The effects of landscape configuration on species richness and diversity in semi-natural grasslands on Öland

A preliminary study

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Degree-thesis in Physical Geography and Ecosystem Analysis

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Abstract

Semi-natural grasslands are amongst our most species rich habitat types and house many threatened plant and animal species. These grasslands suffer from both quality deteriorations due to abandonment, fertilization etc., and from an increasing landscape fragmentation. In fragmented areas patches are smaller and more isolated from each other. If the anthropogenic influence is high, then they also tend to have relatively straight borders and a compact shape. As fragmentation is expected to affected plant and animal populations negatively it is of interest to examine further. The influence of patch size, patch shape and isolation on the vascular plant species richness and diversity in semi-natural grasslands on central Öland is therefore studied. The spatial pattern analysis program FRAGSTATS is used to quantify the configuration metrics and three different statistical methods are used to study the relationships; the t-test, Pearson's correlation coefficient and regression analysis. All three methods contribute with information in the analyses. Mean species richness and mean species diversity on the other hand give very similar results, so for the continued studies in the area it should be sufficient to study one of these metrics.

Although the regression analyses show that only a few percent of the variation in species richness and diversity can be accounted for by size alone all three methods indicate that area, core area and patch perimeter are positively related to both species richness and species diversity. No difference between the influence of total area and core area is found which may indicate that a too narrow edge zone is used when delimiting the core area. Furthermore, the results show that the effects of grazing and eutrophication are stronger than the effect of size.

Shape does not appear to influence the mean species richness and diversity in semi-natural grasslands as significance is low and different conclusions are drawn depending on which metric is used. If there is any influence then it must be relatively weak and depend on more variation in patch shape to show clearly. However, it is likely that the distribution of individual species or plant functional types is influenced by shape. To determine this further studies are required.

Isolation is found to influence species richness and diversity negatively but only a small part of the variation can be accounted for. Furthermore, all of the results are not robust. Patch size is not taken into account in the analyses due to the nature of the used data. Had this been done, then it is likely that the influence of isolation would have been sturdier, especially in the small patches. Interestingly, the negative influence of isolation does not appear to begin until the distance to the nearest neighbour exceeds 70 to 100 meters. Should future studies find similar results this would have implications for conservation work.

Some recommendations for the continued studies in these grassland areas are given in the last section. Size needs to be taken into account when analysing the influence of isolation. By including the historical extent of the grasslands in the analyses it is also likely that more knowledge and a greater understanding can be gained.

Sammanfattning

Semi-naturliga gräsmarker hör till våra mest artrika habitattyper och hyser många hotade växt- och djurarter. Dessa gräsmarker drabbas av både kvalitetsförsämringar, som följd av minskat bete, gödsling o.s.v., och av en ökad landskapsfragmentering. I ett fragmenterat landskap är gräsmarksområdena mindre och mer isolerade från varandra. Om den mänskliga påverkan är hög tenderar de även att ha relativt raka kanter och en kompakt form. Eftersom fragmentering förväntas påverka växt- och djurpopulationer negativt så är dess inverkan av intresse att studera ytterligare. Inflytandet av gräsmarkspatchernas storlek, form och isolering på kärlväxtrikedom och diversitet i semi-naturliga gräsmarker på centrala Öland studeras därför. FRAGSTATS, ett datorprogram för analys av rumsliga mönster, används för att kvantifiera landskapets konfiguration och tre olika statistiska metoder används för att studera sambanden; t-test, Pearson's korrelations koefficient och regressions analys. Alla tre metoder tillför information vid analysen. Genomsnittlig artrikedom och arttdiversitet ger däremot liknande resultat varför det vid fortsatta studier torde räcka med att studera endast en av dessa faktorer.

Trots att regressionsanalysen visar att endast ett par procent av variationen i artrikedom och artdiversitet kan förklaras av enbart storlek så indikerar alla tre metoderna att area, kärnarea och omkrets är positivt relaterade till både artrikedom och artdiversitet. Ingen skillnad mellan inflytandet från total area och från kärnarea framträder vilket kan tyda på att en för smal kantzon används vid avgränsningen av kärnområdet. Vidare, visar resultaten att påverkan från betning och övergödning är starkare än påverkan från storlek.

Form verkar inte påverka den genomsnittliga artrikedomen eller artdiversiteten i semi-naturliga gräsmarker. Endast låga signifikansvärden nås och olika slutsatser dras beroende på vilket index som används. Om det finns någon påverkan så är den relativt svag och beroende av en större variation i form för att framträda tydligt. Det är dock troligt att utbredningen av enskilda arterna eller funktionella växttyper påverkas av formen. Ytterligare studier krävs för att kunna avgöra detta.

Isolering verkar påverka artrikedom och artdiversitet negativt, men endast en liten del av variationen kan förklaras. Dessutom är inte alla resultaten robusta. Som en följd av datans utformning tas ingen hänsyn tas till patchernas storlek vid analysen. Det är troligt att påverkan av isolering hade framträtt tydligare om detta hade gjorts, särskilt i de små områdena. Intressant nog framträder inte den negativa påverkan av isolering förrän avståndet till närmsta granne överstiger 70 till 100 meter. Om framtida studier visar liknande resultat kan det påverka bevarandearbetet.

I det sista avsnittet ges rekommendationer för fortsatta studier av dessa gräsmarker. Hänsyn behöver tas till patchstorlek då påverkan av isolering analyseras. Genom att inkludera den historiska utbredningen av gräsmarker i analysen är det också troligt att mer kunskap och större förståelse kan uppnås.

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1 Introduction

This degree project in physical geography is part of a larger, ongoing study with the aim of determining which factors influence biodiversity in semi-natural grasslands, including historical land-use as well as present factors. The main study is conducted jointly by the Department of Physical Geography and Ecosystem Analysis and the Section of Plant Ecology and Systematics at the Department of Ecology, both at the University of Lund.

1.1 Research objectives

Semi-natural grasslands are becoming increasingly fragmented (Ihse, 1995). As these areas are amongst our most species rich habitat types (Kull & Zobel, 1991) it is of interest to determine the ecological implications of this fragmentation for plant and animal species.

In this degree project the effect of fragmentation on the vascular plant species community is studied by examining the relationship between landscape configuration and vascular plant species richness and diversity in semi-natural grassland patches. There are many aspects to configuration, all of which cannot be examined, so focus is on patch size, shape and isolation. Each of these characteristics can also be quantified in many different ways. Three size metrics, four shape metrics and two isolation metrics are used and an attempt is made to determine which of these, or which combination, is the most appropriate to use.

As a more complex and thorough study is being prepared at the department it is also of interest to evaluate how appropriate the methods used are for this type of study.

1.2 Hypotheses

Below I present my hypotheses regarding the influence of size, shape and isolation along with short explanations to the hypotheses.

Hypothesis 1: *Size* is positively related to species richness and species diversity up to a certain level and once this is reached correlation decreases.

Explanation: Patch area is commonly believed to have a positive influence on biodiversity (e.g. Forman, 1995) and several different explanations to this can be found in the literature. The *habitat heterogeneity hypothesis* states that larger patches contain more microhabitats and therefore more species, while the *equilibrium hypothesis* states that the dynamics between colonization and extinction are the underlying causes to the relationship (Krauss et al., 2004). For a presentation and comparison of these and other theories see Köchy and Rydin, 1997.

Most species-area curves increase steeply at first and then level off quickly once the minimum area point is reached (Forman, 1995). As there are not so many large

patches in the study area it may be difficult to determine the minimum area point at which the importance of patch size declines.

Hypothesis 2: The effect of *shape* is more difficult to predict so the main objective is to see *if* there is any influence from shape.

Explanation: The ecological effects of patch shape have not been studied to the same extent as those of size and are more difficult to predict (Forman, 1995). Straight lines are rare in nature. The more regular the shape of a patch is the more likely it is to have been influenced by man and such influence tends to have a negative effect on species richness. It has also been shown that intermediate anthropogenic influence can produce very irregular patches while natural processes tend to create patches with a more intermediate shape. Based on this, intermediate shape should be connected to the highest species richness.

The more irregular a patch is the longer the boundary with the surrounding areas will be. This enhances migration across the boundary but it also increases the influence from the surrounding areas. Fertilizers, pesticides and herbicides reach the boundary zones from surrounding fields and adjacent forests limit light penetration to the ground. Edge species therefore tend to be generalists that are common in the surrounding landscape while specialist species are found predominantly in the more stable conditions of the patch interior (Forman, 1995). Patches large enough to sustain both edge species and interior species should consequently have the highest total number of species. Furthermore, interior species tend to increase more with area than the edge species do (Forman, 1995). Compact shapes should therefore be positive, as long as the compactness is not the result of anthropogenic activities and the edge undulates enough to allow species to migrate across it.

Much of the variation between differently shaped patches is likely to be found in total species richness and in species composition rather than in the mean species richness and diversity. Due to the sampling methods used neither total species richness nor species composition can be used though. It can not be ruled out that the two metrics used in the study could be affected by shape so I still consider the relationship worth investigating.

Hypothesis 3: Both species richness and species diversity are negatively influenced by *isolation*. The negative effect of isolation is stronger in small patches.

Theory: Increasing isolation leads to a lower rate of colonization and recolonization of species and thereby affects the species number of the patch negatively (Forman, 1995). In large patches the negative effect is less prominent as they sustain larger, and thereby more stable, plant populations making local extinction less common. Furthermore, the chance of a species finding and colonizing a large patch is higher.

1.3 Previous studies in the area

Previously two degree projects, both at the masters' level, have been conducted in the area. The results from these studies are, to a certain extent, used in this project.

In the first degree project (Kindström, 1997) aerial photographs and cadastral maps are used to determine the past and present, i.e. 1994, land use in the area. The results show a great reduction in semi-natural grasslands in the area as well as an increasing fragmentation of the remaining patches.

In the second project (Vandewalle, 2003) the influence of continuity and habitat characteristics such as soil depth, grazing and nutrient-status on present vascular plant species richness is studied. The results show that there are significantly more species in grazed plots than in abandoned ones and that there are no signs of overgrazing in the area. Furthermore, Vandewalle shows that unimproved grasslands are richer in species than those that appear to have been eutrophicated and that the plots with the longest continuity also have more species than the younger ones.

1.4 Disposition

The purpose of the study and the hypotheses used are presented in the first chapter along with a brief summary of previous studies conducted in the area.

The importance of semi-natural grasslands is linked to the history of the landscape so an overview of this is found in the second chapter followed by a section on why semi-natural grasslands are of interest. As landscape ecology is a relatively young science and not traditionally a part of physical geography an introduction to the science, as well as to relevant theories, is given in the background in chapter two.

In the third chapter the study area as well as the methods and programs used are described.

The results are presented in chapter four and discussed in chapter five.

2 Background

2.1 The development of the agricultural landscape

Agriculture was first introduced in Sweden around 6000 years ago (Berglund, 1991) when the slow transition from a hunting and gathering community to a farming one began (Forslund, 2001). By 3000 B.C., most of southern Sweden was affected by agricultural activities (fig. 2.1) (www.sna.se) but farming was still only a complement to hunting (Forslund, 2001).

During the Iron Age (500 B.C.–1050 A.D.) new tools rendered agriculture more effective and it became the main source of income. Permanent settlements with fields and fodder grounds were established (Glimskär & Svensson, 1990) and pastoral grasslands expanded at the expense of forests (Berglund, 1991). By the end of this era agricultural activities had left their mark in the entire landscape. The new human-influenced landscape was more diverse than the pristine one and consisted of a small-scaled pattern of multifunctional land cover types (Skånes, 1996; Berglund, 1991).
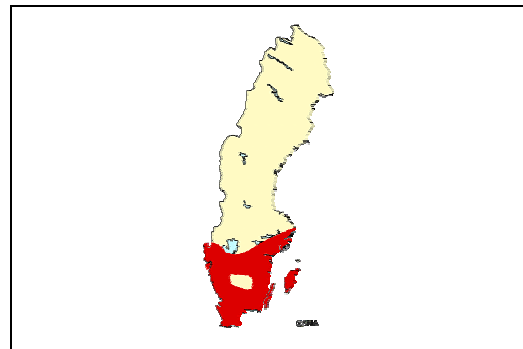
Figure 2.1: The extent of agriculture 5000 years ago (www.sna.se).

The Middle Ages (1050 A.D.–1523 A.D.) brought profound changes to society, an increasing population and land reclamation (Forslund, 2001). Since then, the farming intensity has been increasing continually although the greatest changes began with the enclosure movements of the 18th and 19th centuries and were accentuated by political decisions and technological advances after the Second World War (Berglund, 1991; Skånes, 1991). Both natural and human-influenced landscape types have decreased and consequently so has landscape diversity (fig. 2.2.) (Berglund, 1991).
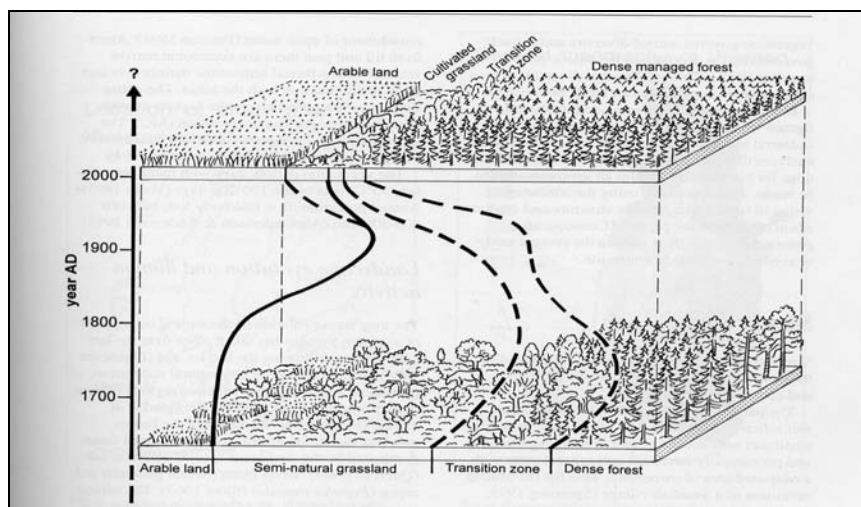
Figure 2.2:Landscape changes over the past 300 years (Skånes, 1996)

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The village landscape that developed during the Iron Age remained relatively stable for over 1000 years and had a permanent infield – outland system (Ihse, 1995). Farms were placed together in small villages surrounded by the infield, *inäga*, which consisted of fields, hay meadows and vegetable gardens and was fenced in to keep animals out (Glimskär & Svensson, 1990). The infield was divided between the farms so that each farmer owned one or several allotments in each type of field. The outland, *utmark,* on the other hand, was common land of poorer quality, further away from the village (NE; Germundsson & Schlyter, 1999). It was used for grazing, gathering wood and hunting and often consisted of forestland or impediment. On Öland special regulations applied to the outland after king Johan III declared the island a royal hunting park (*kunglig djurgårdsinrätting*) in 1569 (Forslund, 2001). All game hunting was banned as was the felling or damaging of valuable trees such as oak and hazel. In 1572 the regulations were expanded to include all animals and all deciduous trees as well as spruce. Game populations grew and damage to the crops increased. An attempt to introduce wild pig enhanced the problems for the farmers.

2.1.1 The enclosure movements

The purpose of the enclosure movements, *skiftes reformer,* of the 18th and 19th centuries was to render agriculture more effective by reducing the number of parcels owned by each farm (NE) and by dividing the outland between farmers (Magnusson, 1999) (fig 2.3).

The first of three land division laws, the *storskifte*, was established in 1749 and although its goals were never completely attained it did result in arable and mowed fields becoming fewer and larger in many areas (NE). On Öland it did not have a large effect though (Forslund, 2001).

In 1807 the more radical *enskifte* was introduced. This obliged framers to move out from the villages to their allotted plot of land and thereby lead to villages being split up, new roads being constructed and property boundaries moved so that the whole landscape picture changed (NE). The extent of the reform was limited to Skåne and parts of Skaraborg, Öland and Blekinge (Magnusson, 1999).

The *laga skifte* of 1827 was more widespread. Villages continued to be split up and outland partitioned and during the 19th century most of Sweden was subjected to these changes (NE).
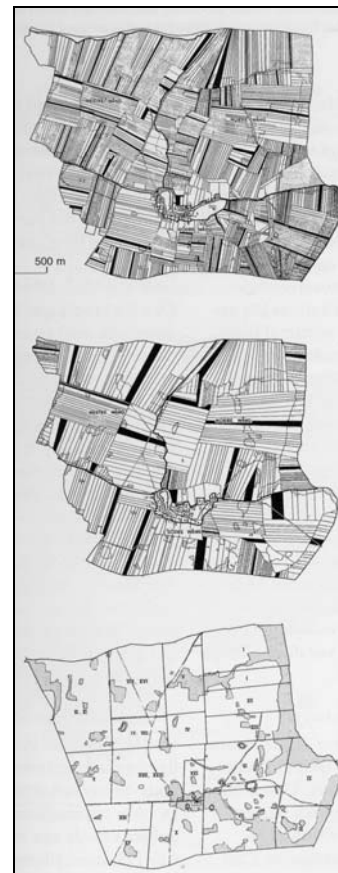

Figure 2.3: The effects of the enclosure movements (Atlas över Skåne, p. 77)

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According to the *kunglig djurgårdsinrätting* the outland belonged to the crown (www.h.lst.se). Farmers were allowed to use it for grazing but the enclosure movement did not affect it and no reclamation of land could occur until after its abandonment in 1801 (Forslund, 2001). The outland was then divided between the villages, except for some parts that were set aside for oak cultivation, construction of roads etc.

The current landscape on Öland is a result of history. Thousands of years of continual grazing created an open landscape (Forslund, 2001) and as much as half of the forest found on Öland today has grown up spontaneously during the past century (Kindström, 1997). After the reforms of the enclosure movement cattle breeding decreased while the cultivation of cereals increased and area of agricultural land more than three-doubled (Forslund, 2001).

2.2 Semi-natural grasslands

In Scandinavia no natural grasslands exist as secondary succession eventually turns any open unmanaged area into forest (Berglund et al., 1991). In the agricultural landscape that began to develop during the Iron Age grasslands non-the-less became an important part of the countryside (Glimskär & Svensson 1990; Forslund, 2001). Fodder grounds and hayfields held a central role in every farm as farmers depended on cattle to get manure for their fields. The continual disturbance that these fodder grounds and hay fields were subjected to, through grazing and / or mowing, prevented shrubs and trees from invading and made it possible for grasslands to persist (Berglund, 1991). These grasslands, that were neither fertilized nor tilled, are referred to as *semi-natural* in this study.

In semi-natural grasslands the vegetation is still dominated by indigenous species but its structure and composition have been affected (Ihse, 1995). The nutrient status of the soil has been lowered by the continual removal of organic matter (Eriksson et al., 1995) and light penetration is kept high which prevents more competitive species such as *Urtica dioica* (stinging nettle) and *Ranunculus acris* (meadow buttercup) from taking over while species like *Scorzonera humilis* (viper's-grass)*, Cirsium helenoides* (melancholy thistle) and *Hypochoeris maculata* (spotted cat's-ear) are favored (Kull & Zobel, 1991; Skånes, 1996).

2.2.1 Threats to semi-natural grasslands

Fundamental changes in land management, with rationalisation and increased efficiency as key words, have led to the small-scaled mosaic of the traditional agricultural landscape being replaced by the large fields and specialized farms of today (Skånes, 1991). These changes are illustrated well in a study from the open plains of southern Sweden where Ihse (1995) shows that, although there is a slight increase in total field area between 1947 and 1978, the number of fields declined from 155 to 32 during the same period. In all of Sweden only 16 000 fields < 2 ha remained in 1966, compared to 120 000 in 1927 (Wilson, 1999).

The expansion of fields has occurred at the expense of grasslands and other biotope types that hold grassland species such as wetlands, linear elements and point

elements. Today only about 10 % of the semi-natural grassland areas found in Sweden 150-200 years ago still remain (Cousins et al., 2002) and, although the percentages vary, similar trends can be seen in other parts of Europe (e.g. Krauss et al., 2004 - Germany; Fuller, 1987 - England; Pärtel et al., 1999 - Estonia). Likewise the vast majority of native prairies in North America have been lost since the European colonisation began (Samson & Knopf, 1994).

Many studies illustrate the drastic decline in quantity of remaining grassland fragments. Skånes (1996) has shown that 61 % of the natural fodder grounds and other non-cultivated grasslands found in her study area in Halland in 1947 had disappeared by 1984 while 67 % were lost between 1938 and 1985 in an area in southern Sweden (Ihse, 1995). There are several explanations to this decline, the main ones probably being changes in land management, the introduction of artificial fertilizers and an increasing population.

