Reversing the habitat fragmentation of British woodlands

by George Peterken

January 2002
About the report

This report is about habitat fragmentation, the damaging effects it has had on wildlife, and the measures that can mitigate its effects. It refers particularly to British woodland – the habitat that once covered the land, but which has been fragmented for millennia. Its aim is to show that conservation of woodland wildlife requires more than a scatter of nature reserves combined with benign policies in woodlands managed for other objectives. In particular, woodland conservation will always be limited until the effects of habitat fragmentation are overcome by re-connecting the fragments. We need “joined-up woodland” just as much as we need joined-up government.

Reversing woodland habitat fragmentation involves five almost distinct processes:

- retaining all or most of the existing woodland;
- increasing the amount of woodland;
- ensuring that the additional woodland is distributed in such a way that it links existing woodland;
- developing forms of woodland management that allow woodland species to experience and use existing and additional woodland fully; and
- designing grassland and other non-wooded habitats to have a close association with woodland.

The sum total of these processes can be labelled “restoring a forest habitat network”. The word “forest” is chosen instead of “woodland” because it accurately conveys the large scale of the enterprise and, like the medieval forests of Britain, clearly encompasses wooded ground and other habitats.

This report comprises four main parts. It:

- describes forest fragmentation, the natural forest and woodland species;
- assesses the impacts of fragmentation on woodland species;
- considers how fragmentation might be reversed by building a forest habitat network; and asks “how well have we been doing?”

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Forest management and silviculture 45
Other habitats within a forest habitat network 46

4 How well are we doing? Past and present policies as a means of generating a network 48
Changes during the 20th century 48
Conservation agencies 50
Current forestry strategies 51

Conclusions 55

Action points 57

References 58
Summary

Britain’s native woodland is rightly described as a fragmented habitat. Originally, natural forests covered perhaps 85-90 per cent of the land, but by the 11th century, clearance had reduced them to 15 per cent in England. Today, the remnants – the ancient woods – cover no more than 1.4 per cent of the land surface. The original, natural woods of England and Wales comprised a single forest of approximately 13.5 million hectares, but now the remnants have been broken up into 28,000 separate woods, only 17 per cent of which extend to more than 20 ha.

Some of the habitats within woodland have been fragmented even further, in particular old stands of great trees with large volumes of dead wood: such old-growth stands were once widespread in natural woodland, but they are now confined to a scatter of specialised woods in forests and parklands. A similar transformation has been wrought in Scotland.

This fragmentation has had profound effects on the native fauna and flora. Woodland species have been much reduced; large mammals, such as bear, wolf and wild cattle, have been exterminated; and the populations of the less mobile species have been broken up into a scatter of separate sub-populations, between which there is little exchange of individuals.

Genetic changes following isolation have forced some species with an inherently slow colonising ability to become even more sedentary. Balances have been shifted between the species that remain: species associated with young stands and edges have prospered relatively, while those associated with mature stands, large pieces of dead wood and the sheltered interiors of forests, have declined disproportionately. In general, ecological isolation between the fauna and flora of individual woods and between the sub-populations of woodland species has become excessive and sustained.

The habitats that replaced woodland provided opportunities and refuges for some woodland species in pastures, meadows, hedges, stream banks and even buildings. The existence of these semi-woodland habitats between woods mitigated ecological isolation. For a proportion of woodland species, the landscape remained an unbroken massif of suitable habitat. Unfortunately, the agricultural intensification of the 20th century has greatly reduced the quality of farmland habitats. The remaining native woods are now more isolated than ever.

This report proposes that a concerted effort should be made to reverse this fragmentation, i.e., to re-connect woodland habitats. New woodland is needed to expand existing woods and fill the gaps between them, thereby allowing more movement of woodland species across the landscape. At the same time, semi-woodland habitats need to be restored on farmland, and woodland in general should be managed to maintain a wide variety of stand structures and ages. All the new components should be located where they will maximise the connections with and between existing woods. Taken together, these elements of “defragmentation” amount to the development of a forest habitat network.

Forest habitat network development has effectively been in progress for 200 years or more. New woods and hedges were created in the 18th and early 19th centuries. Since 1895, the total forest cover of Britain has increased from about 4 per cent to about 11 per cent – but these...
Reversing the habitat fragmentation of British woodlands

developments have not been efficient at reducing ecological isolation. Many early plantations took the form of small, scattered patches remote from the ancient woods that would have supplied them with woodland species if they had been closer. During the 19th and 20th centuries, huge areas of ancient woodland were cleared for agriculture, thus depriving the new woodlands even further of the source populations of woodland species. The 20th century afforestation did at least generate large forests, but they were also mostly remote from ancient woods, and ecological development was restricted by the predominance of poor soils and evergreen conifers.

Today, ecological research underpins the design of forest habitat networks. There is a need for Core Forest Areas, large forests and dense clusters of woods which harbour large and diverse populations of woodland species. These need to be connected by well-wooded belts of countryside, concentrated mainly along rivers and streams, the natural links in the landscape. Throughout, the 30 per cent rule should be applied. Thus, woodland should cover at least 30 per cent of the land within Core Forest Areas and landscape-scale links, for this is the minimum proportion at which the landscape starts to function as if it were a single, large wood for most woodland species.

Individual woods would still be present, both within the network and isolated from it. They need to be enlarged until they exceed the minimum sizes needed to sustain a diverse fauna and flora – approximately 25ha for managed woods and 50ha for minimum intervention reserves. Most woodland needs to be managed to sustain a complete range of age-classes, which incorporates a pervasive element of mature and veteran trees. This will allow the whole network to be experienced as well-connected habitat, even by species with specialised habitat requirements.

The 30 per cent rule emphasises that a forest habitat network would not comprise fence-to-fence woodland. Not only would up to 70 per cent of the ground be unwooded, but grassland, heathland, marsh, etc would also be integral parts of the forest. In fact, “forest” should be understood in its traditional sense as extensive tracts with a mosaic of semi-natural habitats of all kinds, both wooded and unwooded. This is the essence of the “wildscape” or “wildlands” projects that feature in the thinking of the Woodland Trust, and have even been promoted to trans-continental travellers in British Airways’ *High Life* magazine (February 2000).

Forest habitat network development is a matter of decades and centuries. This is inevitable: it takes at least 10 years for new plantations or natural regeneration to develop woodland conditions, 50 years or more for a stand to appear mature, and 100-150 years for large trees and large volumes of dead wood to accumulate. Experience of new woods formed in the past shows that many woodland species move in only slowly over decades, even if the new wood is close to an ancient wood. And, if the new wood is isolated, they may take hundreds of years to colonise. Nevertheless, the long-term benefits outweigh the disadvantages, the short-term benefits are worthwhile, and a start has to be made sometime.

The case for, and the design of, a forest habitat network has been developed around the needs for wildlife. In this respect, it is particularly urgent now because of the 20th century combination of (i) an increase in isolation resulting from agricultural intensification, and (ii) the threat of climatic change, which will require species to adjust their ranges. There would, however, be numerous other benefits, such as opportunities for increased production of quality
hardwood timber, improvements in water quality, long-distance recreational facilities such as walking or cycle tracks, and improvements in property values and urban-rural links.

The concept of a Forest Habitat Network has been incorporated in the current Forestry Strategies of the Forestry Commission in England, Scotland and Wales. Current measures on the ground, especially in Scotland, promise a substantial increase in diverse, multi-purpose forest land in accordance with network design principles. If this effort can be sustained and complemented by restoration of habitats within farmland, Britain’s forest wildlife should become more diverse and resilient in the face of change, and foresters will have greater freedom of management, less restricted by the need to protect relict and otherwise vulnerable populations of native wildlife.
1 Forest fragmentation and its ecological effects

**ORIGINAL-NATURAL FORESTS**

In order to understand the benefits of restoring a forest habitat network, it is helpful to know the principal features of the natural woodlands from which some of our present woodland developed, and in which our woodland wildlife evolved.

Woodland once covered the great majority of the land. Until the Mesolithic peoples started to clear land more than 5,000 years ago, it had developed naturally into a great forest covering perhaps 85-90 per cent of the ground. Other habitats existed as islands (e.g. lakes; montane habitats above the treeline), narrow corridors (e.g. riparian habitats along the major rivers) and on the margins (coastal habitats).

The amount and pattern of unwooded habitats within this matrix of lowland woodland is uncertain. Marshes and bogs remained largely treeless on permanently wet ground, and in a few places inland cliffs and rock outcrops were large enough to remain at least partly open – but the big unknown is the extent of grassland within the woodland (box 1.1).

The best assumption is that some grassland was present, maintained by large herbivores, and that it was found mainly on fertile ground, where vigorous growth of the herbage would have competed strongly with tree seedlings, and would have attracted herbivores. On slopes and thin soils, ground vegetation would have been less vigorous, and the balance would have shifted towards tree growth.

**Box 1.1**

**Natural woodland as wood pasture?**

In recent years, Dutch conservationists have developed a hypothesis that original-natural woodland was more like wood-pasture than dense, closed high forest (Vera 2000). They have formed the view that large herbivores such as bison, cattle, horses and deer, would have maintained substantial tracts of grassland within the forest. Natural woodland therefore comprised a mosaic of (i) open grassland, (ii) scrub developing from grassland into woodland, (iii) groves of dense woodland, and (iv) degenerating groves, where herbivores combined with shade to prevent regeneration. The vegetation at any particular point would pass in a cycle from grassland through scrub to closed woodland and back to grassland again. All grassland and groves would be transient, although grassland and groves would always be present somewhere.

There is evidence for and against this hypothesis. In any case, it seems more likely that natural woodland comprised both closed high forest and more open wood-pasture, and that the debate will be about (i) how much ground was open, (ii) whether some groves and some patches of grassland might be permanent, and where these might be in the landscape, and (iii) the scale of the patchwork.

However this debate is resolved, we should recognise that the sharp and almost permanent divisions in the modern landscape between woodland and other habitats may be an artificial feature and an expression of property boundaries and modern land management, not natural processes. Any attempt to reverse woodland habitat fragmentation must incorporate a more natural integration of woodland, grassland, heathland, marsh, etc.
The structure of the natural woodland probably varied. On permanently wooded ground it would probably have taken the form of dense groves of tall, slender trees, punctuated by gaps where an old tree or a group of trees had died, or had been blown down. Old gaps would be filling with new saplings, and the forest overall would be a patchwork of groups of different ages, each corresponding with a former gap. Extensive even-aged stands would also be present where storms had once blown down swathes of mature trees. Within this dense woodland, shade-bearing species such as lime, beech and wych elm would be abundant, mainly because they could regenerate in shade. A few trees survived to great age, perhaps 500 years, but most would have been unexceptional by modern standards.

Other parts of the natural forests would probably have been more open. Wooded groves would have been bordered by scrub, and some individual trees could have grown spreading crowns and large short trunks, much like modern parkland trees. Fluctuations in grazing and browsing pressure would have allowed some grassland to develop into scrub and thence into closed woodland. In this open woodland, light-demanding trees that can regenerate in grassland (notably oak) would have been common, and shrub species such as hazel and hawthorn would have grown vigorously on the edges.

**THE CHARACTER OF FOREST WILDLIFE SPECIES**

Whatever the balance between closed and open woodland, several important points stand out for woodland wildlife:

1. Wooded habitats were well-connected. Any species that depended on trees or dense woodland could move through the landscape without having to cross hostile territory. This applied both to individual birds and mammals, and to populations of all kinds of wildlife. If any new habitat came available, it could quickly be occupied. If any species lost ground through a disturbance or in competition with other species, it could readily recover lost ground when conditions again became favourable.

2. Wooded habitats were extensive. Those species that naturally exist at low density were still present as populations connected over large areas. Likewise, species with large territories and home ranges (such as the large mammals) had enough contiguous space in which to maintain viable populations.

3. Natural forest contained substantial amounts of dead wood and large timber. Dead wood would have been present in a variety of forms, from fallen wood littering the ground, through standing dead trees, dead branches on living trees, to rotten heartwood in large trunks and branches. This would provide habitats for wood-rotting fungi, wood-using invertebrates, hole nesting birds, and mammals using hollow trees as dens.

4. Natural forest also contained a wide range of microclimates. Whereas some trees would have been deeply shaded, others on the edge of gaps and grassland were well-lit. Likewise, humidity ranged from moist to parched. This, together with large old trees, provided habitats for a wide range of bryophytes and epiphytic lichens.

5. Edge habitats and low scrub were widespread. In modern managed woodlands, edges form some of the richest habitats for wildlife. Equally, species did not have to be associated solely with trees and dense woodland. Many could make use of two habitats, such as green woodpeckers that nest in old trees, but feed on grassland.
Species most strongly associated with grassland or other treeless habitats were an integral part of natural forests. The modern habit of classifying species by their habitats would have been more difficult. Furthermore, in some parts of the landscape, grassland, marsh and other habitats would have been as well-connected as the woodland or tree habitats. The whole assemblage of wooded and unwooded habitats can be envisaged as an intimate, well-connected mosaic.

The distinctive character of forest species can be appreciated by comparison with those of other habitats. Species that occupy isolated habitats such as lakes, or frequently disturbed habitats such as rivers and coasts, had to be good colonists, capable of reaching suitable ground by crossing hostile wooded habitats. The species of trees and woodland, on the other hand, tended to occupy the same ground indefinitely; they did not need to be good colonists to survive. Of course, there were exceptions, in particular the species that occupied gaps in dense forest. These, too, had to react quickly when gaps were created, and thus developed either excellent powers of colonisation, or a capacity to survive for decades as dormant seed in the soil.

HABITAT FRAGMENTATION

Habitat fragmentation comprises four processes: habitat loss, which results in the reduction in the total extent of the habitat; reduction in the patch size of the habitat remnants; an increase in the number of surviving patches; and an increase also in the distances between them. Obviously these processes are linked – for example, patch size cannot be reduced without some woodland clearance – but not absolutely. Thus, it would be possible for a habitat to be pared away from the edges, in which case the number of habitat patches remains at one, and all the remaining habitat stays well-connected.

In the last 5,000 years or so, the great majority of the original woodland has been destroyed (table 1.1). In its place we have farmland, cities, roads, quarries and so-on. Most of this destruction occurred in prehistory, and by the time of the first woodland census – William the Conqueror’s Domesday Book of 1086 – it would be a fair assumption that Britain was largely unwooded. While the Domesday Book contains few details about woodland, it does provide a general picture of woodland distribution across most of England. Its data supports the calculation that between 15 and 20 per cent of Norman England was wooded, all of which is thought to have been managed by that time (Rackham, 1976; Miles, 1999).

