Grazing and the effects on insect communities

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Abstract

Grazing is an important method in managing natural communities. The interaction between grazers and the plant community is relatively well known. The interaction between grazers and insect community is less well known. The vegetation affects the insect community by means of three factors, plant diversity, vegetation height and spatial heterogeneity. Plant diversity positively influences insect diversity, for there are many plants to specialize on. Plant diversity is often positively influenced by grazing. The intermediate disturbance theory can the negative effect. Disturbance itself can be an additional influence on insect communities. An increasing vegetation height can increase the abundance and thereby the numbers of species of insects. Although the height may be a measure of more area for insects to specialize on, the structural complexity of a plant can also increase the insect diversity or species richness. However, both height and complexity are decreased by grazing and thus the overall effect of grazing on insects can differ much. Spatial heterogeneity, or the spatial structure, also positively affects the insect community. The effect of grazing on spatial heterogeneity is most of the times positive, but the result of grazing on heterogeneity may be of similar causes as the plant diversity, namely part of intermediate disturbance. All factors positively effect insects. However, not all factors are positively influenced by grazing. Another cause for different results of grazing is the fact that trophic levels of insects respond differently to changes in vegetation. Mobile/predatory insects respond more to structural changes and immobile/phytophagous insects respond at a smaller scale and mainly at the plant diversity. Disturbance itself can give yet other results of grazing on insects. The best level of disturbance for insects differs with that of plants. The optimal regime for management is therefore hard to find.

Introduction

Increasing or maintaining biodiversity is often the main focus for management of natural communities (Morris 2000). Grazing is a commonly used method to manage natural communities and sometimes the grazers are part of the conservations focus as well. Much research has been done on the interaction between vertebrate grazers and the plant community and the plant community is also the main focus of preserving biodiversity (Olff & Ritchie 1998) (Box 1). Other species groups highly contributing to overall biodiversity in a system are observed less well. Invertebrates are very diverse and abundant, both above ground and in the soil (Morris 2000). The invertebrate community is very complex, with many species and multiple trophic levels. Therefore the focus in this literature study is mainly on above-ground insects and spiders[1]. Grazing by vertebrates has shown an interaction with the insect community (Table 1). This raises the question how does grazing affect the insect diversity?

I hypothesize that the vegetation affects the insect community and that these effects are manipulated by grazing (Figure 1). Herbivorous insects eat plants and other insects eat the herbivorous insects (Haddad *et al.* 2001). Therefore insects may react first of all to changes in vegetation. Based on difference in the vegetation mediated by grazing (Box 1), there are three possible factors to have effect on the insect diversity. These are plant diversity, vegetation height and spatial heterogeneity (Figure 1). Plant diversity may be a direct determinant for the diversity of insects (Figure 1:4). An increase in plant diversity may strongly increase insect diversity. The effect of grazing on the plant diversity should mostly be positive (Box 1 & Figure 1:1). The second factor, vegetation height, may affect the insect abundance and thereby the insect diversity and species richness as a taller vegetation has a possible higher carrying capacity (Srivastava & Lawton 1998) (Figure 1:5). The vegetation height is possibly negatively affected by grazing (Figure 1:2), as grazing decreases biomass (Box 1). At a large scale, spatial heterogeneity, the third factor, is positively affected by grazing (Box 1 & Figure 1:3). These structures may give different microhabitats for insects and thereby affect the insect diversity (Figure 1:6).

Next to indirect effects, some direct effect may occur. An example can be the increased chance of immigration of species due to dispersal by grazers (Figure 1:7), which also occurs with seeds and pollen (Box 1), but I do not expect this to be a major effect of grazing on the insect diversity, for most insects are herbivorous and may therefore depend on the vegetation more.

To investigate the hypothesized scheme, the arrows (see Figure 1) will be investigated one by one. This will be in order to know how vertebrate grazing affects insect diversity. For this we need to know: (1) how grazing affects the plant diversity; (2) how grazing affects the vegetation height; (3) how grazing affects spatial heterogeneity; (4) how plant diversity affects the insect diversity; (5) how vegetation height affects insect diversity; and(6) how spatial heterogeneity affects insect diversity. These subquestions will be covered in the three chapters: Plant diversity; Vegetation height; and Spatial heterogeneity.

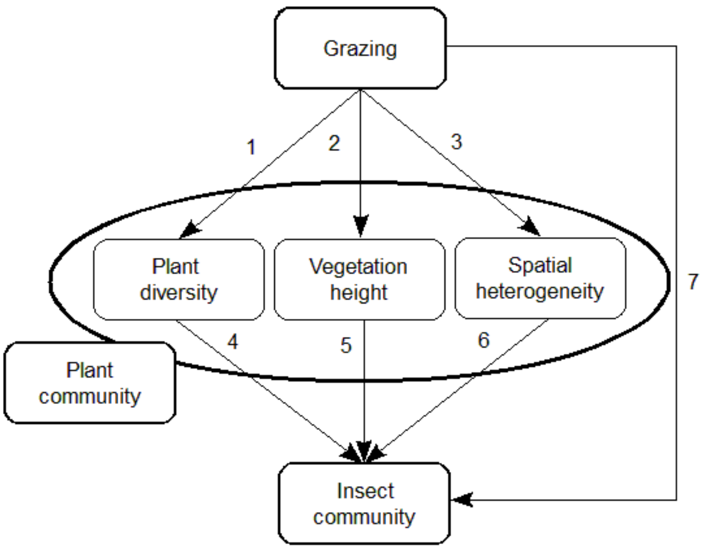

Figure 1: Hypothesized scheme showing direct and indirect interactions of vertebrate herbivores on the insect community. Based on figures from Delibes-Mateos *et al.* 2008, Olff & Ritchie 1998 and Stoner & Joern 2004.