Between 1750 and 1860 Sweden's population almost doubled, from approximately 1.8 to 3.5 million (Magnusson, 1999). More agricultural land was needed (Glimskär & Svensson, 1990) and new technological innovations, such as the threshing-mill and better ploughs and harrows, made it possible to expand onto previously uncultivated land, mainly meadows and parts of the outland (Magnusson, 1999). The area of ploughed, fertilized and drained land therefore increased greatly at the expense of grasslands (Berglund, 1991). During the first half of the 19th century the cultivated area increased from 0.8 to 2 million hectares (Mattson, 1985 - in Glimskär & Svensson, 1990) and in the 1920s, when the extent of agricultural land was at its peak, 3.8 million hectares were cultivated in Sweden (Skånes, 1991).

After the introduction of artificial fertilizers in the mid 19th century (www.lund.se) farmers no longer needed to keep cattle to get manure for their fields (Glimskär & Svensson, 1990). This enabled specialisation and as infrastructure developed the distance between production and consumption could increase, further facilitating specialisation (www. europa.eu.int). This specialisation has lead to the disappearance of many grassland areas and small biotopes containing grassland species (Ihse, 1995). It has also lead to an increasing fragmentation of the remaining patches. The result is a landscape with reduced variability, fewer habitat-types, lower plant diversity and reduced dispersal abilities for the remaining species.

Another effect of demands for increased efficiency is that many of the remaining grasslands have been fertilized (Ihse, 1995) in order to increase their yield and meet the demands for better growth and milk production (Setterby, 2004). Nitrogen and phosphorous are generally the most limiting elements (Crawley, 1997) so the addition of nitrogen-containing fertilizers influences the delicate balance within the plant community and many plant species are lost as a few, more competitive, species take over (Forslund, 2001). The nutrient status of unfertilized areas is also increasing due to atmospheric deposition of nitrogen and in the Netherlands it has been shown that this deposition has influenced the species composition of heath lands (Crawley, 1997). Glimskär and Svensson (1990) find some signs of eutrophication in areas which have not been fertilized but which receive 3-5 kg N/(ha*year) from deposition. In Rockneby, near the study area, 4.2-6.7 kg nitrogen/(ha*year) were deposited between 1997-2003 (www.greppa.nu).

In marginal areas on the other hand many pastures are either reforested or abandoned whereby the openness of the agricultural landscape is lost. The spontaneous forest succession which occurs on abandoned pastures is generally more heterogeneous and open than a forest plantation and will thus provide more possible habitats for grassland species (Skånes, 1996).

The effect of land management on the quality of grasslands has been shown in various studies (e.g. Glimskär & Svensson, 1990; Kull & Zobel, 1991; Skånes, 1991; Eriksson et al., 1995; Wahlman & Milberg, 2002). Many competitive species, which in grazed or mowed grasslands are kept under control, are able to expand at the expense of less competitive species if management decreases or ceases completely (Crawley, 1997). Fogelfors and Ingelög, (1986 – in Glimskär & Svensson, 1990) find that 50 % of the herbs had disappeared 30-40 years after grazing was abandoned while Kull and Zobel (1991) show that a decreased mowing intensity or regularity leads to a decline in species richness. Furthermore they find that approximately 30 % of the species are lost after fertilization while Ihse (1995) shows a 50 % decrease in species number in fertilized grasslands. Ihse also shows that the species composition changes, with a decrease in grassland species and an increase in nitrophile species, and Skånes (1991) finds that nitrofile species still dominate 20-40 years after fertilization.

As previously mentioned, increasing fragmentation is another problem facing the grasslands of today (Ihse, 1995) and the rate at which the fragmentation is occurring makes it difficult for species to adapt to the changes (Swetnam et al., 1997). In a fragmented landscape, the remaining habitat patches are smaller and more isolated from each other than in its non-fragmented counterpart (Hanski, 1999). Both the influence from the surrounding areas and the proportional length of the edge thereby increases. The more stable conditions of the patch-interior on the other hand decrease as does population size and the linkages between nearby patches.

Smaller populations are more prone to extinction than their larger counterparts (Hanski, 1999). They are also more likely to suffer from genetic drift, inbreeding depression and reduced fitness. A decrease in patch area is therefore likely to lead to an increase in extinction rates, while increasing isolation impedes recolonization (Hanski, 1999) and restricts gene flow (Ouborg, 1993).

The nature of the mosaic separating patches has a strong influence on the dispersal abilities of species (Swetnam et al., 1997). Many of the landscape elements that normally act as steppingstones for grassland species, e.g. verges and stone mounds, have disappeared (Ihse, 1995). Borders between patches have become straighter (Ihse, 1995), which affects the dispersal abilities of many species negatively (Forman, 1995). Seed dispersal from the surrounding areas on the other hand is likely to increase when the proportion of edge increases (Simberloff, 1988). As a result, many remnant fragments suffer from biological impoverishment, supporting fewer specialist species and more generalist species (Harrison & Bruna, 1999).

The main problems facing grasslands today are listed below.

1. *Decreasing size* – as the area decreases so does the size of the plant populations. Hence they become less stable and more likely to be subjected to genetic drift or extinction (Hanski, 1999). The influence from surrounding areas also increases while the core area decreases (Ihse, 1995).
2. *Isolation* – as the distance to the nearest neighbouring grassland increases it becomes increasingly difficult for species to spread between patches. Dispersal is also made more difficult by the disappearance of many stepping stones (Ihse, 1995).
3. *Fertilization* – nitrogen and phosphorous are generally the most limiting elements in nature (Crawley, 1997). Many grasslands have been fertilized in order to increase their yield. The delicate balance within the plant community is then affected and many species are lost as a few, more competitive, ones take over (Forslund, 2001). Many studies have shown the negative effect fertilization has on species richness (e.g. Glimskär & Svensson, 1990; Kull & Zobel, 1991; Skånes, 1991).
4. *Abandonment* – an inadequate grazing pressure leads to pastures becoming overgrown and many of the semi-natural grassland areas of today are at the risk of being lost in the near future if management intensity does not increase.

2.2.2 The importance of semi-natural grasslands

Semi-natural grasslands are amongst the most species rich habitat types found in Europe and have been shown to contain up to 63 vascular plant species/m^2 (Kull & Zobel, 1991). Almost one third of Sweden's 2000 vascular plant species are found in semi-natural grasslands (Svensson, 1988 - in Glimskär & Svensson, 1990) and as many as 67 % of the 505 species classified as threatened in the Red Data Book belong to the agricultural landscape (Cousins et al., 2002). Many other species are declining, although not yet threatened, and the fauna dependent on this type of habitat is also affected (Skånes, 1991). Öland has one of the richest insect faunas in the country and many of the species are tied to the agricultural landscape and therefore affected by its decline (Ljungberg, 2002). Furthermore, approximately 500 insect species depend on oak trees for their survival and large, old oak trees are common in grazed areas (Ingelög, 1981).

The high species richness of semi-natural grasslands is likely to be connected to the long continuity in land use this habitat type has been subjected to (Skånes, 1991). Further more it is likely that the pre-agricultural landscape was more open than previously believed and constituted a mosaic of grassland, scrub and forest elements kept open by large herbivores and fires (Vera 2000 in Eriksson et al., 2002). Many of the plants that today depend on management for their survival were probably found in this mosaic landscape long before the development of agriculture and have since then lost their original habitats. (Ingelög, 1981). By preserving the traditional agricultural landscape these species can continue to exist.

Due to the length of the period in which the landscape has been kept open by continual management this habitat type can almost be considered natural. Many traces of the history of civilization are found in the agricultural landscape and it is the only place where the first types of land to be used by man are still to be found (Skånes, 1991). However, it is not only the landscape picture that bears marks of our history.

Many of the grassland species are an important part of our cultural heritage so loosing them would mean loosing part of our history (Ingelög, 1981). Finally, this landscape type is valuable for recreation and outdoor life.

2.3 Landscape ecology

The development of aerial photography opened up a new world for scientists. Not only did the photographs make it possible to study larger areas than before, but they also revealed patterns previously unseen. By moving one step away from earth a whole new perspective had been gained. This opened the doors for the naissance of a new science; landscape ecology.

In landscape ecology the spatial arrangement of the landscape is studied as well as the function of the different ecosystems within the landscape and how these ecosystems have changed over time (Norton, 1991). The questions asked are generally of such a scale that field experiments are not possible. Computer simulations and models are therefore necessary tools and the development of remote sensing techniques, geographical information systems and increasing computer capacities have all contributed to the evolution of landscape ecology and will undoubtedly continue to do so.

2.3.1 Landscape ecological theory

It is not of interest for this thesis to give a complete review of all landscape ecological theory but a short overview of relevant theories is given in this section.

2.3.1.1 The patch-corridor-matrix model

The *patch-corridor-matrix model* provides us with a tool to simplify, and thereby to analyse, our surroundings and to compare different areas with each other or the same area over time (Forman, 1995). According to the model, all landscape elements belong to one of the three different types of spatial structures: patch, corridor or matrix.

Patches are relatively homogeneous non-linear areas that differ from their surroundings (Forman, 1995) e.g. an arable field embedded in a forest, a wetland surrounded by drier areas or an old forest left after a clear-cut. Their shape and size, as well as the number of patches of each particular type, all have an important influence on the biodiversity and productivity of an area.

Corridors on the other hand are linear elements that differ from their surroundings on both sides (Forman, 1995) such as a hedgerow growing between fields or a riverbank meandering through the countryside. Whereas patches mainly act as habitat, corridors have varying functions in the landscape and also act as a dispersal agents or barriers for certain species. As the land-use map over the study area does not show corridors their potential contribution to the dispersal of grassland species is not examined.

Patches and corridors are embedded in the *matrix* which is the land-use type with the most extensive cover (Forman, 1995). It has a high connectivity and / or main control

over dynamics in the area. Well into the 19th century semi-natural grasslands made up the matrix of the study area but by the first half of the 20th century many of these grasslands had disappeared and today only remnant or regenerated patches of grasslands exist in the area (appendix 1).

The type of structure an area belongs to, as well as where the border between the different types is drawn, is determined by scale (www.umass.edu, a). As an example, looking at a small wooded area the forest makes up the matrix, small clearings constitute patches and roads act as corridors. By taking one step away one may realise that in fact the forest previously classified as matrix is now but a patch in a larger matrix of agricultural land and that the small clearings are no longer visible. It is important to realize this when studying the mosaic pattern as a study focused on the wrong scale may not give the desired answers.

2.3.1.2 The island biogeography theory

In 1967 MacArthur and Wilson developed the island biogeography theory which has had a large impact on ecology, conservation biology and landscape ecology (Forman, 1995). The theory states that the species number of an island is determined by a dynamic equilibrium between immigration- and extinction rates which, in their turn, are influenced by island size, isolation and age (Whittaker, 1998; Forman, 1995) (fig 2.4).
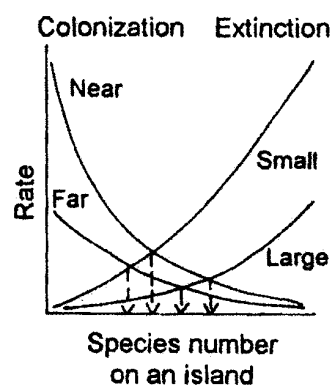
Figure 2.4: The number of species found on an island as explained by the island biogeography theory (Forman, 1995).

Island *size* has a positive influence on species number for several reasons. Not only is a larger island more likely to be discovered by potential colonizers than its smaller counterparts (Forman, 1995) but it will also enable populations to become larger, and thereby more stable (Kiviniemi & Eriksson, 2002; Rosenzweig, 1995), while competition and mortality are kept low. Contrary to size, *isolation* negatively influences the species number of an island as a remote island is less likely to be discovered by potential colonizers (Forman, 1995). Finally *age* is important because younger island have not yet had time to be colonized by so many species (Forman, 1995). The older an island gets the more species will have had time to find, and colonize, it but eventually species number reaches an equilibrium while species composition may continue to change.

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Although the island biogeography theory is based on studies of real islands the model has also been used to study species richness in ecological islands such as grassland patches in an "ocean" of agricultural land. The matrix surrounding such ecological islands is considered neutral which makes the model relatively easy to work with (www.umass.edu, b). However, in reality the matrix is not as unsurpassable as the water surrounding real islands (Forman, 1995) and its properties will have an important influence on the way in which different species spread through the landscape (www.umass.edu, b). In ecological islands, disturbance and succession also have a more prominent influence on species richness and the origin of the patches is more varied than that of most islands.

2.3.1.3 The landscape mosaic model
Some of the weaknesses of the island biogeography model are overcome in the landscape mosaic model. This provides a more realistic, but also more complex, view on how the composition of the landscape affects the organisms within it (www.umass.edu, b). Rather than treating all other land-use types than that of interest as neutral the landscape is viewed as an assemblage of patch types that are more or less similar to each other. This view requires a thorough understanding of the interactions that take place between the study organism and all the land types in the study area. Gaining such an understanding falls outside the time frame of this project but would undoubtedly have added valuable information to the study.

3 Material and methods

3.1 Study area

The study area consists of a rural mosaic landscape and is situated on the central part of the island Öland, of the east coast of Sweden (lat 6284, long 1548) (fig 3.1). It is approximately 2500 ha and is dominated by forest (39 %) and arable land (36 %) (Appendix 2). The forest is part of "Mittlandsskogen", northern Europe's largest broad-leaf deciduous forest below the mountain range (Forslund, 2001).

Great reductions in semi-natural grassland area have occurred in the study area over the past couple of centuries as agricultural land and forests have expanded (Appendix 1). Non-the less, 50 000 ha of semi-natural grasslands remain on Öland and, compared to other Swedish counties, this is a relatively high amount (Forslund, 2001). Today (1994) grasslands, including the for Öland typical alvar, cover 16,5 % of the study area while hamlets, other land use and wetlands make up the remaining 8,5 %. Approximately half of the grasslands are semi-natural. Only 14 % of these are well managed while 47 % are poorly or moderately managed and 39 % are unmanaged. The average species richness is relatively high (25 vascular plant species / 0.25 m^2) compared to similar areas in Sweden (Vandewalle, 2004).
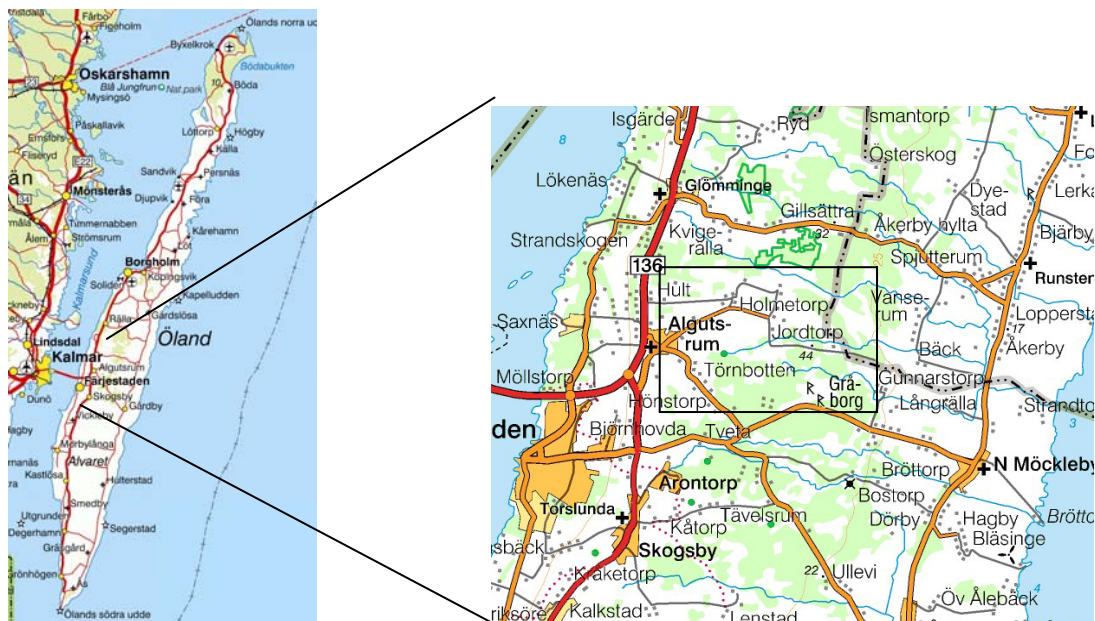
Figure 3.1: The approximate location of the study area (www.lantmateriverket.se).

Öland is surrounded by water and therefore the climate is milder than in many areas on the mainland. As southeastern Sweden is affected by a rain shadow the annual precipitation is low. In Mörbylånga, not far from the study area, the mean annual temperature is 7.4° C while the mean annual precipitation is 475 millimeters (Forslund, 2001). Together with the geological conditions this gives Öland a flora

and fauna that in many ways is unique and the southern part of the island was declared a world heritage area in 2000.

The bedrock is an Ordovician limestone covered by a clayey till (Fredén, 2002) with a measured soil-depth of between 2.8 cm and 40.4 cm (Jonsson et al., in prep). The study area is relatively flat except for the Jordtorp ridge which runs through the central parts of the area. This ridge contains 6 grave-fields and is one of Öland's most well-known ancient remains (Forslund, 2001). There are also areas of national interest for nature conservation, cultural heritage and outdoor life as well as a nature reserve within the study area.

For several reasons the small scaled agricultural landscape persisted longer on Öland than in most parts of the country (Ljungberg, 2002). In 1569 Johan III declared Öland a royal hunting ground, thereby protecting all trees and limiting grazing to the outlands (Forslund, 2001). According to this wildlife establishment (*djurgårds-inrätting*) the outlands belonged to the crown. The enclosure movement did therefore not affect it and no shifts took place until after the abandonment of the establishment in 1801. Further more, connections with the mainland were limited prior to the construction of the bridge in 1972.

3.2 Vegetation data

The vegetation data used for this study comes from an available data set from 1998 (Jonsson et al., in prep.). It contains vascular plant species frequencies in 354 quadrants, located in 92 out of the 225 patches classified as semi-natural grasslands in the 1994/1997 base map of the Jordtorp area (Jonsson et al., in prep. and Kindström, 1997) (appendix 1). The number of quadrants to place in each patch was subjectively determined depending on patch heterogeneity, with fewer quadrants in more homo-geneous patches. The patches contain between one and fourteen quadrants each.

Of the 92 patches, six turned out not to be semi-natural grasslands and were therefore excluded. In another patch, all of the quadrants had been placed in the road verge. As the flora of the verge is likely to differ from that of the rest of the grassland the vegetation data collected cannot be assumed to be representative of that of the rest of the patch so this too was excluded. This left 85 patches and 317 quadrants for which vegetation data was available.

Vascular plant species' frequencies were noted as presence or absence in 25 sub-quadrants in the 0.5 m ^{x} 0.5 m quadrants (fig 3.2). A frequency of 6 consequently means that the species was found in 6 of the 25 sub-quadrants.
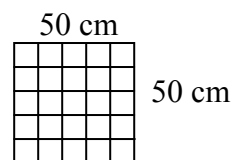
Figure 3.2: The frequency of a plant species is equal to the number of sub-quadrants in which it is found.

Besides information on species frequencies the data set also contains information on nutrient status, grazing and land-use history. The latter was determined by studying historical maps and aerial photographs (Kindström, 1997) whereas the two previous were subjectively determined in the field (Jonsson et al., in prep).

In this study both species richness and species diversity are used to determine the effect of landscape configuration on vascular plant species distribution. *Species richness* refers to the number of species found in each quadrant. It is a commonly used metric when studying grasslands, although the area unit varies between studies. The disadvantage of this metric is that it does not take the relative abundance of each species into account. It may therefore be misleading if one or a few species dominate. The *Shannon diversity index* was therefore used as well (equation 1).

Equation 1: $H = -\sum_{i=1}^{s} P_i \ln(P_i)$

H = Shannon index of species diversity
s = number of species
P_i = the proportion of total sample belonging to the **i**'th species

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s = number of species
P_i = the proportion of total sample belonging to the i'th species

3.3 Quantifying the spatial configuration of the landscape

As previously stated (chapter 2.3) choice of scale and conceptual model will influence the results of the spatial analysis. The analysis is based on a digital map covering an area of approximately 2500 ha. It has 10 land use classes and was created by Kindström (1997) by interpretation of infrared aerial photographs from 940620. The smallest mapping unit is 50m x 50m so no point- or linear elements are shown in the map.

Despite its limitations (see further chapter 2.3.1.2) the island biogeograpic view on the landscape is used. Choosing the landscape mosaic model would have required a more comprehensive understanding of how the plant species studied interact with their environment. Furthermore, it would have been necessary to divide the grassland species into different dispersal groups to account for the different ways in which they spread through the landscape. Doing this was not within the scoop of this study.

