Pollinating Insect Responses to Grazing Intensity, Grassland Characteristics and Landscape Complexity:

Behaviour, Species Diversity and Composition

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Abstract

Pollinators uphold important ecological functions and their economic and ecological importance is considerable. In the present thesis the relationship between management practices and the behaviour, diversity and composition of four flower visitor groups: bees, butterflies, hoverflies and beetles, are examined in grasslands with different grazing intensity and in different landscapes in East-Central Sweden.

Four flower visitor groups were influenced by grazing intensity in different ways. Hoverflies and beetles were positively related to vegetation height, while bees and butterflies were not. In the latter two groups some species were favoured by short vegetation. Hoverflies were more species rich in forested landscapes, whereas butterfly species richness was lower in areas containing many roads.

Bees showed the most complex responses mainly due to their diverse life-history strategies corresponding to different environmental factors. The species richness of nest-parasitic and soil nesting bees was favoured by intensive grazing and the existence of bare soil. Cylinder-nesting solitary bees were little affected by management, and high species richness was associated with eutrophication and low plant species richness. The reproductive output in this group can be measured by produced offspring biomass, and this related mainly to human activity. Bumblebees were influenced mainly by landscape factors and long-tongued species appearing late in the season were especially dependent on landscape connectivity and grassland cover.

To maintain viable populations of flower visitors, alternative grazing strategies are recommended. To maintain a high diversity of flower visitors in isolated grasslands local optimisation of grazing may be the best strategy. In interconnected landscapes a better strategy may be to vary grazing intensity at the landscape level. Grasslands with different grazing management could thus complement each other. In landscapes where conditions are particularly good for specific insects, a third alternative would be to manage the landscape to enhance the diversity of this particular group.

Keywords: Semi-natural grasslands, grazing intensity, behaviour, diversity, Apoidea, Syrphidae, Lepidoptera, Coleoptera, landscape ecology, life-history traits

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Hur påverkas insekter av olika betesintensitet och landskaps-komplexitet

Ängs- och betesmarker utgör viktiga miljöer för biologisk mångfald i det svenska odlingslandskapet. Många arter som återfinns där har i evolutionär tid utvecklat anpassningar för att klara störningar som bete i naturliga gräsmarker. Dessa har i stor omfattning utarmats eller försvunnit. Detta innebär att arterna i våra naturbetesmarker inte har några naturliga tillflyktsorter, utan är beroende av den hävd som mänsklig djurhållning innebär. Från och med skiftesreformerna på 1800-talet har rationaliseringar inom jordbruket konsekvent inneburit att färre personer behövts inom jordbruket. Antalet aktiva lantbrukare har minskat med omkring 80 % sedan 30-talet och antalet betesdjur har minskat med en tredjedel. Parallellt med intensifieringen av bördiga delar av landskapet har många öppna marker i skogsbygder växt igen eller planterats för intensivt skogsbruk. Denna utveckling har medfört at artrika ängs- och betesmarker har minskat i utbredning, vilket ökar värdet av att bevara arealen naturbetesmark som finns kvar i landskapet och ställer samtidigt ökade krav på hävdens kvalité.

Länge har rekommendationer för att bevara mångfald i betesmarker inneburit incitament för lantbrukare att upprätthålla ett intensivt betestryck så att "ingen skadlig ansamling av förna uppträder vid säsongens slut". Ett intensivt betestryck motverkar etableringen av buskar och träd, vilka ses som ett hot mot artrikedomen av växter i gräsmarker. Länge har emellertid denna rekommendation ansetts utgöra ett hot mot mångfalden av insekter. Även om de flesta insektsgrupper påverkas positivt av ett svagt bete finns det finns många undantag inom varje grupp och olika insektsgrupper varierar på olika sätt i förhållande till den omgivande miljön. En grupp som fått liten uppmärksamhet är blombesökande insekter. Detta kan synas märkligt eftersom deras roll som pollinerare av vild och odlad mångfald har utpekats som särskilt värdefull både ekonomiskt och för upprätthållande av ekologiska funktioner.

I denna avhandling studeras effekter av betesintensitet på fyra grupper av blombesökande insekter: bin, fjärilar, blomflugor och skalbaggar. En högre blomrikedom i betesmarkerna ökade antalet blombesökare och beteendet skiljde sig väsentligt mellan kontinuerligt och sent betade gräsmarker. De fyra grupperna relaterade till gräsmarkernas vegetationshöjd på olika sätt. Mångfalden och tätheten av blomflugor och skalbaggar var högre i hög vegetation medan varken fjärilar och eller bin påverkades. Artsammansättningen för dessa båda grupper varierade dock med vegetationshöjd, därför att somliga arter faktiskt var vanligare i betade naturbetesmarker. Artrikedomen av blomflugor gynnades också av närhet till skog medan fjärilsmångfalden missgynnades av tätheten av vägar i det omgivande landskapet.

Bin var den grupp som uppvisade den största variationsvidden i artsammansättning. Detta kan förklaras med bins olika livshistorie-strategier. Boparasiter och solitära bin gynnades i intensivt betade marker med mycket sand, medan humlor var något vanligare i svagt betade marker. Bin som bygger bo i rör var vanligare i odlade landskap med relativt låg artrikedom av blomväxter. Många av dessa arter påverkades av hög vegetation eller täckningsgraden av gräsmark i landskapet. För humlor hade landskapets utseende stor betydelse. Särskilt sent flygande, långtungade humlor var vanligare i vägtäta områden med stor täckning av naturbetesmarker.

När beslut om rekommendationer med avseende på betesintensitet tas bör man ta hänsyn till det omgivande landskapet. För isolerade betesmarker rekommenderas optimering på lokal nivå, generellt relativt svagt betestryck för att gynna många insekter. För betesmarker i landskap som innehåller större antal betesmarker som ligger inom spridningsavstånd från varandra är en optimering på landskapsnivå att föredra. Olika betesmarker bör då ha olika betesintensitet, eftersom enskild optimering på lokal nivå skulle medföra att arter som är beroende av antingen intensivt bete eller obetade betesmarker skulle försvinna. Slutligen finns alternativet att gynna olika grupper i landskap där just dessa grupper av arter har särskilt goda naturgivna förutsättningar.

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Sjödin, N. E. Pollinator behavioural responses to grazing intensity. *Biodiversity and conservation DOI*, 10.1007/s10531-006-9103-0.

II. Sjödin, N E. Bengtsson & J. Ekbom, B. The influence of grazing intensity and landscape composition on pollinator diversity. (Submitted manuscript).

III. Sjödin, N E. Ekbom, B. & Bengtsson, J. Bee (Apoidea) guild variability in semi-natural grasslands. (Submitted manuscript).

IV. Sjödin, N E. Reproductive success in trap-nesting bees found in semi-natural grasslands. (Manuscript).

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Introduction

Pollinators constitute an important functional group that contributes to maintain diversity and viable populations of wild plants and to pollinate crops (Corbet, Williams & Osborne, 1991; Kearns, Inouye & Waser, 1998; Kevan & Phillips, 2001; Kremen *et al.*, 2004; Kremen, 2005; Tscharntke *et al.*, 2005; Klein *et al.*, 2007). Lately dramatically declining pollinator populations have been reported in North America as well as Europe (Allen-Wardell *et al.*, 1998; Cane & Tepedino, 2001; Packer & Owen, 2001; Roubik, 2001; Thomson, 2001; Kremen, Williams & Thorp, 2002; Goulson *et al.*, 2005; Williams, 2005; Biesmeijer *et al.*, 2006). Semi-natural habitats maintain viable populations of many pollinators, and have the capacity to increase their diversity in the landscape (Steffan-Dewenter *et al.*, 2002).

In Sweden and central Europe, semi-natural habitats formerly covered large areas and were managed by traditional hay-making and by grazing animals that foraged in wide forested landscapes (Ihse, 1995; Dahlström & Cousins, 2006). The conservation value of semi-natural habitats is especially high because many of the natural habitats that were the original source of grassland species have been lost (Duffey *et al.*, 1974). Moreover, large areas of traditionally managed grassland have been fertilized, and transformed into arable land. Many pastures have been abandoned (Ihse, 1995; Eriksson, Cousins & Bruun, 2002b) and successively transformed into forest. The remaining semi-natural grasslands comprise only a fraction of their past area, and have a much more fragmented distribution in the landscape. As a result diversity and abundance of different organism groups such as mammals and birds (Andrén, 1994; Donald, Green & Heath, 2001), plants (Luoto *et al.*, 2003) and insects (*e.g.*, Maes & van Dyck, 2001; Biesmeijer *et al.*, 2006) have decreased.

