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Insects and mosaic landscapes

The evolutionary origin of today's nemoral insect fauna took place mainly in the Tertiary and Pleistocene landscapes. During these periods large parts of North America, Asia and Europe were shifting mosaics of different landscape types where grasslands alternated with solitary trees, shrubs and woods, a kind of temperate savannah (Guthrie 1984). The appearance, degree of openness and biological content of this landscape varied, of course, in time and space, but one characteristic was a very high, local diversity of plants, mammals and insects. Numerous herbivorous ungulates lived during these periods, and particularly remarkable were the many species of megaherbivores.

Presumably many insects have a way of life that is adapted to a landscape with a pronounced mosaic structure. The temperate savannah does not exist as a biome today, but many similar structures are found in the small-scale, agricultural landscape (Rackham 1998) and therefore many species have been able to survive there. We must, however, understand the evolutionary history of this landscape to be able to manage it in a way that is appropriate for nature conservation. In this paper we would like to illustrate, through examples from different insect groups, the importance of grazed as well as non-grazed areas and particularly the mosaic structure of the nemoral landscape, and their consequences for the diversity of plants and animals in general and insects in particular. Furthermore, we present arguments for protecting and managing the nemoral woodland and the agricultural landscape as a functional totality.

A very large number of organisms are directly or indirectly dependent on several different habitats during their life-cycles. It is a well-known fact that birds and mammals use different habitats in a landscape (Law & Dickman 1998). Less has been written about the similar dependence on different habitats among a multitude of insects. Furthermore, many insect species use different micro-habitats, e.g. dead wood, patches of bare mineral soil and flower-rich grasslands. A mosaic landscape with a large content of these different habitats and micro-habitats often has a very diverse insect fauna. A diverse insect fauna is vital because many of these mosaic dependent insects have key-functions (e.g. as pollinators) in most terrestrial environments (De Lettre *et al.* 1998, Nilsson 1991, Kullenberg 1991).

Environments that include woods, succession communities/scrub and grazed grassland become species-rich in at least three different ways:

1. Species associated with woodland and species associated with open habitats (pastures and meadows) can live in the same general area.

2. The ecotones (edge communities) are habitats in their own right. Tall herb and shrub fringe communities have typically a species-rich insect fauna.

3. Species that depend on two or more habitats within a relatively limited area thrive in mosaic landscapes.

TOTAL LIVING-SPACE AND PARTIAL LIVING-SPACES

It is often useful to make a distinction between the total living-space and the partial living-spaces of a certain species (Westrich 1989, Wiklund 1977). The total living-space includes all habitats and micro-habitats (partial living-spaces) which are used by a species in different stages of its life-cycle. However, many groups, especially wild bees, sphecid wasps and social wasps, use several partial living-spaces during the period of raising their young (nesting-place, nest material, pollen, nectar, lekking place). These partial living-spaces used contemporaneously are called partial habitats (Westrich 1996). Insects normally have a much smaller home range than vertebrates, and as a consequence they must have access to all vital habitats or elements within a small area (Wesserling & Tscharntke 1995).

Important partial living-spaces for insects are:

1. Lekking places: The adult animals often find their mates in a specific and limited area. Butterflies lek in wood-fringes, around solitary trees, groups of trees or shrubs in open grassland and in glades in woods etc (Wickman 1996). Many insects use the shrubs of wood-fringes as lekking and mating places (De Lettre *et al.* 1998). A flowering hawthorn brightens the landscape and is visible from a long distance. Many beetles and other insects use these shrubs, not only as a food-source but also as an efficient way of finding each other in order to mate (Warren & Key 1991). The branches and leaves of the wood-fringe define a spatial border which is used for lekking by certain moths, e.g. *Adela* spp.

2. Places for larval development: Many insects are highly specialized and use only a single or a group of related plant species as host species for the caterpillars. The host species must also grow in the right place — e.g. the butterfly *Hamearis lucina* preferentially lays its eggs on the leaves of *Primula veris* which are shadowed by trees or shrubs (Kruys 1998, Greif-Andersson 1998). The larval development of other species takes place in different kinds of dead wood. Some species prefer sunny and dry wood while other species live in moist wood in shadowy places (Jonsell *et al.* 1998).

