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Roadside environments as habitats for Lepidoptera

ACADEMIC DISSERTATION

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Over the past 50 years agricultural intensification has resulted in a radical decline in the area of traditional semi-natural grasslands and the associated fauna and flora. Roadside environments may serve as alternative habitats for a variety of grassland species due to their large area and regular mowing management, which somewhat resembles the management of semi-natural grasslands. The approximately 161,000 hectares of open areas along roads and intersections is more than 50 times the total size of the remaining semi-natural grasslands on mineral soils.

The aim of the thesis was to evaluate the importance of open roadside environments as habitats for butterflies and other Lepidoptera using transect count, mark-release-recapture (MRR) and emergence trap methods. Field studies were conducted on four types of roadside environments (intersections, highway, urban and rural road verges), semi-natural grasslands and extensively or non-managed field environments.

Positive plant indicators of semi-natural grasslands were recorded in each roadside environment, which were relatively similar in vegetation structure. The majority of Lepidoptera individuals in roadside environments belonged to meadow species. Butterfly abundance was higher in rural road verges compared to urban road verges, while butterfly species richness was higher along rural roads and highways compared to intersections. Similarly, moth diversity was higher in rural road and highway verges compared to intersections. Semi-natural grasslands were characterised by a higher abundance, species richness and diversity of butterflies and a higher diversity of moths compared to certain roadside environments, while the differences between roadside and field environments were small. The amount of nectar was positively associated with butterfly abundance and high vegetation with moth abundance. Lepidoptera species richness, on the other hand, was positively associated with plant species richness, vegetation quality, the cover of surrounding forests, verge width and age.

The mid summer mown verges had a lower species richness and abundance of butterflies and lower species richness and diversity of moths compared to either late summer or partially mown verges, where intact vegetation remained throughout the summer. Unmown patches preserved along mid summer mown verges offered 'nectar refugia' and shelter for Lepidoptera. Individuals of the butterfly *Aphantopus hyperantus* emigrated more frequently from linear verge habitats compared to non-linear intersections or non-managed field environments. The highway was not a barrier to the movement of *A. hyperantus*. The species richness and cover of low growing plant species and butterfly abundance were lower in *Lupinus polyphyllus* invaded verges compared to non-invaded verges. As the lupin cover approached 100%, fewer butterflies were observed in lupin transects compared to the adjacent non-lupin transects.

The results suggest that roadside environments offer important alternative habitats to a varied group of grassland plant and Lepidoptera species. Their role could be further enhanced by adjusting the mowing management, avoiding two or more total mowings per summer. In future, the road verge management could also be improved by educating the mowing personnel and conducting a thorough survey of the roadside environments of the highest value to biodiversity.

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This thesis is a summary of the following articles, which are referred to by their Roman numerals I-VI in the text.


Some unpublished results are also presented.

I contributed to the study design in papers IV-VI. I gathered all empirical data for paper V and approximately one third of the data for papers II, III, IV and VI. I analysed all the data and prepared manuscripts III-VI, and I participated in preparing manuscripts I-II. I contributed to the study design in the unpublished work on ‘nectar refugia’ and I analysed the empirical data.

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1. INTRODUCTION

1.1. Semi-natural grasslands in the changing landscape

Before the onset of heavy human impact in Europe, it is likely that closed forests predominated the landscape, but open vegetation was common, for example, on flood plains, infertile soils and chalklands (Svenning 2002). Later on, the traditional agricultural practices created a variety of open semi-natural environments such as pastures and meadows, which were used in traditional animal husbandry (Soininen 1974, Olsson et al. 2000). Meadows were cleared in forests and on some occasions the water level of lakes was deliberately lowered to expand the shore meadows, while old slash-and-burn clearings were used mainly as pastures (Soininen 1974). Naturally open areas with herbaceous vegetation on mires and riparian areas were also commonly used as a source of fodder (Soininen 1974). It is likely that mowing and grazing benefited the existence of species that were originally living in areas with open vegetation created and maintained by natural disturbances such as fires, floods, storms, landslides, and grazing by large mammals (Pykalä 2000, Svenning 2002). In semi-natural grasslands mowing and grazing by cattle increase plant diversity by suppressing the dominance of highly competitive species and thus facilitating the coexistence of species with different competitive abilities (Grime 1986, Zobel 1992). A large proportion of these species are native, i.e. they arrived independently of human beings, and would thus probably also occur under present-day natural conditions (Pykalä 2001, Svenning 2002). Due to their high species richness, semi-natural grasslands became essential habitats for maintaining biodiversity in European agricultural landscapes (Duelli & Obrist 2003). They are particularly important for vascular plant and arthropod species (Rassi et al. 2001, Duelli & Obrist 2003).

Over the past 50 years the agricultural practices in Europe have gone through profound changes (Stoate et al. 2001, Robinson & Sutherland 2002). The agricultural landscape has been simplified by intensive management of fields and pastures and, on the other hand, by abandonment of semi-natural grasslands (Fjellstad & Dramstad 1999, Stoate et al. 2001). The intensification has included ploughing the meadows and pastures, the extensive use of agrochemicals, increasing the size of intensively used fields, closing open ditches by sub-surface draining and the removal of a wide variety of landscape features considered to represent obstacles to production, such as remnant islets of semi-natural vegetation, single, or groups of, trees and bushes, hedges, ponds, barns, and stone piles (Agger & Brandt 1988, Ihse 1995, Stoate et al. 2001, Robinson & Sutherland 2002).

In Finland, the nationwide inventory carried out in the 1990s revealed the total area of valuable traditional rural biotopes to be less than 19,000 ha (Vainio et al. 2001). The area of different types of valuable semi-natural grasslands with open vegetation was approximately 9,000 ha, while the area of those on mineral soils was approximately 3,000 ha. The scale and pace of the decline has been alarming. It is estimated that in the 1880s the total area of meadowland was as high as 1,610,000 ha (Soininen 1974). Despite the uncertainty in this estimation due to varying definitions of 'meadows' in different time periods and regions (Soininen 1974), it is clear that a reduction to 1% has occurred during the past century. Semi-natural grasslands have declined throughout Western and Northern Europe (Fuller 1987, Ihse 1995, Linusson et al. 1998, Poschlod & WallisDeWries 2002), which has consequently led to the decline of the associated species (Thomas 1995, Van Swaay & Warren 1999, Rassi et al. 2001, Luoto et al. 2003).

As only fragments of valuable semi-natural grasslands still remain, it has become essential to determine where the grassland species persist in the modern landscape. In agricultural landscapes the potentially most diverse areas include extensively managed areas like abandoned fields, areas around piles of stones, and farm 'cart tracks'. In the
Finnish agricultural landscapes the total cover of these elements and semi-natural grasslands is estimated at less than 5% (Luoto et al. 2004). Non-managed islets surrounded by crops play an important role as refugias for plants (Cousins 2006), but the set-back with all unmanaged agricultural areas is the gradually increasing shading by bushes and trees, which eventually leads to the disappearance of species requiring an early-successional habitat (Erhardt 1985). In addition, agricultural areas with a recent history of ploughing and fertilizing are generally low in plant and insect diversity (Steffan-Dewenter & Tcharntke 1997, Austrheim & Olsson 1999). Although field margins as permanent non-crop habitats are generally considered important refugia for biodiversity in agricultural areas (Marshall & Moonen 2002), margins bordering fields with non-permanent grass and cereal crops are generally species-poor due to the nitrogen and phosphorus fertilizers and herbicides used in the fields (Kleijn & Verbeek 2000, Hald 2002, Smart et al. 2002, Tarmi et al. 2002, Hovd & Skogen 2005). Furthermore, since the 1950s the overall area of the field margins has decreased (Ihse 1995, Hietala-Koivu 2003) and they now cover only approximately 3% of the Finnish agricultural landscapes (Luoto et al. 2004).

Human activities also provide possible refugia for grassland species in the form of road and railway verges, powerline areas, natural gas pipelines, airfields, ruderal areas in towns and cities, abandoned quarries, sand pits and land fills. In Finland, powerline areas offer significant alternative habitats for meadow species and their total area (>20 m wide powerlines) comes to more than 50,000 ha (Kuussaari et al. 2003). Modern railway embankments and railway yards are built on coarse gravel to prevent the emergence of vegetation, but their edges may offer habitats for grassland species. Airfields are mown regularly to maintain visibility and consequently some old sites have become valuable habitats for species of dry meadows (Sundell 2005). In ruderal areas in towns and cities and in abandoned quarries and sand pits the lack of management may be a problem, but well-drained, nutrient-poor soils slow down the emergence of trees and bushes. The abandoned quarries may form particularly important habitats for xerophilous species (Benes et al. 2003). Finally, roadside environments serve as alternative habitats for grassland species due to their large area and regular mowing management, which somewhat resembles the management of semi-natural grasslands (Munguira & Thomas 1992, Persson 1995, Jonsell 2004).

