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Spatial and temporal patterns in the plant community composition of fragmented heathlands

Promotor:
Prof. M. Hermy, K.U.Leuven
Prof. O. Honnay, K.U.Leuven

Leden van de examencommissie:
Prof. G. Volckaert, K.U.Leuven, voorzitter
Prof. H. Gulinck, K.U.Leuven
Prof. R. Marrs, University of Liverpool
Dr. H. Stieperaere, Nationale Plantentuin van België

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Katrien PIESSENS

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SAMENVATTING

De vernietiging van (half-)natuurlijke habitats, en de daaraan gekoppelde fragmentatie, vormt wereldwijd één van de belangrijkste bedreigingen voor biodiversiteit. De verkleinde oppervlakte en de sterke graad van isolatie van de overblijvende delen van deze (half-)natuurlijke habitats, leidt, samen met hun toegenomen hoeveelheid rand, tot veranderingen in de plantengemeenschap die in het habitatfragment aanwezig is. Een voorbeeld van zo'n halfnatuurlijk habitat is heide. Heide nam vroeger aanzienlijke oppervlaktes van het landschap in in gebieden op arme, zure zandgronden, en vormde er een belangrijk onderdeel van het traditionele landbouwsysteem. Door de toegenomen intensivering van de landbouw verloor heide echter zijn economisch belang. Samen met de toegenomen industrialisering en verstedelijking leidde dit tot een sterke achteruitgang van het heide-areaal over heel West-Europa. De gevolgen van deze ver doorgedreven fragmentatie voor de heideplantengemeenschap zijn nog slechts weinig onderzocht. Het doel van dit onderzoek was dan ook om na te gaan hoe fragmentatie de verschillende aspecten van de heideplantengemeenschap beïnvloedt.

Voor de heidegebieden in de Noordvlaamse veldzone (noord-westen van België) werd het fragmentatieproces gereconstrueerd aan de hand van verschillende historische kaarten. Uit deze analyse bleek dat in deze regio minder dan 1% van het heide-areaal aanwezig in 1775, overblijft. Ondanks deze drastische areaalsreductie gaf de studie van historische gegevens over de verspreiding van plantensoorten in het gebied aan dat het verlies aan typische heideplantensoorten relatief beperkt was. 11% van de heidesoorten is uitgestorven in deze tijdspanne. Dit relatief lage extinctie-cijfer kan wijzen op de aanwezigheid van een 'extinction debt', waardoor de effecten van heidefragmentatie nog niet volledig tot uiting gekomen zijn. Bijgevolg kan men verwachten dat in de toekomst nog meer soorten zullen uitsterven, tenzij de omgevingsomstandigheden verbeterd worden door heideherstel en verder oppervlakteverlies van heide voorkomen wordt.

De studie van de plantengemeenschap van de individuele heidefragmenten wees echter op een sterke relaxatie van de heideflora als gevolg van fragmentatie. Ook het voorkomen van ongeveer drie kwart van de heidesoorten werd door fragmentatie

beïnvloed. Hoewel een positieve soort-oppervlakte relatie werd gevonden, bleek isolatie een veel belangrijkere factor te zijn voor veranderingen in soortenrijkdom en soortensamenstelling van de heiderelicten. Ook voor de verspreidingspatronen van individuele heidesoorten was isolatie de voornaamste determinerende factor. Het uitsterven van soorten in fragmenten als gevolg van een verkleinde oppervlakte wordt dus blijkbaar voorkomen door de verbreiding van soorten uit nabijgelegen percelen, het zogenaamde 'rescue-effect'. De beperkte invloed van oppervlaktebepaalde extinctieprocessen wijst op het belang van het behoud van zelfs de kleinste heidefragmenten voor de instandhouding van een zo divers mogelijke heideflora in een bepaalde regio. Bovendien dragen deze kleine fragmenten ook bij tot een verhoogde onderlinge verbinding van de heiderelicten.

Niet alle heidesoorten bleken even gevoelig te zijn voor fragmentatie. Vooral de mogelijkheid tot het opbouwen van een persistente zaadbank verhoogt sterk de overlevingskansen van heideplanten in een sterk gefragmenteerd heidelandschap. De zaadbank buffert de soort tegen uitsterven en kan dus beschouwd worden als een 'rescue effect' in de tijd. Bij het uitstippelen van maatregelen voor heidebehoud en –herstel dient bijgevolg vooral aandacht besteed te worden aan soorten met een kortlevende zaadbank omdat deze soorten het sterkst bedreigd worden door verdere fragmentatie van de heidegebieden.

Als gevolg van een verkleinde oppervlakte hebben gefragmenteerde habitats een relatief grotere hoeveelheid rand vergeleken met continue habitats, wat aanleiding kan geven tot de aanwezigheid van randeffecten. Gegevens om randeffecten te onderzoeken worden meestal verzameld via transecten. De meeste studies over randeffecten houden echter geen rekening met de intrinsieke eigenschappen van transectgegevens. Daarom werd hier het gebruik van linear mixed models voorgesteld als een geschikte benadering voor dit soort gegevens. Hiermee werden significante veranderingen in de abiotische omstandigheden en in de heideplantengemeenschap in de buurt van de rand vastgesteld. In deze zone waren de typische heidesoorten, aangepast aan nutriëntarme, zure omstandigheden nog wel aanwezig, maar is de dominantie er door nutriëntaanrijking verschoven naar soorten kenmerkend voor meer nutriëntrijke omstandigheden. Bij akkers als aangrenzend landgebruik was deze verhoging van het nutriëntengehalte meer uitgesproken dan bij bossen, en werd de karakteristieke dwergstruikvegetatie bijna volledig verdrongen door grassen en soorten typisch voor meer voedselrijke omstandigheden.

Terwijl deze effecten voor de hogere plantensoorten merkbaar waren tot 8m in het heidefragment, waren de randeffecten op de mosvegetatie beperkt tot 2m. Een opmerkelijk randeffect op de mosvegetatie was de verhoogde dominantie van de invasieve soort *Campylopus introflexus* in deze randzone. Daar deze soort een belangrijke bedreiging vormt voor de inlandse mosflora in oligotrofe systemen zoals heiden, dient hiermee zeker rekening gehouden te worden. Hoewel beheer een belangrijke invloed had op de samenstelling van de moslaag, domineerden de effecten van naburig landgebruik, wat er op wijst dat het niet mogelijk is om via een aangepast beheer randeffecten te beperken.

Niet alleen de hoge graad van fragmentatie vormt een belangrijke bedreiging voor het voortbestaan van heidevegetaties. Heidegebieden kunnen enkel overleven als ze ook nog voldoende en op de juiste manier beheerd worden. De huidige hoge niveau's van vermestende en verzurende depositie verhogen deze nood aan aangepast beheer nog. Een veel gebruikte beheersmethode in het huidige natuurbeheer is extensieve begrazing. In het natuurreservaat 'De Maten', één van de belangrijkste heidegebieden in Vlaanderen, is men er met extensieve begrazing grotendeels in geslaagd om over een periode van 25 jaar een diverse en soortenrijke heide in stand te houden. Toch slaagde een lage begrazingsintensiteit er niet in om een hogere bedekking van *Molinia caerulea* en een hogere frequentie van zaailingen van bomen en struiken te voorkomen, wat er op wijst dat een occasioneel bijkomend mechanisch beheer nodig is om vergrassing en successie naar bos tegen te gaan.

SUMMARY

The destruction of (semi-)natural habitats, together with the resulting fragmentation, currently is one of the major threats to biodiversity worldwide. The reduced area and the high degree of isolation of the remaining parts of these (semi-)natural habitats, together with the increased relative amount of edge, can result in changes in the plant community present in the habitat patch. An example of such a semi-natural habitat is heathland. Heathlands used to be present over large areas in regions characterised by nutrient poor, acid soils, and historically formed an important component of the traditional agricultural system. However, due to agricultural intensification heathland lost its economical importance. Together with the increased industrialisation and urbanisation this resulted in a serious decline of the heathland area throughout the whole of western Europe. The consequences of this severe fragmentation on the heathland plant community have hardly ever been studied before. Therefore, the aim of this research was to investigate the effects of fragmentation on the different aspects of the heathland plant community.

For the heaths in north-western Belgium the fragmentation process was reconstructed based on the available historical maps. From this analysis it could be concluded that in this region less than 1% of the heathland present on the map of 1775 currently remains. Despite this serious area reduction, the study of historical data on plant distribution patterns revealed the loss of heathland plant species to be rather limited. 11% of the species characteristic for heathland has gone extinct in this time span. The relatively low extinction number can point at the existence of an extinction debt and the effects of habitat loss may not have fully manifested yet. Consequently, future extinctions are expected to occur unless environmental conditions are improved through heathland restoration and further heathland area losses are prevented.

However, the study of the plant community of the individual heathland patches revealed a strong relaxation of the heathland flora as a result of fragmentation. Furthermore, the incidence of about three quarters of the heathland plant species was influenced by fragmentation. Although evidence was found for a positive species-area relation, patch isolation turned out to be much more important than area in explaining changes in species richness and plant community composition of the heathland relics.

Isolation was also the prime factor in determining the distribution patterns of individual heathland species. Consequently, the extinction of species due to a reduced patch area is probably prevented through dispersal of species from neighbouring patches, a process known as the rescue-effect. The limited importance of area-dependent extinction processes points at the importance of preserving even the smallest heathland patches to assure the conservation of a diverse heathland flora in a region. Additionally, these small patches enhance the connectivity between the heathland patches.

Our analyses showed large differences in fragmentation sensitivity between the different heathland plant species. Especially the ability to build up a persistent seed bank strongly augments the chances of survival of heathland plant species in severely fragmented heathland areas. The seed bank acts as a sort of buffer against extinction and hence can be considered as a rescue effect in time. Consequently, heathland conservation and restoration measures should be primarily aimed at species with a transient or short term persistent seed bank as these species are threatened most by ongoing heathland fragmentation.

As a result of a reduction in area, fragmented habitats show a relatively large amount of edge compared to intact habitats. Data to examine edge effects are generally gathered using transects. However, most studies on edge effects fail to take into account the intrinsic nature of transect data. Therefore, linear mixed modelling was presented to approach this. Significantly altered abiotic conditions and changes in the heathland plant community in the vicinity of the edge were detected. Characteristic heathland plant species, adapted to nutrient poor, acid conditions were still present there, but eutrophication caused a shift in dominance to species characteristic for more nutrient rich situations. Eutrophication effects of cropland on the heathland vegetation and soil were more pronounced than those of adjacent forest, and have resulted in an almost complete replacement of the characteristic dwarf shrub vegetation by grasses and species characteristic for nutrient-rich habitats in the edge zone.

For vascular plant species these effects were present up to 8m into the heathland patch. Effects on the bryophyte layer on the other hand were limited to 2m. One remarkable edge effect in the bryophyte layer was the increased dominance of the invasive species *Campylopus introflexus* in the edge zone. Since this species forms a major threat to native bryophyte species in oligotrophic systems like heathland, this should certainly be taken into account. Although management turned out to be an important factor for the composition of the bryophyte layer, effects of adjacent land use predominated on management effects. Consequently, management cannot act as a tool to mitigate edge effects on bryophyte species in heathlands.

Fragmentation is not the only factor threatening the survival of heathlands. Heathland areas can only sustain when they are properly managed. The present-day high levels of nitrogen deposition and acidification further increase the need for proper management. Extensive grazing is frequently applied in current heathland management. In the nature reserve ‘De Maten’, one of the most important heathland areas in Flanders, extensive grazing has succeeded in preserving a diverse and species rich heathland flora over a 25-year period. However, a low grazing intensity was not able to fully prevent an increased cover of *Molinia caerulea* and a higher presence of shrub and tree species, which pointed at the need of occasional mechanical management to prevent grass encroachment and succession to forest.

CHAPTER 1

INTRODUCTION

Heathland and heathland decline

In large parts of Atlantic Western Europe, heathland is one of the principal semi-natural landscape types and traditionally formed an important component of the landscape (Webb, 1998; De Blust, 2004). Heathland developed about 4000 years ago through human-induced forest degradation and clearing. Subsequently, this land was incorporated into the traditional agricultural systems and formed an important part of it. Heathland was primarily used for grazing and was also cut for fodder or litter in the stable, where it could absorb the excrements of the animals. This material was used afterwards as manure on the fields, giving rise to the so-called plaggen soils (Diemont, 1996; Webb, 1998; Burny, 1999; De Blust, 2004). In Flanders however, the latter are only known from the Campine region (De Beelde, 2003). To maintain a young heathland containing sufficient nutrients both for grazing animals and attractive for bees (honey-production), it was burned regularly. In wet heathlands, sods were cut to be used as fuel (Webb, 1998; Burny, 1999; De Blust, 2004). This intensive use of the heath not only prevented the natural regeneration of forest but also the conversion to other land use types (De Blust, 2004; Verboven et al., 2004).