There would, however, have been significant variation in density of this cover across the country. Clearance continued at intervals throughout the last millennium, and woodland reached an all-time low towards the end of the 19th century, when it occupied no more than 4-5 per cent of the land. Since then, the amount of woodland has multiplied almost threefold, mainly by the addition of large tracts of spruce plantations in the uplands, but Britain still remains one of the least wooded counties in Europe.
Table 1.1. Long-term changes in the proportion of Britain occupied by woodland.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total woodland area (% of land area)</th>
<th>Area of primary or ancient. Semi-natural woodland (% of land area)</th>
<th>Area of coniferous woodland (% of all woodland)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3000 BC</td>
<td>85</td>
<td>85</td>
<td>15</td>
</tr>
<tr>
<td>AD 1086</td>
<td>15</td>
<td>5-10</td>
<td>20</td>
</tr>
<tr>
<td>AD 1895</td>
<td>4</td>
<td>2</td>
<td>25</td>
</tr>
<tr>
<td>AD 2000</td>
<td>11</td>
<td>1.5</td>
<td>70</td>
</tr>
</tbody>
</table>

Source: Peterken (1996:301)

The remnants of the original woodland (primary woodland) are difficult to identify precisely, but they are all contained within the ancient woods, and in many districts it is quite possible that most of the ancient woodlands are primary (box 1.2). Ancient woods, which contain both primary woodland and the secondary woods that originated before 1600, cover just 1.4 per cent of the land (Great Britain). The difference between this and the original 85-90 per cent cover is the true measure of total forest habitat loss.

Box 1.2 Definitions

**Primary woodland:** Land that has been wooded continuously since the original-natural woodlands were fragmented. The character of the woodland varies according to how it has been treated.

**Secondary woodland:** Woodland on land that has been cleared of woodland and used as pasture, cultivated ground etc, at some time since the original-natural woodlands were fragmented.

**Ancient woodland:** Woodland that has existed continuously since at least 1600. These woods will comprise both primary woods and secondary woods originating before 1600.

**Recent woodland:** Woodland that has originated on farmland, abandoned quarries etc, since 1600.

**Semi-natural woodland:** Stands comprising mainly locally native tree trees and shrubs that have mostly originated by natural regeneration or regrowth from stumps, and/or have achieved a mature structure.

The 534,000 ha of ancient woodland in Britain *(Spencer and Kirby 1992, Roberts et al 1992)* might have taken the form of a single very large forest, in which case there would have been no forest habitat fragmentation. In fact, the provision inventories pioneered by the Nature Conservancy Council found 28,000 distinct ancient woods in England and Wales (box 1.3), where the vast majority were small: some 83 per cent of all ancient woods were 20 ha or less, and that did not even count the many that were less than 2 ha.
Box 1.3 the inventory of ancient and semi-natural woods

The Inventory set out to list all the ancient woods of England, Wales and Scotland, and to determine how much of each was semi-natural, and how much was occupied by plantations. Inevitably, the results are provisional: woods not only change, but information sources are incomplete, and there are many woods that fall uncertainly between ancient and recent, and semi-natural and plantation.

When first completed, the Inventory listed 27,688 separate ancient woods in England and Wales totalling 397,702 ha (Spencer and Kirby 1992). Of these, 24,058 woods contained at least some semi-natural stands, and semi-natural stands totalled 236,650 ha. Most woods were small: 12,173 were less than 5ha, and only 500 extended to more than 100 ha. Since the 1930s, 32,001 ha had been destroyed, mostly by clearance for agriculture. These figures have since been revised as new information has become available, but the broad picture remains unchanged.

Information sources in Scotland differed from those in England and Wales, and the woods themselves naturally have a more mobile character. Some 136,126 ha of ancient and long-established woodland of natural origin before 1750 were identified, of which 80,024 ha remained semi-natural (Roberts et al 1992). In addition, these were 18,792 ha of semi-natural woodland growing where there had been plantations in about 1850. Subsequently, Neil Mackenzie in reports to the Forestry Commission found 227,694 ha of woodland dominated by native trees, most of which was in the Highlands.

Thus, the original-natural woodland of England and Wales that once comprised a single forest of approximately 13.5 million hectares has become at least 28,000 separate fragments, only 17 per cent of which extend to more than 20 ha (Spencer and Kirby 1992). Only 500 fragments (i.e. individual woods) extended to more than 100 ha, and very few were larger than 500 ha. On paper, the largest are some of the Highland pinewoods, the remnants of the Ancient Forest of Caledon, which extend to 3000 ha or so, but on closer inspection these are seen to be clusters of separate woods. Some large individual woods survived in England as Royal Forests – Salcey Forest and Wychwood, for example. Other large remnants include the woodland concentrations of southern England and the Welsh Borders such as the Chilterns, Epping Forest, the New Forest, the Weald and the Lower Wye Valley, where several historically distinct woods remain contiguous over several hundred hectares.

Outside these woodland concentrations, ancient woodland covers a small fraction of the landscape. The sample shown in table 1.2 is typical: the amount of woodland, the relative importance of ancient woodland, and thus the distances between ancient woods, all vary substantially from one natural area to another. Large clusters remain in, for example, Rockingham Forest, central Lincolnshire (box 1.4) and along the Cotswold scarp. Most districts have some ancient woods, and these are often clustered on parish boundaries or, in the uplands, along the slopes of main valley sides (fig. 1.1). Some districts have none or few.
Table 1.2. The proportion of land occupied by woodland in the natural areas of part of south-west England

<table>
<thead>
<tr>
<th>Natural Area</th>
<th>Ancient woodland (% of land area)</th>
<th>All woodland (% of land area)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blackdowns</td>
<td>2.2</td>
<td>10.1</td>
</tr>
<tr>
<td>Devon Redlands</td>
<td>0.7</td>
<td>2.9</td>
</tr>
<tr>
<td>Exmoor and the Quantocks</td>
<td>7.0</td>
<td>18.1</td>
</tr>
<tr>
<td>Mendip Hills</td>
<td>3.8</td>
<td>9.1</td>
</tr>
<tr>
<td>Mid Somerset Hills</td>
<td>2.0</td>
<td>4.2</td>
</tr>
<tr>
<td>Somerset Levels and Moors</td>
<td>0.3</td>
<td>1.1</td>
</tr>
<tr>
<td>South Wessex Downs</td>
<td>5.1</td>
<td>10.8</td>
</tr>
<tr>
<td>Thames and Avon Vales</td>
<td>7.0</td>
<td>9.7</td>
</tr>
<tr>
<td>Vale of Taunton and Quantock Fringes</td>
<td>1.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Wessex Vales</td>
<td>3.2</td>
<td>6.8</td>
</tr>
</tbody>
</table>

Source: Purdy and Ferris (1999). The values quoted apply only to those parts of the natural areas falling within the study area.

Box 1.4 Central Lincolnshire woodlands: fragmentation history in relation to wood size

Most of the 89 historically distinct ancient woods in central Lincolnshire are remnants of woods that were larger in historical times. Using a logarithmic size scale:

Two woods of 0.3-1 ha. Both are marginal belts of woods that have been almost completely cleared.

Eight woods of 1-3 ha. Small discrete woods, all the remnants of woods that were known to be much larger in the Middle Ages.

Seventeen woods of 3-10 ha. Small woods, most of which were larger in historical times. Two may be small medieval woods that have survived intact.

Thirty-eight woods of 10-30 ha. Medium-sized woods, some of which are parts of larger clusters. Most are known to have been larger: no more than six show no sign of size-reduction in historical times.

Nineteen woods of 30-100 ha. Larger woods, of which up to 11 may be historically intact.

Five woods of 100-300 ha. Large woods by British standards, but no more than two are historically intact.
Fig. 1.1 The pattern of ancient woodland typical of upland (a) and lowland (b) England.

Source: Spencer and Kirby (1992), reprinted from Biological Conservation, Copyright (1992), with permission from Elsevier Science.

The upland example from the river Coquet catchment in Northumberland could become a dendritic network of woods by infilling the gaps along valley sides. The lowland example, from the north-east of Oxford, shows the strong clustering of ancient woods by parish boundaries. These clusters could be reinforced into small Core Forest Areas by planting alongside or close to existing woods.
**IMPACTS OF FOREST FRAGMENTATION ON HABITATS**

The woodland was replaced by farmland, villages and towns. In terms of habitats, this comprised cultivated ground, artificial habitats such as walls and buildings, and a variety of semi-natural non-woodland habitats such as pasture, meadow, heathland and marsh. The semi-natural habitats probably had near-equivalents in original woodland, and walls would have been roughly equivalent to rock faces, but cultivated ground had no counterpart in natural conditions.

The fundamental change was the transformation of woodland from being the matrix in which other habitats survived as minority, often isolated, habitats, to a new status as island habitats within a matrix of non-woodland habitats. Moreover, the boundaries of woodlands were sharply defined, often with a bank surmounted by a hedge, so the gradual transitions of natural woodland boundaries were severely narrowed. This transformation has reached its logical conclusion in East Anglia and Lincolnshire, where the ancient woods remain as sharply-defined blobs in an arable landscape that is now almost devoid of hedges, hedgerow trees and grassland.

This transformation was mitigated by the presence of semi-woodland habitats within farmland (Box 1.5). This is a cumbersome term that recognises the presence of habitats that have some of the features of woodland, and which provide refuges in farmland for some woodland species. Hedges and trees in farmland are the prime examples, but other less obvious habitats are stream and river banks, which are often shady and moist, and rock outcrops, which provide shaded refuges from grazing. Meadows are another kind of semi-woodland habitat that, like deciduous woodland, provides favourable conditions for spring-growing species that dislike grazing (e.g. wood anemone). In fact, most semi-natural habitats provide opportunities for some woodland species.

**Box 1.5 Semi woodland habitats**

Habitats that are not mapped as woodland, but which provide suitable conditions for some woodland species.

- Hedges
- Non-woodland trees in hedges, fields, moorland, riversides, etc
- Streamsides, especially shaded streams flowing in natural courses
- Rock outcrops
- Limestone pavements
- Sea cliffs and ungrazed mountain ledges
- Meadows
- Bracken
- Undergrazed pasture with spreading scrub

**TREATMENT OF REMNAT WOODLANDS**

The remnants of the original woodlands survived because they were useful. Two main forms of usage can be recognised *(Rackham 1976, 1980)*:

1. **Wood-pastures**: These woods were used as both pasture and sources of wood simultaneously. Deer, cattle, sheep, horses and goats were allowed to range freely among
the trees, and the trees were lopped for wood and leafy fodder. Tree regeneration was inevitably limited in the presence of so many grazers and browsers, but the trees that did get through could grow to great sizes. Today, we recognise wood-pastures and woods that were once wood-pastures by their ancient pollard trees. One of the finest surviving examples in Europe is the New Forest.

2 **Coppices:** These woods were repeatedly cut to the ground, then allowed to grow up again from the stumps. The yield in brushwood and small poles was used as fuel and other applications in the agricultural community. The intervals between cutting were anything from three years to 50 years, but were usually between five and 25 years. Whatever the interval, the woods remained a patchwork of thickets (the “underwood”) of various ages. Some trees (the “standards”) were allowed to grow for 60-80 years to form timber, which was used in larger constructions such as house frames and ships. Most standard trees were oaks, but the underwood was a mixture of species such as hazel, ash, lime, hornbeam, alder and whatever else happened to grow.

Fig. 1.2. Comparison between the components of natural and traditionally managed woodland

<table>
<thead>
<tr>
<th></th>
<th>Natural woodland</th>
<th>Wood pasture</th>
<th>Coppice</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stand structure</strong></td>
<td>Closed, with small gaps. Mature</td>
<td>Parkland Geriatric + scrub</td>
<td>Shelterwood Immature</td>
</tr>
<tr>
<td><strong>Dead wood</strong></td>
<td>Abundant Fallen and standing</td>
<td>Abundant Mainly decay columns</td>
<td>Limited Ancient stools</td>
</tr>
<tr>
<td><strong>Canopy composition</strong></td>
<td>Mixed Changing composition</td>
<td>Simple Mainly oak</td>
<td>Simple Mainly oak</td>
</tr>
<tr>
<td><strong>Underwood</strong></td>
<td>Patchy Changing structure Changing composition</td>
<td>Sparse Dense Dynamic stable structure Mixed stable composition</td>
<td></td>
</tr>
<tr>
<td><strong>Ground vegetation</strong></td>
<td>Mixed shade herbs</td>
<td>Pasture species Mixed shade herbs</td>
<td></td>
</tr>
<tr>
<td><strong>Open ground</strong></td>
<td>Grazed glades Canopy gaps</td>
<td>Pasture matrix Rides Felling coupes</td>
<td></td>
</tr>
</tbody>
</table>

These traditional forms of utilisation can be compared with the original-natural woodlands (Fig. 1.2). The large trees, accumulations of dead wood and grassy openings of the original woodlands survived mainly in the wood-pastures. The woodland ground flora, the intimate mixtures of trees and shrubs, and the dense thickets of young-growth woodland survived mainly in the coppices. In a sense, therefore, the components of original-natural woodland were teased apart: they survived, but components were isolated from each other. This niche-isolation reinforced the absolute isolation generated by woodland clearance and fragmentation.
IMPACTS OF FOREST FRAGMENTATION ON SPECIES

This transformation caused four fundamental changes for woodland species:

1. Many remnant woods were simply too small for woodland species with large territories or home ranges. While some could adapt to landscapes with a low proportion of woodland, most were eliminated. In fact, the decline of many, such as the wolf and wild cattle, was reinforced by hunting.

2. The transformation of woodland from matrix habitat to isolated remnants trapped the sub-populations of slow-colonising woodland species in isolated woods. Many, perhaps most, survived, but any small sub-populations that died out would not have been replaced by new colonists. It seems likely, therefore, that the biodiversity of individual woods declined as extinctions exceeded colonisations.

3. The new habitats in farmland provided opportunities for some woodland species that could survive in cultivated and inhabited land, or that were adaptable enough to survive in semi-woodland habitats, such as hedges.

4. Some woodland species adapted to artificial habitats. Good examples of these are the swift, which transferred its nesting sites from hollow trees to houses, and the death-watch beetle, which expanded from dead wood in woodland to dead wood in the structure of houses.

The outcome for slow-colonising woodland species was that their total population was much reduced, and the remaining population was fragmented into numerous sub-populations in the remaining woods. These sub-populations were probably not completely isolated from each other, but exchange of individuals – and thus genes – between them would be much less than in original woodland (see Part 2). It is impossible to know whether such species were completely eliminated from parts of their range: most likely, outlying populations were most at risk.

Populations of other woodland species that could colonise quickly would also have been reduced, but the exchange of individuals between sub-populations would have remained at natural frequencies. Populations of woodland species that could also thrive in non-woodland habitats might well have expanded (eg, bracken).

Taken together, these changes suggest that woodland species tended to fall into two groups: the slow-colonists that could not survive outside woodland, that were progressively restricted and declined; and the fast-colonists and species with a wide habitat range that could ride out the changes, and even prosper from them. In fact, this divergence may have gone even further at the genetic level, for some slow colonists among the fauna seem to have evolved a more sedentary lifestyle, and thus to have become even less likely to colonise from one wood to another (see Part 2).

This division into two groups that diverged both genetically and as populations is an oversimplification. When we bear in mind that natural woodland must have contained some grassland, marsh, scrub and a wide diversity of edges, even the species of unwooded semi-natural habitats must be seen as part of the natural forest. Against this background, the transformation of the natural landscape was a major change in the balance between the components, not a complete loss. Even within the woods, the changes were a matter of degree. Thus, the coppices retained grassland and edges in the form of a network of rides and ride margins: tree-covered ground and grassland were both present, as in natural woodland, but the configuration of the components became simplified and geometrical.
THE POSITION REACHED IN THE 19TH CENTURY

The area of woodland in Britain reached its nadir towards the end of the 19th century, when woodland of all kinds covered just 4-5 per cent of the land. About half this woodland was ancient, the rest being secondary woodland formed since 1600. Much of this secondary woodland had been planted on farmland in the 18th century when, for example, the parks around country houses were landscaped with clumps and belts, and farmland was embellished with fox coverts. This planting, however, had been counterbalanced by massive clearance of ancient woods during the early and mid-19th century, some of which was facilitated by the removal of Forest status from (for example) Rockingham and Wychwood Forests.