1.2. Roadside environments as alternative habitats

1.2.1. Roads

The total length of motorways, state, provincial and communal roads in the 25 EU member states in 2000-2004 was 4,817,168 km (European Comission 2005). The Finnish road network, totalling approximately 454,000 km in 2006, consists of highways (17%), urban streets (6%) and private roads (77%), including logging roads (Finrra 2006b). The Finnish Road Administration (Finrra) is in charge of the highways (previously regarded as 'public roads'), the length of which has increased from 68,136 km to 78,189 km between years 1940 and 2006 (Finrra 2006a).

The construction and maintenance of roads has radically modified ecosystems throughout most terrestrial landscapes (Bennett 1991, Forman & Alexander 1998, Spellerberg 2002). Road building diminishes and fragments the natural habitats, alters the landscape spatial pattern and causes erosion and changes in water flow (Bennett 1991, Forman & Alexander 1998, Trombulak & Frissell 2000). Chemical pollutants and fertilizing nutrients derived from vehicles and road management affect the surrounding terrestrial and aquatic communities (Spencer & Port 1988, Spencer et al. 1988, Forman & Alexander 1998, Cape et al. 2004), and may change the species composition for a distance of up to 200 m from the road (Angold 1997). Road traffic is an important source of
carbon dioxide emissions, which in 2004 counted for 18% of all carbon dioxide emissions in Finland (Ministry of Transport and Communications 2006). Traffic also kills individuals attempting to cross the road (Mckenna et al. 2001, Spellerberg 2002) while road avoidance and the barrier effect may subdivide populations (Dennis 1986, Munguira & Thomas 1992, Forman and Alexander 1998).

1.2.2. Verges

Along the roads, verges of varying widths have been established and managed on a regular basis to ensure visibility and traffic safety. Estimates on the overall areas of road verges are scarce (Spellerberg 2002). For example, verges are estimated to cover 60,000 ha in the Netherlands (Schaffers 2000) and at least 200,000 ha in Sweden (Sjölund et al. 1999). The exact total area of road verges in Finland is not known, but a crude estimate of the open area along roads and at intersections can be obtained using the statistics on road lengths, the number of intersections, average verge widths, and the average areas of intersections (Table 1). The approximately 161,000 ha of open road verge environments in Finland is more than 50 times the total size of the remaining semi-natural grasslands on mineral soils (Vainio et al. 2001).

Road verges form a network covering almost all continents and geological, soil and climate regions (Way 1977). Road verges are linear edge habitats. Due to variations in the soil and topography they can exhibit a wide array of structural differences and species composition within a small space, harbouring both edge habitat specialists and species from the surrounding environment (Way 1977). Typically, the vegetation varies from the low cover of low growing species in the vicinity of the road edge to the dense cover of tall growing species on the embankments and slopes (Ullmann & Heindl 1989). The management as well varies within the verge, the more intensive mowing often occurring close to the road edge. The third important feature of road verges is the frequent construction work. This includes the building of new roads and the improvement, widening or straightening of the old ones. In addition, pipes, cables or ground water protection layers are installed and ditches are repaired to prevent the water level rising as far as the road surface. These disturbances create a mosaic of different ages and soil structures on the verge network. Intersection reservations (from this point on referred to as intersections), on the other hand, are non-linear roadside environments surrounded by roads and ramps and they more closely resemble semi-natural grasslands in regard to their shape. Intersections also differ from verges in the need for less intensive management and in their vegetation, topography,

<table>
<thead>
<tr>
<th></th>
<th>Length (km)</th>
<th>Verge width (m)</th>
<th>Number</th>
<th>Average area (ha)</th>
<th>Total area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main roads (Class I)</td>
<td>8,579</td>
<td>20</td>
<td>17,158</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main roads (Class II)</td>
<td>4,694</td>
<td>15</td>
<td>7,041</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other highways</td>
<td>28,441</td>
<td>15</td>
<td>42,662</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Local roads</td>
<td>36,482</td>
<td>5</td>
<td>18,241</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urban streets</td>
<td>25,000</td>
<td>2</td>
<td>5,000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Private roads</td>
<td>350,000</td>
<td>2</td>
<td>70,000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intersection reservations</td>
<td>247</td>
<td>4.0</td>
<td>988c</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>All road environments total</strong></td>
<td><strong>161,090</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Finnra 2006b, *Summed width of verges on both sides, based on the average widths of the study sites, *Number of intersections in Finland, according to the database of Finnra, *Summed area of intersection areas surrounded by roads in each intersection, based on the average of the study sites, *Note that in some intersection areas only the edges are managed as open areas.
and possibly lesser exposure to pollutants, dust, salt and physical disturbances.

Road verges offer habitats to native species (Bennett 1991, Munguira & Thomas 1992, Eversham & Telfer 1994, Meurk & Swaffield 2000, Ries et al. 2001, Tikka 2001, Hovd & Skogen 2005). It has also been suggested that linear verges increase the connectivity in fragmented landscapes by providing corridors for native species moving from one habitat patch to another (Bennett 1991, Vermeulen & Opdam 1995, Ries et al. 2001, Tikka 2001). The increasing movement of animals between habitat patches through corridors has been difficult to determine (Rosenberg 1997) but some studies on butterflies have produced positive results (Suitcliffe & Thomas 1996, Haddad 1999a, Haddad & Baum 1999). Range expansions along road verges have also been reported in both butterflies and moths (Dirig & Cryan 1991, Brunzel et al. 2004).

Road verges offer species challenging habitats due to the adverse effects of road maintenance and traffic. The physical environment is characterised by increased dust, noise level, windiness, changes in light conditions, temperature, soil density and water content compared to the adjacent habitats (Ullmann & Heindl 1989, Farmer 1993, Trombulak & Frissel 2000). Mechanical damage caused by snowploughing vehicles, ditch repairs and other construction work on average once every 20-30 years (Mahosenaho & Pirinen 1999) removes vegetation and leaves behind exposed soil. In road verges the soil is often well drained and fairly dry, an important prerequisite for grassland community formation (Cousins and Eriksson 2002). Conversely, exhaust emissions, particles and fluid leaks from vehicles, and deicing salts alter the chemical environment and reduce their quality for wildlife (Liem et al. 1985, Angold 1997, Granby et al. 1997, Forman & Alexander 1998, Günthardt-Goerg et al. 2000, Viskari et al. 2000). In fact, higher degrees of DNA damage have been observed in road verge plants than in non-roadside ones, possibly due to mixed air pollutants (Sriussadaporn et al. 2003). Animals living or using the verges as corridors may also be killed while attempting to cross the road (Ries et al. 2001).

Road verges have often formed footholds and conduits for invasive plant species (Parenedes & Jones 2000, Trombulak & Frissell 2000, Gelbard & Belnap 2003). In some parts of the world, the majority of the road verge flora comprises introduced species (Wester & Juvik 1983, Wilson et al. 2000). Invasions may be facilitated by the frequent disturbances to road verges, which may eliminate or reduce the cover of competitors and/or increase resource levels (Davis et al. 2000). In Finland, one of the most abundant invasive species along road verges is the lupin (*Lupinus polyphyllus*), which nowadays represents a potential threat for generally low growing meadow plants adapted to nutrient-poor conditions. The seeds of non-indigenous grasses are also commonly sown on road verges (Ries et al. 2001, Skrindo & Pedersen 2004, Rentch et al. 2005).

1.2.3. Road verge management

Mowing management started gradually on Finnish road verges in the 1950s but from the 1960s to 1987 verges were also treated with herbicides (Göran Strandström & Karl Bromberg, pers. comm.). The roadside management is based on Finnrna's instructions (Finna 1999, Finnrna 2000). In general, highway verges are mown twice a summer, the verges of urban roads are mown 2–3 times per summer, and the verges of rural roads are mown only once in late summer. The mowings generally take place in mid summer (from mid June to early July) and late summer (from late July to September), but in this respect both years and verges vary. The width of the annually mown area varies depending on the functional classification of the road (Finnrna 2000), and the rest of the open area is managed while removing bushes and other woody plants at regular intervals of 3–5 years. The annual mowing may thus cover either the whole or only part of the
verge. Partial mowings covering a narrow (usually 2 m) strip next to the road are also typical to verges mown completely every year and can occur before or after the complete mowing. The mowing height is approximately 5–10 cm.

Although some road verges and intersections are managed similarly to semi-natural grasslands, there are profound differences in the general management of road environments and traditional biotopes. The management of traditional biotopes included either one mowing event in July or grazing (Heritage landscapes working group 2000). The traditional management also included removal of the cut material, which is rare in roadside environments. Furthermore, the current mowing equipment most frequently used in verge management includes crushing blades instead of the traditionally used cutting blades, which may lead to higher mortality in insects and desiccation and vulnerability to pathogens in vascular plants.

