Comment

BIODIVERSITY CONSERVATION IN BRITAIN: SCIENCE REPLACING TRADITION

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Biodiversity has become part of the language of environmentalists and politicians, all too often without definition. It is easy to make statements of intent to conserve biodiversity, but less easy to understand their implications. However, ecologists have worked on diversity for many years, and their results can be exploited to answer some of the questions commonly asked by conservationists. Their answers are often surprising and controversial. Various meanings of biological diversity are illustrated in Box 1.

Whilst international organisations have been concerned with the conservation of general 'biodiversity' for many years, British conservation has been dominated by enthusiasts for a few popular, but species-poor, groups of organisms. The flowering plants, birds, and butterflies have received attention greatly disproportionate to the number of British species, and the methods for their conservation have often been enshrined in dogma. In addition, British conservationists have relied on a set of ideals founded on 'tradition'. Old dogmas die hard, but some wildlife-managers have now recognised that science, old and new, has relevance to their task, and can give them better results.

It may be a surprise to the public who support British conservation organisations that scientists may see many of their activities as counterproductive. Deep controversies exist about what we should conserve, and how. This would not have serious impact, given Britain's general lack of biodiversity, but because of our potential influence overseas it is important that our philosophy is as objective and consistent as possible, and our methods are reviewed regularly.

Fortunately, scientific research is now being quoted in discussions on site management and environmental-impact assessment. A series of conferences organised by the British Ecological Society (BES) illustrates this process. However, resistance to new ideas is often very strong, and founded on intuitive feelings and sensitivity to suggestions that the management of sites may have been inappropriate for decades. Anyone who has attended meetings on management will know that different people want different things from biological resources, and some views appear irreconcilable. However, ecology and the precision of expression it encourages are beginning to force logically compelling, if unpalatable, conclusions onto managers and the public.

Confusingly, different scientists may recommend different managements, but it is clear that the claims made for the general benefits of some methods are indefensible. Some of the main tenets of conservation in Britain are now being questioned – as we illustrate below.

Should traditional management of nature reserves generally be encouraged?

One of the most deeply held beliefs is that traditional management should be continued or reinstated (e.g. Shirt 1987, Steel & Mills 1988, Warren 1993). In Hampshire, for example, owners are encouraged to 'consider traditional management for all or part of a wood wherever

Box 1 What is biodiversity?

'Biodiversity' is used rather generally to include a number of more precise ecological meanings. Most completely, it is the sum of biological variation on Earth, at levels ranging from molecules to ecosystems. If we are interested in genetic resources, such as new medicines and industrial products, then the units of biodiversity are the genes which produce them. Different species have different numbers of genes. Unfortunately, there are too many genes to conserve individually, and we must aim to protect as many carriers of genes and rare genes as possible. All wildlife, including bacteria and viruses, deserves attention – many medicines are of microbial origin. This aim might be achieved through protecting several different measures of diversity:

Species richness, the length of the species list for a site, is the simplest to understand, but the hardest to measure: no site in the world has a complete or constant species list. So lists for samples or selected taxa are chosen. In addition, we can use *indicator* groups, for which adequate taxonomic, distributional, and ecological data are available. The occurrence of such groups or species must be correlated with features of interest, such as specialists, ancient woodland, rarity – or richness – of other groups which are harder to study.

Species abundance is the population size of a species at a site. The larger the population, the more likely it is to be genetically diverse. Some natural or polluted sites have high species abundance, at low species richness. A species with several populations may be more diverse than one with few.

Habitat diversity is hard to measure, and should include the vertical (architectural) complexity, the availability of cover, as well as the number of successional stages, recognisable communities, soil types and so on per site or unit area.

The diversity of connections between species is another ecological value, again hard to measure. This relates to the complexity, and possibly the stability, of the ecosystem.

It is undesirable to aim obsessively for diversity. Some species or habitats can be *exotic* or damaging, yet add to diversity. Take the Flow Country, an extensive and relatively homogeneous habitat of international importance, and plant some exotic conifer woods: the total species and habitat diversity of the area increases, but the populations of vulnerable species decline. Some types of habitat diversity, such as that created by paths or coppicing, should be near the edge of a woodland, to protect the processes of its core.

