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**Holocene extinctions of British beetles: patterns
of decline in geographical, habitat and bionomic
groups. Publication draft.**

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Summary

Most of the British Coleoptera (beetles) colonised during and following the warming at the end of the Devensian Glaciation (14,000-10,000 BP), since when the relatively stable Holocene climate has probably produced a low natural rate of extinction. In contrast, human impacts probably greatly increased the beetle extinction rate. We combined fossil records and current Red Data Book status assessments to provide estimates of relative past and future rates of extinctions for different bionomic, habitat, and regional groupings. Pine forest, deadwood, dung and terrestrial predatory groups declined significantly earlier than average, woodland species have an average pattern, and heathland, phytophagous and aquatic beetles show significantly more recent decline. Most RDB Coleoptera known as Holocene fossils in southern England survive there today, but with significant weighting towards the more threatened RDB categories. Many southern rarities may be remnants of a formerly widespread lowland beetle fauna now extinct elsewhere in Britain and soon be lost without appropriate conservation initiatives in the South.

Keywords: Coleoptera, extinctions, Britain, conservation

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INTRODUCTION

Insects have proved to be important in the study of environmental change in the past million years or so. Their exoskeletons preserve well in anoxic conditions in waterlogged deposits and have normally not undergone the chemical replacement ('mineralisation') usually associated with 'fossilisation' (Buckland & Coope, 1991). Since the exoskeleton presents most of the characters used to identify modern specimens, the identification of many of these fossil insects is fairly straightforward. Beetles (Coleoptera) are among the best preserved and most easily identified insects preserved as so-called 'sub-fossils', and in higher latitudes at least show a remarkable morphological constancy throughout the last few hundred thousand years; there is no evidence of any evolutionary change amongst Holarctic Coleoptera during this time (Buckland & Coope, *loc. cit.*). Beetles do not then appear to evolve in response to environmental change on the time scale considered in the present work (thousands of years), and so must either migrate or become extinct if environmental changes are sufficiently unfavourable.

To date, fossil beetle assemblages from over a hundred sites have been described from Britain, mainly dating to the last 15,000 years, representing up to 600 sample assemblages from each location, and including in total over 2000 species, more than half of the present British beetle fauna (Coope, 1994). These assemblages can be combined to reflect the Holocene British

beetle fauna, their representativeness being enhanced by the presence of 'background fauna' representing habitats beyond the immediate depositional area (Buckland and Coope, 1991, 11; Kenward, 1975a; 1976a). In this study we compare patterns in the distributions, habitat, and bionomics of the species that are last recorded from Holocene fossils with corresponding patterns in extinctions and decline amongst the rarer British beetles over the past two centuries (IUCN Red Data Book 'RDB' status 1, 2, 3 and Appendix 1; Shirt, 1987). We estimate which regions, habitats and bionomic groups have experienced, or will experience, a comparatively early or comparatively late decline (primarily as a result of human activity) during this period, and consider the implications regarding conservation priorities for Coleoptera.

CAUSES OF BEETLE EXTINCTIONS DURING THE QUATERNARY

The natural background extinction rate

Fossil records indicate that species have a natural lifespan, which may be of the order of 10 million years for invertebrates (May *et al.*, 1995, citing Raup, 1978). As there are now between 3729 and 4000 beetle species in Britain (Kloet & Hincks, 1977; Hyman & Parsons, 1992), a tentative estimate would suggest that only four beetle British species might have become globally extinct during the Holocene. Such extinctions should have been stochastic, and the probability of

species becoming globally extinct be similar for faunal groups of all habitat, distribution and bionomic types.

Species on an island may become locally extinct at a rate determined by its size and distance from a continental landmass (MacArthur & Wilson, 1967). The British land area became separated from the greater Eurasian landmass about 7000 years ago (Funnel, 1995), so a background extinction rate applicable to islands will have affected the British beetle fauna since that time. This extinction rate is predicted to be low according to island biogeography theory, as Britain is a large island with diverse habitats situated very close to continental Europe. For different habitats, geographical areas and bionomies, the overall proportion of species becoming extinct should be the same, even though the numbers of species in each differ. The decline of the whole population from an island should, then, be proportionately matched by the decline in any of its subpopulations.

The Pleistocene Glaciations

The repeated climatic oscillations during the Pleistocene have cloaked Britain in ice or tundra and, for relatively short periods, have permitted the development of temperate forest. With each major climatic fluctuation there has been an associated gradual or sudden local extinction of part of the existing beetle fauna, and colonisation by other species better adapted to the new climatic conditions. Up to 40% of the Coleoptera known to have been present at the end of the last glacial are no longer found in Britain (Buckland & Coope, 1991).

The Ice Ages do not appear to have caused any global extinctions of Coleoptera known to have formerly existed in Britain (Buckland

and Coope, 1991); 'very much less than 1% of the total number [over 2000] of species known from the fossil record [in Britain] may be [globally] extinct' (Coope, 1995). Many species have become extinct from Britain as a result of climatic changes, but they are still to be found elsewhere, albeit in some cases as far away as the Tibetan Plateau, Siberia or Alaska (Coope, 1995). The fierce process of natural selection caused by the global climatic fluctuations of the last two and a half million years has left Britain with a depauperate beetle fauna (less than 4000 species, compared with over 8000 in North Western and Central mainland Europe, Freude *et al.*, 1965). The British beetle fauna consists mainly of mobile species readily able to track climatic changes and colonise the new habitats that developed following the retreat of the glaciers and tundra, although a surprising number of species of low mobility (e.g. flightless weevils) have arrived too.

Given that much of the present British native beetle fauna is adapted to respond to major climatic fluctuations, we consider it unlikely that minor climatic variations during the last 10,000 years will have caused *large-scale* extinctions in the beetle fauna (Buckland & Dinnin, 1993), although the effects of climatic change on beetles may have been amplified by a concurrent human impact.

Extinctions caused by human activity

The modification of the British landscape by humans since the onset of Neolithic agriculture about 6000 years ago (Thomas & Morris, 1995) has been beneficial to some beetle species whilst leading to the decline or extinction of others (Buckland & Coope, 1991; Buckland & Dinnin, 1993; Kenward & Allison, 1994b). The rate of extinctions can be expected to have increased with the rise of the

human population of Great Britain (one estimate of past populations is given by Fowler, 1978), and the habitat destruction consequent upon increasing requirements for resources including living space. Human impact is expected to be the most substantial single cause of extinctions of Coleoptera since early in the present (Flandrian) interglacial.

Expected rates of background, climatic and anthropic beetle extinctions are presented in schematic form in Fig. 1. After the extinctions of the tundra fauna at the end of the Loch Lomond stadial, the rate of background and climatic extinctions will have been more or less constant, compared with the roughly exponential rise in extinctions which might be expected to have been caused by human activity.

