Chapter 5 Effects of vegetation structure on the fauna

'Habitat structure' (Bell et al., 1991), referring mainly to vegetation, influences the species composition and abundance of associated organisms (e.g. birds: MacArthur & MacArthur, 1961; mammals: Rozenweig & Winakaur, 1966; reptiles: Mushinsky, 1985; spiders: Duffey, 1962a, b; Uetz, 1991; insects: Murdoch et al., 1972; Lawton, 1978; Brown, 1991a; soil organisms: Usher & Parr, 1977). The influence is twofold: (a) direct (mainly through mechanical effects, which regulate the distribution of resources for feeding, nesting, resting and basking, mating and egg-laying) and (b) indirect (via microclimate, discussed in the the previous chapters and excellently by Barkman, 1979).

The species composition, abundance, diversity, trophic structure and life-history strategies of virtually all organisms have been shown to change during succession and can often be related or attributed to changes in habitat structure (Brown, 1991a). However, it is not always possible to assign the role to direct or indirect effects. Moreover, several components of vegetation structure (texture and architectural complexity) may determine variation in abundance, diversity and life history of the associated fauna. Vegetation texture includes plant density (the distance between individuals of the same species), patch size (geographical extent of the stand), and vegetation diversity (frequency and identity of non-host plant individuals (see Kareiva, 1983)). Architectural complexity involves both plant size (the spread of plant tissues through different positions in space) and variety of plant structures (number of plant parts, both in form and persistence) (see Southwood et al., 1979; Lawton, 1983). This section mainly considers effects on herbivorous insects and begins with a consideration of the role of host plant selection and the species composition of plant communities in determining distribution and abundance. This is followed by an assessment of the importance of vegetation structure per se on insect herbivore, spider and bird communities.

5.1 Effects of plant species composition

5.1.1 Diet breadth

All herbivores show some degree of selectivity in their feeding, choosing between plant species and between different tissues within the plants. Many herbivore species eat a limited number of plant species (oligophagous or 'specialist'). Others, mainly invertebrates, are restricted to one food plant species (monophagous). Some species (e.g. mammalian grazers) eat a wide variety of plants (polyphagous or 'generalist'). 'Absolute' monophages feed only on one plant species over their entire geographical range, whilst 'functional' monophages concentrate on one species in a given population but take different plant species in different populations (Crawley, 1983).

The range of food plant species is illustrated by the British butterflies. A few species, like the black hairstreak (Strymonidia pruni), feeding on blackthorn (Prunus spinosa) and white admiral (Limenitis camilla), feeding on honeysuckle (Lonicera periclymenum) are strictly monophagous. Some, like the swallow-tail (Papilio machaon), which feeds in Britain only on Peucedanum palustre (milk parsley), are functionally monophagous. Others, while they eat several plant species, are confined to one taxonomic group of plants, such as the green-veined white (Pieris napi), which is restricted to crucifers. A few butterflies can develop on numerous kinds of plants that apparently have little in common. The green hairstreak (Callophrys rubi), for example, feeds on rockrose (Cistaceae), purging buckthorn (Rhaminaceae), gorse, broom, Genista (Leguminosae), bramble (Rosaceae), dogwood (Cornaceae), Vaccinum and Calluna (Ericaeae). Thus, although most British butterflies are oligophagous, a few are monophagous and a few are broadly polyphagous (Crawley, 1983).

5.1.2 Host-plant selection

As well as microclimate (Willmer, 1986), host-plant selection is limited by physical problems of attachment associated with the presence of a hard cuticle, trichomes (Levin, 1973; Lawton, 1986), nutritional problems of plant feeding, such as water, energy and nitrogen content (Edwards & Wratten, 1980) and the presence of secondary plant compounds (Harborne, 1977). Selection comprises two distinct behavioural phases: 'host-finding' (or dispersal) and 'recognition' (actual feeding, Thorsteinson, 1960). The former often involves chemical odours which act as attractants (Edwards & Wratten, 1980), but in the case of Lepidoptera may involve visual stimuli (e.g. leaf shape, Mackay & Jones, 1989). The latter involves tactile, visual, chemotactic, olfactory and gustatory stimuli (e.g. sugars, nitrogen, minerals, organic acids, vitamins, stimuli, plant pigments, glycosides, alkaloids (Thorsteinson, 1960)).