However, from the end of the 18th century onwards, heathland gradually lost its economical importance due to changes in agricultural practices, and was reclaimed or afforested. Additionally, industrialisation and urbanization further led to a decrease of the remaining heathland area (Gimingham, 1976; Webb, 1998; De Blust, 2004; Haaland, 2004). Consequently, the remaining heathland is very fragmented. It is scattered throughout the landscape in small patches surrounded by other land use types. A well known example of this process of heathland decline and fragmentation is the heathland area of Poole Basin in Dorset (United Kingdom) (Fig. 1.1) (Moore, 1962; Webb and Haskins, 1980).

Next to this quantitative decline in heathland area, many heathlands have also deteriorated qualitatively. Since heathlands are restricted to nutrient poor, relatively acid soils, the current rates of atmospheric deposition (in Flanders on average 45 kg N ha^{-1} yr^{-1} (Overloop et al., 2004)) pose a severe threat on this habitat, often resulting in the dominance of grass species such as *Molinia caerulea* or *Deschampsia flexuosa* (e.g. Bobbink et al., 1998; Lee, 1998; Bobbink and Lamers, 2002). In addition, lack of management frequently results in shrub and tree encroachment (e.g. Mitchell et al., 1997; De Bruyn, 2003; De Blust, 2004). Therefore, intact heathlands are now considered as areas of high nature conservation value, which are important both for their biodiversity and as relics of a formerly widespread cultural landscape (Webb, 1998).

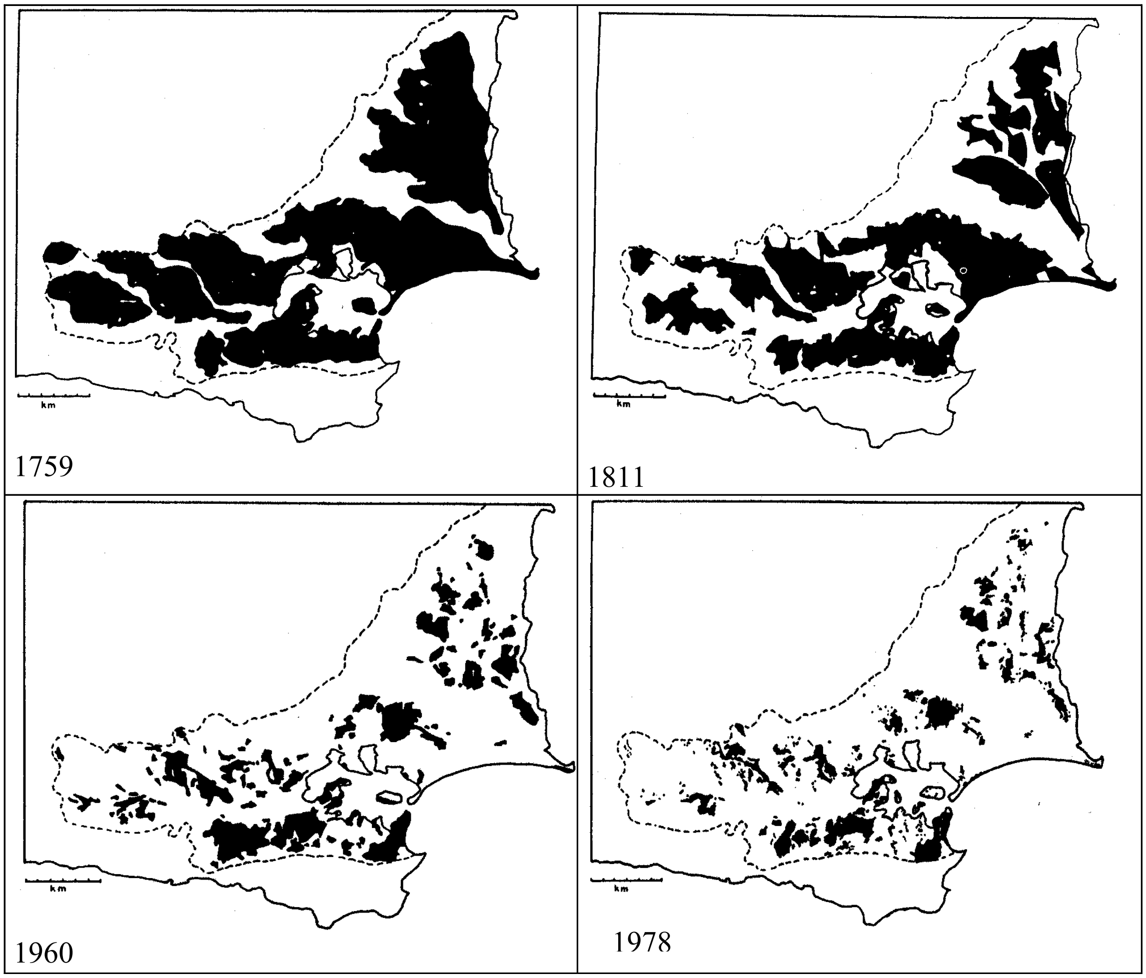

Fig. 1.1 *Fragmentation of heathland in Poole Basin (Dorset, United Kingdom), between 1759 and 1978. Total heathland area was reduced from about 40 000 ha to 6000 ha. In 1759 10 large, continuous heathland areas were present, whereas in 1978 768 heathland patches could be distinguished, of which 80% was less than 4 ha large and 64% less than 1 ha (Moore, 1962; Webb &Haskins, 1980).*

In Flanders and the Netherlands less than 5% of the heathland area present around 1850 remains (Odé et al., 2001). Heathland now occupies about 11 700 ha or 0.21% of the area in Flanders (Hens et al., 2005) (Fig. 1.2). The largest amount of heathland is present in heathland nature reserves (e.g. Mechelse Heide, Kalmthoutse Heide) and military zones (e.g. Groot Schietveld, Zwarte Beek) in the provinces of Antwerp and Limburg. In the central part and in the west, in the provinces of Western and Eastern Flanders, heathland is limited to some very small and isolated relics.

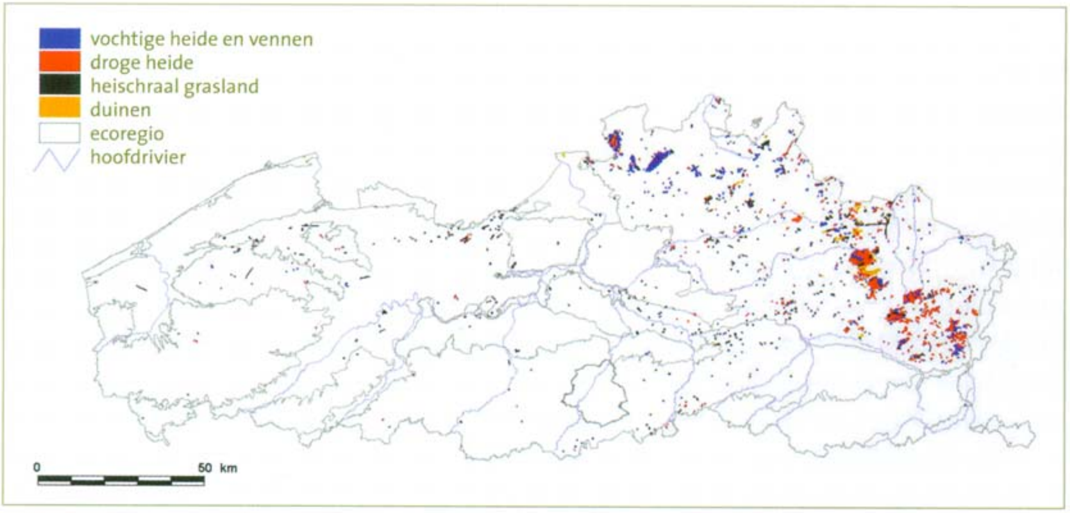

Fig. 1.2 *Heathland in Flanders, based on the Biological Evaluation Map (De Blust, 2004).*

Habitat fragmentation currently is one of the most important threats to biodiversity (e.g. Eriksson and Ehrlén, 2001; Oostermeijer, 2003). Nevertheless, research about how these large area losses and the fragmentation of the remaining heathlands affect the heathland plant community is almost completely lacking. However, studies from other habitat types like forests (e.g. Jacquemyn et al., 2001a; Verheyen et al., 2004; Honnay et al., 2005), grasslands (e.g. Kiviniemi and Eriksson, 2002; Maurer et al., 2003) or dune slacks (e.g. Bossuyt et al., 2003) indicate important changes in the species composition, species richness and plant species distribution patterns in fragmented landscapes. Therefore, this work is primarily aimed at investigating the consequences of heathland fragmentation on the various aspects of the heathland plant community. In this introductory chapter, an overview of the possible effects of habitat fragmentation on the plant community will be provided.

Habitat fragmentation

Habitat fragmentation is occurring in natural habitats throughout the world, and has frequently been found to be a major cause of biological impoverishment (Wilcox and Murphy, 1985; Saunders et al., 1991; Eriksson and Ehrlén, 2001; Harrison and Bruna 1999). Three major components can be distinguished in the habitat fragmentation process: i) loss of the original habitat, ii) reduction of habitat patch size, and iii) increasing isolation of the habitat patches (Andren, 1994). Hence it encompasses more than merely the pure loss of habitat. This may yield changes in different aspects of the plant community (Fig. 1.3).

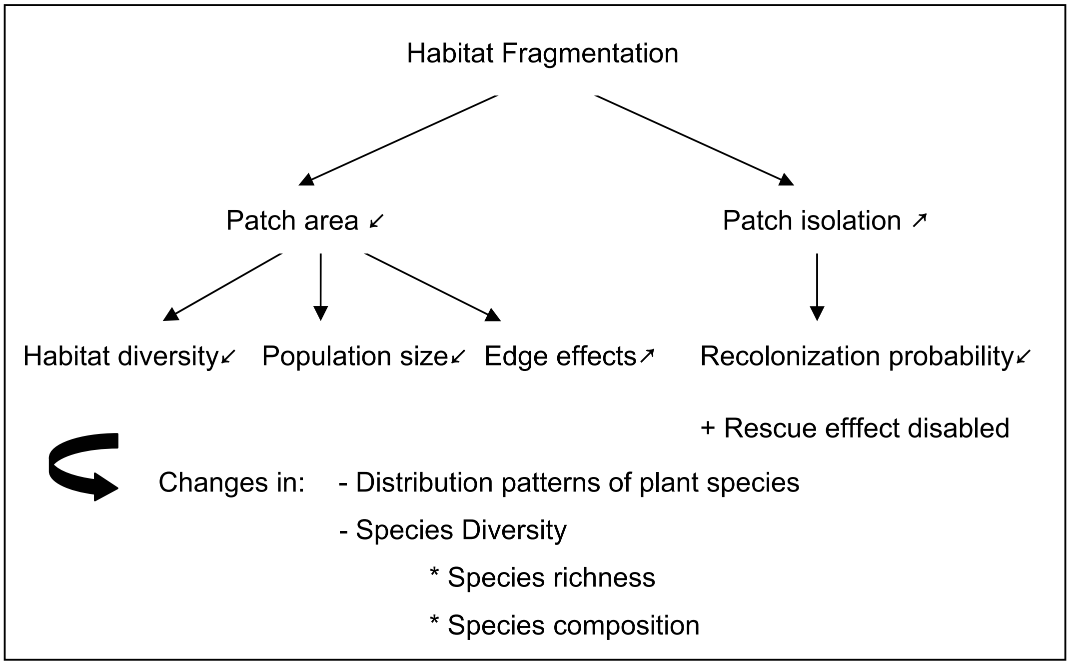

Fig. 1.3 *Effects of habitat fragmentation on the plant community (Honnay, 2000).*

Until present most research on the effects of fragmentation on the different aspects of plant communities has primarily focused on forests (e.g. Grashof-Bokdam, 1997; Honnay et al. 1999a; Jacquemyn et al., 2001b; Verheyen et al., 2004). However, unlike forests, of which some patches disappear and others have been recreated, resulting in a fragmented forest 'landscape' of different aged patches, heathland fragmentation involves almost exclusively the loss of habitat, leading to the subdivision of formerly large heathland areas into small, isolated patches.