CHANGES IN THE RATES OF BEETLE EXTINCTIONS AND DECLINE

To allow us to estimate comparative changes in the rates of beetle extinctions and decline, we adopt the following working assumptions regarding the beetle fauna of Great Britain over the last 10,000 years :

1. Background extinctions will have affected all areas, habitats and bionomic or ecological niche groups equally, and their rate will have been so low that any differentials between groups are insignificant.
2. Although there is evidence for oscillations during the Holocene (Meese *et al.*, 1994, O'Brien *et al.*, 1995), some of them significant to human well-being (Lamb, 1982), it has been a period of unusual climatic stability (Dowdeswell & White, 1995). The small fluctuations will, in general, have affected equally the beetle fauna of all

habitats and bionomic groups in Britain. However, regional distributions of species near their southern or northern limits may have been affected and it is possible that some climatic changes, e.g. in annual patterns of temperature, or in rainfall, had effects which are as yet poorly appreciated.

3. The ecological niche and, in general, the habitats occupied by a species in Britain now are the same as those occupied by the same species at any time during the last 10,000 years. There is ample evidence from Quaternary fossil assemblages that this is indeed so in natural habitats (Buckland & Coope, 1991), with which we are primarily concerned here, but there is equally strong evidence for shifts in habitat amongst certain Coleoptera exploiting human occupation sites (Kenward and Allison, 1994b).

4. Species from any habitat, area or ecological niche are, with certain exceptions (notably water beetles, extreme xerophiles and chalkland species), equally likely to be preserved as fossils, and also to be recovered and identified.

5. All species are equally likely to be recorded by modern collectors and to be found in archaeological deposits. In practice certain cryptic species are rarely encountered by coleopterists today (and therefore rarely recorded), but may be disproportionately more frequently identified in the fossil record, for example some subterranean and burrowing species (Hall and Kenward, 1990, Kenward, 1975b; 1976b; Kenward and Hall, 1995; Kenward and Allison, 1994b). Cryptic taxa account for only a tiny fraction of the overall number of Red Data Book and extinct species, so errors arising from this assumption are likely to be small.

6. The proportion of species undergoing decline in different area, habitat and

bionomic faunal groups will not be the same, since each will contain different proportions of eurytopic and stenotopic species. However, under similar extinction pressure, the ratio of extinct to RDB 'threatened' (etc.) species should be similar in different communities.

7. Human activity (which is selective) will not affect all faunal groups equally, and consequently species in certain localities, habitats or ecological niches may undergo changes in their rate of decline which differ from that of the whole fauna.

8. For analytical purposes the RDB categories can crudely be equated with successive future, though unquantifiable, time periods, (cf. Mace, 1995; Thomas & Morris, 1995). Extinctions are usually preceded by a period of decline. Species can therefore be thought to 'climb the ladder' of the IUCN status classification system for rare species (May *et al.*, 1995). Species that are classified as being 'endangered' are at the terminal stage of their decline (prior to extinction), whilst species that are classified as 'vulnerable' or 'rare' are usually at a less advanced stage in their population decline, but might be expected to proceed to the terminal stage (and ultimately to extinction) if conditions are not alleviated. Many of the species which are now classified as Red Data Book species were formerly more common and/or widespread (e.g. Hyman & Parsons, 1992; 1994). The current list of Red Data Book species therefore can be seen as a list of the species judged most likely to become extinct in the near future. Species now extinct would have been included in Red Data Books if they could have been drawn up in the distant past. The native British beetle fauna is not reflected by the present fauna, since the latter now includes many introduced synanthropic and eurytopic species that are not adversely (and in some

cases are beneficially) affected by human activity. Consequently, the fossil 'sample' of species that have become extinct during the Holocene will have occupied areas, ecological niches and habitats that will more closely match the distribution, ecological niche and habitats occupied by the existing IUCN Red Data Book status 1, 2, 3 and Appendix (extinct) species than the entire contemporary beetle fauna of Great Britain.

Making these assumptions, beetles assigned to any area, habitat or bionomic group considered here should in broad terms have experienced the same pattern of natural decline as any other, and should be equally likely to have been recorded from ancient deposits. The proportions of fossil extinct ('old extinct'), post-Linnean extinct ('recent extinct'), RDB Endangered, RDB Vulnerable and RDB Rare species should therefore be similar within each group and should match the observed ratio for all groups (Fig. 2, solid bars). Any significant deviations from this null hypothesis are likely to result from some selective process, presumably the effect of human activity or of climatic fluctuations. Some area, habitat or bionomic faunal groups may have a faster than average rate of progression to higher 'rungs' of the RDB 'ladder' brought about by human activity, and thus be more threatened, whilst other such faunal groups may be less affected.

METHODS

Distribution, habitat and ecological niche categories for Coleoptera were simplified using a number of faunal groupings for each, these being chosen to represent the range of community types within that category (Table 1). A limit of 20 groups was imposed per category to minimise the occurrence of low expected values in chi-squared analysis.

The Watsonian vice-county distributions, habitats and bionomics of the RDB 'recent extinct', 'endangered', 'vulnerable' and 'rare' beetles of mainland Britain have been abstracted from Hyman and Parsons (1992; 1994). Corresponding data for water beetles (which are not considered by Hyman and Parsons) were obtained from Balfour-Browne (1940-58), Collinson *et al.* (1993), Foster (1981-93), Foster & Spirit (1986), Friday (1988) and Owen *et al.* (1992).

Records of species appearing as fossils from a large number of sites in Great Britain (e.g. Table 3) were obtained from the BUGS database of the Department of Archaeology and Prehistory, University of Sheffield, together with additional data from more recently published work. Habitat and ecological notes on the 'old extinct' species were compiled from Freude *et al.* (1965-1983), Hansen (1927-1966), Lindroth (1985; 1986) and Palm (1959). These sources provide information about the current habitats and ecologies of these species where they still occur in Europe, although it should be noted that a few extant British species occupy a different range of habitats in mainland Europe (cf. Hyman & Parsons, 1992; 1994). Estimates of the former range (from the end of the last glacial to extinction, or to about 1800, as appropriate) of each species can only be produced using the very limited information from the archaeological records, and therefore might show an appreciable bias introduced by the distribution of sites investigated (Table 3). Consequently we did not use these estimates in the analysis of the data.

A contingency table was constructed containing, for each distribution, habitat and bionomic faunal group, the observed frequencies of each of the mutually exclusive status categories (old extinct, recent extinct, endangered, vulnerable and rare), together

with the corresponding frequencies for all other groups combined. These frequencies were examined using the χ^2 contingency test (Everitt, 1977). Significant values of χ^2 indicate that the distribution of species frequencies between the five status categories for a particular faunal group is different from those for all other the groups in that category, i.e. that the species decline *pattern* for that group differs from the overall species decline pattern for all other groups.

RESULTS: FAUNAL GROUPS WITH SIGNIFICANTLY DIFFERENT PATTERNS OF DECLINE

Significant ($P < 0.05$) deviations from the null hypothesis that the pattern of species decline and extinction is even for all beetle faunal groups were found for fourteen groups (Table 2). The deviations from the averaged patterns varied in character, some groups showing a generally earlier decline, and others a more recent, or predicted future, reduction. A significant weighting towards a greater proportion of old extinct species is demonstrated by the 'deadwood' (Fig. 3, solid bars) and the 'pine forest' groups (Fig. 5, solid bars), compared to the pattern for all remaining habitats/niches which contain RDB and extinct species, i.e. the 'non-deadwood' and 'non-pinewood' groups respectively (Figs. 3 & 5, open bars). 'Predatory' and 'aquatic' species show the reverse pattern with a significantly greater proportion of species in the lower RDB threat categories (Figs. 4 & 6) suggesting a relatively higher future rate of beetle extinctions compared to earlier rates. 'Woodland' species, however, demonstrate a pattern of decline that closely matches that for all habitat groups combined (Fig. 8).

