4 Ecology

4.1 Scrub dynamics

4.1.1 The origins and sources of scrub

With a few local exceptions, modern scrub is almost entirely a creation of man's activities, yet scrub vegetation would have occurred in several situations in primeval European landscapes largely unaffected by humans. In terms of contemporary conservation, this is an important point because many species of plants and animals will be adapted to the vegetation structures provided by scrub habitats. Moreover, shrub species were some of the first to colonise after the last ice age and scrub would certainly have been the first type of woody vegetation cover. Since then it has persisted, where climate and man have allowed, as a climax vegetation at the extremes of altitude and oceanity. The forest that followed the scrub would also have expanded to its furthest extent until climate halted its progress. Within these forested landscapes, scrub would have occurred in at least five situations. Examples of each of these **natural types of scrub** can be found in present day Britain but they are rare.

1. As a seral stage wherever primary successions were initiated. These situations would have occurred on stabilized coastal dunes, on eroding coastal cliffs and in river valleys with unstable sediments subject to scouring by floodwater.
2. Wherever extreme climatic conditions, especially windspeed and temperature, restricted the development of full woodland vegetation. In the lowlands these conditions probably pertained mainly to exposed western coasts.
3. In the uplands, montane and sub-montane scrub would have been far more widespread than today (Ratcliffe & Thompson 1988). For example, scrub was widespread in the Outer Hebrides, Shetland, Orkney and Caithness but was destroyed by burning, grazing and clearance about 5000-4000 BP (Birks 1988). Climate change was also a factor in the downward displacement and eastward retraction of scrub during this period.
4. As an ecotone between woodland and open habitats. It is arguable how much open unwooded land existed in primeval lowland Britain. If large herbivores did maintain patches of open grass and heath in some areas, especially those with nutrient-poor soils, it is likely that scrub would have been a constituent of the mosaic of habitats. Substantial areas of willow *Salix* spp. and alder *Alnus glutinosa* scrub would have been a typical component of the vegetation in the major floodplains, especially perhaps at the fringes of the permanent swamp and dry woodland.
5. Natural regeneration within treefall gaps in otherwise continuous forest would, where grazing pressure allowed, have temporarily created scrub-like vegetation structures.

Scrub frequently exists as ephemeral vegetation in the process of active succession from open grass or heath to woodland; Tansley (1939) termed this **seral scrub**. However, much scrub exists in situations where factors such as grazing, periodic fire or cutting prevent the establishment of trees but allow the persistence of scrub; this is effectively an arrested succession which Tansley (1939) termed **subseral scrub**. This type of scrub typically exists as a deflected successional stage or plagioclimax. Most dense thickets of mature scrub, such as blackthorn *Prunus spinosa* and hawthorn *Crataegus monogyna* with no obvious tree regeneration, should be regarded as subseral scrub for these will almost certainly develop into woodland eventually (see 4.1.3). A

different situation arises where climate, salt deposition, substrate stability, soil depth or hydrology are not conducive to tree growth but do permit the development of scrub. Scrub that persists indefinitely as a result of such factors was termed **climax scrub** by Tansley (1939). Extant examples of climatically maintained scrub are found on coastal cliffs in southwest England, on small islands in freshwater lochs in north-west Scotland, in some coastal areas of western Scotland, especially the Inner Hebrides, and in the montane scrub of the Scottish Highlands.

Salt spray appears to be an important factor inhibiting the growth of scrub on upper seacliffs in southwest England and Wales (Hopkins 1996, Oates 1999). Scrub dominated by low banks of blackthorn or gorse *Ulex* spp. are particular features of upper cliff slopes in these regions. Substrate stability is an important factor resulting in the natural persistence of scrub and young woodland on a few cliffs, for example at Axmouth-Lyme Regis Undercliffs, Dorset. Coastal cliff sites with scrub can be considered as among the most natural areas present in Britain, although some will have received past management. Coastal protection schemes can damage these systems where they stabilize slopes. Some spate upland rivers also carry vestiges of scrub on unstable sediments on islands and banksides. There are no surviving lowland examples of natural floodplains in Britain. However, the carrs of the Bure Marshes, Norfolk, provide examples of near-natural wetland scrub structures, with various transitions and intermediate vegetation types between open swamp and closed canopy alder woodland. Perhaps the best example of scrub that is maintained by grazing or fire is gorse on southern heaths.

Scrub development within **primary successions** is a localized phenomenon. It occurs on dune systems in several forms in both wet slacks and old fixed dunes. Within non-calcareous wet dune slacks, low to medium scrub of creeping willow *Salix repens*, eared wilow *S. aurita* and bog myrtle *Myrica gale* is typical; calcareous slacks can have an abundance of creeping willow. The most distinctive scrub associated with fixed dunes is sea buckthorn *Hippophae rhamnoides* which can form extensive tracts, especially on the east coast. Old fixed dunes can, however, develop a wide range of scrub communities. Gorse *Ulex europaeus*, broom *Sarothamnus scoparius* and bramble *Rubus fruticosus* commonly develop on acidic dunes. On non-acidic soils, thickets of blackthorn hawthorn, elder *Sambucus nigra* and privet *Ligustrum vulgare* may all be present. Other primary successions involving scrub may occur on unstable cliffs, scree and along some upland watercourses. However, the most widespread primary successions occurring in the lowlands are those associated with abandoned mineral workings. At dry sites, the scrub that develops depends on nutrient status: chalk and limestone quarries often contain diverse calcareous scrub whereas extraction at more acid sites can lead to gorse, broom and birch *Betula* spp. scrub. Flooded mineral workings often develop fringing thickets of willow scrub.

The majority of contemporary scrub in Britain has arisen through **secondary succession**. In the lowlands, the breakdown of traditional grazing systems on marginal land over the last 100 years has been a stimulant for scrub development. Grazing pressure by domestic animals on downland, heathland, coastal rough grassland and most lowland commons decreased to the point where much of this land was hardly grazed by livestock by the middle of the 20th century. Many of these formerly open sites have been strongly invaded by scrub and woodland but there is

much local variation caused by the exact history of grazing by livestock and rabbits *Oryctolagus cuniculus* and by habitat restoration schemes involving scrub removal. Paradoxically, numbers of sheep escalated throughout most of Britain during the last quarter of the century (Fuller & Gough 1999) but this has taken place in the uplands and on lowland improved productive grasslands. More locally, the abandonment of vegetation cutting and turf cutting has triggered scrub expansion. This has occurred on many of the East Anglian valley mires (e.g. Redgrave Fen, Norfolk) but the best documented example is Wicken Fen where saw sedge *Cladium mariscus* was traditionally cut on a three to four year cycle and peat was also cut (Friday & Colston 1999). These practices declined at the end of the 19th century and in subsequent decades there was massive scrub expansion. The amount of scrub created on lowland marginal land during the 20th century has probably peaked and is now declining as a result of succession to woodland and habitat restoration, though no reliable statistics are available.

Scrub has sometimes been generated within the wider countryside as a consequence of the downturns in the agricultural economy. While this has not occurred in Europe on the scale evident in the eastern and Midwest USA, where large numbers of poor farms were completely abandoned at the end of the 19th century in favour of increased production on more productive land (Whitney 1994), there have been periods of temporarily reduced production here. This occurred most strikingly in the depression years of the 1920s and 30s when grain prices collapsed and arable farming contracted. The drive for self sufficiency in the Second World War and the subsequent intensification of agriculture has, however, removed all traces of pre-war scrub expansion. Abandonment of farmland as a process leading to scrub development in the 21st century cannot be ruled out, especially on poor quality grazing land. Perhaps the most likely large-scale expansion of scrub in the near future is in upland areas, where reductions in grazing pressure may result from abandonment of hill farms and the removal of deer. In the Scottish Highlands, reduction of red deer numbers and associated expansion of scrub is seen as a conservation opportunity by some ecologists and conservationists for ultimately this process will lead to more natural vegetation types (Usher & Thompson 1993, Scottish Natural Heritage 1994, Hester & Miller 1995, Staines *et al.* 1995). Large-scale scrub regeneration, mainly of birch and Scots pine *Pinus sylvestris*, is already taking place on several nature reserves in the central and eastern Highlands, for example at Creag Meaghaidh, Cairngorm NNR, Dinnet NNR and Abernethy RSPB reserve.