In general, an annual mowing regime followed by hay removal has a positive effect on vascular plant species richness on road verges (Parr & Way 1988, Persson 1995, Schaffers 2000). By contrast, among invertebrates many species of Arachnida (Kajak et al. 2000), Orthoptera (Guido & Gianelle 2001), Coleoptera (Morris & Rispin 1988), Diptera (Völkl et al. 1993), Lepidoptera (Erhardt 1985, Völkl et al. 1993, Feber et al. 1996, Gerell 1997, Hogsden & Hutchinson 2004) and Hemiptera (Helden & Leather 2004) suffer from mowing, although some species of these groups may respond favourably (Morris 1981, Morris & Rispin 1988). From the insect point of view it is still unclear whether the verges are successful breeding areas or by contrast form sink habitats, where local reproductive success fails to keep pace with the local mortality (Pulliam 1988) due to intensive mowing. In the worst case, mown road verges could form 'ecological traps', i.e. areas characterised by unsuccessful breeding but which adults prefer over other available habitats (Dwernychuk & Boag 1972, Battin 2004). Regularly mown areas with high quality vegetation could be more attractive to females for egg-laying than the surrounding unmanaged areas, but the consequent mowing may be destructive to the offspring. In the long run, however, mowing has a positive effect on the meadow insects by preventing the growth of bushes and trees (Erhardt 1985).

1.3. Objectives of the study

The aim of the thesis is to study the role of open roadside environments as habitats for butterflies and other Lepidoptera. The specific objectives were to determine the following:
1) Whether roadside environments differ from semi-natural grasslands or field environments as habitats for vascular plants and Lepidoptera, meadow species in particular (I-III).
2) Which environmental characteristics most influence the vascular plant and Lepidoptera communities in roadside environments (I-III).
3) The impact of the mowing regime on Lepidoptera along road verges (IV).
4) How roads affect the movement of butterflies (V).
5) How the invasive lupin affects the vascular plants and Lepidoptera on road verges (VI).

2. MATERIALS AND METHODS

2.1. Study area

All the studies were conducted in South Karelia, SE Finland. The districts of Lappeenranta, Joutseno, Imatra and Ruokolahti belong to the biogeographical province of South Savo and the southern boreal vegetation zone (Ahti et al. 1968). The First Salpausselkä Ridge runs in a SW-NE direction through the four districts. The landscape on the northern side of Salpausselkä is dominated by Lake Saimaa, while the southern side is characterised by a relatively flat field and forest dominated area. A relatively dense road network rami-

10
road, Highway 6, runs along the Salpausselkä Ridge. The area of valuable semi-natural grasslands on mineral soils in the four districts is less than 10 ha (Jantunen et al. 1999). The majority of these have been abandoned and suffer from overgrowth or nutrient enrichment (Saarinen & Jantunen 2001).

Field studies were conducted in 1) open roadside environments ranging from newly built to old, urban to rural, and wide, busy and paved roads to narrow, little used and unpaved gravel roads. Studies did not include farm trails, logging roads with no proper verge, or roads with a narrow verge constantly in the shade. Some studies were conducted on 2) open semi-natural biotopes (from now on referred to as 'grasslands'). Two of the sites were not agricultural grasslands in the sense that the other sites were. They were located on an old airfield, characterised by a long management history and 'valuable grassland' status in the region (Jantunen et al. 1999). The other group used for comparison represented 3) extensively or non-managed field environments located on field verges and abandoned fields. In total, 161 sites were used for the Lepidoptera and vegetation studies.

2.2. Study species

This thesis focuses on butterflies (Hesperioida, Papilionoidea), other Macrolepidoptera (Lasiocampoidea, Bombycoidea, Geometroidea, Noctuoidea) and burnet moths (Zygaenoidea). Butterflies, in particular, have been widely used as indicator species of the change in habitat structure of semi-natural and urban biotopes (Erhardt 1985, Blair and Launer 1997, Söderström et al. 2001). Up to 2006, a total of 120 species of butterflies have been recorded in Finland. The proportion of threatened butterfly species is high in comparison to the other Lepidoptera groups. Two butterfly species are classified as regionally extinct, two as critically endangered, three as endangered, and ten as vulnerable (Rassi et al. 2001). Approximately three-quarters (74 species) of Finnish butterflies with permanent populations inhabit agricultural landscapes (Pitkänen et al. 2001). Species preferring meadows have declined, whereas species preferring field verges or forest edges and clearings have mostly increased (Kuussaari et al. 2005). The majority of butterfly species and virtually all endangered and declining species in Finland are likely to form metapopulations (Hanski & Kuussaari 1995). Metapopulations are collections of subpopulations, which persist in a balance between stochastic extinctions of subpopulations and the establishment of new subpopulations in empty habitat patches (Hanski & Gilpin 1991).

The ecology of the other Macrolepidoptera species is not as well known as that of butterflies (Scoble 1992). Many of these species form metapopulations and their basic ecology is very similar to that of butterflies (Nieminen 1996). The majority of approximately 840 species in Finland are strictly night active, but more than one hundred species are constantly recorded during the daytime (Saarinen & Jantunen 2003). These species represent a continuum from purely day-active to those flying only as a result of being disturbed, these mostly being geometrid moths. The names of the Lepidoptera species used are according to the checklist by Kullberg et al. (2002).

Lepidoptera form a significant proportion of the world's herbivorous insects and in the case of many species the larvae are specialized on certain host plants (Strong et al. 1984). Additionally, nectar is an important resource for the adult stage of many Lepidoptera species, butterflies in particular (Murphy 1983, Scoble 1992). Thus, the quality and structure of the vegetation playing an important role for Lepidoptera was also studied for the thesis. Plants themselves also form an integral part of the semi-natural grassland and road verge communities. The ecology of vascular plants on road verges has been widely studied, e.g. by Persson (1995) and Schaffers (2000). The nomenclature and taxonomy of vascular plants used in this thesis are according to Hämet-Ahti et al. (1998).
In this thesis, special attention is paid to meadow species. Butterflies were divided into species typical of 1) meadows, 2) forest edges and clearings, and 3) field margins, using the classification by Pitkänen et al. (2001). Correspondingly, moths were divided into meadow species and other species, mainly in accordance with Kuussaari et al. (2003). In the case of the vascular plants, positive indicators of semi-natural grasslands ('grassland species') and negative indicators ('weeds') were mainly separated on the basis of the grouping used by Pykälä (2001).

2.3. Vegetation studies

Vegetation studies (I and VI) were based on sample plot data. The abundance of each species on the 1 m x 1 m plot was estimated by projection cover using a percentage scale from 0 to 100. Plots were placed in the middle of the verge between the road edge and ditch. On the narrowest verges plots were partially located on both sides of the ditch.

A comparison of the vegetation between four different types of roadside environments with different traffic densities and widths of road and verge was carried out in 85 sites located in nine areas along Highway 6 (I). The studies were conducted in June and July 2002-2003, before the sites were mown. The four types of roadside environments consisted of intersection areas (17 sites), highway verges (17), urban road verges (17), and rural road verges (17). The two groups used in the comparison included field environments (9 sites consisting of four field verge, and five abandoned field, sites) and grasslands (8 sites consisting of three non-managed, two mown, and three grazed, sites). In each site ten sample plots were systematically located at 25 m intervals along a 250 m transect. In non-linear habitats, the transect of sample plots was projected through the area. Species composition and the number and cover of grassland species were compared between the six groups. Traffic intensity and speed, road width, verge age and width, soil pH, Na, Ca, K, N_{tot}, P_{tot} and C_{org} content of the soil, sandiness and humus content, percentage of fields and forests in the adjacent environment, and the mowing regime, were measured or assessed as the potential factors affecting the flora of roadside environments.

The effect of lupin on other vascular plants was studied on 15 road verge sites. Half of each site represented a lupin-invaded, and the rest a non-lupin, verge with either no lupins or only sporadic stands (VI). The two parts were located adjacent to each other on the same side of the road and ten sample plots were placed symmetrically on the lupin (5 plots), and non-lupin (5 plots), parts. The distance between plots ranged between 3 – 20 m, depending on the length of the study area. The plant species composition was surveyed in July 2005, before the verges were mown. The average vegetation height in the plots, total species richness (i.e. number of species), species richness/m², Shannon's diversity index, lupin cover, cover of other species, and species richness and cover of grassland species, weed species, low growing species (average height < 20 cm), medium height species (20-50 cm) and tall species (> 50 cm) were compared between the lupin and non-lupin parts.