The pattern of decline for the beetles present in southern England since 1800 suggests a relatively earlier decline in this part of Britain compared to the pattern of decline for the rest of the island (Fig. 7), although care must be taken with the interpretation of this result as species extinct prior to 1800 are not been included in this analysis.

DISCUSSION

This study is essentially a preliminary exploration of a technique, and it is undesirable to attempt to place too much significance on the results at this stage. The fossil record is poorly explored and not all the available data could be included here. Many species are difficult to identify as fossils, and little effort has been made to identify the rarer 'natural habitats' species in most urban archaeological assemblages since they are of little relevance to the reconstruction of human activity and living conditions. Certain kinds of habitats may in the past have been inherently unlikely to occur near places where preservation of beetle fossils was possible, and some of these habitats may have housed species differentially affected by human activity. There are clear limitations to the RDB data, particularly resulting from the essentially subjective and somewhat inconsistent criteria used in status classification, the difficulty of distinguishing rarity from threat, and from the under-representation in the catalogue of cryptic species. These things said, our approach appears promising.

A certain proportion of species in any faunal group will be undergoing decline and consequently be susceptible to extinction. Our study concentrates on those species. We are examining variations in the proportions of species in each faunal group which have become extinct, or which have started on the

ladder towards extinction (i.e. have become RDB species). A weighting towards extinct species (particularly old extinct) implies an earlier (faster) decline in the susceptible species of that group, when compared with the overall progression of decline for all groups.

The loss of a component of the Holocene beetle fauna as a result of forest clearance, agriculture and the excessive removal of deadwood has already been noted by previous authors (e.g. Buckland, 1979; Buckland & Coope, 1991; Girling, 1982; Osborne, 1965), and intuitively appears likely. Woodland cover in lowland Britain is estimated to have been reduced from a peak of 95% during the Atlantic period (7-5000 years ago) to 10% by AD 1350 and 5% at present, none of it having escaped some degree of modification (Buckland and Dinnin, 1993; Rackham, 1988; Roberts, 1989). However, the results of our study suggest that the woodland beetle community as a whole, *as opposed to that specifically of deadwood*, has not undergone a significantly faster decline during the Holocene than all other habitat groups combined (Fig. 8). The large number of RDB beetles recorded for broadleaf woodland (Thomas & Morris, 1995) reflects its long-term stability in Britain under the present climatic conditions, with the consequence that woodland species constitute a substantial part of the native Coleoptera fauna (c.f. Warren & Key, 1991, 155-6). Our results suggest that there has throughout the later Holocene been sufficient woodland in Britain to prevent an earlier than average decline of its beetle fauna. Modern initiatives to increase the area of broadleaf woodland may have come just in time to prevent excessive damage to the associated beetle fauna. Renewal of a full range of deadwood habitats must accompany this trend, however.

Species in the pine forest group have fared less well, with a significantly earlier than average decline (Warren & Key, 1991). Native pine forest is now restricted to less than a tiny fraction of its former area in Scotland (Birks, 1996; O'Sullivan, 1977; RSPB, 1993), and is vestigial or no longer present in England and Wales, yet briefly covered much of the British Isles in the early Holocene (Roberts, 1989). An anomalously high proportion of 'old extinct' species in this habitat (see Fig. 5) became extinct from lowland Britain before 1800; and many of these are last recorded from Bronze Age deposits in northern England (e.g. Buckland & Dinnin, 1993; Whitehouse *et al.*, in press), at a time when an increased use of fire and the axe would have led to the rapid loss of the highly combustible non-coppicing pine trees. There were also climatic changes at this time which may have exacerbated the decline of the lowland pine forests (Buckland & Kenward, 1973; Greig, 1996).

Deadwood (in pine forest and deciduous woodland) has been widely noted for its importance both for the conservation of Coleoptera currently listed in the IUCN Red Data Book (e.g. Thomas and Morris, 1995; Speight, 1989; Harding & Rose, 1986) and as a habitat from which many species have already become extinct (e.g. Buckland & Dinnin, 1993; Girling, 1982; Thomas & Morris *loc. cit.*). Our study indicates that deadwood species have indeed declined earlier than average, doubtless as a result of the pressure for firewood even where there was limited woodland clearance. This has not significantly affected the decline of woodland beetles as a whole, even though deadwood species contribute 49% of extinct and RDB beetles in the woodland group. The reason for this is the wide range of other habitats occupied by the RDB and extinct woodland taxa (phytophages 19%; predators 17%; bark dwellers 12%; fungivores 7%;

myrmecophiles 5%; others 4%). Whilst woodland species adapted to the deadwood niche declined much earlier than average, these are balanced by the woodland phytophages and fungivores, which have declined more recently than average.

The significantly later decline of the water beetles (coupled with a low proportion of extinctions compared to the number of RDB species in this group) is of interest, for they are predictably likely to be preferentially preserved in ancient deposits. The proportionately late decline thus seems likely to be real; the major period of threat for water beetles may lay in the future, to judge from the large proportion of 'rare' species (Fig. 6). The more recent decline of water beetles can be ascribed to the widespread post-Industrial Revolution drainage, infilling and pollution of ponds and wetlands, a trend still all too evident and threatening a wide range of organisms (e.g. Dinnin, 1991).

A relatively early decline of heathland beetles may reflect the secondary nature of this habitat, which is in most places artificially maintained by human activity (i.e. fire) in areas that would otherwise revert to other vegetation types, usually woodland or pine forest. Although a discrete native heathland beetle fauna is unlikely to pre-date the advent of human activity (only 5 species of the 480 included in this study are limited to heathlands), the habitat has declined with the virtual disappearance of burnt woodland (Buckland and Dinnin, 1993), and with the recent conversion of heathland to arable agriculture.

The faster decline in the dung, compost and carrion groups is the result of extinctions during the 19th and 20th centuries rather than during the preceding millennia. One possible cause for the decline may be the reduction in the use of horses for transport,

available animal dung being restricted to progressively more isolated fields. Another major cause of more recent changes may be the contamination of dung by prophylactic medication (Ivermectin) given to livestock (R. Buckland and M. Robinson, pers. comm.). There is strong evidence that the 'little ice age' pushed some thermophiles south (e.g. Buckland, 1975; Hall *et al.*, 1983, 219; Kenward *et al.*, 1986, 265; Kenward & Hall, 1995, 781), so perhaps some other species were completely eliminated, at least temporarily.

Phytophagous species demonstrate a slower than average decline, perhaps reflecting their ability typically to utilise a range of foodplants. The significantly slow rate of decline amongst the predatory species as a whole reflects the large proportion of these species which are aquatic (see discussion of water beetles, above). In fact the *terrestrial* predatory species demonstrate a significant deviation from the average change in the rate of species decline as a result of the much larger proportion of species which are currently listed as RDB 'endangered'. The reason for this is not known, but terrestrial predatory beetles might prove to be a barometer for the general 'health' of the communities to which they belong; they will also doubtless have been particularly susceptible to the effects of pesticides concentrated up food chains, perhaps one cause of their recent decline.