Ecological-diversity indices (such as 'William's alpha', 'Simpson's D', or the 'Shannon H': Whittaker 1975) are derived from formulae which have appeal in combining measures of species richness and abundance. They can be used on sample data when sites are too large to get comprehensive species richness for a particular group. High values of such indicators correspond to high equatability of the relative abundance of each species on the list. One of the simplest, Simpson's D, is the probability that two species drawn at random from the community or sample will be different. Equatability is clearly contrary to the trophic pyramid of numbers (one expects fewer predators, for example), but, worse, can give a low score to a site with more of everything. Only after such indices have been calibrated against sites of 'known' quality will they be a useful tool – panels of experts in different taxonomic groups would be needed to draw up the ranking of such sites for calibration. Indices have proved helpful to botanists in assessing chalk grassland, for example, but are of limited value to general conservation biologists.

The life cycles of some species, such as dragonflies, include different habitats as we perceive them. Ideally, large reserves with natural edges between habitats should provide for such species. On a wider scale, a representative diversity of high-quality habitats needs to be protected to provide the requirements of as many specialists as possible.

possible' (Colebourn 1983). Similar claims are made for the benefits of tradition in reedbeds, heaths and damp pastures.

How did this confidence in tradition come to be, and how is it being eroded? Conservationists have perhaps generally been more in favour of the *status quo* than the scientist or the average member of the public. When they encounter a traditionally grazed, flower-rich calcareous grassland, they believe that the best way to preserve it is to maintain the grazing regime. Likewise, if a woodland was coppiced for centuries it may have attractive floral carpets in the spring, encouraging faith in tradition.

These views are acted upon by 'conservation volunteers' and managers throughout the country, who enthusiastically coppice and 'tidy up' woodland, graze grassland and cut reedbeds. What if they are wrong? Does abandonment of tradition always bring disaster?

It is evident in some cases that neglecting a calcareous grassland (non-intervention management) can lead to floristic impoverishment (Smith 1980). Likewise, neglecting some coppice woodlands over the past few decades has sometimes resulted in reduction in ground flora (Steel & Mills 1988), and has been detrimental to a few butterflies (Warren 1993). These are unremarkable observations to those who are familiar with the process of community succession (Box 2).

However, improved understanding of successions, with a shift from 'facilitatory' models to 'inhibitory ones' (Connell & Slatyer 1977), indicates that management can release succession and be counterproductive. Further, studies on the 'Upper Seeds' experiment at Wytham in Ox-

Box 2 Community succession

Succession is the process observed as open habitats, such as rock faces, transform into habitats more typical of the climatic zone, such as forests. If the starting point is a physical substrate, it is a primary succession, whilst secondary successions start on disturbed areas such as tree-falls, old fields and pastures.

It used to be seen as almost inevitable that lowland grassland would progress to woodland if not managed, because each stage of the succession improved conditions for species later in the succession, which then replaced the original community.

Modern successional theory, however, is better able to explain the observed medium-term stability in nettle-beds, scrub, or rank calcareous grasslands, particularly in secondary successions. It has been found that an assemblage of plants and animals may act to *maintain* a particular state, *inhibiting* invasion by the next stage. A catastrophe or other environmental change releases the succession by reducing the smothering influence of the current community, and a new assemblage of species may invade. This latter concept, more compatible with the 'selfish gene' perspective, might predict that initiating grazing on a stable ('neglected') grassland can precipitate scrub growth by creating gaps for scrub seed germination – so producing the very problem of succession that the management was intended to prevent!

As succession occurs, there is a general shift from species specialised to live in transient habitats where factors such as the weather, nutrients and other abiotic stresses constrain their populations, to species for which other factors are more influential. Many late-successional species have specialisation to increase their competitive powers through large size, few and large offspring, long development times and poor dispersal ('K-selected' organisms). Others are specialised to exploit the abundance of life around them. The obvious vulnerability of late-successional species, as compared to the fast-breeding, fast-moving, often tolerant species of early successions, such as grassland ('r-selected' species), gives them priority to a scientist. Internationally and nationally, the 'K-selected' specialists are suffering from habitat destruction and over-harvesting.

To slow down a succession, nutrients (which arrive in rainfall and dust) must be stripped off the land. Controlled grazing with sheep that are gaining weight, mowing with removal of material, and coppicing achieve this.