Insects make up the major part of the diversity in semi-natural grasslands. The quality of grasslands for insects is determined by: (i) natural factors (ii) management history and (iii) present management (Morris, 2000). Diversity differences among semi-natural grasslands are not only caused by local conditions, but also by qualities in the surrounding landscape (Tscharntke *et al.*, 2005; Steffan-Dewenter *et al.*, 2006). Several studies have shown the importance of semi-natural habitats in the landscape for insects (Kleijn *et al.*, 2001; Steffan-Dewenter *et al.*, 2002; Öckinger & Smith, 2006; Moradin *et al.*, 2007). Others have pointed out the importance of the landscape composition around the grasslands (Dunning, Danielson & Pulliam, 1992; Weibull, Östman & Granqvist, 2003; Ouin *et al.*, 2004).

In semi-natural pastures in Sweden the official recommendation to counteract invasion of forest vegetation and to preserve plant diversity, has been intensive grazing (*e.g.*, Bakker, 1998; Ekstam & Forshed, 2000; Klimes & Klimesova, 2001). This recommendation has, however, been argued to be a threat to insect diversity (Hutchinson & King, 1980; Völkl *et al.*, 1993; Carvell, 2002; Steffan-Dewenter & Leschke, 2003), and alternatives with less intensive grazing strategies have been proposed (*e.g.*, Bignal & McCracken, 1996). There are few studies

examining effects of management intensity on different insect groups simultaneously (but see Söderström *et al.*, 2001; Kruess & Tscharntke, 2002b).

Several studies have investigated the diversity and abundance of the insect fauna in semi-natural grasslands, and have demonstrated the importance of low intensity management for certain insect groups: *e.g.* bees and wasps (*e.g.*, Carvell, 2002; Steffan-Dewenter & Leschke, 2003), beetles (Völkl *et al.*, 1993; Dennis *et al.*, 1997), butterflies (Erhardt, 1985), and leafhoppers (Morris & Plant, 1983; Morris, 2000). However, it is unlikely that the same local and landscape factors are important for different taxa (Söderström *et al.*, 2001; Kruess & Tscharntke, 2002b; Vessby *et al.*, 2002; Wolters, Bengtsson & Zaitsev, 2006). Flower visitors have received relatively little attention in relation to management (Morris, 2000; Carvell, 2002). In this thesis four groups of flower visiting insects were studied in grasslands. Abundance, diversity, species, composition, behaviour, reproductive success and life-history traits were examined at different spatial scales and in relation to grazing intensity.

Background

Historic background

Many plant and animal species inhabiting grasslands are adapted to grazing. They colonized the open habitats created when humans cleared forests and later settled down during the Iron Age. From this time the proportion of land used for animal grazing increased until the 19th century. Animals grazed the forests and meadows were used as fodder for stabled animals during the winter (Eriksson, Cousins & Bruun, 2002a).

In a broad sense this agricultural system survived until the mid-19th to the beginning of the 20th Century, when intensification and rationalization transformed the agricultural landscape (Eriksson *et al.*, 2002a). Traditional hay-making and grazing in forests more or less ceased. Most meadows and grasslands were transformed into productive arable land or into productive forest (Ihse, 1995). Only 17.5% of the semi-natural grassland area in Sweden remains compared to 100 years ago (Dahlström *et al.*, 2006) and less than 0.01% of the hay meadows (Person, 2006b). Moreover, the number of farmers and cattle has decreased (Johansson, 2005). One reason for this is centralisation (and marginalisation), where farms in productive areas have become increasingly large, whereas small, isolated farms are abandoned. This process is still going on. Between 1990 and 2005, the number of farms with cattle decreased by 63% (Person, 2006a).

The remaining semi-natural grasslands thus comprise only a fraction of their past area, and have a much more fragmented distribution in the landscape. Grasslands in Sweden today occupy about 600 000 ha pastures (about 500 000 ha semi-natural) and 8700 ha meadows (Person, 2006b), while the area of arable land is 2 660 000 ha and of forest 3 380 000 ha (Johansson, 2005; Person, 2006b).

Traditionally managed semi-natural grasslands may be important in animal production, despite a low productivity. These grasslands can be used for production of meat in combination with production of other values. Such values of grasslands may be their high biodiversity, maintenance of an open landscape, recreation and aesthetic or ethical values. Moreover, grasslands may be vital to maintain viable populations of organisms providing ecosystems with important services such as pollination (Steffan-Dewenter *et al.*, 2002).

Management and plant diversity

Management is often regarded as a disturbance factor. The intermediate disturbance hypothesis (IDH) suggests that the highest diversity is obtained at intermediate disturbance levels (Connell, 1978). Low disturbance may increase competition between species, which ultimately leads to competitive exclusion and the dominance of a few species (Milchunas, Sala & Lauenroth, 1988; Hobbs & Huenneke, 1992). On the other hand, severe disturbance may be harmful for sensitive species. In grasslands a severe disturbance would be excessively intense management like over-grazing.

To be able to understand what intermediate means, present grazing levels must be compared with traditional management systems and the life-history of the species remaining in the community. Annual plant species have disappeared in grasslands because of intense grazing (Shea, Roxburgh & Rauschert, 2004). Traditionally large forested areas were grazed, implying that levels of grazing intensity were much more variable in time and space, and related much more to the activities of the grazing animals than today. Moreover, meadows in fact constituted the major area of the traditionally managed grasslands. Compared to this, our fenced grazing involves huge changes. Animal treading compresses the soil and causes formation of tussocks, and the shorter vegetation causes the soil to be more exposed and sensitive to drought and fluctuating temperature and humidity (Morris, 1969) and animals are forced to graze for a longer time on a small area.

If a species has evolved the ability to survive grazing, this may involve a limitation of adaptation in other ecological functions (Aigner, 2006). When management ceases, all species produce more flowers for a time. Later such grasslands become increasingly covered by species competitively dominant for light, and thus a succession to shrub land forest follows (Ihse, 1995; Hansson & Fogelfors, 2000). The time for abandoned grasslands to move from one successional stage to another varies, but it is probably related to nutrient levels and landscape openness.

Mowing seems to have the capacity to counteract the increase of lignified plants, to drain grasslands from nutrients and at the same time maintaining a complex vegetation structure (Morris, 1969). Mowing therefore results in the highest plant diversity in grasslands (Hansson & Fogelfors, 2000; Stammel, Kiel & Pfadenhauer, 2003). Grazing may also keep dominant species like bushes and trees away (Hobbs & Huenneke, 1992), but only at high intensity levels. The current long-term general recommendation has therefore been to manage old meadows and semi-

natural pastures intensively (*e.g.*, Ekstam & Forshed, 1996; Bakker, 1998; Klimes & Klimesova, 2001).

Management and insect diversity

Grassland management influences insects indirectly through vegetation change. The recommended intensive grazing to ensure long-term plant diversity (*e.g.*, Ekstam & Forshed, 1996) reduces the short-term vegetation complexity that most insect groups rely on (Morris, 1969). Most insect groups are favoured by low grazing intensity, for example, leaf-hoppers (Morris, 1981), scarab beetles (Hutchinson & King, 1980), weevils (Völkl *et al.*, 1993), butterflies (Kruess & Tscharntke, 2002a), trap-nesting bees and wasps (Kruess & Tscharntke, 2002a). However, for many insect groups no significant effect of low intensive grazing has been found: dung-beetles (*Aphodius*) (Vessby, 2001; Vessby *et al.*, 2002), bugs (Heteroptera) (Kruess & Tscharntke, 2002b), Orthoptera (Hutchinson & King, 1980; Tscharntke, 2002a, Stoner & Joern, 2004). Moreover, some species in many groups generally favoured by low intensive grazing are enhanced by intensive grazing, *e.g.* butterflies and moths (Lepidoptera) (Kruess & Tscharntke, 2002a). Some insect groups are also favoured by intensive grazing, like ants (Hutchinson & King, 1980), spider-hunting wasps (Pompilidae), some spiders (Morris, 1969) and large flightless carabid beetles (Cole *et al.*, 2006). The activity of these groups is greater in grasslands containing open ground – often associated with intensive grazing (Morris, 1969).

This variation among insects may indicate that different grassland structures are used (Morris, 1969) but also that different plants and parts of plants are used (Morris, 1969). Root feeders are probably less affected by grazing than species using leaves or stems. Important insect groups feed on seeds, in buds or on reproductive organs in flowers, on pollen or nectar provided in flowers. Therefore, there are often species within each group with contrasting responses and a pattern found in one species group may not be applicable to another (Söderström *et al.*, 2001; Kruess & Tscharntke, 2002b; Vessby *et al.*, 2002; Weibull *et al.*, 2003; Wolters *et al.*, 2006).

