UNIVERSITY OF LJUBLJANA
BIOTECHNICAL FACULTY
DEPARTMENT OF BIOLOGY

Polona BERGOČ

THE EFFECTS OF HABITAT FRAGMENTATION ON PLANT DIVERSITY IN HEATHLAND (DRENTHE, NETHERLANDS)

GRADUATION THESIS

University studies

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VPLIVI DROBLJENJA HABITATOV NA RASTLINSKO PESTROST RESAV (DRENTHE, NIZOZEMSKA)

DIPLOMSKO DELO
Univerzitetni študij

Ljubljana 2010

The thesis work is a completion of university studies of biology. The work was carried out in the Department of Biology, Biotechnical Faculty, University of Ljubljana, Slovenia and in the Department of Biological Sciences, Faculty of Science, University of Amsterdam, the Netherlands.

Diplomsko delo je zaključek univerzitetnega študija biologije. Opravljeno je bilo na Oddelku za biologijo Biotehniške fakultete, Univerze v Ljubljani, Slovenija in na Oddelku za biološke znanosti Fakultete za znanost, Univerze v Amsterdamu, Nizozemska.

The Council of the Department of Biology appointed Professor Alenka Gaberščik, PhD, as supervisor, Professor Gerard Oostermeijer, PhD, as co-advisor and Professor Nejc Jogan, PhD, as reviewer.

Študijska komisija dodiplomskega študija biologije je za mentorico diplomskega dela imenovala prof. dr. Alenko Gaberščik, za somentorja prof. dr. Gerarda Oostermeijera in za recenzenta prof. dr. Nejca Jogana.

Supervisor (*mentorica*): prof. dr. Alenka Gaberščik

Co-advisor (*somentor*): prof. dr. Gerard Oostermeijer

Reviewer (*recenzent*): prof. dr. Nejc Jogan

Podpisana se strinjam z objavo svoje naloge v polnem tekstu na spletni strani Digitalne knjižnice Biotehniške fakultete. Izjavljam, da je naloga, ki sem jo oddala v elektronski obliki, identična tiskani verziji.

Polona Bergoč

Committee for evaluation and defense of the graduation thesis:

Komisija za oceno za zagovor:

Chairman (*predsednica*): doc. dr. Jasna DOLENC KOCE
University of Ljubljana, Biotechnical Faculty, Department of Biology
Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo

Member (*članica*): prof. dr. Alenka GABERŠČIK
University of Ljubljana, Biotechnical Faculty, Department of Biology
Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo

Member (*član*): prof. dr. Nejc JOGAN
University of Ljubljana, Biotechnical Faculty, Department of Biology
Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo

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The results of this thesis are a result of candidate's own work.

Naloga je rezultat lastnega raziskovalnega dela.

Polona Bergoč

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TI	THE EFFECTS OF HABITAT FRAGMENTATION ON PLANT DIVERSITY IN HEATHLAND (DRENTHE, NETHERLANDS)
DT	Graduation thesis, University studies
NO	XV, 75 p., 1 tab., 28 fig., 1 ann., 72 ref.
LA	en
AL	sl/en
AB	This research focused on the effects of fragmentation on the plant diversity of heathlands in Drenthe, a province in the North-East of the Netherlands. We examined the relationship between the number of species and the size of the patch area and the relationship between the number of species and spatial isolation. The data about the number of species used in the research were taken from the floristic inventory scheme of the Netherlands gathered by both professional and amateur/volunteer botanists, coordinated by the foundation FLORON. The results showed that the size of the area and the number of plant species in Dutch heathland patches were in positive correlation. Positive correlation was valid also for the number of the Red Listed species. The relationship between the spatial isolation and the number of plant species showed a negative correlation, the same applied for the relationship between the spatial isolation and the Red Listed plant species. The ratio of edge relative to the area of the fragment (edge effect) showed a negative relation to the number of species present in the area.

KLJUČNA DOKUMENTACIJSKA INFORMACIJA

ŠD	Dn
DK	581.9:502.7.(043.2Drenthe,Netherlands)=111
KG	fragmentacija/resave/vrstna pestrost /izoliranost
AV	BERGOČ, Polona
SA	GABERŠČIK, Alenka (mentor)/OOSTERMEIJER, Gerard (somentor)
KZ	SI-1000 Ljubljana, Večna pot 111
ZA	Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za biologijo
LI	2010
IN	VPLIVI DROBLJENJA HABITATOV NA RASTLINSKO PESTROST RESAV (DRENTHE, NIZOZEMSKA)
TD	Diplomsko delo (univerzitetni študij)
OP	XV, 75 str., 1 pregl. 28 sl., 1 pril., 72 vir.
IJ	en
JI	sl/en
AI	V diplomski nalogi smo raziskovali vplive razdrobljenosti habitatov na rastlinsko pestrost resav v severovzhodni nizozemski provinci Drenthe. Proučevali smo odnos med velikostjo posameznih območij resav in številom prisotnih rastlinskih vrst, ter odnos med izoliranostjo posameznih območij resav in številom prisotnih rastlinskih vrst. Podatke o številu vrst na izbranih območjih smo pridobili iz Nizozemske floristične baze podatkov, koordinirane s fundacijo FLORON, ki zbira podatke s pomočjo amaterskih in profesionalnih botanikov. Dobljeni rezultati so pokazali, da sta bili velikost določenega območja in število prisotnih rastlinskih resavskih vrst pozitivno korelirani. Pozitivna korelacija je veljala tudi za vrste z Rdečega seznama. Odnos med izoliranostjo območij in številom prisotnih resavskih vrst je pokazal negativno korelacijo, tako kot odnos med izoliranostjo območij in številom prisotnih resavskih vrst z Rdečega seznama. Robni efekt (velikost samega roba območja v razmerju s celotno površino območja) je kazal na negativni vpliv na število prisotnih vrst.

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GLOSSARY

Some basic biological and ecological concepts and terms are explained to facilitate further reading and for better understanding of the thesis.

Levels of organization:

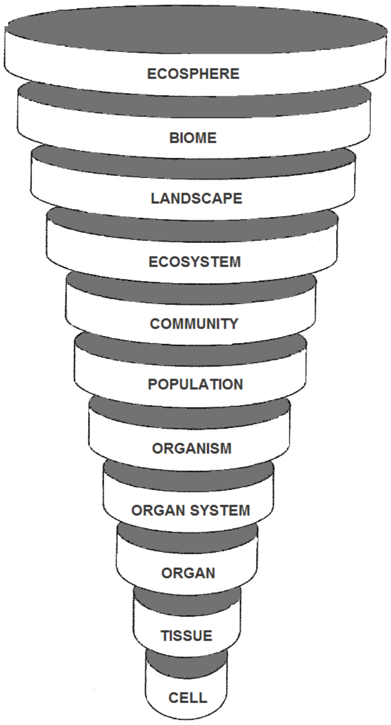

Figure 1: Ecological levels of organization hierarchy (modified from Barrett et al., 1997).

Organism: ‘a living thing: animal, plant or microorganism’
(Hale et al., 1995)

Population: ‘group of individuals of the same species living in a given area or habitat at a given time’ (Odum and Barrett, 2005)

Metapopulation: 'A population of geographically separated subpopulations interconnected by patterns of gene flow, extinction and recolonization.' (Whittaker and Fernández-Palacios, 2008).

Community (sometimes also 'biotic community'): 'includes all the populations inhabiting a specific area at the same time' (Odum and Barrett, 2005)

Ecosystem: 'a biotic community and its abiotic environment functioning as a system' (Odum and Barrett 2005; first used by Tansley, 1935)

Landscape: 'heterogeneous area composed of a cluster of interacting ecosystems that are repeated in a similar manner throughout' (Forman and Gordon, 1986)

Biome: 'large regional or subcontinental system characterized by a particular major vegetation type (such as temperature deciduous forest); biomes are distinguished by the predominant plants associated with particular climate (especially temperature and precipitation) (Odum and Barrett, 2005)'

Ecosphere: 'all living organisms on Earth interacting with the physical environment as a whole (Odum and Barrett, 2005)

Habitat: 'place where an organism lives' (Odum and Barrett, 2005)
'The term habitat is used widely, not only in ecology but elsewhere.' It is the "address" of the organism. 'Habitat may also refer to the place occupied by an entire community. (Odum and Barrett, 2005)

Ecological niche: 'the organism's functional role in the community' (Hale, Margham and Saunders, Collins Dictionary, 1995).
It is the "profession" of the organism. (Odum and Barrett, 2005)

Biodiversity: 'diversity of life forms, the ecological roles they perform, and the genetic diversity they contain; term used to describe all aspects of biological diversity (genetic, species, habitat, and landscape' (Odum and Barrett, 2005)

SLOSS: is an acronym for 'Single Large or Several Small' and refers to whether the reserves should be designed as one big piece of protected land or several smaller reserves. This debate has been mainly referred to the effects of reserve design on species diversity or to the viability of metapopulations by focusing on positive and negative distance effects on population persistence (Meffe and Carroll, 1997).

1 INTRODUCTION

‘Fragmentation, the loss and isolation of natural habitats, is one of the greatest threats to regional and global biodiversity. Whereas natural disturbances and other processes create heterogeneous landscapes rich in native species, human land uses often create islands of natural habitat embedded in a hostile matrix. Such fragmentation reduces or prevents normal dispersal, which is critical to long-term population viability for many species, and increases edge effects and other threats.’ (Meffe and Carroll, 1997).

There are two main consequences of the process of fragmentation: reduction in the total habitat area and isolation of the remaining area into disjunct fragments. Each contributes to a reduction in the number of species supported. (Soulé, 1986; Soulé and Wilcox, 1980). Therefore fragmentation is one of the main causes for many conservation problems.

The influence of the size and the isolation of the area on the species richness was investigated in this study. One of the most famous explanations for the species-area relationship is the equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967). It predicts species richness to increase with habitat area and to decrease with isolation from colonization sources. This theory has been applied to different habitat fragments, and the studies showed very heterogeneous results (Debinski and Holt, 2000). Many studies failed to find support for the theoretical expectations and this is why the effects of patch area and isolation are still important to investigate (Bruun, 2001).

This study focused on the effect of fragmentation in the heathlands of Drenthe, a province in the North-East of the Netherlands. Most of the patches were embedded in a matrix of arable land or forests or meadows. The aim of the study was to examine the relationship between the number of species and the size of the patch area and the relationship between the number of species and the spatial isolation.

Four main hypotheses were set as a starting point of the study:

1. There is a positive correlation between the size of heathland patches and the current number of plant species thriving there.
2. There is a negative correlation between the spatial isolation of heathland patches and the current number thriving there.
3. There is a positive correlation between the size of heathland patches and the current number of the plant Red Listed species thriving there.
4. There is a negative correlation between the spatial isolation of heathland patches and the current number of the plant Red Listed species thriving there.

This graduation thesis bases on a research project that was made in the Netherlands, as a part of an Erasmus student exchange program that I participated during the last year of my studies.

2 REVIEW OF LITERATURE AND RESEARCH

2.1. BASIC GEOGRAPHICAL AND BIOGEOGRAPHICAL CIRCUMSTANCES: THE NETHERLANDS, DRENTHE AND HEATHLAND HABITAT

2.1.1. The Netherlands and Drenthe

The area we chose for the research is situated in the territory of the Netherlands, in particular in the province of Drenthe (Figure 3). The habitat we chose to work with was heathland.

The Netherlands is a constituent country of the Kingdom of the Netherlands, located in the North-West Europe (Figure 2).

Figure 2: The position of the Netherlands (orange) in Europe (modified from Worldatlas).

'The Netherlands' means low-lying country, and indeed, the country is remarkably flat, with large expanses of lakes, rivers, and canals. About 27 % of the country lies below the sea level. Significant areas have been acquired through land reclamation and preserved using elaborate systems of polders and dikes.

With its long coastline on the North Sea, the Netherlands has a temperate maritime climate, with gentle winters, cool summers and significant rainfall in all seasons.

The entire eastern part of the country is in fact a region with sandy soils at higher elevations above sea level. This region forms the main physical geographical region in which we find heathlands, because most of this sand is of glacial origin and is nutrient-poor and hardly buffered. It thus tends to have low pH, which favours heathland formation. (Encyclopedia Britannica; Dutch Ministry of Foreign Affairs…; Statistics Netherlands…, The World Factbook).

There are twenty national parks in the Netherlands, preserving a wide range of landscapes characteristics to the Netherlands, from dunes, tidal flats and stream valleys to woodland, heath and fens (National Parks in the Netherlands).

The fragmented heathland area we worked on is situated in the province of Drenthe. Drenthe is one of the 12 provinces of the Netherlands, located the North-East of the country (Figure 3).

Figure 3: The position of the province of Drenthe (black) in the Netherlands (modified from Dutch Maps).

For long time this province was ill–favoured. The Scandinavian glaciers, which lingered in the north of the Netherlands, left a sandy and not very fertile soil. In some places it is covered with heathland, with a few clumps of oak or pine. In the wetter areas, peat covers the surfaces left by glaciers.

Today, a lot of clearing and the use of fertilizers have modified the landscape. Drenthe is one of the regions in which a nearly continuous area of heathland existed in the past, but currently became extremely fragmented, except for a few larger reserves, such as Dwingelderveld National Park (Machan and Bell, 2005; Netherlands, 1995).

2.1.2. Heathland habitat

Heathland is an open habitat dominated by dwarf-shrubs of the Ericaceae family, found mainly on infertile and acidic soils (Figure 6). In particular, they are normally deficient in available nitrogen and calcium, in some cases also phosphorus (Gimingham, 1972). Heath communities may have different drainage status; dry, humid (moist) or wet (Dolman and Land, 1995; Thompson et. al, 1995, in Price, 2003). UK Biodiversity Steering Group (1995) described that good-quality lowland heathland consist of areas of dry and wet heath, bogs, open water, areas of bare ground and some scattered trees and scrub.' (in Price, 2003). Two of the most common Ericaceae dwarf shrubs are *Calluna vulgaris* (Figure 4) and *Erica tetralix* (Figure 5).

Figure 4: *Calluna vulgaris* (plant-identification.co.uk).

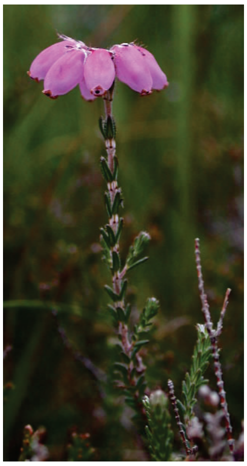

Figure 5: *Erica tetralix* (plant-identification.co.uk).

In North-West Europe heathlands are distributed in the areas that experience a temperate, oceanic (or maritime) climate, lacking temperature extremes, but with abundant rainfall throughout the year (Gimingham, 1972).

The habitat can occur naturally where abiotic environmental conditions such as poor soils and harsh climate prevent tree growth, but it can also develop at the locations where trees are removed and their regeneration is prevented (Gimingham, 1975). In the past heathlands were used predominantly for livestock (sheep and cattle) grazing, and for the production of manure by mixing sheep and cow dung and hand-cut sods in so-called pot stables. This manure was used to fertilize the arable fields in the direct surroundings of the villages. The 'pot-stable system' resulted in a continuous flow of nutrients from the heathlands towards the arable fields that lasted for centuries. As a consequence, the heathlands became even poorer in nutrients, whereas a thick, nutrient-rich organic layer was built up on the arable fields. These fields are still recognizable as low hills in the landscape, the so-called 'enks' or 'engen'. On the extremely nutrient-poor soils, heathlands developed with a not very species-rich, but highly characteristic and specific flora and fauna.

After 1890, as soon as artificial fertilizers had been invented, the heathland habitat had strongly decreased or even fully disappeared, because even the nutrient-poor 'wastelands' could be converted into areas for agricultural production. The last pieces of this semi-natural habitat type are nowadays managed as nature reserves, to conserve the characteristic biodiversity. In the early stages of conservation, the management consisted only of fencing out specific areas and designating them as nature reserves. In the 1980s, it appeared more and more that the characteristic biodiversity was still declining, also in the reserves. After substantial research, ecologists pointed out that the heathland habitat needs to be managed all the time by sod-cutting, burning, mowing or grazing, otherwise it very rapidly develops into dense *Molinia caerulea* or *Deschampsia flexuosa* grasslands or Pine-Birch forest (Price, 2003; Gimingham, 1975).

Figure 6: Heathland (photo: Gerard Oostermeijer).

2.2. BIODIVERSITY

Biodiversity can refer to a broad spectrum of structural elements and levels, which maintain the variety of the living world. It represents the richness of life on the whole biosphere, created by evolutionary processes through billion years of history of life on Earth. Units of biodiversity range from the genetic variability within a species to the great diversity of ecosystems and biomes on Earth. These various levels of biodiversity are best understood in a hierarchical fashion. Kryštufek (1999) distinguished three main hierarchical levels:

- genetic diversity in and among organisms
- species diversity
- ecosystem diversity

These levels are clearly separated and very interrelated at the same time (Kryštufek, 1999; Meffe and Carroll, 1997).

2.2.1. Biodiversity and ecosystem functioning

The relationship between biodiversity and ecosystem functioning is still ambiguous and has led to various debates and controversies. Lots of researches have been made in describing the relationship between species diversity and ecosystem processes, in identifying functionally important species, and in revealing underlying mechanisms. For instance, some experiments (Naeem et al., 1995; Symstad et al., 1998; in Tome 2006) showed that increased species diversity increases some of the functions of ecosystem, like primary production. This shows that more species means better activity of ecosystems. Furthermore, MacArthur (1995) made inferences that more species means more ways of energy flow, which consequently means less sensitive ecosystems (in Tome, 2006). On the contrary, some researches claimed that a higher number of species means a higher number of species interactions and consequently ecosystem may become more sensible about environmental changes (Loreau et al., 2001; Tome, 2006). Considering all different aspects, Loreau et al. (2001), summarized: ‘There is consensus that at least some minimum number of species is essential for ecosystem functioning under constant conditions and that a larger number of species is probably essential for maintaining the stability of ecosystem processes in changing environments. Determining which species have a significant impact on which processes in which ecosystems, however, remains an open empirical question.’

However, since biodiversity is a very important factor in the natural systems and therefore it is an important factor from the aspect of nature conservation, Loreau et al. (2001) concluded: ‘There are many reasons — including aesthetic, cultural, and economic — why we may wish to conserve biodiversity. From a strictly functional point of view, species matter so far as their individual traits and interactions contribute to maintain the functioning and stability of ecosystems and biogeochemical cycles.’