Habitat fragmentation and population viability

Habitat fragmentation can have severe effects on the persistence and viability of a plant population. Small patches often contain small populations (Agren, 1996; Jacquemyn et al., 2002; Bruun, 2005), which are at greater risk of decline or eventually extinction (Shaffer, 1981; Pimm et al., 1988; Ouborg, 1993; Menges and Dolan, 1998; Eisto et al., 2000) as they are much more sensitive to genetic, demographic and environmental stochasticity (Shaffer, 1981; Holsinger, 2000). Isolation can further affect population viability. A higher degree of isolation can hamper individuals from other populations reaching the patch. Such recolonization may prevent the population from going extinct, the so-called rescue-effect (Brown and Kodric-Brown, 1977). Additionally, this also impedes recolonization after extinction, and consequently the build up of a metapopulation (Bullock et al., 2002; Hanski and Gaggiotti, 2004).

Genetic consequences of habitat fragmentation

Reduced size and increased spatial isolation of populations in habitat remnants can lead to genetic erosion and increased interpopulation genetic divergence through genetic drift, increased inbreeding and reduced gene flow between populations (Ellstrand and Elam, 1993; Young et al., 1996; Keller and Waller, 2002; Honnay et al., 2005). Ultimately, the outcome of these processes is reduced fitness, lower population viability, and a limitation of a species' ability to respond to changing environmental conditions (Ellstrand and Elam, 1993; Heschel and Paige, 1995; Ouborg and Van Treuren, 1995; Oostermeijer et al., 1998).

Genetic drift is the random change in allele frequencies that occurs because gametes transmitted from one generation to the next carry only a sample of the alleles present in the parental generation (Ellstrand and Elam, 1993). In small populations this may lead to a reduction in genetic variation and large and unpredictable fluctuations in allele frequencies (Barrett and Kohn, 1991; Ellstrand and Elam, 1993; Young et al., 1996). Furthermore, restricted opportunities for mating in small populations favour inbreeding, leading to an increase in homozygosity (Keller and Waller, 2002). This may result in a reduction in fitness called inbreeding depression (Tallmon et al., 2004). Finally, gene flow is reduced in fragmented populations, resulting in higher genetic differentiation between populations (Young et al., 1996). On the other hand, if the connectivity of the patches is not too low, gene flow through seed and/or pollen flow may counteract some of the deleterious effects of genetic drift and inbreeding in small populations, a process called genetic rescue (Richards, 2000; Ingvarsson, 2001; Tallmon et al., 2004).

Plant-pollinator interactions and pollen and seed flow

Since most plants are insect pollinated (Kearns et al., 1998; Kwak et al., 1998; Wilcock and Neiland, 2002), the plant-pollinator interaction is important for successful reproduction. Pollination success, and consequently seed set and the long-term survival of the plant population, is often reduced in fragmented habitats (Jennersten, 1988; Aizen and Feinsinger, 1994; Agren, 1996; Kwak et al., 1998; Groom, 1998; Lennartson, 2002; Wilcock and Neiland, 2002). Habitat fragmentation can severely reduce the abundance and richness of the pollinator community (Steffan-Dewenter and Tscharntke, 1999; Kearns et al., 1998). Small plant populations are often less attractive for insects (Sih and Baltus, 1987; Wilcock and Neiland, 2002), and hence receive less pollinator visitations and subsequently are less frequently pollinated (Jennersten, 1988; Aizen and Feinsinger, 1994; Jacquemyn et al., 2002). Populations may become too isolated relative to the foraging range of pollinators, again causing reduced pollination (Kearns et al., 1998; Steffan-Dewenter and Tscharntke, 1999). The behaviour of pollinators may also be altered by varying population size and density, factors that are often closely related (Kunin, 1997).

Patch isolation also has an effect on seed dispersal. Experiments in different habitats have shown that distribution patterns of plant species are often dispersal-limited (Eriksson and Ehrlén, 2001). The distances over which seeds can disperse are restricted. Therefore, increased distances between habitat fragments reduce the chances of seed dispersal from one patch to another, consequently diminishing the chances of colonisation and hence the chance of the population being rescued from extinction (Brown and Kodric-Brown, 1977). Not only the demographic effect of the addition of new individuals is important in this context. Seed dispersal, together with pollen flow, can mitigate effects of genetic impoverishment of fragmented populations by replenishing lost alleles, as was mentioned above. However, this remains possible only when inter-patch distances remain relatively limited and do not restrict pollen and/or seed flow.

Seed bank, vegetative reproduction and self-compatibility: traits that help to escape fragmentation effects?

The effects of habitat fragmentation on population viability and persistence are plant trait dependent. Certain plant traits, like the capacity of building a persistent seed bank, the possibility to reproduce vegetatively or through self-fertilization, and the longevity of plant species, can reduce a species sensitivity for fragmentation. Consequently, these traits contribute to a species' capability to form what is called a remnant population (Eriksson, 1996, 2000), a population that is able to persist during extended time periods, despite the negative effects imposed on the species due to fragmentation or other environmental disturbances. As a result, these populations show an extinction debt (Tillman et al., 1994; Hanski and Ovaskainen, 2002). Unless the environmental conditions or the configuration of the habitat patches are sufficiently improved, these populations will eventually go extinct (Hanski and Ovaskainen, 2002).

Most heathland plant species are known to have a long term persistent seed bank (e.g. Stieperaere and Timmerman, 1983; Thompson et al., 1997; Bossuyt and Hermy, 2003; Decleer et al., 2004). For example, *Calluna vulgaris*, the dominant heathland species in dry heathlands, has been found to persist in the soil for over 60 years (Decleer et al., 2004). Some studies even indicate that its seeds may remain viable for more than 80 years (Granstrom, 1988). This characteristic can buffer a population against extinction by making it possible to survive temporally unfavourable environmental conditions or by assuring recruitment after seed production has been reduced by fragmentation.

Also the capacity to reproduce vegetatively can increase the chance of a species to persist in fragmented habitats (Eriksson and Ehrlén, 2001). When sexual reproduction is decreased due to fragmentation, e.g. due to pollen or pollinator limitation, clonal plants still have the possibility to create new ramets, and hence to persist (Honnay and Bossuyt, 2005). Furthermore, these species increase the resilience of a plant community not only by the simple fact of being able to sustain, but also by stimulating the rebuilding of the plant community through positive interactions with other plant species (Eriksson, 2000). However, a prolonged bias in the ratio between sexual and clonal reproduction can eventually lead to genetic impoverishment of the population and the loss of the ability to reproduce sexually (Honnay and Bossuyt, 2005).

Finally, in the absence of sufficient pollen from other individuals due to fragmentation, the ability for self-fertilization can be another possible way to enhance plant persistence. Again this can lead to genetic erosion through increased inbreeding, and consequently in loss of population viability in the long run (e.g. Vange, 2002; Culley and Grubb, 2003). Therefore, the effectiveness of these traits in compensating for pollination decline has been questioned (e.g. Spira, 2001).

Habitat fragmentation and plant community composition

If the above mentioned changes in population viability of plant species result in extinction, this also changes the plant community. Species richness is the most commonly studied quantitative aspect of plant communities. It does, however, not give a complete view because fragments having the same total species number can be made up of completely different species (Kadmon and Pulliam, 1993). Therefore, also plant species composition is important to study (Worthen, 1996).

Species richness in habitat remnants

The species-area relation, or the increase in the number of species as a patch increases in area, is one of the most often found relationships in ecology. The decrease in area would then, in the long term, result in a species number decline. Area-dependent extinction processes (see above) can be underlying this pattern (Shaffer, 1981; Pimm et al., 1988). However, since larger patches often show a higher habitat heterogeneity as well (Honnay et al., 1999b; Brose, 2001), area reduction can also result in the loss of habitat diversity due to a decreased availability of different microsites harbouring different species. In this context it can be important to make the distinction between habitat generalists and habitat specialist, as they may react differently on these area changes. Fragmentation makes communities more susceptible to invasion (Eriksson and Ehrlén, 2001), e.g. as edge effects increase (next paragraph), hence promoting generalists, while specialist species decline (Fischer and Stöcklin, 1997; Harrison, 1999). Reduced connectivity can also have an effect on species richness by preventing or hampering (re)colonisation.

Species composition

Species composition of fragmented habitats frequently shows a non-random pattern. An often studied example is the nested subset pattern. A community can be considered as perfectly nested when each species is present in all patches that are more species rich than the most depauperate patch in which the species occurs (Patterson and Atmar, 1986) (Fig. 1.4). An extensive survey of different datasets showed this pattern to be very common in nature (Atmar and Patterson, 1995).

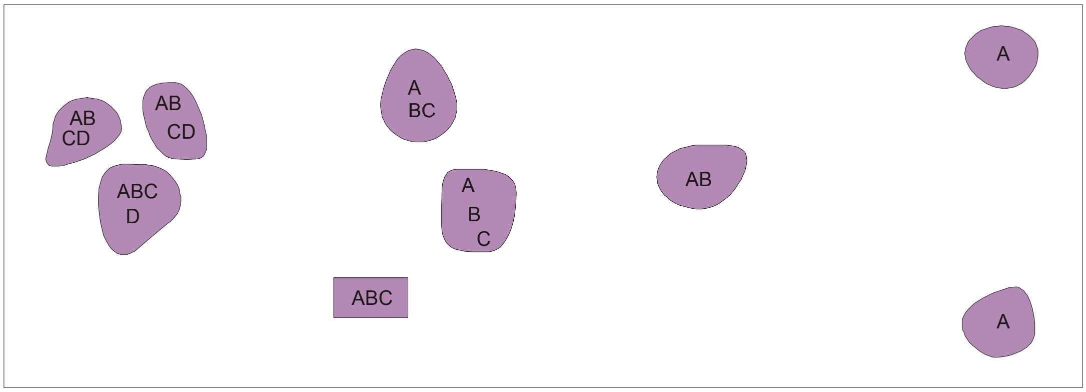

Fig. 1.4 *Schematic representation of a nested subset pattern, where each species (letters A to D) is present in each patch that is more species rich than the most depauperate one in which it occurs.*

Different aspects of habitat fragmentation can be responsible for this pattern. The most often cited underlying factor is that of area-dependent extinction processes (e.g. Patterson and Atmar, 1986; Lomolino, 1996; Hecnar et al., 2002). This can be explained by the process of species relaxation. Each species has a minimum viable population size, below which it is not able to persist. Through the process of habitat fragmentation, patches become smaller, and species will become extinct in a certain, predictable order, depending on their area requirements (Honnay and Hermy, 1998).

Nestedness can also be caused by the process of differential colonization due to differences in the degree of isolation of the different habitat patches (Kadmon, 1995; Sfenthourakis et al., 1999; Butaye et al., 2001). Every species has a certain dispersal capacity and, as a result, a distinct probability of reaching neighbouring patches.

Another potential mechanism is that of nested habitats (Honnay et al., 1999c; Sfenthourakis et al., 1999). Patches having a high habitat diversity will be able to support almost all species, while habitat poor patches can only provide suitable conditions for some generalist species (Honnay et al., 1999c). A final process possibly causing nestedness is passive sampling (Connor and McCoy, 1979; Cutler, 1994). Frequently occurring species have a higher incidence likelihood in a patch than more rare species, purely due to chance events.

Edge effects

Decreased patch area also leads to a higher relative amount of edge, as smaller patches have a higher edge to area ratio compared to larger patches (Laurance and Yensen, 1991). Hence edge effects become more pronounced in more fragmented landscapes. It has even been suggested that the effects of habitat fragmentation through edge effects may be more important than the effects of area and isolation as such (Harrison and Bruna, 1999).

Mechanisms of edge effects

The edge zone can be defined as the portion of a patch where environmental conditions differ significantly from those in the interior of the patch, and hence species composition and abundance also differ (Forman and Moore, 1992). For sessile organisms like plant species, the changes in abundance across habitat edges are mainly caused by three mechanisms: i) ecological flows, ii) resource mapping and iii) species interactions (Ries et al., 2004).

Ecological flows involve the movement of material, species or energy between patches (Wiens, 1992; Cadenasso et al., 2003; Devlaeminck, 2005). The rate of these flows is mainly determined by edge permeability (Strayer et al. 2003; Ries et al., 2004). Plant species composition can be affected directly by these fluxes through the movement of plant propagules across habitat edges (Cadenasso and Pickett, 2001; Devlaeminck et al., 2005a). Indirect effects originate from the differential transfer of light, heat, moisture and wind from a patch to the adjacent patch, which can lead to changes in microclimate in the vicinity of the edge (Matlack, 1993; Cadenasso et al., 1997; Burke and Nol, 1998; Chen et al., 1999), and from the diffusion or deposition of nutrients near the edge (De Schrijver et al., 1998; Weathers et al., 2001; Devlaeminck et al., 2005b). The resulting changes in habitat quality in the vicinity of the edge result in abiotic gradients, and hence gradients in environmental suitability for a certain species, from the edge to the interior of a habitat fragment, thereby leading to changes in species abundances (resource mapping). Finally, also the changed interactions between species near edges influence their distribution patterns within the patch. At the edge predation by animals, both of the plant itself (herbivory) and seed predation, is often enhanced (Jules and Ratchke, 1999; Donoso et al., 2003). Also competitive interactions between plant species can change in this zone (Fagan et al., 1999; Ries et al., 2004), and for example result in a higher presence of invasive species along the edge (Brothers and Springarn, 1992; Honnay et al., 2002a; Yates et al., 2004).