Much of British terrestrial conservation has been a form of our favourite pastime: gardening. Managers subjectively decide where to halt succession. In marine sites, where successions are often fast, conservation managers can usually rest assured that leaving things alone and protecting the sites is the right policy.

ford have confirmed that the fauna of a calcareous grassland may become more numerous and diverse if unmanaged. For example, spring or autumn grazing produces an impoverished community of spiders (compared with neglect), whilst heavier grazing produces a distinct, species-poor, short-grassland assemblage (Gibson *et al.* 1992b).

Experiments at other sites show that many invertebrates suffer under grazing or cutting; sites become less species-rich and support less biomass. A decade ago, Morris and Plant (1983) noted that 'unfortunately, nature conservation continues to be dominated by concepts of grassland management derived from agriculture and other inappropriate sources'. They advocated rotational management which allows a number of stages of succession on the same site. This provides refuges for those organisms which do not appreciate the attention of a sheep's mouth or foot.

By contrast, coppicing involves a rotation which is often too rapid and drastic for woodland species, including many shade- or moisture-loving organisms such as lichens, bryopyhtes, and ferns (Rose 1976). There are even cases where neglect can benefit the flowering plants, whilst coppicing harms them. In Suffolk, one of the county's most eminent botanists caused furore by suggesting that plants had suffered under reinstatement of a coppice regime (Simpson 1989) – partly because of the smothering of the ground by tall herbs and scrub on the now nutrient-rich soil.

Generally, 'neglected' coppice is *improving* gradually as a habitat, and many coppices neglected for decades or centuries are very rich in wildlife and rarities (Duffey 1973; Harding & Rose 1986; Sterling & Hambler 1988; Sterling 1988; but see Key 1990). This improvement could be speeded up by management such as reintroductions and importation of dead wood. Neglected coppice woodlands also store more carbon than active ones (Hambler 1990).

What of wood pastures? Keith Kirby of English Nature suggested at a BES meeting (Kirby & Drake 1993) that we should perhaps depart from the traditional management, by planting flowering scrub as food sources for adult insects; it has also been suggested that deliberately wounding trees could increase their value to dead-wood insects (Bratton & Andrews 1991).

Reedbeds are another of the traditionalists' favourite habitats. However, studies of a broad range of taxa suggest that tradition – which destroys old reeds – is damaging to biodiversity;

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Top A recently coppiced wood, showing timber (habitat) about to be removed or burnt. **Above** A neglected coppice presents a structurally diverse habitat with more ecological niches.

here again, invertebrates were found more likely to thrive under rotational management, or neglect (Bibby & Lunn 1982; Decleer 1990; Tscharntke 1992).

The management chosen should therefore depend on the aims for the site, not on tradition. Experiments are required to devise optimal managements for chosen taxa, with minimal risk to other groups.

Conservationists have often been selective in the types of tradition they support: hunting, for example, is seldom advocated, yet it may lead to woods which are otherwise little disturbed. In marine ecosystems, amongst the most neglected in wildlife conservation, traditional hunting such as lobster-potting is much less damaging than more modern and high-tech scallop-dredging or trawling.

Do species depend on tradition?

It is widely claimed that species 'depend on' coppicing or sheep grazing (e.g. Key 1990). However, such management is unlikely to have

been around long enough, or to have been sufficiently constant, for species to have evolved which depend on it. Coppicing, for example, was performed on a cycle varying from a few years to a few decades, both on the same sites under different owners and in different areas (Peterken 1981). 'Tradition' is difficult to define.

The simpler explanation is that some species have opportunistically exploited extractive agricultural and woodland managements – just as some have exploited modern cereal fields (Speight 1976). The woodland gap and edge conditions coppicing creates from high forest have allowed gap-loving species to usurp the true forest species. A similar process is now being observed amongst butterflies in fragments of rainforest (Lovejoy *et al.* 1986). Other species have spread from cliffs and gaps to the devastated landscapes of calcareous grasslands, where forests have been reduced to a thin smear of life between rock and sun.

Perhaps some species of artificial habitats have now lost their original natural habitats, at least in Britain. However, such early-successional habitats should be easier to re-create, and such species less internationally rare, than the late-successional ones. Some species may have survived here because traditional management prevented woods becoming potato fields, or suffering other short-term exploitation. However, much of Britain's wildlife has survived *despite* traditional management (Sterling & Hambler 1988; Bratton & Andrews 1991).