At the same time, Tome (2006) directed our attention to the fact, that actually all natural ecosystems are stable, otherwise they would not exist on the planet. This phenomenon is called functional diversity and it explains that a community with many species (e.g. tropical ecosystems) cannot be more important that a community with less species (e.g. polar ecosystems). For this reason, in order to reach quality of natural systems does not mean just enlarging the number of species or organisms on every square meter of area, but it is important to maintain the number of species that provides undisturbed ecosystem functioning.

2.2.2. Species diversity

In this research we focused on species diversity. For this type of biodiversity is believed that more species means higher biodiversity. Hence, species diversity is usually presented as number of species per unit area. It is important to know that the diversity level is defined by genetic diversity on one side and that it determines ecosystem diversity on the other side (Kryštufek, 1999; Tome, 2006).

Nevertheless, biodiversity is not just a number of species. For instance, the number of organisms present within particular species or the interactions between different species also play a significant role (Tome, 2006). For this reason Odum and Barrett (2005) divided species diversity into two different components:

1) *Species richness*; 'based on the total number of species present'.
2) *Apportionment*, 'based on relative abundance (or other measures of importance) of species and the degree of dominance or lack thereof'.

Meffe and Carroll (1997) as well distinguished between:

1) *Species richness* as the number of species present in an area
2) *Species diversity* in cases where species are weighted by some measure of their importance, such as their abundance, productivity, or size. To measure species diversity, different indices are used, e.g. Shannon-Wiener index or Simpson index.

Due to the description of these concepts by Odum and Barrett (2005) and Meffe and Carroll (1997), in this research we used the term *species richness* for presenting the relation of the number of species in an area (even the term *species diversity* can be often used for the same relationship).

To describe the complex spatial patterns of biodiversity, ecologist and biogeographers found it useful to divide species richness into different components (Meffe and Carroll, 1997; Tome, 2006; Kryštufek, 1999; Odum and Barrett, 2005):

- *α richness* (within-habitat or within community):
  Refers to the number of species found in a small, homogenous area (Meffe and Carroll 1997). It can also be presented as α diversity (Odum and Barrett, 2005; Tome, 2006; Kryštufek, 1999).
- *β richness* (between habitat richness):
  Refers to the rate of change in species composition across habitats (Meffe and Carroll, 1997). Also presented as β diversity (Odum and Barrett, 2005; Tome, 2006; Kryštufek, 1999).
- *γ richness* (landscape scale areas):
  Refers to the rate of change across larger landscape gradients (Meffe and Carroll, 1997). Also presented as γ diversity (Odum and Barrett, 2005; Tome, 2006; Kryštufek, 1999).

Only α richness was examined in this research. After all, number of species is still one of the most usual methods to describe biodiversity (Tome, 2006). Representing biodiversity as statistics of species number is also very acceptable for the public. ‘We are convinced that biological species is the closest to the optimal model, which illustrates discontinuity of biodiversity’ (Kryštufek, 1999).

2.2.2.1. What is a species?

The species is one of the main players in conservation. Biologists have focused on the species level for centuries. They have developed systems for naming, cataloging and comparing species (Meffe and Carroll, 1997).

Every species of living organisms that science defines as an independent unit is characterized by a double name. Binominal nomenclature was developed by Karl Linné in 1753 and is still in use. In the meantime, more than one million species have been discovered. In particular, approximately 1.5 million species 300 000 fossils species have been described and given scientific names, and there is no doubt that this number is not the ultimate; estimations predict 10 to 100 million species live on the planet (Kryštufek, 1999; Meffe and Carroll, 1997).

Moreover, Karl Linné was also the one who established the concept of the species as a basic unit of classification and therefore also the basic unit of biodiversity (Kryštufek, 1999). Nowadays there are many different ways of defining a species and there is no perfect definition. One of the concepts that received the most attention is the biological species concept of Mayr (1942): ‘Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.’ Even if this is still perhaps the most widely adopted concept, the definition stimulated critiques as well as proposals of alternatives (Queiroz, 2005). Many other species concepts are in use today, like phylogenetic, evolutionary, ecological species concepts and so forth. Different subgroups of biologists advocate different and unfortunately incompatible species concepts. ‘Mayden (1997) listed 24 different named species concepts, and there are even more alternative definitions’ (Queiroz, 2007). Queiroz (2007) proposed a unified species concept and he clearly separated two biological concepts that have commonly been confused in the past: *species conceptualization*, as the conceptual problem of species category, and *species delimitation*, as the methodological problem of interfering the boundaries and numbers of species. Therefore, he proposed a unified species concept that a species simply presents a segment of separately evolving lineages. Considering that the process of speciation is a continuous process, different concepts determinate different boundaries between two different species. Species defining properties (species criteria) result in opposing species concepts due to the fact that these properties arise at different times during the process of speciation. Queiroz (2007) submitted that 'most of the properties emphasized under the alternative concepts should be considered relevant to the issue of species delimitation.' (Kryštufek, 2009)

Meffe and Carroll (1997) summed up: 'Regardless of the practical concept used, it is important to remember that species are dynamic, changing entities containing a great deal population variation that is relevant to conservation efforts.'

Furthermore, grouping organisms into species helps to count the organisms and therefore helps to quantify and to monitor biodiversity in space and time (Kryštufek, 1999; see also chapter 2.2.2. Species diversity).

2.2.2.2. The structure of species

A species is composed of individual populations. If there are no actually or potentially reproductive barriers between them, populations succeed in space and time. All populations are more or less different from each other because living in different conditions evolves specific adaptations. Therefore species is not a homogeneous mixture of individuals, but a mosaic of populations with different adaptations and specific history (Kryštufek, 1999).

2.2.2.3. The role of the species in an ecosystem

The most fundamental processes of ecosystems are the substance circulation and the energy flow. Living organisms are the essential carriers of these two processes. Kos (2009) explained: 'The role of species or populations can be recognized in some basic functional types: they are the carriers of substance circulation and energy flow processes, they maintain exergy, take part in formatting the living space and conditions in it and they form interspecies and intraspecies relations. Inter- and intraspecies relations are complex and have short-term influence on ecosystem state as well as long-term influence on population development and different ecosystem processes. Of course they also indirectly influence the state and characteristics of the whole biosphere on Earth as biogenic planet.'
In addition he added: 'Just co-evolution and mechanisms and population development in dependence of abiogenic component of living species lead to development of complex communities that enable stability and optimal functioning ecosystems.'

Furthermore, every species has a different role in an ecosystem. Some species are more essential for the ecosystem than others. Loosing species, most essential for an ecosystem and therefore fundamental for presence of different other species, can start a chain reaction in the process of extinction, which will keep on eroding the whole ecosystem (Kryštufek, 1999).

2.2.2.4. Red Listed species

The Red List is a list of endangered plant or animal species. The main goal of Red Lists is to convey the urgency of conservation issues to the public and policy makers, as well as to help the international community to try to reduce species extinction. The first Red List was established by the English natural scientist sir Peter Scott in 1960. Nowadays series of Regional Red Lists are produced by countries or organizations, which assess the risk of extinction of species. The world's most comprehensive inventory of the global conservation status of plant and animal species today is the Red List of Threatened Species by the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species. The IUCN is the world's main authority on the conservation status of species. The Red List is never ultimate; it changes and is being completed as the nature changes and as our knowledge about the nature gets more complete. The IUCN Red List is published every year in an improved version. Species are classified in nine groups:

- extinct - no individuals remaining
- extinct in the wild - known only to survive in captivity, or as a naturalized population outside its historic range
- critically endangered - extremely high risk of extinction in the wild
- endangered - high risk of extinction in the wild
- vulnerable - high risk of endangerment in the wild
- near threatened - likely to become endangered in the near future
- least concern - lowest risk, does not qualify for a more at risk category, widespread and abundant taxa are included in this category
- data deficient - not enough data to make an assessment of its risk of extinction
- not evaluated - has not yet been evaluated against the criteria

The aim is to establish a baseline from which to monitor the change in status of species, provide a global context for the establishment of conservation priorities at the local level and to monitor, on a continuing basis, the status of a representative selection of species (as biodiversity indicators) that cover all the major ecosystems of the world (The IUCN Red List of Threatened Species). For this research Red List categories of pant species were obtained from the Red List of the Dutch flora (van der Meijden et al., 2000).

2.2.3. Threats to biodiversity

‘The worst thing that can happen during the 1980s is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within few generations. The one process ongoing in the 1980s that will make millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly that our descendants are least likely to forgive us.’ said Wilson (1985) (Meffe and Carroll, 1997).

Losses of biodiversity are definitely one of the biggest threats to the nature nowadays. However, biodiversity, as any other characteristic of the nature, can not be and has never been a stable condition. All natural processes are dynamic. In the case of species diversity there is a dynamics between the origin and the extinction of species (Tome, 2006). Mršić (1997) described with a wide view: ‘Extinction of species is a process which is not typical only of the present age. Scientists estimate that our planet today inhabited only by 1% of all the species that have existed in the Earth’s history. Species have been dying out through its entire history, however, this process has not been evenly distributed. In the last 600 millions years alone at least five distinct biotic disasters have taken place – a great diminution of the species diversity in a relatively short period of time.’ In addition, he exposed: ‘In the latest period, i.e. with appearance of man, the rate of extinction increased again.’ To illustrate this, he declared that without an effective protection of endangered species, extinction is going to continue with the same rate and consequently 25% of the whole world flora could be lost until the middle of this century.

Indeed, the genetic, species and ecosystem diversity today is in sharp decline. Unfortunately, this time it is a result of human activities. The main reasons causing extinction of species on Earth these days are destruction, fragmentation and degradation of habitats, introduction of non-native species, overharvesting, pollution and toxification, competition for organic substances and other secondary effects. (Mršić, 1997; Meffe and Carroll, 1997; Kryštufek, 1999). In fact, the primary source of all these problems is the fast growth of human population, which needs more and more goods for its growth and functioning (Kryštufek, 1999). Considering the fact that the modern society seems to be addicted with economic growth and the planet has limited natural resources (Mencinger, 2009), all these problems are getting even bigger.

Moreover, loss of habitat and loss of species is not the whole disaster. Probably even more shocking than the wave of extinction is the cessation of significant evolution of new species of large plants and animals. Death is one thing, but the end of birth is something else (Soulé and Wilcox, 1980).

As a reaction on this biodiversity crisis, the field of nature conservation is on the rise. Conservation biology is a multidisciplinary science that tries to understand the interactions between human society and biodiversity. The aim of this science is to conserve the biodiversity of the nature at the same time as to enable sustainable development of human race. (Kryštufek, 1999; Meffe and Carroll, 1997). After all, we are living beings and changes of global biosystem are one of the greater threats also for existence of our species. Often one of the solutions proposed by conservation biologists are national reserves, which try to enable further development of natural systems in space and time (e.g. Dwingelderveld National Park which protects a major area of heathland habitat in Drenthe) . The strategy of such a national reserve is mostly not protection of some defined species, but preservation of ecosystems and habitats as a whole, including essential ecological processes and essential components of biodiversity (Kryštufek, 1999). Much of active management will be required to prevent or overcome ecological imbalance created by fragmentation and other consequences of human activity (Soulé, 1986). Effectiveness of reserves is dependent on some basic critical factors, like their size, diversity and dynamics, placement of the reserve in the environment, corridors, etc. (Kryštufek, 1999).

2.3. FRAGMENTATION

'Fragmentation occurs when a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original' (Soulé, 1986, see Figure 7).

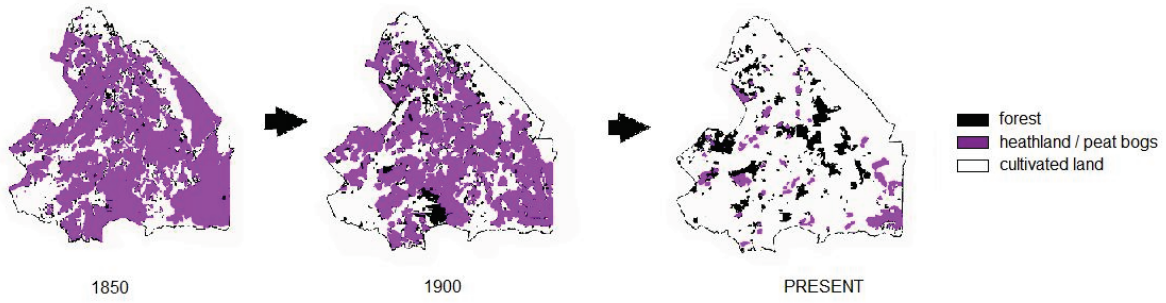

Figure 7: Fragmentation of heathland and moorland in the province of Drenthe, the Netherlands. Fragmented heathland/moorland areas are shown in violet, forest areas in black and cultivated land in white (modified from Oostermeijer).

What kind of consequences does this process have? One is the reduction in the total habitat area or habitat loss (which primarily affects population sizes and thus extinction rate) and the other is redistribution of the remaining area into disjunct fragments or isolation (which primarily affects dispersal and thus immigration rates). Each of them contributes to a reduction in the number of species supported, although different mechanisms are involved (Soulé, 1986; Soulé and Wilcox, 1980).

Meffe and Carroll (1997) suggested five major mechanisms through which biodiversity is reduced as a consequence of fragmentation:

1. Initial exclusion

   Because remaining fragments represent only a sample of the original habitat, many species are eliminated by chance; since they occurred only in the portions of the landscape destroyed by development.

2. Isolation and barriers

   The modified landscape in which fragments exist may be inhospitable to many native species, thus preventing normal movements and dispersal. Structures and habitats, like roads, urban areas, agricultural field or clear cuts, created by humans, can greatly inhibit the movements of many kinds of animals and, potentially, plants, especially those dispersed by animals.

3. Species-area effects

   Small fragments contain fewer habitats, support smaller populations of native species, which are therefore more susceptible to extinction, and are less likely to intercept the paths of dispersing individuals.

4. Edge effects

   Climatic influences and opportunistic predators and competitors from the disturbed landscape can penetrate the fragments, reducing the core area of suitable habitat.

5. Changes in biological communities

   Species composition is alerted in fragmented landscapes because some species are more vulnerable than others to reduced area. Species that have been identified as especially vulnerable to the effects of fragmentation are:

   - rare species
   - species with large home ranges
   - species with limited power of dispersal

- species with low reproductive potential
- species with short life cycles
- species depending on resources that are unpredictable in time or space
- ground-nesting birds
- species of habitat interiors
- species exploited or persecuted by people

Some effects of fragmentation on biodiversity have been conspicuous, others have been subtle and indirect, and some have occurred almost immediately after the initial disturbances, whereas others have developed over decades or are still unfolding (Meffe and Carroll, 1997).

Furthermore, the fragmentation of natural habitats will have different consequences depending on the mobility of organisms and the proximity of isolated fragments (Soulé and Wilcox, 1980). Fragmentation effects vary across organisms, habitat types and geographic regions (Haila, 2002).

2.3.1. Fragmentation and heterogeneity

All landscapes are fragmented and show mosaic patterns on one scale or another. This phenomenon is called natural patchiness. For instance, differences in soil parent material, changes in slope, aspect (which reflects gradients in soil moisture and other proprieties) or elevation (which reflect temperature and precipitation gradients) are reflected in the distribution of vegetation types. Natural disturbances create considerable heterogeneity and generally increase the diversity of habitats, microhabitats and species in an area.

On the other hand, nowadays the fragmentation is often a result of human settlement and resource extraction. Consequently, the landscape has become a patchwork of small areas in a sea of developed land, and mostly the process has negative effects on species diversity.

Main differences between naturally patchy and fragmented landscapes are only beginning to be explored scientifically. There are some major distinctions hypothesized:

- A natural patchy landscape has a rich internal patch structure (lots of tree fall gaps , different layers of vegetation), whereas fragmented landscapes have simplified patches (such as parking lots, cornfields, tree farms with trees all of the same species and size, etc.)
- Natural landscapes have less contrast (less pronounced structural differences) between adjacent patches than fragmented landscapes. Potentially naturally patchy landscape has less intense edge effects.
- Certain features of fragmented landscapes, such as roads and various human activities (drainage, eutrophication, acidification), pose specific threats to population viability.

Therefore, fragmentation creates a landscape different from that shaped by natural disturbances to which species have adapted over evolutionary time (Meffe and Carroll, 1997; Noss and Cooperrider, 1994).

However, the point in the fragmentation process, at which biological integrity declines dramatically, is usually not known. Some studies fail to detect negative impacts of fragmentation on biodiversity, and some even observe positive effects. For this reason, the study of fragmentation remains a topic of active research interest (Meffe and Carroll, 1997).

2.4. ISLAND BIOGEOGRAPHY

'One of the most profound developments in the application of ecology to biological conservation has been the recognition that virtually all natural habitats or reserves are destined to resemble islands, in that they will eventually become small isolated fragments of formerly much larger continuous natural habitat […] Many ecologists and biogeographers have come to recognize the potential importance of studies of islands and other ecological isolates to conservation.' (Wilcox, 1980) The term 'isolate' used here is an ecological community with more or less distinct boundaries and the study of isolate ecosystems is most commonly called 'island biogeography' (Wilcox, 1980)

When the landscape surrounding the fragments (i.e. the 'matrix') is inhospitable to species of the original habitat, and when dispersal is low, remnant patches can be considered as true 'habitat islands' (Soulé, 1986).

There are many different types of islands in addition to those found in the world's oceans, Figure 8 illustrates some of them. In the literature, many forms of 'islands' can be found, from individual thistle plants (islands for the arthropods that visit them) in an abandoned field, to remote volcanic archipelagos like the Galápagos and Hawaiian islands (Whittaker and Fernández-Palacios, 2008).

We may divide islands into two broad types: true islands, being land wholly surrounded by water, and habitat islands, being other forms of insular habitat; discrete patches of habitat surrounded by a matrix of strongly contrasting terrestrial habitats. For example, mountain tops surrounded by desert, woodland fragments surrounded by agricultural land or thistle heads in a field (Whittaker and Fernández-Palacios, 2008).

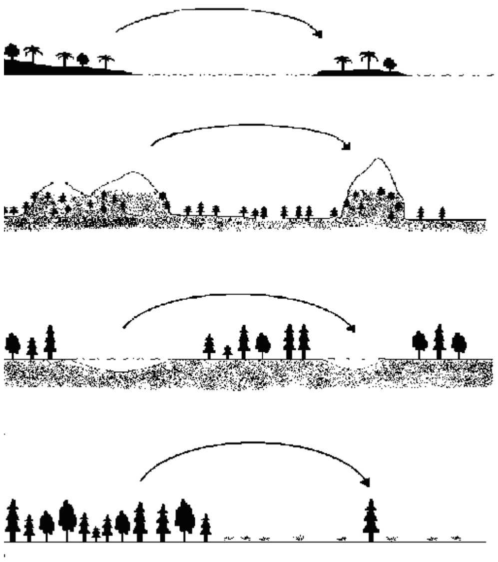

Figure 8: Examples of types of islands (modified from Whittaker and Fernández-Palacios, 2008).