1 When in this thesis it is spoken of insect communities, arachnids are included.

The studies used to find an answer to the main question are shown in Table 1. There are different outcomes of grazing on the insect community. It can have positive (Abensperg-Traun *et al.* 1996, Blaum *et al.* 2009, Gardner *et al.* 1997, González-Megías *et al.* 2004), negative (Baines *et al.* 1994, Woodcock *et al.* 2009), neutral (Rambo & Faeth 1999, Rexroad *et al.* 2007, Stoner & Joern 2004) or both positive and negative (Balmer & Erhardt 2000, Bestelmeyer & Wiens 1996, Gebeyehu & Samways 2003, Morries *et al.* 2005) effects on the invertebrate community (Table 1). The studies differ much from each other. The habitat types of the study site vary, including meadow, grassland, shrubland and woodland. There are also different grazers involved, each of which has their own effect by grazing (Morris 2000). Sometimes the focus of study species lies on one order only, such as *Lepidoptera* or *Orthoptera*, although others include entire insect communities (Arachnids included). Even when it is said that the whole community is sampled, the method of sampling matters. Pitfall traps are not unbiased (Bestemeyer & Wiens 1996), for example they catch mainly mobile epigeal insects (Cole *et al.* 2009), whilst using a sweepnet will only catch the plant dwelling insects (Rexroad *et al.* 2007). The type of study and its duration may also involve in a difference in outcome. Different grazing regimes may also have different effects of grazing on vegetation and on invertebrates (Olff & Ritchie 1998). Still these studies can cover the causes of possible differences of grazing on the insect diversity.

Box 1 – Effects of grazing on vegetation

Grazing has different effects on the vegetation. Olff & Ritchie (1998) describe the interaction between grazing and the plant community clearly. Grazing has both positive and negative influences on grazing. Plant diversity is one of the factors which increases when grazers are introduced. Competitively dominant pants can be eaten and thereby less dominant species have a greater chance to increase their abundance. This increases the plant diversity (Olff & Ritchie 1998). Connected to the increase in plant diversity is the increase in palatible plant abundance and species (Baines *et al.* 1994, González-Megías *et al.* 2004, Olff & Ritchie 1998). When whole plants are eaten, there is a stochastic chance of extintion of species. This also shows that the actual grazing is biomass reduction (Baines *et al.* 1994). A decrease in biomiass can also be a decrease in height. Due to selective grazing and a combination of height reduction and diversity increase, the spatial heterogeneity increases.

Rather less direct effects of grazing on the plant community are dispersal and soil disturbance. Grazers have the ability to carrry along seeds. The relatively long distances which grazers can cover can increase the chance of immigration of species into a community (Olff & Ritchie 1998). The movement of grazers can also have another effect. By trampling or upturning of soil, species may be eliminated, whereas other species find new microhabitats to colonize (Olff & Ritchie 1998).

Table 1: The studies involving the effect of grazing on insect communities. The effect of grazing on insect diversity is either positive, negative, neutral or both positive and negative. The different habitats of grazing, different grazers, different study species and a short discription of the study (study type, longitude of grazing, duration of study) are also given. The longitude of grazing regime is from the time started until the first measurements of the study. The duration of the study is the time from the first measurements until last year of mesurements, either in years following (x yrs) or the years in which measurements have been done (yr x).

Habitat type	Grazers	Invertebrates	Effect	References	Study type	Longitude of regime	Longitude of study
Woodland	wild ungulates	all (sweepnet)	Negative	(Baines *et al.* 1994)	Exclosures	unknown	2 yrs
	sheep	all (pitfall)	Positive	(Abensperg-Traun *et al.* 1996)	Habitat fragmentation, grazed & ungrazed remnants	Longterm	1 yr
	livestock	Hymenoptera, ants	Both	(Bestelmeyer & Wiens 1996)	Exclosure & grazing gradient	8, 18 & 60 yrs	1 yr
Shrubland	sheep	Auchenorryncha	Both	(Morris *et al.* 2005)	Exclosure & rotational grazing	Direct	Yr 1-5
	sheep & wild	Carabidae	Positive	(Gardner *et al.* 1997)	Grazed & ungrazed areas	unkown	3 yrs
	sheep & wild	all (pitfall)	Positive	(Gonzales-Megias *et al.* 2004)	Exclosures	2-3 yrs	Yr 1,2 & 4
	livestock	all (pitfall)	Positive	(Blaum *et al.* 2009)	Shrub cover gradient	unknown	2 yrs
Grassland	wild ungulates	all (sweepnet)	Neutral	(Rexroad *et al.* 2007)	Exclosures	35-55 yrs	1 yr
	wild ungulates	all (sweepnet)	Neutral	(Stoner & Joern 2004)	Grazing & haymaking	Longterm	unkown
	livestock	Orthoptera	Both	(Gebeyehu & Samways 2003)	Ungrazed, non-continously grazed & continously grazed	Longterm	2 yrs
	livestock	Orthoptera	Both	(Balmer & Erhardt 2000)	Grazed, short- & longterm ungrazed	2, 10 & 25 yrs	1 yr
Meadow	Cattle & wild	all (sweepnet)	Neutral	(Rambo & Faeth 1999)	Exclosures & rotational grazing	1 & 8-9 yrs	1 yr
	livestock	all (suction sampler)	Negative	(Woodcock *et al.* 2009)	Exclosure & rotational grazing	Direct	3 yrs

Plant diversity

It is commonly thought that plant diversity and insect diversity are positively related (Haddad *et al.* 2001, Siemann *et al.* 1998). More species of specialist feeders can be present when more species to provide niches are found in a community (Haddad *et al*. 2009, Reid & Hochuli 2007). A recent study by Woodcock *et al.* (2009) shows that there is a positive relationship between plant diversity and insect species richness. However, this effect differs between different functional groups. Predatory insects and spiders do not correlate with vegetation species richness. Herbivorous insects do show a positive correlation with plant species richness. Between groups of herbivorous insects the relation with plant diversity differs. According to Woodcock *et al.* (2009) specialists, like mono- and oligophagous insects, are less dependent on plant species richness than polyphagous insects. Furthermore, Stoner & Joern (2004) found that the effect of the plant community composition differed between trophic levels. Phytophagous insects (*Orthoptera*, *Curculionidae* (*Coleoptera*) and *Lepidoptera*) were strongly affected by changes in the plant community. Predators, in this case *Coccinellidae*, showed no dependence on plant community composition.

