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Patterns, Mechanisms and Rates of Extinction among Invertebrates in the United Kingdom [and Discussion]

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Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom

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SUMMARY

Information about the changing status and extinction rates of invertebrates in the United Kingdom during the past 100–300 years is reviewed. Although historical recording was more thorough in the U.K. than elsewhere, the data are patchy and difficult to interpret. Nevertheless, we conclude that the extinction rates of U.K. invertebrates have matched, and probably exceeded, those of vertebrates and vascular plants in the present century. The main reasons for decline are analysed. No clear pattern of threat was found among aquatic species, but there was a very clear pattern in terrestrial biotopes, where most endangered species inhabit either the earliest or latest successional stages. The former group consists mainly of thermophilous species, which may be relics from a period when U.K. summer temperatures were warmer, and which survived in warm refugia created by the land management of prehistoric man. These types of habitat have largely disappeared from modern biotopes, and their dynamics have also changed. In all systems, many invertebrates are too sedentary to track their habitats in the modern landscape.

1. INTRODUCTION

With about 22 000 species of insect and several thousand other invertebrates, the United Kingdom has a comparatively small invertebrate fauna and few endemics to compensate for the paucity (Kerrich *et al.* 1978). Yet the U.K. is better known than any other comparable area in the world (Bratton 1991; Collins & Thomas 1991), and is probably the only country for which the rates and causes of species loss over the past 100–300 years can be reviewed. Our conclusions apply to much of Europe (Heath 1981; Speight 1989; Erhardt & Thomas 1991; Thomas 1991) and probably elsewhere, for whereas U.K. biotopes were once considered atypical because of management and alteration by man (Rackham 1986; Spellerberg *et al.* 1991; Warren & Key 1991; Thomas 1993), evidence is now accumulating that many third world biotopes have also been shaped by man over recent millennia (e.g. Pimm & Moulton, this symposium). In studying how the invertebrates of low-input low-output agricultural and forestry systems have responded to the agrichemical and silvicultural revolutions of the 20th century, we may therefore illuminate processes to be repeated over much of the world, as human populations grow and societies 'develop'.

2. ESTIMATING EXTINCTION RATES OF U.K. INVERTEBRATE SPECIES

(*a*) *Historical records and modern databases*

Although species lists and status accounts for U.K. invertebrates over the past 200–300 years are unmatched elsewhere (Thomas & Morris 1994), they are far less complete than most biologists suppose. With the exception of well-known groups (e.g. dragonflies, butterflies and molluscs), the British list is still expanding as new species are discovered rather than decreasing as species become extinct (P. T. Harding, personal communication).

A modern era of invertebrate recording began around 1960 with the development of national and local mapping schemes, national site surveys and monitoring schemes (Harding 1992; Thomas & Morris 1994). These have generated a vast database of past and recent records: by 1987 ITE's Biological Record's Centre held 1.25 million records for the 47 national recording schemes it coordinated, encompassing 22 orders and nearly 10 000 species of invertebrate (Harding 1992). Yet substantial gaps remain. The parasitic Hymenoptera (about a quarter of the U.K. insect fauna) have negligible cover, as do many Diptera and some Coleoptera. And the current dearth of young taxonomists means that the past 25 years may be seen as a brief golden age rather than the start of an era of scientific recording in the U.K.

(*b*) *Assessing declines in U.K. Invertebrates*

Past and present recording efforts have been too biased and variable to permit the non-specialist to make objective, quantitative comparisons of changes in the status of invertebrates (Thomas & Morris 1994). The most reliable assessments are those of 95 experts, who recently drew upon all available sources to review their specialist insect groups (apart from Microlepidoptera, Parasitica and some Diptera) using

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Table 1. *The percentage of invertebrate species classified in U.K. Red Data Books and other reviews*

order		no. British species	% presumed extinct	% vulnerable or endangered	% in red data book
insects	Odonata (dragonflies)	41	7	7	22
	Orthoptera (grasshoppers, crickets)	30	0	17	20
	Heteroptera (bugs)	540	1	4	15
	Trichoptera (caddis flies)	199	2	6	17
	Lepidoptera (butterflies)	59	8	5	20
	Lepidoptera (macro-moths)	*ca.* 900	2	3	11
	Coleoptera (beetles)	*ca.* 3900	2	6	14
	Aculeate Hymenoptera (ants, bees, wasps)	580	4	7	28
	Diptera (flies)	*ca.* 6000	0.05	8	14
others	Mollusca (slugs, snails)	*ca.* 200	0	9	17
	Annelida (leeches)	16	0	0	19
	Myriapoda (centipedes, millipedes)	*ca.* 88	0	0	6
	Crustacea (woodlice, amphipods)	64	0	0	9
	Arachnida (spiders, pseudoscorpions)	*ca.* 665	0	8	13