Table 1. *Some possible consequences of intensive grazing that might influence flower visitors. Grazing may affect flower visitors at three levels: individuals (I), populations (P), and communities (C)*

Level	Intensive grazing consequences
I	Presence of grazing animals
I	Floral resources are scattered, because grazing removes flowers
I	Precise location of flowering plants becomes uncertain as grazing removes flowers quite randomly
IP	Vegetation is shorter
IP	Vegetation has less vertical growth with lower structural complexity (Morris, 2000)
IP	Direct trampling (Kearns & Inouye, 1997)
IPC	Sparsely vegetated soils
IPC	Flowers become less abundant, because some of them are grazed
IPC	Grazing sensitive nutrient plants disappear

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Grazing intensity and the behaviour of pollinators

One insect group that has received relatively less attention in relation to management is flower visitors (Morris, 1969; Carvell, 2002). This is especially so for the behavioural responses to grazing intensity.

How would, then, insect behaviour change in response to high grazing intensity (Table 1)? 1. If a higher grazing intensity results in lower flower densities, flower visitors are expected to respond numerically to such variation (Dukas & Real, 1993). There would be fewer visitors in intensively grazed pastures, but each individual visitor should visit a higher proportion of the flowers and flowering plants (Goulson, 2000; Pettersson & Sjödin, 2000). 2. It is unclear how visitation rate would be affected by more scattered flowering individuals in intensively grazed pastures (Chittka, Thomson & Waser, 1999). 3. Shorter vegetation allows insects to move more freely between plants and to find certain flowers more easily (Goulson, 2000; Pettersson & Sjödin, 2000). 4. Short vegetation with lower complexity may also result in lower visitor diversity (Morris, 2000). Plants allowed to grow vertically spread flowers in three dimensions rather than two, in contrast to plants growing horizontally in response to high grazing intensity. 5. The flower visitor response to higher trampling is unclear. Intensive grazing may result in direct trampling of insects and nests (Kearns *et al.* 1998), but trampling might also create sites where vegetation is sparse and serve as suitable nesting sites for some flower visitors (Vulliamy, Potts & Willmer, 2006). 6. The active presence of grazing animals also interferes with insect visitors and changes their behaviour.

Pollinators in grasslands

It has recently been reported that flower visitors in many taxonomic groups are declining in North America (Cane & Tepedino, 2001) as well as in Europe (Kearns & Inouye, 1997; Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998; Cane & Tepedino, 2001; Kevan & Phillips, 2001; Packer & Owen, 2001; Roubik, 2001; Thomson, 2001; Carvell, 2002; Goulson *et al.*, 2005; Biesmeijer *et al.*, 2006). Pollinator loss may affect reproductive success in plants through, *e.g.*, reduced seed set, changed mating system, more self-pollination, decreased heterozygosity, increased expression of deleterious traits and reduced opportunity for pollen competition (Kearns & Inouye, 1997; Kearns *et al.*, 1998). The value of pollinators in ecosystem functioning is well accepted in ecology and their economic importance for crop yield is considerable (Klein *et al.*, 2007). At least two thirds of all flowering plants depend on insects for pollination (Kearns & Inouye, 1997), and many of these are declining in Western Europe (Biesmeijer *et al.*, 2006).

The distance to semi-natural habitats in the landscape has been observed to increase seed-set in plants (Steffan-Dewenter, Münzenberg & Tscharntke, 2001), and the cover of semi-natural grasslands to increase populations of pollinators (Moradin *et al.*, 2007).

The systematics of flower visitors in grasslands

Coleoptera are considered to be the most primitive pollinators. Flower visiting beetles (Coleoptera) constitute a very diverse and heterogenic group that are usually poor pollinators, due to their limited flight ability, smooth bodies and low activity (Kevan & Baker, 1983). Bees (Apoidea) are considered to be the most active flower visitors and probably also function as the most efficient group of pollinators in grasslands (but see Larsson, 2005). This is based on the close connection to plants thorough dependence on both pollen and nectar, but also on their hairy bodies, good flight ability, and variability in size, home range and specialization (Westrich, 1990; Michener, 2000). Butterflies, i.e., true butterflies (Rhopalocera) and burnet moths (Zygaenidae) (Naumann, Tarmann & Tremewan, 1999; Franzén & Ranius, 2004) visit flowers aiming for the nectar resources, for maintenance, and reproductive activities. Adult hoverflies (Syrphidae) mainly feed on pollen while larvae are predators, mainly on aphids, but also on other insects (Gilbert, 1981; Torp, 1994; Sommaggio, 1999). Their ability to pollinate flowers is, however, limited by their smooth and light bodies, by their polyphagous pollen dependence, and due to their small contact area with plant-sexual organs (mouthparts most often only come into contact with anthers).

Adult flower visiting beetles often feed on pollen or hunt in the flowers, but many species also mate and oviposit there. Beetle larvae of flower visiting species are often herbivorous. Some larval groups develop in wood (*e.g.* Cerambycidae and Bupresitdae), others feed on leaves on trees or herbs (*e.g.* Chrysomelidae and Curculionidae) and several groups are seed-predators on herbs (Brentidae and Bruchidae), but there are also several predator groups (*e.g.* Coccinellidae and Cantharidae).

Bees are completely dependent on plant pollen sources for larval development. Bees build nests in different habitats, some depend on sparsely vegetated sandy soil (*e.g.* Andrenindae, Halictidae and Melittidae), others on hollow spaces under ground or in tall vegetation (*e.g.* Apidae) and a third group uses hollow cylinders in dead wood for nest formation (*e.g.* Megachilidae) (Westrich, 1990; Michener, 2000).

Butterflies have long tongues and good flight ability, although their wings may be fragile. The larvae are herbivorous and often depend on a particular resource plant. Larvae of groups within Syrphidae use prey living in different habitats: connected to trees, wet soils, grazing animal droppings or are associated with ants (Torp, 1994; Sommaggio, 1999). Flies are in general very strong fliers and hoverflies are no exception.

Individual behaviour

The behaviour of insects during foraging, mating, ovipositing, nest construction and choice of hibernation sites has consequences for reproductive success. Thus individual behavioural responses to environmental variation have consequences for population persistence and dynamics.

Actions within flowers are determined by specific needs and constraints of the plants and their visitors. Plants pollinated by a certain visitor guild often have features in common. These features are called pollinator syndromes, i.e., groups of characteristics used to identify flowers according to their pollinators (Knuth, 1906; Proctor, 1978; Faegri & van der Pijl, 1979; Kevan & Baker, 1983).

Although insects in general have been shown to restrict their visits to one or a few plant species (flower constancy) (Betts, 1935; Free, 1970; Heinrich, 1976a; Waser, 1986; Goulson, Stout & Hawson, 1997; Goulson & Wright, 1998), they seem to be good at estimating nectar resources and distribute themselves according to available resources (Hodges, 1981; Dreisig, 1995). This has explicitly been studied in bumblebees, where individual foragers now and then switch from the major plant to probe a few minor plants to evaluate changes in reward (Heinrich, 1976a).

Within grasslands insect behaviour influences where to forage. Bumblebees have been observed aggregating in accordance with flower abundance (Cresswell, 1997, 2000; Goulson, 2000), but less is known for other insect groups. Moreover, the ability to discriminate between good and bad patches may be related to scale. Although both honey bees and bumblebees have been observed to respond to aggregations of plants within a grassland, bumblebees lack the ability observed in honeybees to recruit individuals from the colony to resource rich sites in the landscape (Seeley, 1995; Goulson, 2003).

The reproductive success of flower visitors may not only relate to the behaviour during flower visitation, but also during mating and searching for hibernation and larval development sites. In solitary bees holes in the soil or dead wood are used as nests where cells are constructed containing pollen and nectar for the larva. Because the size of bees is often associated with high reproductive success (Heinrich, 1976b; Johnson, 1990; Kim, 1997; Bosch & Kemp, 2004; Giovanetti & Lasso, 2005), the choice of a reproductive female to increase provisioning in each cell may be rewarded. The behaviour of flower visitors thus influences reproductive success.