Others study showing a positive effect of the plant diversity or richness on insect diversity or richness are González-Megías *et al.* (2004) and Rexroad *et al.* (2007). González-Megías *et al.* (2004) concluded that grazing had a positive effect on the insect community. However, by which means this was, either diversity, abundance or richness, differed per site. Arthropod and beetle diversity significantly increased with plant diversity (Figure 2), meaning insects do relate with the diversity, but probably grazing has different effects on the vegetation. Rexroad *et al.* (2007) conclude that the effect of plant diversity on insects is neutral and insects only respond to biomass. Rexroad *et al.* (2007) include in their measurements the species richness of both plants and insects. However, they do not show any possible relation between them. In Figure 3 I plotted the species richness of the plant as a variable for the insect species richness. Although no statistics can be used, there is a positive trend between the richness of insects and plants, except for the insects in May. As a reason, I suggest that the plant richness, which was measured at the end of June, is not a good reflection for the active plant community in May. The results of their study also shows that the difference in species richness of plants is not unidirectional inside and outside exclosures. Therefore, I would add the suggestion that the species richness effects the insect community too.

Unlike the studies above, Gebeyehu & Samways (2003) did not find a positive effect of plant diversity on insect diversity. Instead of diversity they used species richness. Gebeyehu & Samways found that *Orthoptera* richness is not influenced by the plant species richness of their habitat. However, they find both a negative and positive effect of grazing on *Orthoptera* diversity. Continuously grazed lands have a lower abundance and richness of grasshoppers than ungrazed sites. In the rotational grazing regimes the abundance and richness of *Orthoptera* is higher than the ungrazed sites.

Yet other results were found by Balmer & Erhardt (2000). Their results were in line with the intermediate disturbance hypothesis (Box 2). Balmer & Erhardt (2000) found on long-term ungrazed mountain slopes, that forest starts to arise. The vegetation was slowly reaching the final stage of succession. In those sites, the number

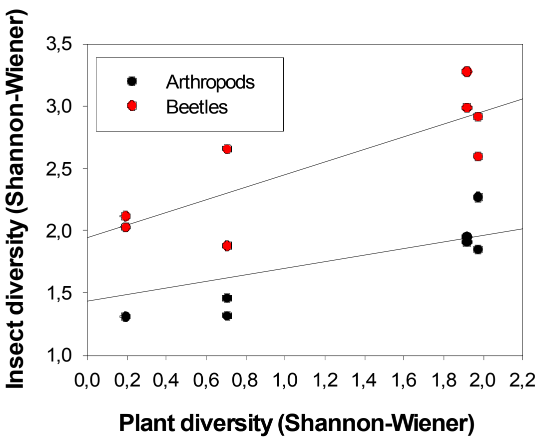

Figure 2: Data points based on results from González-Megías *et al.* (2004). A positive trend between plant diversity and insect dversity.

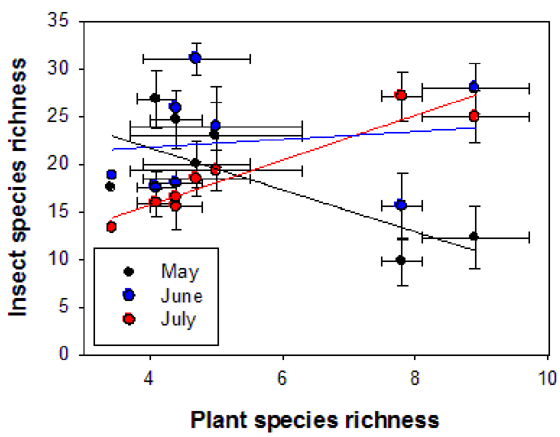

Figure 3: Data point based on results from Rexroad *et al.* (2007). A positive, slightly positive and negative trend for species richness of plants and insects. Error bars are based on mean values of measurements in 2 or 3 sites. Data points without error bars were single measures.

of lepidopteran species and their abundance were dramatically lower than in grazed or ungrazed sites for a few years. And although the grazing had a negative effect on the *Lepidoptera* community, even after two years of non-grazing, it shows that some disturbance is needed to stop the vegetation becoming a forest and decreasing the lepidopteran diversity. The findings of Gebeyehu & Samways (2003) are also in line with the intermediate disturbance theory. Although their regime of continuously grazed sites is extensive, probably the disturbance effect is too high, because the richness and abundance of grasshoppers is lower than in seasonally grazed sites. Also Morris *et al.* (2005) found results corresponding with the intermediate disturbance theory. After exclusion of intensive grazing, the number of many Auchenorrhyncha increased markedly.

Although these studies seem to accept the intermediate disturbance theory, Bestelmeyer & Wiens (1996) found along their land use gradient the exact opposite of the intermediate disturbance theory (Figure 4). They used four disturbance gradients in semi-arid woodlands of Argentina. Highly restored parts (HR) have been ungrazed for 6 years and moderately restored parts (MR) for 3 years. Moderately degraded parts (MD) were less instensively grazed than highly degraded parts (HD) where grazing of cattle and goats has occured for the last 60 years. Their results on species richness in ants do not coincide with the intermediate disturbance theory. Bestelmeyer & Wiens (1996) suggest that the heterogeneity which is of importance to ants may be greater at the extremes of non disturbance and high disturbance.

Intermediate disturbance is not the only cause of a positive relationship between plant diversity and insect diversity. A high species richness of plants creates more different microhabitats. Different levels of palatability, different vegetation structures and different plant structures. More species of plants may result in more specialists or at least more niches to be taken.

