix S2) for 259 water beetle species (see Appendix S3). Dytiscidae was the family with most 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 fossils 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 Alps Maritimes

**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

in France and north-west Italy (Bameul, 1989) and found as fossil in the same area (Ponel *et al.*, 2001).

**Geographical coverage**

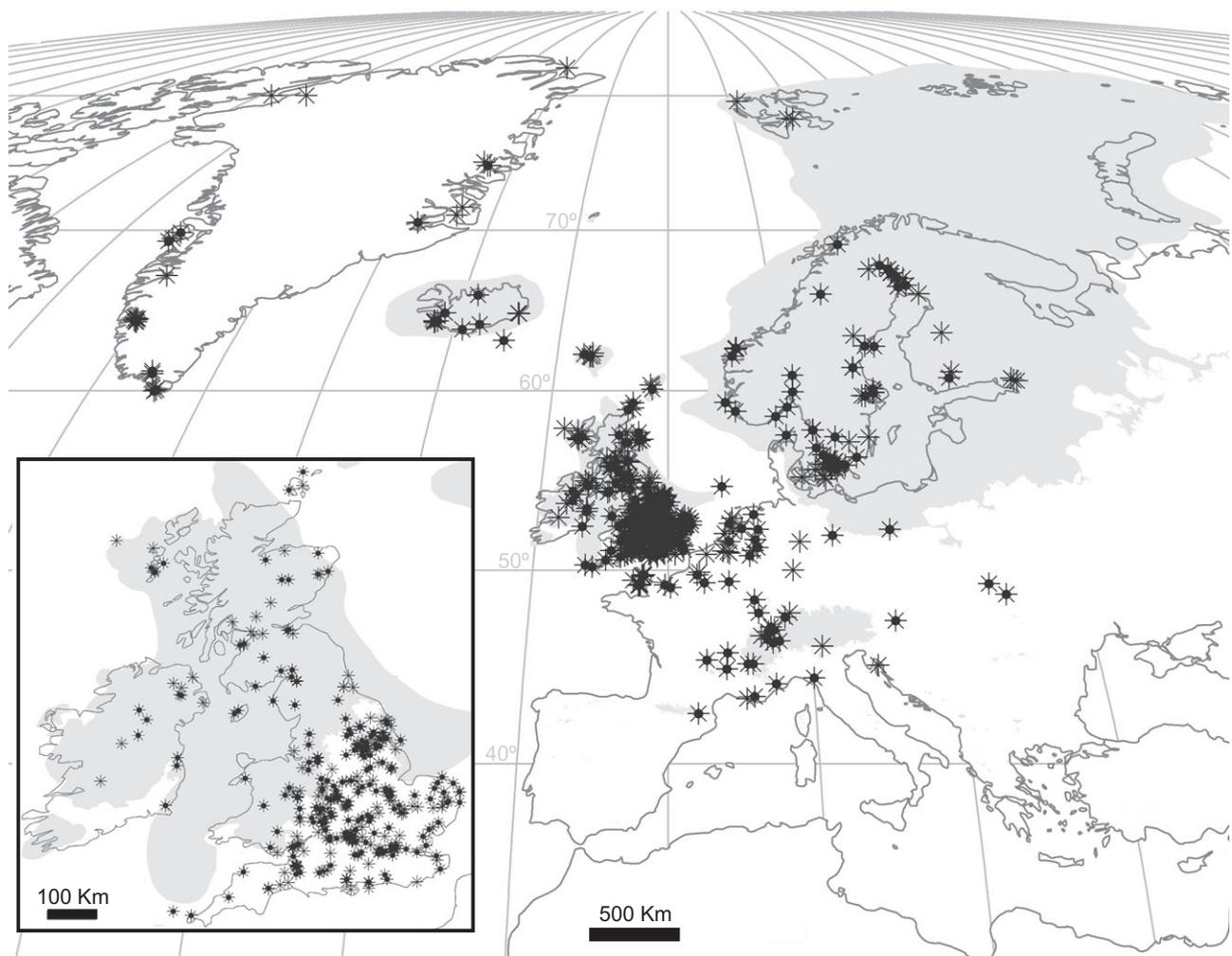
Of the 603 sites with beetle data, a total of 403 sites had records of unambiguously identified water beetles. We excluded some