3.3.1 FRAGSTATS
To quantify the spatial structure of the study area the 3rd version of the spatial pattern analysis program FRAGSTATS was used (McGarigal et al., 2002). This program calculates numerous metrics on three different levels: patch, class and landscape level (www.umass.edu, c). On the patch level each individual patch is considered by itself, e.g. size and shape. On the class level all the patches of a certain type are considered, e.g. average size and shape for each patch type. Finally on the landscape level all patch types are integrated, e.g. the overall diversity of the area.

3.3.1.1 Input data
The 3rd version of FRAGSTATS cannot handle vector data so Arc Map was used to convert the original coverage file to grid format with a pixel size of 1 m [x] 1 m. Only

one specified property remains in the grid file, which was a problem for this study as both patch id and land use were needed for the spatial analyses. The reason patch id was needed is that many of the semi-natural grassland polygons in the area are located next to each other. They have been treated as separate patches because some other feature, e.g. tree coverage or moisture, is different. When the vector data was converted to grid format by using *land use* as separating property this difference was lost and larger patches created. By using *patch id* instead all of the patches kept their original extent but FRAGSTATS interpreted the id numbers as separate classes which made it impossible to determine the degree of isolation. Both of these conversions were therefore made and the patch id conversion used as input file when studying the importance of size and shape while the land use conversion was used to study the influence of isolation.

When running fragstats several choices regarding the setup must be made. First, there is a choice between standard mode and moving window analysis. For the type of input data used in the study only standard mode is appropriate so this was used in all of the runs.

The second choice concerns where to draw the limit between patches. Either the 4-cell rule or the 8-cell rule can be used. With the former only the 4 cells that share a side with the focal cell are considered to be part of the same patch. With the latter, all 8 cells that touch the focal cell are considered to belong to the same patch.

Figure 3.3. illustrates the difference between the options. If the 4-cell rule is chosen the area in the figure will be treated as two separate patches. If, on the other, the 8-cell rule is used the figure will be treated as one patch. As species can spread easily between the two areas I chose to treat them as one patch and consequently the 8-cell rule was used for all of the runs.
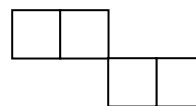
Figure 3.3: With the 4-cell rule this will be considered as two patches and with the 8-cell rule as one.

3.3.1.2 Metrics used

In this study only patch level metrics are used and more specifically size, shape and isolation are to be quantified. All of these properties can be described by several different metrics, many of which are very similar. The metrics used are described below. For a more thorough descriptions see www.umass.edu, c.

Size

Patch area is the most obvious way to illustrate size. In FRAGSTATS the unit used is hectares. However, many species depend on stable conditions and are only found in the interior parts of a patch. *Core area* is used to quantify the interior and represents the area (in hectares) which remains after a specified edge width, in this study three meters, has been removed from the patch. Note that this definition of core area differs from that of Forman (1995) who calls the largest circle to fit within a patch its core area. The *perimeter* (meters) also gives an idea of patch size as well as of the amount of available habitat for edge species. Edge species populations, as well as several

other ecological characteristics, have been shown to correlate better with perimeter length than with patch area (Forman, 1995).

Shape
As noted, both core area and perimeter are influenced by patch size but they are also affected by shape. The more convoluted a patch is the smaller its core area will be in relation to its total area. This relationship is measured by the *core area index* (CAI) (equation 2). Conversely the patch *perimeter* increases with complexity and by simply dividing perimeter by area an estimate of complexity is obtained. However, the *perimeter-area ratio* (PARA) decreases with size and is therefore not used in this study.

Equation 2: $CAI = \dfrac{a_{ij}^c}{a_{ij}}$

a_{ij}^c = core area (m^2) of patch ij based on specified edge depth (m).
a_{ij} = area (m^2) of patch ij.

By using the *SHAPE index* instead (equation 3) the size dependency is avoided as this metric adjusts for a square standard. It is equal to one when the patch is maximally compact, i.e. square. The more irregular the patch is the higher the index value will be (no upper limit).

Equation 3: $SHAPE = \dfrac{p_{ij}}{\min p_{ij}}$

p_{ij} = perimeter of patch ij in terms of number of cell surfaces.
$\min p_{ij}$ = minimum perimeter of patch ij in terms of number of cell surfaces if the patch is maximally compact.

Another shape metric that corrects for the problem of size is the *fractal dimension index* (FRAC) (equation 4). This metric can only take on a value between one and two. One is a maximally compact shape and the closer FRAC is to two the more complex the shape is.

Equation 4: $FRAC = \dfrac{2 * \ln(.25 p_{ij})}{\ln a_{ij}}$

FRAC = Fractal Dimension Index
p_{ji} = perimeter (m) of patch ij.
a_{ij} = area (m^2) of patch ij.

Further more, the *contiguity index* (CONTIG) measures the spatial connectedness of cells within a patch and thereby provides an estimation of patch shape (equation 5). The index value increases with connectedness and ranges from zero to one.

Equation 5: $CONTIG = \dfrac{\left[\dfrac{\sum\limits_{i=1}^{z} c_{ijr}}{a_{ij}} \right] - 1}{v - 1}$

CONTIG = Contiguity Index
c_{ijr} = contiguity value for pixel r in patch ij.
v = sum of the values in a 3-by-3 cell template.
a_{ij} = area of patch ij in terms of number of cells

As appears from the above there are sevral different ways to quantify shape and yet this is but a selection of available metrics. An attempt is made to determine which of

the four metrics studied here, or which combination, is most appropriate to use in this type of study.

Isolation

Two different ways of measuring isolation are used. The first is the *Euclidian nearest neighbour distance* (ENN), which is the shortest straight-line distance from patch ij to the nearest neighbouring patch of the same type. It is based on the edge-to-edge distance, computed from cell centre to cell centre. As a pixel size of one meter is used this means that the actual distance is one meter shorter (0.5 m + 0.5 m) than the results show but this source of error is more than likely negligible compared to the generalisation in the digitalisation. ENN is always > 0 and the higher the value the more isolated the patch is with the extent of the study area as the only upper limit.

ENN measures the shortest distance to the neighboring patch as the crow flies but this is not necessarily the easiest way for a species to spread. A wind dispersed species is more likely to spread downwind and over open areas than upwind and through dense forest. FRAGSTAT also provides a *functional nearest-neighbor distance* (FNN) which calculates the distance in meters to the nearest neighbor along the least-cost path. It requires the user to apply the landscape mosaic model and determine the cost for each plant functional type to pass the different land use types which, as previously mentioned, falls outside the time-frame of this project.

The *proximity index* considers both the size and the proximity of all patches whose edges are within a specified neighborhood of the focal patch (equation 6). Here, three different search radiuses are used; 100, 500 and 1000 meters. The absolute value of the index has little interpretive value, as it is dimensionless, and it is mainly comparative.

Equation 6: $PROX = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$

a_{ijs} = area (m^2) of patch ijs within specified neighbourhood (m) of patch ij.
h_{ijs} = distance (m) between patch ijs and patch ijs based on patch edge-to-edge distance computed from cell center to cell center.

The isolation indices may be misleading for those patches that lie in the outskirts of the study area as the nearest neighbour may well be just outside the border. In that case the ENN value will be too high whereas the proximity index will be too low. This can be avoided by using a boarder around the map. FRAGSTATS then includes the patches in the boarder in the calculations without calculating metrics for the areas in the boarder. However, including such a boarder would have meant either interpreting and digitising the area around the study area or converting part of the study area to boarder and thereby loosing some information. As the surrounding areas do not contain many grasslands, I chose to risk some metrics being misleading rather than loosing parts of the study area or spending time on further digitalisation.

3.4 Statistical analyses

To study the influence of size, shape and isolation on species richness and species diversity three different statistical tests were used: t-test, Pearson's correlation

coefficient and regression analysis. To test for normality the Kolomogorov-Smirnov test was used.

3.4.1 Comparing sample means

With normally distributed data a *t-test* can be used to determine whether or not two sample means are significantly different from each other (Rogerson, 2001). The equation used to calculate the t-statistic depends on whether or not equal variance can be assumed so an *F-test* was first used to determine this.

Based on the results from the structural analyses the patches were divided into groups, e.g. area < 2 ha vs. area > 2 ha or ENN < 50 m vs. ENN > 50. The mean species richness and species diversity of each group was calculated and a null hypothesis of no difference in sample means set up. A t-test was then used to compare the mean species richness, as well as the mean Shannon diversity, of the two groups in order to test the null hypothesis. For each metric several levels of separation were arbitrarily chosen and the t-test used to compare each of these groups.

The method indicates if the studied metric influences species richness and/or diversity but it also has another advantage. Many times the influence of a metric will vary with magnitude, e.g. for most species the nearest neighbour distance is not expected to be as important if the nearest patch is only 10 meters away as when it is 100 or 1000 meters away. By comparing the results from the different separation levels it may be possible to determine in which intervals the species characteristics are influenced by the studied metric.

The tests were performed in Minitab and SPSS and a significance level of 0.05 was chosen for the F-statistic.

3.4.2 Correlation

Correlation coefficients measure the degree of statistical, but not necessarily causal, relationship between two variables (Shaw and Wheeler, 1996). There are several different types of coefficients. The most powerful of these is Pearson's correlation coefficient. It requires the data to be of interval or ratio scale and to approximate normal distribution. As these requirements are fulfilled the coefficient can be used to study the degree of linear relationship between the species variables and the configuration variables in the study area. To account for the expected non-linearity of the relationships the variables are ln-transformed prior to analysis.

Pearson's correlation coefficient was calculated by using the Analysis ToolPack in Excel. In order to strengthen the possible relationships, and to determine in which type of patches configuration metrics influence species characteristics, the data set was divided into seven groups based on the results from a study by Vandewalle (2004). The study shows that grazing and nutrient status influence species richness in the area and that there is a trend for land-use history to be related to species richness although this is not statistically significant. On the basis of this knowledge the data was divided into the following groups:

- Grazed – abandoned
- No / some eutrophication – heavier eutrophication
- Grassland in all time periods – previously arable land – previously forest

To test the null hypothesis of no correlation between the variables the computed coefficient was compared to the required critical value.

3.4.3 Regression analysis

One of the most widely used statistical techniques in geography is regression analysis (Shaw and Wheeler, 1996). This method makes it possible to numerically recreate the way in which one variable controls another and hence to predict the value of y (the dependent variable) based on the value of x (the independent, or explanatory, variable). Besides normal distribution the method also requires the relationship between the tested variables to be linear (Rogerson, 2001). Many relationships however are not linear.

For non-linear relationships it is necessary to (I) determine what the relationship looks like and (II) to transform it so that the requirement for linearity is fulfilled (Shaw and Wheeler, 1996). Failing to do so may have important implications on the interpretation of the results. In order to test what type of curve was the best fit for each of the studied relationships the *curve estimation function* in SPSS was used. Besides the linear curve three other common curve-types (Shaw and Wheeler, 1996) were tested: the power curve, the exponential curve and the logarithmic curve. The power curve was a good fit for all of the landscape metrics so prior to analyses the functions were linearised by ln-transformation according to the following:

Equation 7: $Y = aX^b$

$=> \ln Y = a + b\ln X$

> Y = the estimated value of the dependent variable, here species richness or species diversity
> X = the measured value of the independent variable, here the different species metrics
> a and b are parameters of the equation where a gives the interception point while b indicates the slope of the line.

When using a search radius of 100 m there are several patches which have no other grassland within the search radius and hence receive a proximity index value of zero. As it is not possible to ln-transform zero one unit was added to all of the values prior to the transformation.

As the correlation analysis showed a difference in the strength of the relationships depending on management and land-use history it was of interest to continue to divide the data into the seven categories above. A sub-division of the material according to all of the categories would mean that no less than twelve groups would have to be created. With so many groups the data in each would be limited. By introducing dummy-variables and performing multivariate regression analysis instead all of the factors are taken into account without loosing the advantages of having a large sample.

Qualitative variables, such as grazing, can be included in regression analyses as dummy variables (Andersson et al., 1994). A dummy variable is coded as 0 (e.g. no grazing) or 1 (e.g. grazing). The regression analyses were first performed with just one explanatory variable, e.g. area. In the next step dummy variables for grazing, nutrient status and history were added to the regression analysis. As the history dummy was not significant in any of the regressions it was excluded and the regressions were recalculated using only the dummy variables for grazing and nutrient status.

Both normal and multivariate regression analyses were performed using SPSS and the Analysis ToolPack in excel.

4 Results

4.1 Comparison of sample means

Based on the results from the structural analyses the patches were divided into groups and a t-test was used to compare the mean species richness, as well as the mean Shannon diversity, of each pare of groups. The purpose was to test whether or not they are significantly different (p<0.05). For each metric several levels of separation were arbitrarily chosen. In appendix 2 all of the results can bee found.

4.1.1 The influence of size

All of the size metrics (area, core area and perimeter) were expected to be positively related to both species richness and species diversity. The results indicate that, in the semi-natural grasslands of the study area, this is indeed the case. As area and core area gave very similar results only the area-results are presented here.

4.1.1.1 Area

Of the selected levels of separation 8 are presented in figures 4.1.1. and 4.1.2. Except when the limit was drawn at 0.25 and at 4 hectares there were significantly more species in the larger patches than in the smaller ones (p=0-0.016) (fig 4.1.1). For species diversity all but the last group (< 4 ha vs. > 4 ha) were significantly different (p=0-0.036) (fig 4.1.2).

Figure 4.1.1: The diagram shows that mean species richness in the different area-based groups (SD=3.02-7.25). The non-patterned bars are significantly different (p=0-0.016) whereas the patterned bars are not significantly different (p=0.091-0.87).

As only 9 quadrants were placed in patches > 4 ha it is not possible to draw any conclusions about the upper limit for the importance of size. To do this more samples from large quadrants are needed.

Figure 4.1.2: The diagram shows the mean Shannon diversity in the different area-based groups (SD=0.15-0.32). The non-patterned bars are significantly different (p=0-0.036) whereas the patterned bars are not significantly different (p=0.589).

4.1.1.2 Perimeter

For the patch perimeter 5 different levels of separation are presented. Except when the limit was drawn at 1400 m there were significantly more species in the patches with the larger perimeter than in those with a smaller one (p=0-0.036) (fig 4.1.3). For Shannon species diversity all groups were significantly different (p=0-0.026) (fig 4.1.4).
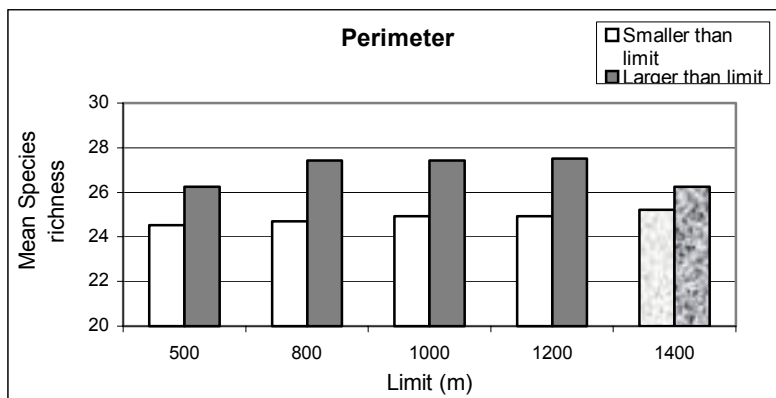
Figure 4.1.3: The diagram shows the mean species richness in the different perimeter-based groups (SD=3.11-5.77). The non-patterned bars are significantly different (p=0-0.036) whereas the patterned bars are not significantly different (p=0.197).

The importance of the influence of patch perimeter on the species metrics is expected to decrease as patch size increases. However, as with area, there are too few large patches to determine if such a decrease does indeed take place. The loss of significance between the groups with a perimeter shorter than 1400 m vs. those with a perimeter larger than 1400 m is once more likely due to the low number of large patches in the area (only 19 have a perimeter of 1400 m or more).
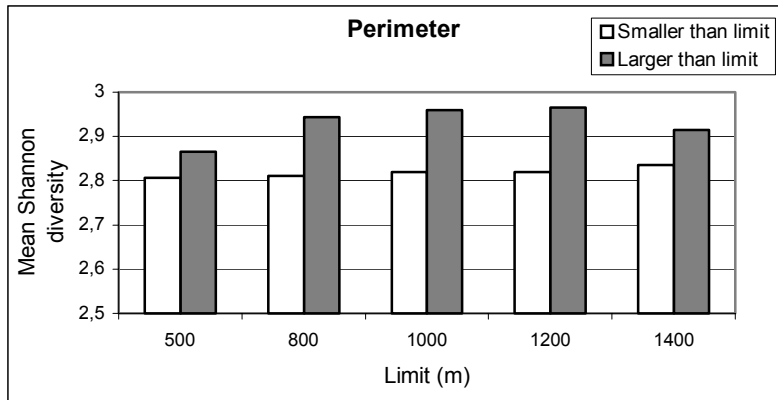
Figure 4.1.4: The diagram shows the mean Shannon diversity in the different perimeter-based groups (SD=0.132-0.248). All bars are significantly different (p=0-0.026).

4.1.2 The influence of shape

To study the influence of shape 4 different metrics were used; core area index, shape index, fractal dimension index and contiguity index. The influence of shape is less clear than that of size and varies depending on what index is used. With the core area index and the contiguity index there is a tendency towards more compact shapes to have more species and a higher diversity. With the other 2 indices the situation appears to be the opposite with a tendency for more species and a higher diversity in patches with a more complex shape.

4.1.2.1 Core Area Index (CAI)

The core area index measures the percentage of the patch constituted by the core area. The more compact the shape of a patch is the higher the index value will be. There is a tendency for the group with a higher CAI-value to have a higher species richness but whether or not the difference is significant depends on where the limit is drawn (p=0.008-0.585) (fig 4.1.5).
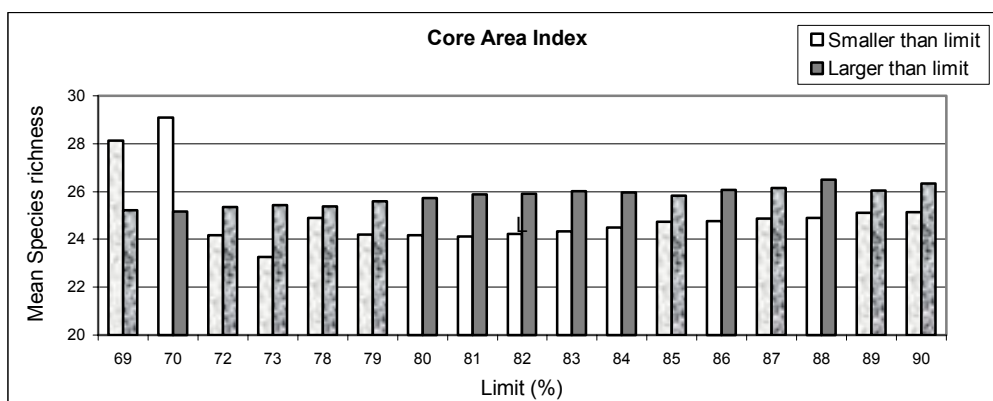
Figure 4.1.5: The diagram shows the mean species richness in the different CAI-based groups (SD=5.29-8.57). The non-patterned bars are significantly different (p=0.008-0.042) whereas the patterned bars are not significantly different (p=0.055-0.617).

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Between a core area index of 79 % and 88 % there is a significantly higher diversity in the patches with a more compact shape, i.e. a higher CAI value (p=0.003-0.021) (fig. 4.1.6). Quadrants placed in patches with a core area index of <78 % or ≥89 % are not significantly different between the 2 groups (p=0.069-0.344).
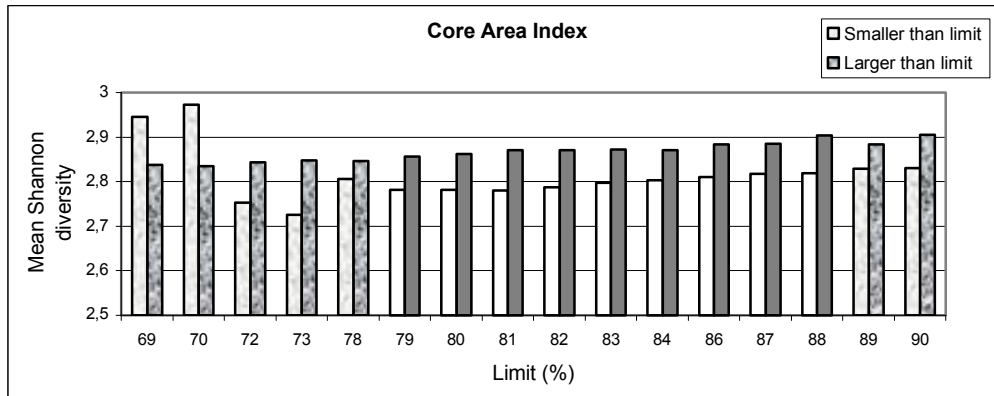
Figure 4.1.6: The diagram shows the mean Shannon diversity in the different CAI-based groups (SD=0.203-0.358). The non-patterned bars are significantly different (p=0.003-0.021) whereas the patterned bars are not significantly different (p=0.069-0.344).