In the light of Brown and Cherrill's work on the wart-biter (Chapter 7), it is worth considering diet selection by members of the Orthoptera (Dadd, 1963; Mulkern, 1967; Brown, 1983). Williams (1954) studied the feeding habits and food preferences of Acrididae and the factors which determine them. He found that grasshoppers preferred grasses to herbs and upright blades of grass to those lying flat and were also affected by leaf toughness and vertical stripe patterns. Bernays and Chapman (1970) found moisture content was also important, but according to Williams (1954) the colour of vegetation has little effect. However, the chemical composition of the plant and particularly the presence of feeding repellents or stimulants are the most important factors. Preferred foods may change during development, e.g. between larvae and adults (Brown, 1990).

5.1.3 Insect distribution and abundance

The distribution and abundance of grasshoppers (Vestal, 1913), and other solely phytophagous groups of insects, is to a large extent determined by the availability of their preferred food (Clark, 1948; Kemp et al., 1990). Insect herbivore abundance and diversity should therefore vary directly with host-plant distribution, abundance and diversity. Larger patches of the host plants often house more herbivore species for a variety of reasons, including increased habitat heterogeneity, increased encounter frequency, and reduced probability of extinction (Kareiva, 1983; Strong et al., 1984). However, several other factors may influence a herbivore's response to increasing host patch size and alter any abundance area relationship. These include 1) the diet breadth of the herbivore, 2) the mobility of the herbivore, 3) the quality, density and size of host plants as they vary with patch area, 4) the abundance, size and allelochemistry of the background non-host vegetation (Tahvanainen & Root, 1972; Rauscher, 1981) and 5) the numbers of parasites, predators and pathogens that may vary with patch size and other components of vegetation texture (Kareiva, 1983). Hence, Brown and Hyman (1986) found that the species diversity of herbs and weevils (herbivorous Coleoptera) is closely related throughout succession.

5.1.4 Species composition in relation to other attributes

In many cases, plant species distribution, abundance and composition may be more important than plant structure in determining associated insect communities. For various guilds of herbivores including sap-feeders, leaf-miners, gall-formers and free-living Lepidoptera, geographic range of host plant accounts for much of the variation in herbivore richness (Strong et al., 1984). Lawton (1983) stated that "on present evidence, range explains approximately 2.5 times more of the variation in insect species richness on British plants than does architecture." Gibson et al. (1992a) found that leaf-miner assemblies were most strongly determined by the effects of grazing on plant species composition (Sterling et al., 1992), while spiders' responses could largely be explained by the effects of grazing on plant architecture. These relationships may change through succession and obviously change from taxon to taxon. Southwood et al. (1979) found that up to a successional age of 16 months, the taxonomic diversities of plants and insects (Heteroptera and Coleoptera) rose, thereafter the diversity of the plant species declined far more than insect diversity. It was concluded that in the later successional stages, the maintainance of a high level of taxonomic diversity of these orders is correlated with the rising structural diversity of the vegetation (Brown & Southwood, 1987).

5.2 Effects of vegetation structure

5.2.1 Insect herbivore communities

a) Species diversity

Lawton and Schroder (1977) were the first to show the relationship between the structural diversity (sensu Lawton, 1986, e.g. size, growth form, seasonal development) of a plant and the richness of its insect fauna and many subsequent studies have supported this finding (Strong & Levin, 1979; Southwood et al., 1979; Moran & Southwood, 1982). Larger, more complex plants with a greater variety and persistence of above-ground parts, should provide more microhabitats, and result in a greater diversity and abundance of herbivores (Lawton, 1978; Strong et al., 1984). Hence, several studies have shown that the number of insect species on trees and shrubs is higher than on forbs and grasses (Lawton et al., 1977; Strong & Levin, 1979; but see Fowler, 1985). Surveys, restricted to particular groups of plants and insects, confirm these broad patterns. For example, Niemeli et al. (1982) found that larger species of Finnish trees have richer macrolepidopteran faunas than smaller species of trees and shrubs. On average, more species of microlepidoptera attack individual species of British trees than are found on shrubs, and both have more species than herbs (Price, 1977). Strong et al. (1984) argue that trees provide a greater variety of niches for insects than herbs in at least three ways: 1) microclimates are more diverse, 2) the degree of phenological change and age differ so that young and mature trees may support different herbivore species and 3) architecturally complex plants provide a greater variety of feeding and oviposition sites, hiding places from enemies, and overwintering sites than do structurally simple plants. For soil insects, Anderson (1975, 1978) found that cryptostigmata species diversity was correlated with microhabitat diversity in six woodland soils with a range of humus forms.