There is a final miscellaneous category of secondary successional scrub that develops on temporarily neglected land of various kinds. These include the fringes of industrial sites and land awaiting development where *Buddleja* often gains a strong hold as well as various forms of native scrub. Railway embankments can support a variety of scrub types, including naturalized and native species.

4.1.2   Mechanisms of scrub invasion

Classical models of successional mechanisms are of three broad kinds: facilitation, tolerance and inhibition (Connell & Slatyer 1977, Finegan 1984). Here we review the extent to which these and other models are likely to apply to the successional establishment of scrub.

The facilitation model applies when the invasion of one species is dependent on change in the environment brought about by another species. Facilitation is potentially most likely to occur in primary successions. Woody plants do not colonise until nitrogen levels have built up to $400 - 1200$ kg ha^{-1} (Crawley 1997). In primary succession the nitrogen is built up mainly through nitrogen fixing species and atmospheric deposition. Most scrub species also require a reasonable depth of soil and moderate

levels of soil organic matter in order to maintain roothold and grow to reasonable stature. Although these processes are driven largely by early successional plant species, they are community processes rather than true interspecific facilitation (Crawley 1997). There is no evidence that facilitation involving interactions between individual species is a critical factor determining the successional invasion of shrubs, nevertheless scrub can usually only flourish in primary successions once the environment has been substantially modified by preceding vegetation. Though technically not facilitation, some bird dispersed shrubs can only gain a foothold once perches are present for birds, hence the invasion of bird-dispersed shrubs may be facilitated by wind-dispersed shrubs. Another example is the protection from browsing animals that some shrubs, such as juniper *Juniperus communis*, can sometimes afford to other plants.

Tolerance models are based on the assumption that later successional species are able to colonise through their ability to tolerate reduced resource levels (light and nutrients) imposed by the earlier, faster-growing colonists. Eventually the latter species are outcompeted by the former (this is also the outcome of facilitation). Inhibition models are fundamentally different to facilitation models in that they assume that early successional species make conditions less suitable for later arrivals and until they die, or are in some way suppressed, the later species are prevented from becoming established. The rate of succession under an inhibition model is linked directly to the longevity of species and to the rate at which local disturbances create opportunities for regeneration by late successional species.

Inhibition is a particularly relevant mechanism in the establishment of scrub in the sense that dense mats of grass, ericaceous shrubs and leaf litter may inhibit regeneration of woody shrubs. This can result in very slow progress of rank grassland towards scrub (Hopkins 1996). The death of individual plants or local disturbances such as trampling and poaching by livestock or fire may be required to establish regeneration. Examples include persistent mats of mat-grass *Nardus stricta* and purple moor-grass *Molinia caerulea* on moorland that may inhibit germination of woody vegetation. A special case of inhibition occurs where grazing holds immature shrubs in check. This may happen if shrubs become established but then become subjected to intensified grazing that is insufficient to kill them but prevents their further growth. Under these circumstances, subsequent relaxation of grazing, may result in rapid release of scrub growth. Hawthorn scrub in grassland can be maintained indefinitely in a low stunted state by sheep grazing, though the sustained use of hill or mountain breeds of sheep that feed less selectively than their lowland counterparts would probably eventually result in the scrub disappearing.

The initial floristic composition model (Finegan 1984, Crawley 1997) is at the opposite extreme to facilitation in that it implies succession is merely driven by the differing life strategies and growth rates of the plant species that are present at the outset. Under this model fast-growing, short-lived species are gradually replaced by slower-growing, longer-lived species. Plant composition in secondary succession may often be driven by such life history differences where a substantial seed bank or parent seed source is present at the outset. However, initial floristics, tolerance and inhibition are not mutually exclusive; these mechanisms may act simultaneously.

Finally, one must consider factors influencing seed dispersal and predation as determinants of the rate and nature of succession. The majority of shrub species produce fleshy fruits and are, therefore, primarily adapted for dispersal by birds. A mutualistic relationship has evolved between berry-bearing shrubs and birds; in Britain the avian dispersers include especially the larger thrushes, the *Sylvia* warblers, robin *Erithacus rubecula* and starling *Sturnus vulgaris* (see 4.2.1.4). Mutualism is potentially far-reaching because there is evidence that birds feeding on juniper avoid selecting fruits that are damaged by insects that predate the pulp or seeds. This has the effect of increasing the

proportion of healthy fruits in the seed rain (Garcia *et al.* 1999). We are unaware of any detailed studies of the dynamics of dispersal of any shrub species in Britain, though the work of Snow & Snow (1988) is valuable as a documentation of the usage made of different fruits by birds. The most detailed European studies of dispersal are of juniper in Spain which show that in addition to wintering thrushes, juniper is dispersed by carnivorous mammals, rabbits and livestock (Herrera 1989, Santos *et al.* 1999). However, the birds are the most effective dispersers (Santos *et al.* 1999). It is likely that mammals also have a dispersal role for some shrubs in Britain. For example, Tansley (1939) mentions that rabbits are important dispersers of hawthorn. Wind dispersed scrub species include alder, willow, birch and pine. It should be noted, however, that although birds do not act as dispersers for these species, they do consume their seeds. Small mammals can exert severe predation on seeds in old fields and this may influence the rate and spatial pattern of shrub and tree establishment (Manson & Stiles 1998).

For all shrub species, the proximity of seed sources is important. This is likely to be especially important in upland areas devoid of existing scrub and tree cover over large areas. Under such circumstances, even when conditions are otherwise favourable for regeneration, scrub development may be a slow process. Finegan (1984) has argued that the behaviour of dispersers, especially birds, is a critical factor in the rate and pattern of succession of woody plants. In the case of bird-dispersed species, invasion may also be slow if birds do not use the receptor site. Deposition of faeces, and hence of seed, can be a slow process if there are few perches (Finegan 1984, McClanahan & Wolfe 1993). Even within established scrub, the dispersal of seed from bushes in small isolated fragments may be less effective than that for bushes of the same species within larger patches of scrub, this being a function of the frequency with which berry-eating birds visit patches of different sizes (Santos *et al.* 1999).

This section has focused on seral scrub but rather different issues may be relevant concerning the potential expansion of montane willow and juniper scrub (D. Gilbert pers. comm.). These include the proximity of male and female plants and so the potential to produce seed. There also appears to be a relationship between population size, volume of viable seed and successful recruitment that requires investigation.

4.1.3 Structural dynamics of scrub development

As scrub colonises open ground and gradually progresses towards woodland there is a huge transformation of physical architecture. These structural changes are extremely important in driving many of the associated changes in animal communities yet they appear not have been documented in detail for any type of scrub in Britain. In the absence of any long-term quantitative studies on the dynamics of scrub vegetation we have based the following account on our own observations of scrub structures made in the course of studies of animal succession within scrub. Three basic situations are outlined below which relate mainly to the pattern of tree regeneration within the scrub.

1. **Lowland thicket scrub** (*sensu* Tansley 1939) occurs when few tree species regenerate within the developing scrub. The scrub itself grows into a dense thicket, which may persist for a considerable length of time though, in the absence of cutting, this will eventually give way to woodland as bushes die and generation opportunities arise for trees. Examples of thicket scrub can include stands dominated by hawthorn, blackthorn and gorse. In describing the typical sequence of structural changes, it is assumed that the scrub is developing on former grassland, that seed sources are readily available for the scrub, that regeneration sites are available for the shrubs and that subsequent grazing pressure by livestock, deer or rabbits does

not arrest or disrupt the development of the scrub. Where the latter happens, low open scrub may be maintained for a considerable period. The structural development of scrub is a continuum. Nonetheless, it is useful to identify three broad main phases which can be defined in terms of the cover and height of the woody vegetation and in terms of the foliage profile i.e. the distribution of foliage across different heights.