Species composition and diversity

In fragmented landscapes, not only quality aspects of the individual grasslands, but also qualities in the surrounding landscape must be considered (Tscharntke *et al.*, 2002). Ecological processes may act at different scales. Scale in this context can be defined as the "physical dimensions of observed entities and phenomena" (O'Neill & King, 1998). Species composition and diversity may be influenced at larger spatial scales in several ways:

1) The species pool, the total number of species in a region may vary in size and composition. The species pool is constrained by geomorphology, climate and weather conditions, as well as evolutionary and ecological history (Leibold *et al.*,

2004). Thus, land-cover, land-use continuity and processes like fragmentation, land transformation and altered management may be important for the species pool.

2) Habitat isolation and population extinction: Meta-population theory and empirical studies have pointed out the importance of dispersal in relation to population extinction rates (Hanski & Ovaskainen, 2000, 2004). Extinction rates may increase in relation to altered land-use and management. Some species groups may be less affected by increased local extinction rates by having good dispersal abilities (Hanski & Ovaskainen, 2000, 2004). Species with intermediate dispersal abilities may be more sensitive to habitat isolation and can only persist if local extinctions are balanced by dispersal. For such species distance between quality habitats and the existence of links between them, like edges, roads, fences and hedgerows may be crucial (*e.g.*, Hill, 1995; Beier & Noss, 1998; Lindborg & Eriksson, 2004; Damschen *et al.*, 2006).

3) Multi-habitat dependence (habitat complementation): Many flower-visitors use different habitats during their life-cycle (Dunning *et al.*, 1992; Ouin *et al.*, 2004). Some groups like butterflies and beetles are often dependent on one larval resource-plant habitat and another adult floral resource and mating habitat. Most hoverflies are predators during the larval stage, and some may use prey in one habitat, whereas the adult feeds on plants in another. Bees construct nests and collect pollen for the larvae. Sometimes nest site preferences do not coincide with pollen resource habitats (Tscharntke, Gathmann & Steffan-Dewenter, 1998; Klein, Steffan-Dewenter & Tscharntke, 2004). When a species depends on different habitats the distance between habitats becomes crucial for persistence (Kruess and Tscharntke 2002). Landscape composition and structure are then crucial, and line elements in the landscape may act as bridges and link distant qualitative habitats (Opdam, Steingröver & van Rooij, 2006).

Aims of the study

The main objective of my studies was to investigate short-term (only a few years) effects of variation in grazing intensity on flower visitor behaviour, abundance, diversity, and species composition. Firstly, some good environmental predictors of grazing intensity with significant association to flower visitors had to be found. Because the landscape has been shown to be an important predictor of diversity in grasslands, analyses of landscape characteristics had to be included and as far as possible considered in relation to local variability. I also asked how information on behaviour, abundance, diversity and species composition can be used in conservation recommendations?

The following questions were asked:
· How do flower visitors and their environment vary in relation to management intensity? (*Papers I-IV*)
· In what ways do flower visitors behave differently in response to grazing intensity? (*Papers I* and *IV*)

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· How important are local and landscape environmental characteristics for diversity of different taxonomic groups of flower visitors? (*Papers II-IV*)
· How do organisms with different life histories vary in relation to local and landscape environments? (*Papers I-IV*)
· How does reproductive success in trap-nesting bees relate to available resources and landscape composition? (*Paper IV*)
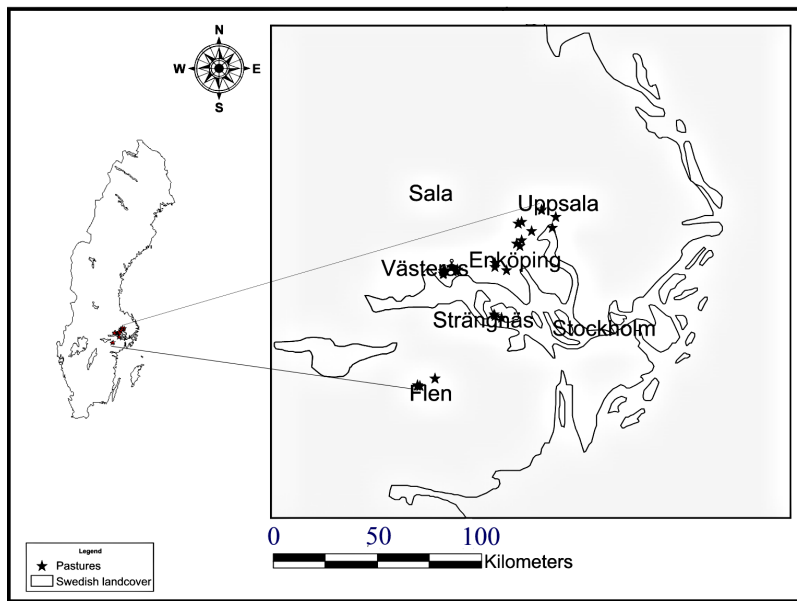

Fig. 1. Eight areas containing 3 grasslands managed at different intensities was studied in East-Central Sweden, in the region around Lake Mälaren 16°28'-17°40' E). The Harpsund site studied in *Paper I* is close to Flen, and the Pustnäs site is close to Uppsala.

Material and Methods

Sites description

All studies were carried out in East-Central Sweden, in the counties of Södermanland, Västmanland and Uppland, situated around Lake Mälaren (between 59°05'-59°50' N; 16°28'-17°40' E) (Fig. 1). In *Paper I* two grasslands were used to study insect behaviour in relation to two levels of grazing intensity. The first site was the commercial farm Harpsund (59°51'N 16°27'E) in the province of Södermanland, and the other was the Pustnäs pasture situated near Uppsala (59°48'N 17°39'E) in the province of Uppland and managed by the Swedish University of Agricultural Sciences. The grazing experiment began in 1997 in Pustnäs and in 2001 in Harpsund, when the pastures were divided into two areas separated by a fence. On one side of the fence grazing by cattle was allowed from the beginning of the season, mid-May, and continued until September ("continuous" grazing). On the other side of the fence grazing was not allowed

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until much later on the season, from mid July, when gates were opened between the two treatments ("late" grazing). In Harpsund both areas were about 6 ha. In Pustnäs the late grazing regime was situated in a 100×50 meter fenced area.

In *Papers II-IV* were performed in eight areas, each with three management regimes: intensively grazed, grazed at low intensity and abandoned grasslands that had not been grazed for at least 10 years. Management history and landscape environment make each grassland be more or less unique and therefore I made a large effort to find comparable grasslands. I used the nationwide inventory of Swedish semi-natural meadows and pastures 1988-1993 (Söderström *et al.* 1993). In the inventory, grasslands were classified according to conservation values based on floral species richness and composition. The eight areas were situated far enough (at least 10 km) from each other to contain different species pools. Within each area the three pastures were situated close enough to have the same species pool, but separated enough to ensure that individual insects would not fly readily between sites (two km). Potential triplets were examined in autumn 2003, and grazing intensity levels were confirmed by examination of litter cover. Grazing intensity measured as vegetation height and litter cover was later shown to follow the classification in the first examination.

Scale definition

Scale in the context of this thesis can be considered as the physical dimensions of observed phenomena (O'Neill & King, 1998). Ecological processes and functions often show scale specific patterns (With, Cadaret & Davis, 1999; Turner, Gardner & O'Neill, 2001; Halley *et al.*, 2004). In the present study several scales were studied and they will be referred to as the plot or micro-scale, i.e. within plots (5 × 5 m) or immediately around trap-nests, local scale occurring within the radius of approximately 300 m, landscape scale 300-1800m and regional scale >1800m. Many ecological processes act between these physical dimensions.

Observation plots

In *Papers I-III* insects were observed in fixed plots, 5 × 5 m. The method is especially suitable for measurement of flower visitor behaviour and mobility, and it may also reflect their importance as pollinators. Such observations are best suited to study bees, but hoverflies and some butterflies are also easily observed. Compared to walking transects, it is easier to detect movement of small insects when walking around one spot and watching the same flowers from many angles. The value of comparing fixed plots is also an increased control of the effect of seasonal variation. On the other hand it may not always be clear how representative the plots are.

In *Paper I* the plots were used to observe insect behaviour. One problem with fixed plots in this respect is that different insects utilize patches at different scales. This means that high visitation rates are more readily found for species visiting flowers adjacent to each other, than for species visiting one plant at a time. Very

few butterflies visited several flowers in a row. One group of bees, large Megachilids (leaf-cutter-bees), visited a few plants in a row, but also seemed to fly quite far between forage sequences.

The plots in *Paper I* were paired along fences between the two treatments; continuous and late grazing. The focus of this study was on pollinator behaviour and visitor choice. In the paired plots flower visitors had free access to choose between treatments. Although pollinators often can be seen following fences, in this study the fences were not permanent and therefore no typical edge zone had developed. Flower visitors were seen flying between flowers crossing the fence. The moisture gradient was opposite the fence separating pairs of plots, which had the effect that pairs represented different vegetation zones. In order to have similar weather conditions plots within pairs were observed directly after one another.