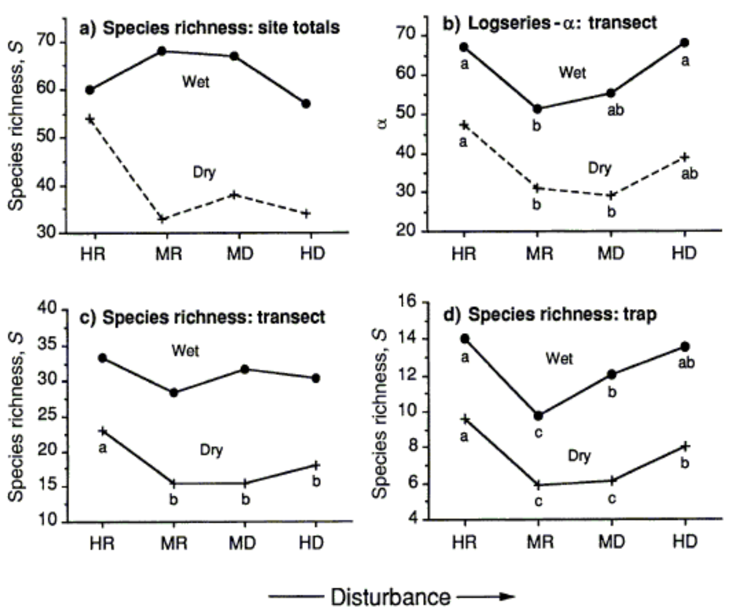

Figure 4: a) n = 1, b) n = 4, c) n = 4, d) n= 20. The three different methods for measuring species richness (a,c,d) and diversity (b) along a disturbance gradient measured in wet and dry seasons. Different letters next to symbols indicate differ significantly (P < 0,05). HR = highly restored, MR = moderately restored, MD = moderately degraded, HD = highly degraded. (Bestelmeyer & Wiens 1996)

Box 2 – The intermediate disturbance hypothesis

The intermediate disturbance hypothesis (Figure 5) is a theory in which the effect of disturbance upon diversity or species richness is described (Krebs 2001). Disturbance is a group of factors which can prevent domination of species with high competitive ability. For example, these factors can be outbreaks of fire, herbivory, predation (Krebs 2001, Morris 2000, Olff & Ritchie 1998). Another example is herbivory seperated in factors, such as soil disturbance and biomass reduction.

When disturbance is very low, hardly any effect shows. An equilibrium arises in which dominant species have competitively have excluded other species and only a few species occur (Krebs 2001) (Figure 5).When a lot of disturbance occurs an equilibrium is prevented. Species which have high rates of increase can survive. Thereby, this state has also low species richness and diversity (Krebs 2001) (Figure 5).

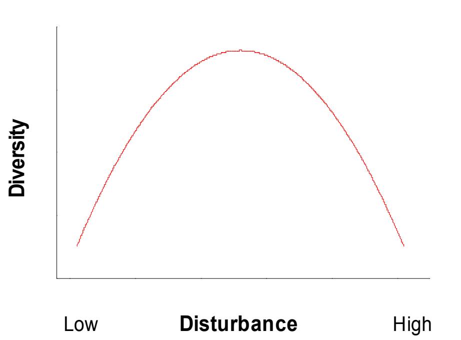

Figure 5: The intermediate disturbance theory of diversity. It predicts that diversity is optimized at levels of intermediate disturbance. (Krebs 2001)

It is hypothesized that in between these high and low disturbance states, the diversity and species richness is higher. At intermediate disturbance levels, the diversity and species richness is optimized (Figure 5). Disturbance allows fast growing species to be present, but be partly outcompeted by dominant species. Disturbance also prevents the dominant species to exclude all other species (Krebs 2001). The effect of grazing on the diversity or species richness on plants can be not always positive, if grazing is to high or to low a disturbance.

Vegetation height

A tall vegetation probably has a high carrying capacity for insects (Baines *et al.* 1994, Haddad *et al.* 2001). Therefore tall vegetation might have more individuals and thereby more species, although not necessarily a higher diversity (Haddad *et al.* 2001, Srivastava & Lawton 1998). As grazing decrease height, this would be a negative effect of grazing. Reasoning the other way round, grazing is actually decreasing pant biomass (Baines *et al.* 1994). When this happens, insects living in or on plants may accidentally be eaten too (Baines *et al.* 1994, González-Megías *et al.* 2004). Assuming grazers do not specifically choose to eat insects, the number of species can be reduced stochastically. Thus the height of vegetation may play an important role in the diversity of insects, not only direct by being accidentally eaten, but also indirect, as the carrying capacity of the vegetation increases with height.

Although some studies did not use height as one of the influencing factors, some studies did, but showed other factors to determine the insect diversity (Blaum *et al.* 2009, Gebeyehu & Samways 2003, Morris *et al.* 2005). There are studies in which the height is in some way responsible for the differing insect diversity. These are elucidated below.

The height of the habitat, e.g. woodland, grassland or shrubland, may have influence on the abundance and the species richness of insects. However, this is only of importance if the grazing regime applied has such an effect on the vegetation. At the study site of Balmer & Erhardt (2000) this is the case. Their long-term ungrazed plot has started to become a forest and their intermediate-term ungrazed plot is dominated by blackthorn. Their grazed and short-term ungrazed plots are grassland and statistically do not differ. Balmer & Erhardt (2000) show that the abundance and number of species butterflies (*Lepidoptera*) is lowest in the forest sites. The species richness is highest in the shrub site and the abundance of species is highest in the grass sites. There is no clear effect of height on the species richness or abundance of these butterflies. It seems that the intermediate disturbance theory is the best explanation for the differences in diversity.

Positive correlation between vegetation height and insect diversity or insect species richness were foudn in sutides of Morris *et al.* (2005), Rambo & Faeth (1999), Baines *et al.* (1994) and Gardner *et al.* (1997). Morris *et al.* (2005) found that *Auchenorrhyncha* were positively related with the vegetation height. However, this was not their main focus and they did not statistically test it. Not all insects are positively related with vegetation height. For example, the butterfly Adonis Blue cannot live in high vegetation. Morris *et al.* (2005) concluded that vegetation was neutrally affected by grazing and grazing neutrally affected the insect community. Both show negative (decreased vegetation height, decreased *Auchenorrhyncha*) and positive (intermediate disturbance, increase Adonis Blue and others) effects of grazing.