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

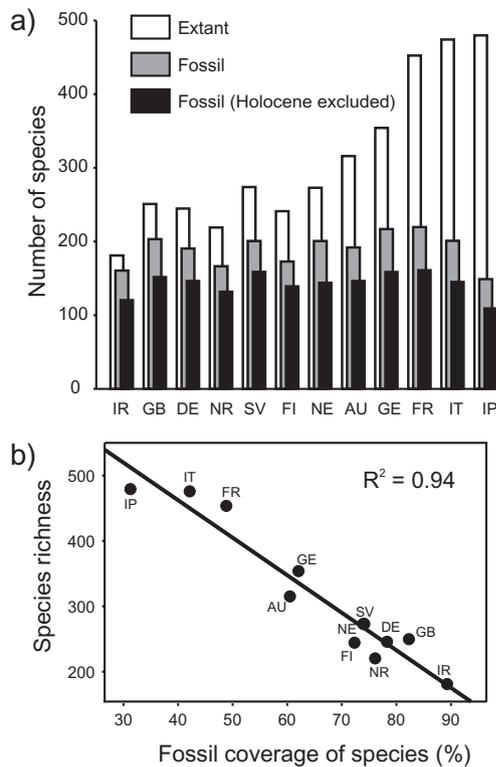
Variable	95% confidence interval (random sampling)	Water beetle data set
Average latitude	54.36–54.88	54.21
Average longitude	−0.17 to −0.03	−0.58
Maximum latitude	80.00–82.45	74.50
Minimum latitude	42.54–43.40	42.54
Maximum longitude	30.07–30.48	24.65
Minimum longitude	−68.00 to −53.83	−53.83

archaeological records from artificial settings and other exclusively anthropogenic samples (none of them with water beetles) which do not represent natural sites and typically have anthropophilic species only. Water beetle sites encompass most of the latitudinal and longitudinal ranges of the overall Coleoptera data set, although the randomization test showed 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 southern France and northern 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



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

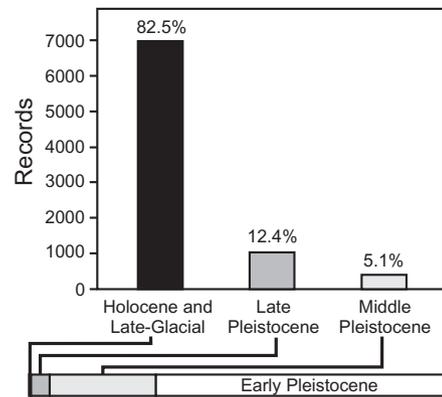


**Figure 2** Fossil versus present water beetle fauna for some European regions. (a) Number of present species (white bars), number of species recorded as fossils (irrespective of the locality; grey bars) and number of species recorded as fossils when Holocene records were removed from the database (black bars). (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.

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 a 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 (Parfitt *et al.*, 2005; Coope, 2006). However, 58.3% are from the Holocene, 36.6% from the Late Pleistocene and only 5.1% have been attributed to the Middle Pleistocene. Most Late Pleistocene fossils actually correspond 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/



**Figure 3** Distribution of the fossil record of water beetles along the Quaternary time-scale (represented by the horizontal bar below the x-axis). Numbers above bars are the percentage of the total data set.

Early Pleistocene deposits for some unambiguously identified species in sites from England (Lesne, 1926) and Greenland (e.g. Bennike & Böcher, 1990).