Although the results of the statistical analysis suggest a slower decline in the Midlands, Northern England, Scotland and Wales, the 'old extinct' category has not been included in the χ^2 contingency analysis, as the prehistoric distribution of these species is not fully known (as opposed to the habitat and bionomic groups, which are assumed to have remained broadly constant throughout the Holocene). Comparing the ratio of RDB and

extinct species that have been recorded in Holocene and Late Weichselian archaeological deposits (Fig. 11) to the overall modern (post 1800) occurrence of RDB species from each region (Fig. 9) suggests that many more species would have formerly occurred in the Midlands and Northern England. This is further reflected by changes in the distribution of beetle species, as approximately half of all the RDB species found as Holocene fossils from the Midlands and Northern England no longer occur there (Fig. 11). Few species have, however, become extinct from these regions since post-Linnaean times (Fig. 10) and it is possible that these regions have had a slower than average rate of decline during the last two and a half centuries because they had already lost a large proportion of their scarcer species. Many of these species may have had the northern or southern climatic limit of their range somewhere in Great Britain, and such species are thought to be especially vulnerable to human activity (Buckland & Dinnin, 1993). Human activity perhaps had a greater early impact on the Coleoptera in Northern England and the Midlands than in the rest of Britain, since these areas contained particularly large numbers of species at the climatic limit of their range.

The paucity of fossil records from Scotland and Wales (with four and three sites respectively yielding RDB and extinct species, compared with 28, 20 and 19 sites from Southern England, the Midlands and Northern England respectively, see Table 3) makes it impossible to produce a meaningful analysis of the Holocene extinction rate in these areas. The patterns for Wales may, on the available evidence, be similar to those of the Midlands and Northern England, where the majority of the RDB species found as Holocene fossils are no longer present, with few extinctions since 1800, and there is

currently a slower than average decline. The opposite is suggested for Scotland, where most of the RDB species recorded as fossils are still found, reinforcing the slower than average rate of decline since 1800. Scotland contains the most sub-arctic climate of Great Britain (because it is northerly and predominantly mountainous) and most of it is unlikely ever to have been colonised by thermophilous beetles which arrived in England and Wales during the Holocene. The SW Scottish 'refugium' area may have lost species through climatic change, but there is currently little useful evidence. A record of *Melasis buprestoides* (Linnaeus) from deposits of early medieval date at Buiston, Ayrshire (Kenward *et al.*, 1994), north of its present range (Hyman and Parsons, 1992, 334), suggests that further investigations in southern Scotland may prove fruitful.

Only a small proportion of the 'scarce' species recorded as fossils from southern England have not been recorded there since 1800 (Fig. 11). This suggests that the proportion of beetle species becoming extinct from Southern England prior to 1800 was lower than in the Midlands and Northern England, yet the more recent (post 1800) decline is significantly faster than elsewhere in Britain (Table 2). In addition, Southern England contains far more RDB status Coleoptera than the other regions of Britain (Fig. 9), and has experienced far more recent extinctions (Fig. 10). The results suggest that southern England is currently suffering a burst of beetle extinctions which may have taken place earlier in the Midlands, Northern England and perhaps also Wales. Coleoptera conservation in Britain is now in a critical period since this retreat back to mainland Europe has almost completed its passage through the British Isles, and has now reached the last strongholds of the native Beetle fauna in areas such as, for woodland

forms, the New Forest (Hampshire), Windsor Great Park (Berkshire) and Blean Forest (Kent), and for some ground-living and phytophagous thermophiles, the south-facing slopes of the south coast. The species at risk are not simply tenuously established marginal thermophiles; they are the remnant of a formerly well-established and widespread lowland fauna. Conservation of whole faunas is unlikely to be adequately served by 'island' nature reserves of restricted extent, and the existing National Parks in Britain principally protect uplands. Perhaps it is time to accept the necessity to designate large areas of southern England as National Park, and to adopt, within them and elsewhere, management strategies suited to these thermophilous species.

This large-scale threat to southern beetles should not detract from our response to the threat to wetland, pine forest and deadwood species throughout Britain; our results support the contention that these groups are relatively highly at risk, as is generally recognised in the literature (e.g. Buckland and Dinnin, 1993; Harding and Rose, 1986).

The list of sites from which archaeological beetle assemblages containing RDB and extinct species have been recovered (Table 3), although incomplete (much work remains unpublished), reasonably represents the uneven distribution of palaeontological work carried out in Britain. Rather few sites in Scotland and Wales have been examined for insect remains, compared with published records from over seventy in the various parts of England. In addition, most of the post Iron-Age fossil records are from urban occupation sites; rural and natural material from the past 2000 years remains virtually unstudied. Certain areas which are currently important for RDB listed species (such as the cliff habitats of the south coast of England) have yet to be investigated for fossil

communities, and are inherently unlikely to provide such evidence. More fossil beetle assemblages are required from Scotland and Wales, and from a range of natural sites of a wider range of dates in England, before a more representative picture of Holocene changes in the distribution of the British Coleoptera can be generated. Sites are undoubtedly numerous, but funds to locate them and to investigate the entomological treasures contained in them are very limited. Both occupation sites and natural deposits should be investigated extensively in order to trace the interaction of climatic change, which is becoming increasingly well documented using a variety of evidence, and human environmental impact, and to provide data for projections of future relative rates of extinctions.

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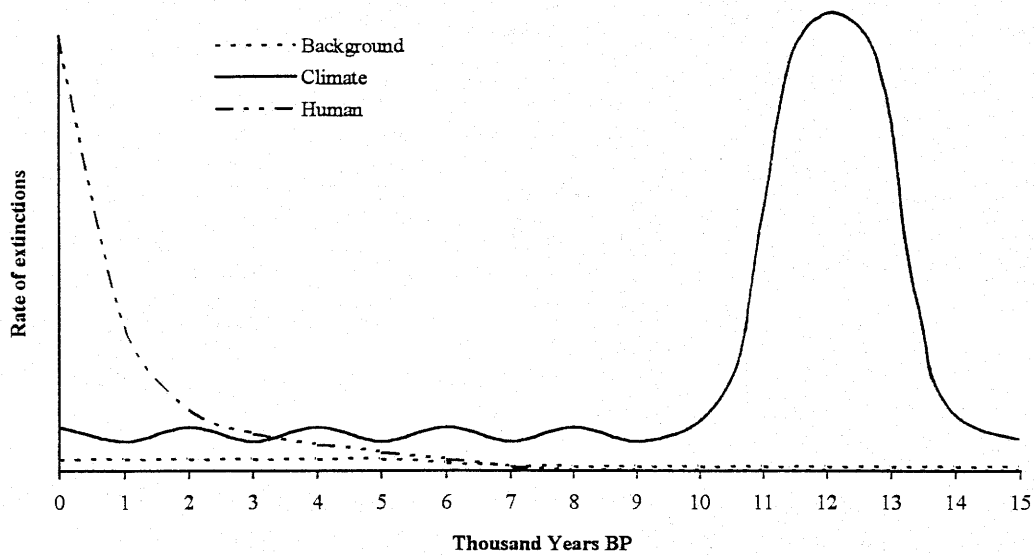


Figure 1. Hypothetical beetle extinction rate in Britain during the Late Devensian and Holocene.