As only 23 quadrants were placed in patches that have a core area index of 73 % or less it is difficult to draw any conclusions about the first 4 groups.

4.1.2.2 Shape Index

The shape index is equal to 1 when the patch is maximally compact and increases with patch irregularity. There is a tendency towards a higher species richness and diversity in the more irregularly shaped patches. In most cases the difference is not statistically significant though (fig. 4.1.7. and 4.1.8). There are more than 30 samples in each group.
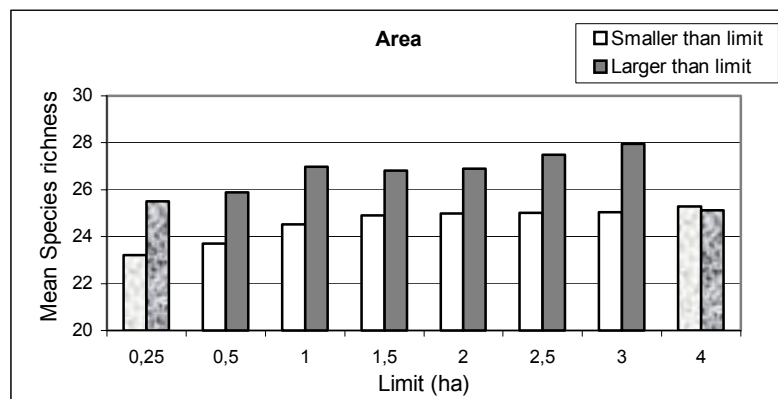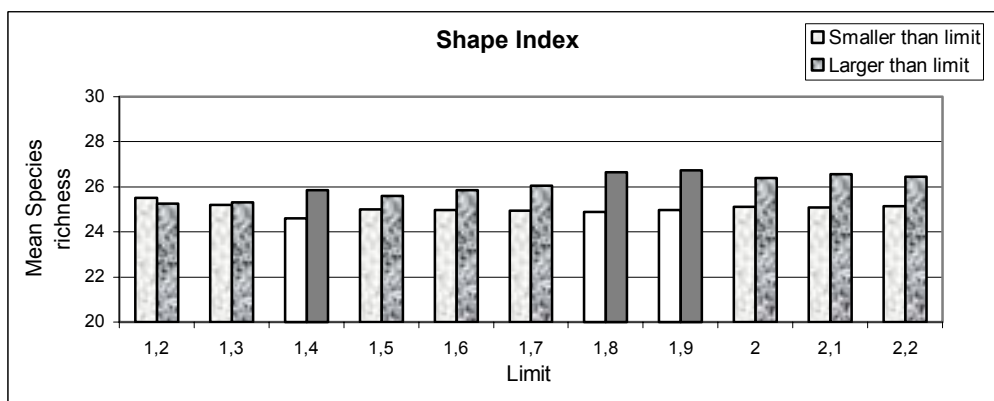

Figure 4.1.7: The diagram shows the mean species richness in the different shape index-based groups (SD=4.8-5.9). The non-patterned bars are significantly different (p=0.018-0.047) whereas the patterned bars are not significantly different (p=0.109-0.871).
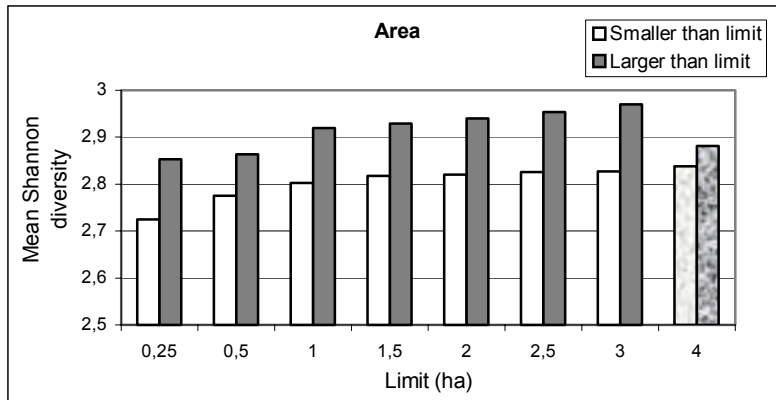
Figure 4.1.8: The diagram shows the mean Shannon diversity in the different shape index-based groups (SD=0.188-0.255). The non-patterned bars are significantly different (p=0.001-0.044) whereas the patterned bars are not significantly different (p=0.092-0.771).

4.1.2.3 Fractal Dimension Index (frac)

Like the shape index the fractal dimension index increases with the complexity of the patch shape but it can only take on a value between 1 and 2. Although statistically significant levels of difference between the groups is reached less than half the time there is a tendency towards a higher species richness and diversity in patches with a more complex shape (fig. 4.1.9 and 4.1.10). There are more than 90 samples in each group.
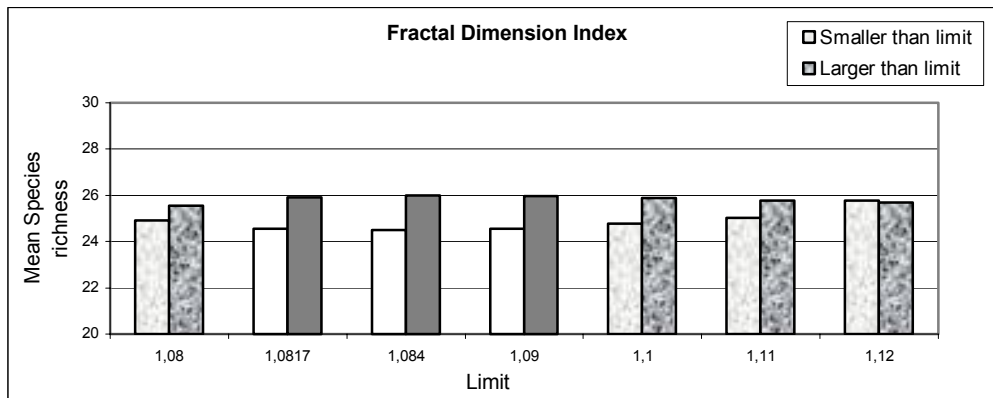
Figure 4.1.9: The diagram shows the mean species richness in the different groups based on the fractal dimension index (SD=4.99-5.86). The non-patterned bars are significantly different (p=0.018-0.033) whereas the patterned are not significantly different (p=0.086-0.396).
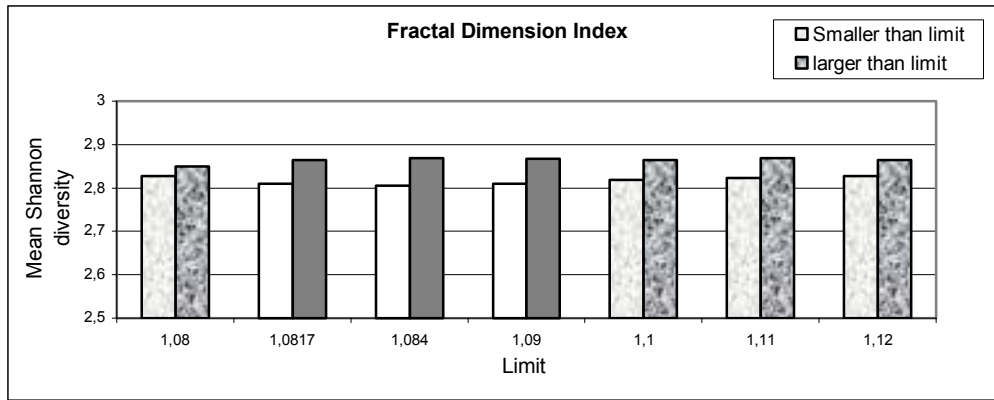
Figure 4.1.10: The diagram shows the mean Shannon diversity in the different groups based the fractal dimension index (SD=0.215-0.252). The non-patterned bars are significantly different (p=0.018-0.036) whereas the patterned are not significantly different (p=0.089-0.409).

4.1.2.4 Contiguity Index (Contig)

The contiguity index is another way of measuring shape, this time by looking at the spatial connectedness of the cells within each patch. The index takes on a value between 0 and 1, increasing with connectedness. There is a tendency towards a higher species richness and diversity in patches with a higher contiguity value (fig. 4.1.11 and 4.1.12). There are 8 samples in the first group and at least 40 in all the others.
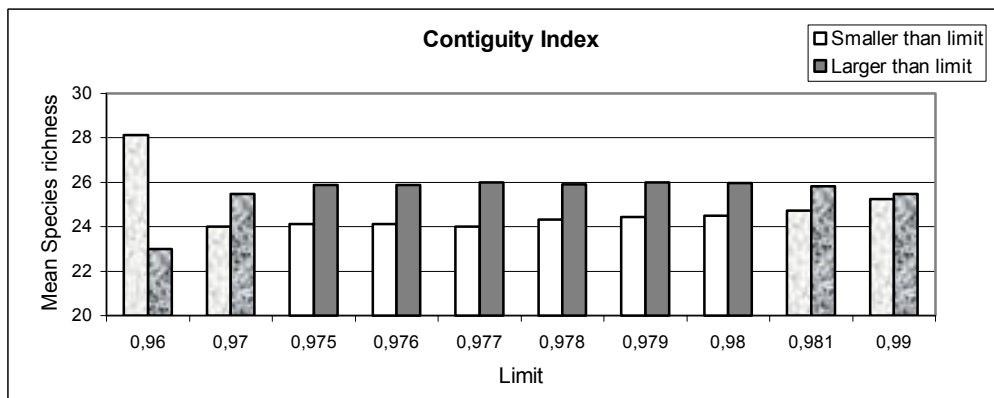
Figure 4.1.11: The diagram shows the mean species richness in the groups based on the contiguity index (SD=5.29-7.61). The non-patterned bars are significantly different (p=0.002-0.019) whereas the patterned are not significantly different (p=0.081-0.768).
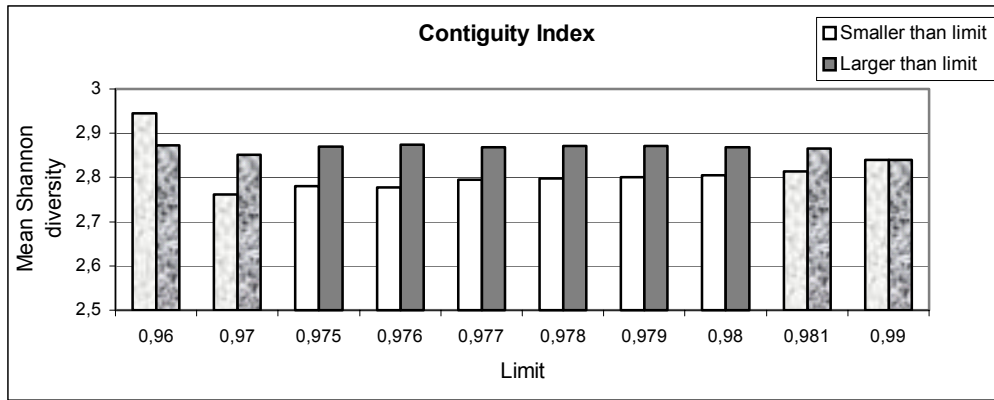
Figure 4.1.12: The diagram shows the mean Shannon diversity in the groups based on the contiguity index (SD=0.216-0.322). The non-patterned bars are significantly different (p=0.001-0.018) whereas the patterned are not significantly different (p=0.058-0.969).

4.1.3 The influence of isolation

Isolation is expected to have a negative influence on species richness and species diversity. Both of the metrics that are used to measure the influence of isolation, the nearest neighbour distance and the proximity index, indicate that this is indeed the case.

4.1.3.1 Eucledian Nearest Neighbour (ENN)

The Eucledian nearest neighbour distance measures the straight-line distance to the nearest patch of the same type (from edge to edge). Isolation appears to have a negative influence on both species richness and species diversity when the distance to the nearest neighbour exceeds 70-100 m (fig 4.1.13 and 4.1.14).
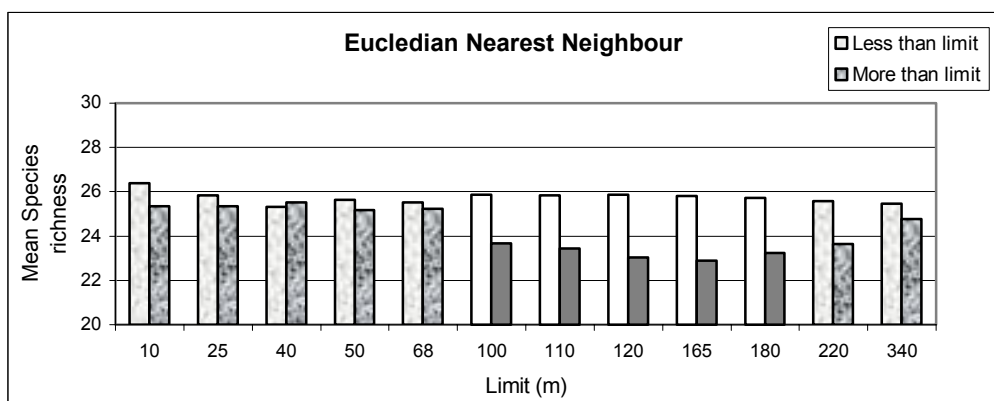
Figure 4.1.13: The diagram shows the mean species richness in the groups based on the Eucledian nearest neighbour distance (SD=5.28-7.37). The non-patterned bars are significantly different (p=0.001-0.012) whereas the patterned are not significantly different (p=0.108-0.744).
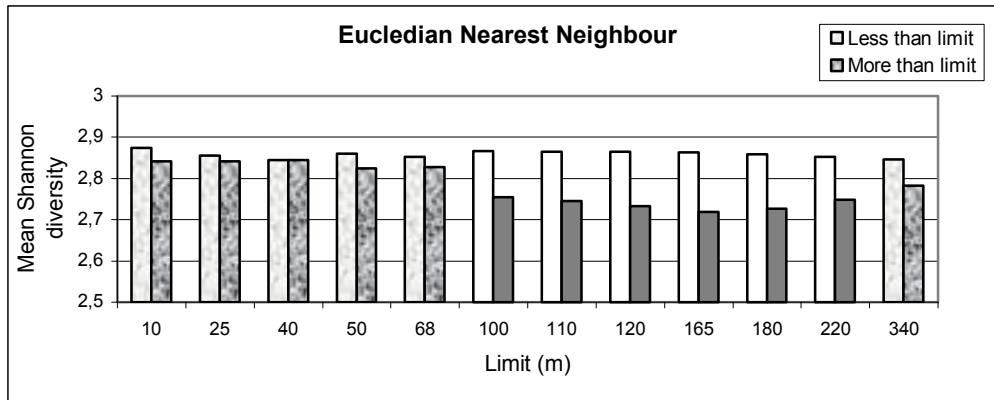
Figure 4.1.14: The diagram shows the mean Shannon diversity in the groups based on the Eucledian nearest neighbour distance (SD=0.207-0.37). The non-patterned bars are significantly different (p=0-0.039) whereas the patterned are not significantly different (p=0.175-0.967).

There are only 20 samples in the first group and less than 25 in the last 2 so the loss in significance does not necessarily mean that isolation is no longer a problem when the nearest neighbour is more than 200 m away.

4.1.3.2 Proximity index (prox)

The proximity index takes both size and proximity of all patches within a specified neighborhood of the focal patch (here 100 m, 500 m and 1000 m) in to account. The results show a tendency for patches with more semi-natural grasslands in their vicinity to have a higher species richness and diversity (figures 4.1.15 - 4.1.20).
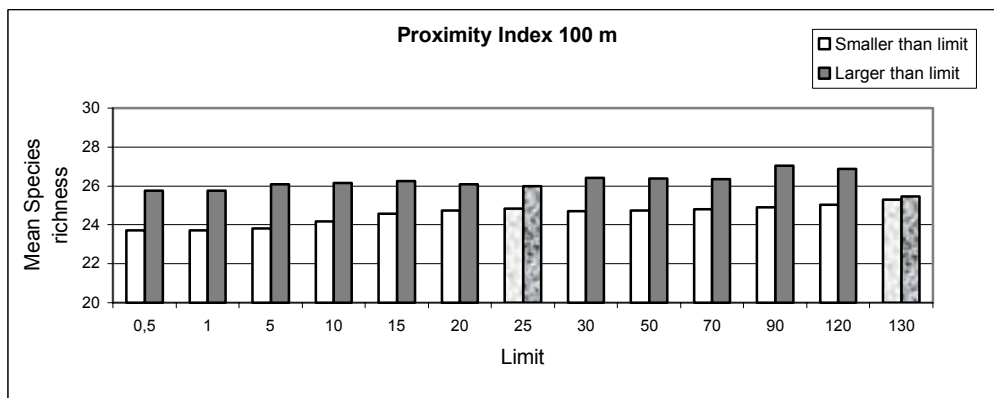
Figure 4.1.15: The diagram shows the mean species richness in the groups based on the proximity index with a search radius of 100 m (SD=5.173-5.933). The non-patterned bars are significantly different (p=0.001-0.031) whereas the patterned are not significantly different (p=0.064-0.889).

There are only 29 samples which have a proximity index of 130 or more within 100 m from the focal patch.
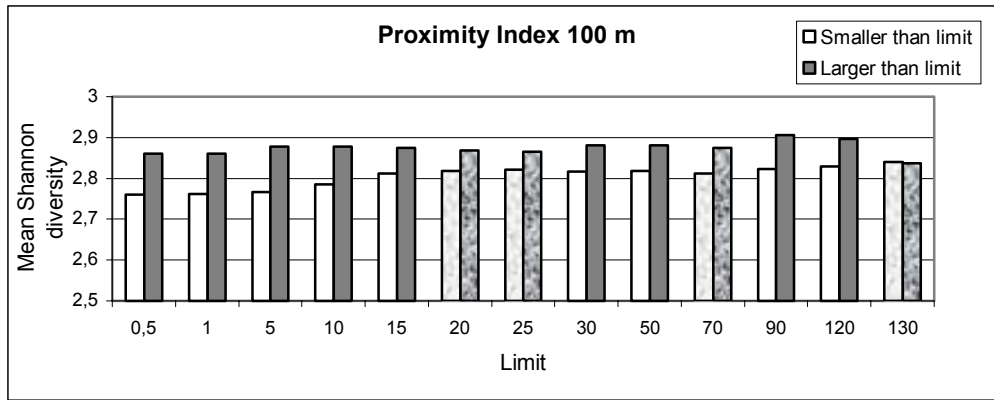
Figure 4.1.16: The diagram shows the mean Shannon diversity in the groups based on the proximity index with a search radius of 100 m (SD=0.196-0.253). The non-patterned bars are significantly different (p=0-0.034) whereas the patterned are not significantly different (p=0.056-0.937).
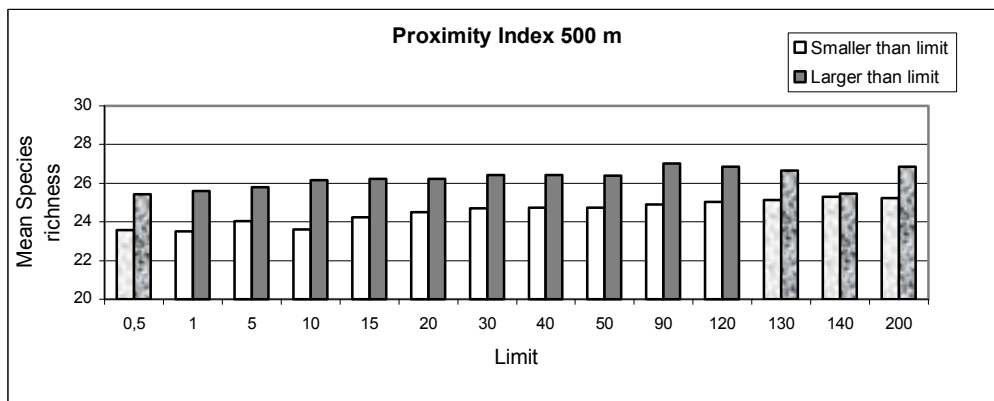
Figure 4.1.17: The diagram shows the mean species richness in the groups based on the proximity index with a search radius off 500 m (SD=4.406-6.564). The non-patterned bars are significantly different (p=0-0.048) whereas the patterned are not significantly different (p=0.083-0.889).
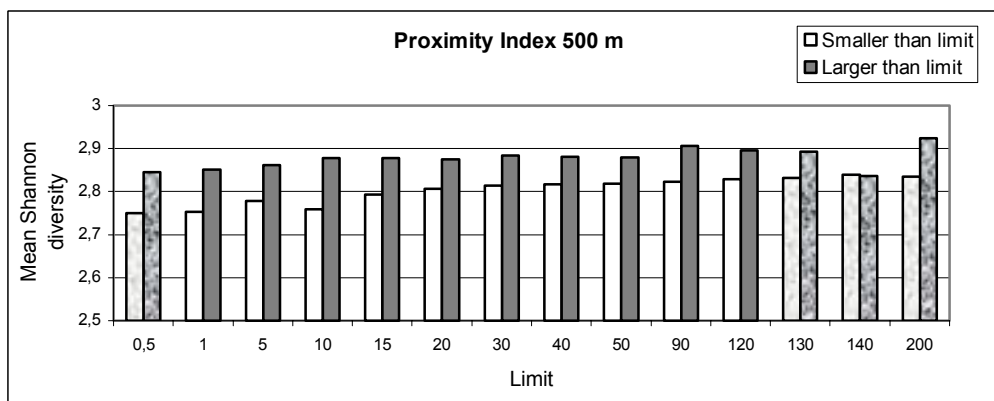
Figure 4.1.18: The diagram shows the mean Shannon diversity in the groups based on the proximity index with a search radius of 500 m (SD=0.182-0.318). The non-patterned bars are significantly different (p=0-0.046) whereas the patterned are not significantly different (p=0.076-0.937).