### Distributional changes

Of the 259 species studied, 50 (19.3%) have Quaternary remains found outside their current distributional range (Tables 1 & 3). All of them are species with current wide (mostly transcontinental) distributions in the Palearctic 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 shifts. When Holocene records were excluded, the database was reduced to 3769 records of 198 species. Of these, 45 experienced range shifts (i.e. only four had exclusively Holocene range shifts), so the percentage of species found outside their current distributional range increased from 19.3 to 22.7%.

Nineteen of the 50 species (38%) 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). Most of these species have been found in deposits from interglacial periods (especially the Holocene) or inter-stadial episodes of glacial cycles (Table 3).

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 Palearctic or Holarctic regions (Table 3, Fig. 4). All these fossil records correspond to deposits from glacial periods (mostly from the last glacial). For four species (1.5% of the fossils, 8% of the range shifts) records represent a western longitudinal extension of their current ranges, all them from the last glacial. For three other species, fossil records represent northern extensions

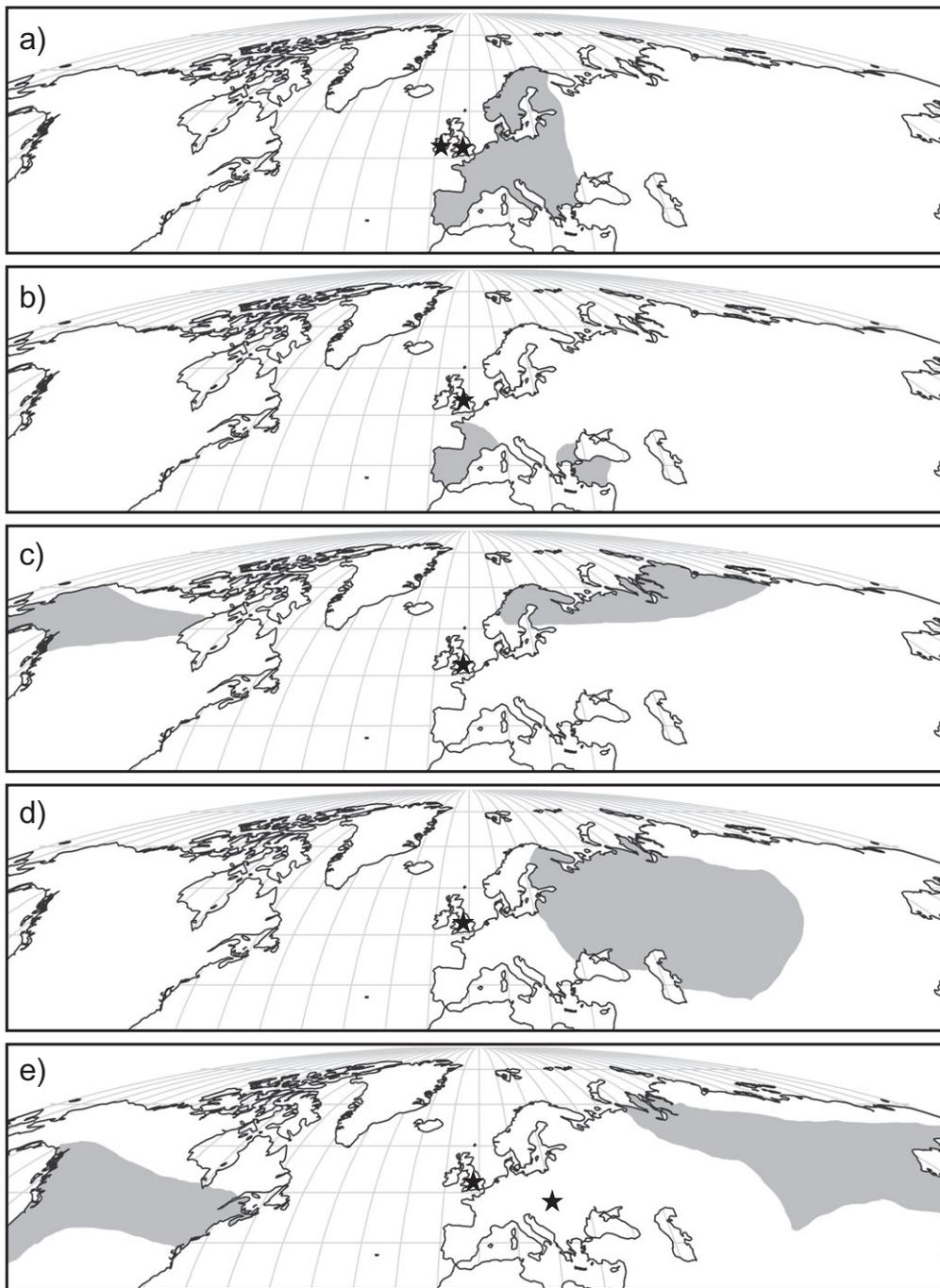
Table 3 Species found as fossils outside their current distribution.