2.4. Lepidoptera transect counts

Data on Lepidoptera was collected using transect counts, where all individuals within a 5 m x 5 m square in front of the recorder were noted (Pollard & Yates 1993). The length of the transect in each site was 250 m, except in the lupin study (VI). In wide verges the transects covered the inner part of the verge only, whereas in narrow verges the ditch and outer part of the verge were also included. All transect counts were conducted weekly from the beginning of June to the end of August. This range was sufficient to cover the seasonal activity in butterflies, but may have excluded some spring flying moths, such as *Archiearisis parthenias*. During each census the temperature, wind speed (1–6, Beaufort scale) and the sunshine percentage (0%, 25%, 50%, 75%, 100%) were measured.
or estimated. The starting time of the censuses varied between 9:00 and 17:30.

Lepidoptera communities on different roadside environments were studied in 51 sites located in nine areas along Highway 6 (II). The sites represented the verges of highways (17 sites), urban roads (17) and rural roads (17). For each road type, 10 sites were studied in 2002 and seven sites in 2003. A comparison of the Lepidoptera communities between intersections and other open grasslands was carried out in nine intersection areas (17 sites) along Highway 6 and nine control areas (17), making a total of 34 study sites (III). The control sites represented field environments (9 sites) and grasslands (8). In both intersections and control areas ten sites were censused in 2002 and seven sites in 2003. All 85 sites used in two transect count studies (II-III) coincided with those used in the vascular plant study (I).

For the thesis, the original data of the two studies (II and III) was combined and reanalysed, using field habitats and grasslands as groups of comparison for the four roadside environments. First, MANOVA was performed using the GLM procedure of the SAS (SAS Institute 1996) to test the overall effect of the habitat group among the response variables, including abundance, species richness and diversity of butterflies and moths, and abundance and species richness of meadow species. Differences in the habitat groups on each response variable were subsequently investigated by mixed-effects ANOVAs conducted by the MIXED procedure of the SAS (SAS Institute 1996). The group was set as a fixed-effect variable, whereas the study area (sites in the vicinity of the same intersection) and the study year were set as the random-effect variables. Tukey pairwise comparison tests were undertaken where significant differences (p < 0.05) were found. The square root transformation was conducted where appropriate to improve the normality.

Three commonly used mowing regimes on road verges were compared in 54 study sites representing the mid summer mown verges (18 sites), the late summer mown verges (18) and the partially mown verges (18) (IV). In the last group at least part of the verge (and transect) remained unmown throughout the study season. The sites included highway verges (n = 19), urban road verges (n = 26) and paved rural road verges (n = 9). Sites were censused during a 3-year period, each site being studied in one year only, viz. 15 sites in 2002, nine sites in 2003, and 30 sites in 2004.

In studies II, III and IV, the compared Lepidoptera variables included species richness (total number of species observed during season), the total abundance (total number of individuals recorded) and Shannon's diversity index. Species assemblages were compared with multivariate methods. The following variables possibly influencing the Lepidoptera in roadside environments were measured or assessed in one or several studies: road width, traffic speed and density, verge width and age, area of intersection, soil moisture and structure (humus, clay, sand), soil pH and the Na, Ca, K, N_\text{tot}, P_\text{tot} content of the soil. In addition, vegetation variables possibly influencing the Lepidoptera in roadside environments were measured or estimated, these being the number of plant or nectar species, the abundance of flowering plants, nectar and host plants, vegetation height, abundance of positive or negative indicators of semi-natural grasslands and origin of the vegetation (artificially sown/naturally established).
uniform in structure, being surrounded by deep sandy slopes with young pine trees. Approximately 10 m wide verges had been constructed using imported top soil and sown vegetation, but native species had also arrived with the soil or from the surrounding environment. In order to study the effect of patches of unmown vegetation, i.e. 'nectar refugia', the area was divided into six 250 m long transects (Fig. 1). These represented two management types: the mown patches were normally subjected to total mowing in mid and late summer in 2004, whereas the refugia were subjected to only partial mowing (a narrow strip next to the road) in mid summer and total mowing in late summer in 2004. Both transect groups were totally mown in mid and late summer in 2005. The weekly transect counts were conducted in June, July and August in the middle of the verge (not covering the partial mown area) during 2004 and 2005. Weekly transect counts were also conducted on a local semi-natural grassland.

Lepidoptera communities on the lupin invaded and non-invaded adjacent verges were studied on 15 road verge transects varying between 100-560 m in length (VI). In each transect, the first half represented lupin invaded, and the second half non-invaded, verge. It was assumed that the lupin stands were random colonisations. Weekly transect counts were conducted between late May and late August 2005.

2.5. Emergence traps

The effect of short term change in the mowing regime on Lepidoptera reproduction was studied with emergence traps (data given in thesis). Tent-shaped emergence traps made of light curtain covered 2 m² (1 m x 2 m). These were pitched so that the highest part was approximately 1 m above the soil. Dichlorvos (DDVP) poison tablets were used in the containers that collected the emerging insects. Traps were located on the refugia and mown verges along a 4-lane motorway described in section 2.4. In 2005, i.e. the summer following the change in the mowing regime, six emergence traps were placed in refugia (n = 3) and mown (n = 3) patches (Fig. 1). Three additional traps were located in local semi-natural grassland representing similar mesic conditions. All traps were emptied on a weekly basis between early June and early August. In addition to the Lepidoptera, the abundance of other insects representing Coleoptera, Heteroptera, Homoptera and Hymenoptera, among others, was also recorded.

2.6. Behaviour and movement of butterflies

Information on Lepidoptera behaviour was collected on lupin invaded, and non-invaded, verges (VI). The behaviour, classified as flying, nectaring, basking or hiding, of each individual was recorded at first sight. In addition, all behaviour relating to lupin, such as nectaring on lupin flowers or basking on lupin, was recorded separately.

The Mark-Release-Recapture (MRR) study on the movement of *Aphantopus hyperantus* was conducted in an approximately 8.6 ha

![](image.png) **Figure 1.** Location of refugia and mown patches and emergence traps in the study area located along the Imatra motorway.
study area located around the Vesivalo intersection (V). The 2.2 km long and 5 m wide line transect running through the study area was composed of 13 sections ranging between 80 – 280 m in length and differing in management and habitat type. Individuals were netted, marked on the wings, released and recaptured on each non-rainy day between 26 June and 8 August 2003.

3. RESULTS AND DISCUSSION

3.1. Vascular plants in roadside environments

3.1.1. Weeds versus grassland species

The quality of the vegetation in roadside environments was highly variable (I), including species typical to semi-natural grasslands, fields, ruderal areas, gardens, forests, bogs and the shores of lakes and seas. Weeds predominated on most roadside environments and the weed species cover was 19–207 times higher than the grassland species cover. The most abundant weeds in roadside environments were *Taraxacum* spp., *Cirsium arvense*, *Elymus repens*, *Anthriscus sylvestris* and *Artemisia vulgaris*, most of them being tall-growing species. The results are in line with Tikka (2001), who previously concluded that road verge vegetation is characterised by both occasionally occurring cultivated species and species typical to disturbed areas. In Scotland, the same was true only for the frequently disturbed inner edge of the road verges, which received the highest deposits of nitrogen and salt (Truscott et al. 2005).

However, many grassland species managed to grow in roadside environments. The most common ones included *Campanula glomerata*, *Lathyrus pratensis*, *Pimpinella saxifraga* and *Vicia cracca* (I). Altogether 37 grassland species were found in road verges and intersections and all roadside environments included sites with several good indicators. No endangered species were found, however, despite 20% of the 225 endangered vascular plant species listed in 1997 in Finland having been recorded somewhere on road verges or ditches (Ryttäri & Kettunen 1997). Nevertheless, our results confirm that in northern Europe road verges do serve habitats for plant species that are grassland specialists (Hæggström 2005, Hovd & Skogen 2005, Cousins 2006).

3.1.2. Roadside environments versus grasslands and field environments

The mean number and the total cover of grassland species in the roadside environments were slightly lower compared to the semi-natural grasslands, but higher compared to field environments (I). However, the only significant difference was the lower number of weed species in grasslands compared to the urban and rural road verges. The small differences in the number and cover of grassland species were probably a result of the broad variation among the road verge and intersection sites. The majority of the roadside environments had a lower species richness compared to the grasslands but the best sites in all roadside environments supported a higher number of grassland species than the average semi-natural grasslands. Thus, roadside environments in general are not likely to replace the disappearing semi-natural grasslands, as also noted by Norderhaug et al. (2000) and Tikka (2001). However, the roadside environments offer valuable habitats, or 'rescue sites' to many grassland species and their role is more important in the modern compared to the traditional landscape (Cousins & Eriksson 2001, Hæggström 2005, Cousins 2006).

Both the number and cover of grassland plant species were slightly higher in roadside environments than in the field environments, although the differences were not significant. Field environments lacked high-quality sites having a higher number of grassland species than average semi-natural grasslands, which were prevalent in all four roadside environments. The inadequate management combined with the herbicides used earlier or on adjacent fields may explain the poorer quality of field environments. Hovd and Sko-
gen (2005) found more grassland plant species growing on road verges than in field environments, but Cousins (2006) concluded that the persistence of grassland species may be higher in more isolated midfield islets compared to the road verges.