Just as the 'Noble Savage' of the tropics has come to be seen as an environmental pillager (Coe 1982; Borgerhoff Mulder 1991), we should recognise that the simple traditional practices of Europeans abused habitats for millennia (Hambler 1990), and were certainly not designed to protect biodiversity. Traditional management developed solely to exploit wildlife, and has narrowly failed to exterminate many of our native species (Box 3). If we continue with tradition, some relatively tolerant species will survive; if we replace old methods with management designed to protect wildlife, then we have a better chance of helping our biodiversity into the hands of our grandchildren – and an opportunity to enhance it.

If you look after the plants, will the invertebrates look after themselves?

The belief that management for flowering plants is sufficient has been complemented by the related saying that 'if you look after the butterflies, many other invertebrates will be well served' (B.U.T.T. 1986; see also Warren 1993).

We need to ask, however, if our mere 1,500 vascular plant species, or a trivial 58 species of butterfly, can indicate the requirements of over 28,500 invertebrate species, some 15,000 fungi, and the unknown diversity of British micro-organisms – including protozoa, bacteria and viruses (Anon. 1994)? How many butterflies live under stones, in damp rank grass, in uncut reedbeds, in mud or rotting wood? Far too few to be taken seriously in all-out biodiversity conservation.

Of course, the reasons why sun-loving flowering plants and butterflies achieve disproportionate interest include their conspicuousness and their aesthetic appeal. These are hardly scientific criteria worthy of consideration in choosing management for conservation. Moreover, it is the very atypicality of these groups which makes them appealing to us. It should be obvious that they cannot represent the best interests of the innumerable cryptic, small, soft and moisture-loving creatures and plants. Most invertebrates are smaller than a butterfly's eye.

Again, consideration of the theory of succession dispels the view that we can simply manage for vascular-plant richness. Late-successional habitats will be poorer in these plant species, but generally richer in invertebrates (Southwood *et al.* 1979), micro-organisms and other predominantly shade-loving taxa (Berg *et al.* 1994). Of course, some invertebrates will benefit from management for flowering plants, and short, heavily grazed calcareous grassland supports some plant-specific herbivores and thermophilous invertebrates such as the blue butterflies, so prized by grassland-managers. But, in general, heavy grazing produces a faunistic assemblage more typical of disturbed ground (Gibson *et al.* 1992a, 1992b).

The fundamental reason for a conflict between invertebrate and plant conservation is that most invertebrates, unlike plants and butterflies, do not exploit the sun's energy directly – indeed, it

Frank Blackburn/Nature Photographers

Adonis Blue butterflies, *Lysandra bellargus*, can be common in southern Europe but are rare in the cooler north.

is hazardous to them. Further, invertebrates often live in and on *dead* plant material. Dead wood and dead grass is of little interest to flowering-plant conservationists, except in so much as it may increase soil fertility and so reduce the floristic diversity. Botanists have long dominated conservation management in Britain, yet few appear to realise that some 70% of the energy flow through a terrestrial ecosystem is through the decomposer community, not the herbivores. Thus, as the pretty plants and their specialist herbivores decline during succession, less loved invertebrates (and many vertebrates) start to thrive, many feeding on abundant decomposer organisms, often in the soil.

In aquatic systems, particularly marine ones, the flowering plants do not dictate management. Several of the marine and coastal environments of Britain are of international significance, and support many threatened animal species. They are also the least cared for of all British natural habitats, and many are much more polluted than would ever be tolerated on dry land. There are encouraging signs (in the Marine Nature Conservation Review, and Anon. 1994) that the difficulties of objectively evaluating the relative biodiversity and conservation value of marine sites are being overcome. Sampling methods for aquatic organisms are improving. It has recently been discovered that there are vastly more microorganisms in marine environments than had been imagined – another challenge for biodiversity conservation.

It is only now that major gaps in our predominantly botanical SSSI designations are being filled, where key sites for invertebrates have been overlooked. The importance of pasture woodland for dead-wood invertebrates and for internationally important lichen communities is being recognised (Harding & Rose 1986), as is the importance of our sub-littoral ecosystems. Landscape aesthetics and public access constrain what can be achieved on some of these sites.

Do rare species deserve priority?

The international conservation community sometimes despairs at the parochial British attitude to wildlife. Internationally rare species and habitats, if rare because of man, deserve the highest priority (Anon. 1994): without help, such species and habitats will be lost globally and forever. By contrast, the loss of a species from the northern end of its climatic range in Europe is a problem mainly for a few geneticists, who could study similar issues elsewhere. Indeed, such species may be unnaturally widespread since man cleared the forests.