Phase I - establishment. Relaxation of grazing or mowing results in growth of the grass and the initial colonization of shrubs. During this phase there is an intimate vertical mixture of grass and woody vegetation, and spatial heterogeneity is high with some patches dominated by grass, others becoming increasingly dominated by shrubs. Once the scrub grows above approximately 1 m and the scrub cover exceeds approximately 50%, the intimate vertical mixtures and horizontal mosaics of grass and woody vegetation start to break down.

Phase II - canopy-closure. Increased growth of the scrub results in conditions where open areas of grass are becoming increasingly scarce through shading and the density of the low woody vegetation, within 1.5 m of the ground, is extremely high, often forming impenetrable thickets. Even when the scrub canopy has fully closed, for a period of time the low woody vegetation will remain dense.

Phase III - post canopy-closure. This is the least structurally diverse stage. Following canopy closure, and with continued growth of individual bushes, the density of low vegetation declines rapidly, both in the field layer and the quantity of low woody vegetation. The biomass of vegetation becomes increasingly concentrated in the scrub canopy and a 'leggy' structure becomes evident to the scrub. Within mature blackthorn and mature hawthorn it becomes possible to walk beneath the canopy with ease.

2. **Lowland woodland scrub** (*sensu* Tansley 1939). The major difference between woodland and thicket scrub is that trees are growing within the former scrub more or less from the outset. Examples of woodland scrub include several formerly grazed commons in the Chilterns where oak *Quercus* spp. grows within hawthorn scrub and regenerating mixtures of ash *Fraxinus excelsior* and hawthorn on limestone. The same sequence of structural changes occurs as for thicket scrub but there is more structural heterogeneity within the establishment and canopy-closure phases. A greater range of shading conditions also exists under woodland scrub which may allow a greater variety of herbs to exist. Perhaps the main difference, however, is in the post canopy-closure phase where the presence of trees results in much greater diversity of structure and a more rapid progression to a woodland structure.

3. **Birch and pine scrub on upland and lowland heath**. This is distinguished as a third type of structural development because, on upland and lowland heathland and moorland, much scrub regeneration usually consists of the tree species that ultimately form the mature woodland. The structural phases of establishment, canopy-closure and post canopy-closure still apply, but the vegetation structures are relatively simple compared with those in much lowland thicket and woodland scrub. Tree and shrub species composition is relatively low so these types of developing scrub tend to have lower diversity of microhabitats and shading conditions.

4.1.4   Spatial patterning, mosaics and edges

Inevitably the above descriptions of structural changes are simplified. There is much variation with the botanical type of scrub and in the spatial uniformity of the process. Patchiness in developing scrub, in both the establishment and canopy-closure phases, is an important habitat feature for many associated plants and animals. The processes by which patchiness develops have not been examined in detail but several factors are likely to be relevant.

The spatial patchiness inherent in the development of much scrub vegetation may have its origins partly in the location of perches for birds. Isolated established bushes will tend to attract birds which deposit more seeds, thus forming a regeneration nucleus (Finegan 1984). The effect may be enhanced where suckering species, especially blackthorn, become established. The behaviour of birds is not, however, the sole factor driving patchiness. Receptive germination sites may not be evenly distributed over the site. Furthermore, seed predation by small mammals may be spatially uneven (Manson & Stiles 1998). Large trees growing within the scrub will also promote patchiness by casting shade and hence inhibiting the growth of shrubs nearby.

Grazing has an important effect on patchiness. An increase in grazing pressure after scrub establishment, or spatial unevenness in grazing, can intensify the patchiness within scrub. On calcareous grassland, rabbits can slow down, and possibly prevent, the expansion of scrub outside regeneration nuclei and thus enhance the mosaic effect.

Where mosaics of scrub and grassland develop, the vegetation structure at the edges of scrub patches is different to that within the patches. Foliage density at the edges of patches is usually denser at the edges and there is often vertical continuity of grass and shrubs forming a complex structure that is not evident within the scrub patch. These complex structures are probably important to a wide range of animals and plants. Hopkins (1996) points out that several plants that are sensitive to grazing may find refuges at the edge of scrub patches where grazing pressure is often less intense. Among the plants he listed are wild parsnip *Pastinaca sativa*, hogweed *Heracleum sphondylium* and false oat-grass *Arrhenatherum elatius*.

Hopkins (1996) has also drawn attention to the concepts of saum and mantel which are well established in a European context but less widely recognised in Britain. Saum and mantel are components of an ecotonal mosaic of vegetation consisting of species-rich grassland, scrub and woodland. Saum is vegetation characterised by tall herbs and sparse shrubs, while mantel is dominated by shrubs. The existence of these different vegetation types in close proximity to one another is usually a product of episodic, low intensity management involving grazing on unproductive land of low nutrient status. Such mosaics are extremely localised in Britain, but Hopkins (1996) gives some examples of locations where they may be found, for example the Derbyshire Dales. In biodiversity terms these mosaics can be extremely rich.

The maintenance of species-rich scrub mosaics represents a conservation challenge. The complex mosaics and edge structures that develop during the successional growth of scrub (and this certainly applies to saum and mantel structures) are rarely evident in scrub that is managed by rotational cutting (Gough & Fuller 1998). This form of management effectively coppices the vegetation, resulting in much regeneration occurring from cut stumps which usually gives a far more uniform appearance to the developing scrub. The structural consequences of starting from open grassland or as regrowth from felled scrub are, therefore, very different. Maintaining biological richness within scrub mosaics is largely dependent on managing the scrub to ensure that it does not reach the closed-canopy stage where nutrient build up occurs (Hopkins 1996).

4.1.5   Environmental changes associated with scrub development

Vegetation succession leads to several alterations in environmental conditions in addition to ones of vegetation structure and floristics. Light regimes are substantially modified by the vegetation changes and the consequences are especially profound for plants growing in the field layer.

Scrub development generates major changes in soils. Nutrient conditions change with succession with build-up of nitrogen, which is enhanced where nitrogen-fixing species are dominant members of the scrub community, for example alder, sea buckthorn and gorse. Phosphorus mining can also occur in scrub, whereby there is enrichment of the soil close to the surface. This can result in dominance by competitive ruderals when scrub is cleared (Grubb & Key 1975). Organic soil content also increases under a scrub canopy with the build up of leaf litter. These processes are particularly important on nutrient poor sites where subsequent attempts to restore a species-rich grassland flora may be hindered by rapid growth of nutrient-demanding rank vegetation (Hopkins 1996).

4.1.6   Mycorrhizal interactions

The occurrence and role of mycorrhizal fungi in scrub communities in Britain and Europe are virtually unknown. The symbiosis between mycorrhiza and host plant relies on the provision of carbon by the host plant to sustain the fungus in return for nutrient (particularly phosphate) acquisition by the fungus (Smith & Read 1997). The mycorrhizal fungus, whether arbuscular or ectomycorrhizal, maybe specific to the plant species. However, the association is variable both within and between species and tends to be more prevalent in nutrient limited soils, often utilised by scrub communities. Mycorrhizal fungi are known to be particularly important in the establishment phase of plants (Gange *et al.*1990) and thus their role in the spread of scrub communities may be considerable. The concept of artificially manipulating mycorrhizal fungal communities is new and yet to be fully researched. However, innoculation of soils with appropriate mycorrhiza, either in the field or nursery, may be a future tool in the restoration of rare species and communities. In addition, the potential for linkages by the hyphae of ectomycorrhiza within or even between species may promote nutrient exchange, reduce plant competition and promote recovery (Amaranthus & Perry 1994). Arbuscular mycorrhiza can also play a role in alleviating drought stress and in the stabilization of disturbed soil by enhanced recruitment of species (Garcia *et al.* 1999).