Species	Distribution	Outsider fossils	Distributional change	Period type	HT
<b>Gyrinidae</b>					
<i>Gyrinus caspius</i> Méné.	Wide Palaearctic	GB	Island extinction	Interglacial (Holocene)	2
<i>Gyrinus colymbus</i> Er.	Wide Palaearctic	GB	Island extinction	Interglacial (Holocene)	2
<i>Gyrinus opacus</i> Sahl.	N Holarctic	DE, FR, PL	Southern extension	Last glacial	2
<i>Orectochilus villosus</i> (Müll.)	Wide Palaearctic	GB IR	Island extinction	Interglacial	0
<b>Dytiscidae</b>					
<i>Agabus arcticus</i> (Payk.)	N Holarctic	DE, FR, GE, PL	Southern extension	Glacial	2
<i>Agabus coxalis</i> Sharp	E Palaearctic, Caucasus	UK	Western extension/ Large range shift	Last glacial	2
<i>Agabus serricornis</i> (Payk.)	N Palaearctic	GB	Southern extension	Last glacial	2
<i>Bidessus grossepunctatus</i> Vorbringer	Wide Palaearctic	GB	Island extinction*	Interglacial (Holocene)	2
<i>Colymbetes dolabratus</i> (Payk.)	N Holarctic	DE, FR, GB, GE, GL	Southern extension	Last glacial	2
<i>Colymbetes paykulli</i> Er.	Wide Palaearctic	GB IR	Longitudinal (W) extension	Last glacial	2
<i>Colymbetes striatus</i> (L.)	Wide Palaearctic	GB	Island extinction†	Last glacial	2
<i>Ilybius angustior</i> Gyll.	Wide Palaearctic	GB	Longitudinal (W) extension	Last glacial	2
<i>Ilybius vittiger</i> (Gyll.)	N Holarctic	GB	Southern extension	Last glacial	2
<i>Hydroporus gyllenhalii</i> Schiöde	W Palaearctic	FA	Island extinction	Interglacial (Holocene)	2
<i>Hydroporus lapponum</i> (Gyll.)	N Holarctic	GB	Southern extension	Last glacial	2
<i>Hydroporus nigellus</i> LeC.	Wide Palaearctic	GB	Island extinction	Last glacial	2
<i>Hydroporus notabilis</i> LeC.	N Holarctic	IR, GB	Southern extension	Last glacial	1
<i>Hygrotus unguicularis</i> Crotch	E Palaearctic	GB	Large range shift	Last glacial	2
<i>Oreodytes alpinus</i> (Payk.)	N Palaearctic	DE, GB	Southern extension	Last glacial	2
<b>Helophoridae</b>					
<i>Helophorus glacialis</i> Villa	W Palaearctic	GB, IR	Island extinction	Last glacial	2
<i>Helophorus aspericollis</i> Angus	E Palaearctic	GB, UK	Large range shift	Last glacial	2
<i>Helophorus sibiricus</i> (Mots.)	N Holarctic	DE, FR, GB, IR, NL, SZ, UK	Southern extension	Glacial	2
<i>Helophorus aquaticus</i> (L.)	Wide Palaearctic	GB	Island extinction†	Glacial and interglacial	2
<i>Helophorus discrepans</i> Rey	W Palaearctic	GB	Island extinction†	Last glacial	2
<i>Helophorus oblongus</i> LeC.	N Holarctic	FR, GB, UK	Large range shift	Glacial	2