A more clear effect of vegetation height on the insect diversity is shown by Rambo & Faeth (1999). Inside exclosures, the vegetation reaches a meter in height. Outside the exclosure, herbivores grazed the vegetation to a height of 10 centimeters. Although a higher plant diversity was found outside the exclosure, in the exclosure there

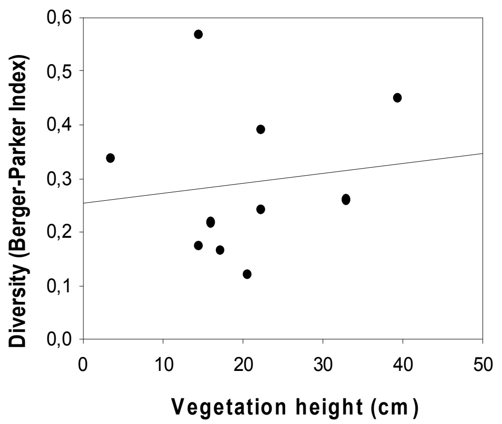

Figure 6: Data points based on results from Gardner *et al.* (1997) showing a slight positive trend between vegetation height and the insect diversity.

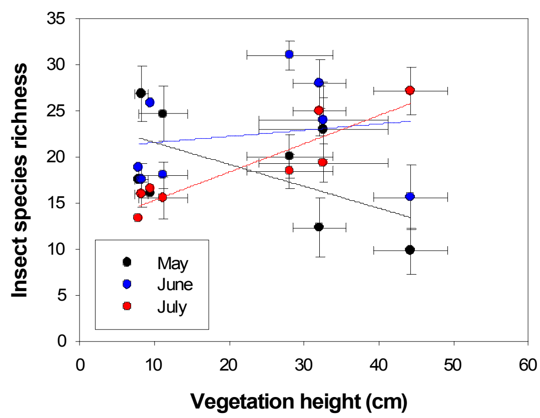

Figure 7: Data point based on results from Rexroad *et al.* (2007). A positive, slightly positive and negative trend for the relationship between vegtation height and insect species richness. Error bars are based on mean values of measurements in 2 or 3 sites. Data points without error bars were single measures.

was a higher insect diversity. This is a good example of the height of vegetation determining the diversity of a community. Therefore Rambo & Faeth (1999) concluded that grazing had a negative effect on the insect community. Baines *et al.* (1994) concluded the same and also for the same reason. The biomass and height of the vegetation was decreased by grazing and the abundance of same larvae was reduced up to a 4-fold. Also Gardner *et al.* (1997) conclude that the vegetation height is one of the two most important components which influence the carabid community, along with the soil organic content. To show this, I plotted their height measurements with the carabid diversity (Figure 6). To calculate their diversity, they used the Berger-Parker Diversity Index. The positive effect found of grazing on the insect community can be partially based on the vegetation height. The height of the vegetation in the ungrazed parts (22,49 cm) is indeed higher than in the grazed parts (17,15 cm).

Although Balmer & Erhardt do not show a clear pattern of height as an explanation for diversity and species richness, other studies do. Blaum *et al.* (2009) found that grazing caused degradation of the vegetation, which gave different percentages of shrub cover and that they reduced vegetation height. These two are correlated. As the percentage of shrub cover shows relationships with different groups of insects, this may be due to the loss or increase of vegetation height. Blaum *et al.* (2009) show that there is a vegetation height optimum at which both abundance (Beetles: P < 0,001, Spiders P = 0,003) and species richness (Beetles: P = 0,045, Spiders P = 0,045) are highest, which lies at about 15% shrub cover. The curve with an optimum may suggest that beetles and spiders are more dependent on the disturbance of grazing. Grasshoppers are both for abundance (P = 0,001) and species richness (P < 0,001) negatively correlated with shrub cover. The abundance of ants (P = 0,008) and scorpions (P = 0,004) is positively related to shrub cover, whilst *Solifugae* abundance is negatively related (P = 0,013). These were the significant results, the other insects (richness and abundance of stick insects and termites) were not affected by grazing (P-values not given, but higher than P = 0,05). The effect of grazing and vegetation height are similar, but different for each insect group.

As mentioned in the introduction, the actual grazing is reducing biomass. As a consequence height is reduced. Not only would one expect that the increase in height would increase the species richness or diversity of insects, an increase in plant biomass would also increase species richness or diversity. Rexroad *et al.* (2007) found such a relationship in their results. To confirm the idea of the height affecting the insect community, I plotted the vegetation height as a variable for the insect species richness (Figure 7). Although no statistics can be used, the graph shows a positive trend between the vegetation height and insect species richness, except for the insects in May. As a reason, I suggest that the plant richness, which was measured at the end of June, is not a good reflection for the active plant community in May. Rexroad *et al.* (2007) conclude that the effect on insects is neutral and insects only respond to biomass increase. This is possible strongly related to the height of the vegetation. And as the effect of grazing on vegetation height is not unidirectional, this is probably the main cause for their findings.

Woodcock *et al.* (2009) did not take height as one of the possible effects on insect communities, instead they used structural complexity. The strucutral complexity could explain the possible increase in insect species better, for more niche differentiation is possible, when the structural complexity is high (Reid & Hochuli 2007). Phytophagous insects can specialize on structures, such as roots, stems and flowers (Morris 2000, Woodcock *et al.* 2009). To predatory insects, complex structures can be used as shelter or for spiders to specialize by different web strucutres. Their results showed that both phytophagous insects (Figure 8(a)) and predators (Figure 8(b)) were strongly related to the structural complexity of the sward. In the models used, for predators 90% was explained by the complexity. For phytophagous insects this was only 50%.