There were no significant differences in the vegetation characteristics between the four roadside environments, but the intersections and urban road verges had the lowest number, and urban road verges the lowest cover, of grassland species (I). In the case of intersections, the likely explanation is the young age and for urban road verges the repeated mowings, which already begin in early summer. The highest number of grassland species among roadside environments was found on the rural road and highway verges, while the cover of grassland species was highest along highway verges.

3.1.3. Factors associated with the grassland flora in roadside environments

Most of the grassland species seemed to favour old sites characterised by a nutrient poor and sandy soil. Old age means a lack of disturbance to soil and a long continuity of regular grassland management, which is also essential for the development of the species rich semi-natural grasslands (Kull & Zobel 1991, Cousins & Eriksson 2002). The development of valuable semi-natural grasslands generally requires continuous management for at least 50, but mostly for over 100, years (Vainio et al. 2001). Due to the present management and other disturbances, this long history is rare among roadside communities.

Sandiness may indicate the other important feature of valuable grasslands, namely the nutrient poor soil. However, Jylhäkan-gas and Esala (2002) concluded that the soil on Finnish semi-natural grasslands was characterised by a high humus content but low nutrient levels. Interestingly, the soil in the studied grasslands was not particularly nutrient-poor compared to the roadside environments (I). This possibly reflects the history of poor management in local semi-natural grasslands during the last decade and the recent removal of top soil in the young roadside environments.

3.2. Lepidoptera in roadside environments

3.2.1. Species composition

A total of 54 species and 16,766 individuals of butterflies were observed in transect counts conducted on road verges and intersections (II-IV, VI and unpublished study on nectar refugia). The most abundant butterfly species recorded in roadside environments included *Aphantopus hyperantus* (28% of all butterfly individuals) and *Thymelicus lineola* (21%). Correspondingly, a total of 83 species and 14,564 individuals of moths were observed in roadside environments, the most abundant species being *Scototeptryx chenopodiata* (45%), *Euclidia glyphis* (21%) and *Scopula immorata* (8%). Some threatened Lepidoptera species (Rassi et al. 2001) were also recorded in road verges and intersections (II-VI): the butterflies *Glaucopsyche alexis* (VU) and *Euphydryas aurinia* (VU) and the hawk-moth *Hemaris tityus* (VU). In addition, *Lycaena dispar* (EN), *Glaucopsyche arion* (CR) and *Cupido minimus* (EN) are among endangered butterfly species recently recorded as breeding or having permanent habitat patches on road verges in South Karelia (Saarinen & Jantunen 2002, Jantunen 2005, Jantunen et al. 2005).

Meadow species were common in roadside environments. 74% of butterfly individuals observed on road verges and intersections belonged to meadow species, while the majority of the recorded species represented either meadow (39%) or forest edge (41%) species and the proportion of field verge species (17%) was rather small (II-IV, VI and unpublished study on nectar refugia). The moth individuals on road verges and intersections were also dominated by meadow species (II-IV). The result indicates that meadow Lepidoptera species, in particular, find nectar and/or host plants in roadside environments. The proportions of species reflect more the classification itself, as 46% of the species prefer meadows, 43%
As road verges are commonly bordered by forests and fields, species typical to these habitats are also present. In fact, the majority of road verges could also be defined either as field or forest edges. The difference is, however, that all field and forest edges are not under the annual mowing management, in contrast to road verges.

3.2.2. Roadside environments versus grasslands and field environments

According to MANOVA, the overall effect of habitat group among all response variables was significant (Wilk's lambda, p < 0.0001). Thus, separate ANOVAs were conducted on each response variable (Figs. 2-6). Grasslands had a higher butterfly abundance, species richness and diversity compared to any roadside environment, but significant differences resulted only when compared to urban road verges (abundance; Fig. 2) or intersections (abundance, species richness and diversity; Figs. 2-4). Also, the meadow butterfly abundance and species richness was higher in grasslands compared to roadside environments, but no significant differences resulted in pairwise comparisons (Figs. 5-6). Sites having a higher meadow species richness or abundance than average grassland were recorded in all roadside environments. It thus seems that roadside environments can offer alterna-

Figure 2. Average (+SE) butterfly and moth abundance (per 250 m) in intersections (n = 17), highway verges (n = 17), urban road verges (n = 17), rural road verges (n = 17), field environments (n = 9) and grasslands (n = 8). Results of ANOVA and Tukey pairwise comparisons tests are reported above bars; groups with separate letters a, b and c differ significantly (p < 0.05).

Figure 3. Average (+SE) butterfly and moth species richness (per 250 m) in intersections (n = 17), highway verges (n = 17), urban road verges (n = 17), rural road verges (n = 17), field environments (n = 9) and grasslands (n = 8). Results of ANOVA and Tukey pairwise comparisons tests are reported above bars; groups with separate letters a and b differ significantly (p < 0.05).

Figure 4. Average (+SE) butterfly and moth diversity in intersections (n = 17), highway verges (n = 17), urban road verges (n = 17), rural road verges (n = 17), field environments (n = 9) and grasslands (n = 8). Results of ANOVA and Tukey pairwise comparisons tests are reported above bars; groups with separate letters a, b and c differ significantly (p < 0.05).
tive habitats to many meadow butterflies and high-quality sites can be found along all types of roadside environments, but the majority of sites in roadside environments are not as high quality as semi-natural grasslands.

In contrast to butterflies, the average abundance of both all moths and meadow moths alone was higher in intersections, highway verges and urban road verges compared to grasslands, although these differences were not statistically significant (Figs. 2 and 5). On the other hand, the species richness and diversity of moths and the species richness of meadow moths were higher in grasslands compared to any roadside environment (Figs. 3-4 and 6). However, these differences were significant only when diversity in grasslands was compared to intersections, highway and urban road verges. Thus, roadside environments do offer good habitats to some meadow moths, but the majority of roadside environments may be of lower quality than the semi-natural grasslands.

Differences in Lepidoptera abundance, species richness and diversity between field and roadside environments were generally small, suggesting that both serve as important alternative habitats to meadow species (Figs. 2-6). The role of uncultivated agricultural habitats for butterflies has been studied more thoroughly than the roadside environments (e.g. Sparks & Parish 1995, de Snoo et al. 1998, Dover & Sparks 2000, Clausen et al. 2001, Kuussaari & Heliölä 2004). Ouin et al. (2004) compared butterfly behaviour in road verges and different types of agricultural environments and suggested that these elements can fulfill different ecological requirements for *Maniola jurtina*.

### 3.2.3. Different types of roadside environments as habitats for Lepidoptera

A comparison of the three road verge types and intersections showed that rural road verges had higher butterfly abundance compared to urban road verges, while rural road and highway verges had higher butterfly species richness compared to intersections (Figs. 2-3). Butterfly diversity, on the other hand, was higher in highway verges compared to intersections (Fig. 4).

By contrast, the (meadow) moths were more abundant on highway verges compared to rural road verges (Figs. 2 and 5). The high abundance of moths on certain intersections,
highway and urban road verges was mainly a result of two common species, *Scototephyx chenopodiata* and *Euclidia glyphica*, which are classified as meadow species but are abundant in various other habitats as well. Even when these species are omitted from the analysis of meadow moth abundances, the differences between the groups remain highly significant (p < 0.0001), the highways having higher abundances compared to rural roads, intersections, urban roads and field environments but not compared to grasslands. No differences resulted in the (meadow) moth species richness among the four types of roadside environments (Figs. 3 and 6). Moth diversity, on the other hand, was higher on rural road and highway verges compared to intersections (Fig. 4).

Intersections were characterised by young age and low vegetation height (I, III), while highway verges had wide verges and high soil pH (I, II). By contrast, urban road verges were characterised by high mowing intensity leading to low vegetation height (I, II), whereas rural road verges were narrow, had low soil pH, tall vegetation and high cover in the surrounding fields (I, II).

These results are not in line with those from agricultural landscapes, where butterflies had higher abundances in non-linear habitats compared to linear ones (Clausen et al. 2001, Kuussaari & Helioä 2004). On the other hand, the low species richness of intersections is in line with previous studies where the high proportion of urban elements, such as roads, in the surrounding landscape has been associated with the low species richness (Kitahara et al. 2000, Söderstrom et al. 2001) and abundance of butterflies (Blair & Launer 1997). In this study, however, the young age of intersections, leading to poor nutrient status on recently exposed soil and low vegetation height, was probably the most likely explanation to their low diversity. This was contrasted by the high Lepidoptera diversity in the oldest intersections studied (III).