4.2 Ecological linkages within scrub systems

This section focuses on four groups of organisms: lichens and bryophytes, ground flora, invertebrates and birds. It reviews the importance of different aspects of the scrub environment for each group in turn. These species groups have been selected because they represent strikingly different life forms, with fundamentally different requirements, and embrace many species considered to be of special conservation importance in the context of scrub. Invertebrates and birds are particularly diverse in their responses to scrub development.

Clearly, scrub can be important to taxa other than those examined in detail here and the following should not be regarded as a comprehensive account. For example, open mosaics of scrub and heath or grassland may be important to reptiles. In the case of the adder *Vipera berus*, Wild & Entwistle (1997) state that 'Scrub is used for cover and is an important feature of many sites'. Successional changes may also affect many other groups of animals including, for example, small mammals (Churchfield & Brown 1987).

The development of increasing structural complexity within seral scrub stimulates a web of indirect interactions between organisms which has been inadequately researched. It is appropriate at this point to touch on the issue of climate change because it is becoming clear that plant communities and their associated invertebrates will be potentially altered, but not necessarily in a predictable way (Masters *et al.* 1998). Hence, it is possible that scrub species may show a variety of responses to changing climate and that this may affect their associated ground floras and invertebrate communities in complex ways.

4.2.1 Effects of scrub floristics

This is concerned with the effects of the species composition and diversity of shrubs.

4.2.1.1 Lichens and bryophytes

For bryophytes, the dominant tree species is generally of secondary importance to microclimate and microhabitat (Hodgetts 1993). Therefore, apparent associations with particular shrubs or trees may merely reflect these other factors. In western Britain, some of the richest assemblages of bryophytes are associated with oakwoods but in north-west Scotland hazel *Corylus avellana* and birch stands can also be rich in bryophytes (Hodgetts 1993). Some of these latter woodlands are, in structural terms, effectively scrub. Ratcliffe (1977) also mentions that stands of northern and western hazel scrub can be rich in bryophytes. Elder *Sambucus nigra* provides a locally important habitat for epiphytic mosses (Ratcliffe 1977). Lichen communities show a certain amount of variation according to tree species (Harding & Rose 1986). This is probably a response to factors such as the texture, chemistry and moisture retention of the bark. These differences appear to manifest themselves mainly on mature, or even veteran, trees so they may not be especially relevant to scrub. Nonetheless, western Scottish hazel stands are of particular interest for lichens, supporting several species endemic to the British Isles. The older, larger hazel stems are the richest in these lichens. Ecological continuity, as well as climate, appears to be a key factor influencing the importance of these stands for lichens.

4.2.1.2 Ground flora

The exact shrub species composition of the scrub is far less significant to plants growing in the field layer than are nutrient conditions, soil dampness and shading. Nonetheless, certain types of scrub stand out as having an especially rich ground flora. These are frequently associated with chalk or limestone and consist of mixtures of shrub species. Where this calcicole scrub exists as a mosaic with rank grassland a diverse ground flora can be present including tall herbs that are intolerant of grazing e.g. bloody crane's bill *Geranium sanguineum*, goldilock's aster *Aster linosyris* and lesser meadow-rue *Thalictrum minus* (Hopkins 1996). Hazel scrub on limestone, as in the Derbyshire Dales, can have a very rich herb flora (Ratcliffe 1977). Montane willow scrub also appears to be associated with sites that have rich ledge and tall herb floras (D. Gilbert pers. comm.). Notwithstanding the above comments, it should be noted that a diverse ground flora does not always occur in scrub. The extent to which there is a rich ground flora depends on factors such as site history and management, proximity of potential colonists and successional stage of the scrub.

4.2.1.3 Invertebrates

The majority of phytophagous insects are specific to plant family and this is discussed in detail in section 3.2.4.1. Non phytophagous insect groups are also closely associated with scrub, though are not generally related to the species composition, but rather to its physical structure and to the biotic and abiotic conditions which this imparts. While parasitoids and predators exploit the increased complexity of structure over herbaceous vegetation, to provide sites for prey capture, resting, basking and mating, other feeding groups are influenced by the scrub cover and related attributes. Scavengers and decomposers, especially primitive insect groups, such as the Collembola or spring tails, and other epigeal invertebrates are often present in large numbers under scrub, because of the shade and higher humidity that the cover provides. The build up of organic matter is also an important factor driving changes in the soil and ground fauna. As with phytophagous taxa, the highest levels of diversity are associated with seral scrub communities, comprising a mosaic of woody and herbaceous species (Brown & Southwood 1987).

Finally, attention should be drawn to the fact that scrub can be important to a wide range of 'dead wood invertebrates', both as nectar sources for adults and as larval food (K. Alexander pers. comm.). The flowers of various species, for example hawthorn and privet, are important sources of nectar. The stem wood and bark of several species of scrub provide specific habitats for saproxylic insects. Examples include the jewel beetles *Agrilus sinuatus* and *Agrilus viridis* which are associated with hawthorn and willow respectively. Old gorse stems support several scolytid beetles. Elder and alder are also important for invertebrates, some associated with the wood itself, others with fungi specific to these trees. More research is needed on communities of dead wood invertebrates, both in climax scrub and in dead and dying stems within seral scrub.

4.2.1.4 Birds

Birds using scrub generally do not show strong associations with particular plant species and are far less dependent on particular shrub taxa than are invertebrates (Fuller 1995, 1996). The structure of the vegetation is probably of greater significance to many birds than its exact species composition. Perhaps the most striking exeption in Britain is the dependence of the Dartford warbler *Sylvia undata* on gorse (see chapter 3). Different species of shrubs create different vegetation structures so it is not straightforward to isolate the effects of structure and floristics. This point is illustrated by a study of bird communities on chalk downland in which a comparison was made of pure hawthorn scrub and mixed scrub containing a diversity of shrubs (Fuller 1987). The samples of scrub were at similar stages of successional development. The hawthorn scrub held higher

densities of breeding birds than the mixed scrub, however this may have been accounted for by the fact that hawthorn scrub tended to be taller than the mixed scrub. Another example is the apparent preference shown by nightingales *Luscinia megarhynchos* for blackthorn scrub in many regions (Fuller *et al.* 1999). This may not reflect a preference for blackthorn *per se*, but rather for the dense thicket structures formed by this rapidly suckering species. Most scrub provides few nest sites for hole-nesting birds such as tits but an important exception is elder which, when old, offers cavities for these birds.

Apart from structural differences, one of the main ways in which scrub species composition is likely to affect birds is through food supply. This applies to both insectivores and frugivores. There have been extremely few studies of the diet of the insectivorous foliage-gleaning species, notably warblers, that are characteristic of scrub. However, it seems likely that the available biomass of invertebrates of suitable size is likely to be more critical to these species than the abundance of particular invertebrate species. We are unaware that estimates of invertebrate biomass are available for different types of scrub. Casual observation, however, would suggest that scrub with considerable quantities of hawthorn or with diverse shrubs such as found on much calcareous soils provides rich feeding for many foliage gleaning birds. Notwithstanding these comments, it is likely that subtle differences exist in foraging ecology and usage of individual plant species between different insectivorous birds.

This was found to be the case in a detailed study of the foraging ecology of *Sylvia* warblers in Mediterranean scrub (Martin & Thibault 1996). Similar work in temperate scrub would be worthwhile.