The status of woodland species was probably not as bleak as the paucity of woodland might imply. Despite widespread enclosure of commons, farmland was still well-stocked with pasture, meadows, hedges and farmland trees, so there were plenty of semi-woodland habitats, and the habitat corridors between woods remained plentiful. Indeed, it was said that a squirrel could cross the country without having to touch the ground. Even though woodland itself was in short supply, a woodland habitat network of sorts functioned for some species. Nevertheless, many species could not use this network: many woodland plants, for example, were quite unable to colonise the new secondary woodlands (see Part 2).

CHANGES DURING THE 20TH CENTURY

During the last century the total extent of forest increased almost threefold, but most of this increase took the form of conifer plantations in the uplands of north and west Britain (Table 1.1). The ecological effects of this afforestation have been vigorously debated, but from the strictly forest point of view, it was the most substantial reversal of forest fragmentation so far to have taken place in Britain.

Simultaneously, fragmentation of native woodland habitats continued in much of the lowlands. This took several forms:

• clearance of 10 per cent of ancient woodlands;
• transformation of 40 per cent of remaining ancient woodlands;
• neglect of many of the remaining 50 per cent of ancient woods;
• substantial loss of semi-woodland habitats in lowland farmland; and
• dislocation of small-scale habitat networks in lowlands.

The final point implies that the condition of woodland habitats is not just a matter of woodland management, but is also influenced by what happens outside woodlands. Figure 1.3 illustrates typical changes in the mostly arable part (horizontal lines) of lowland England. In 1940, two ancient woods (a,b) survived with rides and a coppice-with-standards structure in a matrix of hedges farmland containing fields carved from these woods in the Middle Ages (c) and the 19th century (d); valley grassland with wet depressions (e); and hedgerow trees. By the 1990s, the woods had been neglected (f,g) or converted to a conifer plantation (h), but the woodland area had increased by the reversion of an adjacent field to scrub woodland (j). From a purely woodland perspective, the changes were not too damaging for wildlife, and indeed were beneficial in some respects, but in farmland the losses were almost complete. Most hedges
vanished, the grassland was ploughed and sown as a ley (k), and the river was ditched. Although there is more woodland, the two woods are far more isolated. Trees and other habitats linking the woods have gone. The only grassland is in the woods, but that, too, is no longer linked by habitats between the woods. The influence of events in the surroundings is actually greater than can be shown: drainage of farmland and fertiliser drift from farmland will also have changed the woods subtly.

Fig. 1.3. Changes in the relationship between woods and their surroundings in lowland England since 1940. Left: c 1940, right: 1990s

Of course, there have also been many conservation measures that have mitigated the rate of habitat loss. These are not only a matter of nature reserves, Sites of Special Scientific Interest and the like, but also patches of habitat retained by some individual landowners. Even so, these are sites, not networks. Essential though they are, they remain isolated, and thus vulnerable.
2 Responses of native wildlife to forest fragmentation

This part illustrates the effects of woodland fragmentation and isolation on several groups of native wildlife, and considers some of the effects of wood size, woodland pattern and the character of habitats between woods. Since the early work of Moore (1962) on heathlands, an immense literature has accumulated on habitat fragmentation and its effects on wildlife, and this in turn has led to consideration of the role of links between habitat patches. Valuable reviews of the performance of linking habitats of various kinds in Britain and elsewhere include Hill et al (1994), Dawson (1994) and Bennett (1999).

**CHANGES IN RESIDENT BUTTERFLIES**

The new Millennium Atlas of Butterflies in Britain and Ireland (Asher et al 2001) and an earlier analysis by Thomas (1991) provide a comprehensive analysis of changes from which the significance of habitat fragmentation can be assessed. The contribution of woodland habitats to these changes has been considerable, but cannot be precisely expressed, partly because so many butterfly species depend on other habitats as well as woodland for survival.

Over the last 200 years, five species have become extinct, 29 have declined so much that they have withdrawn from parts of their former ranges, five more species have become far less abundant but still occupy most of their original ranges, five have hardly changed, and 15 expanded their range or recolonised their historical range. Thus, the general decline in butterfly diversity has been considerable, but has been mitigated by some expansion or recovery.

The species that declined had existed perfectly well in a landscape where the woodland had long been fragmented. Some, of course, did not depend on woodland at all, but the majority that did thrived because grassland, edge habitats, hedges, farmland trees and other non-woodland habitats were abundant and well-connected to woodland habitats and each other; grassland and edges in woods were kept open by regular coppicing; the coppice system maintained both mature trees and a constant supply of clearings and freshly regenerating stands; farmland contained numerous trees, many of which were mature; and habitats within woodland were intimately associated with habitats outside woodland. Their decline was due to the reduction and loss of these conditions, specifically:

- loss of grassland and other habitats outside woodland. Brown hairstreak, White-letter hairstreak, Small copper, Common blue, Meadow brown;
- decline of coppicing, resulting in shaded rides, lack of edge habitats within woodland. Chequered skipper, Wood white, Black hairstreak (box 2.1), Silver-washed fritillary;
- loss of mature trees in both woodland and farmland. Large tortoiseshell, Purple emperor;
- habitat mosaics (e.g. of woodland and grassland together) were much reduced. Duke of Burgundy, Pearl-bordered fritillary, High brown fritillary, Heath fritillary, Small pearl-bordered fritillary, Dark green fritillary.
The species that expanded were responding to climate change and land use change. It is difficult to prove that the former caused a change, but correlations have been demonstrated between changes in ranges and increasing average annual temperature, and between the timing of range expansions and periods of warmer weather. The expanding species associated with woodland have also benefited from an increasing area of unmanaged, shaded woodland (e.g. White admiral); the spread of coarse grasses in and outside woodland (e.g. Large skipper, Speckled wood, Ringlet); and climatic changes (e.g. Brimstone, Holly blue, Ringlet, Speckled wood).

What influence has habitat fragmentation had on these changes? When a species declines, population size decreases and small populations become extinct. As the separation between populations increases, so the chance of augmenting small populations and re-establishing lost populations by immigration decreases. Even if the distances have not increased, the potential source populations may also be smaller and the habitats individuals have to cross to reach another population or patch of suitable habitat become more hostile, due to intensification of agriculture. Even expanding species may be restricted by the same factors. And, when lepidopterists try to help poor colonisers by reintroducing species to apparently suitable habitat, the reintroductions usually fail. Summarising, with fragmented habitats:

- small populations cannot be augmented by immigration from stronger, nearby populations;
- local losses cannot be made good by recolonisation;
- even when conditions become more favourable, expansion is restricted; and
- reintroductions fail, partly because they get no help from outside.

The overall effect is that apparently suitable habitats remain unoccupied. Survival of the species depends on a few strong populations and a scatter of small satellite populations that constantly come and go. If the core populations are threatened by a poor season (due, usually, to adverse weather), the whole metapopulation collapses and the species becomes extinct in the district.

Against this background, it is clear that habitat loss is usually the primary cause of local or regional extinction, and that increasing habitat availability or a warmer climate permits expansion. Habitat fragmentation reinforces and magnifies the habitat loss, and restricts the gains. Recognition of the importance of habitat management has enabled foresters and reserve managers to maintain some of the core populations of declining species, usually by maintaining open rides and a regular cycle of coppicing or timber harvesting.

Some of the butterfly species seen in woods are habitat generalists (e.g. Gatekeeper, Wall) and others are migrants (e.g. Painted lady). Neither group is likely to be restricted by habitat fragmentation. It is the habitat specialists that not only require a particular habitat or combination of habitats, but also tend to have inherently limited powers of colonisation, that are limited.
Box 2.1 Black hairstreak

The black hairstreak is a rare butterfly, now confined to 45 colonies in woods on the Midland clays. It feeds on mature blackthorns growing on wood edges or the sunny edges of glades and rides.

Colonies are notably sedentary. Individual black hairstreaks are rarely found outside woods, and then only close to thick hedges. Within large woods, several independent colonies may each survive for 20 years or more. One colony introduced to Surrey spread 1.5km over 30 years, but most colony movement is slower.

This species evidently survives only with continuity of woodland that generates mature (over 20 years growth) blackthorn thickets continuously. Its present range may be partly determined by past woodland management: the ancient woods of the east Midlands not only contained abundant blackthorn, but were also managed as long-rotation coppices. It has declined with the reduction of coppice management and conversion of some woods to plantations. It can establish new colonies, but is most likely to do so close to present colonies and where good habitat links remain to newly suitable blackthorn thickets.


FLOWERING PLANTS AND FERNS

Many people use flowering plants as informal indicators of the history of a wood and in particular as a means of identifying which woods are ancient. An early example was the Norfolk historian Sir Hugh Beevor, who noticed that bluebells were strongly associated with the woods that were the modern survivors of woods mentioned in the Domesday Book of 1086. “Ancient woodland indicators” have also been a basis for conservation assessments. They work as indicators because their populations are strongly biased to ancient woods: that is to say they are far less likely to be found in recent secondary woods, even on site types that are similar to those found in ancient woods.

These AWIs are an expression of habitat fragmentation. They exist because the original woodland was fragmented and they have limited powers of colonisation. The scattered populations in ancient woods have presumably survived more or less isolated from other populations since the original woodland was reduced and left as fragments. A striking example of the failure to colonise comes from the Boulder Clay region west of Cambridge, where the original woodland was reduced to well below five per cent of the land area well before the 11th century. *Mercurialis perennis* is a constant presence in the ancient woods, but not in Papworth Wood and Overhall Grove, which are in fact secondary woods that originated in the 12th and 15th centuries respectively. Even though both woods overlie the same calcareous clay soils that underlie the other ancient woods, this species has failed to colonise, despite having 800 years in which to do so.
The ability of a species to colonise new woodland varies according to circumstances. Some important factors behind this variation are:

- The colonising ability of a particular species tends to reach a minimum towards the margins of its geographic range, and on less suitable soil types. In both circumstances, growth, competitive performance and the amount and frequency of seed production are all likely to be limited.

- The ability of species to find their way into secondary woods is greater if a species can thrive in other habitats, such as grassland. Then, when new woodland is established, there is a chance that the species will already be there. Of course, this comes into play only where land use outside woodlands permits the survival of these other habitats.

- Colonising performance may be influenced by competition with other species. For example, the residual fertility left when woodland develops on former cultivated ground allows a rank growth of shade-bearing weeds (e.g. cow parsley, hogweed) to dominate the ground and exclude low-growing woodland herbs, such as violets and wood anemone. On dry sites, ivy commonly covers the ground in a dense mat in which few other species can grow, but if this mat is disturbed other species move in rapidly.
It follows that some species in ancient woodlands fail to colonise secondary woods (and therefore become AWIs) only where ancient woodlands cover a low proportion of the landscape and the intervening ground is generally hostile to woodland plants. The regions from which AWIs have been most convincingly demonstrated by a combination of botanical survey and historical research are East Anglia, Lincolnshire and the English Midlands (BOX 2.2), where ancient woodland has long been reduced to less than five per cent of the land, ancient hedges are found at relatively low density, and farming is strongly arable.

Contrast these regions with others where the ground flora of ancient woods seems little different from that of secondary woods. Although formal studies are not available to demonstrate the point conclusively, these include districts such as the Chilterns, the Weald, the southern Welsh borderland, central Deeside and Speyside. Significantly, all these districts have about 30 per cent woodland cover or more, a high proportion of the woods is ancient, and the matrix of unwooded land has long retained a fair proportion of semi-natural grassland or heathland as pasture, and a high density of hedges and other semi-woodland habitats. In the Welsh borderland, for example, bluebells, stitchwort, wood melick, wood anemone and many other woodland species are common in hedgerows.

**WHAT ALLOWS WOODLAND SPECIES TO COLONISE?**

The number of ancient woodland species in secondary woods is greatest in those secondary woods that are in contact with ancient woods: colonisation of these woods by vegetative spread and short-distance seeding is possible, and it is not restricted by the need to cross hostile ground. Secondary woods lacking contact with ancient woods have fewer species: the number falls away rapidly as the distance from the nearest ancient woodland increases. In fact, in central Lincolnshire, woods no more than 500m from an ancient wood had no more AWIs than woods up to 7km from an ancient wood, but colonisation is seriously impaired at separations of 200m or less. Some factors affecting colonisation have been identified:

- studies of woodland colonisation into adjacent secondary woods and along attached hedges show that colonisation rates are generally slow, rarely more than one metre per annum (box 2.3);
- where ground conditions are heterogeneous, secondary woods contain more variety, especially where they include both permanently wet ground and dry banks. Secondary woods confined to sites homogenised by ploughing offer fewest opportunities to potential colonists; and
- when a comparison was made of the frequency of Mercurialis perennis in secondary woods between three districts in Eastern England (*Peterken, 1976*), the frequency was high in the district that had always been well-wooded, and low in the district that had been poorly wooded for longest. Since soil conditions and farming history were similar, the difference was most likely to be due to differences in the degree of ancient woodland fragmentation.
Box 2.3 Colonising rates for woodland vascular plants

The rate at which woodland plants colonise new secondary woodland and hedges can be measured by recording the distance the “invasion front” of a species has migrated into an expanded woodland whose date of origin is known. On this basis, Brunet and Oheimb (1998) found rates of zero to 1.0 m/yr, median 0.3 m/yr, for several woodland plants in southern Sweden. Establishment of a field layer comparable with the adjacent ancient woodland proceeded at a rate of 0.3-0.5 m/yr, though some species were missing. Pollard et al (1974) recorded an instance of Mercurialis perennis moving along hedges at up to 0.3 m/yr in the east Midlands. In general, species dispersed by ant or explosive fruit moved only short distances, whereas species dispersed by birds, water and wind move faster by one or two orders-of-magnitude.

Recorded migrations rates into adjacent new woodland are so slow that one wonders how woodland plants managed to colonise temperate woodland after the last glaciation. The species that move at 0.3 m/yr would only move 3km in 10,000 years at that rate, yet on this timescale they have migrated many hundreds of kilometres. This points to the importance of rare instances of long-distance dispersal, even for slow colonisers, the most likely focus of which is along streams and rivers, where propagules may be washed or carried downstream. Even in the modern landscape, woodland plants seem commoner along streams draining from ancient woods. In the modern landscape, the chance that such long-distance dispersal will generate a new population at a distance has apparently been reduced by forest clearance and the intensive cultivation of riparian corridors.

The general conclusion must be that slow-colonising woodland species stand the best chance of entering new woodland if:

- the new woodland is in contact with the ancient woodland or species-rich hedges;
- the distance separating new woodland from ancient woodland is short, and the intervening ground is occupied by hedges, streams, etc. Separations of as little as 50m are significant, and separations of over 200m substantially impair colonisation;
- new woodland has a range of site conditions such as dry banks and wet hollows; and
- new woodland does not inherit excessive fertility from previous cultivation.