Strength of edge effect

Several ecological factors determine how resources are distributed relatively to the edge and how species react to that pattern, and hence affect the strength of the edge effect and the penetration distance of edge effects into the patch (Esseen and Renhorn, 1998; Ries et al., 2004). The most common cited factors influencing edge effects are edge orientation and edge contrast (Murcia, 1995; Ries and Sisk, 2004). Other possible confounding factors are time since edge creation (Matlack, 1994a; Esseen and Renhorn, 1998) and fragmentation effects (Moen and Jonsson, 2003).

Edge orientation has been found to affect the strength of the edge effect (Chen et al., 1995; Honnay et al., 2002a; Ries et al., 2004; Ries and Sisk, 2004; Hylander, 2005). In the northern temperate zone, edge effects are often more pronounced at south-southwest facing edges compared to north-northeast-oriented edges (Chen et al., 1995; Honnay et al., 2002a; Ries et al., 2004), because solar radiation, an important determinant of energy movement, is higher there. In western Europe this effect is enhanced through the dominant southwestern wind direction.

The type of adjacent land use, and more specifically edge contrast or the degree to which neighbouring patches differ from each other, can further influence the intensity of the edge effect. Differences in edge contrast can be caused by differences in vegetation structure (vegetation height and vegetation density) (Murcia, 1995;

Kupfer, 1996; Cadenasso and Pickett, 2000, 2001; Cadenasso et al., 2003) or by differences in habitat quality (Ries and Sisk, 2004).

Objectives and outline of the thesis

The large quantitative and qualitative decline of heathlands in Belgium and most other parts of western Europe urges for their conservation. Therefore, it is important to gain insight into how these changes affect the different aspects of the plant community inhabiting these remnants. Since heathland area has been undergoing a continuous decline during the last decades (centuries), with almost complete lack of heathland restoration, this habitat is extremely suited to study the effects of species relaxation, or the adaptation of the plant community to the conditions of increased patch isolation and reduced patch area.

Consequently, the main objective of this study was to assess the response of different aspects of the heathland plant community to increased heathland fragmentation. The more specific aims of this study were to:

- determine whether the large decline in total heathland area leads to the extinction of species from the regional species pool
- examine how an increased isolation and a reduction in area affects heathland plant community composition and species richness
- uncover the effects of increased isolation on the distribution and persistence of heathland species in the heathland remnants and to assess how certain plant traits might mitigate these effects
- study if the increased amount of patch edge changes abiotic conditions and plant community characteristics
- investigate the effectiveness of management in conserving a diverse heathland flora
- derive management and conservation guidelines to preserve heathland plant diversity

The thesis was subdivided in three main parts (fig. 1.5), dealing with i) direct effects of fragmentation through habitat loss and area reduction and increased isolation of heathland remnants, ii) edge effects, and iii) management effects.

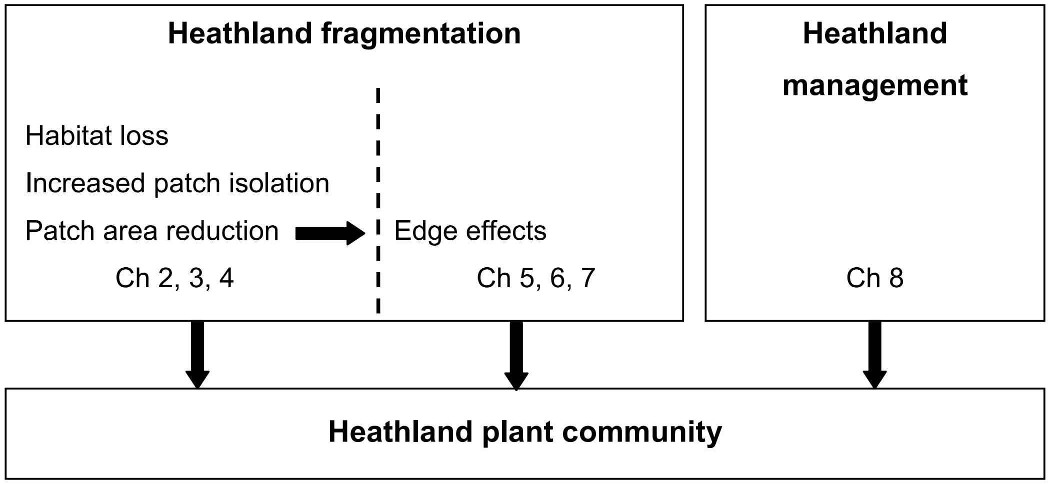

Fig. 1.5 *Schematic overview of the outline of the thesis.*

DIRECT FRAGMENTATION EFFECTS

Chapter 2

The heathland area in the north-western part of Belgium has been dramatically reduced. Of the once dominating heathlands, only small relics remain today. However, this loss has not been quantified yet, so the real extent of this decline is largely unknown. Moreover, little is known about the effects of this drastic reduction in total heathland area on the persistence of heathland species in the region. It can be expected that the longevity of many of these species, together with their often long term persistent seed bank, might have been able to buffer some of the effects of habitat loss. In chapter 2, the former heathland area and the heathland fragmentation process is reconstructed for this region. Historical plant species lists are collected and analysed to gain knowledge of the accompanying changes in heathland diversity.

Chapter 3

The reduction in patch area and the increase in patch isolation associated with this habitat loss forces the heathland plant community to 'adjust' to this new situation, and consequently may result in changes in species diversity and community composition. However, knowledge about the outcome of this process in heathlands is almost completely lacking. Because research in forest ecosystems (e.g. Honnay et al., 1999a; Jacquemyn et al., 2001a) and the more closely related semi-natural grasslands (e.g.

Kiviniemi and Eriksson, 2002; Kraus et al., 2004) have shown that significant community structure alterations are to be expected, it is important to have an understanding of how these processes act in heathlands. In chapter 3, the effects of changes in patch area and isolation on heathland plant community structure are studied, and the relative importance of both processes is assessed.

Chapter 4

Community-level changes reflect the composed response of all heathland species present to the increased fragmentation. However, plant species may vary considerably in their response to habitat fragmentation, leading to differences in distribution patterns. These dissimilarities can result from differences in habitat requirements and in plant traits related to dispersal capacity and local persistence. From a conservation point of view, it is important to know which species (or species groups) are most sensitive to changes in landscape configuration due to fragmentation. Therefore, the individual response of characteristic heathland species to heathland fragmentation is examined in chapter 4. Subsequently, the relation of these patterns with plant traits is investigated.

EDGE EFFECTS

Chapter 5

Edge effects have been extensively studied in the past, again though almost exclusively in forests. Since it has been suggested that a change in vegetation due to edge related deterioration in habitat quality is probably the most important consequence of habitat fragmentation (Harrison and Bruna, 1999), it is essential to have an idea of the type and extent of these effects. Many edge studies, however, fail in taking into account the inherent typical characteristics of this type of data in their statistical analysis. Consequently, this can lead to false conclusions. In chapter 5, these methodological shortcomings are discussed and an appropriate statistical approach is introduced.

Chapter 6

Heathlands can be expected to suffer from impacts of adjacent land use types. Due to its intrinsic character, adapted to nutrient poor and acidic conditions, with species adapted to open, unshadowed habitat, especially changes in microclimate and nutrient conditions are assumed at the edge. The latter has often proved to be responsible for the degradation of many heathland sites (e.g. Bobbink et al., 1998; Lee, 1998). The contrast between heathland and the neighbouring land use is thought to be an important modifying factor for edge effects. Accordingly, this chapter deals with the effects of adjacent land use, both on the abiotic conditions and on the plant community in heathland patches.

Chapter 7

Previous chapters focussed on the vascular plant community of heathlands, which is relatively species poor. On the other hand, the bryophyte layer of most heathlands is very diverse and encompasses an important part of heathland plant diversity. Moreover, since bryophytes do not possess specialised mechanisms for regulating the uptake and loss of water, they can be expected to be more severely affected by possible microclimatic changes taking place at the edge. Management can be an important confounding factor in this aspect. The bryophyte layer is completely covered by the vascular plants, and hence its composition has been found to be strongly affected by the structure of the vascular plant layer, which in turn is mainly shaped by management. The effects of both adjacent forest land use and heathland management and their interactions on the heathland bryophyte layer are considered in chapter 7.

MANAGEMENT EFFECTS

Chapter 8

Heathlands in Western Europe can only sustain when they are properly managed. So even in large heathland patches that have been relatively well spared from fragmentation, the preservation of plant species diversity is not guaranteed. Therefore, changes in different elements of the heathland plant community over a 25 year period in a relatively large heathland reserve are studied in chapter 8. At the start of this period, extensive grazing was set up as the main management type. Since this is now one of the most frequently applied forms of heathland management (De Blust, 2004), this analysis can give important insights in its effects and usefulness, and hence can be of practical use for many heathland managers.

CONCLUDING REMARKS

Chapter 9

In this final chapter, the results of the previous chapters are briefly summarized and discussed. Finally, guidelines for heathland conservation are proposed and possibilities for future research are suggested.

CHAPTER 2

DOES THE HEATHLAND FLORA IN NORTH-WESTERN BELGIUM SHOW AN EXTINCTION DEBT?

Introduction

Human induced land use changes form one of the major threats to biodiversity worldwide (Vitousek, 1994; Vitousek et al., 1997; Sala et al., 2000). Not only land transformation, but also the subsequent fragmentation of (semi-)natural habitats seriously jeopardizes the survival of biodiversity. Yet, in Western Europe, many of the characteristic species and habitats, which are now the focus of nature conservation measures, wouldn't have existed if humans had not managed the land they live on in some way or another (Krebs et al., 1999). An example of such a semi-natural habitat is heathland. Up to the end of the 18th century, and in some countries even until the middle of the last century, heathland formed an important component of traditional agricultural systems in the Atlantic region of Western Europe (e.g. Gimingham, 1976; De Smidt, 1975; Tack et al., 1993). As soon as modern, intensified agricultural practices started to take over, heathland lost its economical value, resulting in a serious decline of heathland area. The latter has been observed all over north-western Europe. In Flanders and the Netherlands, for example, less than 5% of the mid-19th century heathland area is left (Odé et al., 2001).

Little is known about the effects of this large scale destruction on the characteristic heathland plant species. Heathlands are confined to relatively acid, nutrient-poor soils, where some kind of management prevents succession to forest and accumulation of nutrients (e.g. Webb, 1998). These conditions are often difficult to maintain under the high current levels of atmospheric deposition, making the need for regular management even greater, and consequently, threatening intact heathlands and its characteristic plant species even more. However, many heathland plant species are long living and have a persistent seed bank (e.g. Stieperaere and Timmerman, 1983; Pywell et al., 1997; Bossuyt and Hermy, 2003), characteristics expected to delay the plants' responses to habitat loss. Therefore, despite the fact that their threshold conditions for survival are no longer met, many of these species can still be present, although in declining populations. This phenomenon is described as extinction debt (Tillman et al., 1994; Hanski and Ovaskainen, 2002). Eventually, these species will go extinct and a new equilibrium in species composition will be reached. On the other hand, improving the environmental conditions and configuration of the habitat patches sufficiently can prevent these species from going extinct (Hanski and Ovaskainen, 2002).

Evidence for an extinction debt may come from several approaches, e.g. by comparison with relatively stable landscapes (e.g. Berglund and Jonsson, 2005; Helm et al., 2006; Vellend et al., 2006) or relating present day species richness to historical landscape configuration (e.g. Lindborg and Eriksson, 2004). Here a combination of historic records combined with heathland area reconstruction was used. Historic records on plant species distribution data can be a valuable, but often unexploited source to evaluate changes in the flora of a particular area (McCollin et al., 2000; Dutoit et al., 2003; Van der Veken et al., 2004). Relating historical distribution data to the present day occurrence of species in a region provides insights into the extent and rates of species extinction and can help to identify the characteristics that influence species' sensitivities to extinction. Therefore, the aims of this study are to investigate how the loss of heathland area in north-western Flanders has changed the presence of heathland and forest plant species there using historical plant distribution data. By comparing the heathland area and plant species decline it can be determined whether the heathland flora shows an extinction debt. Furthermore, linking the change in species' status with plant traits will make it possible to identify the traits underlying species extinction sensitivity.