A wide range of shrubs provide fruit resources for warblers, thrushes, pigeons, starlings, robins, tits and finches (Snow & Snow 1988). Among especially important sources of food are hawthorn, elder, dogwood *Cornus sanguinea* and sea buckthorn. Most frugivores will feed on the berries of a wide range of shrubs but different species of birds often show apparent preferences for the berries of particular shrub species that are not reviewed here in depth. These preferences are often mediated by the availability of alternative berry supplies in the local area. Complex relationships exist between the birds and shrubs which involve mutualistic relationships in which birds act as seed dispersers. The main avian dispersers of British native shrubs are listed in Table 4.1. Not all birds that benefit from the food resources provided by berry-bearing shrubs actually diperse the seed. Some birds act as seed predators i.e. they consume the seed and do not disperse it. Bullfinch *Pyrrhula pyrrhula*, greenfinch *Carduelis chloris* and tits are examples of species that act mainly as seed predators. Some birds may act as pulp predators i.e. they consume pulp without dispersing the seed. Few, if any, fruit-eating birds depend on a single or a small number of fruit species. This lack of specialisation may be a consequence of different fruits providing complementary resources (Whelan *et al.* 1998).

Table 4.1 The principal avian dispersers of shrubs, trees and climbres with fleshy fruits native to England, Wales and Scotland. Adapted from Snow and Snow (1988).

Species	*Growth form*	*Fruit[1]*	*Principal (minor) bird dispersers[2]*
Cupressaceae			
Juniper *Juniperus communis*	Shrub	fleshy cone	thrushes, (robin)
Taxaceae			
Yew *Taxus baccata*	tree	arillate	thrushes, starling, (robin, blackcap)
Berberidaceae			
Barberry *Berberis vulgaris*	shrub	berry	?
Hypericaceae			
Tutsan *Hypericum androsaemum*	low shrub	fleshy capsule	?
Aquifoliaceae			
Holly *Ilex aquifolium*	tree	drupe	thrushes (robin, blackcap, woodpigeon)
Celastraceae			
Spindle *Euonymus europaeus*	small tree/shrub	arillate	thrushes, robin, (blackcap)
Rhamnaceae			
Buckthorn *Rhamnus catharticus*	small tree/shrub	berry	thrushes, starling, (robin, blackcap)
Alder buckthorn *Frangula alnus*	"	"	?
Rosaceae			
Wild raspberry *Rubus idaeus*	shrub	compound drupelets	thrushes, robin, blackcap
Blackberry *Rubus fruticosus*	"	"	thrushes, warblers, robin, starling
Dewberry *Rubus caesius*	procumbent shrub	"	probably as for blackberry
Field rose *Rosa arvensis*	shrub	fleshy receptacle with achenes	thrushes?
Burnet rose *Rosa pimpinellifolia*	low shrub	"	?
Long-styled rose *Rosa stylosa*	shrub	"	?
Dog rose *Rosa canina*	"	"	thrushes (robin, blackcap, woodpigeon)
Sweet briar *Rosa rubiginosa*	"	"	?
Blackthorn *Prunus spinosa*	small tree/shrub	drupe	thrushes (starling, corvids)
Wild cherry *Prunus avium*	tree	"	thrushes (woodpigeon)
Bird cherry *Prunus padus*	"	"	thrushes (robin, warblers, corvids)
Woodland hawthorn *Crataegus laevigata*	small tree/shrub	"	thrushes?
Hawthorn *Crataegus monogyna*	"	"	thrushes, starling (robin, woodpigeon)
Rowan *Sorbus aucuparia*	tree	pome	thrushes (robin, starling corvids)
Whitebeam *Sorbus aria*	"	"	thrushes (starling, corvids)
Service *Sorbus torminalis*	"	"	thrushes?
Pear *Pyrus pyraster*	"	"	?
Crab-apple *Malus sylvestris*	"	"	blackbird, carrion crow
Grossulariaceae			
Red currant *Ribes rubrum*	shrub	berry	thrushes, warblers, robin
Blackcurrant *Ribes nigrum*	"	"	?
Gooseberry *Ribes uva-crispa*	"	"	blackbird
Thymelaeaceae			
Spurge laurel *Daphne laureola*	low shrub	drupe	robin
Mezereon *Daphne mezereon*	"	"	blackbird (robin? warblers?)
Elaeagnaceae			
Sea buckthorn *Hippophae rhamnoides*	small tree/shrub	drupe-like	thrushes? robin, blackcap, (corvids)
Cornaceae			
Dogwood *Cornus sanguinea*	shrub	drupe	thrushes, starling, robin (blackcap, corvids)
Araliaceae			
Ivy *Hedera helix*	climber	berry	thrushes, robin, blackcap, starling
Cucurbitaceae			

Table 4.1 The principal avian dispersers of shrubs, trees and climbres with fleshy fruits native to England, Wales and Scotland. Adapted from Snow and Snow (1988).

Species	Growth form	Fruit[1]	Principal (minor) bird dispersers[2]
White bryony *Bryonia dioica*	climber	berry	thrushes, warblers (robin)
Ericaceae			
Bearberry *Arctostaphylos uva-ursi*	low shrub	drupe	probably as for bilberry
Cowberry *Vaccinium vitis-idaea*	"	"	probably as for bilberry
Bilberry *Vaccinium myrtillus*	"	"	grouse, thrushes, corvids
Empetraceae			
Crowberry *Empetrum nigrum*	low shrub	drupe	probably as for bilberry
Oleaceae			
Privet *Ligustrum vulgare*	shrub	berry	thrushes, robin, blackcap (corvids)
Solanaceae			
Woody nightshade *Solanum dulcamara*	climber	berry	thrushes, warblers, robin (starling)
Rubiaceae			
Madder *Rubia peregrina*	climber	berry	robin?
Caprifoliaceae			
Elder *Sambucus nigra*	shrub	drupe	thrushes, robin, warblers, starling, (corvids)
Wayfaring tree *Viburnum lantana*	shrub	drupe	thrushes, robin, warblers
Guelder rose *Viburnum opulus*	"	"	thrushes, (robin, blackcap)
Honeysuckle *Lonicera periclymenum*	climber	berry	thrushes, robin (starling)
Liliaceae			
Butcher's broom *Ruscus aculeatus*	low shrub	berry	?
Dioscoreaceae			
Black bryony *Tamus communis*	climber	berry	thrushes, (robin, blackcap)

Notes

[1] Classification of fruit type follows Snow & Snow (1988)

[2] Species listed are those considered to be dispersers i.e. pulp predators and seed predators are excluded. Main sources are Snow & Snow (1988), Boddy (1991). Thrushes = large thrushes where several species are probably involved (i.e. mainly blackbird *Turdus merula*, song thrush *T. philomelos*, mistle thrush *T. viscivorus*, redwing *T. iliacus*, fieldfare *T. pilaris*). Warblers = *Sylvia* species. Species known to be dispersers of seeds on mainland Europe but not recorded as dispersers in Britain are excluded. Scientific names of other birds mentioned above: robin *Erithacus rubecula*, starling *Sturnus vulgaris*, blackcap *Sylvia atricapilla*, woodpigeon *Columba palumbus*, carrion crow *Corvus corone*.

4.2.2 Successional change in habitat factors

Scrub development is accompanied by large changes in the associated biological communities, though successional stage *per se* is of no particular significance. Successional change in communities is largely driven by the massive alteration of physical structure and other environmental conditions that accompany the invasion and growth of bushes. Here we outline successional changes in selected taxa and summarise the key environmental changes that are of particular significance to different groups.

4.2.2.1 Lichens and bryophytes

Habitat quality for both bryophytes and lichen will generally increase with successional age. Critical factors are shade, humidity, exposure and the availability of suitable substrates. Bryophytes are sensitive to hard frost and desiccation so they tend to be most luxuriant in regions and microhabitats that provide suitable temperatures and humidity (Hodgetts 1993). Most bryophyte-rich sites are found in the west of Britain where rainfall and temperatures are relatively high. The richest sites tend to be within woodland or long-established scrub, though Atlantic bryophytes can thrive outside woodland in suitable microhabitats such as ravines or block scree (Hodgetts 1993). Large trees are important to many lichens in terms of the substrate and microclimate they provide (Harding & Rose 1986) though they generally prefer lighter and warmer microclimates than bryophytes (Harding & Rose 1986, Hodgetts 1993). Coastal scrub in western and northern Britain is an important habitat for lichens as discussed above.