the IUCN classifications of Extinct, Endangered, etc. (Mace, this symposium); their conclusions were submitted to a RDB selection committee, which aimed for consistency between taxa. The known habitats and perceived threats to these species were also described, and published with the assessments as the *British Red Data Book of Insects* (Shirt 1987). Other invertebrates have been similarly reviewed (Bratton 1991), covering nine major taxonomic groups but not Protozoa. JNCC or EN have subsequently reviewed or revised the Ephemeroptera and Plecoptera (Bratton 1990), spiders (Merrett 1990), Trichoptera (Wallace 1991), aculeate Hymenoptera (Falk 1991), Hemiptera (Kirby 1992), most Coleoptera (Hyman & Parsons 1992) and pyralid moths (Parsons 1993).

The percentage of each group of invertebrates considered to be Extinct, Endangered or Vulnerable is summarized in table 1. For several taxa, the proportion of threatened species is similar to that in vascular plants (about 7%; Harding & Sheail 1992). However, column 3 undoubtedly underestimates extinctions in taxa that were poorly recorded before the 20th century (i.e. all except butterflies and dragonflies; Thomas & Morris 1994): it is unlikely that butterfly species have declined more over the past 250 years than aculeate Hymenoptera, as both groups are characteristic of the same rapidly disappearing habitat type (§§ 3 and 4) (Falk 1991). The percentages of species in all RDB categories may more accurately reflect the comparative vulnerability of different taxa (table 1, column 5).

Thomas & Morris (1994) also compared extinctions of vertebrates, butterflies and dragonflies in Suffolk, where wildlife recording has been exceptionally thorough over the past 150 years. Invertebrates have apparently experienced more extinctions than other popular groups, in which 3–12% of species have been lost, with butterflies (42% species extinct) being more vulnerable than dragonflies (15% extinct). In corroboration, Thomas (1991) described the extinction of many butterfly species in semi-natural biotopes where the flora is apparently unchanged.

Thus, the extinction rate of butterfly species has probably exceeded those of vascular plants or vertebrates in historical times, and some less popular orders, like aculeate Hymenoptera (Falk 1991) and Orthoptera (Marshall & Haes 1988), may have experienced similarly acute losses. Certainly, several reviewers of specialist groups found that extinctions and declines were considerably greater than previously thought (e.g. Falk 1991). However, some media campaigns have grossly overstated declines: the Butterfly Conservation Society knowingly ran an advertising campaign that was wholly unjustifiable on scientific grounds.

During the same recording periods, a few species in most groups have increased in the U.K. About 9% of butterfly species increased overall this century compared with 74% that declined (Heath *et al.* 1984). The ratio is similar in other groups (Falk 1991).

(*c*) *Predicting future extinctions from current trends*

Vulnerable or Endangered status (table 1) implies extinction for a species in the U.K. in the near or foreseeable future if factors causing its decline continue. More precise predictions of extinction dates have been made for three butterfly species by extrapolating the steep and steady extinction rates of previous decades (Thomas 1983; Thomas *et al.* 1986; Warren *et al.* 1984). However, predictions for *Lysandra bellargus* and *Hesperia comma* were made at their nadir, and more populations exist today than 10 years ago (Thomas & Jones 1993). This occurred because the processes causing their declines were suddenly reversed (§ 4). For this and other reasons, predictions of extinction are likely to be accurate and useful only if the underlying mechanisms are understood.