However, all this variety of islands can also presents variety of islands' characteristics and responses to environmental changes. Whittaker and Fernández-Palacios (2008) noted: 'Habitat islands exist typically within complex landscape matrices, which are often rapidly and dramatically changing over just a few years. Matrix landscapes may be hostile to some but not all species of the habitat islands, and isolation is thus of a different nature than for islands in the sea. It cannot necessarily be assumed that what goes for real islands also works for habitat islands and vice versa' (Whittaker and Fernández-Palacios, 2008).

Moreover, (Pickett et al., 1997) called for attention to the fact that landscapes are dynamic. Even if we call separated patches of habitats islands, it is important to be aware that populations, communities, or ecosystems are not closed, but open to the outside influences. Considering conservation strategies it is important to maintain not only the landscape or populations, but also the dynamic processes that created them.

2.5. SPECIES-AREA RELATIONSHIP

The relationship between an area and a number of species was one of the first ecological relationships to be established empirically. Biogeographers have long known that the area of any insular habitat declines, so does the number of species it contains (Meffe and Carroll, 1997). In 1957 Darlington expressed species-area relationship for the particular case of the herpetofauna of the West Indies: 'Division of area by ten [in going from one island to the next] divides the fauna by two.' (see Figure 9) (MacArthur and Wilson, 1963, 1967).

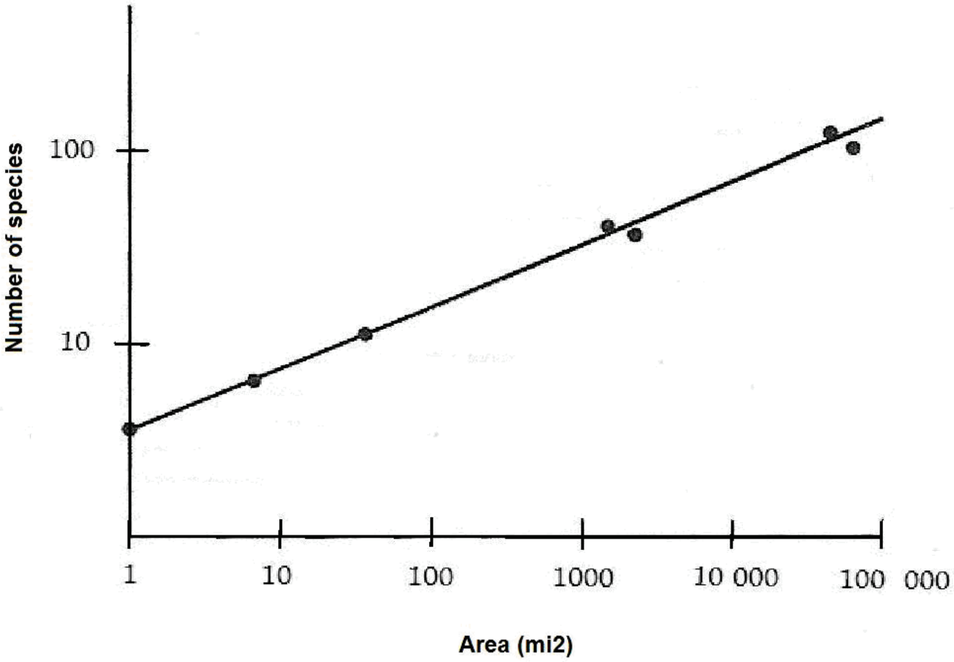

Figure 9: The area-species curve of the West Indian herpetofauna (amphibians plus reptiles) (modified from MacArthur and Wilson 1967).

This relationship was also examined also by Preston in 1962 and MacArthur and Wilson (1963, 1967). Building on previous work, MacArthur and Wilson (1963, 1967) concluded that the island species-area relationship can often be approximated by the power function model (Whittaker and Fernández-Palacios, 2008, see Figure 10):

$$S=cA^{z} \qquad \ldots(1)$$

S is the number of species, A is the area, c and z are the constants determined empirically from the data (MacArthur and Wilson, 1963, 1967; Meffe and Carroll, 1997; Whittaker and Fernández-Palacios, 2008).

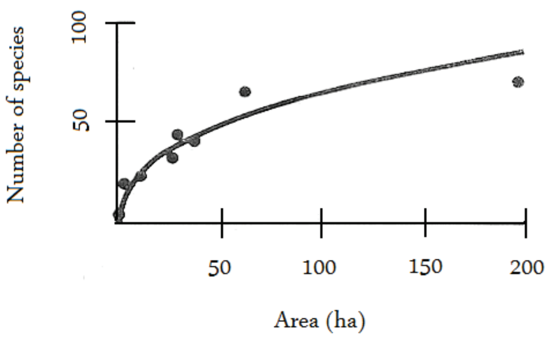

Figure 10: An example of species-area relationship: the number of breeding bird species in different size plots of North American deciduous forest (Data from Preston, 1960; modifided from Soulé and Wilcox, 1980).

With logarithmic transformations the equation becomes:

$$\log S = \log c + z \log A \qquad \ldots (2)$$

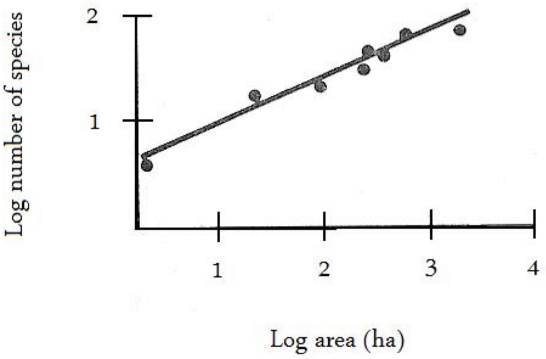

Figure 11: The species-area relation in Figure 10 (the number of breeding bird species in different size plots of North American deciduous forest) plotted on logarithmic axes (Data from Preston, 1960; modifided from Soulé and Wilcox, 1980).

On a logarithmic scale this relationship illustrates a straight line where *c* is the y-intercept and *z* is the slope of the line (see Figure 11). Whittaker and Fernández-Palacios (2008) explained the equation: ‘a low value (slope) means that there is less sensitivity to island area than for a system of high *z* value, while *c* values reflect the overall biotic richness of the study system, and thus vary with taxon, climate and biogeographical region. Values *z* are easy to compare between study systems, but the parameter *c* changes with different scales of measurement used (e.g. km^2 versus $miles^2$), requiring conversion of data to a common measurement scale before they can be analyzed for comparative purposes.’

Z value is a constant for a given group of islands and a given group of organisms. It ranges from about 0.15. to 0.35 over all situations that have been analyzed (Thornton, 2007). Analysis of species-area relationships in different groups of organisms showed that most values of *z* are between 0.20 and 0.35 for islands, and for non-isolated sample areas (nested, subdivided areas within islands or within continents) *z* values are smaller, falling usually between 0.12 and 0.17. Thus, Whittaker and Fernández-Palacios (2008) concluded that ’the slope of the log-log plot of the species-area curve appeared to be steeper for islands, or, in the simplest terms, any reduction in island area lowers the diversity more than a similar reduction of sample area from a contiguous mainland habitat.‘ (MacArthur and Wilson, 1963, 1967; Meffe and Carroll, 1997; Whittaker and Fernández-Palacios, 2008).

‘Although it is possible to find many examples that broadly support this island-mainland distinction, there are also exceptions.’ (Whittaker and Fernández-Palacios, 2008). For example research of Lövie (2006) showed a negative relationship between patch size and number of species.

2.6. THE THEORY OF ISLAND BIOGEOGRAPHY

The causes of species-area relationship have been long debated. It seems that the phenomenon is multicausal (Meffe and Carroll, 1997). There are many explanations about why larger areas support more species. One of them relates to greater habitat diversity (Lack, 1976). Other researches believe that area itself, or some unrecognized factor correlated with area, is more important (Johnson and Raven, 1973). Furthermore, species richness might increase with area because the size of populations increase and it reduces probability of extinction due to stochastic processes (Preston, 1962). The disturbance hypothesis postulates that small islands or habitat islands suffer greater disturbance, and this might remove species, open up sites to colonizations by new species or make sites less suitable for disturbance-intolerant species (McGuinness, 1984; Meffe and Carroll, 1997; Whittaker and Fernández-Palacios, 2008).

Definitely one of the most famous explanations for the species-area relationship is the equilibrium theory of island biogeography, proposed by MacArthur and Wilson (1963, 1967). They suggest that the number of species on an island represents a dynamical balance between immigration and extinction (Meffe and Carroll, 1997; Whittaker and Fernández-Palacios, 2008) (see Figure 12). Thus, species richness on an island is determined by the equilibrium between the immigration of new species and the extinction of those species that are already present (Odum and Barrett, 2005).

Because rates of extinction and immigration depend on the size and isolation of islands, the latter affect the equilibrium. Immigration is affected mainly by island distance from the mainland (near or far, Figure 12) and extinction by island size (large or small, Figure 12). Consequently, the number of species present on an island depends mostly on the isolation and the size of the island (remember that isolation and habitat loss are the main consequences of fragmentation (mentioned above in chapter 2.3. Fragmentation, (Soulé, 1986; Soulé and Wilcox, 1980)).

Figure 12 illustrates how the immigration and extinction, and consequently size of an island and distance of an island to the mainland affect the number of species. Immigration rate declines exponentially and extinction rate rises exponentially. At the point of the intersection of those two curves, the rates of both processes are equal and the equilibrium number of species is defined. Initially empty islands therefore fill up toward their equilibrium species richness. When area and isolation of islands are also considered, it appears that there is a family of curves providing unique combinations of species richness and turnover for each combination of area and isolation. Three equilibrium points are shown as examples in the Figure 12. *S_1* as a small distant island, predicted to have few species, *S_2* as small nearby or large distant island, predicted to have intermediate species richness and *S_3* as large nearby island, predicted to have many species (Odum and Barrett, 2005; Whittaker and Fernández-Palacios, 2008; Soulé and Wilcox, 1980).

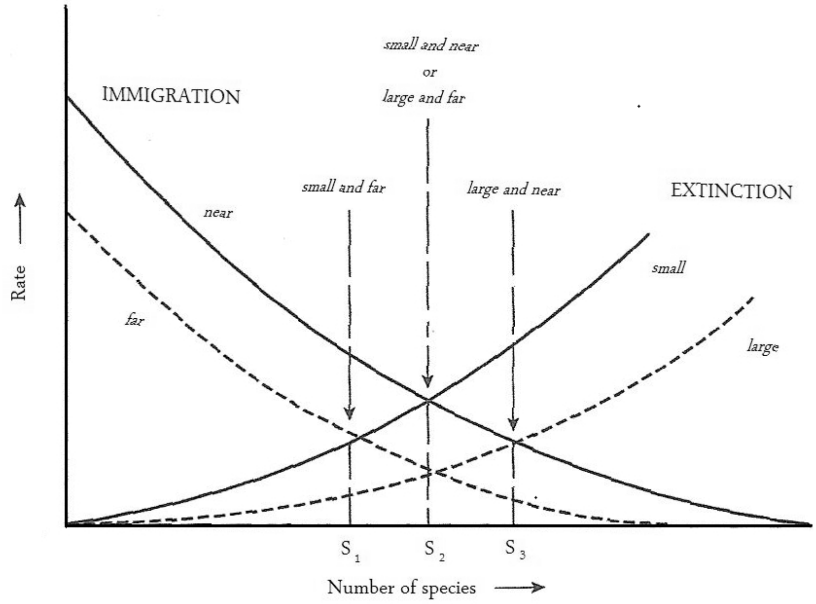

Figure 12: Theory of island biogeography. The number of species on an island is determined by the equilibrium between rate of immigration and rate of extinction. Three points are shown, representing different combinations of large and small islands either near or far from continental shores (after MacArthur and Wilson, 1963, 1967) (Odum and Barrett, 2005).

Furthermore, the equilibrium number of species on an island depends on the characteristics of the island (in particular its size and degree of isolation, as already mentioned) and upon the characteristics of species themselves (in particular their dispersal abilities and population densities) (Soulé, 1986). The present study on heathland fragmentation focuses on the characteristics of the island: the size and isolation of areas and their effects on the diversity of plants.

Moreover, the theory postulates that there are two ways in which islands gain species, by immigration or by evolution of new forms, and two ways in which islands lose species, by emigration or by the death of the last representatives on an island (i.e. extinction). Because of relatively slow rates of evolution, speciation has a smaller effect on equilibrium as well as on emigration. Emigration rarely leads to complete disappearance of a species from an island. Therefore MacArthur and Wilson (1963, 1967) are more focused on processes of immigration and extinction (Whittaker and Fernández-Palacios, 2008).

For mainland situations, we can also conclude that the theory of island biogeography predicts species richness to increase with habitat area and decrease with isolation from colonization sources (Bruun, 2001).

The theory of island biogeography has sometimes been supported by empirical studies and sometimes not (Meffe and Carroll, 1997; Debinski and Holt, 2000). Results of studies differ for different habitats and different taxa. The theory proved useful to explain results of empirical studies on fragments of deciduous woodland in northern Europe (Honnay et al., 1999). However, results on fragments of other habitat types are still ambiguous and facts are unknown (Bruun, 2001). The current study is focused on the heathland habitat in Drenthe, the Netherlands.

However, the model demonstrates the interplay of many fundamental ecological processes which is why the theory is of fundamental importance in the fields of landscape ecology and conservation biology.

2.7. ISOLATION

Following the theory of island biogeography (MacArthur and Wilson, 1963, 1967) (see chapter 2.9) we can predict that island species-area relationship would become steeper with increasing geographic isolation (Whittaker and Fernández-Palacios, 2008) and that species richness decreases with isolation from colonization sources (Bruun, 2001).

Do previous studies verify this hypothesis? Whittaker and Fernández-Palacios (2008) answered: ‘Unfortunately, the increased impoverishment of island biotas with increasing isolation is confounded with variations in other properties of islands, particularly their area. The distance effect has turned out to be difficult to test; moreover, those tests that have been conducted have proved equivocal.’ It appears that the assumptions made in analyzing species-area curves are critical for the outcome of the analysis (Rosenzweig, 1995) (Whittaker and Fernández-Palacios, 2008).

The isolation of islands is not only determined by the distance from a source pool; for real islands it varies also as a consequence of wind and ocean currents and for habitat islands it varies because of the characteristics of the landscape matrix in which they are embedded (Whittaker and Fernández-Palacios, 2008).

Piessens et al. (2005), who investigated the influence of isolation on heathland species in Belgium, mentioned that the possible influence of isolation depends also on the dispersal abilities of species (dispersal mode, mean plant height, seed mass and seed number) and traits that determine the persistence of species (seed longevity, growth form, self compatibility and vegetative propagation).

Lots of past studies used isolation index proposed by Hanski as a measure isolation index (Bruun, 2001; Piessens et al., 2005; Krauss et al., 2004). To make this research comparable with these other studies, we used Hanski’s isolation index as a measure for isolation also in our study.

2.8. EDGE EFFECT

The process of fragmentation creates more and more boundaries that surround the remaining islands. The juncture between the matrix and original habitat is called the edge (Kryštufek, 1999), and the structural contrast between different sizes of the edge causes the so-called edge effect (Meffe and Caroll, 1997). The edge of habitat island is not a line, but rather a zone of influence that varies in width depending on what is measured (Murcia, 1995; Meffe and Caroll, 1997). In other words: 'Edge effects are the result of the interaction between two adjacent ecosystems, when the two are separated by an abrupt transition (edge).'(Murcia, 1995). Because adjacent ecosystems experience flows of energy, nutrients and species across their boundary, the species composition, structure and ecological processes of an ecosystem near the edge may be changed (Murcia, 1995). For example, forest edges have different microclimates, abrupt light changes, substrate and water conditions and are generally rich in microhabitats (Murcia, 1995; Lövei, 2006). Edges may affect the organisms by causing changes in the biotic and abiotic conditions (Murcia, 1995).

The edge effect increases, when edges become proportionately greater relative to interiors. Edge-interior ratio (or perimeter-core ratio) is determined by shape and size (Saunders, 1991):

- smaller fragments have smaller core areas and bigger edge-interior ratio and are more affected by edge effect (Saunders, 1991)
- long, thin areas have smaller core areas and perimeter-core ratio (and are more affected by edge effect (Saunders, 1991)

For many animal and plant species, edge habitat may offer more optimal circumstances from the original habitat or matrix. These species are called edge species (Kryštufek, 1999) and are positively affected by the edge. Some wildlife managers are convinced that habitat edge benefits wildlife. On the other side the pervasiveness of edge effect can cause that habitat patches below a certain size will lack the true interior or 'core' habitat that some species require (Meffe and Caroll, 1997). The theory of island biogeography suggests that reserves should minimize the edge-to-area ratio to maximize the effective core area of the reserve (Debinski and Holt, 2000). As we can see, there is little consensus between scientists on how to measure edge effects and how deleterious they are (Murcia, 1995).

2.9. ABOUT THE SLOSS

Soulé and Wilcox (1980) were convinced that nature reserves are the most valuable weapon in our conservation arsenal. This is why there are so many discussions about the design of the nature reserves, their size, number and arrangement of suitable sites and how these factors influence population persistence. This controversy has come to be known as the SLOSS debate. SLOSS is an acronym for 'Single Large or Several Small' and refers to whether the reserves should be designed as one big piece of protected land or several smaller reserves. This debate has been mainly referred to the effects of reserve design on species diversity or to the viability of metapopulations by focusing on positive and negative distance effects on population persistence (Meffe and Carroll, 1997).

From species-area relationship we could learn that a patch with area size A does not have twice more species than the patch with area size A/2. If two smaller patches together will contain more species than one bigger patch with the same total area size, will depend also on β- and γ-biodiversity. And even if two smaller patches together contain more species, it is important to know if their single areas are big enough to maintain minimum viable population. Besides, a relatively big part of the area can be lost in smaller patches because of the edge effect. However, if we want to preserve the same species richness with several smaller areas and not with a single large one, patches need to be still big enough and interconnected to prevent the cascade of extinction (Kryštufek, 1999).

'There is no single answer to the SLOSS debate because the number, size, and location of habitat patches affect different species differently' (Meffe and Carroll, 1997). For instance, good dispersers will function differently in separated sites than poor dispersers. There is also 'no single 'magic' population size that guarantees the persistence of populations' (Thomas, 1990). Above all, the overall size of complex landscapes that enables effective conservation is very important (Meffe and Carroll, 1997).

Because the present study is focused on effects of fragmentation on heathland plant diversity and therefore as well on effects of area sizes, it also contributes with new empirical data to the SLOSS-debate.