Furthermore, the proportion of individuals belonging to meadow butterfly species was high in roadside environments with the least individuals, i.e. intersections (79%) and urban road verges (77%). The same proportions were 77% in grasslands, 68% in highway and rural road verges and 60% in field environments. The forest edge species, in particular, appeared in low numbers in the intersections, where the cover of surrounding forests was low (III). The same was not true for moths, where a high proportion of meadow moth individuals (> 90%) was recorded in intersections, highway and urban road verges and < 85% in rural road verges, field environments and grasslands, most likely due to the lesser dominance of the *S. chenopodiata* and *E. glyphica* in the latter groups.

### 3.2.4. Factors associated with Lepidoptera abundance and species richness in roadside environments

Nectar abundance was positively associated with butterfly abundance in roadside environments (II, IV). Intensive mowing throughout the summer decreased the availability of nectar, which may explain the low butterfly abundance on many urban road verges (II). The importance of nectar to butterflies has been observed both in road verges (Gerell 1997) and other linear habitats (e.g. Dover & Sparks 2000, Clausen et al. 2001, Pywell et al. 2004, Croxton et al. 2005). Nectar influences the microdistribution of butterflies in their habitat (Loertsch et al. 1995) and the high abundance of both butterflies and nectar on rural road verges suggests that butterflies have concentrated on these narrow verges. In fact, Ouin et al. (2004) suggested that in agricultural landscapes road verges serve mainly as nectaring areas for the studied meadow butterfly species, while other areas are used for reproduction. Despite this, nectar plays an important role in butterfly reproduction, as it increases the longevity and fecundity of individuals (Murphy et al. 1983).

Tall vegetation was positively associated with moth abundance in roadside environments (II), probably because it offers more shelter and hiding places for many nocturnal
moths. Tall vegetation could also offer more resources for feeding larvae, as long as the particular host plants were available. The vegetation height in roadside environments can depend on the soil structure, species pool and mowing regime.

High plant species richness was positively associated with Lepidoptera species richness on road verges (II) and intersections (III). The higher the plant species richness, the higher the number of potential host plant species and the higher the number of potential nectar plant species throughout the summer. However, when the species richness of potential host plants were calculated, no association with Lepidoptera abundance or species richness was observed (IV). The lack of the right host plant was probably not a limiting factor to the presence of most recorded butterflies in roadside environments, as their host plants are typical to road verges and intersections in the region (I). Previously Vessby et al. (2002) concluded that grassland plant diversity was not correlated with butterfly species richness. Although there may not be a direct relationship between plant and butterfly species richness, both probably respond to similar environmental factors (Hawkins & Porter 2003). The high plant species richness does not necessarily represent the high vegetation quality either. However, the abundance of weeds (i.e. negative plant indicators) was negatively associated with butterfly species richness (IV). On the other hand, artificial origin of the vegetation, including imported top soil and sown grasses, was negatively associated with the species richness of all Lepidoptera in intersections (III). Roadside environments with a high abundance of weed species and artificial vegetation may be of lesser value to Lepidoptera, because weeds only include a few important butterfly host plants (*Urtica dioica* and some grasses), while sown seed mixes consist almost exclusively of grasses with no nectar value to adult butterflies.

The forest cover in the surrounding environment was positively associated with Lepidoptera species richness (II, IV) and it probably affected the butterfly species composition (II, III). A forest edge has a positive sheltering and diversifying effect on butterfly species richness (Gerell 1997, Saarinen 2002). Butterfly species preferring forest edges represent a large proportion of all butterfly species in agricultural environments (Pitkänen et al. 2001) and are more likely to be found on road verges bordered by forests.

The verge width was positively associated with butterfly diversity (II) and species richness (IV). Wide verges are likely to offer a greater variety of breeding habitats for butterflies (Munguira & Thomas 1992). The wider the verge, the larger the habitat patches can be. Large patches, in turn, are more likely to be colonised (Hill et al. 1996, Wahlberg et al. 2002). Also old habitat age was associated with high species richness in intersections (III). On recently disturbed roadside environments the barren soil can be exposed or covered with top soil rich in nutrients. Species diversity in both plants and insects increases in the course of time (Steffan-Dewenter & Tscharntke 1997), explaining the higher species richness in older sites. Diverse communities of meadow plants may eventually develop in roadside environments (Hovd & Skogen 2005) but thick nutrient rich top soil and sown seed mixes probably slow down the process.

Several of the environmental factors mentioned above are impossible or difficult and expensive to change in order to improve the quality of roadside environments as Lepidoptera habitats. These include soil structure, width and topography of the verge, the species pool in the surrounding landscape or seedbank and the quality of the surrounding landscape. Nevertheless, several factors could be improved, if only the attitude of both road officials and the public at large would allow it. In the construction phase, the establishment of lawns by spreading a thick nutrient-rich top soil and non-native seed mixes should be avoided. Instead, more roadside environments could be dedicated to the native grassland species even though natural communities may take longer to establish than lawns. When intersections are being built, original top soil should be left
untouched wherever possible. Variation in topography can be created to obtain sunny and sheltered slopes favourable to butterflies (Morris et al. 1994). Shelter can also be created by planting or leaving groups of trees untouched. After the construction, the quality of roadside environments can be improved mainly by avoiding disturbances and adjusting the mowing management.

3.3. The effect of mowing

3.3.1. Timing and intensity

When the three commonly applied mowing regimes in Finnish roadside environments, viz. mid summer, late summer and partial mowing, regimes were compared, the mid summer mown verges had a lower species richness and abundance of butterflies, and a lower species richness and diversity of moths, compared to the verges under the other two regimes (IV). No differences were observed between the late summer and partially mown verges. Similar results were obtained in the MRR study of *A. hyperantus* (V), with the lowest population densities in mid-summer mown verges.

The decline in butterfly abundance after mid summer mowing was mainly a result of two factors that are directly dependent on the mowing: first, the decrease in nectar (Erhardt 1985, Gerell 1997) and second, the breakdown of the vegetation structure (Erhardt 1985) leading to a destruction or conversion of host plants unsuitable for egg-laying at a time when the majority of individuals reach their adult stage. Despite this, the mid summer mowing may also have some positive effects on Lepidoptera, if the area is not mown again in late summer (IV). No differences were observed between the late summer and partially mown verges. Similar results were obtained in the MRR study of *A. hyperantus* (V), with the lowest population densities in mid-summer mown verges.

The adverse effects of mowing during the peak flight period of butterflies has been demonstrated earlier in several studies (Munguira & Thomas 1992, Feber et al. 1996, Gerell 1997, Hogsden & Hutchinson 2004). More interesting was the high Lepidoptera species richness, diversity and abundance in the partially mown verges. This can be explained by the lowest mowing intensity and the highest variation in the timing and frequency of mowing. A time span of approximately three years since the last total mowing on some partially mown verges allows communities to recover from the disturbance. The partial mowing leaves untouched resources such as nectar, host plants and hiding places for adults throughout the flying season. In addition, mowing postpones the flowering and the mid summer mown strip may provide nectar later in the summer. The partial mowing may also destroy fewer Lepidoptera offspring than the total mowing and it leaves untouched resources in the vicinity for the larvae surviving from the mowing, if they are capable of moving on to a new food plant.

3.3.2. Nectar refugia

Besides partial mowing (IV), variety can be created by leaving nectar refugia, i.e. patches of unmown vegetation along the mid summer mown verges. Along the motorway in Imatra, the three patches of nectar refugia were associated with a butterfly abundance comparable to a transect in the semi-natural grassland, while the adjacent normally mown patches had low abundances of individuals throughout the season (Fig. 7). Due to the low number of studied patches, however, the differences in Lepidoptera abundance or species richness between the two mowing regimes were not significant (Table 2). In the following season when all patches were mown uniformly, no differences resulted in transect counts (Table 2, Fig. 7).

The high abundance of adult Lepidoptera on nectar refugia does not necessarily indicate the suitability of the area for reproduction. In fact, the results suggest that the short term change in mowing regime has
short term effects only, and no effect on adult Lepidoptera abundances via enhanced reproduction on nectar refugia was recorded in the following summer. Three explanations are possible: 1) despite the high abundance of butterflies on nectar refugia, butterflies did not lay eggs in these areas, 2) the mandatory late summer mowing destroyed the offspring in refugia patches, or 3) butterfly reproduction is more successful in nectar refugia than on normally mown verges, but the emerging individuals spread to the surrounding area and the differences in adult numbers even out in the following season.

Emergence traps placed on the nectar refugia and the adjacent normally mown patches in the summer following the change in mowing regime indicated no differences in Lepidoptera reproduction between the two treatments. In general, traps produced a low abundance of Lepidoptera individuals (Table 2). Butterflies were not recorded, while one moth individual emerged in both refugia and mown verges. No differences in other insect groups resulted either.