Material and methods

Study area

The study area is situated in the north-western part of Flanders and covers an area of 640 km² (40 4 x 4 km cells) south of Bruges (Fig. 2.1). This region used to have large areas of heathland, which formed an important part of the traditional agricultural system. However, increased population pressure and agricultural intensification resulted in the destruction of these heathlands for forest, industrialisation or urbanisation. Consequently, heathland area declined since the end of the 18th century. Nowadays, only a limited amount of heathland is left, mostly restricted to very small relics.

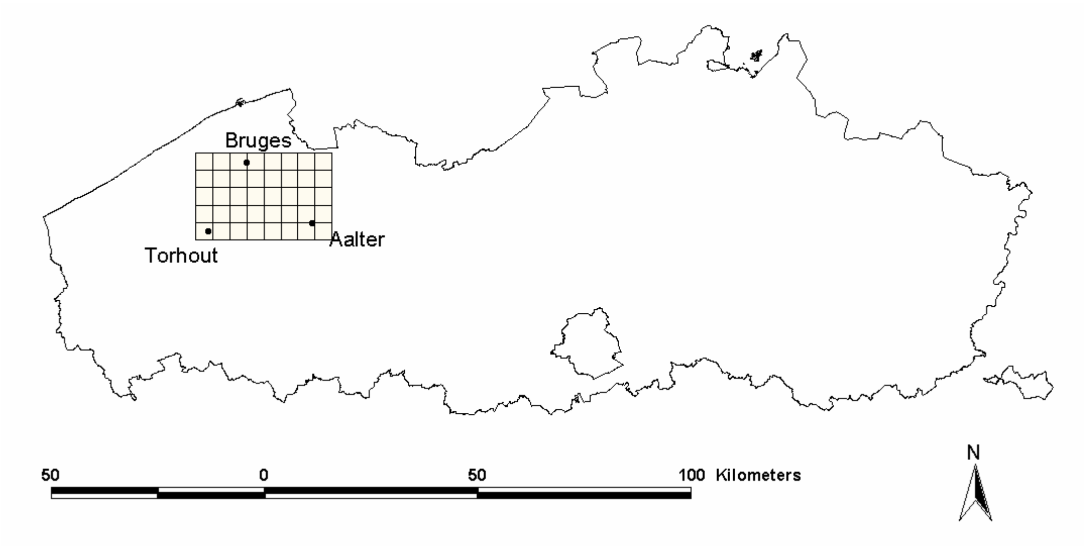

Fig. 2.1 *Location of the study area within Flanders.*

Heathland area decline

The extent of heathland in the past and the process of heathland decline were reconstructed by digitizing heathland area on different, consecutive historic maps. Heathland in the study area reached its maximum extent around the year 1000 (Verhulst, 1995). The area of forest and heathland at that time was globally reconstructed by Verhulst (1995) using several sources. Although this is only a very crude and schematic representation, it gives an indication of the importance of heathland at that time. The first available detailed area-covering map of the region is the topographic map of De Ferraris (1775). The map of Vander Maelen (1850) and the Biological Evaluation Map (1985), a digital land use map containing a land use code for every parcel, were used for successive periods. As afforestation has been one of the main causes of heathland loss, forest area was also digitized on these four maps. Analyses were performed in ArcView 3.2 (ESRI, 2000).

Historic plant species distribution data

Historic data on plant species distribution in the study area were collected from different sources. The books of Roucel (1792, 1803) provide some of the oldest records for the area. Another important source is ‘Prodrome de la Flore belge’ (De Wildeman and Durand, 1898), which compiles most of the floristic data for Belgium published up to that time. Additional records were found in Crépin (1865). Crépin (1860) provides species abundance figures for a broad region encompassing the study area. Furthermore, we systematically surveyed all issues of the three leading Belgian journals dealing with botany or biology in general, being the Bulletin de la Société Royale de Botanique de Belgique (1871-1994) (continued as Belgian Journal of Botany), Botanisch Jaarboek Dodonaea (1889-1932) (continued as Biologisch Jaarboek Dodonaea till 1999), and Dumortiera (1975-present). An overview of the literature sources is given in Appendix 2.1 (this chapter).

These data were supplemented with data from *Florabank* (Van Landuyt et al., 2000), a database compiling data on the Flemish flora. The records in *Florabank* are subdivided into three time periods: before 1940, 1940-1971 and 1972-present. Pre-1940 data were collected from herbaria and different types of publications. Around 1940, the systematic grid-based (4 x 4 km cells) survey of the Belgian flora started. As a result, records from 1940 onwards are composed of data from systematic grid surveys and some additional herbarium and literature sources. In 1972, these data were published and a new area-covering survey started. For the recent period (1972-2003) survey data were supplemented with all other accessible vegetation data in Flanders, and hence give a relatively complete picture of plant species distributions (Biesbrouck et al., 2001).

Recent distribution data were obtained from our own surveys of heathland relics in the area in 2002 (Palmaerts et al., 2004; chapters 3 and 4), and again supplemented with data from *Florabank* (Van Landuyt et al., 2000) for the period 1972-2003.

Data standardisation

As the plant distribution data originate from different sources, they could not be directly combined, and some standardisations had to be carried out in advance. The main adaptations relate to plant species names, the species to include in the analyses and descriptions of the locations where the species were found. Plant species names have often changed during the course of time. Species names in the older records were updated to today’s nomenclature of Lambinon et al. (1998) through synonym lists in Crépin (1860), De Wildeman and Durand (1898) and Biesbrouck et al. (2001). Analyses were restricted to species characteristic for heathland and related vegetation types such as grassheaths and acid grasslands, as they contain a similar species pool. Forest species were also included because many of the present day forests were planted on the former heathlands, and there has always been a strong relationship between forest and heathland (Tack et al., 1993). Finally, only species present in the oldest data set (period before 1940) were included in further analyses because no conclusions on trends in the distribution of other species can be drawn. Historic species lists are hardly ever a complete listing of all species present, but often only mention the rare or ‘special’ species. Consequently, the absence of a species in the oldest data sources does not implicate that the species was not present at that time (see also Van der Veken et al., 2004). The species included in the study are listed in Appendix 2.2 (this chapter).

In *Florabank* species data are stored based on the species’ distributions in 4 x 4 km cells. This grid was used as a base and locations from other sources had to be reclassified and linked to the appropriate 4 x 4 km grid cells. This transformation was relatively easy for the recent data. However, for the older data, this was less straightforward because the descriptions of locations were often quite wide or vague. For example, frequently only the name of the municipality was given. In such cases, all grid cells covering the area possibly indicated by this description were included (Van der Veken et al., 2004).

Data analysis

Comparison of the historic and present dataset revealed the number and identity of species that went extinct. A more detailed trend analysis was performed by fitting a linear regression between the historic abundance categories (Crépin, 1860) and the present number of 4 x 4 km cells occupied (McCollin et al., 2000; Telfer et al., 2002; Van der Veken et al., 2004). This regression line represents the general trend in species abundance over time. Hence the standardized residual for a certain species equals the deviation from the overall trend. Species showing negative residuals have declined more than the average indicated by the total species assemblage, while species showing positive residuals have increased relative to the general trend.

To unravel the environmental factors underlying the changes in species abundance and the ecological characteristics making a species more vulnerable to extinction, their relationship with the standardised residuals was studied. Spearman rank correlations were calculated between the standardised residuals and the species' Ellenberg indicator values for light, temperature, humidity, acidity and soil nutrient content (Ellenberg et al., 1992) and their seed longevity index (Thompson et al., 1997; Bekker et al., 1998). Kruskal Wallis tests with multiple comparisons were used to test for differences in residuals between species showing different seed bank types (transient, short term persistent or long term persistent (Tamis et al., 2004)), plant strategies (C, S, R, CS, SR, CR or CSR (Grime et al., 1988)) and growth forms (ferns (including *Lycopodiaceae*), herbaceous, gramineous and woody species (Biesbrouck et al., 2001)). Differences between generalist (wide ecological amplitude) and specialist species (narrow ecological amplitude) (Runhaar et al., 1987) and between species possessing or lacking the ability to propagate vegetatively (Klotz et al., 2002) were investigated using Mann Whitney tests. Analyses were performed for heathland and forest species separately.

Finally, the effects of changes in heathland and forest area on plant species decline were studied directly. Spearman rank correlations were calculated between the percentage of heathland and forest species that have gone extinct per grid cell, and the percentage of heathland and forest in that grid cell that remained heathland or forest, or was transformed into the other type (i.e. heathland to forest or forest to heathland). To investigate whether the historic heathland and forest area still affect the current diversity of heathland and forest species, Spearman rank correlations were calculated between the number of heathland and forest species present in the recent period (1972-2003), and the area of heathland and forest present on the different historic maps (cf. Lindborg and Eriksson, 2004). All analyses were performed using SPSS 12.0 (SPSS Inc., 2003).

Results

Land use changes

At its maximum extent around the year 1000, heathland occupied some 17 000 ha in the region (Fig. 2.2; Table 2.1). Although this value is only an approximation, it gives an impression of the regional importance of heathland. At the end of the 18th century, destruction of the heathlands had already started (Tack et al., 1993), but large heathland areas were still present. The forest areas surrounding the heathlands were enlarged, while some of the other forests outside the heathland zones were converted to agricultural land. This led to a reduction of the heathland area to about 9040 ha by 1775 (Fig. 2.2; Table 2.1). This process continued during the following centuries. Due to increased human population growth, forests, which were situated on the more fertile soils, were exploited further, while the unfertile heathlands were planted with forest (Fig. 2.2). Consequently, most of the present forest in this region is situated on former heathland. During the 20th century, urbanisation and industrialisation further threatened the remaining heathland and forest, and only a very small amount, about 85 ha, of the once dominating heathlands are currently left (Table 2.1; Fig. 2.2).

Table 2.1 *The areas of heathland and forest in the study area from 1000 to 1985 and some fragmentation characteristics from 1775 to 1985.*

	Forest 1000$^{\$}$	**Forest 1775**	**Forest 1850**	**Forest 1985**	**Heath 1000$^{\$}$**	**Heath 1775**	**Heath 1850**	**Heath 1985**
Total area (ha)	21500	19321	15946	5332	17500	9040	1254	85
Number of patches	NA	693	1336	722	NA	131	134	38
Mean area (ha)	NA	27.9	11.9	7.4	NA	69.0	9.4	2.2
Maximal area (ha)	NA	2333	3698	553	NA	2685	178	12
Total perimeter (km)	NA	1614	2007	865	NA	398	150	34
Mean perimeter/area (m/ha)	NA	83.5	125.9	162.3	NA	44.0	119.4	396.6

$^{\$}$ The values for the year 1000 are an approximation.