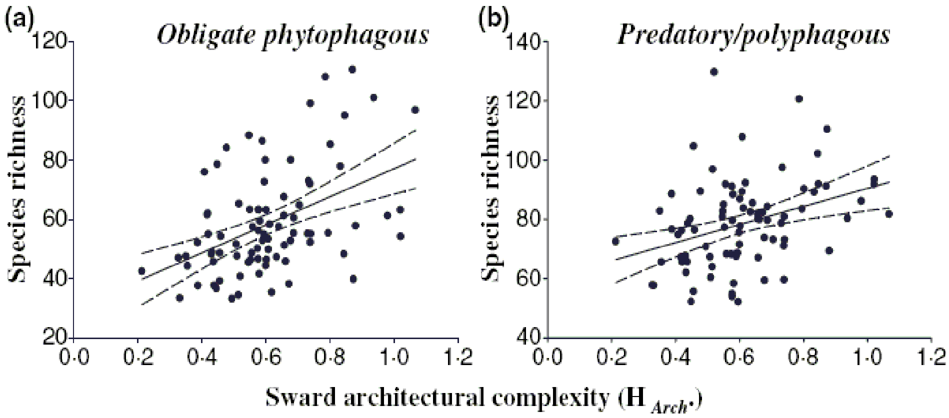

Figure 8: Relationships between structural complexity (sward architectural complexity) and (a) phytophagous insects and (b) predators with a regression line. Univariate 95% interval lines (dashed) providea visual reference for the relationship. (Woodcock *et al.* 2009)

Spatial heterogeneity

Spatial heterogeneity is the diversity on a large, spatial scale. Patches with palatible, grazing tolerant plants where herbivores graze are alternated with patches with unpalatible vegetation, with grazing intolerant plants in between. The patches with palatible, grazing tolerant plants are often lower in height and have are of higher quality than the patches with unpalatible and grazing intolerant plants. Different structures of the patches, such as height and denseness, may provide different microhabitats (Morris 2000, Delibes-Mateos *et al.* 2008). A high spatial heterogeneity is expected to increase the diversity of insect species. As grazing stimulates spatial heterogeneity (Olff & Ritchie 1998), grazing may increase the diversity of insect species.

Concerning the effect of spatial heterogeneity on insects there are two hypotheses. The habitat heterogeneity hypothesis presumes an asymptotic relationship between both an increase in the number of plant species and a higher level of heterogeneity together and the number of species and abundance of insects (Dennis *et al.* 1998). The second hypothesis is the symbiosis between patches hypothesis. This states that the size of a patch has a unidirectional relationship with the number of species and abundance of arthropods. The patches must be large enough to support populations, but small enough that interspersed tussocks provide shelter from weather and grazing disturbance (Dennis *et al.* 1998). In the study by Dennis *et al.* (1998) the area structure showed an asymptotic relation with richness and abundance of insects, supporting the habitat heterogeneity hypothesis However, this does not mean that it holds for all plant-insect community interactions. Blaum *et al.* (2009) did not find such a relationship, not one proposed by the habitat heterogeneity theory and not one proposed by the symbiosis between patches theory. In their results, the insects reacted to the vegetation often in a bell shaped way, with a maximum at 15% shrub cover. Gardner *et al.* (1997) do show that there are some insect carabid communities associated with some special plant communities. When an area is heterogenous with those plant communities and the patches are large enough to support populations (as in the symbiosis between patches theory), there is possible coextistence of both insect communities in the same areas.

Without further elaboration of these theories, for many studies do not recall them, heterogeneity still may show an effect on insect community. The scale of spatial heterogeneity can be large. Abensperg-Traun *et al.* (1996) looked at a large scale heterogeneity, the habitat fragmentation. This was probably a too large scale, for habitat fragmentation was not the factor influencing the insect community, but disturbance was.

Balmer & Erhardt (2000) also performed their research at a high spatial scale, although still a smaller scale than Abensperg-Traun *et al.* (1996). The study sites were in a forest area. There, the long-term ungrazed site is also becoming a forest. As explained previously, this site had a much lower abundance and species richness of insects. This part of the results may be explained by the spatial heterogeneity. The sites, with a size of 1000 m^2, are already becoming a forest and is therefore quite homogenous with the rest of the area. However, it may also still be an effect of a much lower diversity or low disturbance rate than the other sites. Within the other sites, the highest diversity found in the mid-term ungrazed site can be explained by the heterogeneity. The heterogeneity of this site (Average Fisher's $\alpha = 12{,}21$) is significantly larger compared with the grazed site (Average Fisher's $\alpha = 7{,}60$, $P = 0{,}006$) and the short-term grazed site (Average Fisher's $\alpha = 7{,}13$, $P = 0{,}007$). The difference of heterogeneity between the grazed site and the short-term grazed site is not significant ($P = 0{,}901$).

The scale at which heterogeneity is used does matter. Immobile species react at smaller scale differences than mobile insects (Cole *et al.* 2009). Stoner & Joern (2004) also found that in their study. Although phytophagous insects responded strongly to the plant community composition, predators did not. They respond to changes in habitat heterogeneity. However, Bestelmeyer & Wiens (1996) and Gebeyehu & Samways (2003) both suggest that some other spatial heterogeneity is also positively influencing insect communities. Gebeyehu & Samways (2003) state that more colors and substrates can show a positive effect on insect communities, whereas Bestelmeyer & Wiens (1996) suggest that the heterogeneity at extremes, which is probably lower than the optimum created at intermediate disturbance, is of more importance to special insect species or groups, such as ants.

Discussion & conclusion

Five factors are important in the effects of grazing on insect communities. First are the factors which I expected to be of importance, namely plant diversity, vegetation height and spatial heterogeneity. During the literature study, two more important factors became apparent, (intermediate) disturbance and the structural complexity of the vegetation (Table 2). These five factors can be influenced by grazing in different ways and have different effects on the insect community (Figure 9). With these five factors grazing can directly and indirectly influence the insect community. The interaction between plants and insects is assumed to be mainly bottom-up. Plants affect insects, but insects do not affect plants. (Rexroad *et al.* 2007).

The plant diversity is known to be positively affecting the insect diversity, but not always. Most of the studies on the effect of grazing on insects which include plant diversity, find a positive relationship between diversity of plants and insects (Figure 9). This is in accordance with theory, but not all studies show the same results. Even though this effect may be positive, the outcome of grazing on insects can show a different effect. Either grazing does not have a positive effect on the plant diversity, or other factors are of more importance.

Vegetation height is known to be positively affecting the insect diverstiy (Srivastava & Lawaton 1998). In most of the studies, this relationship was indeed found. Normally, grazing has a negative effect on the vegetation height (Figure 9). Therefore grazing can result in a negative effect of the insect diversity. In some cases (González-Megías *et al.* 2004, Rexroad *et al.* 2007) the vegetation height was not always decreased by grazing and therefore grazing resulted in a neutral or positive effect on the insect diversity.