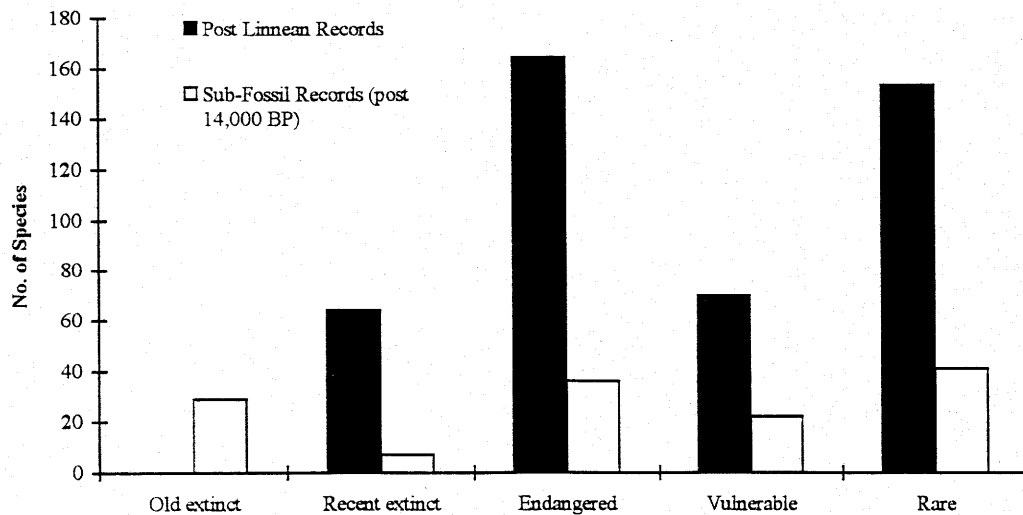
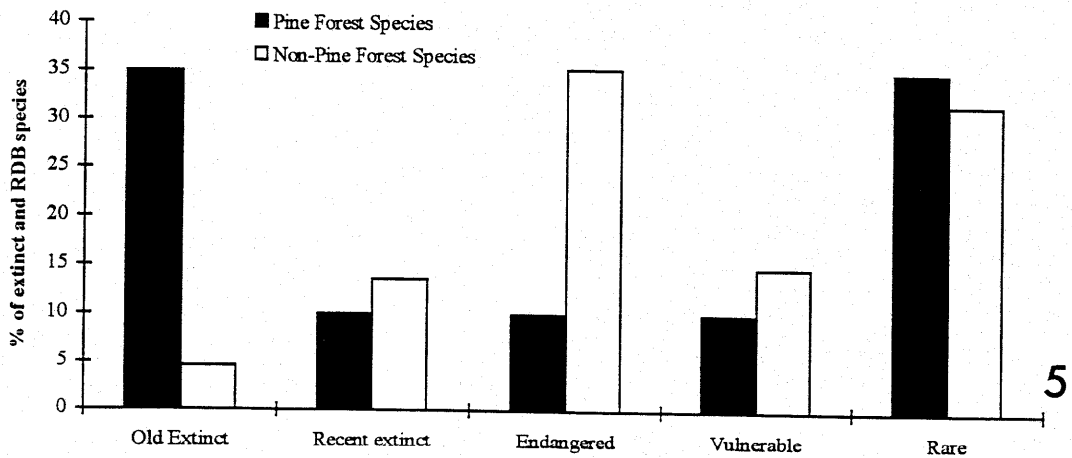
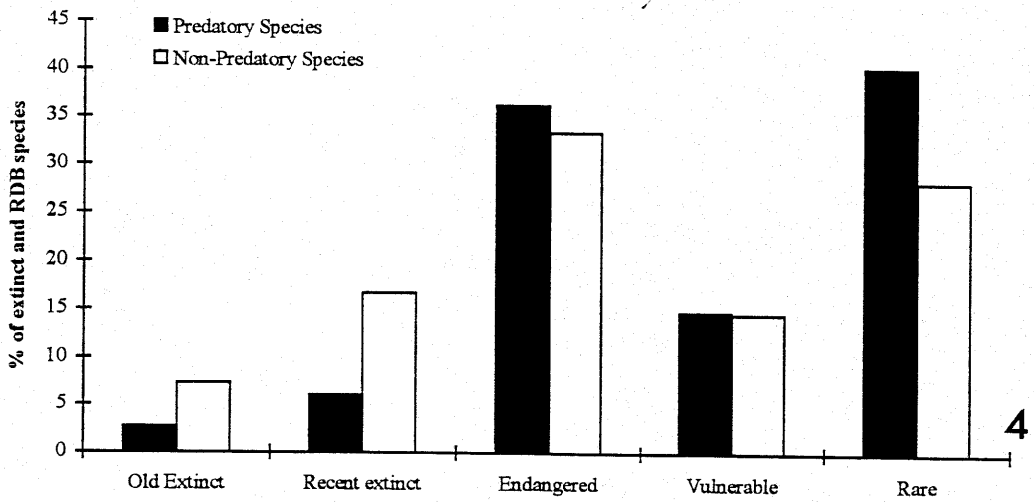
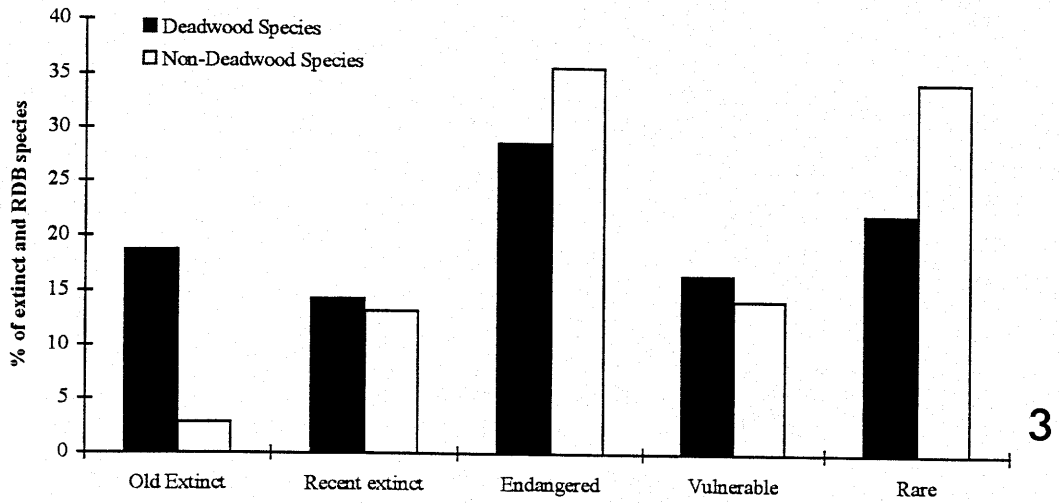
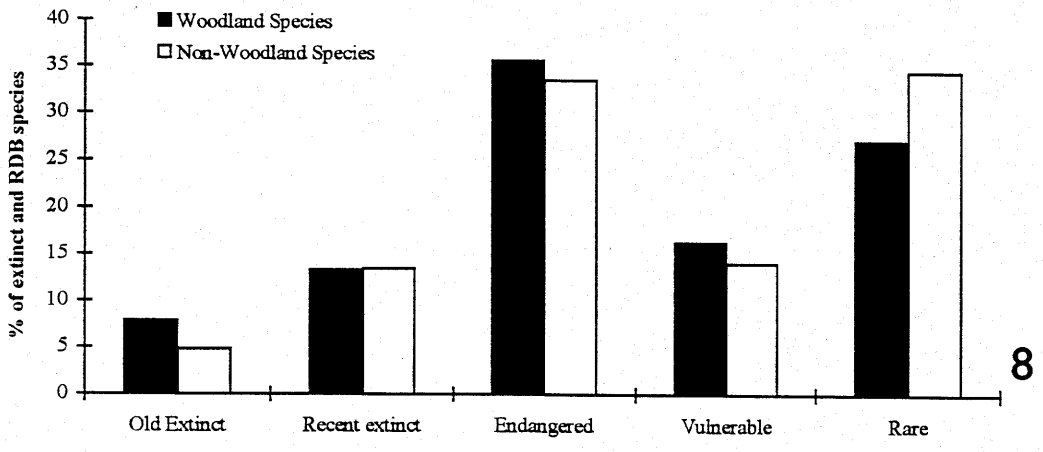
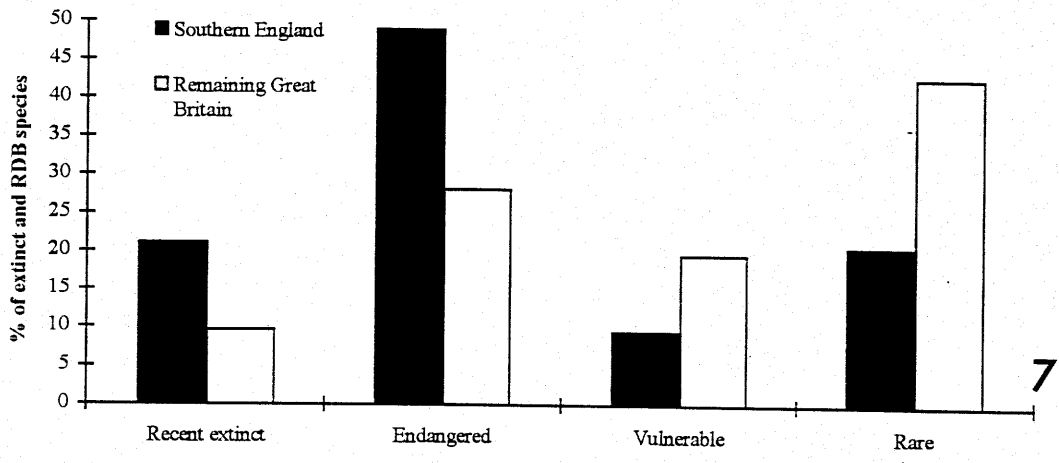
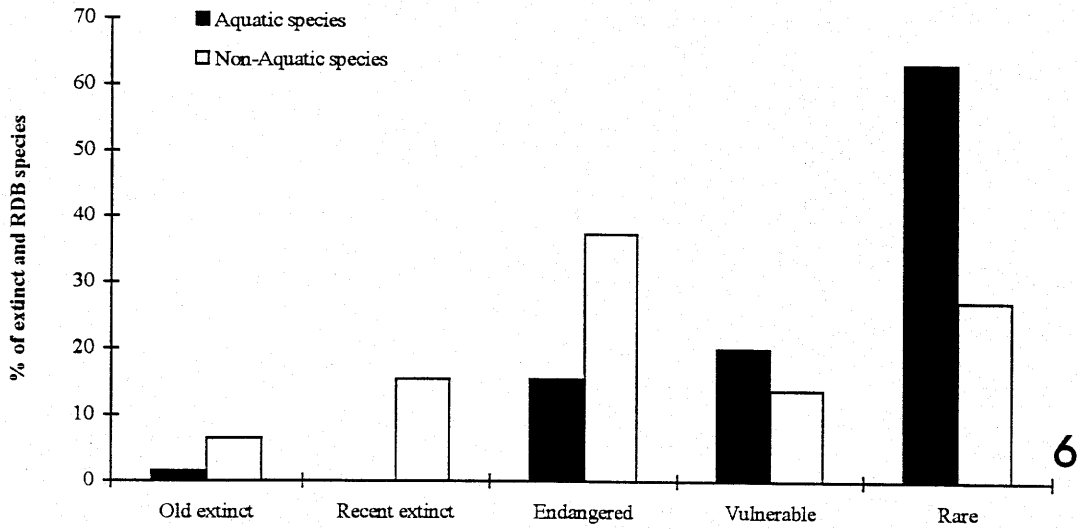