<i>Helophorus splendidus</i> Sahl.	E Palaearctic	GB, GE	Large range shift	Last glacial	2
<i>Helophorus lapponicus</i> Thoms.	Wide Palaearctic	GB	Southern extension	Last glacial	2
<i>Helophorus pallidus</i> Gebl.	N Palaearctic	GB	Southern extension	Last glacial	2
<i>Helophorus orientalis</i> Mots.	N Holarctic	GB, UK	Large range shift	Last glacial	2
<i>Helophorus mongoliensis</i> Angus	E Palaearctic	GB	Large range shift	Last glacial	2
<i>Helophorus praenanus</i> (Lom.)	E Palaearctic	GB, UK	Large range shift	Last glacial	2
<i>Helophorus browni</i> McCorkle	N Holarctic	UK	Large range shift	Last glacial	2
<i>Helophorus khnzoriani</i> Angus	E. Palaearctic	GL, SW	Large range shift	Glacial	2
<b>Hydrochidae</b>					
<i>Hydrochus flavipennis</i> Küster	W Palaearctic	GB	Northern extension	Last glacial	1
<b>Hydrophilidae</b>					
<i>Chaetarthria seminulum</i> (Hbst.)	Wide Palaearctic	IR	Island extinction	Interglacial (Holocene)	2
<i>Hydrobius arcticus</i> Kuw.	N Palaearctic	GB	Southern extension	Glacial	2
<i>Laccobius decorus</i> Gyll.	Wide Palaearctic	GB	Longitudinal (W) extension	Last glacial	2
<i>Coelostoma orbiculare</i> (E.)	Wide Palaearctic	FA, IR	Island extinction	Interglacial (Holocene)	2
<b>Hydraenidae</b>					
<i>Ochthebius figueroi</i> Garrido G.	SW Palaearctic	GB	Northern extension	Last glacial	1
<i>Ochthebius kaninensis</i> Popp.	N Palaearctic	GB	Southern extension	Last glacial	0
<i>Ochthebius foveolatus</i> Germ.	W Palaearctic	GB	Island extinction	Last glacial	0
<i>Ochthebius lenensis</i> Popp.	N Palaearctic	DE, GE	Southern extension	Last glacial	2
<i>Ochthebius pedicularius</i> Kuw.	W Palaearctic	GB	Longitudinal (W) extension	Last glacial	0
<i>Hydraena britteni</i> Joy	W Palaearctic	IC	Island extinction	Interglacial (Holocene)	1
<b>Elmidae</b>					
<i>Dupophilus brevis</i> Muls. & Rey	SW Palaearctic	GB	Northern extension	Interglacial	0
<i>Esolus parallelepipedus</i> (P. Müller)	Wide Palaearctic	GB	Island extinction	Glacial and interglacial	0
<i>Esolus pygmaeus</i> (P. Müller)	Wide Palaearctic	GB	Island extinction	Interglacial	0
<i>Limnius opacus</i> P. Müller	Wide Palaearctic	GB	Island extinction	Interglacial	0
<i>Stenelmis consobrina</i> Dufour	Wide Palaearctic	GB	Island extinction	Interglacial	0
<b>Dryopidae</b>					
<i>Dryops griseus</i> (Er.)	W Palaearctic	GB	Island extinction	Interglacial (Holocene)	1