i) Monocultures

These relationships are most clearly demonstrated in single species monocultures, e.g. of heather (Calluna vulgaris). The lifespan of a single plant is normally 30-40 years (Gimingham, 1979) and during this time the plant undergoes distinct changes in structure from pioneer, through building and mature to a degenerate stage of development (Watt, 1955). This is associated with changes in the aerial biomass and shoot production of both green matter (Chapman et al., 1975a) and litter (Chapman et al., 1975). These affect the microclimatic conditions (Barclay-Estrup, 1971) of each phase which determine seedling germination and establishment (de Hullu & Gimingham, 1984) and vegetative regeneration of the associated flora (Gimingham, 1978), and subsequently the invertebrate fauna. Barclay-Estrup (1973) found significant difference in the total arthropod community between the phases of Calluna, indicating quite different microenvironments. Overall, the degenerate phase seemed to be the most favourable for arthropod activity. However, population peaks for individual taxa are reached in different phases. Ants were most prolific on the bare ground which characterises the pioneer phase. Brian (1964) found that ant colonies were larger where higher insolation produces a more favourable temperature condition and a richer food supply (Brian & Brian, 1951). Spiders preferred the pioneer and degenerate phases, the latter particularly due to the greater food supply. However, phalangids, millipedes and centipedes preferred cool and moist conditions of the building and mature phases and cannot survive the harsh microclimate once the vegetation cover is removed (Barclay-Estrup, 1973). Hence, the soil and litter fauna does not begin to build up until the canopy has closed in the building phase. Barclay-Estrup concluded that of the microclimatic influences which he had studied simultaneously (1971), the humidity change which occurred in the building phase was the most important. However, the distribution and abundance of phytophagous insects in the various phases is likely to be determined more by food quality and supply and less by microclimate.

Brown (1991a, b) and co-workers from 1982-87 used four adjacent sites in southern England representing these main growth phases. They found that spatial and architectural diversity increased with stand age and showed a significant positive relationship with insect species richness. Chewing insects were the main contributors and, in contrast, the abundance of herbivorous insects was greatest at the building stage and gradually declined to the degenerating phase. This was related to the abundance of 'short shoots', i.e. food supply.

Gimingham (1985) studied a heathland in N.E. Scotland and found marked changes in the composition and diversity of the insect fauna as the plants passed through successive phases. In contrast, to studies by Brown (1991a, b), diversity was greatest in the pioneer and degenerate phases and least in the building and mature phases (as found previously by Barclay-Estrup, 1974). However, this was associated with differences in spatial heterogeneity and floristic diversity (Gimingham, 1985). Groups which were best represented in the building and mature phases are chiefly those 1) which flourish upon the unlignified green shoots and 2) sap feeders. By contrast, certain taxa were most abundant in the pioneer and degenerate stands. Some of the species which were particularly numerous in pioneer stands are ground feeders or dwellers rather than those associated with the foliage. Degenerate stands appeared to attract more aphids and coccids.

ii) Managed plant communities

Grasses which produce a persistent thatch have an added component of structural diversity which non producing species lack. Such grasses provide additional feeding and oviposition sites, protection from physical stress, and refuge from enemies, characteristics which increase microhabitat diversity and should lead to an increase in the number of resident herbivores if these thatch-related sites provide new opportunities for exploitation. Two lines of evidence support this: 1) direct positive relationships between herbivore species richness and various components of architecture (Morris, 1971b; Murdoch et al., 1972) and 2) studies where grass architecture is experimentally simplified and changes in herbivore communities measured. Denno and Roderick (1991) decreased the diversity of sap-feeders by reducing the architectural complexity of the grasses on which they feed. Carefully-managed plant communities can be used as a type of natural experiment to demonstrate the effect of modifying plant structure, whilst species composition is held virtually constant. Grazing experiments can manipulate structure to varying degrees, e.g. by different intensities (Hutchinson & King, 1980; Gibson et al., 1987b), or at different times during the season (Gibson et al., 1987a). Work at Wytham, Oxon. In an early old-field succession, Brown et al. (1990) showed that even relatively slight changes in habitat structure, imposed by short-burst grazing by sheep, can have dramatic effects on the abundance and species composition of certain groups of insects (Brown, 1991a, b). Brown et al. (1992) found that leafhopper (Auchenorrhyncha) assemblies, which mainly feed on grasses, were more strongly affected by plant structure than species composition as determined by grazing treatment. At Silwood Park, Stinson and Brown (1983) found that the number of different types of grass structure (as a measure of architecture) account for 79% and 86% of the variance in leafhopper species richness and total abundance respectively, indicating that they require particular features of sward structure as stated by Andrzejewska (1965). Duffey (1975) found that trampling decreased both the abundance and diversity of the invertebrate fauna as a result of reductions in the structure of the litter layer, e.g. the proportion of air space fell from 63% to 38%.