3 MATERIALS AND METHODS

In the research we examined the effects of habitat fragmentation on plant diversity in heathland in the province of Drenthe, the Netherlands.

Main consequences of habitat fragmentation are habitat loss and isolation (see chapter 2.5., Fragmentation). With this in mind, the main question in this research was how the size of an area (of some particular habitat) and isolation affect species diversity. In particular, we focused on plant species diversity, on α richness or α diversity, which refers to the number of species found in a small, homogenous area (see chapter 2.3.2., Species diversity). These small homogeneous areas were areas of heathland habitat in Drenthe, the Netherlands. Furthermore, we were also interested in how the size of an area and isolation affect the number of Red Listed plant species living in the same heathland patches.

To investigate the aim of the study we needed information about:

1. Sizes of the areas.
2. Number of plant species in those areas.
3. Number of plant Red Listed species in those areas.
4. Isolation rate of the areas.

All of the analyses were made with software programs ArcView, ArcMap, ArcInfo (ArcGIS-package by Esri software), Microsoft Excel and SPSS.

Statistical analyses included simple linear regressions.

3.1. SIZES OF THE AREAS

Sizes of the areas were acquired from an electronic, vector-based version of the topographical map of the Netherlands (called TOP10vector). We exported patches of heathland, in particular those situated in a small part of the province of Drenthe (Figure 13 and 14). Using ArcMap, we needed to unite those patches to prepare measurable, closed units. The uniting procedure meant that water surfaces and roads (except the highway) inside of patches were included as part of the heathland patch. This was done to prevent an overestimation of the perimeter of each patch. In the case of each patch, we measured the area, the perimeter and the distance to the nearest other patch.

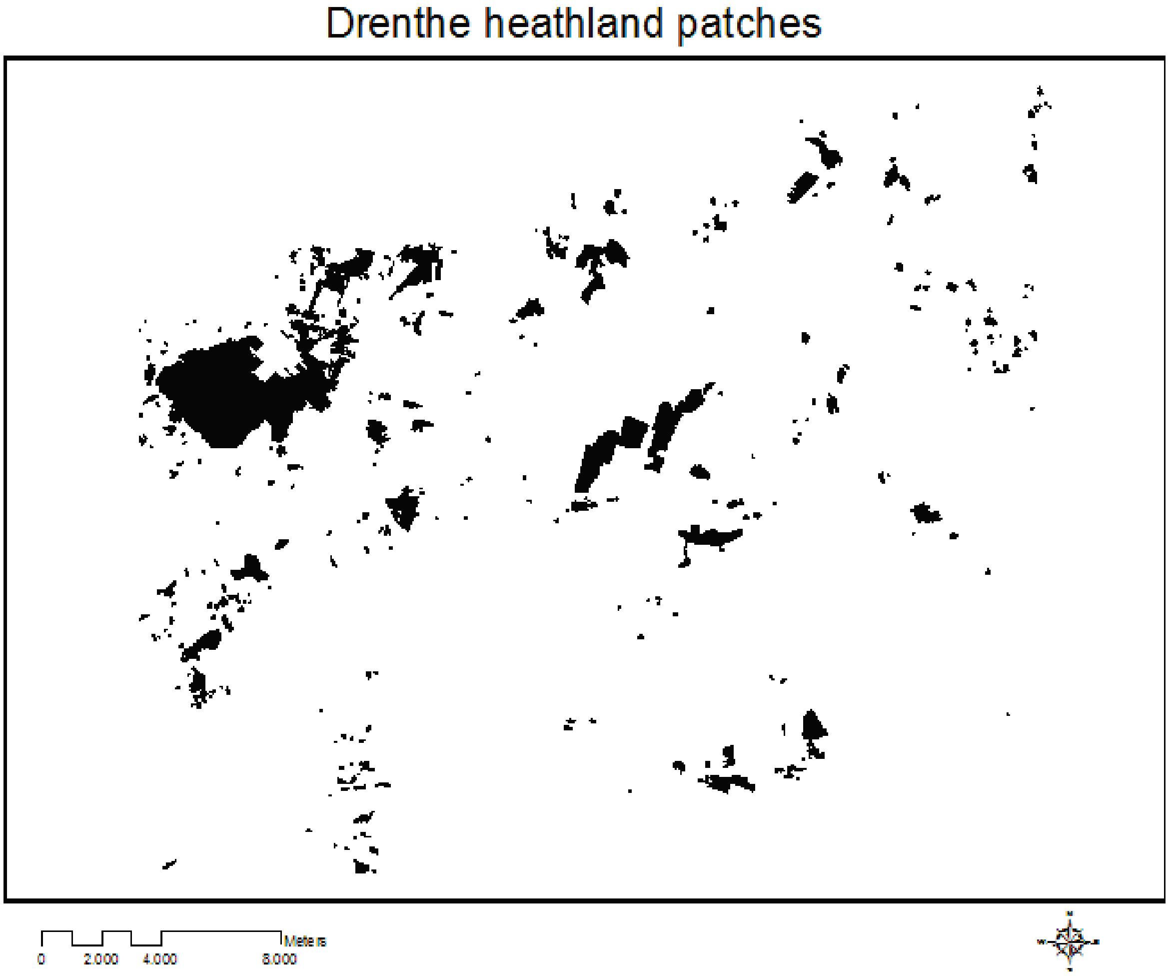

Figure 13: A scheme of the exported heathland patches extracted from the vector-based topographical map of the southern part of the province of Drenthe.

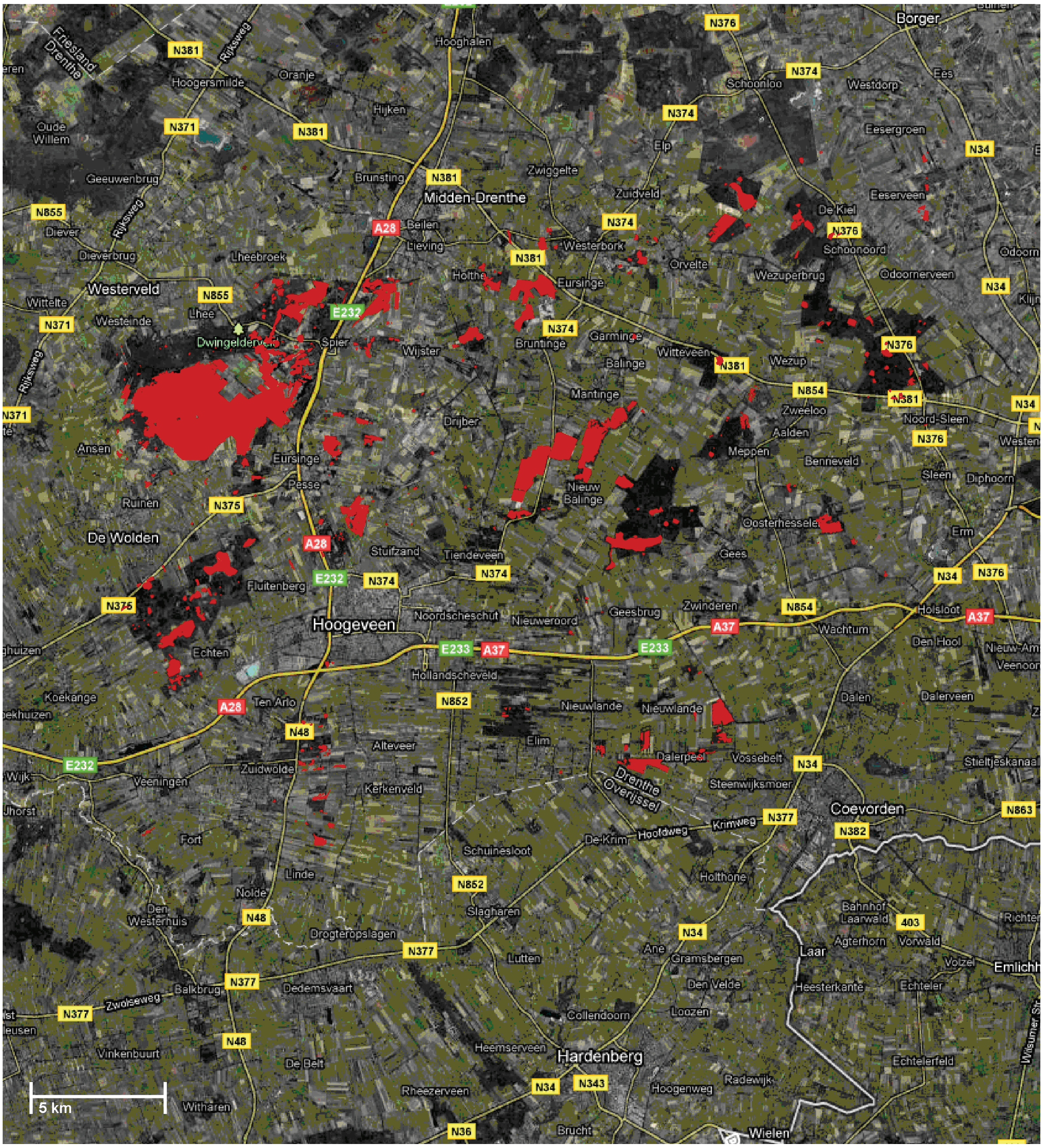

Figure 14: A map of Drenthe overlaid with heathland patces of this research (in red) (modified from googlemaps, a satellite snapshot).

3.2. NUMBER OF SPECIES

The data about the number of species we used in this research were from the floristic inventory scheme of the Netherlands coordinated by the foundation FLORON. The information is collected by both professional and amateur/volunteer botanists. All data on the biodiversity in the Netherlands is brought together in EcoGRID, which holds inventory data for plants, birds, butterflies, grasshoppers, dragonflies, etc.. at a resolution of 1x1 km^2.

First, we compiled a list of typical/characteristic heathland species (Table 1). Using this list, we extracted the number of heathland species for each 1x1 km^2 grid cell, and overlaid this layer in ArcGIS on the abovementioned map with heathland patches (Figure 16).

3.2.1. The list of heathland species

The list of heathland species is derived from the affinity of the species to the different syntaxonomical (i.e. phytosociological) units that are part of the mosaic vegetation complex that are called heathland in the Netherlands. This includes the Oxycocco-Sphagnetea/Ericetalia tetralicis/Ericion tetralicis (wet heathlands), the Calluno-Ulicetea, the Nardetea/Nardetalia/Nardo-Galion saxatilis (dry heathlands and humid grass heaths), and even some elements of the Molinio-Arrhenatheratea/Molinietalia/Junco-Molinion & Calthion (in wet grass heaths). (All the names refer to the English identification guide/table to the plant communities of the Netherlands (Sýkora, 2006)).

64 species were determined as heathland species on the list (Table 1), 44 of those belong to the Red List of the Dutch Flora. According to this numbers, 69% of all current heathland species, present in investigated patches of heathland, are considered as the Red Listed species of the Dutch flora.

Table 1: List of the specific heathland plant species that were used for the analysis of species richness. Species occurring on the Dutch Red List (van der Meijden et al., 2000) are indicated in red and boldface.

Erica tetralix
Molinia caerulea
Drosera intermedia
Rhynchospora fusca
Rhynchospora alba
Drosera rotundifolia
Lycopodium inundatum
Carex panicea
Eriophorum angustifolium
Calluna vulgaris
Gentiana pneumonanthe
Scirpus cespitosus
Juncus bulbosus
Juncus squarrosus
Eleocharis multicaulis
Narthecium ossifragum
Hammarbya paludosa
Myrica gale
Pedicularis sylvatica
Oxycoccus palustris
Deschampsia setacea
Carex dioica
Carex pulicaris
Genista anglica
Hypericum canadense
Polygala serpyllifolia
Succisa pratensis
Nardus stricta
Dactylorhiza maculata
Empetrum nigrum
Danthonia decumbens
Vaccinium vitis-idaea
Platanthera bifolia
Luzula multiflora

Deschampsia flexuosa
Genista pilosa
Juniperus communis
Arnica montana
Galium saxatile
Polygala vulgaris
Cuscuta epithymum
Pinguicula vulgaris
Hieracium vulgatum
Drosera x obovata
Luzula multiflora ssp. congesta
Oxycoccus macrocarpos
Viola canina
Lathyrus linifolius
Cytisus scoparius
Hieracium maculatum
Carex ericetorum
Euphrasia stricta
Filago minima
Antennaria dioica
Botrychium lunaria
Scorzonera humilis
Rhinanthus minor
Radiola linoides
Scutellaria minor
Carex caryophyllea
Trifolium medium
Lycopodium complanatum
Lycopodium tristachyum
Ulex europaeus

3.2.2. 1x1 km² grid cells, overlaid with heathland patches

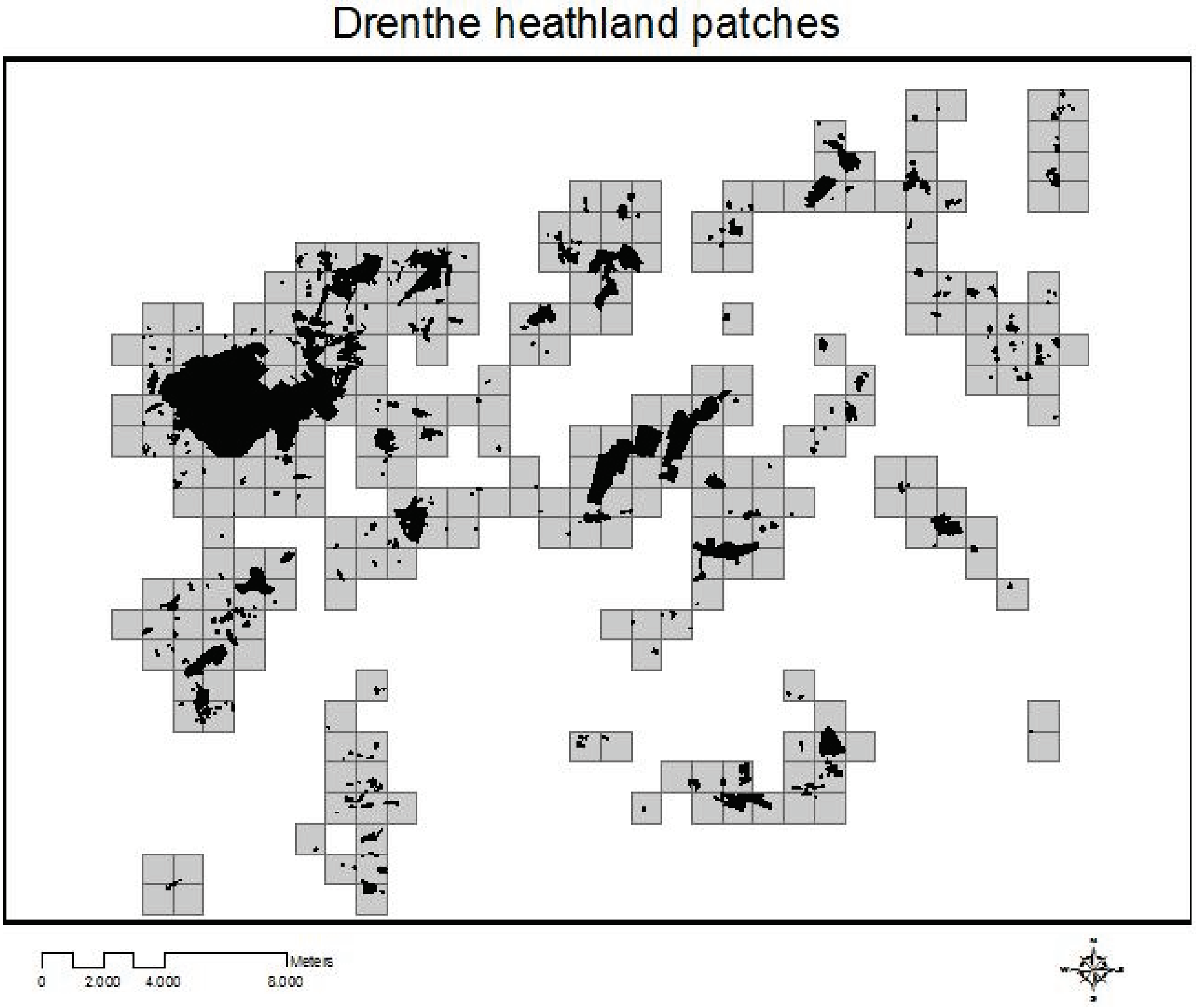

Figure 15: A scheme of the exported heathland patches extracted from the vector-based topographical map of the southern part of the province of Drenthe (shown in black), showing the 1x1 km2 grid-cells (grey blocks) with plant records that were used for the analysis as an overlay.

It was not always easy to assign the species found in an EcoGRID 1x1 km^2 cell to a specific heathland patch (see Figure 15). Frequently, it was not clear to which cell a specific heathland patch belonged, because its boundaries crossed multiple cells. In addition, cells contained more than one fragment, or fragments were secondarily fragmented at a much smaller scale than 1x1 km^2, so that we had to pool them into larger units to be able to assign the plant observations to a single patch (see Fig. 16).

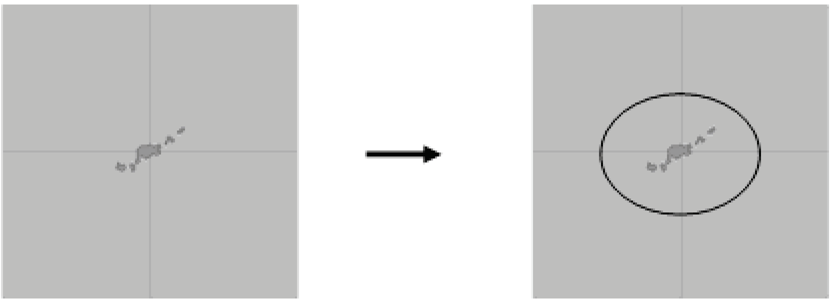

Figure 16: Example showing a case where we decided to merge several patches into a single one, because it was ambiguous to which of the EcoGRID cells the different patches corresponded. The species list for this particular (pooled) patch was assembled from the four EcoGRID cells shown.

This modeling needed specific limits to prevent merging of all the patches into a single one. This is why we developed a system with rules;

- patches were merged together (i.e. considered to belong to the same patch) if they were less than 500 meters apart
- patches were not merged if they were less than 500 meters apart, but separated by a major road (which was believed to form a more severe dispersal barrier than distance alone) (see chapter 2.3., Fragmentation, Isolation and barriers)

Patches that did not suit the decision rules shown above were excluded.