The four observation plots (5×5m) in each grassland in *Papers II-IV* were randomly distributed and established for the duration of the study in dry to moist vegetation (wet areas were avoided) in open parts of the grasslands. In each of the eight areas the three grazing intensity regimes were visited on the same day (if weather allowed) and in random order. Study plots were observed for 10 minutes four times during the summer, between June 7 and August 20, in 2004.

Local environmental variables

In *Papers I-IV* vegetation height was used as the main variable separating grazing intensities and was correlated with litter accumulation (Fig. 4). It was measured by use of a rising plate meter (Sanderson *et al.*, 2001; Correll, Isselstein & Pavlu, 2003).

In *Papers I-IV* the number of pollen and nectar presenting plants and flowers were counted and determined to species. When flowers/inflorescences were counted I used practically separable units ("smallest countable unit"). For the plant families Asteraceae, Fabaceae, Plantaginaceae and Dipsacaceae it was more practical to count inflorescences than flowers and for Apiaceae and Rubicaceae whole plants were counted.

Site-specific characteristics were estimated at the grassland level (Table 2). Three important characteristics are pasture size, cover of tree and bush vegetation and ground structures (Morris, 2000). It is typical for Swedish grasslands to contain scattered trees and bushes, which was also true for the studied grasslands. The number of thick trees, bushes and trees that shadowed parts of the studied grasslands was measured. Especially important to bees are the two measures of ground structures estimated in the grasslands: sand-cover and stones. Cover of vegetation indicating eutrophication was also estimated using indicator plant species and vegetation structures (Ellenberg *et al.*, 1992).

Table 2. *Description of environmental variables at two scales: A. local scale: management (grazing related) characteristics measured in plots within grasslands and site characteristics. B. Landscape scale: measured at three landscape scales in the grassland surroundings (600, 1200, 1800 m radius around each grassland)*

Variable	Description
A. Local scale	
Vegetation height	Mean of 9 measurements using a rising plate meter (Sanderson *et al.*, 2001). The measure combines effects of vegetation height and density
Litter cover	The proportion cover (in 5% intervals) of visual dead plant material as means from four plots at the end of the season
Microstructures	The number of cattle dung droppings, distinct tussocks, bare ground surfaces, visual ant hills, visual stones and small grazed bushes (Morris 1969)
Vertical temperature variation	The ratio between air and ground temperature. The temperature in shadow was measured 10 cm above and at ground level.
Plant species richness	Number of flowering plant species.
Flower abundance	Counts of flowers per species for all herbs presenting pollen and/or nectar. For the plant families of Asteraceae, Fabaceae, Plantaginaceae and Dipsacaceae it was more convenient to count inflorescenses than flowers and for Apiaceae and Rubicaceae whole plants were counted.
Pasture characteristics	
Stones	Estimated from stone 1 (poor) to 5 (rich)
Sandy soil	Estimated as % cover (in 5% intervals)
Eutrophication	Proportion of the grassland with vegetation affected by vegetation and species indicating eutrophication
Tree cover	The proportion of the grassland covered by trees and bushes
Thick trees	The number of large trees (>2.0 m perimeter at breast height) in the whole grassland
Bush cover	Proportion of the grassland covered with bushes (in 5% intervals)
Pasture size	Estimated as proportion grassland cover from map-component at 300m around the mid-point of four study plots
B. Landscape scale	
Arable land	Proportion (in 1% classes) arable land cover
Grassland	Proportion (in 1% classes) grassland cover
Water	Proportion (in 1% classes) water cover
Forest	Proportion (in 1% classes) forest cover
Buildings	Number of buildings per circle area in the landscape
Road length	The length of roads per circle area in the landscape
Edge length	The length per circle area of edges between two map components

Landscape parameters

In *Papers II-IV* I examined the influence of the landscape surrounding the pastures on abundance, species composition, diversity, and reproductive success of different flower visitors. In the first two studies, GIS analyses were made within circles at three different radii (600, 1200, and 1800m) surrounding the mid-point of the four study plots in each grassland (Table 2). Different radii were used because flower visitor groups have been shown to respond at different scales within this range.

Butterflies may be an exception as they may respond to landscape variation at even larger scales (Bergman *et al.*, 2004).

The Swedish terrain map (vector map) was used, obtained from the Swedish Land Survey Authority (classes included arable land, forest, grassland, and water cover). Landscape diversity was measured by examination of the cover of all included land-cover elements individually (no diversity measure was used). As a measure of landscape heterogeneity total edge length per unit area of these land-use categories was used. Connectivity in the landscape was measured indirectly by two measures of linear elements in the landscape, roads, and edges per unit area. Human presence and influence was represented by two measures, roads per unit area and density of buildings. (Table 2)

The method of measuring landscape characteristics with cumulative area at different radii has certain constraints and may be misinterpreted. At small scales cover measures relate mostly to element proximity and size, whereas at large scales measures say more about landscape composition. The diversity of insects may be affected by distance to elements rather than their cover and distribution in the landscape. Some important influences acting at short distances are many severely negative effects such as the use of pesticides or fertilization of arable fields, but also other effects related directly to individual and behavioural insect responses. This is the reason why I believe that insect behaviour and reproductive success should be studied at smaller scales (*Paper IV*).

Isolation can generally be expected to be associated to actual distances between patches, but line-elements may function as corridors or greenways connecting distant habitats. Line elements may serve three ecological functions for flower visitors: 1) increased habitat size or complementing the main habitat, 2) link qualitatively good habitats, and 3) change the behaviour of individual foragers (Haddad & Baum, 1999; Haddad, Rosenberg & Noon, 2000). In addition, in analyses based on circles in the landscape large radii are wrongly judged to be as important as small radii. To reduce the effect of large radii, however, may be arbitrary and the significance of large-scale effects should in my view instead be interpreted with care.

Moreover, measures at different scales are not independent. And in my opinion, scales may act in a hierarchical way, i.e. measures at small scales are more affected by large scales than the opposite. I therefore doubt the value of explicitly comparing relation strength between scales. The within scale relationships, identities and the scale in itself comprise important information about biodiversity. It can be expected that species and processes are affected by different factors and this will depend on the scale studied.

In the landscapes studied, the mean proportion cover of arable land (42.3% ± 4.3) and forest (38.4% ± 3.4) was high and quite equal, whereas grassland cover (10.9% ± 0.9) and water cover (7.2% ± 2.6) constituted only small fractions of the landscape. Because my observations were carried out in grasslands, the fraction occupied by this element was highest at the smallest circle sizes with a rapid

decrease in cover between the two smallest circle sizes (300m and 600m) (Fig. 2). This effect was so prominent that, in fact, the smallest circle mainly reflects the size of the grassland. In addition, grassland fragmentation (measured as perimeter per unit area) was not used in the studies because it was strongly and negatively correlated with grassland cover in the landscape (r_s= -0.48; p=0.017).
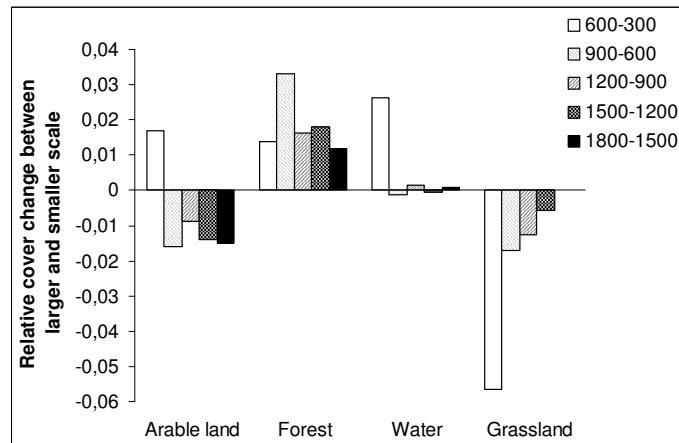

Fig. 2. The mean proportional change in proportional land-cover between areas resulting from an increased circle radius of 300 m (from the mid-point in grasslands to 1800 m.

Landscape diversity (1-D (Simpson diversity index)) was strongly correlated to water cover. This is explained by an increased evenness between land-cover elements when high proportions of the landscape were covered with water. This means that where water was present, it increased evenness among landscape elements and thereby also the diversity index. In my studies landscape diversity was negatively correlated to cover of arable land (r_s= -0.57; p=0.0034), positively with water cover (r_s= 0.63; p=0.0011) and edge length (r_s= 0.53; p=0.0075).