Plants, unlike most woodland fauna, can readily be introduced to new woodland by seeding or transplants. Seeding can take place inadvertently, as the classic study of a fox covert in Lincolnshire (Woodruffe-Peacock 1918) showed at the dawn of scientific ecology in Britain. (This was the study that asserted the importance of trouser turn-ups for transporting plants!)

Recently, successful attempts have been made to enrich new secondary woodlands with a wide range of woodland plants (Francis and Morton 2001). Up to a point, therefore, the effects of isolation that are inherent in fragmented habitats can be overcome by planting not just the trees and shrubs, but also the rest of the flora. However, “translocating” the rest of the flora and fauna is far more difficult. Even if it were practicable, the result would not be ancient woodland, but rich new woodland – a facsimile of ancient woodland.

Mammals

Habitat fragmentation is possibly the greatest threat to the survival of some woodland mammal populations (Bright 1993), and it was presumably a factor in the extinction of the large mammals in the primaeval forests. Admittedly, white cattle – possible survivors of free-roaming, primitive herds – have survived in Chillingham Park for centuries, but they have been
vulnerable to periodic population crashes, and the outbreak of foot and mouth disease in 2001 elicited special pleading for their vaccination in the national press. The surviving species that seem most vulnerable to habitat fragmentation are those of semi-natural habitats that exist at low population density, breed slowly, and have poor mobility.

The importance of spatial factors can be illustrated by red squirrels and dormice, two popular native mammals that have received a good deal of conservation attention in recent years (boxes 2.4, 2.5). Both species depend first and foremost on a stock of suitable woodland, respectively coniferous and broadleaved, and the red squirrel appears to come second in competition with grey squirrels, but otherwise the factors that most influence their distribution are the size and distribution of woodland and the suitability of the matrix for dispersal.

Box 2.4 Red squirrels

The red squirrel is a native species that has retreated in the face of the advancing grey squirrels. The metapopulation dynamics of this species have been investigated, so we can consider how it responds to forest habitat patterns on a landscape scale (Apeldoorn et al 1994, Delin and Andrén 1999, Rodríguez and Andrén 1999).

Red squirrels prefer mature coniferous stands, whereas broadleaved and immature stands are sub-optimal. Home ranges may be as large as 6.8ha in sub-optimal habitat, but are generally much less. Maximum daily movements reach 2,800m for individual males and 680m for individual females. Young squirrels rarely disperse more than 1km through suitable landscapes.

Over a wide range of forest patch size (0.1-500ha), the number of red squirrels in a patch depends on the area of suitable habitat within a patch. If it is less than 600m from another patch containing red squirrels, there is a 90 per cent probability that it will be occupied. In fact, a landscape is functionally continuous for this species if (i) the separation between woodland patches does not exceed the ordinary movements of individuals, which in this case will be around the 680m maximum daily movements of females, and (ii) the matrix habitat is not hostile. Put another way, it is the spatial arrangement of patches and the quality of the matrix habitats that determine whether fragmentation and isolation become significant factors.

In the absence of complicating factors (which, given the presence of grey squirrels, is not the case here), the measures available to maintain red squirrel populations at a landscape scale include (i) supplying some optimal habitat in the form of mature conifer stands, and (ii) the following landscape-scale actions:

- supplying forest patches that are large enough to maintain populations continuously without augmentation from outside;
- reducing isolation of smaller patches to within the dispersal and colonising capacity of the species, thereby allowing the species to function as a metapopulations; and/or
- improving the quality of the matrix habitats to minimise mortality of individuals on the move.
Box 2.5 Dormice

A study by Bright et al (1994) of dormice populations in the woods of Herefordshire provides a fine example of how fragmentation influences a woodland mammal in lowland Britain. Dormice occur at low population densities in deciduous woodland, where they are sedentary and tend to move only in trees and bushes.

The survey of 238 woods covering a range of sizes from 2ha upwards showed that the species was far more frequent in both ancient and larger woods. It was present in 20-30 per cent of the secondary woods of 6-50ha and in 30-80 per cent of ancient woods in the same size range. Its occurrence in secondary woods was influenced by isolation and connectivity. Thus, it was in 40 per cent of woods less than 800m from the nearest ancient wood, but was rarely found more than 1km from an ancient wood. For a given distance and area, its presence in a secondary wood was correlated with the number of hedges making contact with the wood (thus linking it with other woods).

The survey suggested that dormice populations could be maintained in woods of 20ha and above. Their conservation depended mainly on appropriate management of ancient woods, which in this instance amounted to continued coppicing while maintaining contiguous patches of mature underwood. They do colonise new woodland, especially if it is close to ancient woodland and connected by hedges.

Slugs and snails

One of the earliest accounts of the effects of woodland fragmentation on wildlife came in a presidential address to the British Ecological Society about the habitats of slugs and snails. Boycott (1934) listed 49 “woodland species” that were not absolutely confined to woods, but also occurred in related habitats such as hedges, scrub, sea cliffs and limestone screes. Most of these species were anthropophobic in the sense that they did not flourish in cultivated ground and around habitations. Moreover, many were strongly associated with ancient woodland: their ability to colonise new woodland was limited.

For example, according to Boycott “the woodland species living in the old forests on the South Downs and the Cotswolds have not spread into the neighbouring beech plantations which were made so freely from about 1750”. Some species would not become established in apparently suitable ground even if they were placed there by hand. Two slugs, *Limax cinereoniger* and *L.tenellus* occur throughout Britain, yet they are found only in woods “which have every appearance of being ancient and which are generally large”. Furthermore, “they do not occur in woods which look like or are known to be plantations, and their discovery is probably as good a piece of evidence as can be had that a wood is on a primaeval site”. Other species he listed and which are still believed to be strongly associated with ancient woodlands are *Acicula fuca*, *Acanthinula lamellata* and *Ena montana*.

While these observations give only limited encouragement to the belief that additional woodland would enable these species to expand, observation from Cambridgeshire (Paul, 1978) reinforce the suggestion that the problem is isolation, not the habitat. Whereas an ancient woodland had about 25 species in a standard sample, and isolated secondary woods had about 15-16 species (including secondary woods originating in the early Middle Ages), a secondary woodland that was in direct contact with the ancient wood had 23 species, even though it originated only in the 20th century.
Wood-using beetles and other saproxylic groups

The term “saproxylic species” has been coined to include species that depend on large trees, and/or dead or dying wood at some stage in their life. Groups with numerous saproxylics include epiphytic lichens, fungi and several groups of invertebrate. Hole-nesting birds such as woodpeckers are also included. In the original-natural forests, which are believed to have contained numerous large trees and much rotting wood, these species were important. In fact, some 20 per cent of all the invertebrate species of original broadleaved forests in Europe were saproxylic (Speight 1989). This is understandable, given that the volume of dead wood of all kinds mature, near-natural temperate broadleaved stands is likely to exceed 100 m³/ha (Kirby et al 1998).

Inevitably, many saproxylic species have been hugely restricted since forests were cleared and trees were utilised in the remaining woods. Today, many timber-using beetles occur in remarkably small populations, often separated by great distances. Typically, they are found in ancient trees in parkland (e.g. the old oaks of Windsor Great Park) and other kinds of woodland-pasture (e.g. the ancient beech-oak woods of the New Forest), where large volumes of dead wood, large old trees with rotten trunks and branches, and open spaces that provide nectar sources have all been present continuously for at least hundreds of years (BOX 2.6).

These populations are presumably survivors from the original-natural forests. They survived because the mature timber habitats have always been present. A high proportion colonise slowly, partly because the habitat itself takes well over a century to develop into a suitable state.

Protection of the sites where these species survive is the obvious priority, and one might expect that a network would have little relevance to such sedentary species. However, Alexander (1998) takes a more positive line:

“Old forest invertebrates are not all inherently immobile. Their mobility may be relatively low but it is not zero. Today’s reservoirs of these species are the results of historical accidents. We must find ways of allowing them to spread so that they can become part of ‘everyday nature’ again, [for they are] part of natural nutrient cycling, breaking down [of] dead wood, recycling [of] minerals and releasing them for other organisms to use. Their future lies in a wider acceptance of old trees as a desirable feature of the countryside in general, not just in special sites.”

Box 2.6 Some of the richest woods in terms of the number of saproxylic species of beetle recorded

<table>
<thead>
<tr>
<th>Code</th>
<th>Name and location</th>
</tr>
</thead>
<tbody>
<tr>
<td>365</td>
<td>Windsor Forest and Great Park, Berkshire</td>
</tr>
<tr>
<td>256</td>
<td>Epping Forest, Essex</td>
</tr>
<tr>
<td>241</td>
<td>Moccas park, Herefordshire</td>
</tr>
<tr>
<td>235</td>
<td>Richmond Park, Surrey/Greater London</td>
</tr>
<tr>
<td>222</td>
<td>Ashtead Common, Surrey</td>
</tr>
<tr>
<td>170</td>
<td>Powis Castle Park, Powys</td>
</tr>
<tr>
<td>171</td>
<td>Chirk Castle Park, Wrexham</td>
</tr>
<tr>
<td>157</td>
<td>Dinefwr Estate, Carmarthenshire</td>
</tr>
<tr>
<td>151</td>
<td>Dunham Massey Park, Greater Manchester</td>
</tr>
</tbody>
</table>

Source: Roger Key in Harding and Wall (2000). The New Forest was counted as a district and has been excluded, but it would otherwise have come second to Windsor.
DO HABITAT CORRIDORS AID THE MOVEMENT OF WOODLAND SPECIES?

Dawson (1994) reviewed the notion that species move along hedges and other small-scale corridors, but found very little firm evidence. For example, Pollard et al (1974) calculated that *Mercurialis perennis* moved at up to 0.3m/yr along hedges in Northamptonshire (box 2.3). Peterken & Game (1981) found that *M. perennis* was more frequent in hedges close to ancient woods in central Lincolnshire, but interpreted this as the combined effects of survival in woodland relics, the tendency of such hedges to be close to existing ancient woods, and short-distance colonisation from ancient woods. Baudry (1988) found more species in hedges within 500m of woods. Petit & Usher (1998) found that woodland beetles moved into hedges, but were limited by isolation and the effects of pasturage. Hedges, however, helped black hairstreaks (box 2.1) and dormice to reach new woodland (box 2.5).

Nevertheless, both Dawson (1994) and Hill et al (1994) remained sceptical about the role of corridors. Dawson concluded that all-purpose corridors do not exist. They are unlikely to help rare and specialised species unless their (presumably rare and specialised) habitat is part of the corridor. Many species cross hostile territory easily, while others hardly move. Some species use corridors more as stepping stones: that is to say they are more likely to cross hostile territory than move laboriously along corridors. The most likely beneficiaries are species of intermediate mobility with some degree of habitat specialisation.

Insofar as one can generalise about woodland species, they appear to reach habitat patches in farmland by crossing fields as much as by movement along hedges. However, even for species that venture across fields, hedges are useful staging posts. The woodpecker that flies out from one wood may explore a hedgerow tree before moving on to another wood.

Riparian corridors can be important for woodland species on a larger scale. The recent discovery of colonies of barbastelle bats in ancient beech-oak-holly woodland in a well-wooded part of Sussex (Greenaway 2001). The colony foraged over an area of 242 sq km, concentrating along rivers and streams up to 18km from the roost.

Recognition that the population of a species often takes the form of separate sub-populations in discrete patches of suitable habitat has led to the concept of the metapopulation, i.e. the aggregate of these separate populations. The survival of a species may depend on the degree of interaction between sub-populations. Where individuals frequently move between sub-populations, each sub-population is reinforced by immigrants, and newly available habitat is rapidly colonised. The strong sub-populations effectively support the weaker ones. The metapopulation concept draws attention to the importance of movement between habitat patches and the particular configurations of habitats that facilitate movement.

INTERIOR HABITATS

In countries where original forests have remained unfragmented until recently, and where large blocks of forest remain, there is considerable emphasis on “interior species” – those that habitually live in the forest interior and abhor woodland edges. In Britain it is difficult to believe that any interior species could have survived: after all, not only has woodland been fragmented for millennia, but the remaining woods are also divided by rides, have repeatedly been cut down, and in the uplands they are often thinly drawn out along valley sides. There are few
points in British woods that are not close to an edge of one kind or another, where light and air temperature are higher than in the interior of a stand, soil moisture is lower, the trees tend to grow larger but suffer higher rates of canopy damage and mortality, bird density and plant diversity are higher, but nest predation and turnover of species due to dispersal and invasion is also higher (Murcia 1995).

Despite this, there may be some forest interior bird species in Britain. Those listed in box 2.7 are all British woodland birds that show some affinity with forest interiors, or some reluctance to breed in small, isolated woods, in at least part of their European range. However, this collection merely demonstrates that interior habitats are rarely essential for British birds. As Fuller (1995) says, the capercaillie is the only species that shows some need for the interiors of large forests in Britain, and most of the rest are familiar species of mixed countryside with small woods and non-woodland trees. Only the sedentary nuthatch and marsh tit seem reluctant to colonise isolated but otherwise suitable woods.

**Box 2.7 British woodland birds of interior forest habitats**

<table>
<thead>
<tr>
<th>Blue tit</th>
<th>Garden warbler</th>
<th>Nuthatch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capercaillie</td>
<td>Golden oriole</td>
<td>Pied flycatcher</td>
</tr>
<tr>
<td>Chaffinch</td>
<td>Great spotted woodpecker</td>
<td>Redstart</td>
</tr>
<tr>
<td>Chiffchaff</td>
<td>Hawfinch</td>
<td>Song thrush</td>
</tr>
<tr>
<td>Coal tit</td>
<td>Jay</td>
<td>Treecreeper</td>
</tr>
<tr>
<td>Crested tit</td>
<td>Lesser spotted woodpecker</td>
<td>Willow tit</td>
</tr>
<tr>
<td>Crossbill</td>
<td>Marsh tit</td>
<td>Wood warbler</td>
</tr>
</tbody>
</table>


Perhaps the most plausible “interior” species remaining in British woods are those oceanic bryophytes that are sensitive to both edges and canopy removal, even in the extremities of the western Highlands (Ratcliffe 1968).

**GENETIC CHANGES DUE TO ISOLATION**

The impact of long-term isolation on the character of slow-colonising woodland species themselves is only now being evaluated, but there are indications of genetic change in carabid beetles and other insects (den Boer 1990, Dempster 1991).

It is easy to see how these changes might come about. If the amount of movement varies between individuals, the adventurous ones are more likely to move outside woodland than sedentary ones. If, further, the surroundings provide unsuitable habitat, mortality rates of adventurous individuals would be higher, so sedentary genes would increase in the population. If suitable habitat were available nearby, adventurous individuals might be rewarded for their enterprise by access to new habitat without competition. Thus, isolation above a certain level actually decreases the ability of a species to colonise, but habitat fragmentation in which related habitats remain nearby might actually enhance colonising ability.
DECLINE IN DIVERSITY DUE TO ISOLATION?

Theoretical considerations suggest that the number of species in isolated woods will steadily decline through a process known as “relaxation”, whereby the rate of species extinction in a site exceeds the rate of colonisation from outside. The population size of all species will fluctuate to some extent, and when this happens to a species present only in low numbers there is a danger that it will die out. Such local extinctions would not matter in a large forest, for recolonisation from the surrounding woodland would be straightforward. When there is no surrounding woodland, however, recolonisation will be improbable or impossible. Local extinction will be more likely in a small woods than a large wood, for populations will be proportionately smaller. The combination of local extinction and failure to recolonise would be most severe in small, isolated woods.