NA: not available

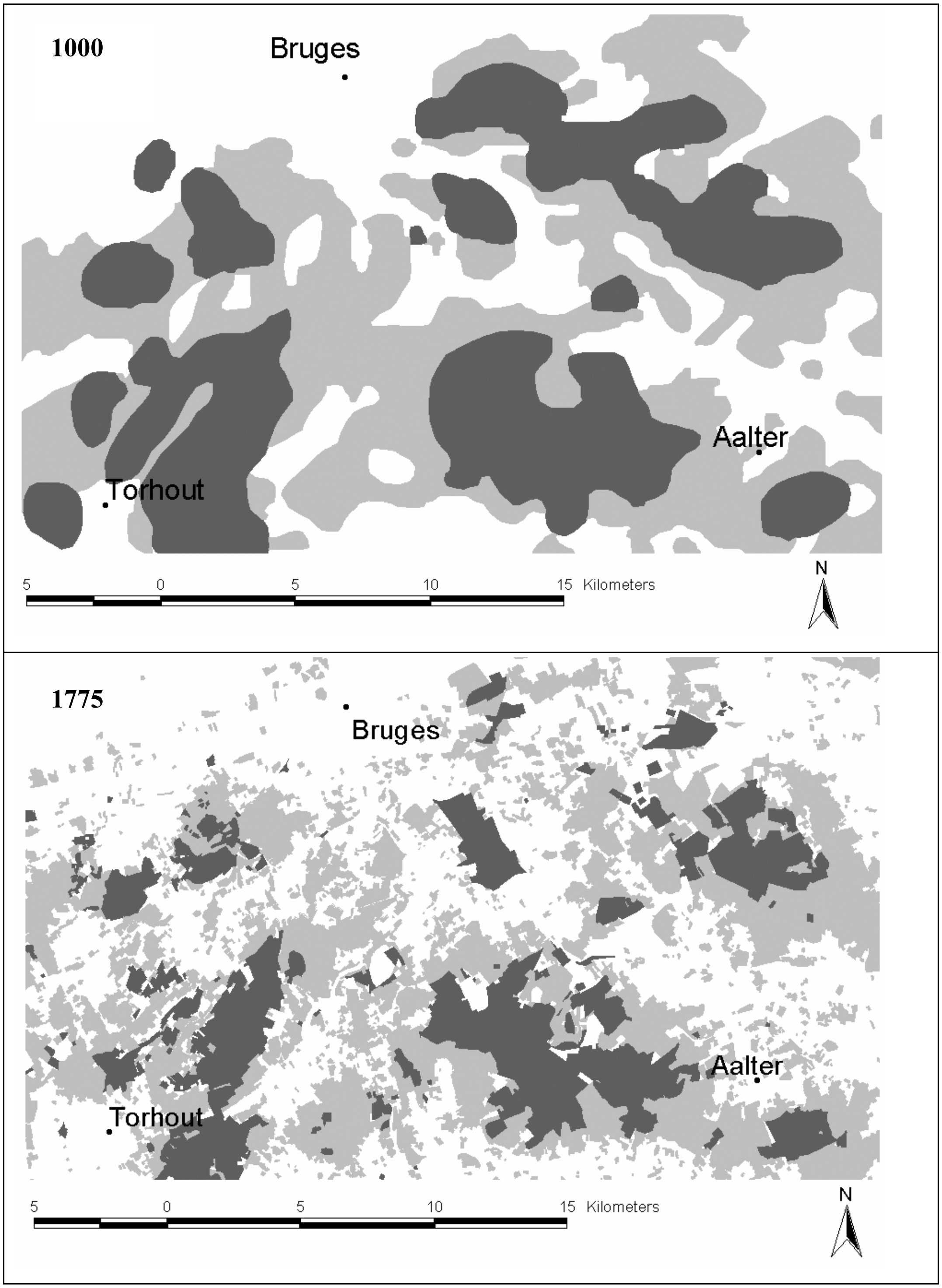

Fig. 2.2. *The areas of heathland (dark grey) and forest (pale grey) in the study area from around 1000 till 1985.*

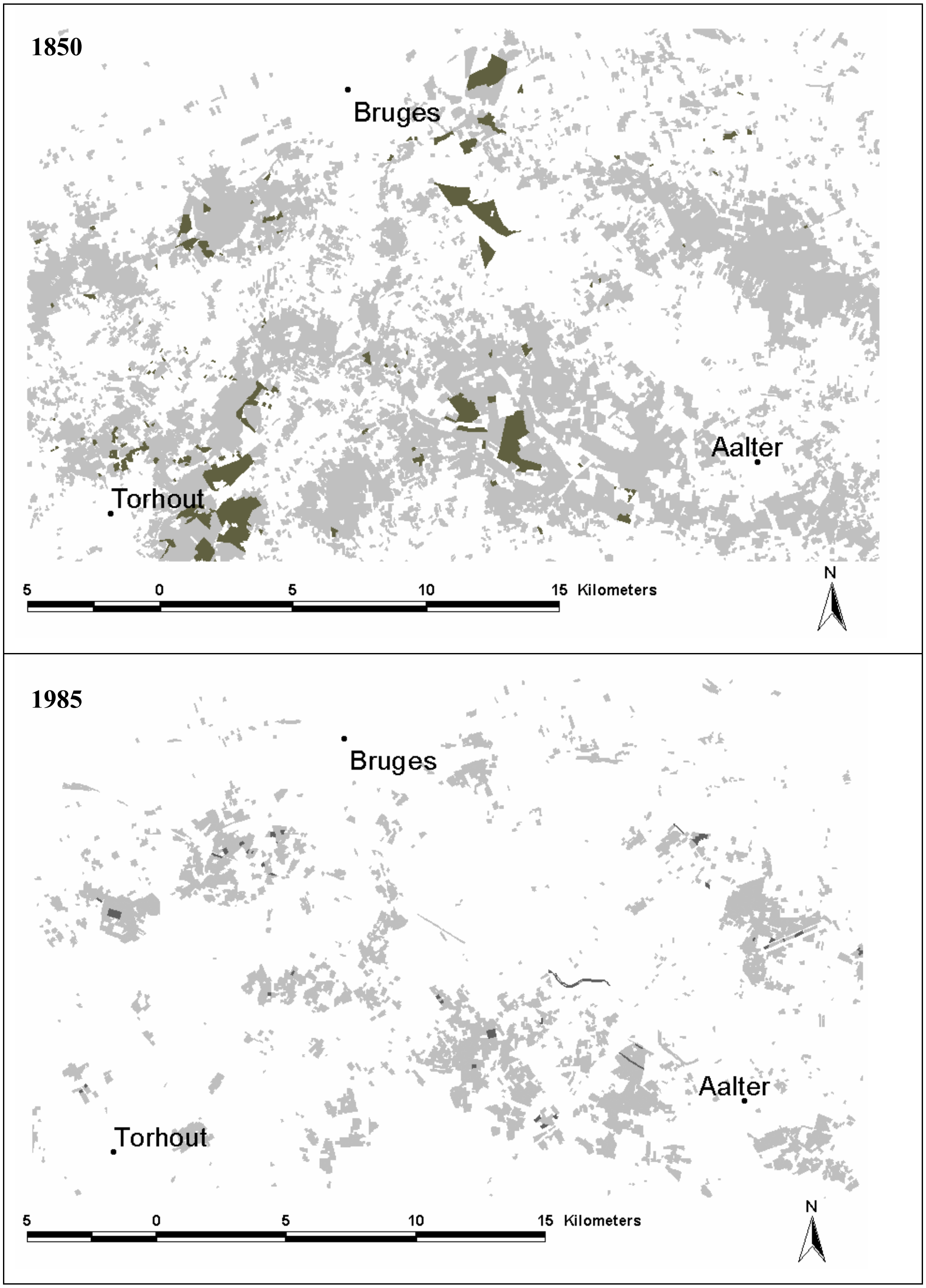

Fig. 2.2. *The areas of heathland (dark grey) and forest (pale grey) in the study area from around 1000 till 1985 (continued).*

Species extinction

Over a time span of about 210 years, 19 of the 174 (11%) species characteristic for heathland and forest have gone extinct (Table 2.2). Heathland (10 out of 91 species or 11%) and forest species (9 out of 83 species or 11%) show a comparable rate of decline.

Table 2.2 *Species that have gone extinct during the study period, and their habitat.*

Species	**Socio-ecological group***	**Reference$^{\$}$**
Antennaria dioica	dry heath	33
Carex punctata	acid grassland	37
Carex strigosa	forest	10
Cuscuta epithymum	dry heath	25
Diphasiastrum tristachyum	dry heath	10
Gentiana pneumonanthe	wet heath	10, 16, 33, 36, 37
Gymnocarpium dryopteris	forest	10, 36
Huperzia selago	acid grassland	10, 37
Inula conyzae	forest edges	37
Juncus filiformis	wet heath	10, 37
Lysimachia thyrsiflora	wet heath	10
Monotropa hypopitys	forest	10, 36
Montia fontana	forest	36
Neottia nidus-avis	forest	10, 36, 37
Polystichum aculeatum	forest	10
Pyrola minor	forest	10, 26, 36, 37
Thymus serpyllum	acid grassland	9, 36
Vaccinium vitis-idaea	dry heath	10
Viscum album	forest	10

* according to Stieperaere & Fransen (1982); $^{\$}$ numbers refer to appendix 2.1

The linear regression between the number of presently occupied 4 x 4 km cells and the historical abundance categories was highly significant (F_{162}=94.32; $p<0.001$; R^2= 0.37) (Fig. 2.3). For forest species, these standardised residuals were significantly positively correlated with the Ellenberg indicator value for soil nutrient content (Table 2.3). For heathland species, this relationship was only marginally significant (Table 2.3).

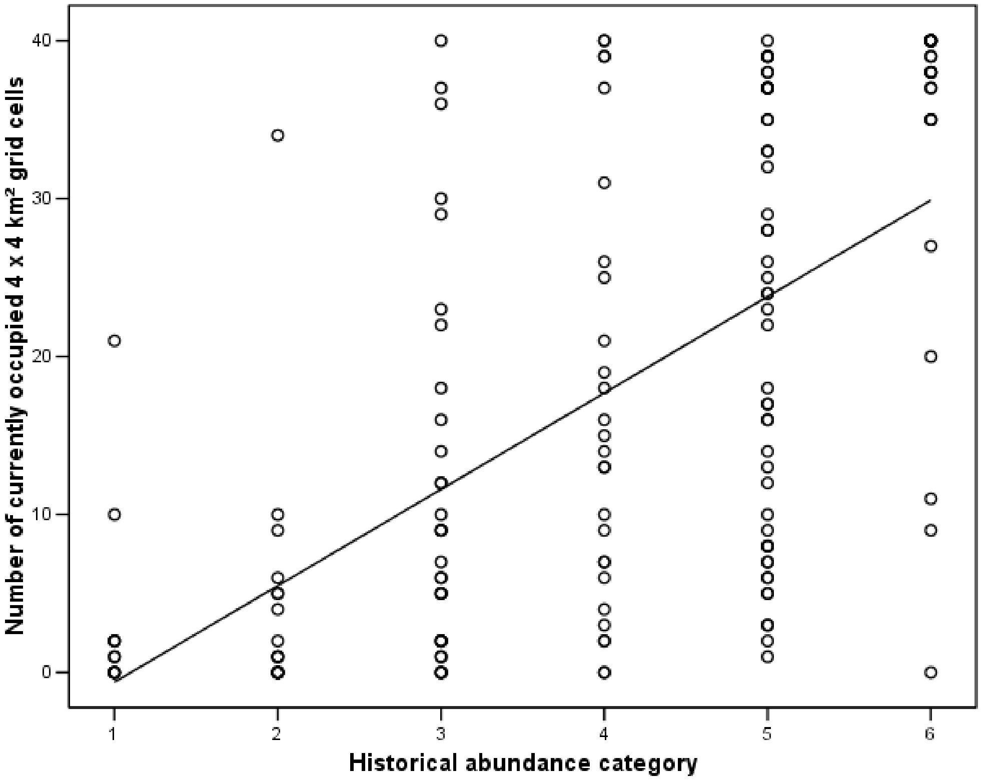

Fig. 2.3. *Linear regression between the number of presently occupied 4 x 4 km cells and the historical species status categories according to Crépin (1860) ranging from 1= very very rare to 6= very common (n=163; R²=0.365; Y= -6.555 + 6.071X).*

Table 2.3 *Spearman rank correlation coefficients between the change in species status during the study period, as depicted by the standardised residuals of the regression relating past and present species abundance, and plant traits.*

	Heathland species	Forest species
L[a]	-0.167	-0.103
T	0.023	-0.080
F	-0.144	0.029
R	0.004	0.015
N	0.197 (*)	0.272 *
Seed longevity index	0.221 (*)	0.016

*: 0.01<p≤0.05; (*): 0.05<p≤0.1

[a] Ellenberg indicator values for light (L), temperature (T), soil moisture content (F), soil acidity (R) and soil nutrient content (N) (Ellenberg et al., 1992).

Although seed bank characteristics show no relationship with the standardised residuals for forest species, they significantly affect the survival of heathland species (Tables 2.3 and 2.4). The seed longevity index of heathland species is positively correlated with the standardised residuals (Table 2.3). Furthermore, heathland species having a long term persistent seed bank show higher values for the standardised residuals than species having a transient seed bank, while species with a short term persistent seed bank show intermediate values (Table 2.4).

Table 2.4 *Kruskal-Wallis and Mann Whitney U tests testing the relation between the change in species status, as depicted by the standardised residuals relating past and present species abundance, and plant traits.*

	Heathland species		Forest species	
Plant strategy[a]	$\chi^2=3.971$		$\chi^2=15.441$	*
Ecological amplitude[b]	z=1.144		z=1.858	(*)
Seed bank type[a]	$\chi^2=6.697$	*	$\chi^2=2.088$	
Vegetative spread[b]	z=2.055	*	z=1.484	
Growth form[a]	$\chi^2=1.282$		$\chi^2=8.541$	*

*: $0.01<p\leq 0.05$; (*): $0.05<p\leq 0.1$

[a]: Kruskal Wallis test; [b]: Mann Whitney test

Forest species having different plant strategies have evolved differently over the last centuries. A significant difference was found between the standardised residuals of stress tolerators on the one hand and stress tolerant competitors on the other (Table 2.4). Species showing a strong S-component have declined, while stress tolerant competitors show predominantly positive residuals. Other plant strategies show intermediate values. Plant strategy does not affect extinction sensitivity of heathland species (Table 2.4).