The scale of spatial heterogeneity can differ. Most studies including spatial heterogeneity find a positive effect of increasing spatial heterogeneity on insect diversity. Grazing regularly influence the spatial heterogeneity positively (Figure 9). A point of discussion can be made here. The introduction of grazers or the exclusion of grazers may have different short term effects on the vegetation. Depending on the growth rate of competitive dominant plant species, the effect of introduced grazers may take longer to decrease enough dominant plant species to really increase diversity and heterogeneity. This would also mean that short-term studies might show no effect of grazing in a few years. The results of Balmer & Erhardt (2000) can be an example for that, as they found no difference between grazed and 2-3 years ungrazed. Back to spatial heterogeneity, another result found is that the size of the area observed may differ between groups of insects. Mobile insects react to a larger area than less mobile insects.

One of the two factors which I unexpectedly found is the structural complexity of the vegetation. It is quite similar to the responses on spatial heterogeneity, but this is a much smaller scale. One could also call this the vertical structure. Woodcock *et al.* (2009) showed the insect community has a positive relationship with increasing structural complexity. As Woodcock *et al.* (2009), Morris (2000) and Reid & Hochuli (2007) state, complex structures can provide more niches on which species can specialize. Grazing has a negative effect on the complexity (Figure 9) (González-Megías *et al.* 2004), but as this is only one study, it is interesting to know if in other communities, the same effect is found. The second factor unexpectedly found, was the effect of disturbance, which will be discussed later on.

The four factors summarized above are not isolated factors. Therefore, and for possible different effect of grazing on these factors, it is hard to predict how the plant community affects the insect community when exposed to grazing (Figure 9). In short I will discuss the interactions between the factors, but the main discussion should be about the interaction between insects and grazing and not plants affected by grazing. Diversity and vegetation height are probably related. As the height of

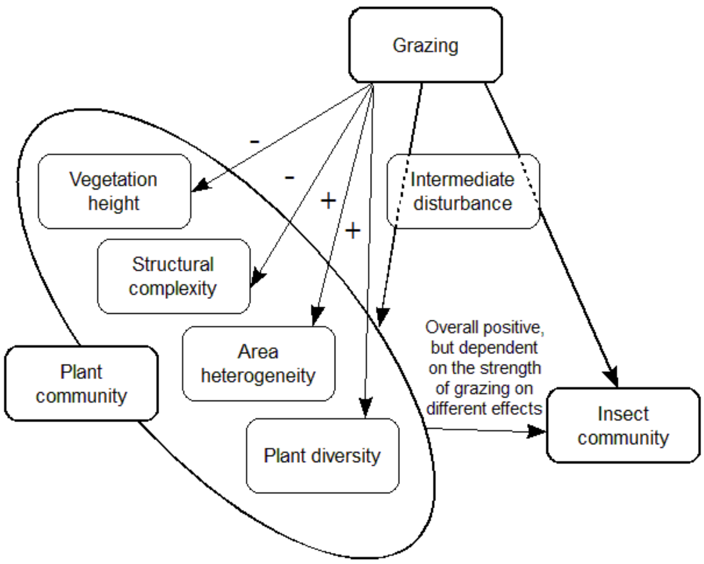

Figure 9: Scheme with conclusions of effect of grazing on the insect community through the plant community. All factors in the plant community influence the insect community positively. The effect of grazing on the plant community is direct, either positive or negative. Grazing can effect the indirectly by intermediate disturbance, but also directly by intermediate disturbance. The effect of this is dependent on the level of disturbance.

Table 2: Concluding effects of grazing on insects, the effect of grazing on plants and the factors of importance between plant and insect communities. Bold tekst shows the factor which is most important. Positive effect is +, negative effect is – and neutral effects is o. Multiple effects can also occur.

References	Grazing~insects	Grazing~plants	Plants ~ insects
(Gardner *et al.* 1997)	+	+	**Vegetation height**
(Abensperg-Traun *et al.* 1996)	+	o	**Intermediate disturbance**
(Blaum *et al.* 2009)	+	-	**Intermediate disturbance**, vegetation height
(Gonzales-Megias *et al.* 2004)	+	-	**Diversity**, vegetation height
(Balmer & Erhardt 2000)	+/o/-	+/-	**Heterogeneity**, intermediate disturbance, height
(Bestelmeyer & Wiens 1996)	-/+	+/-	Heterogeneity, intermediate disturbance
(Morris *et al.* 2005)	+/-	+/-	Vegetation height, intermediate disturbance
(Gebeyehu & Samways 2003)	+/-	-	**Intermediate disturbance**, heterogeneity
(Rexroad *et al.* 2007)	o	+/-	**Vegetation height**, diversity
(Rambo & Faeth 1999)	o	-	**Vegetation height**
(Stoner & Joern 2004)	o	-	Heterogeneity, structural complexity, height
(Baines *et al.* 1994)	-	-	**Vegetation height**
(Woodcock *et al.* 2009)	-	-	**Structural complexity**, species richness

the vegetation increases, competition for light gets more important. This will favour competitively dominant plant species and thereby decrease diversity. For the entire insect community this could be a kind of trade-off. Vegetation height has a higher carrying capacity for individuals, but the vegetation diversity offers more specialization for insects, especially phytophagous insects. Diversity can also be related to the spatial heterogeneity, for different plant species occur in different patches. When there are many patches, the diversity of plants will be higher. This is similar for the diversity and the structural complexity. Many plant species can increase the structural complexity, as different species have different structures. Both with heterogeneity and complexity, the interaction with diversity is unidirectional in their effect on the insect community. Diversity, heterogeneity and structural complexity all increase the diversity and species richness of insects.