3. PATTERNS AMONG DECLINING SPECIES

Probably many different factors have caused declines among invertebrates, given the diversity of change in the U.K. countryside (Rackham 1986): more than 50 different threats are listed in the Red Data Books. However, autecological studies and reviews of dragonflies (Moore 1976), butterflies (Thomas 1984, 1991)

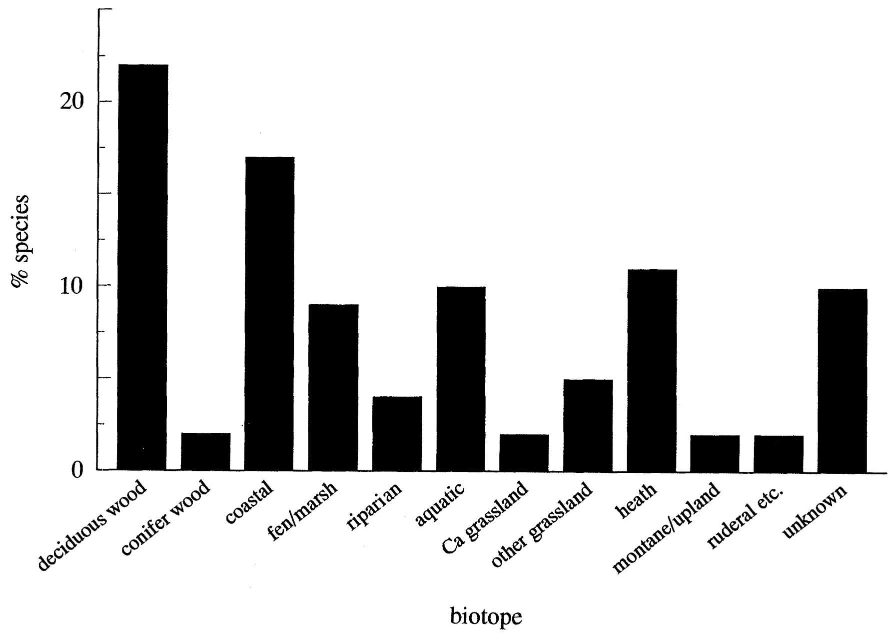

Figure 1. The percentage distribution of all RDB and Notable invertebrates ($n = 2518$) in 12 principal types of biotope (after Welch 1993).

and the beetles of woodland (Warren & Key 1991) and fresh water (Foster 1991, 1992) suggest that some factors are particularly important, and that taxa with certain life styles or habitat types may be especially threatened. Information in Red Data Books and other reviews was therefore analysed for patterns among declining species, concentrating on their habitats because nearly every species account implies some sort of habitat change as the main threat. (See also Thomas & Morris 1994.)

Welch (1993) classified the biotopes of all RDB and notable species of U.K. invertebrate (figure 1), and obtained similar patterns for Endangered and Vulnerable species alone. Most inhabit deciduous woodland, coastal and aquatic (freshwater) biotopes or heathland, whereas upland, calcareous and other grasslands contain comparatively few. The low 'score' of calcareous grassland is surprising, given its conservation emphasis. However, these figures show where the most threatened species live rather than the fauna as a whole.

Welch also found considerable variation in biotope occupancy by threatened species in different taxonomic groups. Deciduous woodland proved particularly important for Diptera and Coleoptera, heathland for Aculeate Hymenoptera and spiders, and aquatic biotopes for snails (Thomas & Morris 1994).

In a review of European butterfly conservation, Thomas (1991) distinguished between extinctions caused by the fundamental destruction of biotopes (e.g. conversion of heathland to agriculture), and those caused by the less obvious disappearance of species' habitats within surviving biotopes, usually through successional change. The second process has caused more extinctions of butterflies in recent decades, and autecological studies of other endangered terrestrial invertebrates reached the same conclusion (e.g. Cherrill & Brown 1990*a*,*b*; L. K. Ward, personal communication). The pattern of threatened invertebrates in biotopes (figure 1) suggests this may apply to other taxa. There is no correlation between the extent by which biotopes have declined in historical times and the number of threatened species they contain; indeed, greater proportions of deciduous woodland, heathland and most coastal biotopes have survived than calcareous and other lowland grasslands, fens and marshes (Warren 1993), yet the first three biotopes have more threatened and extinct species than the latter group (rank correlation $r = 0.60$, $n = 5$).

We therefore classified all Extinct, Endangered and Vulnerable terrestrial invertebrates by their habitats rather than by the broad biotope they occupied. Where possible, species were assigned to one of six successional stages:

1. Bare ground and very early, including dunes but not shingle, pioneer heath, woodland floors in the first five years after coppicing or clearing, grassland within 2 years of perturbation or maintained as a plagioclimax below 3 cm tall.
2. The building phase of heaths, 5–10 year regrowth after coppicing or woodland clearing, 4–10 cm tall grassland.
3. Mature heath, grassland above 10 cm tall, including woodland glades and rides.
4. Shrubs.
5. Healthy trees.
6. Saproxylic, defined as dead or dying, standing or fallen wood, or the fungi growing on it, or species supported by other saproxylic species (Speight 1989), such as mymecophiles of *Lasius brunneus* nests.