Trap-nests

In *Paper IV* trap-nests were used to study reproductive success of inhabitants to local and landscape qualities in the nest surroundings. Previous studies have pointed out the value of using trap-nests to evaluate ecological change and habitat quality (Gathmann, Greiler & Tscharntke, 1994). Two trap-nests were placed in 2004 and 2005 in the open, but near to a tree or bush (within 10m), on a pole at the edge of the grassland with cylinders pointing towards the grassland. One trap-nest was a bundle of paper cylinders constructed to suit the red mason bee, *Osmia rufa* (Oxford bee company Ltd., 40 Arthur Street, Loughborough, Leicestershire LE11 3AY). Each of these contained 29 (150 mm long) paper cylinders of three different diameter widths, 12 of 7 mm, 10 of 8 mm and 7 of 9 mm. The second trap-nest consisted of a bundle of common reed (*Phragmites australis*) cylinders containing 150 mm long cylinders cut at the nodes forming one front with cylinder-entrances and one back where the node forms a wall. Common reed cylinders were generally smaller in diameter and trap-nests contained about 70 cylinders of common reed.

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The bundles of paper- and common reed cylinders were removed from the field-sites in October and stored in four paper cages (23×36×50 cm) outside (under a roof) at winter temperatures. They were brought inside (20°C) for insect hatching on April 9, 2005 and February 29, 2006. All insects that hatched from each paper-cylinder and from common reed bundles were collected each day and stored in 25 ml tubes in the freezer. All frozen insects were determined to species, sexed, and individually weighed. All cylinders were individually opened for counting insects that failed to hatch.

Statistics

In *Paper I* differences between treatments for both environmental variables and variables describing insect behaviour were examined in a repeated measures analyses with site as the random factor (procedure MIXED). Residuals were visually examined in relation to time (week). Using the Akaike´s information criterion (AIC), the covariance structure autoregressive order 1 was used (Littell *et al.*, 1996).

In *Paper II* all multivariate analyses were done in CANOCO (ter Braak & Verdonschot, 1995; ter Braak & Smilauer, 2002). To choose the appropriate analysis, the gradient length first was estimated in a detrended correspondence analysis DCA. The gradient length was intermediate. Since unimodal methods (CCA) are more frequently used for species diversity (Ulf Grandin, Dept. Environmental Assessment, SLU, personal communication), the analysis continued with a canonical correspondence analysis (CCA), which has been shown to be as good as linear methods for shorter gradients (Oksanen, 2006). The influence of local and landscape variability was estimated for each scale separately.

In *Papers II* and *III* the differences between grasslands was investigated using the mean (of the four plots) of the sum of observations over the summer in the former and as means per plot per grassland in the latter paper.

The papers in this study used stepwise (forward) regression analyses. This traditional method is easy to understand but has some limitations (Whittingham *et al.*, 2006). One is that the first environmental variable constraints which other variables that may be accepted in the model. In *Papers I-III* correlation analyses was used to select variables that were not associated in the subsequent analyses. This may have the effect that important information is lost (Whittingham *et al.*, 2006). In *Paper IV*, a principal component analyses was used instead. Multi-dimensional regression lines are fitted to the environmental variables. Scores from three PCA-axes may be used to substitute a range of environment factors in the subsequent analyses. A third option, not used here, may be to use a likelihood-based measure (Akaike's information criterion) to find models explaining most of the variation (Mazerolle, 2006). This method was not used because the choice of best model also involves arbitrary judgments. In *Papers II-III* regression analyses were used to examine community structure. In *Paper IV* regression analyses were

conducted on the numbers of produced individuals and their size were only compared for sites were the species were present.

Results and Discussion

Behaviour and grazing intensity

Insects clearly responded behaviourally to the different environments caused by the different grazing intensities (*Paper I*). The foraging behaviour differed between scales levels. At the micro-scale (within flowers), visitors behaved differently in flowers in continuous grazing compared to the late grazing environment. At the intermediate scale, the flower visitation and switching behaviour between flowers did not differ between grazing intensities. At the largest scale, more flower individuals chose to forage in the late grazing regime and their behavioural repertoire was more diverse (Table 3).

Table 3. *Differences in species richness, abundance, visitation and behavioural variables in relation to intensive and low intensive grazing. Significantly (p<0.05) higher values in low-intensive grazing are indicated by a "<" between management effects*

Level	Intensive		Low intensity	Unit
Paper I: Visitor behaviour				
Decision level 1				
visitor abundance	4.44 ± 0.90	<	7.38 ± 0.90	$Ind.\times m^{-2}\times min^{-1}$
visitor species richness	3.41 ± 0.44	<	5.15 ± 0.44	$Spp.\times m^{-2}\times min^{-1}$
Decision level 2				
visitation rate	0.063 ± 0.025	n.s.	0.12 ± 0.025	
# of plant species visited	2.65 ± 0.53	n.s.	3.43 ± 0.53	$Spp. \times plot^{-1}$
prop. flowers visited	0.22 ± 0.03	n.s.	0.26 ± 0.03	$Ind.. \times ind.^{-1} \times plot^{-1}$
# of switching visitors	0.59 ± 0.46	n.s.	0.80 ± 0.46	$Ind.. \times plot^{-1}$
prop. switching visitors	0.12 ± 0.11	n.s.	0.21 ± 0.11	$Ind. \times ind.^{-1} \times plot^{-1}$
Decision level 3				
visitor activity diversity	0.58 ± 0.074	<	0.90 ± 0.074	H' (ind ~ act.class^{-1})
Paper II: Diversity between grasslands				
Abundance				
Bee abundance	51.75 ± 7.43	n.s.	62.50 ± 7.43	$Ind.\times site^{-1}\times 40min^{-1}$
Butterfly abundance	22.75 ± 3.53	n.s.	22.87 ± 3.53	$Ind.\times site^{-1}\times 40min^{-1}$
Hoverfly abundance	28.25 ± 5.47	<	35.38 ± 5.47	$Ind.\times site^{-1}\times 40min^{-1}$
Beetle abundance	4.50 ± 2.36	<	6.88 ± 2.36	$Ind.\times site^{-1}\times 40min^{-1}$
Species richness				
Bee species richness	20.88 ± 1.53	n.s.	21.25 ± 1.53	$Spp.\times site^{-1}\times 40min^{-1}$
Butterfly richness	9.37 ± 0.72	n.s	9.13 ± 0.72	$Spp.\times site^{-1}\times 40min^{-1}$
Hoverfly richness	7.50 ± 1.22	<	9.88 ± 1.22	$Spp.\times site^{-1}\times 40min^{-1}$
Beetle richness	2.75 ± 0.60	<	3.75 ± 0.60	$Spp.\times site^{-1}\times 40min^{-1}$

Flower visitor responses to grazing intensity

The papers in this thesis examined how different components of the diversity of flower visitors were related to grazing intensity (*Paper II*). Insect groups showed contrasting responses to management intensity (Fig. 3). Hoverflies and beetles

were favoured by tall vegetation, i.e. the environment characteristics of abandoned grasslands or where grazing intensity was low. Bees differed in their response to management. Although the correlation with vegetation height was not significant, the slope was significantly different from that for beetles and butterflies. For both butterflies and bees many species were related to tall vegetation, but other species were also more common in grasslands with short vegetation.
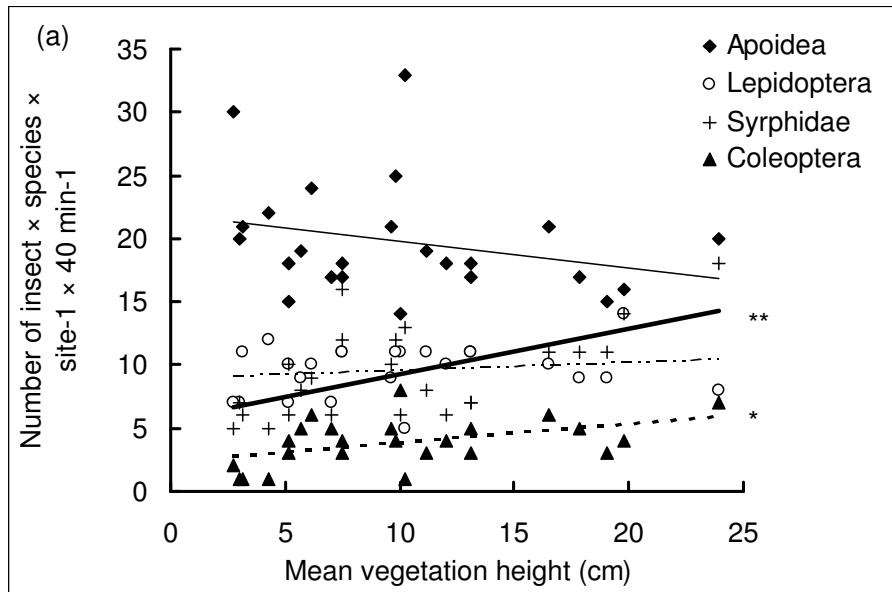