At the same time, emergence traps on the local semi-natural grassland caught six individuals representing five moth species of the families Lasiocampidae, Geometridae and Noctuidae. Although the data is small and statistical comparison impossible, a six-fold abundance in grassland vs. motorway verges per trapped surface area suggests that young road verges are mainly sources of nectar for butterflies and hiding places for other species, but that they are of less importance to Macrolepidoptera reproduction. Different life stages may need different elements of the landscape, thus requiring individuals to travel between patches (Dunning et al. 1992). In the case of butterflies, young, but nectar rich, road verges probably attracted individuals from the surrounding environment, but
this does not explain why the moths were also abundant on the nectar refugia. The high abundance of other insects captured suggested that the trapping method functioned well. Possibly with larger traps or higher replication it would be possible to reveal the value of these areas to Lepidoptera reproduction.

According to a sweep net study conducted on old late summer and mid summer mown verges, areas under both of these mowing regimes can serve as reproduction habitats for at least some Lepidoptera species (unpublished data). A total of 25 larvae representing 12 taxa of Macrolepidoptera were netted in May 2006, from 10 verge sites mown the previous August (swept surface 100 m$^2$ in each). The butterflies *Albulina*

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**Table 2. Results of the field experiment on short term change in the mowing regime. 2004 = year of experiment, 2005 = year after the experiment. Transect counts of refugia (n = 3), normally mown verges (n = 3) and grassland (n = 1). Emergence traps on refugia (n = 3), normally mown verges (n = 3) and grassland (n = 3). Tests with paired samples t-test.**

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<th>Refugia SD</th>
<th>Mown Average</th>
<th>Mown SD</th>
<th>t-test p$^a$</th>
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$^a$none of the differences are significant after sequential Bonferroni correction (significance level 0.10), $^b$cannot be computed because the standard error of the difference is 0.
optilete and Plebejus argus/idas, along with some geometrid, arctiid, noctuid and burnet moths were recorded. Furthermore, 95 larvae representing 10 taxons of geometrid and noctuid moths were recorded in July 2006 from 10 verges (100 m² each) mown 3 or 4 weeks before. Although it is known that eggs, larvae and pupae are sensitive to mowing (Courtney & Duggan 1983, Erhardt 1985, Feber et al. 1996) there are probably differences between the species in this respect (Swengel 1995), as suggested by this data.

3.4. Behaviour and movement of Lepidoptera on road verges

3.4.1. What do Lepidoptera do on road verges?

Butterfly behaviour on road verges (not invaded by lupin) was characterised by flying (65% of individuals), nectaring (20%), and basking (15%) (VI). Flying may be habitat-related behaviour, representing, for example, patrolling or searching for the next nectar or host plant, but it may also indicate that the individual is just passing by. A high number of individuals flying may also be the result of disturbance from traffic or the counting. The results indicate that road verges are frequently used as nectaring areas. In French road verges, nectaring was the most common behaviour expressed by individuals of Maniola jurtina, measured against time (Ouin et al. 2004). Moth behaviour was dominated by hiding in the vegetation (86% of individuals), but also included flying (10%), nectaring (2%), and basking (2%).

A behavioural trait verifying that adults accept road verges as breeding habitats as well would be egg laying. Signs of this were not observed during transect counts, which are not optimal for the purpose. However, records of butterflies laying eggs in roadside environments have been obtained on other occasions. In a study where the movement paths of three meadow butterflies were recorded in 2005, two satyrid butterflies, Aphantopus hyperantus and Coenonympha glycerion, did not lay eggs while being followed, whereas the third species, Lycaena virgaureae, frequently oviposited on Rumex acetosella on both road verges and habitat patches (unpublished data). During the field studies between 2002 and 2005 (II-IV), Papilio machaon and Lycaena hippothoe were observed to lay eggs on host plants growing in roadside environments. Eggs and small larvae of Lycaena dispar were also found close to a busy highway edge.

3.4.2. Are roads barriers and verges corridors?

Although the majority of A. hyperantus individuals were sedentary, the proportion of recaptured individuals which had crossed one or more roads was 23% (V). 10% of all recaptured individuals had crossed the 11 m wide highway. The MRR study also suggested that a dense network of roads may decrease the movement of this species. This effect can be both behavioural (the individual refuses to cross an unsuitable area) or physical, if the traffic and wind gusts prevent crossings (Dennis 1986, Munguira & Thomas 1992).

Although the roads do not isolate the A. hyperantus populations, thereby forming a barrier to the gene flow of the species, wider roads or those built on high embankments may have a stronger barrier effect. Neither can the results be directly generalised to all butterfly species, which can have various reactions to different barriers and boundaries in agricultural landscapes, such as roads, walls, trees or shade (Fjellstad 1998, Norberg et al. 2002). For example, a lower proportion of butterflies of the family Lycaenidae crossed the road compared to other butterfly species (Fjellstad 1998). Roads have also been reported to restrict the movements of bumblebees (Bhattacharya et al. 2003) and some small sedentary butterfly species, while larger and more mobile butterfly species are less affected (Munguira & Thomas 1992, Fjellstad 1998, Ries & Debinski 2001).

The proportion of highway crossings was
the highest and the proportion of sedentary individuals the lowest on mid summer mown verges (V). In other words, the individuals of *A. hyperantus* in the high-quality habitats were less likely to take the risky decision to enter the matrix habitat and cross the road. Thus, individuals flying to, or emerging from, mid summer mown verges are likely to leave the verge and find nectarating and reproduction areas elsewhere. This may also lead to a lower number of laid eggs and emerging individuals the following season. In conformity with this, Ries et al. (2001) reported a relatively higher traffic-induced mortality and a higher proportion of butterflies crossing roads along road verges planted with non-native grasses compared to verges with native prairie vegetation. The individuals were also more likely to exit linear habitats than non-linear habitats (V). On linear verge habitats the edge-to-size ratio (ESR) is high compared to non-linear habitats and should lead to higher emigration from linear patches (Stamps et al. 1987).

Movement along boundaries is common in butterflies and the barrier and corridor functions of a certain landscape element may be inseparable (Fjellstad 1998). In forested landscapes open corridors facilitate the dispersal of *A. hyperantus* (Sutcliffe & Thomas 1996) and other butterfly species (Haddad 1999a) from one open habitat patch to another. Species reactions depend on the behaviour of individuals at habitat boundaries (Haddad 1999b). For example, butterfly individuals, which 'reflect' off boundaries between a habitat patch and forest rather than continue to enter the forest, will move a longer distance in the habitat patch, which increases the probability of encountering the corridor opening (Haddad 1999b). This might be, for example, a road verge running next to the habitat patch and continuing through the forest. In the same way, biased turnings at the road vs. verge, or verge vs. forest, boundaries may direct the movements along the verge corridor (Haddad 1999b). According to Fjellstad (1998), both road and trees created a similar boundary to butterflies, where approaching individuals frequently turned back. Even if the road itself does not direct the movements, the forest edge on the other side of the road may do so. Therefore, it is likely that road verges, too, serve as corridors for some butterfly species in forest dominated landscapes.

As far as *A. hyperantus* was concerned, the corridor effect of road verges was difficult to observe in a heterogenous landscape consisting mostly of elements other than forests (V). Any generalisation on the corridor effect is also difficult, as only one habitat patch was unconnected by verges to another. However, we found evidence that there were more movements among the sections connected by a verge than in any other type of section and that linear habitats encouraged individuals to leave more often than non-linear habitats. It is possible that intensively mown road verges, if not suitable as reproduction habitats for the *A. hyperantus* individuals, may at least form corridors, but further research on this matter is needed.

3.5. Invasive *Lupinus polyphyllus* as a threat to grassland species

The vascular plant species richness and diversity and cover of species other than lupin were lower in lupin invaded road verges compared to the adjacent non-invaded road verges (VI). The adverse effect of lupin was particularly severe for the low growing (< 20 cm) species. It is likely that the lupin has filled the unused space above the original verge vegetation and the low growing species have been outcompeted due to the shading. Although the invasion of nitrogen-fixing plants may increase the originally low species richness on barren soils by encouraging further invasive species to settle (Vitousek & Walker 1989), no such effect was observed.

Consequently, the decline in cover and variety of possible host and nectar plants had an adverse effect on Lepidoptera, the abundance of butterflies in particular (VI). The higher the lupin cover, the lower the number of butterfly individuals found on the lupin
verges compared to the adjacent non-lupin verges. Furthermore, individuals in flight at
different times of the summer and during the
different phases of lupin growth, from
vegetative growth in early summer to flow-
ering in mid summer and withering in late
summer, were all adversely affected. Most
probably lupin did not provide significant
food resources for any stages of Lepido-
ptera. In lupin invaded verges the butter-
flies found nectar in plants growing in the
gaps within the lupin stands, explaining
why the nectaring decreased as the cover of
lupin approached 100%. The discrepancy
between the high cover of lupin and the
few visitors to lupin flowers suggests that
the lupin is a poor nectar plant or does not
serve nectar, and the few butterfly and
moth visits to its flowers were abortive
attempts at obtaining nectar. On the other
hand, the lupin canopy grows tall in the
early summer and provides more hiding
places for the less active moths compared
to the adjacent lower vegetation (VI). The
rapid withering of lupin might explain the
decline of moths on lupin verges in the late
summer.