Structural complexity, spatial heterogeneity and vegetation height also have their interactions. Structural complexity and spatial heterogeneity can actually be seen as the same measures, namely structural diversity. The difference is that structural complexity is more in vertical direction and on small scale, while spatial heterogeneity is more focused on patches with often differences in height and is focussed on a larger scale. This last part also explains the interaction between heterogeneity and height. Heterogeneous areas can have the same mean height as homogeneous areas, but in heterogeneous areas the variation in height measurements is much larger. On average the height decreases with grazing, and in the same time heterogeneity decreases. However, structural complexity might increase again, but this may be more related to the plant diversity. Many studies included height measures in finding the effect of grazing on insects (Blaum *et al.* 2009, Gardner *et al.* 1997, Rambo & Faeth 1999, Rexroad *et al.* 2007). The effects found in these studies can still be caused by structural complexity, as they did not specifically measure this. The effect of grazing on the insect community is therefore hard to predict, as these factors are not unidirectional influenced by grazing and due to the interactions also are not unidirectional in their effect on the insects.

Probably the most important factor for the effect of grazing on insect communities is intermediate disturbance. The intermediate disturbance theory has already been explained. At intermediate disturbance there is a balance between plants with low competitive ability and slower growing plants with high competitive ability (Krebs 2001). The diversity and species richness of the plant community is on its highest point. The fact that intermediate disturbance causes an optimum in vegetation diversity, also explains why some studies have a neutral effect of grazing on plants (Table 2). By using different grazing treatments, some are past the optimal disturbance and are even lower in diversity or richness than ungrazed sites. In those studies, grazing has both a positive and a negative effect on the plant community (Balmer & Erhardt 2000, Bestelmeyer & Wiens 1996, Gebeyehu & Samways 2003, Morris *et al.* 2005).

Disturbance is known to influence the diversity and species richness, but I suggest that it also can affect the heterogeneity directly. Trampling is an example of this. Trampling can create bare patches and effect the substrates directly, which can also be of importance for the insect communities. (Bestelmeyer & Wiens 1996, Gebeyehu & Samways 2003). In fact, this can be seen as a direct disturbance effect on insects. Another can be the eating of biomass. For plants factors of intermediate disturbance have often been elucidated. But what disturbance and therefore intermediate disturbance is for insects is still questionable. Still, the basis of this theory should be applicable to the insect community. Without disturbance, the insect community should not be diverse or species rich and with too much disturbance is low as well. For some part this can be true. Polyphagous insects can occupy highly disturbed sites. They can occupy large niches or are plastic in choosing a smaller niche. When disturbance is lower, specialists can come in and take small niches, driving polyphagous insects into niches left over. The last part, when disturbance gets very low and apparently specialists should take over can be true. On the other hand polyphagous insects can take over as well, for the disturbance is very homogeneous and less specialization opportunities occur and a monoculture is expected. This can possibly be explained as a direct effect of disturbance and as an indirect effect of disturbance, responding through the plant community.

The effects of disturbance on polyphagous and specialist insect may differ, so can the trophic level, or indeed the insect group have different effects (Haddad *et al.* 2009, Woodcock *et al.* 2009). The methods used (sweepnetting, pitfall, D-Vac) may be of influence on the results, for only specific insects group can be caught (Cole *et al.* 2009). It is possible to discuss this, but the different groups now allow us to distinguish between the effects of grazing on different groups. Gibson *et al.*(1992) also state this. They suggest that different groups can be indicators for different conditions. For a start, the effects of changes in the plant community are less strong in higher trophic levels, such as *Carabidae* and spiders (Haddad *et al.* 2001, Haddad *et al.* 2009, Siemann *et al.* 1998, Woodcock *et al.* 2009). Also mobile insects are reacting stronger to vegetation structures, such as complexity and heterogeneity than less mobile insects (Cole *et al.* 2009, Morris 2000, Woodcock *et al.* 2009). These structures can be higher both in grazed and ungrazed sites, thus a strong conclusion on the effect of grazing on mobile insects is hard. It is convenient that mobile species are often predators (Stoner & Joern 2004). Both a cause and a result of the lack of response of predators to plant species richness or diversity is their stronger response to structure changes. As we discuss differences in responses of groups, it may also occur that some specialists or some entire groups, do not live in certain vegetation at all (Morris *et al.* 2005) and therefore there are species shifts or even functional groups shifts in the insect community as a response to grazing (Haddad *et al.* 2009).

For management not only a problem arises as species may disappear entirely when grazers are introduced or excluded, but when the species richness or diversity of both plants and insects are to be maintained or maximized too. By using grazing as a management regime, this brings along disturbance. For plants and insects the level of disturbance which creates the most heterogeneous, diverse or species rich community can differ. I would call this a disturbance mismatch (Figure 10). Although the optimal disturbance for insects is hard to measure, if this optimum for insects is higher than that for plants, then the vegetation will slowly degrade to a stage which is similar to that of high disturbance. If the optimal disturbance for insects is lower than that of plants, the vegetation will slowly be driven by competition towards a climax stage, similar to that of low disturbance.

As insects are not isolated from changes in vegetation by means of vegetation height, plant diversity, spatial heterogeneity and structural complexity, I would suggest that management would maintain areas at the disturbance levels which optimize the plant community. Thorough, long-term research on the effects of grazing on both plant and insects communities should be done to find out what the optimal management method is. But it is not a simple matter of conserving the areas to give the highest diversity or species richness. Areas with other forms of management, left undisturbed or highly disturbed, ought to be maintained too. This would provide habitats for specialists which may not be able to exist in the sites which are not present with the suggested form of management (Balmer & Erhardt 2000, Bestelmeyer & Wiens 1996, González-Megías *et al.* 2004). And even a level higher, management is not only for diversity of both plants and insects, but also for other animals, which may be dependent on both, such as birds (Cole *et al.* 2009).

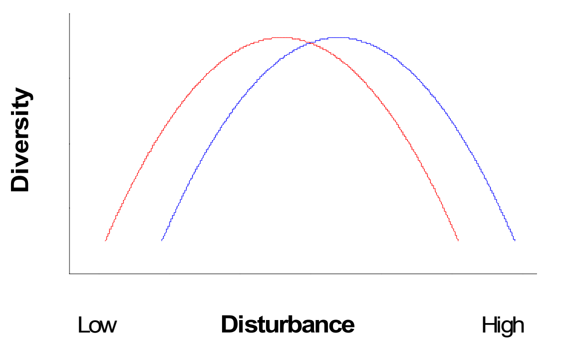

Figure 10: A mismatch between the optimized disturbance levels between different groups.

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