This dilemma is worse since many species may not be locally rare. This is epitomised by the peculiar situation in a reserve in England, where grassland is being grazed with the intention of encouraging blue butterflies, at the expense of one of the country's largest populations of Great Crested Newts, *Triturus cristatus*. The newts would much prefer long damp grass. Blue butterflies (and that other popular group, the grassland orchids) are abundant in Europe on waste ground and roadsides, whilst Great Crested Newts are in decline even in their last substantial European population – Britain's.

A further problem is that populations on the edge of their range are responsive to climatic changes which may negate or render redundant resources which have been devoted to them. The rapid rise and fall of butterfly populations illustrate this. Our efforts could be better spent on more tractable problems than trying to create the micro-climate of Spain on English grasslands.

Rarity should be assessed *globally*, if consistent priorities are to be set to conserve species from ultimate, not local, extinction. Mature forest, and wetlands, are in decline internationally, as are many of their specialists.

Should management aim to increase diversity?

This problem is complex, because few people distinguish the different ecological definitions of 'diversity' (Box 1). Indeed, since there are many conspicuous species in open habitats, high habitat diversity which includes open areas may lead to a mistaken impression of high species richness.

Should maximum species richness be a goal? Or, given the inevitable conflicts of interest between those interested in different taxa, should some species receive more weight? Scientists are beginning to suggest that some should be treated more seriously than others: 'species quality' counts for more than quantity. Fortunately, the quality of biodiversity in an area may be measured more easily than total biodiversity. If sites with indications of high quality are conserved, then we shall protect a wider range of genetic resources in specialist species.

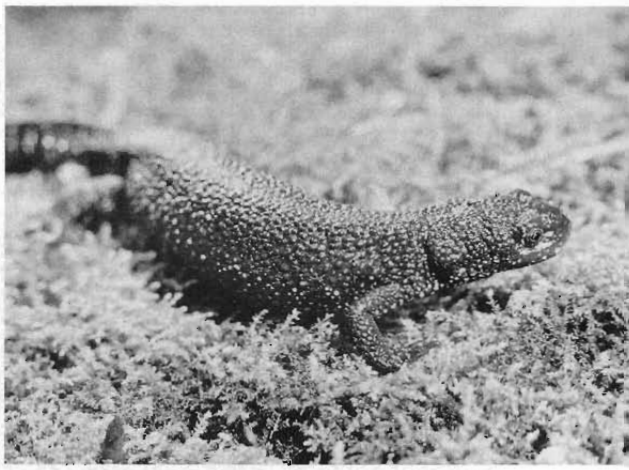
Quality and quantity of biodiversity

The important species are not those which are prettiest, or easiest to see, but include those which are endemic, threatened or are 'keystone' specialists which are fundamental to their ecosystems. These might include burrowing or detrivorous organisms. Researchers and environmental consultants are starting to consider the 'quality' of species on site lists, concentrating on specialist and 'indicator' species and discounting vagrant 'tourist' species, or very common and tolerant species, from measures of community value.

Richness of species and quality of species would not necessarily be expected to correlate, except in late-successional habitats, where interactions between species are stronger. This is because the species of temporary habitats are more mobile than those of established habitats, and mobile species will often be more common and widespread. For various British organisms, Prendergast *et al.* (1993) have already found that rarity and richness do not coincide.

Habitat diversity

High diversity of habitat is clearly an undesirable general goal: the costs and benefits depend on the scale of the habitats. A diverse park or garden may have more landscape or educational appeal



Gary Smith/Aquila

The Great Crested Newt is declining in most of Europe. This species needs undisturbed terrestrial habitat.

than a dense, dark oak or spruce monoculture, and more species of vascular plants – but more specialist, vulnerable, and globally rare species could inhabit the woodland. Mud and sea lochs may not be diverse, but are important habitats.

Coppicing, which turns woodland into glorified scrub, is again a useful example. It is often thought to increase habitat diversity since the rotational cutting of patches of the coppice woodland gives an impression of variety. However, this may be an artefact of the way people see habitats: fractal geometry shows that architectural diversity is scale-dependent, and to many organisms there may be more habitat diversity in a mature woodland although it may seem homogeneous to an animal as large as a human. The smaller the organism, the greater the rate of loss of habitat as felling occurs. A large late-successional habitat, such as a forest with natural treefall gaps, will often have a high habitat diversity – with both very high species richness and quality.