Seven experts helped us categorize their specialist groups (see acknowledgements). All mymecophilous

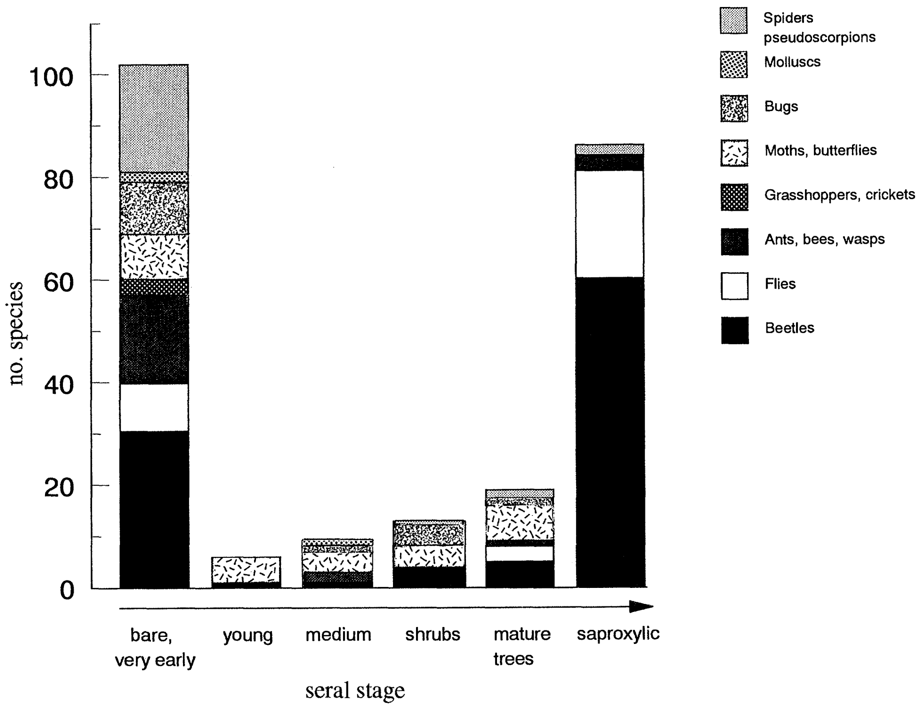

Figure 2. The seral stages inhabited by extinct, endangered and vulnerable RDB species in woods, grassland, heaths and dunes (a further 65 species could not be classified).

species characteristic of woodland clearings (except those associated with *L. brunneus*) were assigned to category 1; where two categories were used during a life cycle, the seral stage needed by early stages was preferred because they have more exacting requirements than the adults (N. W. Moore, personal communication; Thomas 1991). Exceptions, such as *Decticus verrucivorus* which requires a mosaic of category (1) and (3) seral stages (Cherrill & Brown 1990*b*), were scored as half in each. The one bumble bee listed was tentatively scored category (3) due to the critical adult need in this group for abundant nectar.

Forty-five species had unknown or very specialized habitats, such as Coleoptera known only from animal artefacts or dung, and inhabitants of cliffs and quarries (possibly category 1). We had insufficient information to assign a further 65 species to such precise seral stages. However, the remaining 232 species revealed a remarkably clear pattern, most being inhabitants of very early or very late seral stages (figure 2). This confirms, quantifies and extends the hypothesis that the most threatened groups of woodland insect in U.K. depend on the extremes of the woodland succession (Warren & Key 1991). The species that require early successional stages are taxonomically varied, but the saproxylic group consists almost entirely of Coleoptera and Diptera (figure 2).

Habitat data for all U.K. invertebrates are lacking, but the pattern is probably a rough mirror image of figure 2 (although less extreme), with fewest species in the earliest successional stages and most inhabiting mature trees. The dependence of endangered species on the extremes of seres is discussed in § 4.

4. MECHANISMS CAUSING DECLINES

(*a*) *Terrestrial species*

(i) *Early successional and thermophilous invertebrates*

In addition to the Extinct, Endangered and Vulnerable species, many 'nationally notable' invertebrates listed in reviews inhabit this seral stage (see Falk 1991). And for all changes in butterflies, we found a significant correlation between the intensity of decline (or increase) and the earliness of the seral stage inhabited (no U.K. species is saproxylic) ($p < 0.05$, $n = 54$).