3. Feeding places of adults: In a large number of insect species the adults depend on totally different environments to the caterpillars. Tall herbs like teasels (*Dipsacaceae*), thistles and golden rod (*Asteraceae*) are very important food plants for adult butterflies of many species, while the caterpillars of the same species may use totally different host-plants. Many of the wood-living longhorn beetles (*Cerambycidae*) also need flower-rich places with a large supply of nectar and pollen during their time as adults. These flowers must grow within reach of suitable places with dead wood. Many hoverflies, solitary wasps and wild bees have a similar need of access to flowers and dead wood.

4. Hibernation places: Some insects need particularly sheltered places to be able to live through the winter. This especially applies to the species that hibernate as adults. Important habitats in this respect are decaying wood, dead trees, rough and fissured bark, branches with plenty of lichens, grasslands with dry tall herbs, mounds of stones and places with an accumulation of leaf litter or tall grass.

BUTTERFLIES

Most butterflies have become less common in the last few decades and many species have now a diminished distribution (Thomas 1991, 1995). A quarter of the Swedish butterfly fauna, 31 species, is included in the national red list (Gärdenfors *et al.* 2000). Several studies during the last ten years or so have pointed out two important factors that limit butterfly distribution:

- The habitat demands of the larvae (Erhardt & Thomas 1991)
- The size of the habitat patches and their isolation in relation to the butterflies dispersal abilities (Dennis *et al.* 1998, Ebenhard 1995, Hill *et al.* 1996)

Scrubbing over of pastures and meadows and clearing and close cutting of roadsides and similar microhabitats are generally considered as the most important reasons for the decline of many butterfly populations (Oates 1995, Götmark et. al. 1998) but many other reasons have also been discussed (Warren 1992). The current theory thus states that a reduced level of grazing and mowing leads to the deterioration of conditions for many of the larval host-plants and thereby, in the long run, leads to reduced sizes of the habitat patches and increased levels of isolation. The area of meadows and pastures in Sweden has indeed decreased dramatically during the 20th century (Eriksson & Hedlund 1993).

This is however — as we see it — a simplified explanation, partly because many butterfly populations have decreased in spite of the fact that their host-plants are still common, and partly because many of the species in decline are dependent on successional

Figure 1. *The butterfly* Apatura iris. *A male from Kullen, province of Skåne, Sweden. This species depends on willow shrubs in sunny places during the larval period. The mature butterflies are mostly seen in tree-tops of different trees. Photograph by Anders Amandusson.*

stages that are not well-grazed or mown (Greiff-Andersson 1998). The eight butterfly species on the Swedish red list that are dependent on the agricultural landscape use the following host-plants:

Fabriciana niobe	*Viola*
Hamearis lucina	*Primula veris*
Hesperia comma	*Poa, Festuca*
Maculinea arion	*Thymus serpyllum, Origanum vulgare*
Mellicta britomartis	*Plantago, Veronica*
Pyrgus alveus	*Agrimonia, Potentilla*
Pyrgus armoricanus	*Fragaria vesca, Potentilla*
Stymonnidia pruni	*Prunus spinosa* (preferably older, shaded bushes)

It is striking that most of these host-plants do not belong to groups of species that decrease rapidly in the absence of grazing or mowing — only *Thymus* belongs to this group (Grime, Hodgson & Hunt 1988). Many of the host-plants mentioned are, on the contrary, species that belong to early stages of overgrowing grasslands such as *Primula veris, Origanum, Agrimonia, Fragaria* and *Prunus*. Furthermore, many species depend on tall herb vegetation to find protection and food. As a result the butterfly fauna is generally most diverse in poorly grazed lands, and the greatest species-richness is often found in places which have not been grazed during the last 10 or 15 years (Götmark *et al.* 1998). In areas with only well-grazed grasslands the butterfly fauna will be impoverished. Scrublands and forest edges provide important micro-habitats for the caterpillars but also suitable places for lekking and mating (Wickman 1996). Oates (1995) points out several important factors to take into consideration when working with butterfly conservation and two of these can be summarised as follows:

• The length and timing of the grazing period. Considering butterflies, the best management regime is to have grazing animals in a specific location only in late summer and autumn. It is important to have grass swards with varying vegetation heights since many butterflies prefer a rather high grass vegetation (8-30 cm).