Fig. 3. Mean number of species per site of four insect groups in relation to vegetation height (VH) (ANCOVA: Group × VH; F=5.01**). Bees (♦, solid line) =22.0 - 0.22 × VH (R^2 = 0.076 n.s.); Butterflies (○, dashed broken) =9.0 + 0.06 × VH (R^2 =0.032 n.s.); Hoverflies (+, solid line)=5.63 + 0.67 × VH (R^2 =0.36; F=12.11**); Beetles (▲, dashed line)=2.36 + 0.15 × VH (R^2 =0.21; F=5.86*). Insect and vegetation measures were made in 24 grasslands grazed at three intensity levels. Significant regression lines are shown with bold lines, significance levels are indicated as p=: *<0.05, **<0.01.

Local or landscape variability

Vegetation height

Vegetation height and litter accumulation separated grasslands managed at the three intensity levels (*Paper II*) (Fig. 4). Sites with tall vegetation also had more bushes and less thick trees. Studies have shown that butterfly composition is determined by different succession stages when grasslands are abandoned (Balmer & Erhardt, 2000). Many beetles and hoverflies that use hollow trees for larval development dependend on the existence of large trees. Litter accumulation and the invasion of bushes are both associated with decreasing plant species richness (Hansson & Fogelfors, 2000). The diversity of hoverflies and beetles showed the opposite pattern (Fig. 3, Table 3).
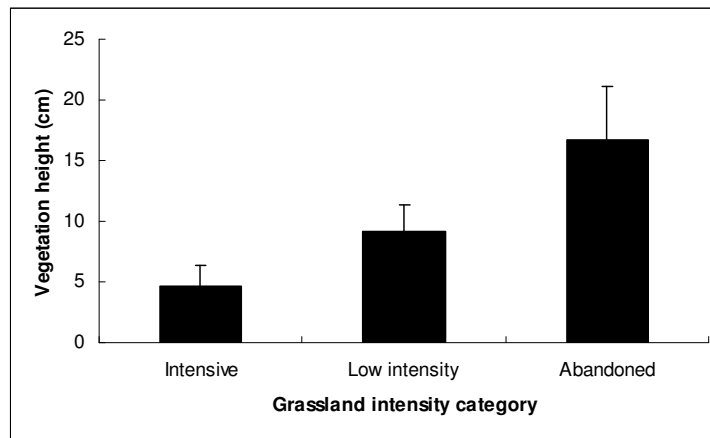
Fig.4. The relation between mean vegetation height from grasslands, in eight areas, managed at three intensity levels: intensively grazed, low intensive grazing and abandoned. Mean vegetation height per grassland (± s.e.) originates from measures with a rising-plate meter: nine measures in four plots, four times during the season in eight pastures for each treatment.

Flower abundance

In *Paper I* the relation between low grazing intensity and high flower abundance was established. In *Papers II-IV* this relationship was not found. The reason for this may be that only plant species rich grasslands in each region were used. It may be that the chosen grasslands were not completely representative for grasslands in general, *e.g.* the sampled abandoned grasslands had not suffered too much from overgrowth and shadowing from trees and bushes.
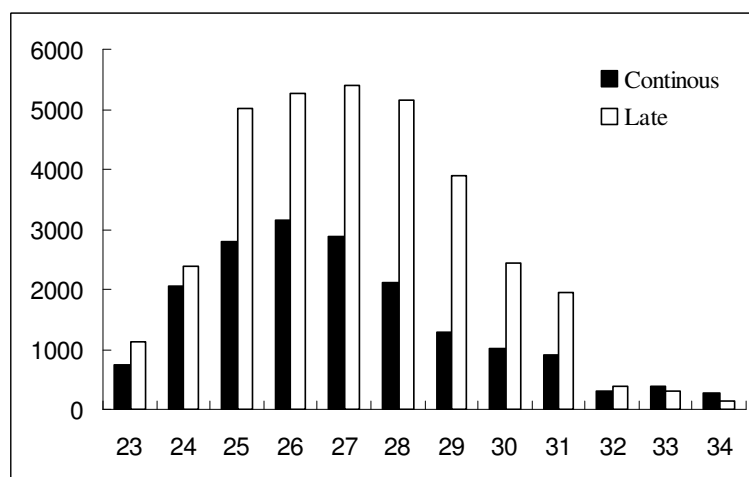
Fig.5. The change during the season (in 2003) in flower abundance between continuous and late grazing. The sum of flowers from four plots is shown.

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In *Paper I* flower richness was higher in late grazing (Fig. 5), and insect behaviour was obviously related to plant species richness by directing species and individuals to flower rich patches and in relation to the plant species visited. However these relationships were not observed on larger scales. Plant species richness did not differ between grasslands grazed at different intensity levels, and plant species richness did not influence insect composition.

Landscape characteristics

In *Papers II-IV* a number of landscape characteristics were important for reproductive success, species richness and composition of different flower visitors.

Forest cover

In *Paper II*, forest cover was a good predictor of hoverfly diversity, in accordance with previous studies (Haslett, 2001; Ouin *et al.*, 2004). At sites in open landscapes, species related to trees are less common, since a large group of hoverfly species' larvae eat aphids specialised on specific tree species (Torp, 1994; Sommaggio, 1999).

Roads

In *Paper II*, there were contrasting effects of roads on bees and butterflies. Species richness in the former increased whereas the latter decreased. Roads constitute linear elements that may function as corridors connecting foraging patches in the landscape (Beier & Noss, 1998; Tewksbury *et al.*, 2002; Damschen *et al.*, 2006). Among bees, mainly species richness of bumblebees and oligolectic bees were enhanced as the number of roads increased (see *Paper III*). Roadsides may be used as an alternative habitat providing pollen and nectar. But, because roadsides are linked to human activity, this may also cause direct mortality, especially for butterflies. Roadsides may be used as habitat for larvae in both groups (Erhardt, 1985; Westrich, 1990; Balmer & Erhardt, 2000). Roads may, however, constitute sink habitats for butterflies (Dias, 1996; Battin, 2004) since dust and mowing might be detrimental to the unprotected larvae.

Buildings

In *Paper IV*, the importance of human presence in the landscape to trap-nesting bees was shown (*e.g.* Fig. 6). . Many structures such as large trees, timbered houses, wooden fences and thatched roofs are traditionally connected to buildings and may function as important nest-substrates for cylinder nesting bees. Also an increased diversity of floral resources is connected to traditional management methods, such as mowing, gardening and extensive grazing (Hansson & Fogelfors, 2000; Jensen & Meyer, 2001; Stammel *et al.*, 2003).

Life-history strategies

In *Paper II*, the analyses on species composition revealed a large variation in community structure in bees. In *Paper III* different life histories and nest-preferences within bees were shown to explain much of this variability.

Solitary, soil-nesting bees

Soil nesting bees and nest-parasites increased with grazing intensity, in contrast to other groups. In line with a previous study from the Mediterranean (Vulliamy *et al.*, 2006) this was found to be a result of their dependence of open sandy soil for the nest construction (*Paper III*). The same trend was found in bees hibernating as larva and adults.

Nest-parasites

In *Paper III,* species richness of nest-parasites increased with increased grazing intensity. In *Paper IV* the reproductive success of a nest-parasite in terms of size and number of offspring produced was shown to depend on three alternative hosts. Because hosts used different parts of the landscape, this had consequences reproductive output.

Fig. 6. The reproductive output for *Hylaeus communis* related to building proximity and density in the landscape. The female completes a nest cylinder with mucus 2006-07-24.

Cylinder nesting bees

Papers III and *IV* examined diversity and reproductive success in cylinder nesting bees in relation to local and landscape variables. Results from these studies indicate that this group may not be as severely affected by landscape-wide intensification, by means of eutrophication, as many other groups of bees. Some reasons for this may be good flight ability, generalist plant use, and late appearance

during the season, when flower abundances generally are higher. The nesting strategy is connected to dead wood and tree cover, which in this study was correlated with indicators of eutrophication in the grasslands (R^2=0.21, p=0.023). In *Paper III* human presence and activity was shown to enhance reproductive success for cylinder nesting species (*e.g.* Fig. 6). This points out another important part of landscape intensification, i.e. centralisation and marginalization. These processes increase the extent and sizes of farms in productive areas, whereas small, isolated farms are abandoned (Ihse, 1995). For cylinder nesting bees this means loss of farm availability in the landscape.