b) Insect life-cycles strategies

Changes in several life-cycle strategies of the herbivorous insects can be related to the increase in habitat structure during succession, while reproductive potential and niche specialisation are a direct result of changes in species composition (Brown & Southwood, 1983). The high occurrence of multivoltinism in early succession is a result of the rapid turnover of plant structure and individuals, which provides suitable nutrition throughout the growing season. This is in direct contrast to the mid- and late-successional species where the host plant may only provide food in a suitable form for a limited period each year, a feature favouring selection for a univoltine life cycle. In terms of individuals, 90% of the early colonizing insects are multivoltine, whereas only 5% of the late successional individuals have more than one generation a year (Brown, 1986).

Wing polymorphism and/or ability to fly is associated with the durational stability (Southwood, 1977, or degree of permanence) of the habitat, with more stable habitats tending to select for aptery or brachyptery (Brown, 1991a). The strategy of overwintering as an egg increases as succession proceeds with around 50% of both species and individuals overwintering in this way in late succession. In early and mid succession, overwintering as an immature is common and is probably related to the fact that many perennial plants die back in winter and suitable foliage for egg-laying is not apparent until late in the season. In the case of insect species associated with late successional trees and shrubs, the 'structure' of the plant is already present in spring and insects overwintering as eggs can exploit the early flush of spring foliage for larval feeding (Brown, 1986).

As for reproductive potential, Brown and Llewellyn (1985) found that aphids associated with herbaceous plants (annual, biennial and perennial herbs) were more fecund than those on woody trees and shrubs. Within these categories, aphids on annuals generally have higher fecundity than those on biennials and perennials, whereas shrub-associated aphids are potentially more fecund than aphids on trees. Brown and Hyman (1986) found that niche breadth declined through early and mid-succession (Brown & Southwood, 1983), but there was a dramatic reversal in late succession. Brown (1982b) found that the range in size and shape of Heteroptera increased with successional age and exhibited a similar trend to the structural diversity of the vegetation. Species characteristic of early successional habitats were somewhat intermediate in size and tended to be fairly consistent both in size and shape, whereas late successional species were very much more variable in body form. This is related to the diversity of niches which increases as succession proceeds.

5.2.2 Spider communities

Physiognomy or physical structure of environments has important influence on the habitat preferences of spider species, and ultimately on the composition of spider communities, for two reasons. Firstly, many spiders build webs for prey capture, and the attachment of these webs to surrounding structures often requires the presence of specific architectural features or arrangements. Secondly, the nature of both web-building and and non web-building spiders' primary sensory modalities dictates that they perceive their environment using tactile and vibratory cues (Uetz, 1991).

Habitat structure plays an important role in web-site selection because of the potential for reduction of damage (Cherrett, 1964). This was demonstrated by Robinson (1981) who constructed modular habitat units, consisting of cubes of chicken wire supporting various arrangements of jute rope, tied in configurations representing several combinations of parallel and intersecting axes, and varying densities. Several common spiders showed statistically significant preferences for specific structural orientations, and a number of species differed significantly in their choice of structure type.

a) Species composition

In a study of the spiders of the dunes along the shores of Lake Michigan, Lowrie (1948) noted that the spider community changed with the physical structure of the plant community over dune succession. As the vegetation matured, becoming more dense and stratified, more species and families of spiders were present. Lowrie attributed the increase in diversity to the moderation of weather factors and creation of diverse microclimates, as well as the increased availability of web attachment sites for orb-weavers and other web-builders. Elsewhere, Barnes and Barnes (1954) noted that drift lines on beaches provided unique structural habitats for a number of spider species.

Luczak (1963, 1966) studied spider communities in pine plantations of different ages in Poland. Despite essentially identical plant species composition in all stands, the different-aged stands showed marked differences in the species composition and relative abundance of spiders. These differences were related to the height distribution of trees and associated shrubs and herbaceous vegetation beneath the pine canopy. Stratton et al. (1979) compared the species composition of spiders in three coniferous tree species within the same plant community and microclimate, which differed primarily in architecture. The primary structural differences were in needle and cone type and branching arrangements, which in turn influence the presence and absence of spider species known to utilize specific microhabitats within them.