Following this system, 77 groups of heathland patches were modeled. These modeled grups of heathland patches represented our operative sample units. Some of those 77 sample units still could not be used in the following analyses. The reasons were:

- Two or more operative sample units belonged to the same 1x1 km^2 grid cell, therefore it was impossible to define which species belonged to which sample unit. These sample units were excluded.

- Some of the 1x1 km^2 grid cells had only very old observations. All sample units that belonged to 1x1 km^2 grid cells with no data collected after 1990 were excluded. The number of records in the Florbase database has strongly increased since 1990.
- Some of the sample units needed to be excluded, because the data about the species were unreliable as a result of incomplete sampling. For example, when the database contained just one heathland species for particular sample unit, like *Succisa pratensis*. This is an example of a species that is often found in heathland habitats but just by itself does not really represent heathland habitat.

As a result, a lot of sample units had to be eliminated. 30 of the initially 77 operative sample units were used for the statistical analysis (Figure 18 and 19). The biggest (merged) operative sample unit measured 1537.4 ha, the smallest 0.2 ha and the average size of the area of all thirty sample units was 81.7 ha.

In addition, the system of merging patches caused that the operative sample units of heathland in this research were on average bigger than areas of heathland patches in reality in the Netherlands (Figure 17).

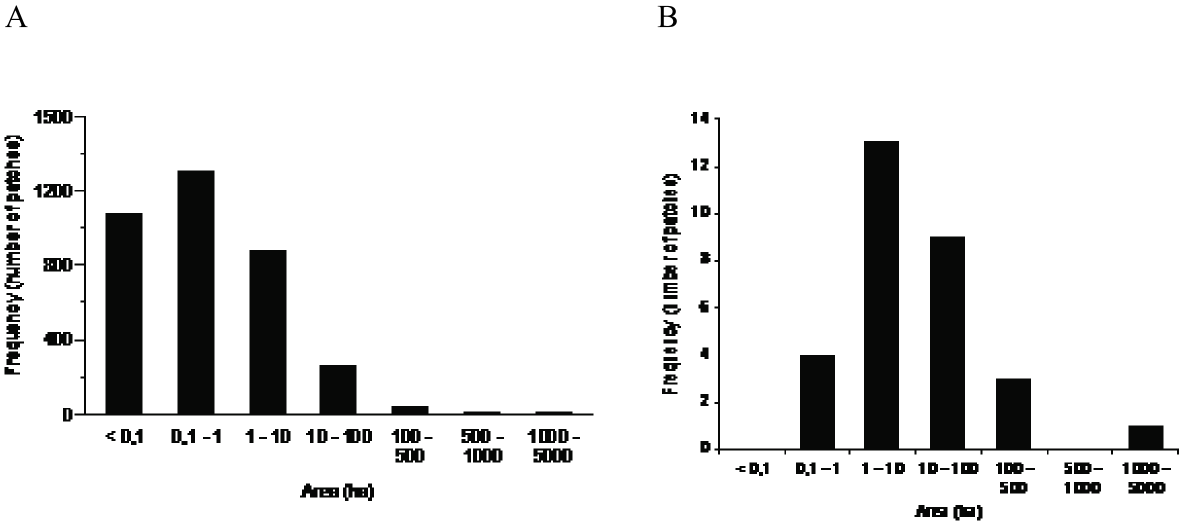

Figure 17: A-frequency distribution of the areas of heathland patches in the Netherlands (Dutch website - compendium for the environment), B-frequency distribution of the areas of heathland patches in Drenthe, after selection and merging as described in the methods.

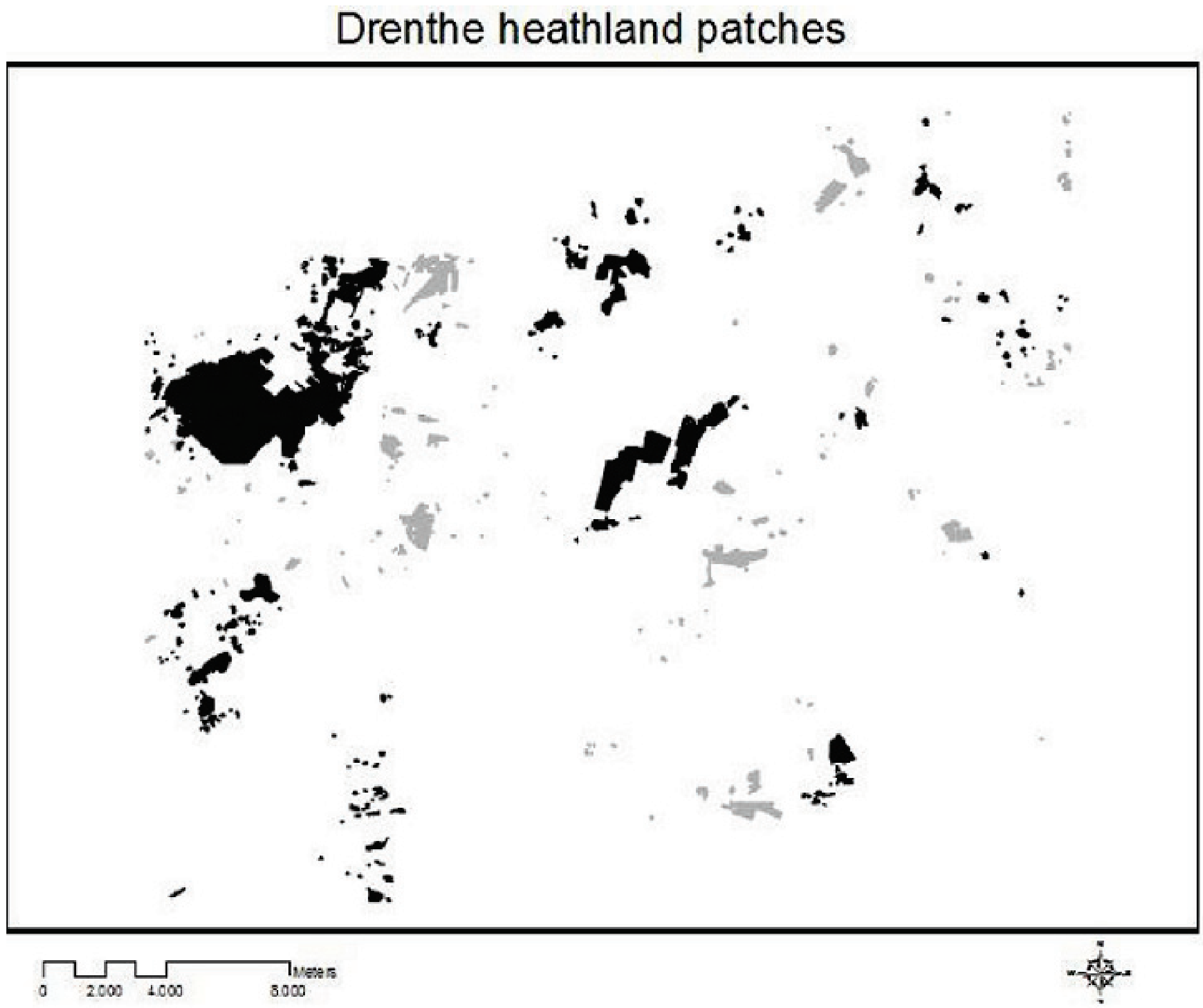

Figure 18: Map showing the final 30 out of 77 selected sample units (in black). The remaining 47 patches (shown in grey) had to be discarded because they did not meet our selection criteria (see Materials and methods).

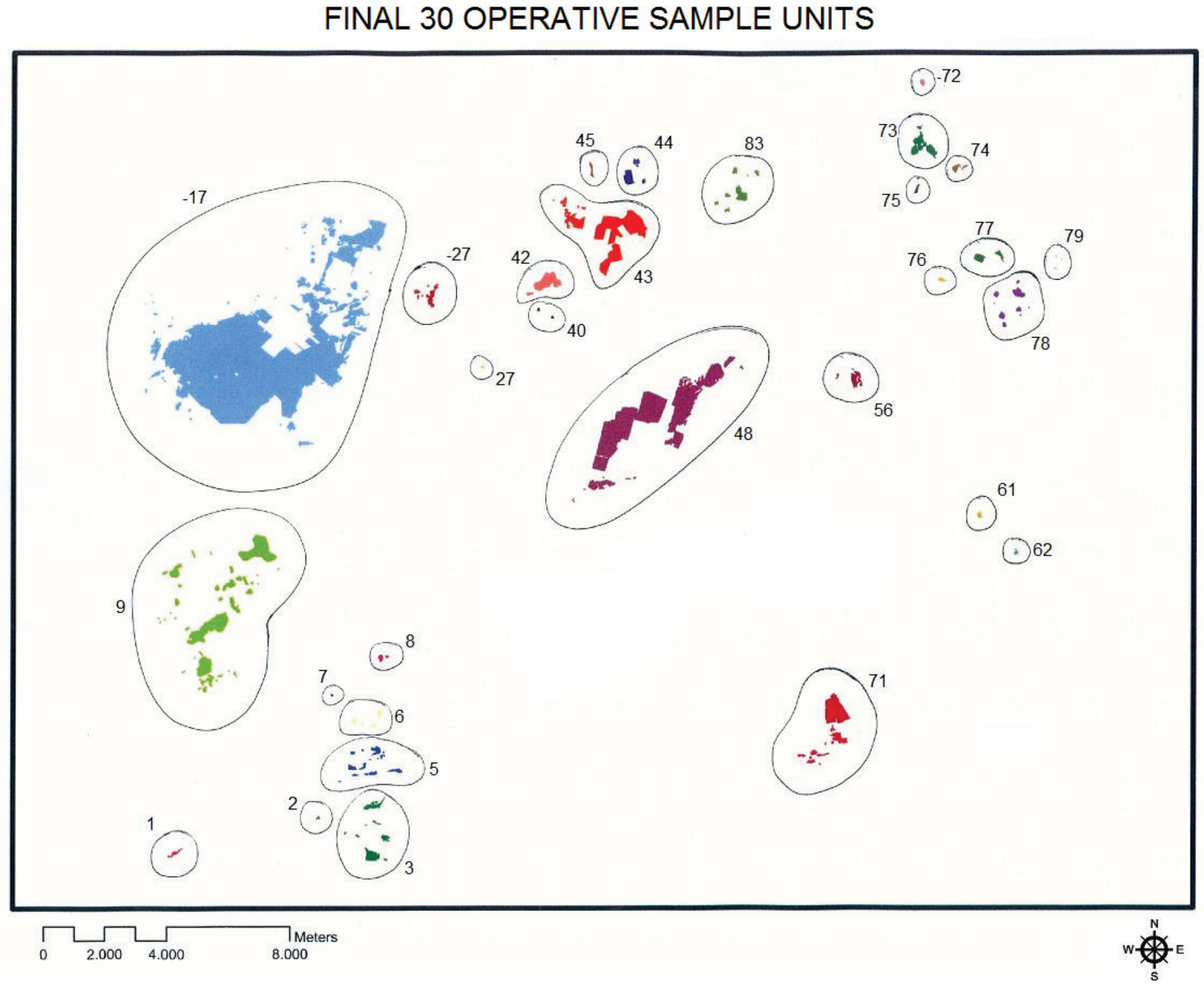

Figure 19: A scheme representing final 30 sample units used for statistical analyses. Every operative sample unit is colored differently, it is encircled and has a number beside, which represents just the name of the sample unit.

3.3. NUMBER OF RED LISTED SPECIES

Because the Red Listed species may be considered especially vulnerable to the effects of fragmentation, we were also interested in the influence of the area and the isolation of a heathland fragment on the number of currently observed Red Listed plant species. Hence, the same analyses that were made for all typical/characteristic heathland species were also executed separately for heathland plant species that occurred on the Red List of vascular plants of the Netherlands (van der Meijden *et al.*, 2000).
These species are indicated in Table 1 (indicated in red and boldface).

3.4. ISOLATION

To estimate the isolation of an area, we used Hanski's (1994) isolation index (see chapter 2.7. Isolation). The formula of this index is:

$$\mathbf{S_i = \sum_{i \neq j} \exp(-\alpha\, d_{ij})\, N_j} \qquad \textbf{(Hanski)} \qquad \ldots(3)$$

Where: S_i = isolation index

i = measuring population

j = other population with possibility of migration to patch j

α = describes how fast the numbers of migrants from patch j decline with increasing distance

d_{ij} = straight-line (Euclidian) distance between patches i and j

$N_j = p_j A_j$

P_j = equals 1 for occupied and 0 for empty patch

A_j= the area of the patch j

This measure of population/patch isolation should reflect the expected numbers of immigrants arriving to the patch. Immigrants may arrive from several populations. Generally we expect that the contribution of the population *j* to the patch *i* increases with the size of the population *j*, but decreases with its distance from the patch *i.* The measure of isolation above (Formula 3) takes these effects into account (Hanski, 1994). The original formula was a little simplified in similar studies. We used the same formula that Bruun (2001) used for patches of grassland and heathland in Denmark:

$$I_i = -(\sum \exp(-d_{ij})*A_j) \qquad \textbf{(Bruun)} \qquad \ldots(4)$$

The sum of 5 closest sample units was calculated. All 77 basic sample units were used for the calculations of the isolation index.

The distances between patches were measured in ArcMap (with measure tool). Distances were measured from edge of one sample unit to the edge of the other sample unit. We did not use any unit of measure for the isolation index. There was no case when two sample units would be the same distance away from the focal sample unit.

3.5. EDGE EFFECT

The results of the number of species were also presented in the relationship to the perimeter/area ratio of the sample unit (perimeter of the sample unit/ area of the sample unit). This perimeter/area ratio was a measure for edge effect, which is one of the major mechanisms through which biodiversity is being reduced as a consequence of fragmentation (Meffe and Carroll, 1997, see chapter 2.3 Fragmentation and chapter 2.8. Edge effect).

4 RESULTS

4.1. RESULTS FOR SPECIES-AREA RELATIONSHIP

The size of heathland patches was positively correlated with their species richness of heathlands (Figure 20). Bigger patches apparently contained more species. Species richness increased rapidly with increasing area. The relationship showed a power function model. After logarithmic transformation the power model presented a linear relationship (Figure 20). This accorded with many other studies that explored species-area relationship (Rosenzweig, 1995, see also chapter 2.5. Species-area relationship). The equation for linear function became log S = log $c + z$ log A (where S was the number of species, A was area, c and z were constants determined empirically from the data (MacArthur and Wilson, 1963, 1967)). Simple linear regression for correlation between size of the area and species richness (Figure 20) corresponded to the equation y = 0.1628x + 1.0993. Therefore the z value was 0.1628 and c value was 1.0993.

Z value presented a slope of the regression line. A low value (slope) means that there was less sensitivity to island area than for a system of high z value (Whittaker and Fernández-Palacios, 2008, see chapter 2.5.Species-area relationship). *Z* value (Figure 20) matched the ranges of z values from previous researches; from 0.15 to 0.35 (Thornton, 2007). The value was a bit lower than usual for islands (most values of z are between 0.20 and 0.35 for islands (MacArthur and Wilson, 1963, 1967; Rosenzweig, 1995; also see chapter 2.5. Species-area relationship).

C values reflect the overall biotic richness of the study system, and thus vary with taxon, climate and biogeographical region. Values of the parameter c also change with different scales of measurement used (e.g. km^2 versus miles^2). Therefore values of c are not easy to compare within different studies (see chapter 2.5. Species-area relationship).

The value of correlation of coefficient (R) was 0.82, and the value of coefficient of determination (R^2) was 0.68 (Figure 20), which means the correlation was positive and strong. When the correlation between two variables is positive, large values of one variable are associated with large values of the other variable. In particular, when the area (on average) of the patch of our sample units was bigger, the number of species present in there (on average) was bigger as well.

The correlation was statistically significant ($p \leq 0.001$, Figure 20). It means that there is less than 5 % ($p \leq 0.05$) possibility that the observed relationship occurred by chance. The relationship is therefore correlated.

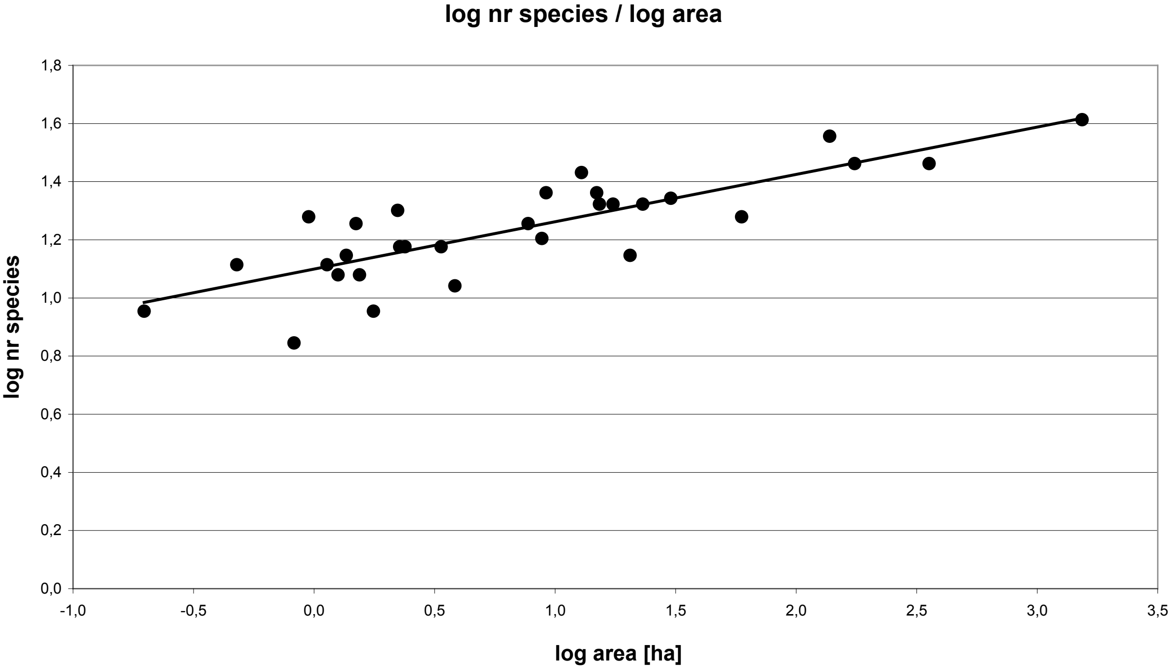

Figure 20: Correlation between the number of plant species and the areas of heathland patches in which they occur in the province of Drenthe, the Netherlands.
Regression equation: $y = 0.1628x + 1.0993$
$R = 0.82$, $R^2 = 0.68$, $p \leq 0.001$

When the analyses were made only for the number of the Red Listed species, the results were very similar (Figure 21). The number of the Red Listed species increased with fragment area (Figure 21). The correlation of coefficient (R) was 0.71 and the coefficient of determination (R^2) was 0.50, which means the correlation was positive and medium.