Figure 2. Numbers of 'old extinct' and RDB Coleoptera species recorded from postglacial fossil assemblages and post-Linnean data. Species last known from Late Glacial deposits have been excluded.



(see next page)



Figures 3-8. Comparisons between the pattern of decline of various geographical, habitat and bionomic groups of Coleoptera in Great Britain and those for all other groups combined: (Figure 3) dead wood (n=91) and non-deadwood (n = 388); (Figure 4) predatory (n = 149) and non-predatory (n = 330); (Figure 5) pine forest (n = 20) and non-pine forest (n = 459); (Figure 6) aquatic (n = 65) and non-aquatic (n = 414); (Figure 7) species limited to southern England (n = 180) and species not limited to, or occurring outside, southern England (n = 271); (Figure 8) woodland (n = 165) and non-woodland (n = 314). For explanation of categories see text.

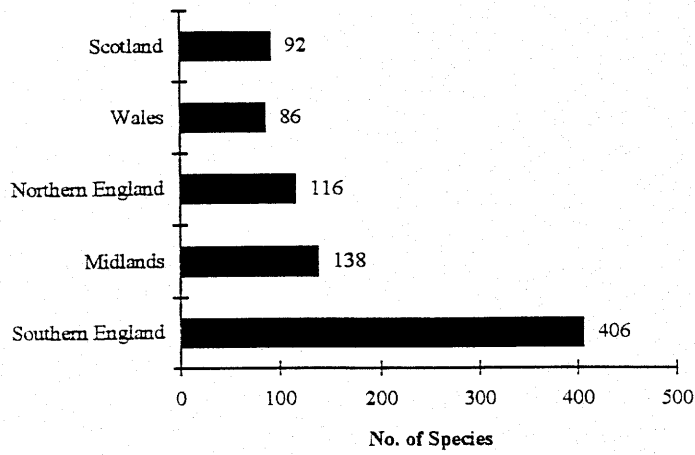


Figure 9. Occurrence of RDB status Coleoptera in Great Britain by region.