Within 500 m from the focal patch there are only 18 samples from patches with a proximity index value lower than 0.5 and less than 30 samples from patches with an index value larger than or equal to 140.

30
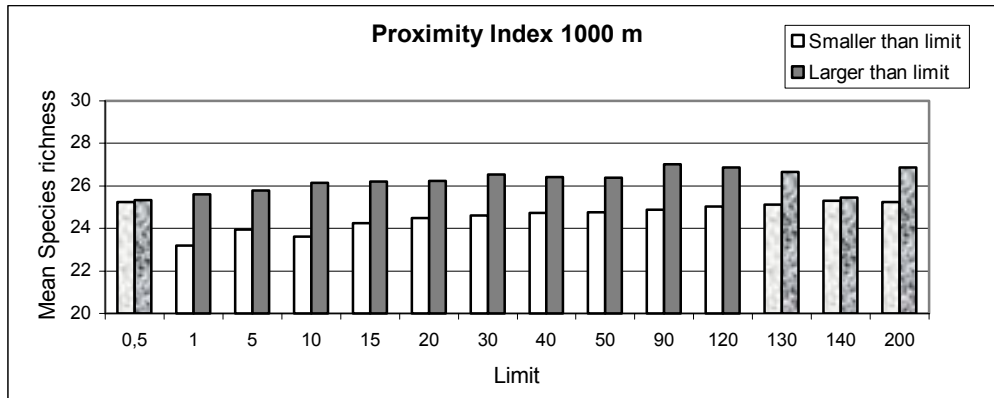
Figure 4.1.19: The diagram shows the mean species richness in the groups based on the proximity index with a search radius of 1000 m (SD=4.406-7.106). The non-patterned bars are significantly different (p=0-0.034) whereas the patterned are not significantly different (p=0.083-0.979).
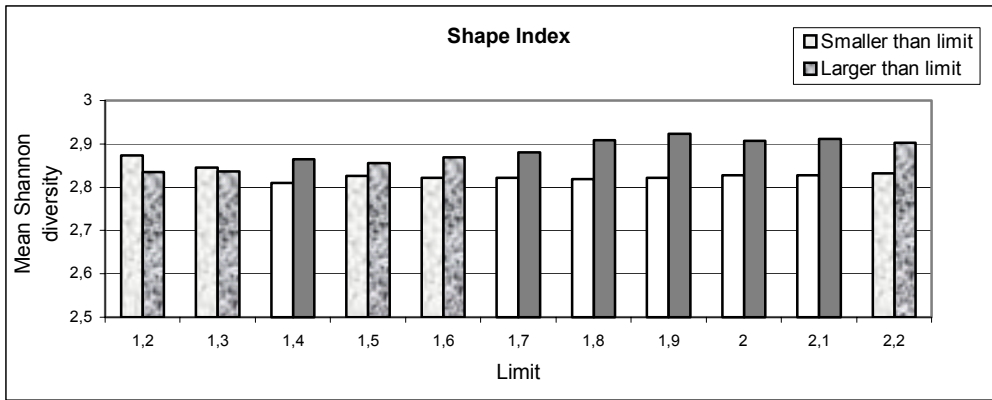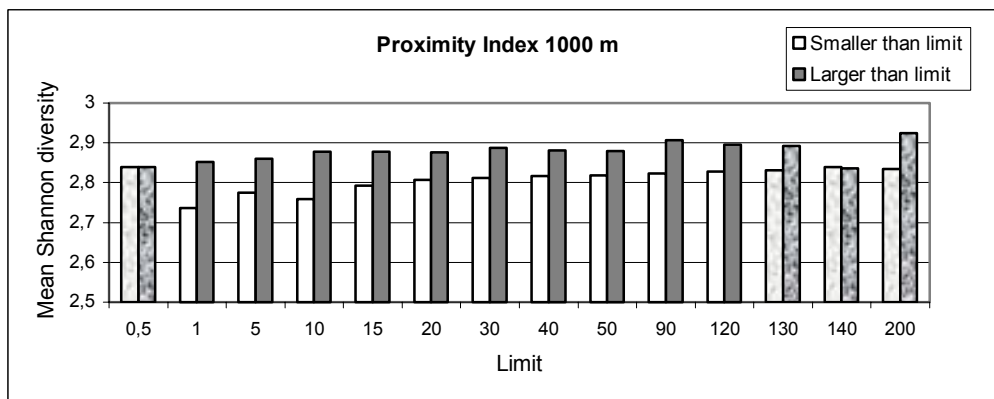

Figure 4.1.20: The diagram shows the mean Shannon diversity in the groups based on the proximity index with a search radius of 1000 m (SD=0.182-0.297). The non-patterned bars are significantly different (p=0-0.034) whereas the patterned are not significantly different (p=0.076-0.998).

Within 1000 m from the focal patch there are 8 samples from patches with a proximity index value lower than 0.5 and less than 30 samples from patches with an index value larger than or equal to 140.

4.2 Pearson's correlation coefficient

To determine the covariation between the chosen metrics and the species characteristics Pearson's correlation coefficient was calculated. The coefficient was calculated not only for all of the patches together but also for each of the chosen groups, i.e. grazed, abandoned, no / some eutrophication, heavier eutrophication, grassland in all time periods, grassland that was previously arable land and finally grassland which was previously forest. To account for the expected non-linearity of the relationships the variables were ln-transformed prior to analyses.

All patches
When looking at all of the 317 quadrants at once there is a statistically significant positive correlation between size and both of the species metrics (table 4.2.1). Except for the fractal dimension index the shape indices are also positively correlated with

the species metrics (table 4.2.2). The nearest neighbour distance and the proximity index 100m+1 are negatively correlated with the species metrics while the proximity indices 500m and 1000m are positively correlated (table 4.2.3).

Grazing
It appears that the effect of grazing overrules the effect of size on species richness and diversity (table 4.2.1). In abandoned areas there is a significant positive relationship between all three size metrics and the species metrics. In grazed areas on the other hand there is no significant correlation between size and species richness and only a weak positive correlation between Shannon diversity on one side and area and core area on the other.

Grazing also appears to influence the effect of shape but, contrary to size, the influence of shape on the species metrics is stronger in the grazed areas than in those that have been abandoned (table 4.2.2). The influence of isolation is also stronger in grazed areas although there are no strong correlations (table 4.2.3).

Nutrient status
In eutrophicated areas the correlation between size and the species metrics is lost while it remains positive in areas with a low nutrient status (table 4.2.1). None of the shape metrics reach significant levels of correlation in eutrophicatied areas while some of the shape indices retain their significance in the non-eutrophicated areas. Finally, for isolation there is only a small difference between the two types of areas.

Land use history
In old grasslands and grasslands on former forest a positive relationship between species richness / diversity and size is found whereas no relationship is found in grasslands on former arable land (table 4.2.1). Irregardless of history class none of the shape metrics are significantly related to the species metrics (table 4.2.2) while the isolation metrics are significantly correlated with the species metrics in the grasslands with the longest continuity but not in any of the younger grasslands (table 4.2.3).

Table 4.2.1: The table shows Pearson's correlation coefficient for species richness and species diversity and the chosen size metrics. All variables have been ln-transformed. When bold font is used the two factors are significantly correlated. The history categories are G=old grassland, A=former arable land and F=former forest. The critical values are for p=0.05 and come from www.psychstat.smsu.edu.

SIZE		All	Grazed		Nutrient status		History		
			Yes	No	Low	High	G	A	F
Critical value (5 %)		0.1103	0.1205	0.274	0.118	0.576	0.1691	0.2106	0.2765
ln(Species Richness)	ln(Area)	**0.1792**	0.09	**0.4285**	**0.1546**	0.202	**0.2504**	0.0249	**0.4336**
	ln(Core)	**0.1786**	0.0902	**0.4252**	**0.1533**	0.2039	**0.2493**	0.0241	**0.4407**
	ln(Perim)	**0.1851**	0.085	**0.4749**	**0.1625**	0.1889	**0.2499**	0.0315	**0.4036**
ln(Shannon diversity)	ln(Area)	**0.2102**	**0.124**	**0.4596**	**0.1835**	0.3248	**0.2783**	0.076	**0.4616**
	ln(Core)	**0.2096**	**0.1238**	**0.4579**	**0.1823**	0.3226	**0.2762**	0.0761	**0.4686**
	ln(Perim)	**0.1851**	0.1145	**0.4983**	**0.186**	0.3156	**0.2848**	0.0696	**0.4161**

Table 4.2.2: The table shows Pearson's correlation coefficient for species richness and species diversity and the chosen shape metrics. When bold font is used the two factors are significantly correlated. The history categories are G=old grassland, A=former arable land and F=former forest. The critical values come from www.psychstat.smsu.edu.

SHAPE		All	Grazed		Nutrient status		History		
			Yes	No	Low	High	G	A	F
Critical value (5 %)		0.1103	0.1205	0.274	0.118	0.576	0.1691	0.2106	0.2765
ln(Species Richness)	ln(CAI)	**0.1457**	**0.2207**	-0.074	**0.1663**	-0.486	0.0081	-0.034	-0.078
	ln(Contig)	**0.1359**	**0.2067**	-0.051	**0.1575**	-0.483	0.0173	-0.033	-0.186
	Ln(Frac)	0.0859	0.11	-0.018	0.0811	0.239	0.0861	-0.013	0.1265
	Ln(Shape)	**0.1168**	**0.1507**	-0.042	0.1156	0.1769	0.103	-0.02	0.0996
ln(Shannon diversity)	ln(CAI)	**0.1719**	**0.2441**	-0.058	**0.2006**	-0.495	0.0149	-0.003	-0.051
	ln(Contig)	**0.1613**	**0.2286**	-0.033	**0.1919**	-0.482	0.027	-0.007	-0.163
	Ln(Frac)	0.0852	0.1095	-0.057	0.0766	0.3481	0.0955	-0.072	0.1455
	Ln(Shape)	**0.1239**	**0.157**	-0.078	**0.121**	0.2922	0.1176	-0.083	0.1228

Table 4.2.3: The table shows Pearson's correlation coefficient for species richness and species diversity and the chosen isolation metrics. When bold font is used the two factors are significantly correlated. The history categories are G=old grassland, A=former arable land and F=former forest. The critical values come from www.psychstat.smsu.edu.

ISOLATION		All	Grazed		Nutrient status		History		
			Yes	No	Low	High	G	A	F
Critical value (5 %)		0.1103	0.1205	0.274	0.118	0.576	0.1691	0.2106	0.2765
ln(Species richness)	ln(ENN)	**-0.117**	-0.024	0.0009	-0.073	-0.546	**-0.188**	0.0014	-0.034
	ln(Prox100+1)	**-0.134**	0.0394	-0.0085	-0.116	-0.358	**-0.198**	0.0584	-0.168
	ln(Prox500)	**0.1981**	**0.125**	-0.0052	**0.1546**	**0.6847**	**0.2945**	0.0385	0.0978
	ln(Prox1000)	**0.192**	0.1182	-0.0203	**0.1496**	**0.682**	**0.293**	0.0331	0.0757
Shannon diversity	ln(ENN)	**-0.12**	-0.027	-0.0347	-0.068	**-0.672**	**-0.186**	-0.031	0.0412
	ln(Prox100+1)	**-0.124**	0.0488	-0.0192	-0.106	-0.334	**-0.217**	0.0669	-0.061
	ln(Prox500)	**0.2003**	**0.1306**	0.0086	**0.1517**	**0.7382**	**0.296**	0.0659	0.0086
	ln(Prox1000)	**0.1941**	**0.1221**	0.0017	**0.1465**	**0.7379**	**0.2957**	0.0594	-0.01

4.3 Regression analyses

4.3.1 The importance of size

The simple regression analyses show that an increase in patch size leads to an increase in both species richness (table 4.3.1) and species diversity (table 4.3.2) in the patch. If patch area increases by one percentage point then species richness increases by 0.050 percentage points while species diversity increases by 0.021 percentage points. A one percentage point increase in core area leads to a 0.046 percentage point increase in species number and a 0.020 percentage point increase in species diversity. Finally, if the patch perimeter increases by one percentage point then species richness increases by 0.080 percentage points while species diversity increases by 0.033 percentage points.

As can be expected, the size variables lose in power when the dummy variables for grazing and nutrient status are included in the regressions but they remain significant at the 10 % level (table 4.3.1 and 4.3.2). Further more, the equations containing the dummy variables have a higher R^2-value than the simple regressions and hence they

explain more of the variation in species richness and species diversity. While the simple regressions only explain 3-4 % of the variation in species richness and diversity the multiple regressions explain around 15 % of the variation in both of the variables.

Table 4.3.1: The results from the simple and multiple regression analyses between species richness and the size parameters. A and b refer to the parameters of equation 7. The level of significance is noted by: *** if p < 0.01, ** if p < 0.05 and * if p < 0.1.

Independent Variables	Dependent Variable: Species richness					
Constant *(a)*	3.214***	3.031***	3.222***	3.035***	2.697***	2.738***
Ln(area) *(b)*	0.050***	0.027*				
Ln(core) *(b)*			0.046***	0.025*		
Ln(perim) *(b)*					0.080***	0.046*
Graz_cat		0.220***		0.220***		0.219***
N_cat		-0.177***		-0.177***		-0.177***
R^2	0.032	0.149	0.032	0.149	0.034	0.151
Adjusted R^2	0.029	0.141	0.029	0.141	0.031	0.142
N	317	317	317	317	317	317

Table 4.3.2: The results from the simple and multiple regression analyses between species diversity and the size parameters. A and b refer to the parameters of equation 7. The level of significance is noted by: *** if p < 0.01, ** if p < 0.05 and * if p < 0.1.

Independent Variables	Dependent Variable: Shannon diversity index					
Constant *(a)*	1.045***	0.982***	1.048***	0.984***	0.831***	0.845***
Ln(area) *(b)*	0.021***	0.013**				
Ln(core) *(b)*			0.020***	0.012**		
Ln(perim) *(b)*					0.033***	0.021**
Graz_cat		0.075***		0.075***		0.075***
N_cat		-0.060***		-0.060***		-0.061***
R^2	0.044	0.149	0.044	0.149	0.045	0.150
Adjusted R^2	0.041	0.141	0.041	0.140	0.042	0.142
N	317	317	317	317	317	317

4.3.2 The importance of shape

Apart from the fractal dimension index, which does not significantly influence either of the species metrics, an increase in the shape indices leads to a significant increase in both species number (table 4.3.3) and species diversity (table 4.3.4) in the simple regressions. The R^2-value is low though and only 1-3 % of the variation in the species variables can be explained by the simple regressions. By adding the dummy variables to the analyses the regression equations' abilities to predict the species variables increase but the significance of the shape indices is lost. This indicates that the results are not robust.

Independent Variables	Dependent Variable: Species richness							
Constant (a)	1.147	1.948**	3.228***	3.064***	3.158***	2.991***	3.194***	2.987***
Ln(CAI) (b)	0.465***	0.243						
Ln(contig) (b)			3.898**	1.986				
Ln(frac) (b)					0.505	0.317		
Ln(shape) (b)							0.126**	0.079
Graz_cat		0.225***		0.225***		0.229***		0.227***
N_cat		-0.183***		-0.186***		-0.200***		-0.195***
R^2	0.021	0.146	0.018	0.145	0.007	0.143	0.014	0.146
Adjusted R^2	0.018	0.138	0.015	0.137	0.004	0.135	0.010	0.137
N	317	317	317	317	317	317	317	317

Independent Variables	Dependent Variable: Shannon diversity index							
Constant (a)	0.164	0.440	1.076***	0.999***	1.024***	0.996***	0.019***	0.963***
Ln(CAI) (b)	0.198***	0.112*						
Ln(contig) (b)			1.670***	1.010*				
Ln(frac) (b)					0.181	0.115		
Ln(shape) (b)							0.048**	0.032
Graz_cat		0.078***		0.078***		0.080***		0.079***
N_cat		-0.063***		-0.064***		-0.072***		-0.070***
R^2	0.030	0.143	0.026	0.141	0.007	0.135	0.015	0.139
Adjusted R^2	0.026	0.143	0.023	0.133	0.004	0.127	0.012	0.131
N	317	317	317	317	317	317	317	317

4.3.2 The importance of isolation

Two different types of metrics are used to quantify isolation. The first type, the proximity index, calculates the amount of semi-natural grassland found within a specified distance of the focal patch. When this distance is set to 100 m there is no significant influence on the species variables (table 4.3.5 and 4.3.6). If the search radius is instead set to 500 m (prox_500) or 1000 m (prox_1000) 3-4 % of the variation in the species metrics can be explained by the regression equations. A one percentage point increase in prox_500 leads to a 0.023 percentage point increase in species richness and a 0.008 percentage point increase in species diversity. A one percentage point increase in (prox_1000) leads to an increase in species richness by 0.240 percentage points and an increase in species diversity by 0.009 percentage points. These results are not robust though as significance is lost when the dummy variables are added to the equations.

The second type of isolation metric which is used is the nearest neighbour distance (ENN). As this distance increase by one percentage point the species richness decreases by 0.028 percentage points while the species diversity decreases by 0.010 percentage points. Only around 1 % of the variation in the species metrics is

explained by the equations. These results are not robust either as significance is lost when the dummy variables are added.

Table 4.3.5: *The results from the simple and multiple regression analyses between species richness and the isolation perimeters are presented. A and b refer to the parameters of equation 7. The level of significance is noted by: *** if p < 0.01, ** if p < 0.05 and * if p < 0.1.*

Independent Variables		Dependent Variable: Species richness							
Constant	(a)	3.185***	2.996***	3.139***	3.006***	3.134***	3.004***	3.311***	2.998***
Ln(prox_100)	(b)	0.120	0.005						
Ln(prox_500)	(b)			0.023***	0.009				
Ln(prox_1000)	(b)					0.240***	0.009		
ENN	(b)							-0.028**	0.004
Graz_cat			0.242***		0.217***		0.218***		0.238***
N_cat			-0.172**		-0.225***		-0.226***		-0.238***
R^2		0.009	0.113	0.039	0.155	0.037	0.154	0.014	0.150
Adjusted R^2		0.005	0.102	0.036	0.147	0.034	0.146	0.011	0.142
N		317	317	317	317	317	317	317	317

Table 4.3.6: *The results from the simple and multiple regression analyses between species diversity and the isolation perimeters are presented. A and b refer to the parameters of equation 7. The level of significance is noted by: *** if p < 0.01, ** if p < 0.05 and * if p < 0.1.*

Independent Variables		Dependent Varaible: Shannon diversity index							
Constant	(a)	1.036***	0.968***	1.016***	0.970***	1.014***	0.970***	1.079***	0.972***
Ln(prox_100)	(b)	0.004	0.002						
Ln(prox_500)	(b)			0.008***					
Ln(prox_1000)	(b)					0.009***	0.004		
ENN	(b)							-0.010**	0.001
Graz_cat			0.085***				0.075***		0.082***
N_cat			-0.048*				-0.078***		-0.082***
R^2		0.007	0.106	0.040	0.145	0.038	0.145	0.014	0.140
Adjusted R^2		0.003	0.095	0.037	0.137	0.035		0.011	
N		317	317	317	317	317	317	317	317

5 Discussion

5.1 Possible sources of error

5.1.1 Sampling methods

The reliability of any result is dependent on the quality of the data used in the analysis. As the species data used here was neither gathered for this study, nor intended to be used in this type of analysis, it is one of the main sources of error. The intention was merely to get an overview of the study area so a time effective, but not entirely reliable, sampling method was chosen. One of the problems with the data set is that sampling was not standardized with regards to humidity, nutrient status, light-penetration etc. Other underlying differences may therefore disturb the interpretation of the results. Furthermore, only one or a few quadrants were placed in patches considered homogeneous, regardless of patch size, while more samples were taken from more heterogeneous patches. If sampling intensity is not proportional to patch size, which it was not, then more information is likely to be missing from the large patches (Forman, 1995). When studying the effect of size a consistent under-estimation of species richness in larger patches is likely to influence the results by weakening the co variation found between the variables.