Although the lupin may have positive
effects on some species, e.g. bumblebees
and other insects collecting lupin pollen
(Söderman & Leinonen 2003), its uncon-
trolled spread poses a real threat to
meadow plant and Lepidoptera species
living on road verge environments. Lupin
decreases the area of potential alternative
habitat for the vascular plants of semi-
natural grasslands. Although adult Lepido-
ptera can move to unininvaded areas, the
decrease in host plant and nectar resources
will affect future generations.

*Lupinus* species are commonly used in
land reclamation processes, but the prob-
lem has been their vigorous growth and the
effects of nitrogen transferred to other fast
growing species, which often become dom-
inant (Bradshaw 2000). Studies on
the control of lupin are urgently needed, but
meanwhile regular mowing before the
lupins have shed their seeds, together with
the removal of the cuttings, should be or-
ganised. In addition, manual eradication on
or close to sites where rare or endangered
species occur may be necessary. Possible use
of biological control agents, either plant
pathogens or herbivores, should also be
studied (Harvey et al. 1996). Finally, as the
lupin has imposing flowers, it is possible that
some people deliberately spread lupin seeds
for decorational purposes along road verges.
Thus, greater public awareness of the effects
of lupin and other invasive species is needed.

### 3.6. Suggestions for management

The results confirm that the mowing of
roadside environments should preferably be
delayed until late summer (Anderson 1995).
However, roadside environments with tall
vegetation predominated by a few plant
species should already be mown early in the
season (Hellström 2004). To minimise
the effect of mowing on all life stages of Lepido-
ptera there should be only one mowing per
summer. The intensive mowing regime typi-
cal to many urban verges treated as lawns
and mown repeatedly is the most harmful
one. Verges which naturally support low
growing vegetation which does not restrict
visibility could be left unmown in certain
years. This could enable the reproduction of
the most sensitive species, e.g. those with
larvae feeding in flowers, to take place.

Variation in the timing of mowing ensures
that species with different life cycles and
different sensitivity to mowing can breed in
roadside environments. Nowadays the vari-
ation is greatest on wide, partially mown
highway verges, where part of the verge is
mown once every 3-5 years, keeping these
areas open, but minimising the disturbance to
Lepidoptera. On the other hand, the low veg-
etation next to the road, created by frequent
mowing, can offer different resources and
conditions compared to the taller vegetation
further from the road. In fact, the annual
mowing is not optimal for butterflies, al-
though many may benefit from the diverse
vegetation created by this regime. Erhardt
(1985) concluded that recently abandoned
grasslands were the most species rich butter-
fly habitats, but eventually the lack of man-
age will lead to rapid degeneration of these
sites. Variation in the mowing intensity can also be created by leaving nectar refugia on road verges in conjunction with mid summer mowing. Mosaic-like mowing is often suggested as being the most beneficial to Lepidoptera (Munguira & Thomas 1992) and other invertebrates (Morris & Rispin 1988, Bakker 1989, Völkl et al. 1993).

The short term goal in improving the management of roadside environments should be the avoidance of two or more total mowings and replacement of mid summer mowing by late summer mowing. If not a threat to visibility, distant parts of the verge could be mown only every 3-5 years. Regular mowing, as required on road verges, is expensive. In Finland the verge management accounts for 12% of all road management costs (Finra 2000) and the annual costs of mowing are approximately 6 million euros (Heikki Lappalainen, pers. comm.). Thus, lowering the mowing intensity by avoiding total mowing twice a season and using partial mowing instead, may lead to substantial savings in money and energy (IV). It is promising that, as these recommendations were recently published in Finra project reports (Jantunen et al. 2004, Saarinen et al. 2006), the mowing instructions in the study districts were changed by the 2006 summer to favour partial mowing, while lupin stands are also being mown in mid summer.

A median term goal in improving the management of roadside environments could be achieved by educating mowing personnel to recognise certain characteristics and to vary the mowing on the basis of the vegetation. Tall growing and hay dominated verges, or those with easily identified negative plant indicators of grasslands, such as Anthriscus sylvestris and Epilobium angustifolium, could be mown twice. For example, the increased abundance of Anthriscus sylvestris on meadows and road verges during the last few decades is recognized as a threat to grassland plant species, but one mowing event in late summer will only increase the abundance of this species, so that a more intensive mowing regime is needed (Hanson & Person 1994). On the other hand, low growing verges could be left occasionally unmown, to decrease the adverse effect of mowing management on Lepidoptera (Erhardt 1985, Nieminen & Kaitila 2000). Nectar refugia patches could be created on road verges with plenty of flowering plants. In addition, the impact of different mowing machinery on plants and insects should be studied and the least harmful blades should be fitted to new machinery.

Finally, the long term goal could be a thorough survey of the most diverse habitats on road verges and intersections. The least harmful mowing regime should be tailored to sites with positive indicators of semi-natural grasslands or endangered plant and insect species. If possible, disturbance should be avoided on these sites. Databases on road verge flora and fauna have already been created elsewhere in Europe for selecting the best management measure for each road verge site (Siepel 1997). An initiative has been taken in SE Finland, where the local road administration has been collecting information on valuable road verge sites from the public (Kaakkois-Suomi Road Region 2005).

4. CONCLUSIONS

Roadside environments are a mosaic-like network of habitats varying considerably in width, soil, history, disturbance, management and surrounding environment. Thus, roadside environments also offer highly variable habitats for a variety of organisms, including vascular plants and Lepidoptera. The main conclusions of this thesis are as follows:

1) There were relatively small differences in vegetation between the four roadside environments compared. However, rural road verges had a higher butterfly abundance compared to urban road verges, while highways had a higher butterfly species richness and diversity compared to intersections. Some meadow moths reached high abundances on intersections, highway and urban road verges, but moth diversity was particularly low in intersections. Differences in
plant and Lepidoptera species richness, abundance and diversity between roadside and field environments were smaller than those between roadside environments and grasslands. Grasslands were characterised by a lower number of weed species, and a higher abundance, species richness and diversity of butterflies than certain roadside environments. Nevertheless, in terms of grassland plant species richness and meadow butterfly abundance and species richness, sites better than the average grasslands were found in all roadside environments. While moth abundance was slightly (but not significantly) lower in grasslands compared to intersections, highway and urban road verges, the diversity was higher in grasslands compared to all these roadside environments.

2) The availability of nectar was positively associated with high butterfly abundance in roadside environments, and the vegetation height with moth abundance. On the other hand, species richness among Lepidoptera in roadside environments was possibly influenced by several environmental factors, including plant species richness, vegetation quality, the surrounding environment, verge width and site age. Old age and nutrient poor sandy soil, on the other hand, were positively associated with the cover of grassland plant species in roadside environments.

3) Mowing had an adverse effect on both butterflies and moths, most probably due to the disappearance of nectar, host plants and sheltering vegetation. Nevertheless, mowing is essential for keeping the verges open and suitable for grassland Lepidoptera in the long term. For the adult stages of both butterflies and moths, mid summer mowing caused the most severe reduction in abundance compared to late summer mowing or partial mowing, where only a narrow strip next to the road is mown in mid summer. Besides the partial mowing, variation in mowing regimes can also be created by leaving some unmown patches within mid summer mown verges. These areas could offer nectar refugia and shelter for Lepidoptera.

4) The majority of *A. hyperantus* individuals in all roadside environments, except on mid summer mown road verges, were sedentary. However, more emigration from linear verge habitats was observed compared to non-linear intersections or non-managed field environments. The highway was not a barrier to the movement of *A. hyperantus*, but it is possible that a dense network of roads may decrease the movement of this species.

5) The ongoing spread of *Lupinus polyphyllus* in roadside environments is a threat to vascular plant and Lepidoptera species. The species richness and cover of low growing plant species and butterfly abundance, in particular, were lower in lupin invaded verges. As the lupin cover approached 100%, fewer butterflies were observed in lupin transects compared to the adjacent non-lupin transects.

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References


Courtney SP, Duggan AE 1983. The population biology of the Orange Tip butterfly Anthocharis cardamines in Britain.


Ihse M 1995. Swedish agricultural land-
scapes – patterns and changes during the last 50 years, studied by aerial photos. Landscape Urban Plann. 31: 21–37.


Parr TW, Way JM 1988. Management of...


Sjölund A, Eriksson O, Persson T, Ham-


Tikka PM 2001. Threatened flora of semi-
natural grasslands: preservation and restoration. Jyväskylä studies in Biological and Environmental Science 93, Jyväskylä.