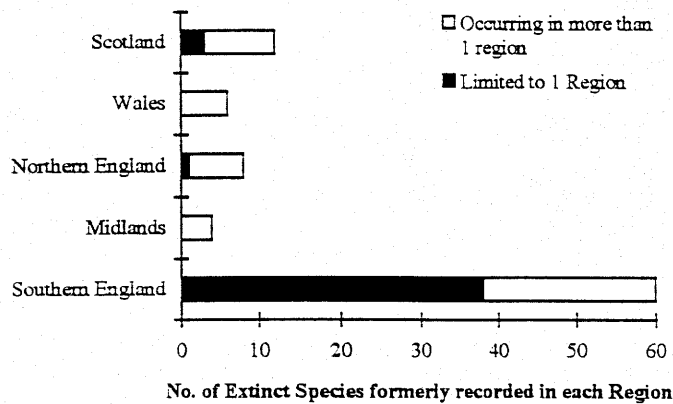


Figure 10. Extinctions of Coleoptera in Great Britain since 1750 by region.

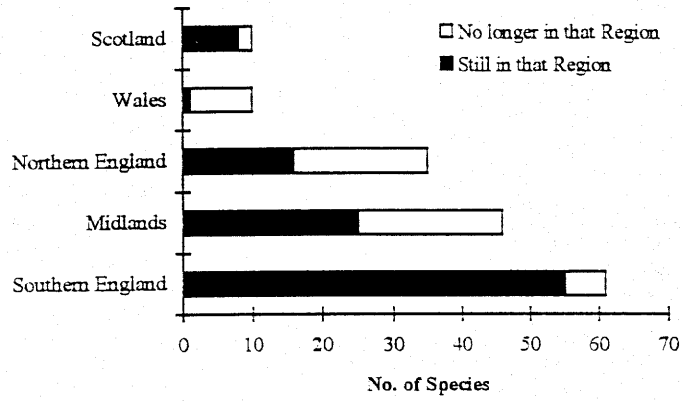


Figure 11. Occurrence of RDB status Coleoptera in sub-fossil records in Great Britain by region.

TABLE 1. Status, distribution, habitat and bionomic groups. For the distribution category, numbers in parentheses indicate the numbers of species whose distribution in Britain is limited to the region concerned, while the number outside the parenthesis indicates the total number of RDB and extinct species recorded in that region.

Category	Group	Notes	n
Status	Old Extinct	Species extinct prior to 'modern' collections, i.e. before 1800	28
	Recent Extinct	Species extinct from 1800 to 1900	64
	Endangered	Red Data Book classification 1	170
	Vulnerable	Red Data Book classification 2	70
	Rare	Red Data Book classification 3	153
Distribution	South-East	Kent and Sussex extending into Essex and Surrey.	27 (21)
	Southern England	Includes the south-eastern and south-western distributions. Extends as far north as Gloucestershire, Oxfordshire, Buckinghamshire, Bedfordshire, Huntingdonshire, Cambridgeshire and Norfolk	397 (180)
	South-West	Cornwall, Devon, Dorset and Somerset	24 (11)
	Midlands	Broadly Herefordshire, Worcestershire, Warwickshire, Northhamptonshire and Lincolnshire north to Shropshire, Staffordshire, Derbyshire and Nottinghamshire	138 (3)
	East	Only occasionally used where a particular distribution appears to be limited to the former fenland areas of Suffolk, Norfolk, Cambridgeshire and Lincolnshire	9 (7)
	North West	Cheshire and south Lancashire which appear to include a number of distinct records. Cumberland is also included which also has some distinct records	25 (1)
	North-East	Yorkshire to the Scottish Border	8 (-)
	Northern England	From Cheshire and Yorkshire to the Scottish border. Includes the NE and NW distributions	116 (7)
	S.Wales	Glamorgan and/or Monmouthshire, which contain a number of species not recorded elsewhere for Wales	36 (-)
	NW.Wales	Anglesey, Merionithshire and Caernarvonshire which appears to be another area with some isolated records	18 (1)
	Wales	Includes S.Wales and NW Wales	86 (2)
	Scotland		92 (25)
Habitat	Grassland	Natural and semi natural grassland, as well as downland and calcareous grassland	59

Category	Group	Notes	n
	Pasture	Indicates man-made grazing land (often ploughed and sown with exotic grasses)	9
	Woodland	Includes ancient woodland and pasture woodland	165
	Wooded bog	Differs from woodland in that the trees are developed on marshy, boggy ground	9
	Scrub	Indicates an early stage in succession, either following heavy disturbance to natural and semi natural vegetation, or regeneration of waste ground	20
	Water edge	Indicates habitats on the margins of freshwater, either riversides, the edges of ponds and lakes, as well as drainage ditches and dykes.	48
	Wetland	Include bogs (non-wooded), fenland and peat bogs	43
	Coast	Includes cliffs and beaches, shingle, saltmarshes and sand	65
	Sand	Indicates habitats with a sandy substrate, and could include dunes	14
	Eurytopic	From two to many of the other habitat types	18
	Saltmarsh		7
	Hedge		4
	Subterranean	Cryptic species living under ground	1
	Mountains		4
	Aquatic	Water beetles	65
	Pine Forest	Coniferous forest (upland and lowland)	20
	Dunes	Exposed coastal sand dunes as opposed to sandy substrate habitats	5
	Cliffs	Coastal cliffs. Always a subset of the Coast habitat	16
	Cultivation		7
Habitat/niche	Parasites	Usually on other insects, especially bees.	10
	Phytophages	Plant eaters	148
	Deadwood	Includes damp, rotting timber as well as dry timber	91
	Predators	Often on other beetle species	149
	Myrmecophiles	Species living in association with ants	11
	Compost	Includes all types of rotting non-woody vegetation and plant matter	16
	Dung	Dung beetles	21

Category	Group	Notes	n
	Carrion		13
	Bark	Species found under bark, both during hibernation and for feeding	27
	Flowers	Species found on flowers, e.g. nectarvores	4
	Fungi	Puffball and rotting wood fungivores	17
	Detritivores	Species found in association with beach shingle detritus	3

TABLE 2. Groups in which the ratios of old extinct: recent extinct: RDB Endangered: RDB Vulnerable: RDB Rare species is significantly different from the ratios for all other groups in that category. Only groups in which the number of observed species equals or exceeds 20 are given, to avoid errors associated with low expected values of χ^2 . * - does not include old extinct species as distributions of these species can only be inferred from fossil records, which are inadequate samples of an unknown overall distribution.

Category	Faunal group	n	χ^2 probability (%)	Cause
Habitat (inclusive)	Heathland	23	4.68	Later decline
	Aquatic (Water beetles)	149	<0.001	Later decline
	Pine Forest	20	<0.001	Earlier decline
Ecological niche (inclusive)	Deadwood	91	<0.001	Earlier decline
	Phytophagous (inc. flowers)	148	3.25	Later decline
	Compost, Carrion, Dung	39	4.20	Earlier decline
	Predatory species (all)	149	1.67	Later decline
	Predatory species (Terrestrial)	88	0.70	More endangered species
Distribution* (exclusive)	South-east England	21	<0.001	Earlier decline
	Southern England	180	<0.001	Earlier decline
Distribution* (inclusive)	Midlands	138	<0.001	Later decline
	Northern England	116	0.03	Later decline
	Wales	86	2.23	Later decline
	Scotland	92	0.19	Later decline

APPENDIX 1: THE SUB-FOSSIL RECORD

Sub-fossil Coleoptera assemblages from the present (Flandrian) interglacial and the period of climatic amelioration at the end of the Devensian (last) glacial have been described from over 100 sites in Britain. Sites giving RDB and extinct species analysed in this study are listed in Table 3, as recorded on the BUGS database of the University of Sheffield. Species last recorded as fossils in Late Glacial deposits have not been included for analytical purposes.