Bumblebees

Papers I and *III* examineed bumblebee behaviour, diversity and abundance. Bumblebees aggregate in flower rich areas, but within the landscape flower rich grasslands did not increase bumblebee abundance and diversity. Not all species were positively influenced by low grazing intensity with the generally higher flower abundances.

Fig. 7. *Bombus ruderarius* (Müller 1776) ♂ feeding on a *Centaurea jacea* L. 2004-09-04. Relates to road length and grassland cover in the landscape (*Paper III*), a species appearing late in the season that decreases in Western Europe.

Many of the threatened bumblebee species in Western Europe have long tongues, fly late in the season, have small colonies, and build nests in vegetation rather than underground (Williams, 1986; Goulson *et al.*, 2005) (*e.g.* Fig. 7). Species with these features were among those influenced by grassland cover and road length. Why are these species especially sensitive? There are good reasons for building colonies later in the season: taller vegetation for nest formation, avoidance of risks with early season fluctuating weather, and escape from nest-parasites. On the other hand, colonies formed late may suffer from increased competition for floral resources and have a shorter time for development. The longer tongue in

many late flying species may be an adaptation to handle the deep late-blooming flowers, or alternatively necessary equipment for late-flying species to be able to compete with early fliers (Ranta & Lundberg, 1980).

The quality of the surrounding landscape is crucial for production of large bumblebee colonies (Goulson, 2003). As floral habitats are becoming increasingly scattered, those species dependent on fast colony development will suffer the most. Bumblebee species forming colonies late are therefore most vulnerable as they depend on good resource patches that are either close to the nest, or easily reached through line-elements in the landscape (*Paper III*).

Diversity and conservation practises

The goal to preserve biodiversity is not politically controversial, and is part of environmental policy. However diversity as such is often not a useful measure for decisions on conservation issues in practice. Three fundamental questions have to be answered first: 1) On what scale should diversity be preserved? 2) What diversity should be preserved? 3) What are the prerequisites in terms of grassland and landscape qualities, degree of isolation, complementation and landscape distinctive characteristics? I think that a target scale for decisions and species in focus for conservation actions has to be explicitly stated: local or landscape.

Conservation actions taken to preserve species at one scale may involve a decrease in diversity on another scale. For example, my results suggest that managing grasslands in an optimal way to enhance local diversity of insects entails less intensive grazing than what is recommended today on the basis of plants. However, species positively influenced by extreme intense management would probably disappear in the landscape as a whole, if this strategy were used for all grasslands in a landscape. On the other hand, managing landscapes to enhance diversity at the landscape level may decrease local diversity in grasslands.

Let us say that we want to preserve grassland diversity. But it is not possible that all grasslands will contain all species and that all landscapes have the prerequisites to contain all kinds of organisms. Many studies have shown that the diversity (richness) and abundance of different organism groups are not correlated (Kruess & Tscharntke, 2002b; Vessby *et al.*, 2002; Weibull *et al.*, 2003; Wolters *et al.*, 2006). This means that even if we have perfect information on all species, it is not possible to design single management programs that will enhance all species at the same time. This leads to more questions: Which species should be preserved and should they be found in each grassland or landscape?

Finally, it is important to ask which species should be the focus of conservation actions. Perhaps threatened species should be considered first. In Sweden, the Swedish species information centre evaluates decreasing species and species with limited distributions, which every fourth year results in a revised list containing Regionally threatened species (Gärdenfors, 2005). Another approach may be to base conservation efforts on the economic importance to human welfare that

different species possess (Kevan & Phillips, 2001; Kremen, Williams & Thorp, 2002; Roubik, 2002; Klein, Steffan-Dewenter & Tscharntke, 2003; Kremen *et al.*, 2004; Veddeler, Klein & Tscharntke, 2006; Klein *et al.*, 2007). Then pollinators and decomposers are are among the groups that provide important ecosystem services. But it may be even more important to investigate the ecological importance of different species (Chapin *et al.*, 1997; Loreau *et al.*, 2001; Lundberg & Moberg, 2003; Larsen, Williams & Kremen, 2005). Which species are needed to maintain ecosystem diversity and its functions? Many attempts have also been made to find species that are especially sensitive to environmental change and species that react in the same way as many other species. Such species may function as key-species, umbrella-species or indicators. Flower visitors acting as pollinators fulfil most of the above mentioned grounds for extensive care, but no single group appears to be useful as an indicator of the other and members from all groups are needed to maintain diversity.

Recommendations

How is it possible to use contrasting responses of organisms in different groups or within groups, such as those detected here, in conservation actions for preservation of biodiversity? One way may be to provide alternative strategies for conservation actions in the future. It has been suggested that landscape planning may be a useful tool to conserve diversity (Opdam, Foppen & Vos, 2002; Opdam, Steingröver & van Rooij, 2006). Several alternative strategies may give rise to similar diversity although species composition will be different. I suggest four alternative strategies that may be the foundations for conservation actions for flower visitors in different landscape settings and in relation to special characteristics.

A) Highly fragmented landscapes. In landscapes containing very isolated grasslands, conservation actions may best be applied at the grassland level. A diversity of local environmental factors can be assumed to increase diversity in each grassland. Low intensity grazing may then be recommended as a standard method to maintain areas in grasslands containing sparsely vegetated soil (important for some solitary bees), but also tall vegetation for nests (for some bumblebees) and flower abundances large enough to maintain viable populations each year. The behaviour of grazers will result in local variability in grazing intensity. Additional actions to reduce invasive tree and bush vegetation might be necessary. Whether or not isolated grasslands may maintain viable populations of pollinators also depends on grassland size (e.g. MacArthur & Wilson, 1967; Öckinger & Smith, 2006).

B) Landscapes containing linked grassland habitats. Grasslands that are well connected in the landscape may be suited to complement each other. Some grasslands may be managed to enhance nesting sites for bees and therefore intensively grazed, whereas other grasslands may be managed as foraging patches and therefore grazed at a lower intensity. Abandoned grasslands may also be a part of the larger interconnected system of semi-natural grasslands. If the target is to preserve species, variation in management at the landscape level is preferable to

variation within grasslands, as it ensures that local populations are large enough to survive. In addition, a good option at the landscape level could be to rotate between intensive and low-intensity grazing on a longer time-scale (Bengtsson *et al.* 2003). This should be done asynchronously at the landscape level, mimicking the wax and wane of grazing pressure in the traditional landscape (Dahlström, 2006).

C) Grasslands with distinctive characteristics. Grasslands containing certain special features of high conservation value should be treated in a special way: Geology, moisture, tree-cover, sand cover, presence of rare plants or, for flower visitors, important nutrient plants or adjacent land cover types may be grounds for special treatment. Although not studied here, moisture gradients have been shown to affect plant species composition and productivity considerably. A higher grazing pressure may have to be considered to suppress dominant grasses. Tree and bush cover and adjacent land cover types may be important for some flower visitors e.g. hoverflies. In such grasslands low intensity management may be considered. Sand cover increases the diversity of soil nesting bees and intensive management may enhance as the availability of nesting sites. Certain nutrient plants may be required for some flower visitors and grazing intensity may be adjusted to favour those plants.

D) Landscapes with distinctive landscape and traditional characteristics. An alternative option to complementary grasslands may be to design management strategies in a landscape to suit a particular group of flower visitors. A landscape containing many sandy ridges may be especially suitable for sand nesting bees. Grasslands in landscapes containing many old trees or wooden houses with thatched roofs may be suited for enhancing the diversity of cylinder nesting bees and forested regions may be appropriate for increasing diversity of hoverflies. This option requires a consensus about management strategy within a landscape and a regional variation of management strategies suited to favour different organism groups in different landscapes.

The knowledge about the different responses in flower visitors may be used as background information when decisions about management are made. Traditional land-use, knowledge of residents and the preferences of stakeholders may form the basis for decisions on management in different landscapes (Treu *et al.*, 2000; Opdam, Verbom & Pouwels, 2003; Opdam, Steingröver & van Rooij, 2006). One of the most important issues for conservation in the future may be to handle increased fragmentation and abandonment of the countryside. The diverse responses of pollinators make them good indicators reflecting health of different parts of agricultural landscapes at the local to landscape scales.

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