• Do not graze the whole area of a specific location every year but leave some patches ungrazed (rotational grazing). Many dry locations do not need to be grazed every year but only every third or fourth year.

Another reason for the decline of butterfly populations could be the fact that many species are dependent on mosaic landscapes since the imagos often use different habitats than the caterpillars. A limited number of tall herbs with flowers rich in nectar determine to a large extent the distribution of the

Figure 2. Zygaena filipendulae. *Butterflies within the family of* Zygaeinidae *are rather sessile animals that have a rather poor dispersal ability. They are usually seen in flowers in pastures with high grass swards. They are poisonous and the clear red blue colours are warning signals. Hibernating pupae are attached at the uppermost parts of tall herbs and grasses and they are therefore sensitive to intensive grazing or mowing. Photograph by Anders Amandusson.*

imagos and thereby also where egg-laying will take place (Murphy et. al. 1984, Loertscher et. al. 1995). The butterflies preferably use sunny and warm patches when the air temperature is low and then move to more exposed patches as the temperature rises (Shreeve 1984, Davies 1978, Dennis 1982). The small patches with raised temperature close to bushes are particularly important for insects in northern Europe (Thomas 1993).

Some examples of species that use different habitats or mosaic landscapes during their life-cycle:

*Lopinga achin*e lives in open woodland (crown density 65-85 %) with a large supply of edge-zones (Bergman 1998). The female prefers to lay her eggs on the sedge *Carex montana* growing in the half-shade of wood-fringes. A possible interpretation is that this behaviour has evolved in an environment where large grazing animals have created abundant glades in the deciduous woodland (Bergman 1996).

Coenonympha pamphilus normally lives in open and well-grazed pastures. The butterflies do not visit flowers very often but occupy themselves with reproduction. The caterpillars feed on several grass species, usually *Festuca ovina*. The males often gather around shrubs or solitary trees in the pasture where they perform a kind of lekking behaviour to compete for females (Wickman 1996).

Gonepteryx rhamni are among the earliest butterflies in spring since they hibernate as adults. The butterflies do not visit flowers very often in spring but devote their time to mating and egg-laying. The caterpillars feed mainly on *Frangula alnus* growing in woodland and on lake shores. The new generation fly in late summer and then the butterflies visit tall herbs rich in pollen and nectar, e.g. *Succisa pratensis* and thistles growing in field-margins and wood-fringes. The butterflies need a good supply of nutrition to be able to live through the winter (Jennersten 1980).

The caterpillars of *Anthocharis cardamines* feed on seeds of several crucifers, mainly *Cardamine pratensis* and *Arabidopsis thaliana*. Mating and egg-laying take place in spring and sometimes the butterflies visit spring flowers such as *Primula veris*. In rainy summers the caterpillars survive better on *Arabidopsis* and in dry summers on *Cardamine*. To succeed well *Anthocharis cardamines* therefore needs both dry and moist grassland within a small area (Wiklund & Åhrberg 1978, Dempster 1997).

Leptidea sinapis flies in early summer and the females lay their eggs on leguminous plants such as *Lathyrus pratensis* and *Vicia cracca* growing in open grassland. The butterflies search for food and mate in open woodland where they almost exclusively use *Lathyrus linifolius, Viola riviniana* and *V. canina* (Wiklund 1977).

WILD BEES

Insect pollination is the most important type of mutualism between plants and insects. Wild bees are the most important pollinators in temperate ecosystems (Weislo *et al.* 1996). In the last few years there has been a growing awareness of the serious and rapid reduction of biodiversity in this group (Götmark *et al.* 1998, Kearns et. al. 1998, Banaszak 1995, Williams 1995, Westrich 1996, Cederberg 1999). This reduction is particularly serious as it is accompanied by a considerable change in the flora and in the structure of the landscape. Many conservationists think that these interactions should receive more attention (Kearns & Inouye 1997).