Table 3. Records of fossil beetle assemblages from Great Britain which include species now classified as RDB extinct, endangered, vulnerable or rare, of species not recorded in Great Britain since 1800 and of species last recorded from Great Britain during the Holocene.

Reference	Age (years BP unless otherwise given)	Distribution	Site Type
Amsden & Boon, 1975	1st - 4th C AD	S. England and Wales	Roman occupation
Ashworth, 1972	<12,160; 10,580; 9800	Northern England	Natural site
Ashworth, 1973	<10,300; 10,300;10,670, >10,670	Midlands	Natural site
Bishop & Coope, 1977	9040, 11,205; ca. 11,700; 12,441; 12,940; LL; 10,898	Scotland	Natural site
Blair, 1935	early Holocene	Southern England	Washed up moorlog
Buckland, 1976	4 C AD	Northern England	Roman occupation
Buckland, 1979	2980; 3000; ca. 3100	Northern England	Flooded Woodland
Buckland, 1980	4 C AD	Northern England	Roman occupation
Buckland, 1981	ca. 2600	Midlands	River
Buckland, 1982	10280; 10280/10,550; >10,280/10,550	Midlands	Peat under blown sand
Buckland & Johnson, 1983	<2980	Northern England	Flooded Woodland
Buckland & Sadler, 1985	Iron Age - Roman	Northern England	River, peat deposits
Buckland <i>et al.</i> , 1991	ca. 3345	North/Midlands	River
Chowne <i>et al.</i> , 1986	2350	Midlands	Iron-Age occupation

Reference	Age (years BP unless otherwise given)	Distribution	Site Type
Coope, 1967	13,560	East Anglia	Natural site
Coope, 1968	approx. 11-12,000	Scotland	Marsh
Coope, 1971	12,160	Isle of Man	Natural site
Coope, 1977	12,112; 12,645; >12,645; 13,185; 14,557	Wales	Natural site
Coope, 1982	13,450; 11,230	South-east England	Natural site
Coope & Brophy, 1972	12,556; >12,556; 14,468	Wales	Natural site
Coope & Joachim, 1980	<11,180; >11,500; <12,560; 12,560	North-west England	Natural site
Coope & Osborne, 1968	4 C AD	Southern England	Roman well
De Moulins, 1990	1-2 C AD	Southern England	Roman occupation
Dinnin, 1991	Early modern	Northern England	Lake
Girling, 1976	Bronze Age	South-West England	Fenland
Girling, 1977	10,600; 4210; >4210	South-West England	Raised acid bog
Girling, 1979a	2130-2340	South-West England	Fenland
Girling, 1979b	ca. 5150; 5625	South-west England	Fenland
Girling, 1979c	< ad 375	Southern England	Roman occupation
Girling, 1980	ca. 3950; 4950, >4950	South-West England	Woodland
Girling, 1984a	Mid 15 C AD	Midlands	Natural site
Girling, 1984b	ca. 5150	South-West England	Fenland with carr
Girling, 1985	4470; <4470	South-West England	Woodland
Girling, 1989	Zone VIIa; VIIb	Southern England	Woodland
Girling, 1991	2175/2260; 2380; 2970- 4420	Wales	Natural site

Reference	Age (years BP unless otherwise given)	Distribution	Site Type
Girling & Robinson, 1987	4840; >4840; 6100; >6320	South-West England	Occupation and natural
Girling & Robinson, 1989	<ad 1323; <ad 375; Zone VIIa-b	Northern England	Semi-natural (moat)
Hall & Kenward, 1990	2 - 4 C AD (300 assemblages)	Northern England	Roman-Med. occ.
Hall <i>et al.</i> , 1980	4 C AD	Northern England	Roman well
Holdridge, 1987	2830	Northern England	River
Keepax <i>et al.</i> , 1979	10 C AD	Midlands	Saxon occupation
Kelly & Osborne, 1965	ca. 400; 4830	Midlands	Woodland
Kenward, 1984	Roman	North-West England	Roman occupation
Kenward, 1988	Roman	Northern England	Roman occupation
Kenward & Allison, 1994a	9410 - 1200	East Anglia	Aquatic, Water edge
Kenward & Hall, 1995	9 - 11 C AD (c. 600 assemblages)	Northern England	Viking occupation
Kimmins, 1954	Late Iron-Age - Roman	Northern England	I. A.-Rom. occupation
Osborne (in Girling, 1982)	ca. 4300	Midlands	Woodland
Osborne, 1969	3160	Southern England	Open grassland
Osborne, 1971a	2 C AD	Midlands	Roman occupation
Osborne, 1971b	43-75 AD	Southern England	Pre-Roman occ.
Osborne, 1972	VIIb [3-4000]; VIIa [6-7000]; <11,048; >11,000; 11,790; >11,790; 13,555; >13,555	Midlands	Woodland
Osborne, 1973	11,700	Midlands	Natural site

Reference	Age (years BP unless otherwise given)	Distribution	Site Type
Osborne, 1974	9450; 9470; 9510; 9550	Midlands	Marsh, Woodland
Osborne, 1979	Iron Age	Midlands	Iron-Age occupation
Osborne, 1980	12165; 9305; 9080; 2890/2880	Midlands	Natural site
Osborne, 1984	1090; 1110; 1080	South-West England	Saxon occupation
Osborne, 1988	2880	Midlands	River
Osborne, 1989	3160	Southern England	Bronze-Age well
Peake & Osborne, 1971	10,130	Southern England	Natural site
Pearson, 1961	13,560	Southern England	Natural site
Robinson, 1979	250 ad; >350 ad	Southern England	I.A.-Rom. occupation
Robinson, 1980	Roman	Southern England	Roman occupation
Robinson, 1991	3500-5400; 1000-850 bc	Southern England	River, Woodland
Robinson, 1992	2830; >2830	Southern England	Fenland
Rose <i>et al.</i> , 1980	11,940	South-east England	Natural site
Shackley, 1976	4210, 4180	Southern England	River, Woodland
Shotton & Coope, 1983	9860; <12,570; 12,570	Midlands	Natural site
Shotton <i>et al.</i> , 1977	8320	Midlands	Natural site
Skidmore, 1970	mid Holocene	Northern England	Wooded bog
Walsh, 1992	nd	Scotland	Natural site
Whitehead, 1989	ca. 3390; 2 C AD	Midlands	Roman occupation
Whitehead, 1992	2 C AD	Midlands	Roman occupation
Whitehouse, in press	approx. 3000	Northern England	Flooded Woodland