To saproxylic organisms, species requiring large or complex structures, or abundant foliage, coppicing does not increase diversity. Sterling & Hambler (1988) and Waring (1988) have found coppicing damaging to woodland spiders and moths. It may benefit butterflies such as the Pearl-bordered and Heath Fritillaries, *Boloria euphrosyne* and *Mellicta athalia*. However, such butterflies have alternative habitats on woodland edges, rides, and even on grasslands and heathlands respectively (Thomas 1986). Is it ethical to

Box 3 The message from the Red Data Books

The continuing decline of Britain's wildlife resource can be seen clearly in the Red Data Books of British insects and non-insect invertebrates (Shirt 1987; Bratton 1991). The international Red Data Books have for several years proved powerful tools in indicating key sites for global conservation (Collar & Stuart 1988). The same approach can now be used for the 600 species in the British Books for which the habitat requirements are clearest.

Of the 150 woodland species, 65% are threatened by removal of dead wood or old trees. Such 'saproxylic' organisms often require trees which foresters might call 'over-mature', but which are just beginning to be of use to some hoverflies, soldier flies, or click beetles.

Only three species (0.5%) are specifically threatened owing to lack of the commonest traditional woodland management – coppicing. Roughly 20% of woodland species require open conditions (often in Scottish Caledonian relict forests). In deciduous sites open conditions used by some gap-demanding species can be provided on woodland edges and rides, whilst in the native pine forests natural age structures must be encouraged.

Why are woodland invertebrates so vulnerable, both nationally and internationally (Speight 1989; Berg *et al.* 1994)? Specialist beetles, feeding on the scarcely nutritious dead wood, take several *years* to mature, and have poor powers of dispersal because their food supply is very abundant and continuous in extensive natural forests. They are suffering the fate of similar late-successional specialists and K-selected species globally.

Charles Elton stated (1966) that when we remove the dead wood in our over-tidy management 'we remove one of the two or three greatest resources of the woodland habitat'. Practitioners often ask how much dead wood should they leave. About *half* the timber in a British forest should be dead or dying, to judge by more natural forests in Europe. Numerous invertebrates require fungi, mosses, tree-holes, loose bark and other habitats available continuously only in large woods.

Unsurprisingly, the greatest proportion (35%) of the Red Data Book invertebrates are wetland species threatened by drainage, pollution and other habitat losses. Wetlands and woodlands are the major habitats which have been largely eliminated from the British landscape. The species requiring large wetlands are confined to tiny relicts of what must have been a gloriously wet natural landscape. The British love the sun, but our native wildlife requires the rain! When evaluating and managing ponds, the Red Data Books should be considered – ponds are too often styled according to fashions or favourite taxa.

Grassland species in the Red Data Books are often specialists of short grass, which has become very local in Britain since myxomatosis decimated the rabbits. Most are common in Europe.

How fast are we losing species? Between 1900 and 1987, 43 species appear to have become extinct amongst the taxa covered by the Insect Red Data Book (64% of the insects). This extrapolates to one insect species becoming extinct in Britain nearly every other year. Since each may carry specific endoparasites, and other major taxa such as fungi are also declining, we may be losing biodiversity at a rate of over one species a year.

'diversify' or create habitat for them at the expense of the woodland species such as the epiphytic 'lower' plants – the true natives of much of our landscape, with nowhere else to go except extinction? Woodland nature reserves are supposedly secure as woodland habitats – and large ones are the best places to aim for true forest conservation. Common habitats should not be created from rare ones to increase diversity.

A further problem with habitat diversity is that it may be created at the expense of large, homogeneous blocks of habitat between small habitat fragments, and therefore more edges are created. In some circumstances, edges are beneficial, but a rapidly increasing scientific literature suggests that organisms of the edge and matrix around a habitat can be inimical to those of the interior.

Woodland specialists and edge effects

Woodland, once the dominant habitat of Britain, now covers about 10% of the land. If we want to conserve the ecological processes of forests, woodland specialists should be given priority over species which have a greater range of potential habitats, and which are more tolerant of stressful, open environments. Woodland interiors are coming to be seen as very different from their edges (Soulé 1986; Laurance & Yansen 1991). Edge biology has enormous implications for the shape of woodlands, and the positions of clearings such as rides and roads within them.