After logarithmic transformation, there was a positive linear relationship, with equation $y = 0.3031x + 0.4307$, with $z = 0.3031$ and $c = 0.4307$ (Figure 21). Also for the Red Listed species z value matched the ranges of z values from previous researches; from 0.15 to 0.35. The z value for equation of the Red Listed species was actually very typical for islands in past researches (most values of z were between 0.20 and 0.35 for islands) (see chapter 2.5.Species-area relationship). The z value was much higher for the Red Listed species ($z = 0.3031$) than for all of the species present in particular area ($z = 0.162$). This means that the slope was steeper for the Red Listed species and that any reduction of the area lowers species richness for the Red Listed species more strongly than species richness for all of the species together (Rosenzweig, 1995). In other words, we can conclude that the Red Listed species were more sensitive to area reduce (Whittaker and Fernández-Palacios, 2008, see chapter 2.5. Species-area relationship).

The correlation was statistically significant ($p \leq 0.001$, Figure 21).

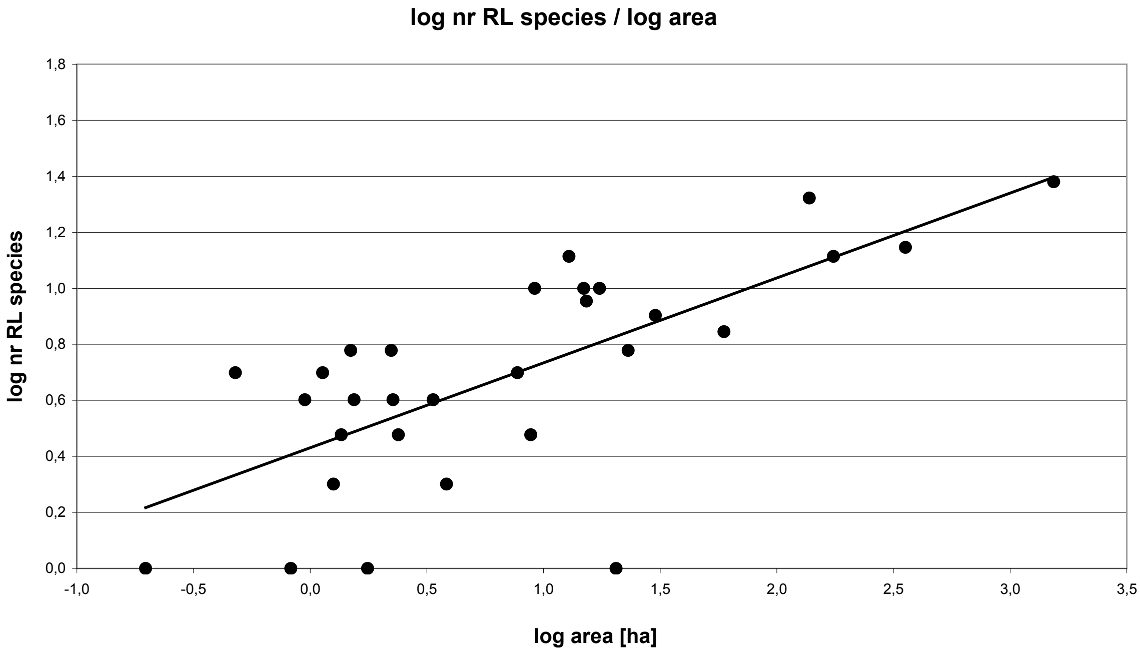

Figure 21: Correlation between the number of the Red Listed plant species and the areas of heathland patches in which they occur in the province of Drenthe, the Netherlands.
RL = Red Listed species
Regression equation: $y = 0.3031x + 0.4307$,
$R = 0.71$, $R^2 = 0.50$, $p \leq 0.001$

The proportion of the Red Listed species also increased with the size of the area (Figure 22).

For linear regression we used the angular transformation ($y=\arcsin(\sqrt{x})$) of proportion of the Red Listed species. The regression equation was $y = 0.1456x + 0.4502$. The correlation of coefficient (R) was 0.59 and the coefficient of determination (R^2) was 0.35, which corresponds to positive and medium correlation.

In bigger (on average) areas, bigger (on average) proportion of the Red Listed species was found. This means that proportionally more Red Listed species have been lost from smaller than from larger fragments.

The correlation was statistically significant ($p = 0.001$, Figure 22).

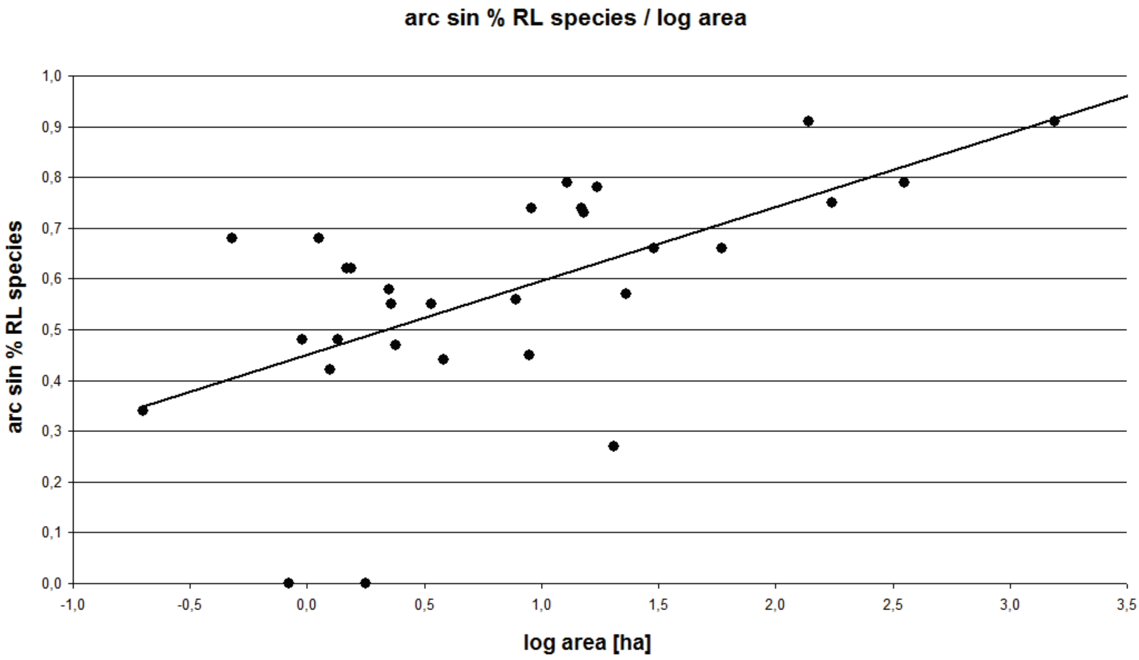

Figure 22: Correlation between the proportion of the Red Listed plant species and the areas of heathland patches in which they occur in the province of Drenthe, the Netherlands.
RL = Red Listed species
Regression equation: $y = 0.1456x + 0.4502$,
$R = 0.59$, $R^2 = 0,35$, $p = 0.001$

4.2. RESULTS FOR ISOLATION

The isolation index showed a negative correlation between the spatial isolation of heathland patches and the current number of species in them (Figure 23, 24 and 25).

The correlations were not as strong as the correlations with the size of the area and the number of species, but still statistically significant ($p \leq 0.05$). The coefficients of determination (R^2) of correlations for isolation index were all lower or the same than 25, which already contributed to low correlation (Figure 23, 24, 25). Compared to correlations of the size of the area and number of species (Figure 20, 21, 22), where the coefficients of determination (R^2) were higher or the same than 35, which contributed to medium or strong correlation.

In Figures 23, 24, and 25 there were only 29 patches included in calculations, because the deviation of one patch was too big to keep results evident in the graph.

Correlation between the number of all plant species present in heathland patches and the isolation index (Figure 23) was negative and low (the correlation of coefficient (R) was -0.47 and the coefficient of determination (R^2) was 0.22). Therefore less species were found in more isolated heathland patches (smaller numbers of species were found in areas with bigger isolation index).

The log-transformation was a straight line. The regression equation was y = -0.4573x + 1.1386 (Figure 23).

The correlation was statistically significant ($p = 0.010$, Figure 23).

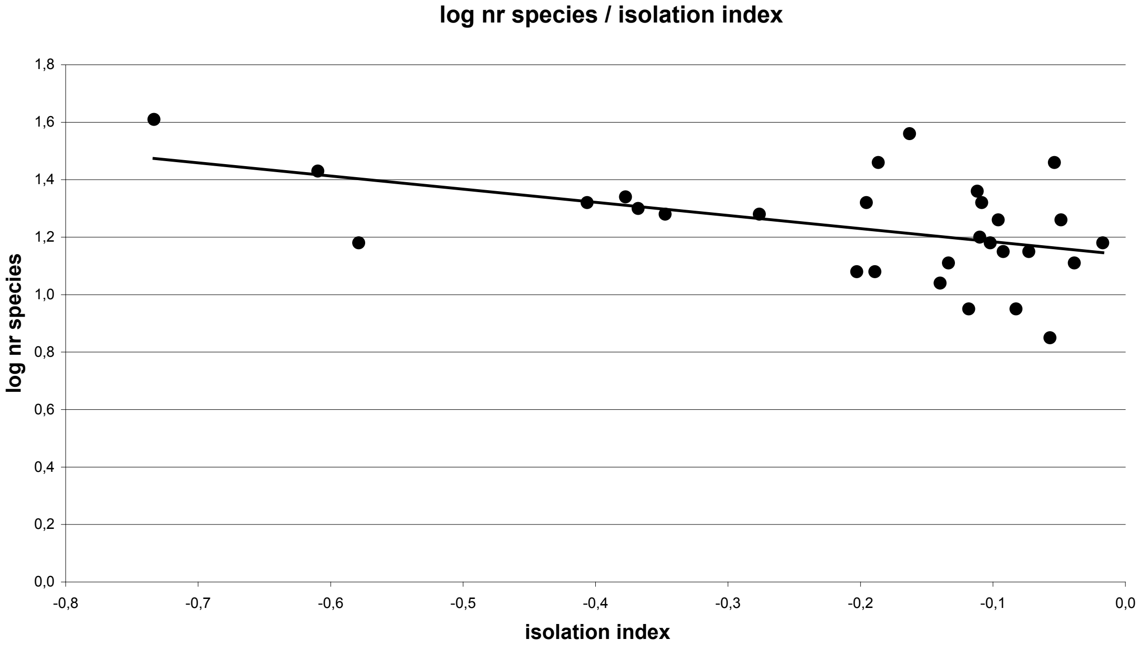

Figure 23: Correlation between the number of plant species and the isolation index of heathland patches in Drenthe, the Netherlands.
Regression equation: $y = -0.4573x + 1.1386$
$R = -0.47$, $R^2 = 0.22$, $p = 0.010$

Negative correlation can again be noted between the Red Listed species present in heathland patches and the isolation index (Figure 24). It means less Red Listed species were found in more isolated areas (the same was true for all species present in areas (Figure 23)). The strength of the correlation was low (coefficient (R) was -0.45) and the coefficient of determination (R^2) was 0.21. The log-transformation was a straight line and the regression equation was y = -0.9508x + 0.4804. The slope was again steeper in the case of the Red Listed species (Figure 24) than in the case of all species present in heathland patches (Figure 23). Similar phenomenon was already noted above with the correlations of number of species present in different area sizes. Any increasing of isolation of the areas lowered species richness for the Red Listed species more strongly than species richness for all of the species together. We can suggest that the Red listed species were more sensitive to area isolation as well as to area reduction.

The correlation was statistically significant (p = 0.013, Figure 24).

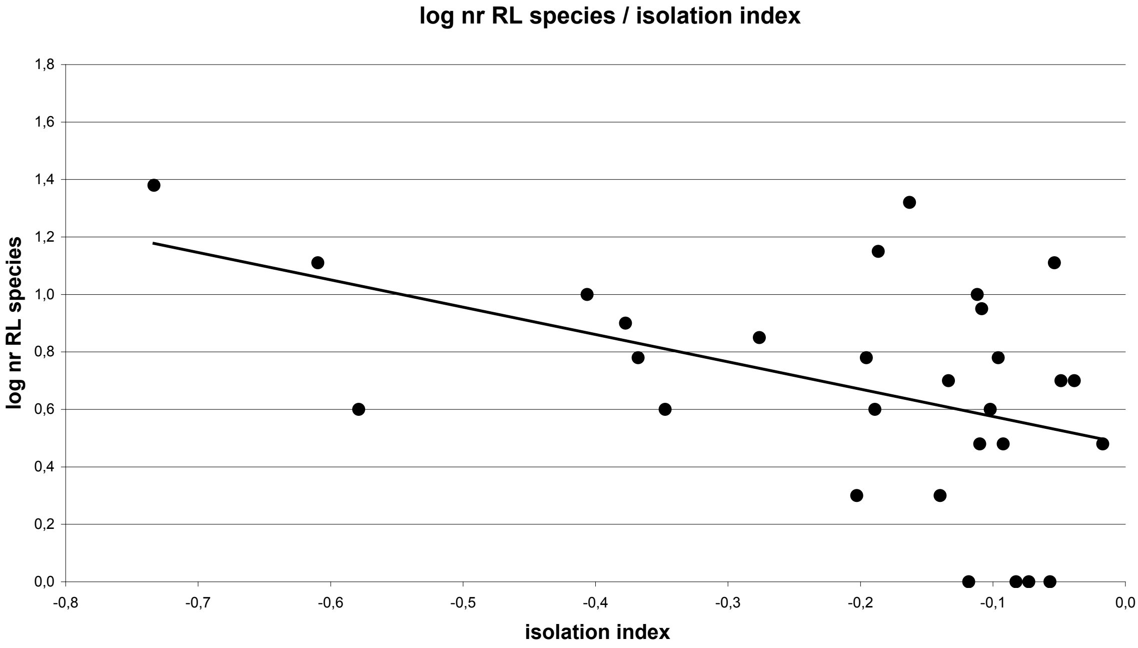

Figure 24: Correlation between the number of the Red Listed plant species and the isolation index of heathland patches in Drenthe, the Netherlands. RL = Red Listed species
Regression equation: y = -0,9508x + 0,4804
R = 0.45, R^2 = 0.21, p = 0.013

Even the proportion of the Red Listed species in relation with isolation showed negative correlation (Figure 25). We could see a trend of decrease in proportions of the Red Listed species when the isolation of areas was increasing; more isolated areas included a lower proportion of the Red Listed species. The strength was low (the correlation of coefficient (R) was -0.41 and the coefficient of determination (R^2) was just 0.17), but still statistically significant ($p = 0.026$).

For linear regression we used the angular transformation ($y=\arcsin(\sqrt{x})$), the same as we did with the correlation of proportion of the Red Listed species and area size. The regression equation was $y = -0.4959x + 0.4654$. We could saw a trend of decrease in proportions of the Red Listed species when the isolation of areas was increasing.

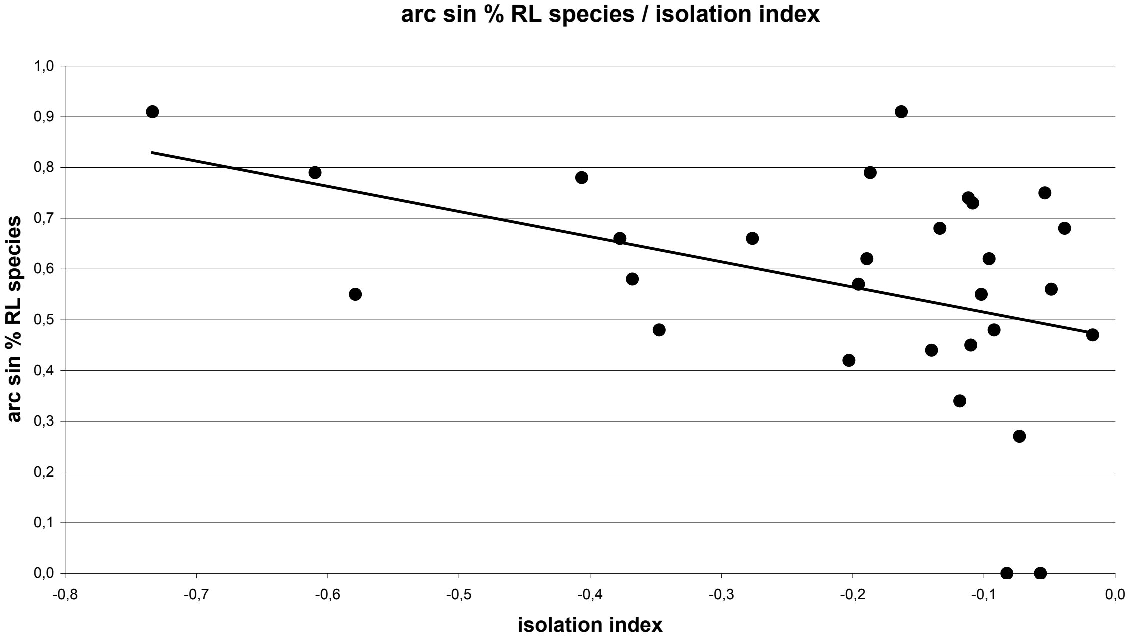

Figure 25: Correlation between the proportion of the Red Listed plant species and the isolation index of heathland patches in Drenthe, the Netherlands. RL = Red Listed species
Regression equation: $y = -0.4959x + 0.4654$
$R = -0.41$, $R^2 = 0.17$, $p = 0.026$

4.3. RESULTS FOR EDGE EFFECT

For a measure of Edge effect we used the perimeter/area ratio (see chapter of methods 3.5. Edge effect). The correlation between the number of species and the perimeter/area ratio was negative (Figure 26). The correlation of coefficient (R) was -0.76 and the coefficient of determination (R^2) was 0.57, which means the correlation was negative and medium. Areas with higher perimeter/area ratio included less Red Listed species than areas with lower perimeter/area ratio. This suggests that the edge effect, for which this ratio is a measure, contributed to the reduced number of species in smaller heathland patches (Figure 26). The same was true for the number of Red Listed species (Figure 27) and the proportion of Red Listed species (Figure 28).

After log-transformation the relationship was linear, the regression equation was:
$y = -0.4846x + 0.5388$ (Figure 26). The correlation was statistically significant ($p \leq 0.001$, Figure 26).