The results of a study by Cousins and Eriksson (2002) show that in open, dry to mesic, semi-natural grasslands the diversity within the plot (i.e. the α-diversity) is high, while the diversity between plots (the β-diversity) is relatively low. This means that in a homogeneous patch most species are found in a relatively fine-scaled sample and hence the problem with few quadrants may not be so great. Non-the-less, with only one or a few quadrants in each patch one can not be confident that the found species composition is representative of that of the entire patch, nor can the total species richness of the patch be determined. A more systematic sampling would therefore have been appropriate.

Despite its limitation the available species data was used. This is a preliminary study intended as a preparation for a larger, ongoing study of the area. The main purpose is to get acquainted with the methods used and to see if landscape configuration appears to influence the species metrics. In the main study, species data is collected in a more systematic and thorough way which will make the results more reliable.

5.1.2 FRAGSTATS

The 3rd version of FRAGSTATS does not support input data in vector format so the land use map was converted from vector to raster format prior to analysis. Such a conversion leads to an upward bias of patch perimeter and influences not only the perimeter, but also those shape metrics that are based on the perimeter, namely the shape and fractal dimension indices. As all of the patches are subjected to this bias, and a small pixel size (one meter) is used, I believe that the effect on the interpretation of the results is negligible.

Only semi-natural grasslands within the study area are taken into account when the isolation metrics are calculated. This means that there is a risk of the isolation being overestimated for patches located near the outskirts of the study area. By adding a boarder the width of the largest search radius (here 1000 m) this can be avoided. However, as a general examination of the surrounding areas showed that there are not many grasslands in the vicinity of the study area, the likelihood of such a boarder changing the results to any great extent is low.

The main problem regarding the metrics calculated by FRAGSTATS concerns the scale at which the patches are delimited. Only one property can be keep when converting the original coverage file to a grid file. As discussed in section 3.3.1.1. this means that either all of the patches are treated as separate classes or patches located next to each other are joined together in new, larger patches. Depending on which criteria one wishes to use to delimit the patches, either of these can be the correct approach. If the original extent is kept, then only the relatively homogeneous areas originally considered to constitute a patch will be regarded as suitable habitat. If on the other hand, patches located next to each other are joined together, then the entire new patch will be considered equally suitable as habitat even though the area is likely to be very heterogeneous. None of these approaches is likely to reflect reality entirely. It is more likely that each species will have a certain type of habitat in which it is most abundant but that it is still able to survive and spread through some of the other habitat types found in the vicinity. I would have preferred to use the original extent of the patches for all of the analyses but this was not possible as land use class had to be used in the studies of isolation. When looking at size and shape the original structure of the landscape was maintained though which means that two different scales are used.

5.2 Evaluation of the results

Three different methods are used to study the relationship between each of the patch metrics and the species metrics. By comparing the results with each other it is possible to draw conclusions regarding their reliability. If all three methods point towards the same sort of relationship, then it is more likely that such a relationship does indeed exist. If, on the other hand, one method results in a positive relationship, while the other indicates that there is no relationship, or even that it is negative, then the results are obviously less reliable. Such a comparison is therefore made below.

5.2.1 Size

Regardless of whether area, core area or patch perimeter is used to quantify size the *t-tests* show that species richness and species diversity are higher in larger patches than in their smaller counterparts. In all of the cases where the difference is not significant the sample size is below 30, which means the results are not reliable. Hence my hypothesis regarding the influence of patch size on species richness and diversity is supported. Regarding the possible existence of a minimum area point, i.e. an upper limit for the effect of size, no conclusions can be drawn due to the small number of samples taken from large patches.

All three size metrics were positively correlated with both species richness and species diversity, so the *correlation coefficients* also support my hypothesis regarding the influence of size. When grazing, nutrient status and land use history, factors known to influence species richness in the area, were taken into account additional information was gained. In grazed or nutrient enriched areas species richness and diversity were not influenced by patch size. As grazing is known to influence the species metrics positively and eutrophication is known to have a negative influence it is perhaps not so surprising that the effect of size is overruled in these areas. However, only 14 samples have been collected from patches considered to be eutrophicated. This is too small a sample to be confident that the effect of nutrient enrichment is stronger than that of size.

Finally, the *regression analyses* also show that an increase in size leads to an increase in species richness and diversity. However, the R^2-value shows that a regression equation with size as the only explanatory variable only explains a few percent of the variation in the species metrics. By adding dummy variables for grazing and nutrient status the explanatory degree of the regression equation increases to around 15 %. This makes it a more interesting model to work with, although much of the variation in species distribution is still left unaccounted for.

The same conclusion regarding the influence of size is drawn with all three methods. It is therefore likely that size has a positive influence on the species metrics in the study area. As there is no reason to believe that the grasslands of the study area differ from other grasslands the results should be applicable in other semi-natural grassland areas as well. Previously, the importance of patch size in semi-natural grasslands has been studied with varying results. In most studies on plants and area, the island biogeography theory has not been found to fit well (Forman, 1995). Eriksson et al. (1995) find that pasture area has no significant influence on species richness. A possible explanation is that the species richness is not in equilibrium with the current landscape picture. When area decreases, species numbers are expected to follow but there is a certain time-lag between habitat loss and species respons. This means that species which are bound to go extinct eventually may be able to survive in the area for years. Several studies have also found a positive relationship between size and species richness. Krauss et al. (2004) find that habitat area has a positive effect on both generalist and specialist plant species and Bruun (2000) finds that both long- and short-lived plant species are affected positively by perimeter length. Furthermore, Grashof-Hopdam (1997) finds that forest species richness in the agricultural landscape increases with area as does Jaquemyn et al. (2003).

5.2.2 Shape
When a *t-test* was used to examine the influence of shape, varying results and levels of significance were found. No conclusions regarding the influence of shape can therefore be drawn based on the results. While the *core area-* and *contiguity indices* show a tendency towards a higher species richness and diversity in more compact patches, the *shape-* and *fractal dimension indices* show the opposite. In all cases, significance varies depending on where the limit is drawn. Contrary to size, the lack in significance can not always be explained by a small sample.

The *correlation coefficients* show similar tendencies to the t-tests. Although the fractal dimension index shows no significant co variation with the species metrics the other three shape indices are positively correlated to them. This once more implies that both a compact and an irregular shape is good for the species richness and diversity and makes it difficult to interpret the results. When the analysis was performed on separate groups, based on land use history, level of grazing and eutrophication, most of the correlation was lost. It remained significant only in nutrient poor and grazed areas, the two largest groups. With a large sample, the correlation required to reach significance is lower than that required with a small sample. This may explain why the grazed and nutrient poor areas are significant and not the others.

When simple *regression analysis* was performed, a positive relationship between the species indices and the CAI, shape index and contiguity index was found. The R^2-value was low and only a few percent in the variation could be accounted for though. The fractal dimension index lacked significance. After adding the dummy variables the explanatory degree of the regression equations increased greatly but most of the shape indices lost their significance indicating that they are not robust in the model.

The influence of patch shape is more difficult both to predict and to interpret. Not only is significance low, but different conclusions regarding the importance of shape are also drawn depending on which metric is used to quantify it. Shape therefore does not appear to influence the mean species richness and diversity in semi-natural grasslands. If such an influence does exist it must be relatively weak and dependent on more variation in patch shape to show clearly. In the study area the dispersion in patch shape is low. This is likely to be the case in most areas as semi-natural grasslands depend on disturbance to persist and are mainly found in the agricultural landscape where most borders have been influenced by man.

While the results do not show that shape is of ecological importance this is still likely to be the case. In this study only mean species richness and diversity are taken into account. Different species thrive in different types of environments though. As an example, a species dependent on stable conditions is expected to be positively related to the contiguity index. A species that prefers living in the edge zones, on the other hand, should be negatively related to the same index. If the species had been divided into different functional types prior to analysis, and each plant type had been analyzed separately, it is possible that a totally different picture of the importance of shape would have emerged, but Saunders et al. (1991) find that shape is only important in relatively small patches.

5.2.3 Isolation

The results of the *t-tests* support my hypothesis that isolation has a negative influence on species richness and diversity. The results also show that the negative influence begins as the distance to the *nearest neighbour* exceeds 70 to 100 meters. Prior to this, no significant influence is seen and there are sufficient samples to conclude that the negative influence of isolation has not yet begun. Naturally, individual species may be adversely affected by isolation long before, but the mean species richness and diversity do not appear to be. When the nearest neighbour is 220 meters or more from the patch the negative influence of isolation seems to disappear. However, a small

sample size (23 samples or less) is once more the most probable reason. For the three *proximity indices*, no upper or lower limits to their influence appear. With a few exceptions, all when a search radius of 100 meters is used, any loss in significance is linked to a sample size below 30.

If my hypothesis regarding isolation is correct, then *Pearson's correlation coefficient* should be negative for the nearest neighbour distance and positive for the proximity indices. Only the proximity values obtained with a search radius of 100 meters deviate from the expected pattern. For some reason, they are negatively related to species richness and diversity. That the amount of nearby grasslands should have a negative impact on species richness and diversity appears highly unlikely. Prox_100 was the only group containing zero values. It is possible that my handling of these cases was not correct and that it has somehow influenced the results. Ln-transformation was required in order to account for the expected non-linearity of the relationships. As zero can not be ln-transformed I added one to all of the Prox_100-values and used lnProx_100+1 in the calculations instead. Perhaps it would have been better to simply exclude the zero values.

Much of the co variation between isolation and the species metrics is lost when the patches are divided into groups according to the different categories. The smaller the groups are the stronger the co variation needs to be to be considered significant which may be part of the reason for the loss in significance. It is not the whole explanation though as the influence remains significant in eutrophicated areas (14 samples) but not in old arable land (85 samples).

The simple *regression analyses* support my hypothesis regarding the influence of isolation but only a small part of the variation can be accounted for. When the dummy variables are added and multivariate regression analyses are performed then the isolation metrics loose their significance. This means that they are not robust in the regression equations.

Isolation was expected to be negatively related to species richness and diversity. If the prox_100 is neglected, then two out of three methods support the hypothesis while the third indicates that it may be correct. I therefore conclude that it is likely that isolation has a negative influence on species richness and diversity in the study area. As with size, previous studies have come to different conclusions regarding the influence of isolation. Neither Krauss et al. (2004) nor Eriksson et al. (1995) find any significant effect of isolation on species richness. Bruun (2000) on the other hand finds that isolation plays a significant role in small patches and that it negatively affects short-lived species. Furthermore, his results indicate that while local extinction occurs in small isolated patches, populations in similarly sized patches located near a source may survive. Franzén and Eriksson (2003) study the effect of isolation on four different plant species and find that three of these are affected negatively. Finally, Jaquemyn et al. (2003) and Grashof-Hopdams (1997) study forest species and find that they are negatively influenced by isolation, especially those with a low dispersal capacity. Interestingly, Grashof-Hopdams also finds that most species are affected either by area or by isolation but generally not by both and that for species spread by animals the distance between patches should not exceed 100 meters. This coincides well with the results found in this study, where the effect of isolation on grassland

species appears around 70 to 100 meters. Many grassland species are distributed by wind rather than by animals but the comparison is still interesting.

One of the weaknesses with the isolation studies is that patch size is not taken into account although it is believed to be of importance. As discussed in section 5.1.2 patches located next to each other were joined together in the input file which was used to calculate the isolation metrics. In the new file only 37 patches remained which is not enough to separate them into groups and treat small and large patches separately. Furthermore, as most of the new patches are larger than the original ones they are not believed to represent the size that is of ecological importance. Including size might therefore be more misleading than informative.

5.3 Evaluation of the methods

It took a while to get acquainted with the computer program Fragstats but once it was up and running it proved to be effective for calculating various metrics. Only a small part of the capacity was used and I believe more knowledge about the landscape configuration and its consequences can be gained.

The results show that the mean species richness and mean species diversity are affected in a similar way by the landscape configuration of the study area. If the grasslands had been impoverished, then diversity would have been lower and the results might not have corresponded so well with each other. However, they appear to be alike so both metrics do not need to be taken into account in the continued exploration of the area. Species richness is the most commonly used metric in this type of study.

Three different *statistical methods* were used to explore the various relationships. The *t-test* had the advantage of being illustrative. It also showed if, and where, relationships change which was especially useful for isolation. *Pearson's correlation coefficient* made it possible to determine in which types of areas the influence of a landscape metric was the strongest. The main problem was that some of the groups contained few samples, which made the results less reliable. Finally, the *regression analyses* could be used to quantify the relationships, showing not only if there was a relationship but also how much of the variation in the dependent variable could be explained by the independent variable. When multivariate regression analyses, with dummy variables for grazing and nutrient status, were performed 10-15 % of the variation could be accounted for. This shows that many more factors need to be taken into account to get the full picture.

5.4 Suggested improvements and future research

One of the reasons that large patches are expected to contain more species than their smaller counterparts is that they contain more microhabitats. While some species thrive in the stable conditions of the patch interior others are found in the transition zones of the patch edges. Some species live in the moister low lying areas while others are found in the drier, higher parts of the grassland patches. Two patches with the same mean species richness can therefore be very different. In a homogeneous patch the same species will be found in many of the quadrants and the difference

between mean and total species richness will not be so great. In a heterogeneous patch on the other hand the species composition in the quadrants will vary much more and the difference between mean and total species richness will be greater. By using a more systematic sampling method, with sampling intensity proportional to patch size, it would be possible to compare the total number of species in each patch as well. It is likely that the difference between small and large patches would then be greater.

The results show little, or no, difference between area and core area. As edge width, which is used to determine core area, was rather subjectively chosen it would be interesting to see if the results change with a different edge width. If the influence from the surrounding areas was underestimated then the areas considered to be core area were not core area after all. That would explain why so little difference was found between total and core area. Also, edge width varies depending on the surrounding areas, on the dominating wind direction etc. (Forman, 1995). All of this variation can not be taken into account but it should be given some thought when the width is determined.

For the isolation metrics several things could have been done differently or need further exploration. The results show that isolation begins to have a negative effect as the nearest neighbour distance exceeds 70 to 100 meters. All of the search radiuses used when calculating the proximity indices exceed this limit. It would be interesting to include a proximity index with a smaller search radius, e.g. 50 meters, to see how species richness was influenced by this. If time and knowledge allow, it would also be appropriate to include the *functional nearest neighbour* in the analyses. This metric requires a thorough understanding of how the dispersal of different plant functional types is influenced by the surrounding environment. It calculates the distance to the nearest neighbour along the least cost path, rather than the shortest distance and is therefore a better reflection of reality, providing that the costs are correctly set. But even if the functional nearest neighbour can not be calculated then corridors and stepping stones which enhance dispersal and the land use in the surrounding landscape can be of interest. As an example, Söderström et al (2001) find that there are fewer plant species in semi-natural grasslands with more arable fields in the surrounding landscape. Finally, patch size should be included in the study of isolation. It was not taken into account here due to the limitations in the input data discussed in section 5.1.2. In the larger, ongoing study of the area a one meter edge has been removed from all of the grassland polygons. They then become separated from each other and keep their original extent in raster format which means that the same input file can be used regardless of which type of metric is calculated. Patch size can then be included in the analysis and the belief that small patches are more affected by isolation can be tested. Some indication regarding the minimum size needed to avert the negative effects of isolation can also be sought. From a conservation point of view such information is very interesting as resources are often limited and choices must be made regarding which grasslands to manage. Other taxa, such as insects and lichen, may also be of interest to study from a conservation point of view as they too can be dependent on the semi-natural grasslands for their survival.

Another factor which would be interesting to include in the analysis is the history of the area. Grasslands are dominated by perennial plants so there is a time-lag in the response between an aerial change and changes in species distribution. The current species composition is therefore more likely to be in equilibrium with the past habitat

distribution than with the current one (amongst others Eriksson et al., 2002 and Bruun 2000). Bringing the historic extent of grasslands into the analysis could therefore enhance the understanding of the processes which act in the agricultural landscape.

Should the possible effects of shape be investigated further it would be appropriate to divide the plants into different functional types prior to analysis or to look a few, chosen, species. If it were possible to find a study area with a greater number of large and irregular patches I believe that it would be better. With a low variation in shape, potential patterns are hard to find.

There is a risk that the relationships found during the different types of statistical analyses are caused by a simultaneous response from the two studied variables to a third variable and not by an actual relationship between them (Shaw and Wheeler, 1996). As an example, many of the grasslands in the study area have been abandoned or have too low a grazing pressure to keep them open. Should small patches have been abandoned to a greater extent, which is not unlikely, then they will be more overgrown than the larger ones. The observed difference in species richness may then be a consequence of lower light penetration and not of a smaller size. It would therefore be wise to make sure that the results are not an effect of a simultaneous response to e.g. openness.

5.5 Conclusions

In this study both species richness and species diversity are compared to the different landscape metrics. As the results are very similar, only one of the two needs to be used in future studies. Species richness is more common so it is easier to compare the results with other studies if this metric is chosen.

None of the landscape metrics explain more than a few percent of the variation in species richness and diversity on their own. By taking grazing and nutrient status into account the explanatory degree increases for most of the metrics but around 85 % of the variation is still left unaccounted for.

The results indicate that size affects both species richness and species diversity positively. The chosen edge zone of three meters is likely to be too narrow as no difference is found between the influence of area and core area.

Shape does not appear to influence the species metrics. It is possible that the species composition is influenced by landscape fragmentation, with an increase in generalist species in fragmented areas, but further studies are required to determine this.

Isolation seems to influence the species negatively as the distance to the nearest neighbour exceeds 70 to 100 meters. By including patch size and land use history in the analyses further knowledge should be gained.

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http://www.umass.edu/landeco/research/fragstats/documents/Conceptual%20Background/Patches%20and%20Patchiness/Patches%20and%20Patchiness.htm#PATCHES%20&%20PATCHINESS:%20%20LEVELS%20OF%20LANDSCAPE%20METRICS

University of Massachusetts, Landscape Ecology Program. Collected 23/5-04. Last updated 12/9-03.

Appendix 1

The pictures show how the land use has changed over time in the study area.