\*Record by Foster &amp; Carr (2008).

†Doubtful island extinction (see Discussion).

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.



**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) (*Laccobius decoratus*); (e) large range shift (*Helophorus orientalis*). The grey area represents the current distributional range of the species and the black stars are the sites where they have been found as fossils outside their present ranges.

of species currently distributed in the south-west of the Palearctic region (Table 3). For one of these species (*Dupophilus brevis* Mulsant & Rey) the fossils correspond to interglacial deposits from the Middle Pleistocene, while for the other two (*Ochthebius figueroi* Garrido, Valladares & Régil and *Hydrochus flavipennis* Küster) fossils are from an interstadial episode within the last glacial period (Angus, 1993).

Finally, 10 species (3.8% of those with fossils, 20% of the species with range shifts) have fossil records far outside their current distribution, since at present they do not occur in western Europe (Table 3, Fig. 4; see also Appendix S4). They are all from deposits from the last (Weichselian, Devensian) glaciation. 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*) (Table 3, Appendix S4). In the case of *A. coxalis*, there is one subspecies of uncertain taxonomic status in the Caucasus (*A. coxalis schmidti* 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 (Appendix S5). Although they are currently found in the same regions where 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% lotic and 38% 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 4), even when only the central and northern species are considered (i.e. removing Iberian, Italian and other exclusively Mediterranean species;  $P < 0.0001$ ). Among the species with fossil remains there was no association between habitat and range shift ( $P = 0.16$ ; Table 4), 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 4). 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

**Table 4** Chi-square test on the contingency tables of the number of species of aquatic Coleoptera found as fossils for association between habitat type (lotic, lentic, both).

Contrast	$\chi^2$	d.f.	$P$
Current European species			
All species	80.4	2	0.000
Excluding Mediterranean species	27.2	2	0.000
Species found outside current range			
All	3.7	2	0.160
Excluding 'island extinctions'	4.6	2	0.100
Large range shifts	7.0	2	< 0.050
British species	3.8	2	0.150

d.f., degrees of freedom of the contrast.

(18.6%) but still not significantly different from a random sample of the British fauna ( $P = 0.15$ ; Table 4).

## 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, 1978; 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 for the Iberian, Italian, Balkan and Anatolian peninsulas and North Africa, the areas with the highest concentration of endemics (Greuter, 1991; Myers *et al.*, 2000; see Ribera *et al.*, 2003, for aquatic Coleoptera) and the least affected by the Quaternary glaciations. At the Last Glacial Maximum (23–18 kyr BP) the European ice sheet extended north of 52° N, with permafrost north of 47° N (Dawson, 1992), while the Mediterranean peninsulas had a more temperate climate and vegetation (e.g. Huntley, 1988; Hewitt, 2000).

#### Temporal bias

The temporal extent of the Quaternary aquatic beetle record is markedly biased towards the present. 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 coleopteran fossil record, and is probably related to the rarity of Early Pleistocene sites and the decreasing probability of preservation with increasing site age. There is an important palaeontological 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 chitinous fossil insect remains more than 1 Ma are extremely rare (Elias, 2007), largely being restricted to Arctic and sub-Arctic regions (Elias *et al.*, 2006; Elias, 2007), where the long-term preservation of chitinous exoskeletons is greatly facilitated by permanently frozen ground or permafrost. The 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 (especially for the first half) represents a serious limitation to drawing

general conclusions about the role of Quaternary climatic cycles on speciation events, since vast majority of available information covers only the last glacial cycle. Some molecular studies place the diversification events at the first half of the Quaternary (e.g. Carisio *et al.*, 2004; Ribera & Vogler, 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 commonly recovered from 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, 1994). 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, 1994). This ecological bias can also be related to 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 fossil water beetle data set concerning the role of climatic changes in altering the distributions of species during the late Quaternary. The fossil data compiled here show that for c. 80% of the species their fossil remains have been found within their current distributional ranges. This percentage was only slightly smaller (c. 77%) when the Holocene records were excluded from the database. However, this does not necessarily indicate 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, determination of absences is less reliable, 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 inter-glacial, 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 has been a continuous

presence of populations in the area or if there were successive local extinctions and recolonizations – 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 recolonization during the Holocene (see, e.g. Coope, 1978, for other examples in terrestrial Coleoptera).