In a small-scale mosaic landscape the species-richness and abundance of wild bees is particularly high, as their demands for nesting places, food-plants and lekking places are satisfied in such a landscape (Sörensson 2000). Effective conservation work must take into account that these animals use different

TABLE 1 : BUTTERFLIES DEPENDENT ON MOSAICS
(compiled from several butterfly fieldguides and handbooks and the Swedish red data lists (www. dha.slu.se)

Species/group	Hibernation	Caterpillar	Imago (feeding)	Imago (reproduction)
Parnassius mnemosyne	tree base	woods/wood fringe	wood fringe/grassland	grassland
Nymphalidae (many species)	woods	woods	wood fringe/grassland	wood fringe/grassland
Gonepteryx rhamni	woods/wood fringe	woods	wood fringe/grassland	wood fringe/grassland
Euphydryas maturna	wood fringe	wood fringe/grassland	wood fringe	wood fringe
Lopinga achine	wood fringe	wood fringe	wood fringe	wood fringe
Strymonidia pruni	wood fringe	wood fringe	wood fringe/grassland	wood fringe/grassland
Carterocephalus palaemon	wood fringe	wood fringe	wood fringe/grassland	wood fringe/grassland
Leptidea sinapis	grassland	grassland	woods	woods
Anthocaris cardamines	dry/moist grassland	dry/moist grassland	wood fringe/grassland	grassland/wood fringe
Maculinea arion	dry grassland/wood fringe	dry grassland/wood fringe	wood fringe/grassland	grassland/wood fringe
Aricia nicias	wood fringe	wood fringe	wood fringe	wood fringe
Lycaeides argyrognomon	wood fringe	wood fringe	wood fringe/grassland	wood fringe/grassland
Heodes virgaureae	grassland	grassland	grassland/wood fringe	grassland/wood fringe

habitats which are often widely separated in space by unused habitats (Westrich 1996). Wild bees and solitary wasps (*Sphecidae, Eumenidae*) use their partial living-spaces contemporaneously and not sequentially as do most other insects. The different partial habitats must exist within the feeding range of the bees, which varies from a few metres up to five kilometres (the honeybee *Apis mellifera*). Most solitary wild bees must have access to their partial habitats within a range of 500 metres (Wesserling & Tscharntke 1995).

Different kinds of bare mineral soil are interesting partial habitats. Most of the wild bees nest in colonies in such patches. Important landscape elements with suitable nesting places are abandoned sand and gravel pits, eroded stretches along roads, naturally eroded river-banks and steep lake shores as well as dry pastures where the trampling of livestock creates bare patches. The species nesting in dead wood use elements like dead trees, logs and unpainted wood-constructions. Other species nest in dry stems of tall forbs or empty snail-shells. There is a distinct relationship between the occurrence of these partial habitats and the occurrence of wild bees (Steffen-Dewenter & Tscharntke 2000).

Some wild bees line their nests with special parts of plants, which may be found in another partial habitat. *Macropis europaea* lines its nest with glandular hairs from the petals of *Lysimachia* while *Anthidium* use hairs from *Verbascum* and *Stachys*. The leaf-cutter bees *Megachile* cut pieces from leaves and petals of particular plants.

Other very important partial habitats are localities with food-plants. Many species are oligolectic, i.e. they collect pollen for their offspring only from one or a group of related plants. A few scattered plants are not enough, but the food-source must be sufficiently abundant. Sometimes these oligolectic bee species use other plants for collecting nectar.

Finally some species swarm and mate at particular landscape elements. The large bumblebee *Bombus lapidarius* swarms around treetops, a habitat where they do not normally occur (Bergman 1997).

The wild bees constitute an important and neglected group of insects which may see their living-space disappear in spite of conservationists carefull managing sites of natural value, like meadows, pastures and wood reserves. The wild bees could be favoured by preserving and restoring the mosaic structure of the landscape and identifying this structure as a natural feature in its own right (Cederberg 1999).