Extinction probabilities differ between forest species having a wide or narrow ecological amplitude (Table 2.4). Specialist forest species have a higher chance of extinction than generalist forest species. Also growth form affects the likelihood of extinction solely for forest species (Table 2.4). Standardized residuals for herbaceous forest species are significantly lower than those for woody forest species, with grass species and ferns showing intermediate values. On the other hand, the ability for vegetative regeneration enhances the chances of survival for heathland species only (Table 2.4).

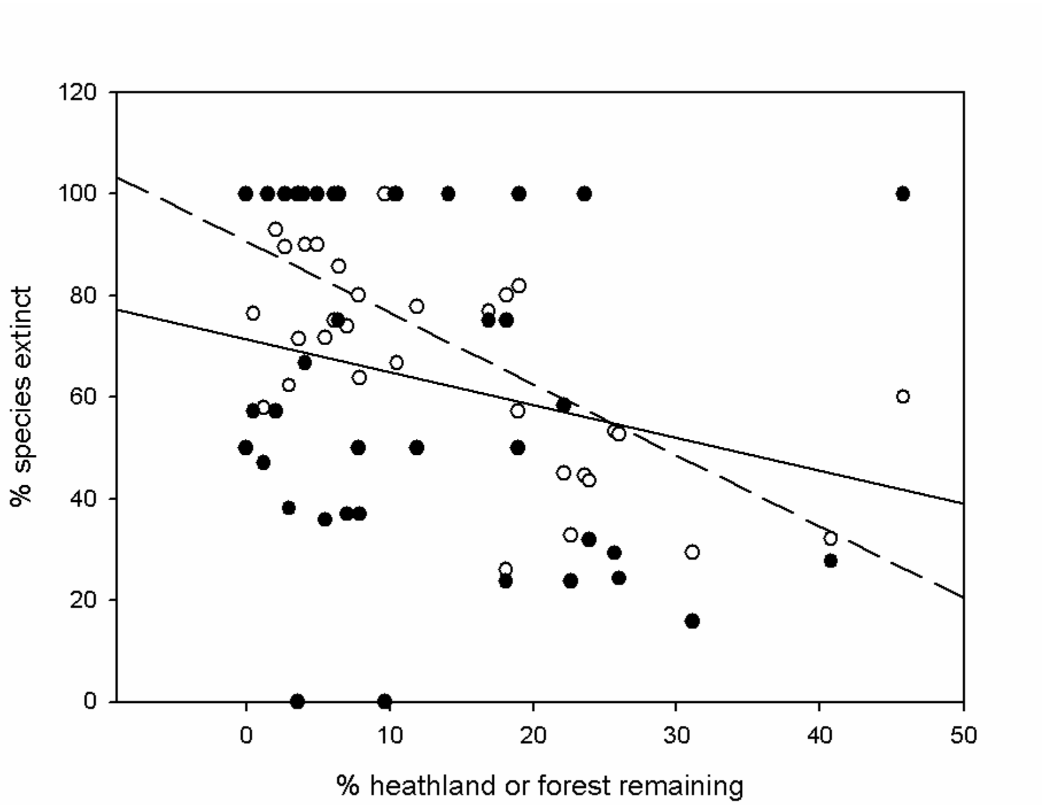

Fig. 2.4 *Relation between the percentage of heathland (open dots; dashed line) and forest (closed dots; full line) species that has gone extinct, and the amount of heathland and forest present in 1775 that remained heathland or forest until now, based on 4 x 4 km cells.*

Furthermore, the extinction of heathland and forest species in the study area is significantly linked with changes in land use. The percentage of heathland (r_s= -0.641; p<0.001) and forest (r_s=-0.281; p=0.079) species per grid cell that has gone extinct is significantly negatively correlated with the relative amount of heathland and forest present in 1775, that remained forest or heathland until now (Fig. 2.4). Consequently, grid cells where larger amounts of heathland and forest have been transformed into agricultural land, industrial areas or built-up zones, have lost a higher number of heathland and forest species. Additionally, the current number of heathland species per grid cell is significantly positively correlated with the heathland area per grid cell on the map of 1775. The same holds for the number of forest species (Table 2.5). Both are also significantly related with the forest area in 1850 (Table 2.5). Hence the former presence of heathland or forest in the area still affects current heathland and forest species diversity. The significant correlation between the number of heathland species and forest area on the Biological Evaluation Map further confirms the strong link between forest and heathland in the study region (Table 2.5).

Table 2.5 *Spearman rank correlations between the current number of forest and heathland species and the area of heathland and forest per grid cell on the different historic maps.*

	Number of heathland species		Number of forest species	
Heathland 1775	0.535	***	0.347	*
Forest 1775	0.323	*	0.408	**
Heathland 1850	0.258		0.145	
Forest 1850	0.615	***	0.549	***
Heathland 1985	0.649	***	0.398	*
Forest 1985	0.743	***	0.710	***

***: $p<0.001$; **: $0.001 \leq p<0.01$; *: $0.01 \leq p<0.05$

Discussion

Species loss

Despite the large losses of habitat, especially for heathland (over 99% since 1775, and probably a lot more as the map of 1000 indicates), extinction numbers calculated in this study (11 % for both heathland and forest species over a 210 year time period) are relatively small. The historic records which yielded these figures date from different periods over a time span of about 150 years (1792-1939). As a result, it is difficult to calculate the rate of species extinction from these figures, as a species could have gone extinct since the recording of the oldest record (1792) or at the end of the period studied (1939). Consequently, the worst case scenario indicates an extinction rate of 0.30 heathland or forest species or 0.18% per year (period 1939-2003). At best, an extinction rate of 0.09 species or 0.06% per year can be determined (period 1792-2003). However, since the oldest list showing extinct species dates from 1874 (Vander Meersch, 1874), an extinction rate of 0.15 species or 0.09% per year over this 130-year period is more realistic.

These values are small compared with those given in other studies investigating species loss (e.g. cities and surrounding: 1 species or 0.22% per year (Turnhout, Belgium) (Van der Veken et al., 2004), 1.5 species or 0.36% per year (Boston, US) (Drayton and Primack, 1996), 3 species or 0.26% per year (Plzen, Czech Republic) (Chocholouskova and Pysek, 2003); forests and prairies: between 0.36% and 2.2% per year (Waller and Rooney, 2004)). This could be explained by the fact that most records date from times when large areas of heathland had already been lost, so some species possibly were already extinct at that time. Additionally, most heathland and forest species possess certain plant traits that have often been linked to prolonged survival after habitat loss or deteriorating environmental conditions, like a long term persistent seed bank (heathland species) or a long life-span (forest species). Hence these extinction rates probably represent an extinction debt, indicating that the effects of habitat loss have not fully manifested yet.

Ecological drivers of plant species decline

Soil nutrient content (Ellenberg et al., 1992) turned out to be a major determinant of changes in plant species distributions, especially for forest species. Species adapted to nutrient-poor conditions are significantly more threatened than species characteristic for nutrient-rich habitats. This is a general trend found in many studies (e.g. Bobbink et al., 1998; McCollin et al., 2000; Van der Veken et al., 2004; Smart et al., 2005). As the study area is situated in one of the most intensive areas of livestock industry in Belgium, atmospheric deposition in this region is very high, amounting to over 60 kg N/ha.yr^{-1}, and locally even to more than 70 kg N/ha.yr^{-1}. These values are far above the mean yearly average for Flanders (45 kg N/ha) (Overloop et al., 2004) and the mean critical loads for forests, heathlands and acid grasslands (Van Avermaet et al., 2004). Greater levels of atmospheric deposition became obvious since the beginning of the seventies (Overloop et al., 2004), which coincides with the start of the period for which recent abundances were calculated (1972-2003).

Increased atmospheric deposition rates have been found to be one of the major threats to the biodiversity of natural and semi-natural habitats in Europe in recent decades (e.g. Bobbink et al., 1998). Many of these ecosystems are nutrient-limited, and their plant species are adapted to these conditions. Increased nitrogen addition results in changed competitive interactions and the outcompeting of species adapted to these nutrient-poor conditions by nitrophilic species (Bobbink et al., 1998; Lee, 1998). In heathlands for example, atmospheric deposition has been shown to be responsible for decreasing species diversity, especially related to the extinction of endangered characteristic heathland species, and changes in species composition, mainly a shift in dominance from dwarf shrub to grass species (e.g. Bakker and Berendse, 1999; Roem and Berendse, 2000; Roem et al., 2002).

This importance of changed nutrient conditions in the decline of many of the species studied, especially the forest species, is further confirmed by the significant differences in standardized residuals between forest species' plant strategies (Grime et al., 1988). Competitive species have increased at the expense of species with a strong S-component, hence species adapted to some kind of stress, in this case especially nutrient-poor conditions due to the intrinsic nature of the habitats studied (and for forest species also limited light availability). The lack of a significant effect for the heathland species can be due to the fact that these species are almost exclusively stress tolerators, and other strategy types are underrepresented.

Also most other plant traits affecting the survival probability of the studied species differ between heathland and forest species. For heathland species, the possibility to build up a long living seed bank and the ability to propagate vegetatively form the most important traits enhancing a heathland plant species' chances for survival. Since many of the characteristic heathland species have a long term persistent seed bank, this probably explains the relatively limited extinction rate of these species in the region, despite the catastrophic reduction in heathland area. The species can survive in the forest that replaced many of the heathlands, and when conditions become favorable again, e.g. when forest parcels are clearcut, or along forest roads or in open places in the forests, they can reappear and replenish the seed bank, assuring their survival for another few decades.

For forest species, growth form and ecological amplitude are the traits related most with species survival. Woody species show much lower chances of decline than herbaceous species, with fern and gramineous species having intermediate values. This is probably related to the much longer life span of the woody species, compared to the other species groups. The effect of life span itself however is difficult to test as most of the studied species are perennials. Moreover, since values for the mean number of years a species can survive are hardly available, effects of life span as a continuous variable cannot be tested either, and growth form is probably the best surrogate for life span.

Effects of land use change

Extinction rates are highest in grid cells that lost a large proportion of forest or heathland, i.e. in grid cells where these (semi-) natural land use types have been replaced by agriculture, industry, housing and other infrastructure. The highly significant correlation between the current number of heathland species in a 4 x 4 km grid cell and the area of heathland on the map of Ferraris further indicate that most characteristic heathland species can still be found there, and probably survive in the forests that replaced the heathlands through their seed bank, or in some of the remaining small heathland relics.

Strengths and limitations of using historic data

Past criteria and methods do often not match present day standards. Working with historical data thus inherently incorporates some difficulties. Floristic records from different time periods and different sources can differ in recording effort and the species surveyed. Historical floristic data rarely give a complete view of the plant community present in a certain area. Usually the focus was on the rare species, and species that were too frequent or not considered to be botanically interesting were not included (e.g. Pâques, 1880). Consequently, it is not known what other species were present at the time of recording or how they evolved, and only species decline can be studied.

Another problem in comparing older and recent vegetation data is retrieving the exact location of the older data. Early botanical records, e.g. Roucel (1792), often only provide a rough description of where a certain species was found. Hence they cannot be assigned to one exact place, and have to be allocated to a larger area where the record could have been made. However, since almost no direct comparisons of grid cells over the different time periods were involved in the analyses used, this is not expected to bias results.

Despite their limitations and difficulties, historic records can provide valuable insights in the evolution of the flora of a certain area over a large time span. Analyses of this kind can document how the flora has changed as a result of human activities in the past and can reveal the categories of species especially sensitive to extinction. This knowledge can be a very useful tool in focusing conservation efforts to prevent future extinctions.

Guidelines for conservation

Despite the high area losses, the number of extinct heathland plant species is relatively low. This can probably be explained by the fact that many heathland species can survive in the forests that replaced most of the heathlands in the study area. The ability to build up a long term persistent seed bank (e.g. Bossuyt and Hermy, 2003) is one of the most important traits ensuring the survival of heathland species. However, the changed forestry practices, promoting indigenous deciduous forest species with much longer rotation times, can be a severe threat for these species. Furthermore, this relatively low number of species extinctions can point at the presence of an extinction debt (Tillman et al., 1994). It can be expected that the heathland plant community has not fully adapted yet to the drastic area losses, because specific plant traits delay the plant’s responses to the changed conditions. Hence the new equilibrium species number has not been reached so far and future extinctions are expected unless environmental conditions are improved (Hanski and Ovaskainen, 2002). Heathland restoration and the prevention of further heathland area losses are needed. For the heathland species, especially species that cannot build up a long term persistent seed bank or do not possess the ability for vegetative propagation are threatened most. Consequently, conservation efforts should focus on these species.