In any case, the overall conclusion is that most late Quaternary fossil remains of aquatic beetles from central and northern Europe are of species currently present in the same area. This is particularly so for the Holocene remains, which represent the vast majority of the Quaternary fossil record and can be considered part of the current fauna, but also, although to a lesser extent, for the remains of the last glacial and interglacial, with as many as 25% of the recorded species having experienced a range shift. 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; Losos & Glor, 2003).

The percentage of the current north European fauna represented as Quaternary fossils is remarkably high, with values of c. 70–90% of the species for the most northerly countries and 30–50% for the most southerly ones (Fig. 2). These values decreased to, respectively, 50–70% and 20–40% when the Holocene records were excluded from the database (Fig. 2, Appendix S1). Despite the dominance of very recent fossil remains (mid to late Holocene), the fact that there are no known fossils of any of the species with current restricted distributions in the Mediterranean region can be taken as a strong evidence that these species were not present in central and northern Europe during at least the last glacial cycle (with the unavoidable caveat of the potential incompleteness of the fossil record). This may not be the case for other families of Coleoptera, such as Carabidae and Scarabaeidae, for which several species with restricted distributions within the Mediterranean have been recorded as fossils as far north as Britain during warm interglacial periods (e.g. Coope, 1990). However, the lack of a quantitative analysis does not allow us to assess how frequent these range movements were. In the case of the aquatic Coleoptera, the absence of Mediterranean restricted species of water beetles, together with the general stability of ranges shown above, outlines a scenario for the last glacial cycles 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 latitudinal or, to a lesser extent, longitudinal range shifts (rarely more than a few thousand kilometres) in response to climatic change. Nevertheless, given the strong western European bias of the data set, it is difficult to be certain of the extent of these latitudinal and longitudinal range shifts. 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; Zinoviev, 2006; Kuzmina *et al.*, 2008), and (although with still incomplete data) to the whole Pleistocene (Elias *et al.*, 2006). The existence

**Table 5** Number of species and geographical variables used for regression models and results obtained.

Region	Predictor variables			Con (Present) (km)	Con (late glacial) (km)	Predicted S (late glacial)	Predicted S (Present)
	Area (km <sup>2</sup> )	Total S	sLat (deg.)				
Corsica	8680	192	41.3	0	0	121.6	141.5
Ireland	81,638	181	51.5	0	170	194.1	96.9
Sardinia	24,090	237	39.0	0	0	144.2	200.1
Sicily	25,708	235	36.5	0	0	176.7	243.8
Mallorca	3640	141	39.3	0	0	145.4	141.7
Britain	230,977	253	50.0	0	430	274.3	129.5
Holland	41,526	272	51.3	330	330	237.3	188.0
Iberia	583,254	469	36.0	400	400	831.5	948.7
Norway	385,252	219	58.0	510	510	147.9	176.6
Sweden	449,964	273	55.0	510	510	188.5	226.9
Denmark	43,098	244	54.5	73	330	182.6	122.2
Germany	357,021	358	47.5	875	875	402.0	409.9
Italy	251,536	478	38.0	580	580	789.6	743.2
France	551,695	460	42.5	940	940	611.6	647.3
Finland	338,000	243	60.0	1140	1140	155.3	165.4
Iceland	103,000	11	64.5	0	0	17.5	38.2
Faroe Islands	1400	12	61.4	0	0	24.3	23.1

S, total number of species; sLat, southernmost latitude; Con, length of the connection with mainland ('connectivity').

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 glacial) 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). The relative role of climatic and geographical factors (e.g. isolation in peninsulas) in the increased speciation levels in the south is still an open question. Given the virtual lack of sites with fossil data in the Mediterranean region, this conclusion has still to be considered hypothetical, as only the discovery of fossils of the southern endemics in their current distributional areas, together with the absence of more northern, European species, will provide direct evidence to support this scenario.