4.2.2.2 Ground flora

Increasing shade from the growth of woody plants is the overriding factor driving successional change in the field layer, though nutrient status may also be important. Once the cover of woody plants exceeds some 50%, shading starts to have a serious effect on the field layer (Ward & Jennings 1990a). Species that are dependent on short grazed swards are rapidly replaced by tall, coarse grasses (Ward & Jennings 1990b) and by tall herbs sensitive to grazing which are often associated with the edges of the scrub itself (Hopkins 1996). While these latter situations may be shaded to a certain extent, unchecked growth and expansion of scrub will eventually lead to loss of the open grassland and associated flora. As stressed above, the pattern of change in the ground flora will be strongly influenced by whether scrub is freshly colonising open grassland or whether it is regrowth from cut scrub. The change to a woodland flora will generally be slow due to the lack of nearby colonists in many landscapes and to the poor dispersal ability of many of the species. Changes in the seed bank are inevitable under long-established scrub with gradual reduction of viable seeds of species associated with the open vegetation. This was illustrated in a study conducted across a grassland-scrub-woodland gradient in Surrey by Davies & Waite (1998) which found that few species were recorded in the seed bank along the entire gradient.

4.2.2.3 Invertebrates

Many of the invertebrates associated with scrub are associated with specific vegetation structures. Unimpeded successional change in scrub habitats therefore results in an ongoing change in niches and in the composition of the invertebrate fauna. Invertebrate turnover does not necessarily proceed at a uniform rate. The effect of vegetation structure on invertebrates is considered in greater detail in 4.2.3.

Successional studies have, understandably, focused on changes in the vegetation in terms of species composition and structure. The few studies which have encompassed invertebrates (e.g. Southwood *et al.* 1979, Brown & Southwood 1987, Brown 1990) have also demonstrated clear successional trends. These are mainly related to the transition in plant growth forms as succession proceeds. Clearly, the invasion of woody scrub species into a perennial grass and herb community introduces not only new plant species for specialist herbivores, but additional and different structural and architectural complexity for groups with other trophic affinities. Indeed, the integral mix of scrub species, or of a single species at different seral stages, provides a complexity of 3-dimensional structure far in excess of grassland communities.

As succession proceeds, specialist predators and parasitoids either track the changes in the phytophages directly or benefit from using scrub as 'an interceptor' in the grassland sward for host capture, resting, basking or mating. In addition, male bush crickets (Orthoptera: Tettigoniidae) also select scrub as a substrate on which to stridulate and thereby project their courtship song (e.g. Cherrill & Brown 1987).

Knowledge of the subterranean invertebrate community is extremely limited and, to our knowledge, there have been no studies specific to scrub. Even so, such faunal groups are likely to provide key resources for birds and small mammals, especially the larval stages of holometabolous insects.

It is interesting that some phytophagous insect species are only found associated with specific stages of scrub succession or indeed after scrub clearance. While many of these species are associated with the scrub species themselves, others are related to herbaceous plant species tracking the changes in the scrub species. One such species of flea beetle, *Epitrex atropae*, feeds on deadly nightshade *Atropa belladonna* which is a successful early coloniser of cleared scrub.

Invertebrate communities vary seasonally as well as successionally, a trend even seen in the soil micro-arthropod community (Parr 1978), even though subterranean taxa tend to be buffered from changes in abiotic conditions. Such temporal variation is an important dimension in the role of invertebrates as a source of food for higher trophic levels.

4.2.2.4 Birds

In lowland calcareous scrub, the numbers of species and of individuals of breeding birds increases rapidly with scrub encroachment. The relationship is not a linear one, however, for numbers do not increase, and perhaps even drop, after canopy closure (Fuller 1987, 1995). As with invertebrates, birds show a large turnover in species composition with growth of the scrub. This is summarised in Figure 4.1 for birds breeding in scrub on the escarpment of the Chiltern Hills. Species show considerable individuality in their distribution across the habitat gradient. Some species are confined to the earliest stages (skylark *Alauda arvensis* and pipits *Anthus* spp.), others are associated with open-canopy scrub and rapidly disappear once the canopy has closed (e.g. yellowhammer *Emberiza citrinella* and linnet *Carduelis cannabina*), while some reach greatest abundance around canopy-closure (e.g. garden warbler *Sylvia borin*, lesser whitethroat *Sylvia curruca*). Densities of breeding warblers can be extremely high in the canopy-closure phase but decrease thereafter. Long-distance migrants contribute an exceptionally high proportion of the total songbird territories in these early and mid stages of secondary woodland succession and their densities are also highest at that stage (Helle & Fuller 1988).

The rates of turnover in species composition are greatest in the early stages of scrub development (Figure 4.2). An increase of scrub from 5 to 25% cover has a larger impact on species composition than does an increase from 35 to 60% cover. This effect occurs partly because grassland species will tolerate only a limited amount of scrub encroachment. But it also arises because several species that live in old scrub will actually colonise scrub at a relatively early stage of growth, before the canopy closes. This turnover in bird species is driven mainly by the species-specific responses to the ever changing physiognomy of the scrub, defined

as its canopy openness, its height and its foliage density. Effects of scrub structure on birds are examined further in 4.2.3.

Successional changes in breeding bird communities of upland scrub have been studied in birch, pine and juniper scrub in the central and eastern Highlands (Gillings *et al.*1998, Gillings & Fuller 1998, Fuller *et al.* in press). Avian species richness increases across the series: moorland – open birch scrub – closed birch scrub – old birch woodland. This is broadly consistent with the pattern for lowland scrub described above, but in other respects the findings were different. The numbers of species and densities of birds in all stages of scrub development were relatively low. The commonest breeding birds of scrub – tree pipit *Anthus trivialis*, willow warbler *Phylloscopus trochilus* and chaffinch *Fringilla coelebs* – were widely distributed in woodland