Figure 3.
*A woodliving wild bee (*Osmia sp.*) at the entrance of its nest. Photograph by Mats W. Pettersson.*

Figure 4. *A wild bee within the genus* Anthidium *collecting hairs from a tall herb - the garden plant* Stachys byzantina. *Photograph by Mats W. Pettersson.*

TABLE 2.
WILD BEES DEPENDENT ON MOSAICS
(compiled mostly from Westrich 1989 but also from other Swedish and German handbooks and the Swedish red data lists (www. dha.slu.se)

Genus	Nest habitat	Nest material	Feeding	Lek
Osmia	dead wood/ snail-shells	exposed clay/earth/ gravel, leaves/ petals	*Salix* (shrub land)	
Eucera	sand/ earth in open aeras	-	*Corydalis* (woods)	-
Anthophora	sand/ earth in open aeras	-	*Pulmonaria* (woods)	-
Lasioglossum	sand/ earth in open aeras	-	*Asteraceae* (mostly in open grasslands)	-
Bombus	successions communities/ vole burrows etc	-	(willow scrubs, woodland, open land)	tree tops /shrubs
Apis	woods/hollow trees	-	open land/shrub land	tree tops /shrubs
Macropis	sand/ earth in open aeras	*Lysimachia*	*Lysimachia* (shaded and sunny habitats)	tall herbs
Andrena	sand/earth in open aeras	-	vernal herbs, often in deciduous forests, and *Calluna, Vaccinium myrtillus, Veronica, Potentilla*	- shrubs (many species)
Anthidium	sand/ earth in open aeras	Verbascum hairs	weed-ridden areas	-
Colletes	sand/earth in open aeras	-	*Asteraceae* and willows (mostly in open habitats)	-
Halictus	sand/earth in open aeras	-	*Lamiaceae*, *Scrophulariaceae* (shaded and sunny habitats)	-
Chelostoma	dead wood, mostly in sunny habitats	-	*Campanula, Ranunculus* (open woodland/grassland)	*Campanula*

HOVERFLIES

Hoverflies (*Syrphidae*) form a species-rich family and many hoverflies depend on access to different kinds of partial living-spaces. The adult flies are important pollinators (Torp 1994). They mainly visit flowers with easily accessible pollen, e.g. rosaceous flowers like apple-blossoms. Hoverflies are mainly found in wood-fringes, glades and tall herb communities. A large group of the hoverflies have larvae that feed on aphids. The larvae, which normally are polyphagous and hunt several aphid species, live in trees and shrubs. The larvae of other species hunt caterpillars in similar habitats.

The high biodiversity of mosaic landscapes is enhanced by the fact that many predators rely on hoverflies as their main or only prey. The wood-living fly *Laphria flava*, the dung-living robber fly *Asilius crabroniformis* and the sand-living wasp *Bembix rostrata* all feed primarily on big hoverflies. The solitary wasp *Ectemnius ruficornis* (= *E. planifrons*) nests in dead wood and hunts only hoverflies as food for its larvae.

Among the wood-living hoverflies are many typical cambium-feeders such as the genera *Temnostoma, Spilomyia, Xylota* and *Chalcosyrphus*. On damaged branches and trunks with sap-flows one may find species like *Hammerschmidtia ferruginea, Pocota personata, Ceriana conopsoides* and *Lejota ruficornis*. Some hoverfly larvae (e.g. *Mallota cimbiciformis* and *Myathropa florea*) develop in water-filled cavities in old trees together with many other specialized flies and gnats. The rove beetle *Quedius truncicola* is a top predator in this ecosystem. The wood-living hoverflies depend on moist and shaded wood or old trees for larval development. They represent a group of wood-dependent insects that occupy a habitat different to that of many beetles which live in sunny and dry wood habitats (Nilsson & Baranowski 1994, 1996, Ranius & Jansson 2000). Nonetheless, the adult hoverflies of this group still require sunny habitats nearby for the flowers on which they feed and mate.

THE FORMING OF THE MOSAIC LANDSCAPE

It is interesting to speculate on the formation and maintenance of the mosaic landscape (temperate savannahs sensu Rackham (Rackham 1998), wooded pastures sensu Vera (Vera 2000)) and its evolutionary history. The appearance and biological content of such mosaic landscapes varied of course in time and space. During the Holocene period it is possible that the savannah-like forests were restricted to more warm and arid regions within the former nemoral biome and that the savannah-structure in more cold and humid regions (e.g. England, Denmark and Scandinavia) may have been less pronounced. Some authors stress, however, that the northern parts of Europe also had rather open forests during the Holocene (see for example Vera 2000).

The evolutionary history of the mosaic landscape mainly took place in the Pleistocene and Tertiary periods and it is also therefore necessary to consider these periods if we want to understand the grassland-deciduous woodland ecosystem(s) of today.