A considerable proportion of the species that shifted ranges may have done so as the result of island extinctions. As noted above, the Holocene rise 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 in isolation (Rosenzweig, 1995), perhaps as the result of local extinction without the possibility of recolonization due to the opening of the English Channel (e.g. *Gyrinus colymbus* Erichson during the medieval Little Ice Age; Girling, 1984, and Table 3). Results of regression models were in agreement with this hypothesis. The total species number in the 17 regions considered was predicted with good accuracy based on the three geographical parameters (Table 5) for the two different scenarios, present ( $R^2 = 0.76$ ) and the late glacial period ( $R^2 = 0.87$ ). When Britain and Ireland were con-

sidered islands, their species number was consistently underestimated, but when they were peninsulas (situation at the late glacial) their species richness was overestimated (194 species in Ireland against the current 181, and 274 species in Britain against the current 253; Table 5). 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 late glacial as peninsulas towards the equilibrium as islands.

The possibility that some of the species considered to be potential 'island extinctions' could have become extinct for ecological reasons must also be considered. Potential examples are species restricted to more continental areas, such as *Helophorus aquaticus* (Linnaeus) or *Helophorus discrepans* Rey, or typical of snowfields, such as *Helophorus glacialis* Villa (R.B.A., 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 regional 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 (e.g. 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. Our results show a consistent pattern of these range movements in relation to climate fluctuations. The southern or western extensions in the range of species with current northern distributions were associated with cold (glacial) episodes. Correspondingly, the fossils of species found north of their current distributions in the south-west of the Palaearctic region were from warm episodes (inter-glacials or inter-stadials within the last glacial). For most of the species these range movements correspond to relatively limited expansions south or west of their current ranges, but 10 can be said to have undergone 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, in agreement with the pattern reported here (Coope, 1990, 2004).

At least in the case of the water beetle fauna, the 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 (although the percentage of fossils identified at the species level for this family, c. 40%, does not seem to be higher than for other well-represented groups such as Dytiscidae, Hydraenidae or Elmidae, with between 54 and 78% identifications to species level), 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 to climatic changes in a different manner from 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 it difficult to determine the effects of Quaternary climatic changes on their diversification and extinction. The only southern species of aquatic Coleoptera with a restricted range found as a Quaternary fossil was *Rhithrodytes crux*, in a site within its current range (Ponel *et al.*, 2001). *Ochthebius figueroi* (found in British Pleistocene deposits; Angus, 1993) was believed to be an Iberian endemic, but it has since been recorded from Morocco (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., *Ochthebius (Asiobates) cantabricus*

Balfour-Browne, known only from the types in a single locality in the north-west of Spain but recently recorded from north-east Turkey; 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 expected. However, for the latter group differences were not significant, probably due to the small 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 highlight the spatial and temporal limitations of a fossil record largely restricted to widespread species from central and northern Europe for the last glacial cycle.

Caution needs to be exercised when generalizing conclusions obtained from the fossil record to other areas or periods for which there are no fossil data, since extrapolating from what we know of widespread, northern taxa may be misleading. Although our results may go some way towards explaining the discrepancy between the fossil record and several recent molecular phylogenetic studies that suggest speciation in southern peninsulas during the Quaternary (e.g. Ribera & Vogler, 2004; Previšić *et al.*, 2009), only the study of fossil data in these areas would provide direct evidence with which hypotheses based on molecular data could be contrasted.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Species of aquatic Coleoptera for 12 regions of western Europe, indicating those recorded as fossils.

**Appendix S2** Available records for aquatic Coleoptera used in the analyses.

**Appendix S3** List of species of aquatic Coleoptera represented in the Quaternary fossil record and areas where they have been found.

**Appendix S4** Species which have suffered major range shifts. Extant distribution and fossil sites where they have been found are indicated.

**Appendix S5** Species recorded from deposits older than the Last Glacial Maximum (LGM) in sites that were covered by ice sheets during the LGM.

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## BIOSKETCH

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