as well as in scrub habitats. The scrub was not characterised by concentrations of scrub specialists, such as the *Sylvia* warblers so typical of southern scrub. Those scrub specialists that were present occurred at very low density, for example black grouse *Tetrao tetrix*, redpoll *Carduelis flannea*, yellowhammer, whinchat *Saxicola rubetra* and stonechat *Saxicola torquata*. Fuller *et al.* (in press) made several predictions about the consequences for birds of large-scale expansion of scrub and woodland in this region. Scrub expansion would be beneficial for the above scrub specialists and this was highly desirable in the black grouse which is in serious national decline. However, a wider range of species would benefit from the long-term development of old woodlands through natural regeneration.
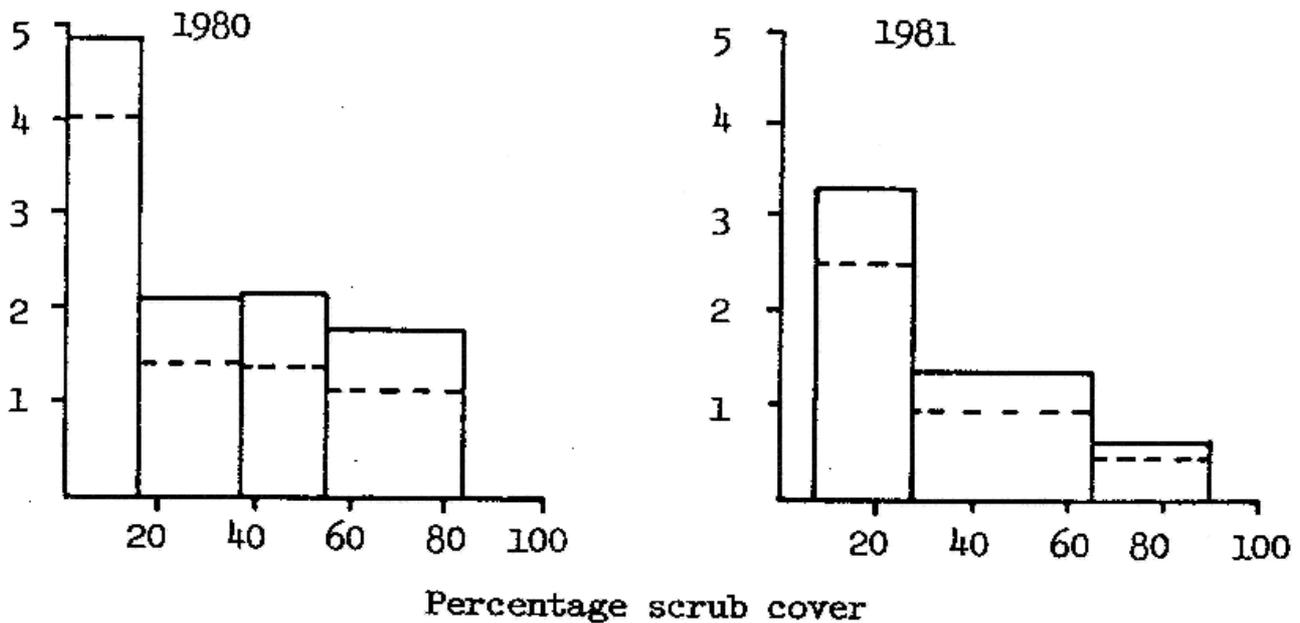
Figure 4.1 Abundance of breeding birds on the escarpment of the Chiltern Hills in relation to scrub growth. Based on point counts conducted in 1980 and 1981. The index of abundance is derived from numbers of birds counted within a 50 m radius at more than 90 locations. Reproduced from Fuller (1995) with the permission of Cambridge University Press.
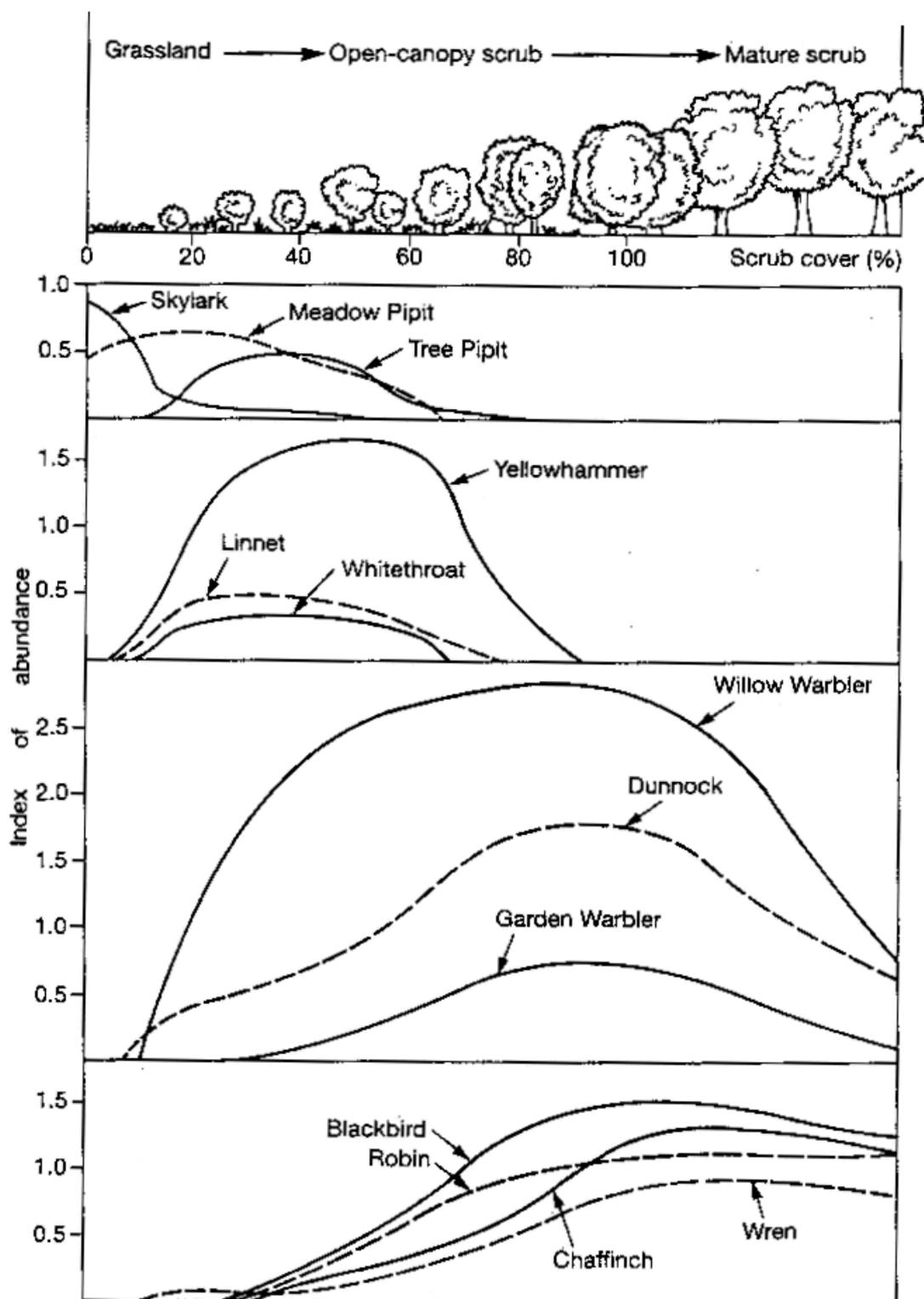
Figure 4.2 Turnover rates in bird species composition between successive stages of scrub development on the escarpment of the Chiltern Hills. Stages are described in terms of scrub cover. Solid lines indicate turnover rates as shown by the Jaccard Index, and broken lines by the Sorensen Index. The bars of the histograms are positioned centrally according to the average scrub cover of the sampling points in each stage. Reproduced from Fuller (1987).

4.2.3   Vegetation structure

4.2.3.1   Invertebrates

Very little published work exists on the effect of physical architecture on scrub invertebrates, but in general, the significance of vegetation structure to invertebrates cannot be overestimated (Kirby 1992). The architectural complexity of the host plant influences herbivore species richness and abundance. Larger, more structurally complex plants provide a greater variety of microhabitats, resulting in greater diversity and abundance of insect herbivores (Lawton 1978, Southwood 1978). For example, a greater variety of microhabitats support richer assemblages of sap feeders than simple-structured hosts (Denno & Roderick 1991). Habitat architecture has a major influence on the habitat preferences of spider species (both web and hunting taxa) (Rushton 1988, Uetz 1991) and may have a greater impact on spatial distribution than host plant species.

Many invertebrate species are so small that the microclimate they inhabit is profoundly influenced by the architecture of apparently similar plant species, and the wider the range of growth forms in which a plant species grows, the larger the assemblage of invertebrates it can support (Kirby 1992). In one of the few studies looking at invertebrates on scrub, Rushton *et al.* (1990) found that ground beetle communities under three scrub management regimes at Castor Hanglands NNR, Cambs, were very different. Vegetation structure was believed to be important in determining the composition of these beetle communities.

Plant architecture may influence invertebrate life-history traits, for example, aphids on trees need a sufficiently long stylet to pierce phloem elements in the host tree bark, and hence have a larger body size than herb-feeding taxa (Dixon 1985). A similar trait is shown by planthoppers, leaf hoppers and aphids which can exist in winged or brachypterous forms. Wingless forms are rare in arboreal habitats, with most late successional vegetation types, e.g. trees, exploited by winged taxa. Strong *et al.* (1984) suggests that trees provide a greater variety of niches for invertebrates than herbs, due to i) the greater diversity of microclimates available, ii) the range of phenologies and changes linked to plant age, and iii) the architectural complexity of a tree that provides a greater diversity of feeding and oviposition sites, hiding places from enemies, and overwintering sites than do structurally simple plants.