Studies of British woodlands using advanced environmentally benign 'knockdown' sampling methods have shown that forest-specialist invertebrates may suffer in a way similar to the forest-specialist birds of the Americas when their habitats are fragmented (Ozanne 1991). Specialists decline rapidly near the woodland edge, and are rare on isolated trees. These results are supported by work on the ground faunas of woods near York (Usher *et al.* in prep.). We have found that detrimental edge effects penetrate at least 25m into an Oxfordshire conifer woodland (Ozanne *et al.* in press). Further studies will clarify whether this is a general pattern of relevance to minimum forest sizes and corridor widths.

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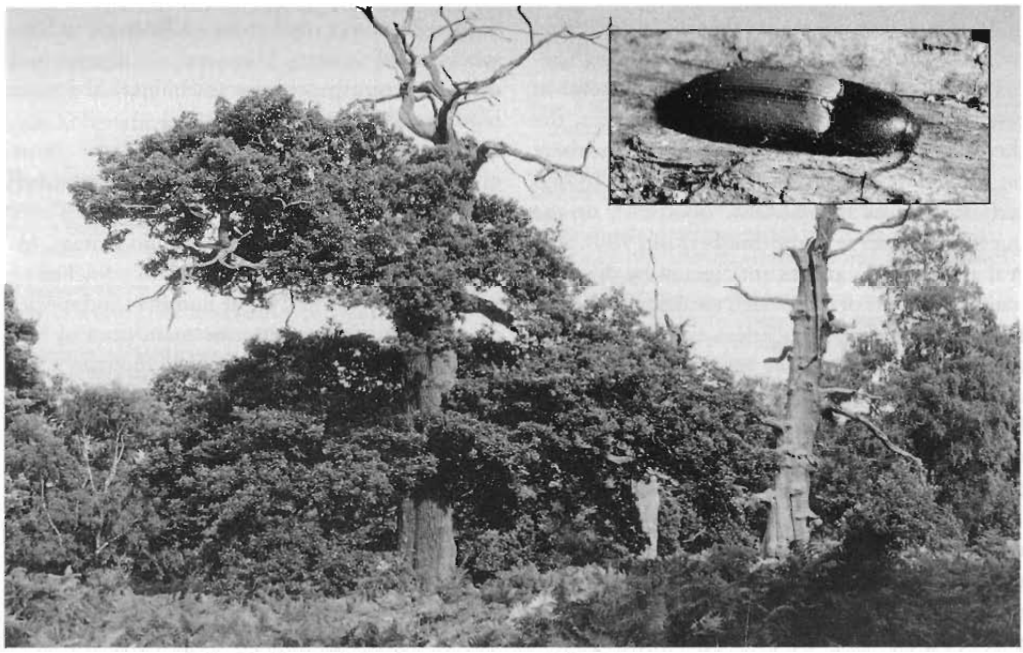

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Old hollow trees, such as these in Sherwood Forest, are important for saproxylic invertebrates. **Inset** *Ampedus cardinalis*, a Red Data Book species of click beetle which depends on rotting oaks.

Britain has presumably lost most woodland-specialist mammals and birds which inhabited its great forests before they were destroyed: few vertebrates thrive on short grass, and the species that live in forest gaps generally are mobile and have alternative habitats. Many birds require tree holes and dead wood, and there is a paucity in certain elements of our avifauna (such as woodpeckers) in comparison with larger and more natural woods in Europe. Unfortunately, we cannot be sure what we have lost. Are we still losing specialist invertebrates? Examination of the Red Data Books shows that we are (Box 3; also Kirby & Drake 1993).

Other dogmas, old and new

Several common phrases echo around debates on conservation. 'We should let in more light' suggest the botanists, unaware perhaps that the high surface-volume ratios of most micro-organisms and invertebrates render them vulnerable to the environmental stresses of open habitats. A dead tree in the sun is only slightly more use than no dead tree at all, since it will tend to petrify rather than become a home for decomposers.

'Set-aside (ex-arable) land should be in strips' may be a fledgling modern dogma supported by the idea of corridors. But the corridors will not be adequate for the species that need them most: the late-successional, poorly dispersing, edge-sensitive, K-selected species which are most at risk on land in Britain. These will not be functional corridors to many saproxylic organisms. Better perhaps to have large blocks of grass or heath or real woodland than strips, which will be of as little use to specialists as are cereal fields. Ironically, field-edge habitats may be worse than none at all, if predation and other edge effects now being discovered in temperate and tropical America (Soulé 1986; Laurance & Yansen 1991) are general ecological phenomena. We already know that small heathlands do not support true heathland communities, but are influenced strongly by vagrants (Webb 1989).