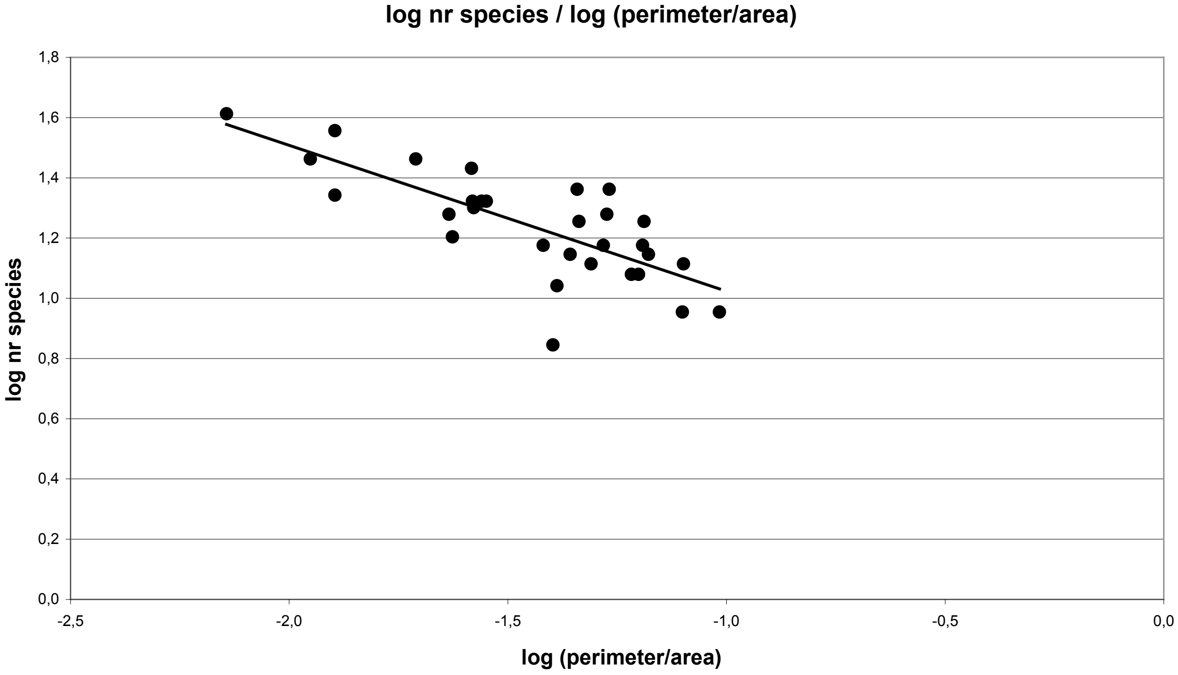

Figure 26: Correlation between the number of plant species and the perimeter/area relation of heathland patches in which they occur in the province of Drenthe, the Netherlands.
Regression equation: $y = -0.4846x + 0.5388$
$R = -0.76$, $R^2 = 0.57$, $p \leq 0.001$

The correlation between the number of the Red Listed species and the perimeter/area ratio was also negative (Figure 27). The correlation of coefficient (R) was -0.68 and the coefficient of determination (R^2) was 0.46, which corresponds again to negative and medium correlation (see the interpretation above).

The regression equation was $y = -0.9409x – 0.6686$. The slope of the regression line for the perimeter/area ratio was steeper for the Red Listed species than for all species present in the particular area. This suggests that enlargement of edge effect affected the Red Listed species more than all species in the particular area.

The correlation was statistically significant ($p \leq 0.001$, Figure 27).

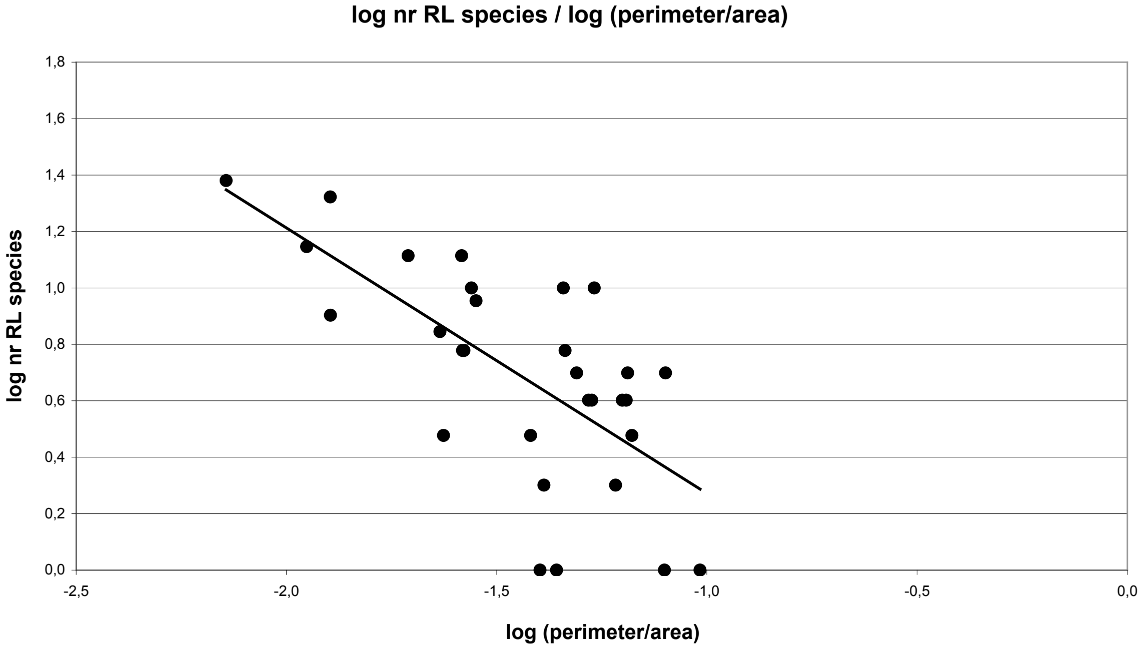

Figure 27: Correlation between the number of the Red Listed plant species and the perimeter/area relation of heathland patches in which they occur in the province of Drenthe, the Netherlands.
RL = Red Listed species
Regression equation: $y = -0.9409x – 0.6686$
$R = -0.68, R^2 = 0.46, p \leq 0.001$

The proportion of the Red Listed species also decreased when the edge effect (perimeter/area ratio) was increasing (Figure 28). The correlation was negative and medium (the correlation of coefficient (R) was -0.55 and the coefficient of determination (R^2) was 0.30). The regression equation was y = -0.4379x – 0.0576. We can conclude that sample areas with higher perimeter/area ratio (which represents higher edge effect of the area) included lower proportion of the Red Listed species.

The correlation was statistically significant (p = 0.002, Figure 28).

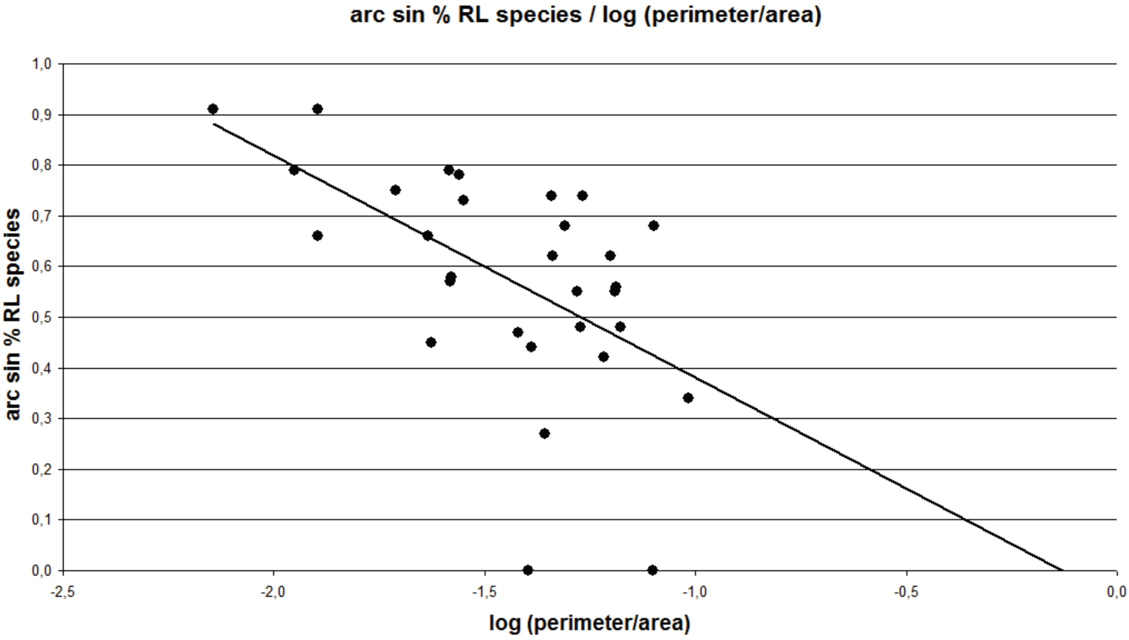

Figure 28: Correlation between the proportion of the Red Listed plant species and the perimeter/area relation of heathland patches in which they occur in the province of Drenthe, the Netherlands.
RL = Red Listed species
Regression equation: y = -0.4379x – 0.0576
R = -0.55, R^2 = 0.30, p = 0,002

5 DISCUSSION

Fragmentation is one of the primary causes for extinction of species in the world (Soule and Wilcox, 1980) and it has been also identified as a major threat to the survival of wild plant populations (Oostermeijer et al., 2003). As the theory of island biogeography (MacArthur and Wilson, 1963, 1967) predicts and as many past studies had confirmed, extinction is a strongly area-dependent process (Soule and Wilcox, 1980) and this was also shown in our study. One consequence of fragmentation is the reduction in the total habitat area or habitat loss, but isolation or redistribution of the remaining area into disjunct fragments is the other consequence of the same process. Both of them contribute to a reduction in the number of species supported (Soulé, 1986; Soulé and Wilcox, 1980). Therefore fragmentation is one of the main causes for many conservation problems. Considering the importance of habitat fragmentation in conservation, many observational and experimental studies refer to the effects of fragmentation in different habitat types and on different plant or animal species within habitats (overviewed in Debinski and Holt, 2000). Due to variable results and because of a considerable lack of consistency in results across taxa, habitat types and experiments (Debinski and Holt, 2000), the topic is still interesting and ambiguous for scientists nowadays. Effects of fragmentation and the species area relationship in general are actually one of the oldest topics that have fascinated ecologists but they are still very important and they still raise many questions.

In short, island biogeographical theory suggests that the number of species on an island represents a dynamical balance between immigration and extinction (MacArthur and Wilson 1963, 1967; Meffe and Carroll, 1997; Whittaker and Fernández-Palacios, 2008). This theory predicts species richness to increase with habitat area and to decrease with isolation from colonization sources (Bruun, 2001). Results of the present study show that the size of the area indeed has a significant effect on the number of species (Figure 20, 21). Thus, even though we are talking about habitat islands in a matrix of unsuitable environment, the results for Dutch heathlands support the equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967), on which our first hypothesis is based. This hypothesis, predicting that there is a positive correlation between the size of heathland patches and the current number of plant species in them, is therefore valid. Larger patches are expected to have a higher diversity of microhabitats and larger populations, as well as their extinction probabilities are lower.

Size of the area was an important determinant of species richness also in many other studies (Kohn and Walsh, 1994; Benedick et al. 2006; Whittaker and Fernández-Palacios, 2008; Rosenzweig, 1995) including in the research of Bruun (2001), where the relationship between species richness and patch area, of patches of grassland and heathland in Denmark were examined, and in the research of Krauss et al. (2004), made on German grasslands patches. In contrast, in research of Piessens et al. (2005), exploring fragmentation effects on remaining heathland patches in Belgium, almost none of the species seemed to be negatively affected by a reduced patch area.

Larger areas contained more species and this was even more significant for the Red Listed species (Figure 21). This shows that also our third hypothesis, predicting that there is a positive correlation between the size of heathland patches and the current number of the plant Red Listed species in them, is valid (Figure 21).

The correlation between the size of heathland patches and species richness (in the case of all species present and in the case of the Red Listed species) presented a linear relationship after logarithmic transformation (Figure 20 and 21). This accords with many other studies that explored species-area relationship (reviewed in Rosenzweig, 1995). Also our *z* values matched the ranges of z values from previous researches of species-area relationship (Thornton, 2007) (Figure 20 and 21). The slope of the regression line for only Red Listed species is steeper than the slope of the line for all heathland species (*z* is higher for the Red Listed species). This implies that any reduction of the area has lowered the number of Red Listed species more strongly (Rosenzweig, 1995). The Red listed species are apparently more vulnerable to area reduction.

In addition, isolation (the other process that affects the equilibrium between immigration and extinction) also seems to have important influence on the number of species, although the correlation of isolation on the number of species was not as strong as the correlation of area (Figure 23 and 24). More isolated fragments contained less heathland species (Figure

23), less Red Listed heathland species (Figure 24) and also had a lower proportion of the Red Listed species (Figure 25). The slope of the regression line for the Red Listed species was steeper than the slope of the regression line for all heathland species (Figure 23 and 24), the same as in the case of species area relation mentioned above. Based on these results we can suggest that the Red Listed species are also more vulnerable to isolation. These results also support the equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967) and confirm our second and forth hypothesis, which predict that there is a negative correlation between the spatial isolation of heathland patches and the current number of plant species (second hypothesis) or Red Listed plant species (forth hypothesis) in them. Here we can note differences between our results and results from Bruun's research, examined on heathlands and grasslands in Denmark. Spatial isolation was not important factor determining species richness in his research (Bruun, 2001). Comparatively, habitat isolation did not have significant effects also in German grasslands (Krauss et al., 2004). On the other side, the effect of isolation was proved in the study of Piessens et al., (2005). They investigated how the fragmentation of Belgium heathland patches affects the distribution patterns of heathland plant species. The result of their study was that the species isolation was the most important factor determining their presence or absence in a heathland patch (64% of heathland species showed a significant negative effect of isolation).

The perimeter/area ratio, in other words the amount of edge relative to the total area of the fragment, showed negative correlation, which implies a negative influence on species richness (Figure 26, 27, 28). This result provides evidence for the existence of edge effects that reduce the amount of available habitat in smaller fragments even more strongly (Sauners, 1991). Such edge effects can be caused by interactions of heathland islands and surrounding matrix, compounded of arable land, forests or meadows. There is energy and nutrient flow between island and matrix, which can affect the species composition, structure and ecological processes in heathland patch (Murcia, 1995).

All the information about how size, isolation or shape of the areas affect species richness become very applicative in design of the nature reserves. How this factors influence population persistence are frequently asked questions in many discussions about reserve design (Meffe and Carroll, 1997). Considering that the biggest sample unit of our research belongs to a natural reserve (Dwingelderveld National Park), our results might be useful for their (or any other reserve including heathland patches) managing or designing.

Natural reserves are one of the solutions often proposed by conservation biologist to enable future development of natural systems in space and time (Kryštufek, 1999). Nevertheless, losses of biodiversity are definitely one of the biggest threats to the nature of the world nowadays (Tome, 2006). The strategy of such natural reserves is the preservation of ecosystems and habitats as a whole, including essential ecological processes and essential components of biodiversity (Kryštufek, 1999). Two of the most fundamental processes of ecosystems are the substance circulation and the energy flow, and living organisms of different species are essential carriers of those two processes (Kos, 2009). Species as their individual traits and interactions therefore contribute to maintain the functioning and stability of the ecosystems and biogeochemical cycles (Loreau et al., 2001). Moreover, scientists are convinced that biological species is one of the closest to the optimal model, which illustrates discontinuity of biodiversity (Kryštufek, 1999). It is believed that more species means bigger biodiversity (Kryštufek, 1999; Tome, 2006). Species richness (as a component of species diversity) is therefore a good 'indicator' of biodiversity and is also very interrelated with other hierarchical levels (like genetic diversity and ecosystem diversity). It was used as a basic unit also in our study. To preserve bigger biodiversity in natural reserves we therefore want to preserve bigger species richness. And what kind of management will be required to retain species richness and to prevent or to overcome ecological imbalance created by fragmentation and other human activities? Effectiveness of reserves is dependent on some basic critical factors, like their size, isolation, or placement of the reserve in the environment, etc. (Kryštufek, 1999). How to design a nature reserve to preserve some necessary level of species richness and to retain natural systems the most effective and stable? These kinds of questions have bothered scientists already for decades. The debate about them is known as the SLOSS-debate (Single Large or Several Small) (Soulé, 1986; Meffe and Carroll, 1997; Wiersma, 2005).

'You will find more species if you sample a larger area' (Rosenzweig, 1995). This observation forms the basis of the species-area relationship and it can also be understood as: you will conserve more species if you conserve a larger area. Others believe that conviction that refuges should always consist of the largest possible area, can be incorrect under variety of biological feasible conditions (Simberloff, 1976). They believe, that several smaller areas, adding up to the same total area as the single large area, are not biogeographically equivalent to it. Consequently, larger areas can tend to support a smaller number of species in total (Simberloff, 1976).

This research demonstrated that size of the area and its isolation (which at the same tine actually means its connectivity) are important factors when considering plant diversity in Dutch heathlands. A larger number of species would be protected, especially the Red Listed species, if we conserve larger and less isolated areas as natural reserves. Results show that also edge effect can negatively affect species richness, thus also the shape of the area is important, which especially affects smaller patches with smaller habitat core. Bigger and more rounded patches will support more species also from this perspective. Of course, it does not imply that smaller patches are not important in the concept of conservation. Based on the negative isolation effects showed in our results, we can conclude that these separated heathland patches are still interconnected (if there would be no connection there would be no correlation between isolation and species richness). And if patches are interconnected, smaller patches can always function as a ‘rescue effect’ to prevent extinction in other surrounded patches as a possible source of colonization. Besides, if we only conserve large areas with large number of species in them, some very rare species that still occur in a number of small fragments would perhaps lose a large fraction of their populations. This would mean a large loss of genetic variation and an increased risk of metapopulation extinction. Moreover, Piessens et al. (2005) were convinced in their study that smaller heathland patches are important. Considering the high importance of isolation of heathland patches in their research (mentioned above), they concluded that for most species even small patches are important for their survival and this is why management and conservation should not focus only on the larger heaths but also on smaller patches. A high connectivity of the patch may increase the species chances of survival.

All the results are valid for heathland; other habitat types may act differently. Land use classes are not equal from biodiversity perspective. The effects of fragmentation may vary across organisms, habitat types and geographic regions (Haila, 2002). Nevertheless, the processes of extinction, colonization, edge effects, inbreeding, etc., that affect populations in fragmented landscape can be similar for habitat types, but not for all individual species. Hence, different species in the group of heathland species (Table 1) may be affected by fragmentation differently, depending on their own characteristics, like their population densities, dispersal abilities (dispersal mode, mean plant height, seed mass and seed number) or traits that determine the persistence of species (seed longevity, growth form, self compatibility and vegetative propagation) (Soulé, 1986; Piessens at al., 2005). In this research only general species richness was estimated, we have not looked at the identity of the species. We must not forget, that regression analysis we used in the research estimates the conditional expectation of the dependent variable given the independent variables — that is, the *average value* of the dependent variable when the independent variables are held fixed.