Does relaxation happen in practice? Clearly it does in the case of species whose numbers naturally fluctuate greatly, such as dormice and some butterflies (above). Clearly not in the case of some populations of woodland plants that are known to have survived for decades or longer as small populations in hedges and small woods. Woods that were reduced in the mid-19th century have just as many woodland plant species as woods that were reduced several centuries earlier, which suggests that the rate of relaxation is slow (Peterken and Game 1984).

No doubt relaxation rates vary between wildlife groups. In theory, they should be greatest in groups of species that have fluctuating populations and low rates of colonisation. The outcome would be under-representation of species in small, isolated woods. Relaxation may be a problem for all groups, but it is most likely to be serious for the fauna. The fact that it happens at all emphasises the dangers of further isolating existing habitats and the need to enlarge small woods and minimise isolation.

OPEN SPACE HABITATS IN WOODLAND

Rides, glades and other open spaces in woodland have long been recognised as rich habitats for invertebrates and birds. This value emerges clearly from the account (above) of woodland butterflies. Open spaces also contribute a remarkably high proportion to the total plant list for a wood, often well over half of all species.

A recent analysis of the open space flora of woods in central Lincolnshire (Peterken and Francis 1999) found that the number of species increased with the area of the wood, as one would expect, but also that the relative importance of the open space flora increased in steps (box 2.8). In very small woods, open spaces were either transitory or totally absent, with the result that shade-intolerant herbs were sparse and confined to margins. On the other hand, above about 3ha, access rides were usually incorporated in the design, so open space habitats were generally present. However, smaller woods often went through periods of neglect when the rides became totally shaded, so the variety of shade-intolerant species was still circumscribed. Only in woods of about 20ha and above were rides and clearings permanently suitable for shade-intolerant species, due to a regular stream of forestry operations and cutting associated with game keeping or public access. In the larger woods, therefore, slow-colonising ride species always found suitable conditions somewhere in the wood, whereas in smaller woods they would be periodically excluded by edge-to-edge shade.
It would be wrong to dismiss the grassland on rides as an artificial and unimportant habitat. Rides provide refuges for the many grassland and marsh species that cannot survive in modern farmland (fig. 1.3). Rides can also be regarded as a modified version of the woodland-grassland association that may once have been part of the original-natural forests (box 1.1). In central Lincolnshire, one of the truest ancient woodland indicators was *Carex pallescens*, a species that was confined to unshaded situations in rides.

Box 2.8 Open space habitats in woodlands of different sizes

<table>
<thead>
<tr>
<th>Size of Wood</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Extremely small woods (&lt; 1 ha)</td>
<td>Usually lack open spaces. Few open space species on margins.</td>
</tr>
<tr>
<td>Very small woods (1-3 ha)</td>
<td>Rarely contain rides. Tracks usually shaded. Generally poor open space flora.</td>
</tr>
<tr>
<td>Small woods (3-10 ha)</td>
<td>Rides usually included. Stands rarely have a balanced age/class distribution, so rides periodically completely shaded. Open space flora can be rich, but usually moderate or poor.</td>
</tr>
<tr>
<td>Medium-sized woods (10-40 ha)</td>
<td>Rides invariably included. As woodland size increases, so too does the probability that the wood is subject to regular forestry operations. Open space flora usually moderate or rich, usually 30-50 per cent of the total flora in the wood.</td>
</tr>
<tr>
<td>Large woods (&gt; 40 ha)</td>
<td>Too large to neglect, these woods invariably have a programme of management and thus some permanently open rides etc. Open space flora usually rich – often more than half the total flora of the wood – but even here it would be far less if a large wood were left wholly unmanaged and thus lacked open spaces.</td>
</tr>
</tbody>
</table>

Source: Peterken and Francis (1999).

**THRESHOLDS**

The previous study revealed thresholds of about 3ha and 20ha in the relationship between wood size and a component of biodiversity. Thresholds are important, for they could suggest targets in the design of a forest habitat network.

Three kinds of threshold may be significant:

- **Minimum areas of individual woods.** In isolated woods, the probability that particular woodland bird species will breed does not approach 100 per cent until wood area exceeds 10ha, and marsh tits are sure to be breed only in woods of 25ha or more (*Hinsley et al., 1994*). A 50 per cent probability is achieved at about 5-10ha for treecreeper, jay, garden warbler and chiffchaff. Great spotted woodpeckers will breed in small woods, but 50 per cent probability is reached only in woods approaching 100ha (*Moore & Hooper, 1975*). Dormouse populations can be sustained only in woods of 20ha or more (box 2.5).

- **Threshold separations between woods.** Female red squirrels move up to 680m in one day, which limits colonisation in sparsely wooded landscapes (box 2.4). Dormice rarely colonise secondary woods more than 800m from an ancient wood (0 2.5). Many ancient woodland plants appear rarely to colonise woods over 200m from ancient woods. Invertebrate species that evolve a more sedentary behaviour in isolated woods surrounded by a hostile matrix will presumably retain or recover a more mobile behaviour where woodland covers a
greater proportion of the area and the matrix is more favourable, and there must be a watershed state between these two evolutionary flows.

- **Minimum woodland density.** As a general rule, at least 30 per cent woodland cover is needed to allow most woodland mammals to function as if the landscape is one wood (Andren, 1994). This value will be reduced in landscapes where hedges and non-woodland trees are abundant between woods, i.e. matrix quality influences the threshold. In a fragmented woodland landscape, there is a 90 per cent chance that red squirrels will be present if a wood is greater than 10ha and less than 600m from a source population (Rodriguez & Andren, 1999). Likewise, on heavy clay soils in eastern England, *Mercurialis perennis* is found more frequently in the secondary woods of districts that have maintained a high cover of ancient woodland (Peterken 1976).

**CONCLUSIONS: IMPACTS OF FOREST FRAGMENTATION ON SPECIES**

Fragmentation has had several effects on forests as habitats for wildlife species. The sum total of forest habitats has been reduced, of course, and in addition (i) edge habitats have been increased in relation to interior habitats, (ii) small woods have been created that may not be large enough to support some species, and (iii) barriers have been created between remaining forest patches that restrict the movement of individuals and populations. Furthermore, (iv) a new woodland type – secondary woodland isolated from both original woodland and ancient woodland – has been generated. Inevitably, too, there have been (v) indirect effects on management, for small woods cannot be used in the same way as large woods. Furthermore, the “external relationships” of forest habitats have been changed by (vi) disrupting the natural relationships with other habitats, such as grassland and watercourses, and by (vii) creating a matrix of non-forest habitats, some of which are extremely artificial.

Fortunately, a large proportion of forest species has been able to ride out these changes. They remain in the modern world of fragmented forest habitats by several means:

- Surviving as small, isolated populations in ancient woods. Survival has been possible only if the particular habitat niche has also survived, as the saproxylic species demonstrate. These are the “ancient woodland indicators”.
- Making use of mixed countryside containing small woods and non-woodland trees and shrubs.
- Using non-woodland vegetation such as meadows, or surviving in semi-woodland habitats such as stream sides, hedges, etc.
- Adapting to artificial habitats. Swifts, starlings and death-watch beetles are all species that have “moved” into buildings from mature timber habitats in natural forests.
- Retaining an efficient mechanism for colonising new, suitable habitat rapidly. These are the forest species that appear first when new woodland is created.

Nevertheless, forest fragmentation has fundamentally changed the circumstances of woodland species. Before fragmentation, in original-natural circumstances, they were components of the matrix habitat and the species of other habitats were confined and isolated to patches and corridors within forests. After fragmentation the positions were reversed – other habitats became the matrix and remaining woodland was isolated – but the character of woodland species remained the same. Evolutionary adaptations that were suitable for life in the matrix
habitat were no longer suitable for life in isolated habitat fragments. Thus, fragmentation has left its mark on forest wildlife, in several ways:

- as a contributory factor in the loss of the original large mammals, etc;
- by restricting many species of the original forests to small, isolated populations, often in specialised woodland types such as those with mature timber, where they are vulnerable to local extinction;
- excluding some forest species from small woods, and thus from parts of their natural range and from some otherwise suitable habitat;
- by progressively reducing the numbers of species in remaining small woods by the process of relaxation;
- an impaired ability to colonise due to genetic changes in isolated woodland populations; and
- increasing competition from species in non-woodland habitats, and from non-native species (which are usually first introduced into non-woodland habitats). Several naturalised species such as the grey squirrel and the sycamore colonise better than otherwise comparable native species.

The outcome for slow-colonising woodland species is that their total population has much reduced, and the remaining population has been fragmented into numerous sub-populations in the remaining woods. These sub-populations have probably not been completely isolated from each other, but exchange of individuals – and thus genes – between them has probably been much less than it would have been in original woodland. It is impossible to know whether such species have been completely eliminated from parts of their range: most likely, outlying populations have been most at risk.

Populations of other woodland species that could colonise quickly must also have been reduced, but the exchange of individuals between sub-populations has remained at natural frequencies. Populations of woodland species that could also thrive in non-woodland habitats, such as bracken, might well have expanded.

Taken together, these changes suggest that woodland species tend to fall into two groups: the slow-colonists that rarely survive outside woodland, that have been progressively restricted and reduced; and the fast-colonists and species with a wide habitat range that have been able to ride out the changes, and even prosper from them. In fact, this divergence may have gone even further at the genetic level, for some slow colonists among the fauna seem to have evolved a more sedentary life-style, and thus to have become even less likely to colonise from one wood to another.

This division into two groups that diverged both genetically and as populations is, of course, an over-simplification. When we bear in mind that natural woodland must have contained some grassland, marsh, scrub and a wide diversity of edges, even the species of unwooded semi-natural habitats must be seen as part of the natural forest. Against this background, the transformation of the natural landscape took the form of a major change in the balance between the components, not a complete loss. Even within the woods, the changes were a matter of degree. Thus, the coppices retained grassland and edges in the form of a network of rides and ride margins: tree-covered ground and grassland were both present, as in natural woodland, but the configuration of the components became simplified and geometrical.
Logically, the consequences of fragmentation listed above would be reversed if several measures were implemented. Recreation of extensive habitats might permit the reintroduction of the lost mammals. Relict habitats, notably mature stands that support populations of saproxylic species should be maintained and expanded. Existing woods generally should be expanded and linked. The presence of naturalised species may have to be accepted, but native species are more likely to survive in large, heterogeneous tracts of woodland.

**WOULD THE RESTORATION OF A FOREST HABITAT NETWORK BE SUCCESSFUL?**

The effectiveness of some elements of a forest habitat network seems assured. Large woods certainly contain more species, larger populations, and some species that abhor small woods. Where woodland remains a substantial element (30 per cent or more of the land area) in the landscape, many woodland species evidently behave as if the woodland has not been fragmented. New woodland next to existing woodland is fairly readily colonised by woodland species. There have also been some successful transfers of slow-colonising woodland species into new woodland, although these can never be enough to allow the whole woodland assemblage to adjust.

But will the restoration of links between woodlands alleviate the effects of fragmentation? If so many of the vulnerable woodland species are slow colonists, will they actually make use of new woodland? There are some encouraging signs. We know that many woodland species use corridors of woodland and semi-woodland habitats, although we are less sure of the degree to which such habitats enable them to spread across fragmented territory. There is much uncertainty about the effectiveness of corridors as links: perhaps their function as stepping stones (small, isolated habitat patches) is more important for most woodland species.

Nevertheless, the combination of observation and ecological common sense suggests that all problems would be solved for woodland species if we can reconnect woodland habitats in a well-designed forest habitat network. Experience elsewhere, however, indicates that a network would help some species, but not all; that it may take a very long time to be effective; and, that it could actually cause problems.

Experience in the eastern US, where native forests have returned during the last century to cover the landscape (Foster 1992), and bears and wild turkeys are becoming familiar even in suburban estates, reveals that many plants are still almost confined to the ancient woods that survived through the peak of agriculture (Whitney and Foster 1988). In Britain, the soils of new woodland formed on farmland show the residual effects of drainage, ploughing and fertilisers many decades or centuries later: the altered soils encourage rank weed growth, which in turn offers stiff competition to any woodland species that attempts to colonise. In any case, many woodland species that depend on large timber and dead wood will have to wait for these habitats to develop. Complete or nearly-complete ecological restoration of a woodland network is a matter of decades and centuries.

We must also remember that a restored forest network may have disadvantages for native forest wildlife. In theory, by enticing woodland species to venture out into narrow corridors, we may inflict higher levels of predation from species on the edges and in the matrix. More realistically,
the spread of naturalised species such as grey squirrel, muntjac, sycamore and rhododendron would be facilitated. However, at this point the words “horse”, “locking”, “bolted”, “stable” and “door” come to mind: even in a landscape of fragmented woodland, these species have been able to spread.

Despite these reservations, experience in the districts where woods have always covered 30 per cent or so of the land and have remained connected by a network of forest habitats, combined with evidence from the spread of forest species into 20th century upland plantation forests (Avery and Leslie 1990, Good et al 1990), suggests that the benefits greatly outweigh the disadvantages. These forested districts – ancient and modern – have retained or are developing a distinctive character in which agriculture is not dominant, there is a diversity of semi-natural habitats, and the diversity of native species is high. Restoration of a forest habitat network is a long-term goal, but even at the outset the trends would be in the right direction.
3 Reversing fragmentation: building a forest habitat network

Forest fragmentation has created numerous problems for wildlife. Many woodland species have been broken up into a scatter of isolated sub-populations that are vulnerable to changes in the distribution of woodland and its management. Now, because of 20th century intensification of agriculture, this vulnerability has been extended to native grassland and its associated species. As a result, open habitats within woodland have taken on an added significance, but have themselves become extremely vulnerable to change. At the same time, the advent of accelerated climatic change induced by human activity has increased the need for species to be able to respond to change.

The solution to this dilemma is to regenerate a forest habitat network. In essence, this involves adding new woodland to the landscape where it will enlarge small woods and link scattered woods of all sizes; keeping existing woods and managing them to retain habitat diversity throughout the woodland area; and associating other habitats with the woodland.

The issue is: how should such a network be designed? Certain thresholds and fundamental characteristics need to be appreciated before the detail can be fleshed out into a practical programme.

One principle that must be incorporated is design efficiency. We must aim to maximise connections between woodland with the minimum amount of additional woodland. This is not just a matter of cost-effectiveness, but is also recognition that agriculture, living space, communications and other land uses will inevitably restrict the land available for a forest network.

**STRUCTURE OF A NETWORK**

A network can be visualised as an array of nodes connected by links, both set in a contrasting matrix (fig. 3.1). A forest habitat network comprises forested nodes and links in a matrix of other habitats.

This structure can be recognised at a range of scales. The smallest nodes are individual woods, which may be linked by hedges, incised streamsides and other linear semi-woodland habitats. This is the familiar structure of the traditional lowland countryside that has been so disrupted over the last 60 years by hedge clearance, stream ditching, etc (fig 1.3). At a much larger scale, however, one can also recognise much large nodes, known as “Core Forest Areas” (CFAs), comprising concentrations of forested land and dense clusters of woodland. CFAs come in several forms, from the massive 20th century plantation forests of Kielder and Thetford Chase, to the ancient concentrations of ancient semi-natural woods in, for example, central Speyside, Borrowdale, the Maentwrog valley and the Lower Wye Valley.