'Conifer monocultures are poor for wildlife' is another view which may soon change. Studies of exotic plantations in southern Britain have shown that, when the previously neglected tree canopy is sampled, woodland specialists and other invertebrates can be found in very great abundance (Ozanne 1991). Conifer leaves live a long time, and present a lot of cover even in winter, and many inconspicuous animals graze the microfungi on their surfaces.

An interesting dogma, in that it is propagated by many scientists, is that the Equilibrium Theory of Island Biogeography (ETIB) is useful in reserve design (Diamond 1975). However, the theory actually contributes nothing to the debate on single large or several small reserves (popularly known as the 'SLOSS' question), or the question of reserve shape (Simberloff 1986). Several assumptions are, as anticipated by the original proponents of the model, unrealistic. Worse, ETIB predicts species richness, not quality. Fortunately, modern studies revealing the importance of perimeter/area and edge/core ratio effects have generally led to the same conclusions as those claimed to be derived from ETIB, and can predict the abundance of specialists (Temple 1986; Laurance 1991). We have perhaps ended up with the right general strategies for the geometry of reserves (large and circular) but for the wrong reasons! At least searching for equilibria made us think. Similarly, 'metapopulation' models ignore edge effects. Doubtless, other dogmas will come and go, but science should reduce the duration and impact of each.

Conclusion

With increasing amounts of Britain's wildlife coming under the control of a few landowners and conservation groups, the diversity of land management itself may decline. It is therefore crucial that conservationists keep up with and employ research in ecology. Recent conferences, and the Biodiversity Action Plan (Anon. 1994), suggest that communication between practitioners and researchers is improving. Researchers have often found their results unpalatable to practitioners, but should not give up collecting and disseminating them. Practitioners must come to appreciate the scope of their responsibilities to wildlife in its fullest sense, and be less swayed by their fondness for charismatic species.

Conservationists should always remember what Charles Elton (1966) called the 'importance of Cover'. As structural complexity increases, so does the microclimatic amelioration, and so does the availability of sites and plant structures suitable for animals' oviposition, overwintering, web-building, crypsis, courtship etc. There is more damp material for decomposers, more substrate for microbes, more prey for predators. There is simply more niche space in late-successional habitats. In general, the damper and more structurally complex the habitat, the more biodiversity it can support.

Therefore, most organisms become more numerous as succession proceeds. In marine systems, this can be witnessed by snorkelling over sub-littoral rocky substrates around Britain. Invertebrates and micro-organisms (including viruses) form the bulk of the numbers and species of organisms in any site: the main pool of biodiversity; these will increase until biomass accumulation stabilises naturally – a point seldom reached in Britain, where traditional and other managements interrupt successions. Late-successional and damp habitats are often heavily exploited. Biodiversity conservation should emphasise these habitats, and, although a case can of course be made for conservation of early-successional stages as well (Usher 1993), we suggest that the philosophy of conservation will be more consistent if we see a paradigm shift to give late-successional environments more emphasis.

Biodiversity is so immense, even in temperate regions, that we cannot hope to elucidate the individual requirements of all the species we wish to conserve. In a search for tractable, yet biologically sensitive indicator species, the birds are emerging globally as a valuable tool to short-cut some of the research required. The ICBP biodiversity programme shows the way forward (ICBP 1992). But for smaller areas, birds cannot represent all the fungi, microbes, protozoa and invertebrates that comprise most of our biodiversity. Other groups, such as leaf miners and spiders, can represent some specialists on plant species and structures (Sterling *et al.* 1992; Sterling & Hambler 1988), whilst ancient-woodland indicator beetles can contribute by revealing a historical continuity of woodland habitat (Harding & Rose 1986; Speight 1986).

Finally, we expose ourselves to accusations of hypocrisy from other countries if we encourage them to protect their forests, while recommending that we continue to chop down our own by traditional methods. We should submit a scientific, not traditional, approach for the world's scrutiny. Scientific paradigms may be challenged more often, and be less damaging, than those of dogmatists – and may slow the loss of British

species. However, a diversity of conservationists may benefit biodiversity, and the intensity of the current debate about such controversial issues should benefit wildlife in general.

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