The U.K. niches of 12 species studied that inhabit the earliest stages of seres (one ant, one orthopteran, ten butterflies) are even narrower than described, because all are also restricted to southerly facing slopes and most to southern England (Cherrill & Brown 1990*a*,*b*, 1992; Thomas 1984, 1991, 1993). These species do not need early successions per se, but the exceptionally warm microclimates associated with these situations in which to develop (Thomas 1983; Cherrill & Brown 1990*b*; Warren 1994). Thus under the warmer climate of lowland central France, the same species occur on all aspects of land except south-facing slopes (which are too hot), and in tall rather than short swards or in semi-shaded woodland (Thomas 1993). This may not apply to all the other 98 species in this category (figure 2), but as many reach the northern limit of their ranges in south England, most are probably thermophilous, ground-dwelling species that can inhabit only the hottest patches available here.

Most species in several groups of invertebrate reach the northern limits to their ranges in southern Eng-

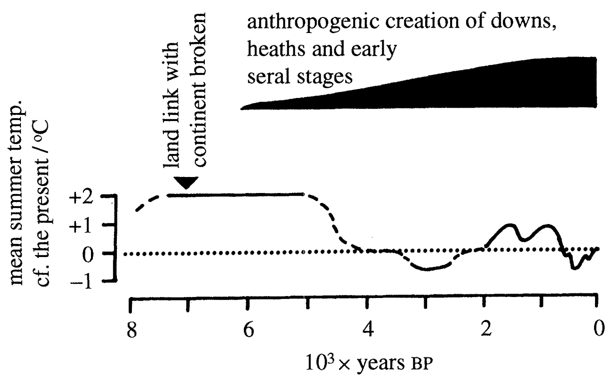

Figure 3. Summer temperatures and the availability of warm habitats in Britain (from Thomas 1993).

land, for example Orthoptera, Odonata and butterflies (Heath *et al.* 1984; Eversham 1993). The constraint caused by the extra requirement of an exceptionally warm local climate has been calculated for a heathland butterfly, *Plebejus argus*, using descriptions of its habitat from the extreme north of its range and from further south, where summer temperatures are 2°C warmer: the number and size of habitat patches that would be suitable for it under each climate were plotted using the Dorset Heathlands Database (84 sites) (Thomas 1991). Under the cooler climate, only seven small islands of habitat would exist in just four heaths, whereas under a warmer climate, precisely the same biotopes would contain a 70-times greater area of *P. argus* habitat distributed as 112 islands within 45 sites. The probability of local extinction is clearly greater near the edge of *P. argus*' range because individual populations are smaller, and the probability of recolonization is lower due to the greater distance between colonies. Moreover, butterfly populations near the edge of species' ranges undergo much greater fluctuations than those further south (Thomas *et al.*, in preparation) again increasing the probability of extinction in unfavourable years.

In fact, thermophilous species have survived in the U.K. for long periods on a few restricted sites, so long as their specialist habitat requirements were maintained. *Melitaea cinxia*, for example, has maintained its status on the crumbling undercliffs of the Isle of Wight for at least 150 generations (Thomas 1991). However, most declining species of early seral stages have depended entirely on man (or rabbits) to create their ephemeral habitats since historical records began, 150–200 years ago (Thomas 1993). Their absence from eroding cliffs is possibly explained by the fact that although they need warmth, they are not xerophilous; ironically, several thermophilous butterfly species experienced population crashes in the hottest summers of recent years, because these resulted in severe droughts (Thomas 1983).

One explanation for the many thermophilous species in Britain is that they colonized the country in 9000–7000 BP, before the land-link was broken (figure 3). During that period, summer temperatures were about 2°C warmer than today, enabling them to inhabit the broader niches currently occupied in central Europe: these habitats are commoner and less ephemeral, and would not have required man to maintain them. Thomas (1993) suggests that these species should really have become extinct in the U.K. about 5000 BP when the summer climate cooled. However, by then man had been creating warm habitats within woods, heath and grassland for at least 1000 years (figure 3), providing refuges where thermophilous species could survive.