Legen - land use in the study area

Symbol	Land use
	Agricultural field
	Cultivated grassland
	Semi-natural grassland
	Other grassland
	Alvar
	Closed forest
	Pasture like forest
	Hazel
	Wetland
	Built up area / Other land use

1938

1959

1994
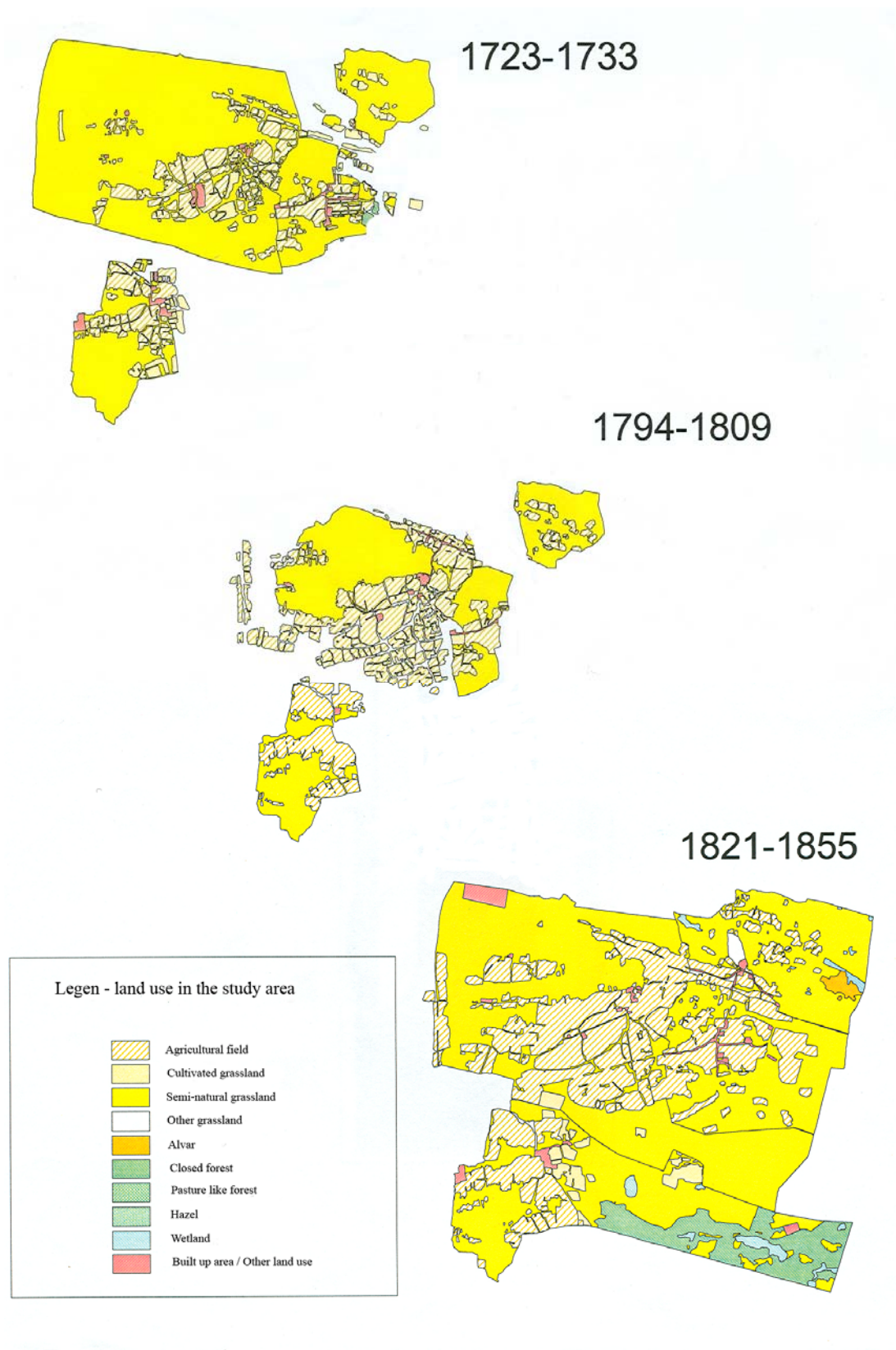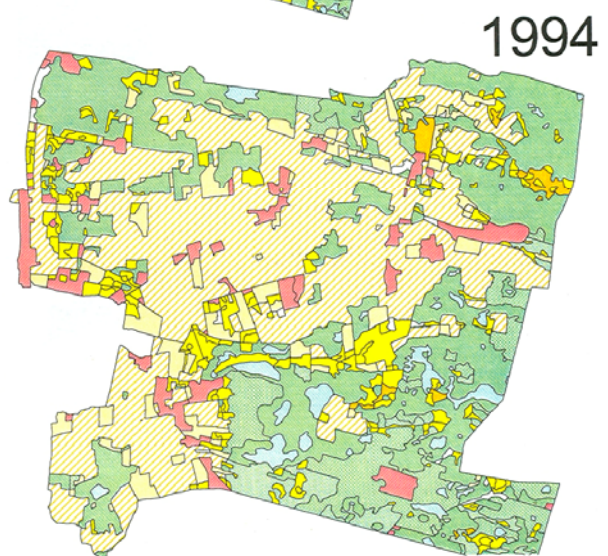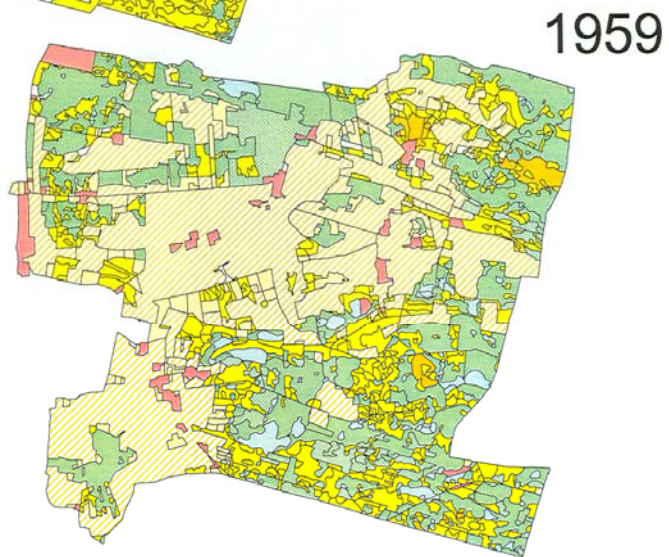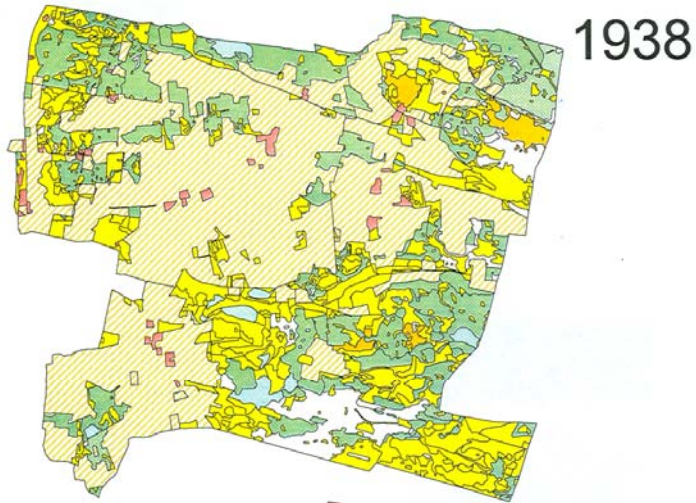
Appendix 2

All of the results from the t-test are presented in the tables below.

NoSpp	N	Avg	SD			N	Avg	SD	p
Area < 0,25	32	23,22	7,25	Vs.	Area > 0,25	285	25,52	5,35	0,091
Area < 0,5	88	23,72	5,41	Vs.	Area > 0,5	229	25,89	5,57	**0,002**
Area < 1	218	24,52	5,62	vs.	Area > 1	99	26,97	5,09	**0**
Area < 1,5	255	24,91	5,74	vs.	Area > 1,5	62	26,82	4,7	**0,016**
Area < 2	266	24,97	5,75	vs.	Area > 2	51	26,9	4,46	**0,009**
Area < 2,5	283	25,02	5,71	vs.	Area > 2,5	34	27,5	3,97	**0,002**
Area < 3	290	25,03	5,66	vs.	Area > 3	27	27,96	4,13	**0,002**
Area < 4	308	25,29	5,66	vs.	Area > 4	9	25,11	3,02	0,87
Area 0-0,5	88	23,72	5,41	vs.	Area 0,5-1	105	25,06	5,79	0,085
Area 0-1	218	24,52	5,67	vs.	Area 1-2	48	27,04	5,73	**0,006**
Area 1-2	48	27,04	5,73	vs.	Area 2-3	24	25,71	4,59	0,325
Area 2-3	24	25,71	4,59	vs.	Area 3-4	18	29,39	3,91	**0,009**
Area 3-4	18	29,39	3,91	vs.	Area 4-5	9	25,11	3,02	**0,008**

Shannon	N	Avg	SD			N	Avg	SD	P
Area < 0,25	32	2,724	0,323	vs.	Area > 0,25	285	2,852	0,223	**0,036**
Area < 0,5	88	2,775	0,245	vs.	Area > 0,5	229	2,864	0,23	**0,003**
Area < 1	218	2,803	0,244	vs.	Area > 1	99	2,92	0,201	**0**
Area < 1,5	255	2,817	0,246	vs.	Area > 1,5	62	2,93	0,174	**0**
Area < 2	266	2,82	0,244	vs.	Area > 2	51	2,94	0,166	**0**
Area < 2,5	283	2,826	0,242	vs.	Area > 2,5	34	2,954	0,156	**0**
Area < 3	290	2,827	0,24	vs.	Area > 3	27	2,97	0,165	**0**
Area < 4	308	2,838	0,24	vs.	Area > 4	9	2,882	0,15	0,589
Area 0-0,5	88	2,775	0,245	vs.	Area 0,5-1	105	2,821	0,243	0,166
Area 0-1	218	2,803	0,244	vs.	Area 1-2	48	2,899	0,232	**0,013**
Area 1-2	48	2,899	0,232	vs.	Area 2-3	24	2,907	0,163	0,886
Area 2-3	24	2,907	0,163	vs.	Area 3-4	18	3,014	0,158	**0,038**
Area 3-4	18	3,014	0,158	vs.	Area 4-5	9	2,882	0,15	**0,047**

NoSpp	N	Avg	SD			N	Avg	SD	p
Perim < 500	139	24,54	5,68	vs.	Perim > 500	178	25,87	5,48	**0,036**
Perim < 600	200	24,96	5,46	vs.	Perim > 600	117	25,84	5,81	0,179
Perim < 700	233	24,8	5,67	vs.	Perim > 700	84	26,63	5,2	**0,01**
Perim < 800	248	24,69	5,65	vs.	Perim > 800	69	27,41	4,88	**0**
Perim < 900	269	24,84	5,75	vs.	Perim > 900	48	27,75	3,89	**0**
Perim < 1000	273	24,94	5,77	vs.	Perim > 1000	44	27,41	3,79	**0**
Perim < 1200	275	24,94	5,76	vs.	Perim > 1200	42	27,52	3,78	**0**
Perim < 1300	288	25,11	5,74	vs.	Perim > 1300	29	27,03	3,62	**0,014**
Perim < 1400	298	25,22	5,72	vs.	Perim > 1400	19	26,26	3,11	0,197
Perim < 500	139	24,54	5,68	vs.	Perim 500-1000	134	25,36	5,86	0,242
Perim 1000-1250	15	28,13	4,12	vs.	Perim > 1250	29	27,03	3,62	0,368
Perim < 1000	273	24,94	5,77	vs.	Perim 1000-2000	39	27,67	3,87	**0**
Perim 1000-2000	39	27,67	3,87	vs.	Perim 2000-3000	2	27,5	2,12	0,952
Perim 2000-3000	2	27,5	2,12	vs.	Perim >3000	3	24	1,73	0,133
Perim <1000	273	24,94	5,77	vs.	Perim 2000-3000	2	27,5	2,12	0,532
Perim <1000	273	24,94	5,77	vs.	Perim >3000	3	24	1,73	0,788
Perim 1000-2000	39	27,67	3,87	vs.	Perim >3000	3	24	1,73	0,114
Shannon		N	Avg	SD		N	Avg	SD	p
Perim < 500	139	2,806	0,248	vs.	Perim > 500	178	2,866	0,227	**0,026**
Perim < 600	200	2,823	0,233	vs.	Perim > 600	117	2,867	0,243	0,113
Perim < 700	233	2,813	0,246	vs.	Perim > 700	84	2,912	0,197	**0**
Perim < 800	248	2,81	0,242	vs.	Perim > 800	69	2,944	0,187	**0**
Perim < 900	269	2,816	0,244	vs.	Perim > 900	48	2,967	0,142	**0**
Perim < 1000	273	2,82	0,244	vs.	Perim > 1000	44	2,959	0,141	**0**
Perim < 1200	275	2,82	0,244	vs.	Perim > 1200	42	2,965	0,141	**0**
Perim < 1300	288	2,828	0,242	vs.	Perim > 1300	29	2,949	0,144	**0**
Perim < 1400	298	2,835	0,242	vs.	Perim > 1400	19	2,915	0,132	**0,024**
Perim < 500	139	2,806	0,248	vs.	Perim 500-1000	134	2,835	0,241	0,323
Perim < 1000	273	2,82	0,244	vs.	Perim 1000-2000	39	2,966	0,144	**0**
Perim <1000	273	2,82	0,244	vs.	Perim 2000-3000	2	3,0085	0,012	0,277
Perim <1000	273	2,82	0,244	vs.	Perim >3000	3	2,838	0,0867	0,899
Perim 1000-1250	15	2,979	0,137	vs.	Perim > 1250	29	2,949	0,144	0,51
Perim 1000-2000	39	2,966	0,144	vs.	Perim 2000-3000	2	3,0085	0,012	0,681
Perim 1000-2000	39	2,966	0,144	vs.	Perim >3000	3	2,838	0,0867	0,141
Perim 2000-3000	2	3,0085	0,012	vs.	Perim >3000	3	2,838	0,0867	0,079

NoSpp	N	Avg	SD			N	Avg	SD	p
CAI < 69	8	28,13	7,61	vs.	CAI > 69	309	25,21	5,54	0,146
CAI < 70	10	29,1	7,02	vs.	CAI > 70	307	25,16	5,52	**0,028**
CAI < 72	17	24,18	8,57	vs.	CAI > 72	300	25,35	5,4	0,585
CAI < 73	23	23,26	8,12	vs.	CAI > 73	294	25,44	5,34	0,218
CAI < 78	55	24,89	6,57	vs.	CAI > 78	262	25,37	5,39	0,617
CAI < 79	70	24,2	6,12	vs.	CAI > 79	247	25,59	5,42	0,067
CAI < 80	89	24,16	5,94	vs.	CAI > 80	228	25,72	5,41	**0,025**
CAI < 81	108	24,12	6,02	vs.	CAI > 81	209	25,89	5,29	**0,008**
CAI < 82	119	24,23	5,93	vs.	CAI > 82	198	25,92	5,31	**0,009**
CAI < 83	137	24,34	5,73	vs.	CAI > 83	180	26,01	5,4	**0,008**
CAI < 84	146	24,48	5,59	vs.	CAI > 84	171	25,97	5,53	**0,018**
CAI < 85	158	24,73	5,67	vs.	CAI > 85	159	25,83	5,49	0,081
CAI < 86	191	24,76	5,72	vs.	CAI > 86	126	26,07	5,34	**0,042**
CAI < 87	212	24,86	5,69	vs.	CAI > 87	105	26,14	5,35	0,055
CAI < 88	242	24,9	5,58	vs.	CAI > 88	75	26,51	5,54	**0,03**
CAI < 89	258	25,11	5,64	vs.	CAI > 89	59	26,05	5,42	0,244
CAI < 90	279	25,14	5,62	vs.	CAI > 90	38	26,34	5,41	0,215
CAI < 75	35	23,34	7,47	vs.	CAI 75-85	123	25,13	5,02	0,19
CAI < 75	35	23,34	7,47	vs.	CAI > 85	122	25,69	5,51	0,091
CAI 75-85	123	25,13	5,02	vs.	CAI > 85	122	25,69	5,51	0,408
CAI 80	190	25,6	5,42	vs.	CAI 90	38	26,34	5,41	0,442
CAI_min 10%	32	23,16	7,77	vs.	CAI_max 10%	32	25,84	5,58	0,117

Shannon	N	Avg	SD			N	Avg	SD	P
CAI < 69	8	2,945	0,233	vs.	CAI > 69	309	2,837	0,237	0,204
CAI < 71	10	2,972	0,215	vs.	CAI > 71	307	2,835	0,237	0,072
CAI < 72	17	2,753	0,358	vs.	CAI > 72	300	2,844	0,229	0,312
CAI < 73	23	2,725	0,341	vs.	CAI > 73	294	2,848	0,226	0,103
CAI < 78	55	2,806	0,294	vs.	CAI > 78	262	2,846	0,224	0,344
CAI < 79	70	2,782	0,269	vs.	CAI > 79	247	2,856	0,226	**0,021**
CAI < 80	89	2,781	0,267	vs.	CAI > 80	228	2,862	0,221	**0,012**
CAI < 81	108	2,78	0,265	vs.	CAI > 81	209	2,87	0,216	**0,003**
CAI < 82	119	2,787	0,262	vs.	CAI > 82	198	2,871	0,216	**0,004**
CAI < 83	137	2,797	0,253	vs.	CAI > 83	180	2,872	0,22	**0,005**
CAI < 84	146	2,803	0,247	vs.	CAI > 84	171	2,87	0,225	**0,012**
CAI < 85	158	2,814	0,246	vs.	CAI > 85	159	2,865	0,226	0,058
CAI < 86	191	2,811	0,248	vs.	CAI > 86	126	2,883	0,214	**0,008**
CAI < 87	212	2,817	0,245	vs.	CAI > 87	105	2,885	0,216	**0,016**
CAI < 88	242	2,819	0,237	vs.	CAI > 88	75	2,904	0,228	**0,006**
CAI < 89	258	2,829	0,239	vs.	CAI > 89	59	2,883	0,226	0,121
CAI < 90	279	2,83	0,241	vs.	CAI > 90	38	2,905	0,203	0,069
CAI_min 10%	32	2,72	0,349	vs.	CAI_max 10%	32	2,888	0,208	0,024
CAI < 75	35	2,731	0,338	vs.	CAI 75-85	123	2,838	0,209	0,082
CAI < 75	35	2,731	0,338	vs.	CAI > 85	122	2,852	0,231	0,052
CAI 75-85	123	2,838	0,209	vs.	CAI > 85	122	2,852	0,231	0,603
CAI 80	190	2,854	0,224	vs.	CAI 90	38	2,905	0,203	0,192

NoSpp	N	Avg	SD			N	Avg	SD	p
Shape < 1.2	37	25,51	5,05	vs.	Shape > 1,2	280	25,25	5,68	0,791
Shape < 1,25	57	25,16	4,78	vs.	Shape > 1,25	260	25,31	5,77	0,852
Shape < 1,3	93	25,2	5,78	vs.	Shape > 1,3	124	25,32	5,54	0,871
Shape < 1,35	115	24,68	5,68	vs.	Shape > 1,35	202	25,63	5,54	0,147
Shape < 1,4	142	24,59	5,81	vs.	Shape > 1,4	175	25,85	5,38	**0,047**
Shape < 1,45	160	24,73	5,84	vs.	Shape > 1,45	157	25,85	5,3	0,073
Shape < 1,5	173	25,01	5,8	vs.	Shape > 1,5	144	25,61	5,35	0,343
Shape < 1,55	185	24,9	5,88	vs.	Shape > 1,55	132	25,82	5,16	0,152
Shape < 1,6	201	24,96	5,9	vs.	Shape > 1,6	116	25,84	5,01	0,176
Shape < 1,65	216	25	5,8	vs.	Shape > 1,65	101	25,89	5,12	0,187
Shape < 1,7	220	24,95	5,79	vs.	Shape > 1,7	97	26,04	5,09	0,11
Shape < 1,75	236	24,93	5,67	vs.	Shape > 1,75	81	26,31	5,29	0,056
Shape < 1,8	245	24,88	5,62	vs.	Shape > 1,8	72	26,65	5,36	**0,018**
Shape < 1,9	262	24,98	5,7	vs.	Shape > 1,9	55	26,73	4,89	**0,035**
Shape < 2	271	25,1	5,68	vs.	Shape > 2	46	26,39	4,99	0,147
Shape < 2,1	274	25,08	5,66	vs.	Shape > 2,1	43	26,56	5,11	0,109
Shape < 2,2	285	25,15	5,62	vs.	Shape > 2,2	32	26,44	5,4	0,22
Shape 1-1,5	173	25,01	5,8	vs.	Shape 1,5-2	98	25,24	5,49	0,746
Shape < 1.32	106	24,74	5,76	vs.	Shape 1.32-1.643	103	25,4	5,92	0,414
Shape 1.32-1.643	103	25,4	5,92	vs.	Shape > 1.644	108	25,71	5,11	0,679
Shape < 1,32	106	24,74	5,76	vs.	Shape > 1.644	108	25,71	5,11	0,191
Shape lägsta 10 %	32	25,03	5,1	vs.	Shape högsta 10 %	32	26,44	5,4	0,288