Results may also support calculations for predictions for the loss of species from fragmented landscapes. We agree with a thought: '…Rather than asking how many species will be lost if a landscape is fragmented, the question can be turned around to as how many species will be gained by protected area network if more landscape is added to the network' (Desmet and Cowling, 2004).

6 CONCLUSIONS

- There is a positive correlation between the size of the heathland patches in Drenthe, the Netherlands, and the current number of plant species in them. After logarithmic transformation the power model presents linear relationship, with z = 0'16.

- There is a negative correlation between the spatial isolation of the heathland patches in Drenthe, the Netherlands, and the current number of plant species in them.

- There is a positive correlation between the size of the heathland patches in Drenthe, the Netherlands, and the current number of the plant Red Listed species in them. After logarithmic transformation the power model presents linear relationship, with z = 0'30.

- There is a negative correlation between the spatial isolation of the heathland patches in Drenthe, the Netherlands and the current number of the plant Red Listed species in them.

- There is a negative correlation between the perimeter/area ratio (which is a measure for edge effect) and the number of plant species in heathland fragmented patches in Drenthe, the Netherlands.

- There is a negative correlation between the perimeter/area ratio (which is a measure for edge effect) and the number of the Red Listed plant species in the heathland fragmented patches in Drenthe, the Netherlands.

7 SUMMARY

7.1. SUMMARY

Fragmentation, the loss and isolation of natural habitats, are threats to regional and global biodiversity. This research focused on the effects of fragmentation on the plant diversity in the heathlands in Drenthe, a north-east province of the Netherlands. The relationship between the number of plant species and the size of the patch area and the relationship between the number of plant species and the spatial isolation were examined.

It was hypothesized that (1) the size of heathland patches is positively related to the current number of plant species thriving there, (3) the size of heathland patches is positively related to the current number of plant Red Listed species thriving there (2) the spatial isolation of heathland patches is negatively related to the current number of plant species thriving there and that (4) the spatial isolation of heathland patches is negatively related to the current number of plant Red Listed species thriving there.

The data about the number of species used in the research were taken from the floristic inventory scheme of the Netherlands gathered by both professional and amateur/volunteer botanists, coordinated by the foundation FLORON.

The analyses revealed a positive correlation between the number of species (and the number of the Red Listed species) and the size of the area and a negative correlation between the number of species (and the number of the Red Listed species) and the spatial isolation Moreover, the amount of edge relative to the area of the fragment (edge effect) also shows a negative relation to the number of species present in the area.

7.2. POVZETEK

Drobljenje, izgubljanje in izoliranje habitatov dandanes predstavljajo temeljno grožnjo regionalni in globalni biodiverziteti (Meffe and Carroll, 1997). Medtem ko naravne motnje lahko ustvarjajo heterogene pokrajine z bogato vrstno pestrostjo, človeški posegi v naravo pogosto pustijo za seboj le fragmente oziroma otoke naravnih habitatov (Meffe and Carroll, 1997). Ti otoki so ločeni med seboj z novonastalim habitatom (t.i. matriksom), ki je drugačen od prvotnega. Proces nastajanja takšnih otokov imenujemo fragmentacija. Je proces, v katerem večji in sklenjeni habitat preide v več izoliranih fragmentov z manjšo skupno površino. Kryštufek (1999) razlaga: ‘Kadar matriks vrstam prvotnega habitata ne omogoča preživetja, potem fragmenti postanejo otoki z vsemi posledicami, ki izhajajo iz modela otoške biogeografije.’

Fragmentacija ima namreč dve glavni posledici: prva je zmanjševanje prvotnega habitata, kar prizadene dejansko velikost populacij in s tem vpliva na stopnjo izumiranja. Druga posledica je izolacija preostalih fragmentov, kar vpliva predvsem na zmanjšano disperzijo med njimi in s tem na stopnjo imigracije oz. naseljevanja. Oba učinka povzročata zmanjševanje števila vrst prisotnih v določenem območju (Soulé, 1986; Soulé and Wilcox, 1980). Odnose med številom vrst, naseljevanjem in izumiranjem sta MacArthur in Wilson (1963, 1967) razložila z modelom otoške biogeografije znan tudi kot model dinamičnega ravnotežja (Kryštufek, 1999). Po tej teoriji je število vrst na posameznem otoku posledica ravnotežja med dvema nasprotnima si procesoma: izumiranjem in naseljevanjem oz. imigracijo.

Fragmentacija predstavlja danes enega izmed glavnih problemov varstva narave. Veliko dosedanjih raziskav je bilo narejenih na področju vplivov fragmentacije na različne habitatne tipe in na različne tamkaj prisotne živalske in rastlinske vrste (Debinski and Holt, 2000). Rezultati so zelo raznoliki, zato fragmentacija ostaja aktualen problem današnjih znanstvenikov.

Pri naši diplomski nalogi smo se osredotočili na vplive procesa fragmentacije na vrstno bogastvo nizozemskih resav. Glavni namen je bil ugotoviti kakšen vpliv ima velikost površine in stopnja izoliranosti habitata na rastlinsko pestrost nizozemskih resav. Zgoraj omenjena teorija otoške biogeografije (MacArthur and Wilson, 1963, 1967) predvideva, da vrtno bogastvo narašča s povečano površino habitata in da vrstno bogastvo upada s povečano izoliranostjo od drugih kolonizacijskih virov (Bruun, 2001). Na osnovi teorije otoške biogeografije smo postavili štiri hipoteze:

1. Med velikostjo resavskega območja in številom prisotnih vrst je pozitivna korelacija.
2. Med stopnjo izoliranosti resavskega območja in številom prisotnih vrst je negativna korelacija.
3. Med velikostjo resavskega območja in številom prisotnih vrst z Rdečega seznama je pozitivna korelacija.
4. Med stopnjo izoliranosti resavskega območja in številom prisotnih vrst z Rdečega seznama je negativna korelacija.

Hipoteze smo preverjali na preostalih fragmentih resavskih območij v severovzhodni provinci Drenthe na Nizozemskem.

Za preverjanje hipotez smo potrebovali podatke o velikosti posameznih območij, podatke o številu prisotnih vrst, podatke o številu prisotnih vrst z Rdečega seznama in stopnjo izolacije območij.

Informacije o velikost resavskih območij smo pridobili iz elektronske topografske mape Nizozemske (TOP10vector).

Podatke o številu vrst na izbranih območjih smo pridobili iz Nizozemske floristične baze podatkov koordinirane s fundacijo FLORON, ki zbira podatke s pomočjo amaterskih in profesionalnih botanikov. Podatki so zbrani v t.i. mreži, velikosti 1km x 1km, imenovani EcoGRID.

Iz celotne baze podatkov smo izvzeli 64 rastlinskih resavskih vrst (Tabela 1), ki se nahajajo na tamkajšnjih območjih. 44 od 64 vrst pripada Rdečemu seznamu vaskularnih rastlin Nizozemske (van der Meijden *et al.*, 2000). Mrežo s podatki resavskih vrst (1km x 1km) smo nato povezali s posameznimi območji fragmentov resav (Slika 15). Ta povezava ni bila vedno preprosta, saj lahko več območij resav pripada enemu samemu kvadrantu mreže in je nemogoče določiti, kateremu območju pripada določena vrsta s seznama. Iz tega razloga smo se odločili za združitev posameznih resavskih območij (bližjih od 500m) v večje enote. Nekatere enote tudi po združitvi niso bile združljive s seznamom, zato smo jih izločili iz nadaljnjih opazovanj. Izločili smo tudi tiste enote, katere so vsebovale le podatke o prisotnih vrstah iz popisov, izvedenih pred 1990. Po selekciji nam je ostalo 30 osnovnih operativnih enot (Slika 18 in 19), katere so bile vključene v nadaljnjo analizo.

Stopnjo izolacije smo ocenili s pomočjo izolacijskega indeksa (Hanski, 1994, enačba 3), katero je uporabil v svoji raziskavi tudi Bruun (2001, enačba 4), izvedeno na resavskih in travniških območjih na Danskem.

Preverili smo tudi ali razmerje med obsegom in površino določenega območja, kar predstavlja t.i. robni efekt, vpliva na vrstno bogastvo.

Meritve in obdelave podatkov smo izvedli s pomočjo programov, kot so ArcView, ArcMap, ArcInfo, Microsoft Excel in SPSS. Statistične analize so vključevale linearno regresijo.

Rezultati so pokazali, da je med velikostjo resavskega območja in številom vrst prisotnih znotraj njega pozitivna korelacija, kar je potrdilo prvo hipotezo in je podprlo teorijo otoške biogeografije (MacArthur and Wilson 1963, 1967) (Slika 20). Ravno tako je bila pozitivna korelacija opazna med velikostjo resavskega območja in številom prisotnih vrst z Rdečega seznama (Slika 21). Ta rezultat je potrdil tudi tretjo hipotezo. Razmerje med velikostjo območja in številom vrst (ter številom vrst z Rdečega seznama) je prikazalo eksponenten odnos oz. po logaritemski transformaciji linearen odnos, kar se sklada s sorodnimi raziskavami (Rosenzweig, 1995) (Slika 20, 21). Tudi naklon linearne linije (z) lahko umestimo znotraj mejnih vrednosti, ki so bile predstavljene v preteklih raziskavah

(Rosenzweig, 1995). Naklon regresijske linije v primeru vrst z Rdečega seznama (Slika 21) je bil večji od naklona regresijske linije v primeru vseh vrst prisotnih na resavskem območju (Slika 20). Z drugimi besedami, *z* je bil višji v primeru vrst z Rdečega seznama, kot v primeru vseh prisotnih vrst. To nakazuje, da bi zmanjšanje površine določenega območja povzročilo večje zmanjšanje števila vrst z Rdečega seznama kot števila vseh prisotnih vrst. Lahko sklepamo, da so vrste z Rdečega seznama bolj občutljive na zmanjševanje površine habitatov.

Razmerje med stopnjo izolacije in številom prisotnih vrst (Slika 23), in tudi številom vrst z Rdečega seznama (Slika 24), je prikazalo negativno korelacijo. Z logaritemsko transformacijo smo dobili linearen odnos. Ta rezultat je potrdil tudi tretjo in četrto hipotezo in ponovno podpira teorijo otoške biogeografije (MacArthur and Wilson 1963, 1967). Tudi v primeru izolacije je bil naklon regresijske linije strmejši v primeru vrst z Rdečega seznama kot v primeru vseh prisotnih rastlinskih vrst, kar kaže na večjo občutljivost vrst z Rdečega seznama tudi na izolacijo.

Tudi razmerje med obsegom in površino določenega območja (kar predstavlja t.i. robni efekt) je pokazalo negativno korelacijo s številom prisotnih vrst v resavskem območju (Slika 26). Negativna korelacija je veljala tudi za razmerje med obsegom in površino določenega območja in številom prisotnih vrst z Rdečega seznama (Slika 27). Ta rezultat kaže na negativni vpliv robnega efekta na vrstno pestrost.

Vsi rezultati se nanašajo na resavska območja, drugi habitatni tipi se lahko odzivajo drugače na spremembe velikosti in izoliranosti območja ter na robni efekt. Tudi različne vrte znotraj skupine resavskih vrst se lahko odzivajo drugače na fragmentacijo, glede na njihove lastnosti, kot so populacijske gostote, disperzijske sposobnosti (npr. število in masa semen, povprečna višina rastlin ali oblika disperzijskih elementov) ter 'trdoživost' samih vrst (dolgoživost semen, rastne oblike, vegetativno razmnoževanje ipd.) (Soulé, 1986; Piessens et al., 2005).

Vse informacije o tem, kako velikost, izoliranost, oblika in umeščenost nekega fragmenta v okolje vplivajo na vrstno pestrost (in s tem na celotno biodiverziteto), lahko postanejo uporabne pri načrtovanju in oblikovanju naravnih rezervatov (Meffe and Carroll, 1997). Glede na to da je naša največja vzorčna enota pripadala naravnemu rezervatu Dwingelderveld (Dwingelderveld National Park), bi lahko bili naši rezultati uporabni pri njihovem načrtovanju in upravljanju. Seveda so rezultati lahko uporabni tudi za katerikoli drugi naravni rezervat z resavami.

O tem, kako naj bi bili oblikovani naravni rezervati, že dolgo poteka diskusija, imenovana SLOSS (Single Large or Several small) (Soulé, 1986; Meffe and Carroll, 1997; Wiersma, 2005), ki še vedno ni pripeljala do poenotenja stališč (Kryštufek, 1999). Glavni namen diskusije je ugotoviti, kaj je bolje: en velik rezervat ali več manjših z enako skupno površino. Naši rezultati vsekakor potrjujejo pomembnost velikosti zaščitenih območij za ohranjanje vrstnega bogastva. Večja območja navadno vsebujejo več vrst. Tudi robni efekt kaže na to, da bodo večja območja (ki imajo manjše razmerje med obsegom in površino) in bolj zaokrožena območja (z večjim jedrom osnovnega habitata) vrstno bolj bogata. Vsekakor pa to ne pomeni, da manjši fragmenti niso pomembni v varstvu narave. Glede na to, da v naši raziskavi izolacija kaže na negativni vpliv na vrstno pestrost, lahko sklepamo, da so posamezna resavska območja še vedno povezana med seboj. Manjša območja so torej lahko pogosto ‘rešilna bilka’ za ponovno naseljevanje že izumrlih vrst sosednjih območij in lahko zmanjšujejo izumiranje metapopulacij. Seveda bi izgubljanje manjših območij pomenilo tudi izgubljanje genske raznolikosti prisotnih metapopulacij, ki so vir pestrosti celotne populacije neke vrste.

Rezultati bi lahko bili uporabni tudi, kadar želimo predvideti, kolikšno izgubo vrstne pestrosti bodo utrpela fragmentirana območja. Tukaj bi se strinjali z Desmetom in Cowlingom (2004), ki pravita, da bi se bilo bolje vprašati koliko vrst bo pridobljenih z dodajanjem novih območij v mrežo zavarovanih delov narave, kot da se sprašujemo, koliko vrst bo izgubljenih s fragmentacijo določenih območij.

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ANNEX

Annex A: The results of measurements and calculations of final 30 patches (Figure 19)

nr – the number of a sample unit, **name** - the name of the sample unit, **nr patches** - the number of patches included in the sample unit, **kmxkm** - the number of grid cells (km x km) that belongs to the sample unit, **perimeter (m)/area (m^2)** - the ratio of perimeter of sample unit and area of sample unit, **nr species** - the number of species present in a sample unit, **nr species RL** - the number of the Red Listed species present in a sample unit, **% RL species** – proportion of the Red Listed species present in a sample unit, **isolation index** – isolation index (Bruun 2001)

nr	name	perimeter [m]	area [m^2]	area [ha]	perimeter(m) / area(m^2)	nr patches	kmxkm
1	1	1398,73	17640,77	1,76	0,08	5	4
2	2	381,34	4782,49	0,48	0,08	1	1
3	3	8999,48	204910,85	20,49	0,04	14	4
4	5	8031,07	148813,40	14,88	0,05	18	5
5	6	1760,78	33655,30	3,37	0,05	5	2
6	7	190,09	1972,90	0,20	0,10	1	1
7	8	909,37	23866,81	2,39	0,04	2	1
8	9	34092,44	1749623,70	174,96	0,02	45	17
9	-17	110559,63	15373776,63	1537,38	0,01	88	42
10	-27	4182,45	91763,45	9,18	0,05	8	3
11	27	331,41	8261,38	0,83	0,04	1	1
12	40	506,10	9499,82	0,95	0,05	2	2
13	42	3843,61	301964,73	30,20	0,01	3	2
14	43	17530,06	1377555,85	137,76	0,01	8	10
15	44	3358,98	128627,60	12,86	0,03	6	4
16	45	1457,76	22675,60	2,27	0,06	1	1
17	48	39789,91	3559635,72	355,96	0,01	21	21
18	56	5011,80	77301,20	7,73	0,06	7	2
19	61	972,51	15443,37	1,54	0,06	2	2
20	62	554,73	11318,07	1,13	0,05	2	1
21	71	13775,18	594051,91	59,41	0,02	13	7
22	-72	588,10	22247,27	2,22	0,03	1	2
23	73	6060,02	230918,60	23,09	0,03	6	3
24	74	1574,40	38417,60	3,84	0,04	4	1
25	75	763,55	12587,11	1,26	0,06	1	1
26	76	687,07	14935,13	1,49	0,05	1	2
27	77	2084,57	88192,71	8,82	0,02	2	1
28	78	4315,59	152792,79	15,28	0,03	9	4
29	79	902,94	13607,65	1,36	0,07	3	2
30	83	4795,65	174121,93	17,41	0,03	8	5

nr	name	nr species	nr species RL	% RL species	last observation	isolation index
1	1	9	0	0,000	1999	-0,08247153
2	2	13	5	0,385	2001	-0,13352599
3	3	14	1	0,071	1993	-0,07281582
4	5	23	10	0,435	2002	-0,11177068
5	6	15	4	0,267	1996	-0,10194865
6	7	9	1	0,111	1993	-0,11827608
7	8	15	3	0,200	1990	-0,01700194
8	9	29	13	0,448	2001	-0,05353357
9	-17	41	24	0,585	2002	-0,73334398
10	-27	23	10	0,435	1995	-4,34872270
11	27	7	0	0,000	1992	-0,05683769
12	40	19	4	0,211	1999	-0,34734191
13	42	22	8	0,364	2001	-0,37727472
14	43	36	21	0,583	2001	-0,16287666
15	44	27	13	0,481	1994	-0,60959614
16	45	15	4	0,267	1990	-0,57875151
17	48	29	14	0,483	2000	-0,18656965
18	56	18	5	0,278	1994	-0,04855196
19	61	12	4	0,333	2002	-0,18906117
20	62	13	5	0,385	1990	-0,03846149
21	71	19	7	0,368	2000	-0,27631112
22	-72	20	6	0,300	1994	-0,36778272
23	73	21	6	0,286	1995	-0,19546652
24	74	11	2	0,182	1990	-0,13988065
25	75	12	2	0,167	1992	-0,20279952
26	76	18	6	0,333	2002	-0,09599811
27	77	16	3	0,188	1991	-0,10990818
28	78	21	9	0,429	1998	-0,10836245
29	79	14	3	0,214	1991	-0,09217765
30	83	21	10	0,476	1995	-0,40633627