Whatever the merits of this hypothesis, archaeology and history indicate that man's traditional land management of the U.K. resulted in the frequent and regular regeneration of early successional stages on an increasingly large scale within woods, heaths and grasslands from about 6000 BP until the late 19th century (Rackham 1986). But in the 20th century, there was a shift towards later seral stages as coppicing was replaced by high forest, and heaths and unfertilized grassland abandoned (Smith 1980; Webb 1986; Warren & Key 1991). Thermophilous butterflies, and presumably other taxa, experienced numerous local extinctions as their southern habitats became shaded and experienced the equivalent cooling (−4°C) of transportation to the Orkneys. Grassland species survived longer because rabbits briefly replaced domestic herbivores on abandoned grassland. But from the mid 1950s onwards, myxomatosis was introduced, and resulted in a spate of extinctions. In the 1970s, only one of 43 former *Maculinea arion* sites had a suitably short sward, and the species became extinct in the U.K. (Thomas 1991). *Lysandra bellargus* and *Hesperia comma* survived on a few farmed chalk hillsides (Thomas 1983; Thomas *et al.* 1986). Both have partly recovered with the return of rabbits, although only restored habitats that are within a kilometre or so of surviving populations have been recolonized (Thomas *et al.* 1992; Thomas & Jones 1993; § 4*c*). All these changes were quite independent of the survival of biotopes. Woodland of all types has doubled in area during this period, but early successional habitats within woods became rare and isolated (Warren & Key 1991).

(ii) *Saproxylic species*

The threatened invertebrates of dead or dying wood are difficult to study and few autecological studies have been made. Reviews by Speight (1989) and Warren & Key (1991) are sufficiently thorough for us to comment only briefly on some similarities and differences between these species and those inhabiting early stages of seres.

One similarity is that most species of this stage are specialists inhabiting extremely narrow and specific niches (Warren & Key 1991). These have been categorized into 20 broad types. So specialized is the habitat of some species that only about 1% of ancient trees may contain it at any one time (Stubbs 1972).

Microclimate is important in determining whether dead wood will develop a species' habitat (Warren & Key 1991), but unlike the early successional insects, most saproxylics cannot survive in hot microclimates. Many require very wet conditions and some only inhabit wood that has fallen into water; others occur in arid, red-rotted wood or fire-scorched timber.

Warren and Key found no consistent patterns of extinction among saproxylic insects; Caledonian pine forest species have declined particularly severely in historical times, whereas those associated with decaying exotic softwoods have increased. Declines presumably started with the major forest clearances around 4000 BP, which reached a maximum in the 19th century. Since then the woodland biotope has doubled, but most modern woods are middle-aged, managed, and contain very little dead wood. Saproxylic habitats have also declined in ancient parks and forests, for moribund trees are regarded as untidy, dangerous to the public, and a source of infection to sound trees.

(*b*) *Wetland and freshwater species*

Perceived threats and causes of loss to the large number of threatened and extinct invertebrate species associated with various wetland biotopes (figure 1) are difficult to interpret, with several factors sometimes listed for the same species. This may genuinely reflect the diversity of factors harming wetland habitats in the British countryside, but more research is needed to clarify this: only information on water beetles (Foster 1991) and Odonata (e.g. Moore 1976) is reasonably clear. Foster (1991) reviews the numerous perceived threats listed in RDBs. Our figures, from slightly different sources, are very similar: the main factors blamed are drainage (62 citations), pollution and/or eutrophication (26 citations) and inappropriate management (13 citations).

(*c*) *Fragmentation and dispersal*

Little is known about the mobility of threatened invertebrates. U.K. butterflies can be divided crudely into mobile species with open populations (about 15%) and those that are colonial (85%) (Thomas 1984). No pattern is discernible in the mobility of the few extinct species. *Aporia crataegi* and *Nymphalis polychloros* lived in predominantly open populations, forming several local colonies in woods, hedgerows or orchards for a decade or two before experiencing local extinctions (Heath *et al.* 1984). *Carterocephalus palaemon*, (extinct in England) is also comparatively mobile, with individuals regularly flying several kilometres (Ravenscroft 1992). However, three other extinct butterfly species lived in closed populations, and *M. arion* was highly sedentary (Thomas 1991). The other butterflies that have declined severely this century appear also to be sedentary, and have usually failed to track the rate at which their habitats have been created, most being incapable of crossing barriers of > 1–10 km (J. A. Thomas 1991; Thomas *et al.* 1992; Thomas & Jones 1993; C. D. Thomas 1994).