A great number of grazing and browsing ungulates existed during these periods and particularly notable is the large number of huge herbivores, so called megaherbivores (Owen-Smith 1988). There are many theories that try to explain the phenomenon of mosaic landscapes and we will here give a short introduction to some of these that we find particularly interesting in this context.

Guthries theory of mosaic pattern

The American paleobiologist Guthrie (1984) states that large areas of the North American and Eurasian continents during the late Tertiary and Pleistocene periods consisted of a varied landscape where grasslands, tall grass and herb vegetation, shrublands or fringe-vegetation, old trees, dead wood, groves and woods formed shifting mosaics. He shows that the non-ruminating herbivores are dependent on vegetation mosaics. He also states that when the landscape turned more uniform (end of Pleistocene) the number of ungulate species declined dramatically. The Northern Hemisphere was at that time inhabited by huge herbivores such as rhinoceroses, proboscideans and giant ground sloths. As opposed to the ungulates that dominate the grassland-ecosystems today the huge herbivores were non-ruminants and unable to synthesize certain amino acids and vitamins. Their digestive system made them more vulnerable to large amounts of toxic plant substances. The non-ruminants were thus dependent on a very varied diet containing grass and herbs as well as twigs and leaves and for this nutritional reason they were restricted to living in mosaic landscapes. The elephants and rhinoceroses that exist today have similar habitat demands.

The megaherbivore theory

Due to their impressive body size, large herbivores need to consume considerable amounts of food to survive. An adult African male elephant eats 300 kilos of plant material each day. Approximately 50% consists of grass and the rest of leaves, twigs and herbs (Law 1970). The huge body size functions as an effective protection against carnivores and population sizes are therefore regulated by food supply (Owen-Smith 1987, 1988, 1989). These features make them highly capable of influencing the landscape structure (Muller-Dumbois 1972, Jachman & Bell 1985). Considering this, the megaherbivores were very likely to play a major role in the forming of the vegetation-structures during Tertiary and Pleistocene periods (see also Zimov *et al.* 1995). If parallels are drawn to the African savannahs of today a herd of elephants can, for example, transform a woodland into an open or semi-open savannah - and then leave it as the vegetation turns too homogenous (Caughley 1976, but see also Prins & Van der Jeugd 1993). The megaherbivores are unique in the sense that they can create a mosaic landscape also from forested areas.

The theory of "cyclical turnover of vegetation"

In recent years a lot of research has been done in large nature reserves in the Netherlands and Germany concerning grazing animals and their impact on the vegetation (Olff *et al.* 1999, Vera 2000). This research has produced a theory that describes how grazing animals create a cyclic succession where different stages of successions co-exist in close proximity to each other. The mechanism behind this process is based upon "associational resistance" which causes palatable plants to be proportionally less grazed by large herbivores when unpalatable species reach higher relative abundance. According to this theory most herbivores will contribute to the maintenance of vegetation mosaics, and the result would be a landscape dominated by "wood pastures" with grasslands, fringe-vegetation and groves.

The "high forest theory"

There is also a possibility that the insects adapted to a landscape with a pronounced mosaic structure could satisfy their ecological requirements in forests with internal dynamics only, and in absence of big herbivores. This theory is in concordance with the classical view of north European botanists, of the "mixed oak forests" that are believed to have existed during Holocene. Eemian pollen data from Jutland in Denmark, show virtually no pollen grains from plants indicative of open conditions (Bradshaw & Mitchell 1999).

It could be argued that for example the hoverflies, mentioned by us earlier, could survive in a closed-canopy woodland with gaps and without grazing being a necessary requirement. Shrubs such as *Crataegus laevigata*, which is more shade tolerant than *C. monogyna*, and tall herbs in wood margins and gaps could possibly supply nectar and mating sites. This is also in concordance with their floral preferences (Branquart & Hemptine 2000).

Ranius and Jansson (2000), on the other hand, show that the old trees with abundant dead wood are more valuable when found in open growing conditions. The saproxylic insects connected with oaks (and sometimes conifers) also prefer sunny parts of dead wood (Nilsson & Baranowski 1994, 1996). Natural gaps are in that sunny state for only a short period (Elofsson & Gustafsson 2000) and not long enough to meet the ecological requirements of these species. Wild bees need plants from open situations in abundant populations, and could certainly not survive in a closed canopy forest with internal dynamics only. According to our opinion, it is therefore unlikely that the multihabitat use has evolved and survived in so many groups of insects, in a landscape only consisting of high forests.