4.2.3.2   Birds

Many birds have specific requirements for certain vegetation structures and configurations (James 1971). These ecological differences underpin the large turnover in bird species that occurs with succession from open grassland or heathland to closed canopy scrub (section 4.2.2.4). For example, species such as whitethroat *Sylvia communis* and yellowhammer require open relatively low scrub structures, whereas garden warbler and blackcap *Sylvia atricapilla* are associated with much denser, more closed scrub. The functional basis of this habitat selection is probably mainly a combination of foraging needs and predation risk. Important though they are, these broad differences among species in structural habitat use are rather obvious to any competent naturalist. Less obvious are the microhabitat differences shown by often closely related species within particular successional stages. Some of these differences are subtle and many are likely to be adaptive i.e. associated with enhanced fitness (Martin 1998). There is, for example, growing evidence that nest site selection is linked to nest predation (Martin & Roper 1988, Kelly 1993, Martin 1993). Food availability probably also has a major effect on breeding success but this is far harder to measure.

Of particular interest in the context of scrub habitats is the coexistence of several species of closely-related warblers within broadly similar vegetation structures. The mechanisms of this coexistence have long been debated especially in the context of Mediterranean scrub where several species of *Sylvia* live in close proximity. Cody & Walter (1976) have argued that interspecific competition among Mediterranean warblers causes observed patterns of habitat selection among these species. This is refuted, however, by recent evidence demonstrating that fine-scale differences exist between foraging warblers in the plant species used, the height of individual shrubs used and the vegetation structures that are selected (Martin & Thibault 1996).

Similarly subtle differences of foraging habitat selection almost certainly occur in warbler communities in temperate scrub but they have not been described. However, distributions of territory-holding warblers have been examined in relation to scrub structure on the Chiltern Hills escarpment (R.J. Fuller, unpublished data). These data show that species differ considerably in the structural profiles that they use. Willow warbler has by far the widest habitat amplitude using scrub that ranges from 1.3 to 4.5 m in height and approximately 40 to nearly 100% canopy cover. Its habitat profile overlapped that of the other four warbler species present in the study area. Respective figures for the other warbler species were: whitethroat 1.4–2.3 m, 31–64 % cover; lesser whitethroat 2.1–2.7 m, 67–85% cover; garden warbler 1.0–3.8 m, 61–91% cover; blackcap 1.8–4.2 m, 56– 95% cover. Whilst there was considerable overlap in habitat use between the latter four species, each occupied a distinctive scrub structure. Lesser whitethroat showed the narrowest habitat amplitude.

Several of the migrant species that use scrub have a particular requirement for moderate to tall scrub with extremely dense low vegetation. This applies especially to nightingale and garden warbler, but to some extent to blackcap and lesser whitethroat. The preferred habitat structures of nightingale have been described in detail by Fuller *et al.* (1999). Once the scrub has grown to an extent where the low growth is completely shaded out and it becomes 'leggy' the habitat quality for migrants is greatly reduced.

4.2.4   Scale and spatial arrangement of habitats

At any one site, scrub is frequently extremely heterogenous. It may exist as patches of differing size mixed with other vegetation, especially grassland and woodland. The scrub patches themselves may differ in size, height and foliage density. The significance of this patchiness is discussed here for invertebrates and birds.

These two groups respond to habitat heterogeneity on very different scales. Many invertebrates are affected by extremely fine-grained habitat variation. Availability of preferred food plants and critical microclimates may alter within a few centimetres. Furthermore, large populations of invertebrates can be maintained within a few square metres of suitable habitat. This contrasts with the requirements of birds which are satisfied on a vastly larger scale. The majority of songbird species typical of scrub have territories that are at least 0.25 ha, frequently much larger. Most breeding birds probably respond to the relatively coarse-grained physiognomy of the environment in selecting potential habitat, though exact selection of foraging sites within the territory may be a more subtle process. A further contrast is that many, but certainly not all, invertebrates meet their full life cycle requirements on one small patch of land. This is rarely true of birds that use scrub. Many of the breeding birds of scrub overwinter in other habitats or regions. Conversely, species that feed on the berries offered by scrub often derive from distant breeding populations. Birds are able to exploit these localised resources through their great mobility.

4.2.4.1   Invertebrates

Most invertebrates have very specific habitat requirements that may vary at different stages of their life cycle. Many species also

have a relatively low mobility, or a low instance of long distance dispersal. Sufficient resources to fulfill all aspects of a taxa's life cycle may therefore be needed within an area of only a few square centimetres or metres. This requires a diverse mosaic of ages and species of scrub within a small area.

In general, a close-knit mosaic of vegetation age, structures (including edges) and species is more useful to invertebrates than large uniform blocks (Kirby 1991, Hopkins 1996). Scattered scrub may support different invertebrates to mature scrub. Large, isolated bushes may be major sources of food for nectar and pollen feeding insects, and provide favourable conditions linked to architecture such as shelter, in addition to supporting their associated communities.

The character of the habitat mosaic which includes scrub vegetation may be as important as the shrub species themselves, although this is difficult to demonstrate (Hopkins 1996). Edges are particularly important, as they provide the warm but sheltered conditions favoured by many invertebrate species (e.g. Kirby 1991). An intimate mix of grassland, scrub and woodland may be an advantage to many invertebrate species, providing a range of conditions in close proximity. Several invertebrates associated with scrub may be more usefully defined as woodland/grassland transition species, for example the Duke of Burgundy butterfly *Hamearis lucina*, which lays its eggs on the lush leaves of cowslip and primrose growing in shaded areas, and uses sunny, sheltered glades and clearings for basking and nectaring.

Herbivorous invertebrates are strongly influenced by host plant chemistry. The chemical composition of plant parts (e.g. leaves, sap, phloem contents) varies enormously in relation to many factors including water stress, herbivory history, disease and climatic conditions (Masters & Brown 1995). All of these factors will be influenced by the age and location of a shrub at a site, and will impact on the availability of niches to invertebrate taxa.

4.2.4.2 Birds

Mosaics consisting of patches of scrub at different ages, mixed with open grassland, tend to support extremely rich assemblages and high densities of breeding birds because a wide range of habitat structures and microhabitats are present.

In extremely patchy situations, individual birds may hold territories that comprise spatially separate patches of scrub (Haila & Hanski 1987). This may merely reflect an ability to exploit a mosaic rather than a particular requirement for a mosaic. However, there are several instances where birds do appear to have a requirement for a mosaic of habitats that incorporates scrub. One of the most striking is the black grouse. Essentially a bird of the moorland-woodland edge, the black grouse benefits strongly from mosaics of moorland, scrub and woodland. In the case of wetlands, mosaics of bushes and fen vegetation appear to be preferred by marsh warbler *Acrocephalus palustris* and Cetti's warbler *Cettia cetti*, rather than areas of dense scrub (Wotton *et al*. 1998). On lowland heathland, the presence of both gorse and heather appears to be a determinant of habitat quality in the Dartford warbler (Bibby 1979 a,b).

Mosaics of scrub and grassland probably offer two advantages to breeding birds though this has not been studied in detail. First, they may provide high quality habitats for species that forage in short open vegetation but nest in dense scrub. Blackbirds *Turdus merula* and song thrushes *Turdus philomelos* are examples of species that may benefit in this way. Second, the structure of scrub vegetation may be much denser at the edge of a scrub patch than the interior. This is likely to confer an advantage on birds such as nightingale and garden warbler that require dense low foliage. The edges of suckering blackthorn thickets often provide ideal cover for these birds (Fuller *et al*. 1999).

At a landscape scale, the songbirds breeding in upland scrub may provide important food resources for birds of prey nesting in adjacent moorland. This is especially true for upland raptors such as merlin *Falco columbarius* and hen harrier *Circus cyaneus* (see 4.3.3).