The matrix itself may also vary in its degree of hostility or affinity to woodland species. Thus, perhaps the most hostile matrix is intensive arable agriculture with large fields and few
remaining hedges and non-woodland trees. The most benign would be extensive agriculture
with a low density of stock and a wealth of semi-woodland habitats. From the standpoint of
woodland species, these contrasting landscapes would be the ends of a range from low- to high-
quality matrices.

**Fig. 3.1. The basic structure of a network.**

Nodes (circles) are joined by links (lines), and the spaces between form the matrix. The mesh
size of the matrix is determined by the size of the discrete panels separated by links. A forest
habitat network comprises nodes and links, but its performance also depends on the quality of
the matrix for woodland species. The basic structure applies at a range of scales. Thus, the
nodes might be large Core Forest Areas, clusters of woods, or individual woods.

**WOODLAND IN RELATION TO THE WHOLE LANDSCAPE**

The properties of a network are controlled by some fundamental characteristics of patchworks.
These properties have been explored by means of computer simulations of model landscapes.
They reveal two important thresholds at about 30 per cent woodland cover and about 60 per cent
woodland cover.

When woodland is added randomly to a landscape, the properties follow the pattern shown in
fig. 3.2. As new woodland is added to a hitherto unwooded landscape, the degree of isolation,
amount of edge and the amount of interior habitat do not increase linearly. Edge habitats peak at
50 per cent woodland cover. Isolation becomes minimal at about 30 per cent cover and vanishes
altogether at under 50 per cent cover. The development of interior habitats depends on how they
are defined, but on most definitions they do not start to develop until about 50 per cent cover.

Two other significant network properties are not shown on fig. 3.2. At low woodland cover, the
landscape comprises scattered woods, but at about 60 per cent cover these woods coalesce into a
single wood with holes in it. At low woodland cover it is not possible for an animal to cross the
landscape without going outside woodland, but from about 45 per cent cover upwards a
complete traverse in woodland becomes possible, albeit by crossing at corners from one wood
to the next.
Fig. 3.2. Changes in some spatial properties in relation to woodland as a proportion of the landscape in a model grid of 10 x 10 squares

These thresholds will be different if the accumulation of new woodland is not random. For example, if a rule is imposed that all new woodland has to be adjacent to existing woodland from five per cent cover upwards, interior habitat would develop at a lower cover, all new woodland from five per cent upwards would be next to existing woodland (so isolation would be minimal), but edge habitats would be reduced and traverses across the landscape would only become possible at much higher cover than 45 per cent. This finding is general: design rules that allow one network attribute to increase or happen at lower cover are paid for by reducing or delaying another network attribute.

The baseline relationships in fig 3.2, allow us to characterise woodland in relation to the landscape by reference to three ranges defined by the 30 per cent and 60 per cent thresholds (box 3.1). However, since Britain has only 11 per cent forest cover, and most parts of Britain have five per cent cover or less, the 0-30 per cent range is arbitrarily divided at five per cent cover into sparse and not-so-sparse ranges.
Box 3.1 Forest in relation to the whole landscape

Forest cover between 60 per cent and 100 per cent: This is a single forest punctuated by clearings, which represents the first stage of forest fragmentation. It differs from natural conditions in possessing much more edge habitat and much less forest interior habitat. All forested land is well-connected, although barriers to species movement may arise if clearance is particularly associated with internal networks, i.e. along watercourses. Almost all new woodland that springs up on cleared ground would not be isolated, but connected to existing forest and rapidly colonised by forest species.

Forest cover between 30 per cent and 60 per cent: The forest comprises a dense array of separate patches of various sizes and shapes. Edge habitats are maximal, but forest interior habitats are much reduced and survive mainly in the cores of the largest patches. Movement of species within patches is generally not restricted, except for species which naturally depended on internal networks, notably stream corridors. Movement across the landscape involves crossing non-forested land, although the gaps (and the risks) are small. Most new woodland added to this landscape will be close to existing woodland and will tend to extend and link existing patches of forest.

Forest cover between 5 per cent and 30 per cent: Landscape containing a scatter of separate woods with few large woods. Edge habitats decline as cover falls below 30 per cent and forest interior habitats are either absent or reduced to tiny areas within the largest patches. Movement of species across the landscape depends on crossing non-forest land. Any new woodland added to this landscape may be isolated from existing patches and thus not readily colonised by forest species. If new woodland develops mainly as marginal expansion of existing woodland, colonisation by woodland species should be rapid, but movement across the landscape will remain limited.

Forest cover below 5 per cent: Landscape containing a sparse scatter of generally small woods. Isolation is substantial, edge habitats are limited, interior habitats are absent or extremely limited, and movement of species across the landscape requires long traverses of unwooded land. New woodland is most likely to be isolated from existing woodland.

The notion that 30 per cent cover represents a significant threshold is supported by observations on woodland species. Ancient woodland indicators among vascular plant species are hard to recognise in landscape that has always been at least 30 per cent wooded (see Part 2). Andren (1994) mentioned that 30 per cent cover of suitable habitat represents a maximum fragmentation threshold for many mammals. Wiktorak et al (2001) found that the reproductive performance of woodpeckers falls off once suitable foraging habitat falls below about 25 per cent of the landscape. Thus, theoretical considerations and field observations come together to indicate that at a woodland cover of 30 per cent or more, woodlands are ecologically resilient: isolation is so small that woodland species can respond to changes in the pattern of woodland. In other words, these cease to experience the landscape as a scatter of woods separated by hostile territory, and start to use it as a single wood.

This enables us to propound the 30 per cent rule. The land within a forest habitat network should have at least 30 per cent woodland cover. Thus, a Core Forest Area would be a landscape in which woodlands are well-distributed, well-connected, and cover at least 30 per cent of the land. Put another way, a CFA need not be a vast tract of fence-to-fence trees, but could consist of predominantly (up to two-thirds) unwooded land.
REVERSING THE HABITAT OF BRITISH WOODLANDS

The emphasis in rebuilding forest habitat networks will understandably be on creating new woodland, but the priority must be to keep existing woods. It would be pointless to destroy woods when the general objective is to increase woodland. More specifically, existing woods are the sources of species from which new woodland would be restocked.

This consideration applies with particular strength to ancient woods. These have many virtues, including their long historical associations with their locality: they are historical monuments and enduring components of the local landscape. They are also the richest woods for wildlife and usually the only sources for ancient woodland indicator species. Furthermore, in the most intensively cultivated parts of Britain, they are often the richest places for the species of native grassland and wetland.

THE SIZE OF INDIVIDUAL WOODS

However successful we may be in regenerating a forest habitat network, the landscape will still contain discrete, individual woods, both within Core Forest Areas and the links between them, and in the rest of the countryside. Most existing woods are small, perhaps too small – 83 per cent of all ancient woods larger than 2ha in England and Wales cover less than 20ha. So how large should a wood be? And should networks be designed to include only large woods?

It is easy to assume that larger is better, given that the number of species increases with area. However, the number of species in a given area of woodland actually increases with the degree of fragmentation: a single 100ha wood contains fewer species than ten 10ha woods, although it may be the only place where large-territory species can survive. This paradoxical finding is explained by the greater variety of site types that can be included if a fixed total woodland area is spread out over a larger district. Practical considerations also apply: a single large wood requires less fencing and less management time. This dilemma is probably best resolved by ensuring that a CFA contains a range of sizes, concentrating particularly on developing some large woods.

What is meant by a “large” wood? In ecological terms it must be large enough to maintain a normal age-class distribution, minimise edge effects, and support large-territory species. Thus, woodland coppiced in a 30-year rotation in which re-growth forms a closed canopy after five years, would have to be cut in not less than six operations in every rotation if pre-thicket stands are to be maintained permanently. If each coppice block has to be as large as practicable – say at least 5ha, to mitigate deer damage (Kay, 1993; Putman, 1994) – the wood must extend to at least 30ha in order to maintain a dynamic steady state of habitats. Edge effects generally penetrate 50m (Murcia, 1995), so the smallest wood that can contain stands that are free of edge effects is a circular wood of 0.8ha. This, however, would be far too small for, say, an interior-dependent bird species to hold territory: even some small bird and mammal species benefit from having woods of at least 25ha.

Another approach to defining appropriate sizes emerges from considering species associated with open spaces, such as felled woodland, rides, clearings, pools, watercourses and the woodland margin. Much of the biodiversity of woods is associated with these habitats, and in much of arable England, woodland rides and clearings may be the only places where grassland
and marshes remain which are not directly affected by agriculture. As far as open space plants are concerned, there appear to be thresholds at about 3ha and 25ha (Peterken & Francis, 1999). Below 3ha woods rarely contain permanent open spaces, and open space species comprise only 0-30 per cent of the flora. From 3ha upwards woods generally contain rides, and above about 25ha it is rare for rides ever to be completely shaded. In the larger woods, open space species comprise 40-60 per cent of the total flora. On this basis there is a case for ensuring that very small woods are brought above 3ha (which more or less ensures that rides will form part of the design), and that larger woods are brought above 25ha (a size at which woods are rarely left totally unmanaged).

THE SHAPE OF NEW WOODLAND

What shape of new woodland is desirable? New woods must first acquire woodland species and then keep them if they are to be functional components of a network.

Theory suggests that long, thin woods are better at “catching” species moving through the landscape, but that compact woods are better at retaining species once they have been caught (Game, 1980). In practice, shape seems to have no significant impact on the number of plant species. Even in small woods, where shapes tend to be least compact, my records from central Lincolnshire showed no effect of wood shape on the number of plant species present. Ecological processes may provide a basis: for example, linear woods along streams would have ecological advantages. In the absence of clear guidance from ecology, shape may best be determined by visual principles, which in any case tend to be based on some concept of “natural” patterns and proportions.

LOCATION FOR NEW WOODLAND

Various strategies for locating new woodland were tested on four sample districts in England by Buckley and Fraser (1998). These included random planting, placing new woodland close to existing woods, expanding existing woods, and connecting ancient woods by belts, among others. Each pattern had it particular consequences. Thus, compared with the other patterns, linking ancient woods by belts yielded large increases in mean wood size, wood perimeter and shape irregularity, but only small increases in perimeter, and only small reductions in nearest neighbour distances. As with other patterns, the results varied according to the inherited density and pattern of woodland, suggesting that there may be no general “best” solution for ecologically effective new woodland creation.

EXPANDING EXISTING WOODS

Despite the above findings, the priority for new woodland in most districts should be to expand existing woods. New woodland situated next to existing woodland will be colonised faster than isolated woodland, because ecological isolation is minimal and the adjacent new woodland is likely to be on a similar site types and thus the species in the existing wood are likely to be suited to the new woodland.
If new woods cannot be adjacent to existing woodland, what separations are acceptable? Both the fauna and flora include species (such as some wood ants) that rarely colonise new woodland by crossing hostile territory, but will move slowly into contiguous woodland (Puntila, 1996). Separations of 100-200m may be reasonable for many woodland plants, but even this would probably present problems to some invertebrates. There will always be species that will tolerate little or no separation, and these, together with large-territory species, effectively require that landscapes function as a single wood.

At a larger scale, the aim should be to reinforce clusters of existing woods until 30 per cent woodland coverage is achieved within the clusters. The general approach should be to build upon what already exists. This reverses the intuitive answer: under the conditions prevailing in most of Britain, new woodland is particularly needed where there is already some woodland. If, alternatively, we simply scatter the new woodland around evenly (“pepper-potting”), we would only add to the already large number of isolated small woods, and homogenise the landscape – minimal ecological benefit and a loss of locally distinct landscapes.

**TYPES OF GROUND FOR NEW WOODLAND**

What ground should be chosen for new woodland? The immediate impression is that the greatest gains will be achieved by concentrating new woodland on existing cultivated ground, since the latter is largely devoid of conservation interest in its cultivated state. However, there is no doubt that the richest secondary woods are those that developed on old pasture, marshland, or some other semi-natural habitat. This is because the precursor habitats usually survive in some form in woodland rides, and the soils are not so heavily fertilised that only rank weeds can grow in the shade. Unfortunately, such habitats are in such short supply in lowland Britain that transformation of the remaining examples into woodland would incur a net loss of conservation value, if not of species. The best approach would be to locate new woodland on arable or leys next to old grassland, heath or marsh, thereby facilitating colonisation of open space habitats within the new woodland.

**THE PATTERN OF CORE FOREST AREAS**

The pattern of CFAs is in many ways already determined by the inherited pattern of woodland. Thus, we have large concentrations with a high proportion of ancient woodland in many places already mentioned (Chilterns, Cotswolds, western Weald, New Forest and adjacent areas, Forest of Dean and Lower Wye Valley, Highland fringes and major valleys). In the 20th century we created new concentrations in, for example, Kielder and the Borders, Galloway, Thetford Chase, Argyll and the northern Cairngorms – all areas with a hitherto small wooded proportion. Some of this afforestation was in reasonably well-wooded districts, such as Coed y Brenin forest and the Mawddach estuary in southern Snowdonia. We are also generating more – notably the New National Forest in northern England, and the Community Forests around selected cities.

New CFAs should be also be generated by augmenting concentrations of scattered ancient woods. From the woodland point of view, a productive approach might be to concentrate on those districts that have had concentrations of ancient woodland throughout the historical period, such as Rockingham Forest in Northamptonshire, central Lincolnshire, high Suffolk, and the district north-east of Oxford. A small-scale precedent exists at Chambers Farm Plantations...
in central Lincolnshire, where a cluster of five ancient woods linked by ancient hedges was filled in by plantations in the 1930s and later to produce a large, rich and diverse tract of woodland.

**CREATING LINKS BETWEEN CORE FOREST AREAS AND INDIVIDUAL WOODS**

Once CFAs have been developed and individual woods have been expanded, the need is to generate or restore links between them.

**Links between individual woods**

The traditional lowland landscape of woods in a matrix of hedged fields and other non-woodland habitats provided a well-connected local network – but it did not benefit all woodland species, as the existence of ancient woodland indicators testifies. Even so, it was certainly better than the present condition, in which hedges have been much reduced, scrub has been largely eliminated, streams have been ditched, trees in farmland have been reduced to a tithe, and grasslands have largely been replaced by leys and arable.

The need is to restore some of the hedge network and to develop strips of mixed habitats by retaining uncultivated field margins. Habitat strips could be developed along existing linear features such as roads, railways and stream sides. Including some trees in hedges and adding small field-corner plantations would also help. Within all this is the need to keep what we still have: like the ancient woods, these will be the richest farmland habitats.

**Links between Core Forest Areas**

Long-distance links between CFAs are more difficult to envisage. Elongated concentrations of woodland are found in the English landscape, notably along the Chiltern and Cotswold scarps, and on Wenlock Edge. They are actually more frequent in the uplands, where concentrations of woodland are confined within the major valleys. Thus in Highland Scotland, Deeside, Speyside and the Great Glen are both CFAs and long-distance links in a network. Elsewhere, manufacturing links is more problematical, and would require building upon existing woods between CFAs. So for example, the ancient woods along the middle Clyde and its tributaries would be the best basis for linking the concentrations of woodland along the southern edge of the Highlands with the large new forests in Galloway and the Borders.