Shannon	N	Avg	SD			N	Avg	SD	p
Shape < 1.2	37	2,873	0,2	vs.	Shape > 1,2	280	2,835	0,242	0,359
Shape < 1,25	57	2,861	0,185	vs.	Shape > 1,25	260	2,835	0,248	0,37
Shape < 1,3	93	2,845	0,246	vs.	Shape > 1,3	124	2,837	0,234	0,771
Shape < 1,35	115	2,818	0,248	vs.	Shape > 1,35	202	2,851	0,231	0,239
Shape < 1,4	142	2,809	0,255	vs.	Shape > 1,4	175	2,864	0,22	**0,042**
Shape < 1,45	160	2,816	0,251	vs.	Shape > 1,45	157	2,863	0,221	0,077
Shape < 1,5	173	2,826	0,247	vs.	Shape > 1,5	144	2,855	0,225	0,271
Shape < 1,55	185	2,822	0,248	vs.	Shape > 1,55	132	2,864	0,22	0,122
Shape < 1,6	201	2,822	0,248	vs.	Shape > 1,6	116	2,869	0,216	0,092
Shape < 1,65	216	2,824	0,245	vs.	Shape > 1,65	101	2,873	0,219	0,089
Shape < 1,7	220	2,822	0,244	vs.	Shape > 1,7	97	2,88	0,217	**0,044**
Shape < 1,75	236	2,819	0,24	vs.	Shape > 1,75	81	2,898	0,222	**0,01**
Shape < 1,8	245	2,819	0,237	vs.	Shape > 1,8	72	2,909	0,228	**0,004**
Shape < 1,9	262	2,822	0,243	vs.	Shape > 1,9	55	2,924	0,188	**0,001**
Shape < 2	271	2,828	0,243	vs.	Shape > 2	46	2,907	0,194	**0,038**
Shape < 2,1	274	2,828	0,241	vs.	Shape > 2,1	43	2,911	0,199	**0,032**
Shape < 2,2	285	2,832	0,24	vs.	Shape > 2,2	32	2,903	0,208	0,113
Shape 1-1,5	173	2,826	0,247	vs.	Shape 1,5-2	98	2,831	0,235	0,856
Shape < 1.32	106	2,818	0,253	vs.	Shape 1.32-1.643	103	2,833	0,238	0,653
Shape 1.32-1.643	103	2,833	0,238	vs.	Shape > 1.644	108	2,866	0,22	0,308
Shape < 1,32	106	2,818	0,253	vs.	Shape > 1.644	108	2,866	0,22	0,144
Shape lägsta 10 %	32	2,854	0,2	vs.	Shape högsta 10 %	32	2,903	0,208	0,35

NoSpp	N	Avg	SD			N	Avg	SD	p
Frac < 1,08	138	24,92	5,56	vs.	Frac > 1,08	179	25,56	5,63	0,311
Frac < 1,0817	147	24,56	5,75	vs.	Frac > 1,0817	170	25,91	5,41	**0,033**
Frac < 1,084	150	24,5	5,73	vs.	Frac > 1,084	167	25,99	5,4	**0,018**
Frac < 1,09	152	24,55	5,71	vs.	Frac > 1,09	165	25,96	5,43	**0,024**
Frac<1,1	173	24,79	5,64	vs.	Frac>1,1	144	25,88	5,51	0,086
Frac < 1,11	207	25,02	5,86	vs.	Frac > 1,11	110	25,77	5,06	0,258
Frac < 1,12	219	25,77	5,86	vs.	Frac > 1,12	98	25,68	4,99	0,396
Frac<1,06	99	24,86	5,72	vs.	Frac1,06-1,1	74	24,7	5,57	0,858
Frac1,1-1,15	105	25,55	5,61	vs.	Frac>1,15	39	26,74	5,22	0,251

Shannon	N	Avg	SD			N	Avg	SD	p
Frac < 1,08	138	2,827	0,238	vs.	Frac > 1,08	179	2,849	0,237	0,409
Frac < 1,0817	147	2,809	0,252	vs.	Frac > 1,0817	170	2,865	0,222	**0,036**
Frac < 1,084	150	2,806	0,251	vs.	Frac > 1,084	167	2,869	0,221	**0,018**
Frac < 1,09	152	2,809	0,251	vs.	Frac > 1,09	165	2,867	0,221	**0,03**
Frac < 1,11	207	2,823	0,246	vs.	Frac > 1,11	110	2,869	0,219	0,1
Frac<1,1	173	2,819	0,244	vs.	Frac>1,1	144	2,864	0,228	0,089
Frac < 1,12	219	2,828	0,246	vs.	Frac > 1,12	98	2,864	0,215	0,212
Frac<1,06	99	2,832	0,238	vs.	Frac1,06-1,1	74	2,8	0,253	0,4
Frac1,1-1,15	105	2,844	0,235	vs.	Frac>1,15	39	2,917	0,2	0,087

NoSpp	N	Avg	SD			N	Avg	SD	P
Contig < 0,96	8	28,13	7,61	vs.	Contig > 0,96	309	23	6,8	0,146
Contig < 0,97	41	24	7,16	vs.	Contig > 0,97	276	25,47	5,32	0,211
Contig < 0,975	108	24,12	6,02	vs.	Contig > 0,975	209	25,89	5,29	**0,008**
Contig < 0,976	114	24,12	6,02	vs.	Contig > 0,976	203	25,89	5,29	**0,002**
Contig < 0,977	126	24,02	5,91	vs.	Contig > 0,977	191	26	5,3	**0,012**
Contig < 0,978	137	24,32	5,8	vs.	Contig > 0,978	180	25,92	5,38	**0,008**
Contig < 0,979	143	24,43	5,64	vs.	Contig > 0,979	174	25,99	5,48	**0,013**
Contig < 0,98	147	24,49	5,59	vs.	Contig > 0,98	170	25,97	5,54	**0,019**
Contig < 0,981	158	24,73	5,67	vs.	Contig > 0,981	159	25,83	5,49	0,081
Contig < 0,99	253	25,24	5,52	vs.	Contig > 0,99	64	25,47	5,96	0,768
Contig 0,95	8	28,13	7,61	vs.	Contig 0,96	33	23	6,8	0,069
Contig 0,96	33	23	6,8	vs.	Contig 0,97	106	24,68	4,87	0,195
Contig 0,97	106	24,68	4,87	vs.	Contig 0,98	156	26,03	5,53	**0,043**
Contig 0,98	156	26,03	5,53	vs.	Contig 0,99	14	25,29	5,78	0,631

Shannon	N	Avg	SD			N	Avg	SD	p
Contig < 0,96	8	2,945	0,233	vs.	Contig > 0,96	309	2,873	0,237	0,204
Contig < 0,97	41	2,762	0,322	vs.	Contig > 0,97	276	2,851	0,221	0,096
Contig < 0,975	108	2,78	0,265	vs.	Contig > 0,975	209	2,87	0,216	**0,001**
Contig < 0,976	114	2,777	0,26	vs.	Contig > 0,976	203	2,874	0,217	**0,001**
Contig < 0,977	126	2,795	0,258	vs.	Contig > 0,977	191	2,868	0,219	**0,01**
Contig < 0,978	137	2,797	0,253	vs.	Contig > 0,978	180	2,872	0,22	**0,005**
Contig < 0,979	143	2,801	0,249	vs.	Contig > 0,979	174	2,871	0,223	**0,009**
Contig < 0,98	147	2,805	0,247	vs.	Contig > 0,98	170	2,869	0,225	**0,018**
Contig < 0,981	158	2,814	0,246	vs.	Contig > 0,981	159	2,865	0,226	0,058
Contig < 0,99	253	2,839	0,237	vs.	Contig > 0,99	64	2,84	0,241	0,969
Contig 0,95	8	2,945	0,233	vs.	Contig 0,96	33	2,718	0,328	0,074
Contig 0,96	33	2,718	0,328	vs.	Contig 0,97	106	2,822	0,211	0,093
Contig 0,97	106	2,822	0,211	vs.	Contig 0,98	156	2,869	0,228	0,097
Contig 0,98	156	2,869	0,228	vs.	Contig 0,99	14	2,869	0,204	0,997

NoSpp	N	Avg	SD			N	Avg	SD	P
ENN < 10	20	26,4	5,44	vs.	ENN > 10	294	25,36	5,51	0,416
ENN < 18	28	25,79	5,14	vs.	ENN > 18	286	25,4	5,54	0,721
ENN < 25	53	25,83	5,28	vs.	ENN > 25	261	25,35	5,55	0,562
ENN < 30	126	25,43	5,45	vs.	ENN > 30	188	25,49	5,56	0,816
ENN < 40	151	25,32	5,46	vs.	ENN > 40	163	25,53	5,56	0,744
ENN < 50	174	25,64	5,52	vs.	ENN > 50	140	25,16	5,48	0,444
ENN < 66	202	25,82	5,33	vs.	ENN > 66	112	24,73	5,76	0,094
ENN < 68	213	25,52	5,52	vs.	ENN > 68	101	25,24	5,49	0,671
ENN < 100	252	25,87	5,44	vs.	ENN > 100	62	23,66	5,44	**0,005**
ENN < 110	260	25,84	5,4	vs.	ENN > 110	54	23,44	5,61	**0,003**
ENN < 120	264	25,88	5,4	vs.	ENN > 120	50	23,04	5,49	**0,001**
ENN < 165	274	25,8	5,37	vs.	ENN > 165	40	22,88	5,82	**0,002**
ENN < 180	279	25,71	5,37	vs.	ENN > 180	35	23,23	6,12	**0,012**
ENN < 200	283	25,56	5,48	vs.	ENN > 200	31	24,23	5,69	0,2
ENN < 220	291	25,57	5,44	vs.	ENN > 220	23	23,65	6,15	0,108
ENN < 230	296	25,54	5,43	vs.	ENN > 230	18	23,67	6,51	0,162
ENN < 340	301	25,46	5,42	vs.	ENN > 340	13	24,77	7,37	0,659

Shannon	N	Avg	SD			N	Avg	SD	p
ENN < 10	20	2,874	0,21	vs.	ENN > 10	294	2,842	0,234	0,554
ENN < 18	28	2,839	0,199	vs.	ENN > 18	286	2,845	0,236	0,906
ENN < 25	53	2,855	0,207	vs.	ENN > 25	261	2,842	0,238	0,715
ENN < 30	126	2,841	0,229	vs.	ENN > 30	188	2,847	0,236	0,815
ENN < 40	151	2,845	0,225	vs.	ENN > 40	163	2,844	0,24	0,967
ENN < 50	174	2,86	0,226	vs.	ENN > 50	140	2,824	0,24	0,175
ENN < 66	202	2,867	0,217	vs.	ENN > 66	112	2,803	0,254	**0,018**
ENN < 68	213	2,853	0,231	vs.	ENN > 68	101	2,827	0,237	0,356
ENN < 100	252	2,866	0,224	vs.	ENN > 100	62	2,755	0,247	**0,001**
ENN < 110	260	2,865	0,222	vs.	ENN > 110	54	2,745	0,257	**0,001**
ENN < 120	264	2,865	0,222	vs.	ENN > 120	50	2,733	0,257	**0**
ENN < 165	274	2,863	0,221	vs.	ENN > 165	40	2,719	0,272	**0**
ENN < 180	279	2,859	0,221	vs.	ENN > 180	35	2,726	0,29	**0,013**
ENN < 220	291	2,852	0,226	vs.	ENN > 220	23	2,748	0,296	**0,039**
ENN < 340	301	2,847	0,226	vs.	ENN > 340	13	2,783	0,37	0,55

NoSpp	N	Avg	SD			N	Avg	SD	p
PROX_100 < 0.5	67	23,72	5,54	vs.	PROX_100 > 0.5	250	25,75	5,607	**0,009**
PROX_100 < 1	69	23,71	5,459	vs.	PROX_100 > 1	248	25,77	5,626	**0,007**
PROX_100 < 5	108	23,81	5,933	vs.	PROX_100 > 5	209	26,1	5,342	**0,001**
PROX_100 < 10	132	24,17	5,709	vs.	PROX_100 > 10	185	26,14	5,468	**0,002**
PROX_100 < 15	176	24,57	5,811	vs.	PROX_100 > 15	141	26,25	5,308	**0,008**
PROX_100 < 20	183	24,74	5,889	vs.	PROX_100 > 20	134	26,1	5,216	**0,031**
PROX_100 < 25	185	24,83	5,919	vs.	PROX_100 > 25	132	26	5,185	0,064
PROX_100 < 30	205	24,72	5,768	vs.	PROX_100 > 30	112	26,41	5,267	**0,009**
PROX_100 < 50	208	24,75	5,733	vs.	PROX_100 > 50	109	26,39	5,337	**0,012**
PROX_100 < 70	212	24,81	5,695	vs.	PROX_100 > 70	105	26,35	5,426	**0,02**
PROX_100 < 90	253	24,89	5,688	vs.	PROX_100 > 90	64	27,03	5,173	**0,004**
PROX_100 < 120	266	25,02	5,693	vs.	PROX_100 > 120	51	26,86	5,173	**0,025**
PROX_100 < 130	291	25,31	5,677	vs.	PROX_100 > 130	26	25,46	5,383	0,889

Shannon	N	Avg	SD			N	Avg	SD	P
PROX_100 < 0.5	67	2,761	0,253	vs.	PROX_100 > 0.5	250	2,86	0,229	**0,004**
PROX_100 < 1	69	2,762	0,249	vs.	PROX_100 > 1	248	2,861	0,23	**0,004**
PROX_100 < 5	108	2,766	0,261	vs.	PROX_100 > 5	209	2,877	0,216	**0**
PROX_100 < 10	132	2,785	0,248	vs.	PROX_100 > 10	185	2,878	0,222	**0,001**
PROX_100 < 15	176	2,812	0,246	vs.	PROX_100 > 15	141	2,874	0,222	**0,018**
PROX_100 < 20	183	2,818	0,247	vs.	PROX_100 > 20	134	2,869	0,222	0,056
PROX_100 < 25	185	2,821	0,247	vs.	PROX_100 > 25	132	2,865	0,222	0,093
PROX_100 < 30	205	2,817	0,241	vs.	PROX_100 > 30	112	2,881	0,226	**0,02**
PROX_100 < 50	208	2,818	0,24	vs.	PROX_100 > 50	109	2,88	0,228	**0,025**
PROX_100 < 70	212	2,812	0,239	vs.	PROX_100 > 70	105	2,875	0,231	0,057
PROX_100 < 90	253	2,822	0,243	vs.	PROX_100 > 90	64	2,906	0,204	**0,006**
PROX_100 < 120	266	2,828	0,243	vs.	PROX_100 > 120	51	2,896	0,197	**0,034**
PROX_100 < 130	291	2,84	0,241	vs.	PROX_100 > 130	26	2,836	0,196	0,937

NoSpp	N	Avg	SD			N	Avg	SD	P
PROX_500 < 0.5	18	23,56	6,564	vs.	PROX_500 > 0.5	299	25,42	5,581	0,252
PROX_500 < 1	40	23,5	6,148	vs.	PROX_500 > 1	277	25,58	5,532	**0,048**
PROX_500 < 5	87	24,05	5,803	vs.	PROX_500 > 5	230	25,8	5,522	**0,016**
PROX_500 < 10	104	23,61	5,852	vs.	PROX_500 > 10	213	26,15	5,361	**0**
PROX_500 < 15	143	24,24	6,014	vs.	PROX_500 > 15	174	26,21	5,175	**0,002**
PROX_500 < 20	167	24,5	6,035	vs.	PROX_500 > 20	150	26,23	5,043	**0,006**
PROX_500 < 30	203	24,69	5,786	vs.	PROX_500 > 30	114	26,44	5,226	**0,006**
PROX_500 < 40	205	24,72	5,768		PROX_500 > 40	112	26,41	5,267	**0,009**
PROX_500 < 50	208	24,75	5,733	vs.	PROX_500 > 50	109	26,39	5,337	**0,012**
PROX_500 < 90	253	24,89	5,688	vs.	PROX_500 > 90	64	27,03	5,173	**0,004**
PROX_500 < 120	266	25,02	5,693	vs.	PROX_500 > 120	51	26,86	5,173	**0,025**
PROX_500 < 130	278	25,13	5,715	vs.	PROX_500 > 130	39	26,67	4,986	0,083
PROX_500 < 140	291	25,31	5,677	vs.	PROX_500 > 140	26	25,46	5,383	0,889
PROX_500 < 200	302	25,24	5,695	vs.	PROX_500 > 200	15	26,87	4,406	0,188

Shannon	N	Avg	SD			N	Avg	SD	P
PROX_500 < 0.5	18	2,75	0,318	vs.	PROX_500 > 0.5	299	2,845	0,231	0,231
PROX_500 < 1	40	2,753	0,293	vs.	PROX_500 > 1	277	2,852	0,226	**0,046**
PROX_500 < 5	87	2,779	0,25	vs.	PROX_500 > 5	230	2,862	0,229	**0,008**
PROX_500 < 10	104	2,759	0,26	vs.	PROX_500 > 10	213	2,879	0,216	**0**
PROX_500 < 15	143	2,793	0,257	vs.	PROX_500 > 15	174	2,878	0,213	**0,002**
PROX_500 < 20	167	2,807	0,253	vs.	PROX_500 > 20	150	2,876	0,214	**0,009**
PROX_500 < 30	203	2,815	0,242	vs.	PROX_500 > 30	114	2,883	0,225	**0,012**
PROX_500 < 40	205	2,817	0,241		PROX_500 > 40	112	2,881	0,226	**0,02**
PROX_500 < 50	208	2,818	0,24	vs.	PROX_500 > 50	109	2,88	0,228	**0,025**
PROX_500 < 90	253	2,822	0,243	vs.	PROX_500 > 90	64	2,906	0,204	**0,006**
PROX_500 < 120	266	2,828	0,243	vs.	PROX_500 > 120	51	2,896	0,197	**0,034**
PROX_500 < 130	278	2,832	0,243	vs.	PROX_500 > 130	39	2,892	0,189	0,076
PROX_500 < 140	291	2,84	0,241	vs.	PROX_500 > 140	26	2,836	0,196	0,937
PROX_500 < 200	302	2,835	0,239	vs.	PROX_500 > 200	15	2,925	0,182	0,086

NoSpp	N	Avg	SD			N	Avg	SD	p
PROX_1000 < 0.5	8	25,25	7,106	vs.	PROX_1000 > 0.5	309	25,32	5,617	0,979
PROX_1000 < 1	36	23,19	6,246	vs.	PROX_1000 > 1	281	25,59	5,517	**0,034**
PROX_1000 < 5	79	23,94	5,956	vs.	PROX_1000 > 5	238	25,78	5,475	**0,017**
PROX_1000 < 10	104	23,61	5,852	vs.	PROX_1000 > 10	213	26,15	5,361	**0**
PROX_1000 < 15	143	24,24	6,014	vs.	PROX_1000 > 15	174	26,21	5,175	**0,002**
PROX_1000 < 20	167	24,5	6,035	vs.	PROX_1000 > 20	150	26,23	5,043	**0,006**
PROX_1000 < 30	201	24,61	5,755	vs.	PROX_1000 > 30	116	26,55	5,251	**0,002**
PROX_1000 < 40	205	24,72	5,768		PROX_1000 > 40	112	26,41	5,267	**0,009**
PROX_1000 < 50	208	24,75	5,733	vs.	PROX_1000 > 50	109	26,39	5,337	**0,012**
PROX_1000 < 90	253	24,89	5,688	vs.	PROX_1000 > 90	64	27,03	5,173	**0,004**
PROX_1000 < 120	266	25,02	5,693	vs.	PROX_1000 > 120	51	26,86	5,173	**0,025**
PROX_1000 < 130	278	25,13	5,715	vs.	PROX_1000 > 130	39	26,67	4,986	0,083
PROX_1000 < 140	291	25,31	5,677	vs.	PROX_1000 > 140	26	25,46	5,383	0,889
PROX_1000 < 200	302	25,24	5,695	vs.	PROX_1000 > 200	15	26,87	4,406	0,188

Shannon	N	Avg	SD			N	Avg	SD	P
PROX_1000 < 0.5	8	2,84	0,269	vs.	PROX_1000 > 0.5	309	2,839	0,237	0,998
PROX_1000 < 1	36	2,737	0,297	vs.	PROX_1000 > 1	281	2,852	0,226	**0,03**
PROX_1000 < 5	79	2,775	0,258	vs.	PROX_1000 > 5	238	2,861	0,227	**0,009**
PROX_1000 < 10	104	2,759	0,26	vs.	PROX_1000 > 10	213	2,879	0,216	**0**
PROX_1000 < 15	143	2,793	0,257	vs.	PROX_1000 > 15	174	2,878	0,213	**0,001**
PROX_1000 < 20	167	2,807	0,253	vs.	PROX_1000 > 20	150	2,876	0,214	**0,009**
PROX_1000 < 30	201	2,812	0,241	vs.	PROX_1000 > 30	116	2,887	0,224	**0,006**
PROX_1000 < 40	205	2,817	0,241		PROX_1000 > 40	112	2,881	0,226	**0,02**
PROX_1000 < 50	208	2,818	0,24	vs.	PROX_1000 > 50	109	2,88	0,228	**0,025**
PROX_1000 < 90	253	2,822	0,243	vs.	PROX_1000 > 90	64	2,906	0,204	**0,006**
PROX_1000 < 120	266	2,828	0,243	vs.	PROX_1000 > 120	51	2,896	0,197	**0,034**
PROX_1000 < 130	278	2,832	0,243	vs.	PROX_1000 > 130	39	2,892	0,189	0,076
PROX_1000 < 140	291	2,84	0,241	vs.	PROX_1000 > 140	26	2,836	0,196	0,937
PROX_1000 < 200	302	2,835	0,239	vs.	PROX_1000 > 200	15	2,925	0,182	0,086

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