Duffey (1962a, b) conducted detailed studies of the microdistribution of spiders within a meadow in England, and was able to correlate the distribution of spiders with habitat features. While it may not seem surprising that associations were found between web-building species and plant types or structures (living and dead), strong plant-structure associations were also noted among the hunting spiders. Similarly, de Keer et al. (1989) studied the distribution of spiders in islets of higher grass and short-grazed patches during the day and night. Spiders active during the night showed a preference for higher vegetation and day active spiders prefer short vegetation. The spider fauna of grikes in limestone pavement is strongly influenced by spatial properties, e.g. width which determine web distribution (Colebourn, 1974). These studies indicate that habitat structure may have a more important influence than microclimate (Enders, 1973) or prey availability (Cherrett, 1964).

b) Spider diversity

In most of the studies mentioned, the abundance and species richness of spider fauna are greater in vegetation associated associated with later stages of ecological succession, or in plant communities with greater structural complexity. This is because these habitats allow greater opportunities for coexistence. Several studies have shown that web-builders occupy different size and structurally diverse spaces in forest or old-field vegetation, and may thus have access to different prey types and sizes (Enders, 1974).

i) Correlative studies

Studies conducted by Uetz (1975, 1979) on the influence of deciduous forest leaf litter environments on the species diversity of hunting or wandering spiders revealed consistent patterns. Spider species richness and diversity were correlated with litter depth as well as interstitial space. With increased depth and complexity of litter, the overall amount of habitat increases, as does the diversity of microhabitat space within litter. This may relate to variation in prey abundance or microclimate. Similarly, Greenstone (1984) found a significant correlation between a measure of vegetative complexity and the diversity of web-building species, but no correlation with prey abundance.

ii) Experimental studies

Since the influence of habitat structure is complicated by interaction with associated variables, several experimental studies have sought to separate these influences. Bultman and Uetz (1982) compared spider communities in both artificial litter (vinyl plastic) and natural litter of varying structure. They found litter depth was more influential than structural complexity or nutritional content of litter in organising the forest floor spider community. Hatley and MacMahon (1980) experimentally altered vegetative structure of sagebrush communities by respectively clipping branches to reduce, and tying branches together to increase, complexity. The number of spider species was significantly higher in shrubs with branches tied together and lower in shrubs with clipped branches. This suggests that structurally more diverse shrubs can support a more diverse spider community. Gibson et al. (1992a) found that spider assemblages were most affected by the effects of grazing on plant architecture, in contrast to other invertebrates which were more strongly affected by plant species composition.

8.2.3 Bird communities

Long-term population changes in British birds probably result mainly from changes in the extent and nature of bird habitats caused either by climatic change or (increasingly) human activities. However, Root (1988) examined the environmental factors associated with avian distributional boundaries in North America. He found that both climatic factors (e.g. minimum January temperature, mean annual precipitation) and biotic interactions were important in determining range limits. Moreover, man has also influenced bird populations by deliberately reducing pest species and introducing or conserving selected species. Since they are warm-blooded, well insulated, relatively waterproof and mobile, it is rare for birds to suffer immediate physical damage due to cold, heat or storm. Birds do, however, suffer at such times because food becomes less available (Marquiss & Newton, 1990).

A general pattern in many bird communities is an increase in species composition and density with increased heterogeneity in habitat structure. Red grouse tend to nest at greater densities on heather moorland when the ground is structurally more complex and where the heather has been burnt in small patches. Burning increases the abundance of more nutritious, young heather shoots and also the structural heterogeneity of the heather habitat, providing more shelter from predators and more 'edges' which cocks may use as reference points for territorial boundaries (Hudson, 1988). Fuller and Moreton (1987) observed changes in breeding bird populations in relation to the age and development of coppiced woodland. Warblers, finches and buntings (and migrants) were most abundant in young coppice, but thrushes and tits increased with the age of the coppice.

MacArthur and MacArthur (1961) found that bird species diversity in North American deciduous forests could be predicted in terms of the height profile of foliage density and bore no relationship to plant species diversity (Erdelen, 1984). In Australia, Recher (1969) similarly found that habitat diversity, as measured by foliage profile, is a good predictor of bird species diversity. This indicated that the number of bird species which a habitat can support is determined by its structural complexity and the degree of specialization reached by coexisting species. Karr (1971) showed that avian communities may subdivide the vegetation profile similarly in Panama and Illinois. Cody (1968) showed that species of grassland birds coexist by a combination of vertical and horizontal specializations in use of food and space. Studies in a range of both temperate and tropical habitats have shown that bird species diversity is linearly related to foliage height diversity and curvilinearly related to per cent vegetation cover (Karr & Roth, 1971; Willson, 1974; Erdelen, 1984).