As it happens, the creation of long belts of new woodland would not be without precedent. In the 16th century, Russian rulers created the “abatis lines”, huge belts of woodland stretching hundreds of miles, to keep out the Asian hordes (*Ponomarenko 1994*). On a much smaller scale, shelter-belts were commonly established around English country houses in the 18th century.

**Riparian links**

Whether on a large or a small scale, artificial belts of woodland crossing geometrically over the natural grain of the land have strong drawbacks links in a network. For example, a species that requires wet ground would be unable to move through the dry parts of the belt, which would effectively put up internal barriers within the network. Far better would be to work with the grain, and this leads directly to a preference for links based on the natural pattern of drainage.
Streamside and riversides already provide habitats for woodland species. They tend to be humid and sheltered, and provide niches protected from grazing. They are also the natural foci for movement of species on a landscape scale. Valleys also tend to have varied habitats and site types: not only does the watercourse through a mosaic of wet and dry sites on the floodplain, but the proximity of the valley side and possible rock outcrops also enhances the diversity. In montane districts, valleys will inevitably determine the pattern of woodland. Admittedly, riparian forces work mainly in one direction, and the network they form is dendritic with its own isolated headwaters, but these are small drawbacks beside the benefits.

So, on a local scale we should be looking to line small streams with trees, and leave buffer zones of uncultivated ground on each side. On a large scale, we should be planning to concentrate woodland into and around certain valleys, such as the Clyde.

**URBAN CONSERVATION AND A FOREST HABITAT NETWORK**

Surprising though it may seem, urban environments have something in common with woodland habitats – protection from grazing and intensive agriculture; trees and shrubs contributing to a complex vegetation structure – so it is entirely understandable that blackbirds, foxes and other woodland species have colonised cities. Moreover, cities have so expanded that many ancient woods have become incorporated within their boundaries, where they usually function as public open spaces.

A study of plant species in habitat fragments within Birmingham ([Bastin and Thomas 1999](#)) found that many species, including woodland plants, were more likely to be found in ancient and long-established woods, and that generally their presence was more likely in larger woods and those close to other woods. In other words, ecological isolation had some effect on the occurrence of these species. They nevertheless took the view that “narrow ribbons of open space” were unlikely to benefit slow-colonising species, and that the best strategy for urban plant conservation was to maintain the large, old habitat patches (including woods), and the connections between them.

If conurbations are to be part of, rather than barriers to, a forest habitat network, there is a strong case for linking urban greenspace to woodland on city fringes. It may benefit only the common and adaptable, many of which will find their way to isolated urban habitats without planned links, but good links will work the other way by allowing people greater access to forest habitat networks.

**FOREST MANAGEMENT AND SILVICULTURE**

Many forest species have a strong association with either the open phase of growth before a stand forms a closed canopy (young-growth stands, usually less than 20 years since establishment), or the mature phase, when a stand contains large trees, a complex structure and large amounts of dead wood (old-growth stands, usually more than 150 years old) ([Peterken, 1996](#)). These species will not experience a forest habitat network as a network if their specialised requirements are poorly distributed.
Young-growth associates are easier to satisfy, since most are necessarily good colonists. But suitable conditions are more ephemeral, lasting less than a decade in most forest types. They require that felling and other forest operations continue on a regular, well-dispersed programme that maintains pre-thicket stands permanently in at least some part of each wood or cluster of woods that are well-distributed through the network.

Old-growth associates are more exacting, in that a high proportion are slow colonists and suitable conditions may take 150 years or so to develop. Many are saproxylic species that depend on dead wood or large timber (e.g. Harding & Rose, 1986). On the other hand, suitable conditions generally persist indefinitely in temperate forests once they have developed. These species require that existing stands at or approaching old-growth are retained as long as possible, together with individual large old trees. In the long term, it will be necessary to maintain mature conditions by growing some stands on very long rotations before harvest; retaining a core of minimum-intervention enclaves; including continuous-cover or shelterwood among the suite of silvicultural systems; and allowing a scatter of trees in or on the margins of all woods to die naturally in situ.

Almost all woodland in a forest habitat network should eventually be felled and harvested, but forestry should be planned to maintain continuity of both young- and old-growth habitats, and contiguity of old-growth. This can be achieved by working towards a normal age-class distribution and ensuring a network of old-growth and mature trees within woodland. An even flow of forestry operations will also ensure the continuity of open glades, which are crucial for many woodland invertebrates (Greatorex-Davies et al, 1992).

OTHER HABITATS WITHIN A FOREST HABITAT NETWORK

The importance of open space habitats in diversifying woodland (fig. 1.3, box 2.8), the possibility that some original-natural woodland took the form of wood-pasture (box 1.1), and the recognition that woodland isolation becomes negligible once woodland covers at least 30 per cent of the land (fig. 3.2), raises the general question of the relationship between tree-covered ground and other habitats. There are positive and precautionary points: open space habitats are an integral part of forests, but in constructing a forest habitat network, we must not also construct barriers for the species of other habitats.

One approach is that promoted by WWF, the global environment network, which considers forest defragmentation at a landscape scale. The practical realisation of this would be the restoration of our traditional forest habitats within a mosaic of other associated semi-natural habitats such as wetlands, heathlands, downland and coasts. Critical to the success of this approach is the promotion of both ecologically and economically sustainable rural development practices built around agricultural reform, delivered mainly through reform of the Common Agricultural Policy.

The Woodland Trust has also suggested that all semi-natural habitats should be considered collectively as a habitat network. This approach is particularly appropriate to lowland habitats, where arable and much other farmland contrasts sharply as habitat with all semi-natural habitats; remnant semi-natural grassland etc often occurs in close association with woodland; and the woodland edge habitats not affected by agriculture are those between semi-natural
habitats. This extensive mosaic of woodland and unwooded habitats was the essence of traditional forests, and should be a key feature of forest habitat networks.

**Simulating strategies for ameliorating fragmentation**

The study by *Buckley and Fraser (1998)* in lowland England is one of several that have explored the effects of different location strategies for reducing the effects of fragmentation. Another has recently been published which deals with Snowdonia, a contrasting region in the oceanic uplands, which broadly supports the approach adopted in this report (*Gkaraveli et al 2001*). Some 15.1 per cent of the National Park carries woodland of some kind, mostly conifer plantations (10.1 per cent), with minority proportions of mixed conifer-broadleaved plantations (0.6 per cent), broadleaved woodland (3.8 per cent) and scrub (0.6 per cent). This is not evenly distributed: there are concentrations in the Coed y Brenin and Gwydir plantation forests and the broadleaved Meantwrog valley. Overall, the broadleaved woodland fell into 2,110 fragments with an average size of 3.9ha and a mean nearest-neighbour distance of 118m. After simulating the effects of different strategies for increasing the area of broadleaved woodland in sample districts, the authors concluded that the priority was to retain the ancient woods, and then to adopt a mix of converting conifers to broadleaves, reforesting agricultural land, and establishing wooded buffer zones around existing woods. Provided the exact combination chosen was suited to the inherited pattern, this was the most efficient method of increasing both interior habitat and connectivity between woods.
4 How well are we doing? Past and present policies as a means of generating a network

**CHANGES DURING THE 20TH CENTURY**

Since the Board of Agriculture census of 1895, the area of British woodland and plantations has increased from a historic low point in the late 19th century of 4-5 per cent of the land area to about 11 per cent. How much has this threefold increase contributed to a forest habitat network?

Most of the increase has been taken the form of conifer plantations in the uplands. New plantations have been strongly concentrated into certain districts, governed partly by the economies of scale. This has created some substantial Core Forest Areas in the northern Pennines, Galloway, Argyll, the northern Grampians, Snowdonia and other areas. In the English lowlands, a new CFA was created in Thetford Chase, with lesser concentrations on other heathland districts.

The ecological development of these new CFAs has necessarily been restricted while the plantations were passing through the first rotation, but it has also been limited by their location, mostly remote from ancient woodland, and on soils that are not suitable for many woodland species. Where new CFAs have been developed on better soils and in association with existing woodland, as has happened in Coed y Brenin (southern Snowdonia) since the late 1920s, the forests have developed strongly as habitats.

At the same time, we have lost substantial number of ancient woods, thus removing the source populations. In approximately 60 years from the 1920s to the 1980s, some nine per cent of all English ancient woodland was destroyed through clearance and the land used for agriculture, roads, urban and industrial development, quarries, etc.

Over the same period, ancient woods have also been transformed by neglect or abrupt change from coppice to plantations. In England, some 37 per cent of English ancient woodland had been converted to plantations by the 1980s, and most of the rest were not managed. At least these still exist as woods, but the changes have been damaging. Conversion to plantations has damaged the native tree communities and their species, but the rides and other open space habitats have been kept open. Conversely, neglected woods have retained their native tree mixtures and associated species, but open space habitats have been much reduced and actually eliminated from most small woods.

Until the 1980s, despite a threefold increase in the area of woodland of all kinds, the 20th century saw a net retreat from a forest network. Whereas some CFAs were generated and some species prospered as a result, there was substantial loss and degradation of the ancient woodlands upon which a network would have to be based, and only limited creation of new native woodland. Moreover, the hedges, natural streams and other small-scale linkages across farmland were massively reduced.
Recent improvements

Latterly, there have been many improvements. The prospects for ancient woodland improved in the early 1980s under provisions of the 1981 Wildlife and Countryside Act and particularly the 1985 Broadleaves Policy (Thomas et al. 1997). These measures and subsequent developments have:

- much reduced the rate of destruction of ancient woodland;
- greatly reduced the rate of conversion to conifer plantations;
- increased forestry operations designed to maintain woods as mixtures of locally native tree species under comprehensive guidance appropriate to each main semi-natural woodland type;
- encouraged a substantial restoration of semi-natural woodland on ancient woods that had been converted to plantations of conifers; and
- incorporated a spatial and size element into current FC grants, i.e. proposals that would plant next to existing woodland are now favoured.

Current policies towards ancient woods are thus increasingly rigorous. Despite this, there is still evidence that ancient and semi-natural woodlands are threatened and sometimes destroyed: see the Woodland Trust’s report Ancient woodlands under threat, the WWF/FC Protected forest areas in the UK report and the WWF Forest scorecards. Nevertheless, the current position is a huge improvement on the position before 1985.

The passage of time has allowed many upland plantations to develop both a degree of stand maturity and a range of age classes. Moreover, woodland species have had more time to move in. This increasing diversity was further enhanced by changes in management, including:

- planting and encouraging the natural regeneration of broadleaves on a fraction of the ground;
- retaining some plantations well beyond commercial maturity;
- enlarging open spaces of all kinds; and
- removing plantations from riparian corridors.

Unfortunately, the conservation gains in woodland and forestry have not been matched by improvements in agriculture and farmland habitats, nor in the management of water resources. In fact, several trends have led to considerable loss of habitat and biodiversity outside forested land, in particular:

- continuing loss of lowland habitats;
- continued ageing of farmland trees and deterioration of old hedges;
- massive fertiliser use, leading to eutrophication of remaining lowland habitats;
- substantial over-grazing in the uplands;
- land drainage; and
- continuing control of river flows, channel movement and flooding.
This analysis has been largely confirmed by the Countryside Survey 2000 (box 4.1). The effect of these pressures and changes has been a continuing decline in semi-woodland habitats within farmland and increasing ecological isolation of woodland.

**Box 4.1 Habitat change in the British countryside, 1990-1998**

Recent broad changes in habitats have been quantified by the Countryside Survey 2000, carried out by the Centre for Ecology and Hydrology on behalf of the DETR. Some of the findings are important in assessing progress to or from a forest habitat network.

- **Broadleaved woodland** area has increased by five per cent (p.8). However, some woodland has been lost to development in England and Wales (p.11).
- **Coniferous plantation** area has not changed significantly (p.8).
- **Hedges**. The total length has remained the same (p.15), but there has been some turnover (p.7). Of all the hedges present in 1990, two per cent has been lost completely, and five per cent has been changed into lines of trees or shrubs, relict hedges, fences or banks and grassy strips.
- **Streams**. Although water quality has improved, streamside vegetation has become overgrown, and plant diversity has decreased by 11 per cent (p.15).
- **Neutral grassland** has continued to decline. Bracken and species that respond to eutrophication (false oat-grass, common nettle, cleavers) have increased substantially, whereas the characteristic species of semi-natural grassland (meadow vetchling, glaucous sedge, quaking grass, sneezewort) have decreased (p.6).
- **Roadside verges** also show evidence of increased nutrient levels and losses of plant diversity.

Source: Accounting for nature: assessing habitats in the UK countryside, an overview. CEH/DETR, 2000.

Admittedly, there have been small improvements. Re-creation of lowland habitats has taken place on a limited scale and damaging trends have been mitigated by agri-environment schemes. Consideration has been given to river restoration and habitat buffers along watercourses. These gains have been welcome, but they have been very limited. Perhaps now, after the 2000-01 winter of flooding and the later outbreak of foot and mouth, we may see further changes, such as:

- allowing rivers a limited freedom to flood, combined with a measure of river restoration;
- reduced upland grazing pressures and moor gripping;
- agri-environment schemes that allow farmers to retain and restore habitats;
- cross-compliance; and
- reduced use of fertilisers.

Habitat Action Plans recognise the need for habitat expansion. However, they provide for particular habitat types, not all semi-natural habitats in general. Even if they were fully implemented, they would go only part of the way towards achieving a forest habitat network.

**CONSERVATION AGENCIES**

The Conservation Agencies turned their attention to forest habitat networks in the 1990s. Scottish Natural Heritage in particular noted ideas for a European Ecological Network and proposals for large-scale native woodland creation by the Scottish Wildlife and Countryside Link and the Native Woodland Policy Forum. It also commissioned a report, which developed...
the idea of a forest habitat network for Scotland (Peterken et al 1995). Subsequently, this has been followed up by consideration of woodland conservation on a large scale in the Cairngorms, Clyde Valley, around Loch Sunart and in the Western Highlands generally. It has also sponsored Macaulay Land Use Research Institute to produce maps of potential woodland types, which form a basis for woodland restoration. English Nature has also considered reversing habitat fragmentation in Kirby (1995) and commissioned several research projects.

CURRENT FORESTRY STRATEGIES

The Forestry Commission has issued separate strategy documents for England, Scotland and Wales. On the basis of the statements in these documents, how far will the current strategy of the Forestry Authority go towards creating a forest habitat network?

England

The England Forestry Strategy (Forestry Commission 1998a) endorses the concept of a forest habitat network in the following terms (p.23):

“Over 20 per cent of our woodlands are of ancient and semi-natural origin. Many of these are fragments of historically more extensive woodlands. One of the consequences of this fragmentation is that their continued ecological viability is threatened. One way of overcoming this is to restore ancient semi-natural woodlands on the nation’s forest estate. A priority will be to work towards reversing this fragmentation by encouraging the creation of new native woodlands located to create more viable woodland units. Using locally native trees and shrubs helps to conserve the ecological value of native woodlands.”

Several programme actions explicitly implement elements of forest habitat network development, in particular:

- **Review the effectiveness of the existing measures for protecting ancient semi-natural woodlands and, if necessary, introduce new measures for giving them added protection.** This safeguards the base from which an ecological network can be developed.