NATURE CONSERVATION AND THE MOSAIC PRINCIPLE

The flora and fauna of the agricultural landscape has been seriously impoverished during the last few decades (Swedish Environmental Protection Agency 1994). The insect fauna has not been studied as the thoroughly as flowering plants, but the threats to the insects are certainly not less serious (Thomas 1991). Insects have many unique characteristics which make it necessary to pay special attention to them in conservation work. Apparently the insects depend on a small-scale landscape where there is a variety of partial habitats within a small area.

Accordingly, the diversity of habitats is very important in conservation work. Many insects have temporary populations in small areas (e.g. a stump, a carcase or a heap of twigs). They live there for a short time and then become extinct in that particular locality. Hopefully some individuals manage to colonize a new area before the local extinction occurs. Such population dynamics are dependent on constant access to these small and often temporary habitats. One can therefore expect that just a few years of unsuitable environmental conditions would lead to the extinction of vulnerable species. Specialized herbivores and pollinators are dependent upon access to a sufficient amount of suitable plants. Most species in temporary habitats are good dispersers and are able to find new localities within reasonable distances (a few kilometres). Therefore it often pays conservationists to create new insect habitats.

In conservation work one should make the best use of the knowledge of interactions between the organisms of deciduous woodland and those of the agricultural landscape. For example it is of great importance to include grassland and areas of developing scrub in new woodland reserves, even if the prime purpose is to preserve an old deciduous wood. Many conservationists maintain that the proper way of protecting the wildlife of the agricultural landscape is an intensive management with traditional practices. The restoration of agricultural landscapes from the 18th and 19th century is often seen as the best way of creating optimal conditions for the wildlife of small-scale agricultural landscapes.

The composition and qualities of adjacent woodland are seldom included in these restoration and management projects. The conservation strategies are built upon the demands of a few flowering plants which depend on intensive grazing or mowing. Successional vegetation is often seen as unwanted vegetation types that must be controlled. However, the major part of biological diversity - and most insects - is dependent on complex ecological interactions rather than intensively managed and uniform grassland areas.

Nature reserves consisting of deciduous woodland have too often been left to a free development without grazing or any other management. In these habitats conservationists have endeavoured to restore an allegedly natural landscape, the virgin forest.

The growing knowledge of the interactions between grassland and woodland must, however, lead to an understanding of the importance of grazing in woodland as well as the importance of non-grazed areas in grassland. As disturbance in the form of grazing and browsing historically has had a key-role in the nemoral biome, various kinds of grazing and browsing ought to be an important part of the management of this landscape (see for example Ranius & Jansson 2000).

The habitat directive of the European Union (Natura 2000 network) uses a system of static habitat types. Such a system makes it hard to argue for incorporating unmanaged grass and shrub lands within a pastured grassland reserve or within a woodland reserve, although this would favour - and often is a prerequisite of - the entomological diversity. Unfortunately we still are inclined to believe that deciduous woodland, if left unmanaged, will revert to some kind of "natural ecosystem", to which all species are adapted.

Deciduous woodland and agricultural land are often treated as two separate entities without any connections. Forestry is meant to take responsibility for the biodiversity in forests and woodlands, and agriculture is meant to do the same thing in meadows and pastures. This kind of thinking is, in our view, sub-optimal when it comes to conserving biodiversity in deciduous woodland and agricultural land.

Instead we propose that one should look upon deciduous woodland and grasslands not as separate units, but as a whole, the remnants of the temperate savannah, where pastures, tall grass and herb vegetation, scrubland or fringe-vegetation, old trees, dead wood, groves and woods form mosaics•

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Figure 5. *A pasture landscape with abundant thorny shrubs. The shrubs are an important pollen and nectar resource for many insects and they also maintain regeneration niches for different trees. Hard grazing will lead to a complete exclusion of woody species but if grazing is held at moderate levels, patches of regeneration will eventually appear, thereby creating a diverse stand-structure and re-establishing the succession of trees. Illustration by Nils Forshed*

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