There is anecdotal evidence that many other declining U.K. invertebrates have very sedentary populations, especially saproxylic species (Warren & Key 1991). This is expected from templet theory (Southwood 1977), but the low dispersal rates of species with ephemeral, early-successional habitats is surprising. Thomas (1991) argued that, having lived in anthropogenic habitats for 1000–5000 generations, they may have evolved sedentary local races adapted to the unusual dynamics of early successional patches generated by traditional forms of land management: they are undoubtedly ill-adapted to the dynamics of early-successional habitats in the modern landscape.

5. CONCLUSIONS

Many invertebrate species are declining at rates that match and probably exceed those of vertebrates and vascular plants in the U.K.. Although few recorded national extinctions have occurred, many species are close to extinction. A similar or worse situation exists in the Netherlands (Tax 1989) and parts of Germany (O. Kudrna, personal communication). More thorough scientific recording is essential if declines are to be recognized; a shortage of taxonomists is a major problem in U.K.

It is important to understand the underlying mechanisms if successful predictions are to be made about how invertebrate populations will change in modern landscapes and, probably, under changing climates. The preponderance of thermophilous species among threatened invertebrates was a surprise; with the prospect of global warming, conservationists should nurture these populations, for they may multiply in the future.

The extent to which man has altered both the biotopes of invertebrates and species habitats within them is clear. In the U.K., the species of the two extremes of succession are especially threatened. These types of habitat are often scarce on nature reserves. Management should create (or leave) more of them, and new habitat patches should be close enough in space and time to be utilized by sedentary species. These same habitat types have become rare at similar latitudes across Europe and at higher altitudes further south (Erhardt & Thomas 1991), but elsewhere saproxylic species form a much more threatened group, as is likely to be the case in other continents. However, conservationists in third world countries should not ignore the possibility that populations of some invertebrate species may also have become confined (or adapted) to antique anthropogenic habitats that were maintained by prehistoric forms of land management.

The exact requirements of only a few representative invertebrate species can be studied, but in U.K. more autecological information is required from saproxylic and aquatic taxa, which may reveal clearer patterns about causes of decline. Finally, the lack of knowledge of dispersal by endangered invertebrates is a major constraint for conservationists trying to apply metapopulation concepts to their conservation (e.g. Thomas 1994). This will be particularly important if there is a redistribution of invertebrates following climate change. But even under the status quo, the practical questions of how often, how large, and how far apart species habitat patches should be remain largely unanswered.

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Discussion

C. Hambler (*Department of Zoology, University of Oxford, U.K.*). I am concerned that Dr Thomas has overemphasized the importance of very early successional habitats. First, although species within them may be rare in Britain, they are often common in continental Europe. In contrast, species of late successional habitats are often internationally rare and declining.

Secondly, my own examination of the British Red Data Books suggests the importance of anthropogenic early successional habitats is nowhere near as great as the importance of late successional habitats.

It should be remembered that the Red Data Books do not cover many taxa of small organisms, which do not favour abiotically stressful early successional habitats.

J. A. Thomas. I agree that the British species of early successional habitats are, with some exceptions, much less threatened internationally than the species of late seral stages; I made that point in my paper. However, I was invited to review the threats to U.K. invertebrates, and our analyses indicate that the largest threatened group of *terrestrial* invertebrates here inhabit early seral stages. I am aware that Red Data Books do not cover many taxa of small organisms, but until these groups are assessed (and their habitats described) it is impossible to generalize about the types of habitat of the *declining* species within these taxa.

I am more concerned that Mr Hambler obtained different results from an examination of the British Red Data books. Small discrepancies are inevitable because in our classification (and perhaps vice versa) we sometimes drew upon unpublished habitat descriptions that were unavailable to him, or were advised by specialists whom he did not consult. This enabled us to make some generalizations, for example in the classification of threatened myrmecophilous species: details are given in our written paper. But I suspect the discrepency lies in the fact that Mr Hambler included 'Rare' species in his analyses. We only classified the Extinct, Endangered and Vulnerable species, because the designation 'Rare' need not imply decline, simply that the species is rare. As I stressed, the patterns shown by declining species may not reflect where most species in taxa live, merely where the small proportion that is threatened do. We actually suspect that early successional habitats have the lowest biodiversity of all seral stages, and would therefore expect a different pattern of occupancy if the many rare or nationally notable species were included in analyses.