- **Target grants through the Woodland Grant Scheme to reverse the fragmentation of existing native woodlands, conserve priority species, and help with the preparation of management plans for semi-natural woods.** Grant applications that would expand existing woods above certain threshold areas are now preferred, other things being equal.

- **Create new woodlands along transport corridors as part of a programme of environmental improvements.** This would generate long-distance links in a forest network.

- **Promote a network of forest tracks suitable for cycling as part of the National Cycle Network and our Integrated Transport Policy.** Insofar as the cycleway network and new woodland creation are mutually reinforcing, this will help to generate long-distance links.

- **Give priority to acquiring freeholds of leasehold land in areas close to centres of population, particularly in the Community Forests and the National Forest, when there is a shortage of existing woodland access.** This reinforces work already well under way to generate Core Forest Areas.
• Support research to improve understanding of the value of the environmental benefits of trees, woodlands and forests and the environmental processes that they perform, particularly in relation to aerial and water-borne pollution. This hints at reinforcing the links between woodland and watercourses, partly as a buffer against pollution, that would generate a natural pattern of riparian links in a network.

• Introduce long-term plans to guide the management of woods and forests. This long-established, but often neglected aspect of forestry, would help maintain the “network within the network” – a beneficial distribution of age-classes throughout a developing forest network.

More generally, the England Forestry Strategy has several elements that can facilitate forest network development indirectly. Thus, there will be support for research into the implications of CAP reform for the transfer of land from farming to forestry. Large-scale thinking is manifested in support for strategic development of woodland resources (sustained timber production, support for craft uses, etc), the promotion of forestry through land-use planning, support for incorporating forestry within the work of Regional Development Agencies, and support for highlighting forestry within regional and national planning guidance. Support for new urban forestry initiatives and promotion of forestry as a means of restoring waste and quarried land would improve links between urban greenspace and a rural forest network.

Scotland

The Scotland Forestry Strategy (Forestry Commission 1998b) explicitly endorses Forest Habitat Networks, and recognises the contribution made by Scottish Natural Heritage to developing the concept. In fact priority action PCE2 is “extend and enhance native woodlands by developing Forest Habitat Networks”. It explains (p.26) that:

“New native woodlands are especially valuable if they are located where they expand and create links between existing native woodland. The concept of Forest Habitat Networks has been developed to provide an ecological basis for planning woodland expansion. Forest Habitat Networks can enlarge and reconnect existing woods, thus alleviating the disadvantages of fragmentation. Riparian woodlands can often provide these links, as well as benefitting aquatic habitats. There is also the important role for treeline, or montane, woodland, providing a link between forest and mountain habitats.”

Other priority actions are closely related, though not explicitly tied to the network idea. For example, PCE6, Contribute to a radical improvement in the quality and setting of urban areas, provides links into urban greenspace, and FFR1, Expand the area of well designed productive forest, would also contribute to a network. The commitment to Indicative Forestry Strategies will tend to promote the development of Core Forest Areas.

The strategy has a clear regional priority: “Particular attention must be paid to lowland Scotland because there is a much lower proportion of native woods south of the Highland Boundary Fault. This recognises that much has already been done to generate a forest network in and around the Highlands, and that a special effort is needed in the lowlands, where woods generally remain small, scattered and separated by intensive farmland or urban development.

The strategy also quantifies the restoration and expansion targets for native woodland (Table 4.1), and explicitly links this to “targeting expansion to fit in with Forest Habitat Networks, for
example, using riparian woodlands to create strategic linkages between core areas of native woodland” (p.27).

Table 4.1. Restoration and expansion targets for native woodland in the forestry strategy for Scotland.

<table>
<thead>
<tr>
<th>Woodland type</th>
<th>Estimated area now (ha)</th>
<th>Restoration (ha)</th>
<th>Expansion/creation (ha)</th>
<th>Completion date</th>
<th>Intended total (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upland birchwoods</td>
<td>64,000</td>
<td></td>
<td></td>
<td></td>
<td>64,000</td>
</tr>
<tr>
<td>Upland oakwoods</td>
<td>30,000</td>
<td>3,000</td>
<td>3,000</td>
<td>2005</td>
<td>33,000</td>
</tr>
<tr>
<td>Native pinewoods</td>
<td>30,000</td>
<td>5,500</td>
<td>30,500</td>
<td>2005</td>
<td>60,500</td>
</tr>
<tr>
<td>Upland mixed ashwoods</td>
<td>12,000</td>
<td>800</td>
<td>2,000</td>
<td>2015</td>
<td>14,000</td>
</tr>
<tr>
<td>Wet woodlands</td>
<td>12,000</td>
<td>1,600</td>
<td>2,200</td>
<td>2015</td>
<td>14,200</td>
</tr>
<tr>
<td>Lowland mixed deciduous woods</td>
<td>3,000</td>
<td></td>
<td></td>
<td></td>
<td>3,000</td>
</tr>
<tr>
<td>Lowland wood pasture and parkland</td>
<td></td>
<td>150</td>
<td></td>
<td>2010</td>
<td>150</td>
</tr>
</tbody>
</table>

**Wales**

The Wales Forestry Strategy, *Coetiroedd i Gymru (2001)*, also incorporates network concepts. As part of its aim (2.5.1) to conserve and enhance the biodiversity of their woodlands, it recognises that the success of its strategy “will be shown if we can improve the quality of these woodlands, linking and expanding their habitat networks without compromising other valued habitats or historic features. The prospect of global climate change demands that we consider how robust our woodland habitats are, so that we concentrate our conservation efforts on habitats that will be sustainable in the long term”. Specific provisions include:

- “We will increase the quality of native woodlands for wildlife and implement the Biodiversity Action Plan targets for their restoration and extension, creating links between fragmented woodlands.
- “We will increase the biodiversity of coniferous woodlands through the use of continuous cover-systems, developing multi-aged structures through natural regeneration and the incorporation of native species.
- “We will increase the area of native woodlands, targeting extension and connection of existing woods and incorporating the concept of increasing the core area of native woodland habitats.
- “We will encourage owners to incorporate different habitats, such as heath and bog, within woodlands, to maximise the connections between similar habitat types”.

Furthermore, as part of its general aim (2.5.3) to better integrate woodlands with other countryside management:

- “We will use catchment management planning to develop the role that woodlands can play in the management of water and the reduction of flood risks.
• “We will work to prevent further loss of ancient and semi-natural woodland, building on the National Inventory of Trees and Woods to improve our knowledge of the status of native woodlands in Wales and to assist in their protection.

• “We will work to develop appropriate links between woodlands and wider countryside management through Tir Gofal and other environmental schemes.

“We will continue to support scientific research into the interactions between woodlands and other land uses in the wider countryside, to develop our policies for the environment”.

Comment
The aspirations expressed in these strategies can be implemented up to a point through the work of Forest Enterprise, and substantial progress has been made through, for example, Forest Design Plans and the restoration of plantations on ancient woodland sites (PAWS) to native woodland. Since 1919, the Forestry Commission has created or reinforced many Core Forest Areas, albeit in the form of conifer plantation forests, but these are being steadily diversified. However, Forest Enterprise is hardly expanding its land holdings, and cannot therefore generate many components of a network.

If there are criticisms to be made or reservations to be expressed, they are fourfold:

1 Targets are not always specific and quantitative. This is perhaps to be expected in a strategy statement, but the broad values given for native woodland in Scotland give a clear indication of what is envisaged.

2 Although the strategies incorporate ecological concepts, spatial elements and large-scale thinking, the shape (literally) of the long-term future pattern of forests remains vague. Clearly, the future pattern will be substantially determined by the present pattern, but a more detailed statement of the desired forest network at national, regional and local authority scales would give clarity and precision to the strategy’s targets.

3 Many action points stand back from reality on the ground – for example, by “seeking opportunities to consider”, “supporting research” and “exploring ways” of doing things. This mode of expression is inevitable, especially as much of the Forestry Commission’s role is to promote and control forestry in the work of others. Nevertheless, the pressures from agriculture and water resource management still run strongly against trees and woodland, and the resources available to these land users exceed those available to forestry, to the extent that some aspects of the strategies may be difficult to implement.

4 There are suggestions, most obviously in the Scottish strategy, that a Forest Habitat Network is to do with native woodland. In fact, all forest land will contribute. Large conifer plantation forests devoted primarily to timber production are an essential component: if they were not, they would represent substantial barriers to network development. In the long term, the concept of a network could break down distinctions between native woodland and conifer timber plantations, and between nature reserve woodlands and the rest.

Nevertheless, there is little doubt that current forestry strategies endorse the concept of forest habitat network, and this is much to be welcomed. More flesh is now needed on the bones.
Conclusions

Nature reserves have been an effective mechanism for conservation for more than a century. Numerous species owe their survival at a county scale to protection of rich and representative habitats, and there have been many other benefits in education, research and the pleasure they have provided. They and other rich wildlife habitat are the sources from which a rebuilt habitat network would be restocked.

Even so, nature reserves should be regarded as a necessary but insufficient means of protecting wildlife. Their failures are obvious from, for example, the analysis of local extinctions of native vascular plants (Marren, 2001): over recent decades, between 0.3 and 1.4 species have been lost each year from the English counties. Even when managers have manipulated protected habitats to provide ideal conditions for the most important constituent species, most reserves are too small and too isolated to provide long-term security for the species they contain. This much was made clear by the multiple losses of butterflies from Monks Wood National Nature Reserve after it became an NNR. The damaging effects of management in surrounding land cannot be excluded. Populations of wildlife species in reserves may be so small that eventually they are extinguished by short-term fluctuations or adverse conditions. Once a species has been extinguished in an isolated reserve, it may be unable to recolonise if the nearest surviving population is some distance away, and the intervening ground is hostile to its survival.

This lack of resilience of some apparently protected wildlife populations in small, isolated reserves has long been recognised, and attempts have been made both to enlarge reserves and to manage them to sustain the habitats of the most important and sensitive species. However, with the advent of climatic change and the consequent need for wildlife populations to adjust their ranges to changing conditions, the prospects for trying to protect wildlife in a scatter of isolated reserves have deteriorated. We need joined-up thinking not only in government, but also in nature conservation, because we need to plan for nature conservation on a larger scale.

Fortunately, several concepts have evolved to facilitate this larger-scale perspective (Angelstam 1997, Forman 1995). During the last 30 years, landscape ecology has developed to study the effects of the pattern of habitat patches, the processes that operate between them, and the influence of people in forming and changing the pattern. As far as individual wildlife species are concerned, the concept of metapopulations has developed to allow particular species to be visualised as a collection of more-or-less distinct populations between which there is a greater or lesser degree of exchange on individuals. Furthermore, the effects of ecological isolation have become increasingly recognised, both in scientific research and in popular concepts, such as ancient woodland indicators.

The new concept in conservation is the habitat network, which provides a comprehensive basis for the restoration of forest habitats. Sure, the rationale of network design continues to evolve, and we have hardly started to solve practical issues of inserting new woodland into our ancient, evolved pattern of land use and ownership. Moreover, we must consider how a forest network might impact on other habitats, such as moorland habitats in the uplands. But, undeveloped as it is, the network concept has much to recommend it.
Although we have presented the case in terms of nature conservation benefits, the approach to reversing habitat fragmentation on the basis of a forest habitat network would have many benefits in addition to the benefits for wildlife. It not only matches the current preference for organisations to work in partnerships, but also has several more specific benefits for multi-purpose forestry:

**Timber** New woodland on the fertile soils of the lowlands should offer opportunities to grow more hardwoods in Britain and diversify the timber harvest. There is no reason why most of the woodland in a network should not be productive of timber. In fact, a network would offer foresters what they have largely been denied: a chance to grow quality hardwoods on some of the better land.

**Forest management** If wildlife populations become more resilient in the face of habitat change, foresters will have correspondingly more flexibility in their management. It is possible even to envisage circumstances in which the various landscape and nature conservation designations could be more sparingly deployed.

**Water quality** If streams and rivers are more extensively buffered from arable agriculture by mixed habitats including woodland, there would be good prospects for improving water quality by decreasing both fertiliser run-off and sediment load.

**Landscape** This is a subjective judgement, but many people would welcome a more arborescent landscape, especially in regions where the number of hedgerow trees has greatly diminished in the last 50 years.

**Recreation** As an example, long-distance corridors of mixed habitats would be good places to route long-distance footpaths and cycle tracks.

**Urban-rural links**

The mixed habitats of a forest network could be linked to networks of urban greenspace. This is already happening in the case of various Community Forests. The benefits for woodland wildlife may be limited, but the benefits for people in the form of access to a forest habitat network would be considerable.

The obvious question – one that is often asked in policy-making circles – is how much more woodland is needed? In this instance direct and simple answers tend also to be arbitrary. The priority is to develop the large network components – Core Forest Areas and the habitat-rich corridors between them – each containing at least 30 per cent woodland cover, and to enlarge the size of individual woods, especially those now covering less than 20ha. But it is the mesh size – the relative sizes of the network and the matrix – that would also determine the overall amount of woodland.

The number of CFAs and the mesh size of the network cannot be determined on purely ecological grounds. Existing occupation of the land presents obvious limitations on the freedom of design, and other demands on land will compete for opportunities for expansion. Nevertheless, the idea of a forest habitat network is sufficiently broad, flexible and founded on ecological understandings to provide a unifying concept for forest restoration.
Action points

1. Forest cover should be increased to 15 per cent of the land area of the UK, with a minimum target of 30 per cent cover in particular districts. This reiterates a proposal previously expressed by WWF in its *Greenprint* document (WWF, 2001).

2. The Forestry Commission, having endorsed the network concept, should develop a more comprehensive forest habitat network strategy. This should be based on the multi-habitat definition of forest.

3. Core Forest Areas should be identified. Their management might be coordinated within CFA management plans or strategy that incorporates a well-connected, multi-habitat design, a well-distributed range of age classes, and a spread of habitat maturity throughout the CFA.

4. Potential new CFAs should also be identified, and incentives should be devised to bring these up to the scale and connectivity of CFAs. Natural Areas and the Inventory of Ancient and Semi-natural Woodland should form a basis for planning new CFAs.

5. In general, incentives for new woodland should include a stronger spatial element, designed to increase the size of small woods, increase linkages between woods, and develop CFAs and landscape-scale links.

6. Records of new woodland should include information on spatial characteristics, in order to assess with other data progress towards a Forest Habitat Network.

7. County and regional authorities should be encouraged to restore forest habitats on the basis of a network, considering both connections within the area and linkages to adjacent areas.

8. It is important that safeguards for ancient woodland be maintained and strengthened, and that plantations on ancient woodland sites continue to be at least partly replaced by native woodland.

9. Network design should be developed and improved through continuing research into the movement of wildlife species over the landscape, and the survival of individual sub-populations of wildlife species.

10. The benefits of a Forest Habitat Network for recreation, water quality, hardwood timber production, etc., should continue to be explored and developed.

11. More detailed analysis of and prescriptions for the reform of existing instruments (such as the Common Agricultural Policy, particularly the Rural Development Regulation, the Woodland Grant Scheme and the Farm Woodland Premium Scheme) is needed. This will enable the agricultural and forest authorities to jointly develop effective support for retention and restoration of wooded landscapes habitats within farmland.
References


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