Appendix 2.1 Overview of historical sources used the study

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2. Baguet, C., 1891. Notes sur quelques localités nouvelles de plantes rares ou assez rares de la flore Belge. Bulletin de la Société Royale de Botanique de Belgique 30, 177-191.
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4. Crépin, F., 1860. Manuel de la flore de Belgique. Gustave Mayolez, Bruxelles.
5. Crépin, F., 1865. Notes sur quelques plantes rares ou critiques de la flore belge. Hayez, Bruxelles.
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7. De Langhe, J. E., 1943. Quelques notes floristiques. Bulletin de la Société Royale de Botanique de Belgique 75, 137-140.
8. Delvosalle, L., 1961. A propos de certaines cartes de dispersion. Bulletin de la Société Royale de Botanique de Belgique 93, 137-150.
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19. Fabri, R., 1991. *Oenanthe peucedanifolia-Oenanthe silaifolia* (*Apiaceae*), une confusion tenace. Notes sur deux autres Oenanthe de la flore Belge. Bulletin de la Société Royale de Botanique de Belgique 124, 47-59.
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Oostkamp (prov. West-Flanders, Belgium). Bulletin de la Société Royale de Botanique de Belgique 114, 125-139.

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27. MacLeod, J., 1893. Over de bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen. Botanisch Jaarboek Dodonaea 5, 156-452.
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Appendix 2.2 List of the heathland and forest species found in the historical sources, their standardized residuals and plant traits.

Species	H/F	StRes	HA	PA	SLI	L	T	F	R	N	EcolAmp	SB	Strat	VegSp	GrF
Aegopodium podagraria	F	1.882	4	40	0.33	5	5	6	7	8	0	1	CS	1	2
Agrimonia eupatoria	F	-0.228	4	15	0.10	7	6	4	8	4	1	1	CSR	0	2
Agrostis canina	H	-0.658	5	16	0.49	9	5	9	3	2	1	3	CSR	1	3
Agrostis capillaris	H	0.852	6	40	0.66	7			4	4	1	3	CSR	1	3
Aira caryophyllea	H	-0.658	5	16		9	6	2	4	1	0		SR	0	3
Aira praecox	H	0.439	5	29	1	9	6	2	2	1	0	3	SR	0	3
Alliaria petiolata	F	-0.245	6	27	0.43	5	6	5	7	9	1	2	5CR	0	2
Antennaria dioica	H	-0.979	3	0	0	8		4	3	2	0		S	1	2
Asplenium scolopendrium	F	-0.042	2	5		4	5	5	8	4	0		S	0	1
Athyrium filix-femina	F	1.114	5	37		3		7		6	0		C	1	1
Betula alba	F	0.684	6	38	0.45	7		8	3	3	1	3	C	0	4
Blechnum spicant	F	1.123	4	31		3		6	2	3	0		S	0	1
Botrychium lunaria	H	-0.295	2	2		8		4		2	1		SR	0	1
Bromus sterilis	F	0.768	6	39	0	7	6	4		5	1	1	R	0	3
Calamagrostis epigejos	F	1.114	5	37	0.43	7	5			6	1	2	C	1	3
Calluna vulgaris	H	0.599	6	37	0.88	8			1	1	1	3	CS	1	4
Campanula rotundifolia	H	-1.764	6	9	0.40	7	5			2	0	2	S	0	2
Carex binervis	H	0.371	3	16	0.60	7	5	7	1	1		3	S	1	3
Carex echinata	H	-0.650	4	10	0.17	8		8	3	2	0	1	S	1	3
Carex elongata	F	-0.557	3	5	0	4	6	9	7	6	0		CS	1	3
Carex lasiocarpa	H	-0.810	3	2	0.50	9	4	9	4	3	0		CS	1	3
Carex nigra	H	-0.836	6	20	0.19	8		8	3	2	1	1	S	1	3
Carex panicea	H	-0.734	4	9	0.35	8		8		4	0	2	S	1	3
Carex rostrata	H	-1.418	5	7	0.20	9		10	3	3	1	1	CS	1	3
Carex strigosa	F	0.051	1	0		3	6	7	7	6	0	3	S	1	3
Carex sylvatica	F	0.034	3	12	0.67	2	5	5	6	5	0	3	S	1	3
Carpinus betulus	F	1.553	3	30	0	4	6				0	1	CS	1	4
Centaurium erythraea	F	0.279	4	21	1	8	6	5	6	6	1	3	SR	0	2
Ceratocapnos claviculata	F	0.962	3	23		5	6	5	3	6	1		SR	0	2

Species	**H/F**	**StRes**	**HA**	**PA**	**SLI**	**L**	**T**	**F**	**R**	**N**	**EcolAmp**	**SB**	**Strat**	**VegSp**	**GrF**
Chaerophyllum temulum	F	0.430	6	35	0.67	5	6	5		8	1	3	R	0	2
Clematis vitalba	F	0.043	2	6	1	7	6	5	7	7	1		CS	0	2
Comarum palustre	H	-0.379	2	1	0.13	8		9	3	2	0	1	S	1	2
Corydalis solida	F	0.136	1	1	0	3	6	5	7	7	0		CSR	0	2
Corynephorus canescens	H	-1.755	5	3	1	8	6	2	3	2	0	3	CS	0	3
Crataegus monogyna	F	0.852	6	40	0	7	5	4	8	4	1	1	CS	0	4
Cuscuta epithymum	H	-0.979	3	0						2	1	3		0	2
Cytisus scoparius	H	1.283	5	39	0.67	8	5	4	3	4	0	3	CS	0	4
Dactylorhiza maculata	H	-1.249	5	9		7		8		2	1		S	0	2
Danthonia decumbens	H	-0.067	5	23	0.29	8			3	2	1	2	S	1	3
Deschampsia flexuosa	F	0.026	4	18	0.08	6			2	3	1	1	S	1	3
Diphasiastrum tristachyum	H	-0.464	2	0		8	6	5	1	1	0		CSR	1	1
Drosera intermedia	H	-0.903	4	7	1	9	5	9	2	2	0		S	1	2
Drosera rotundifolia	H	-1.333	5	8	1	8	4	9	1	1	1	3	S	1	2
Dryopteris cristata	H	0.220	1	2		4	6	9	5	6	1		CS	1	1
Dryopteris filix-mas	F	1.114	5	37		3		5	5	6	1	1	CS	1	1
Epilobium angustifolium	F	1.798	4	39	0.57	8		5	5	8	1	3	C	1	2
Epilobium palustre	H	-1.240	4	3	0.33	7	5	9	3	2	0	2	S	1	2
Epilobium roseum	F	-0.987	4	6	0	7	6	9	8	8	1		CSR	1	2
Epipactis helleborine	F	1.469	3	29		3	5	5	7	5	1		S	1	2
Erica cinerea	H	0.380	2	10	0.75	7	6	5	2	1	0	3	S	1	4
Erica tetralix	H	-0.489	5	18	0.41	8	5	8	1	2	1	3	S	1	4
Eriophorum polystachion	H	-1.840	5	2	0.15	8		9	4	2	1	1	S	1	3
Fagus sylvatica	F	2.144	3	37	0	3	5	5			1	1	CS	0	4
Filago minima	H	-1.755	5	3	0.33	9	6	2	4	1	0	1	SR	0	2
Fragaria vesca	F	-0.574	5	17	0.35	7		5		6	1	2	CSR	1	2
Frangula alnus	F	1.114	5	37	0	6	6	8	4		1	1	C	0	4
Galium palustre	H	0.852	6	40	0.26	6	5	9		4	1	2	CR	1	2
Galium saxatile	H	0.017	5	24	0.50	7	5	5	2	3	1	3	S	1	2
Galium uliginosum	H	-0.219	3	9	0.12	6	5	8		2	1	1	S	1	2
Genista anglica	H	-1.333	5	8	0	8	5	5	2	2	0	1	CS	0	4
Genista pilosa	H	-1.418	5	7	0	7	5		2	1	0		CS	0	4
Gentiana pneumonanthe	H	-0.979	3	0		8	5	7		1	0		CSR	0	2
Geranium robertianum	F	0.684	6	38	0.47	5				7	0	2	R	0	2

Species	H/F	StRes	HA	PA	SLI	L	T	F	R	N	EcolAmp	SB	Strat	VegSp	GrF
Glechoma hederacea	F	0.852	6	40	0.17	6	6	6		7	1	1	CSR	1	2
Gnaphalium sylvaticum	F	-1.156	4	4	1	8		5	4	6	0	3	SR	1	2
Gymnocarpium dryopteris	F	-0.464	2	0		3	4	6	4	5	0		S	1	1
Hieracium lachenalii	F	-1.587	5	5		5	5	4	4	2			S	1	2
Hieracium sabaudum	F	-0.472	3	6		5	6	4	4	2	0		S	1	2
Holcus mollis	F	1.283	5	39	0	5	5	5	2	3	1	1	C	1	3
Huperzia selago	H	0.051	1	0		4	3	6	3	5	0		S	1	1
Hydrocotyle vulgaris	H	0.692	5	32	0.27	7	5	9	3	2	1	3	CSR	1	2
Hypericum perforatum	H	1.367	5	40	0.90	7	6	4	6	4	0	3	CR	1	2
Hypericum pulchrum	F	0.101	5	25	1	4	6	5	3	2	0	3	S	0	2
Inula conyzae	F	0.051	1	0	1	6	6	4	7	3	1		S	1	2
Jasione montana	H	-0.152	5	22	0	7	6	3	3	2	0	1	S	0	2
Juncus acutiflorus	H	0.355	5	28	0.64	9	6	8	5	3	0	3	CS	1	3
Juncus conglomeratus	H	0.684	6	38	0.51	8	5	7	4	3	1	2	C	1	3
Juncus filiformis	H	0.051	1	0	0.36	7	4	9	4	3	0	2	CSR	1	3
Juncus squarrosus	H	0.541	3	18	0.86	8	5	7	1	1	0	3	S	1	3
Lamium album	F	0.852	6	40	0.65	7		5		9	1	3	CR	1	2
Lapsana communis	F	0.852	6	40	0.95	5	6	5		7	0	3	R	0	2
Lathyrus linifolius	H	-0.379	2	1	0		5	5	3	2	0		S	1	2
Listera ovata	F	-0.396	4	13		6		6	7	7	0		S	1	2
Lonicera periclymenum	F	1.798	4	39	0	6	5		3	4	1	1	CS	0	4
Luzula campestris	H	0.852	6	40	0.37	7		4	3	3	1	2	S	1	3
Lycopodiella inundata	H	-0.042	2	5		8	4	9	3	1	0		CS	1	1
Lycopodium clavatum	H	-0.379	2	1		8	4	4	2	2	0		S	1	1
Lysimachia thyrsiflora	H	-0.464	2	0	0	7	6	9		4	0	1	C	1	2
Maianthemum bifolium	F	-0.143	4	16	0	3		5	3	3	0	1	S	1	2
Melampyrum pratense	F	-1.595	6	11	0	6	5	5	3	2	0	1	SR	0	2
Mibora minima	H	-0.126	2	4	1	8	8	3	4	3	0		R	0	3
Moehringia trinervia	F	2.060	3	36	0.69	4	5	5	6	7	0	3	SR	0	2
Molinia caerulea	H	1.114	5	37	0.36	7		7		2	1	2	CS	1	3
Monotropa hypopitys	F	-0.464	2	0	0	4		5	3	2	0			1	2
Montia fontana	F	-1.494	4	0	0.50	8	4	9	5	4	1	3	R	1	2
Mycelis muralis	F	-0.472	3	6	0.50	4	6	5		6	1	1	CSR	0	2
Myosotis arvensis	F	0.599	6	37	0.75	6	6	5		6	1	3	R	0	2

Species	H/F	StRes	HA	PA	SLI	L	T	F	R	N	EcolAmp	SB	Strat	VegSp	GrF
Myrica gale	H	-1.333	5	8	0	8	6	9	3	3	0	1	CS	1	4
Nardus stricta	H	-0.827	5	14	0.20	8			2	2	1	1	S	1	3
Narthecium ossifragum	H	0.220	1	2	0.50	8	4	9	2	1	0		S	1	2
Neottia nidus-avis	F	-0.464	2	0		2	5	5	7	5	0			1	2
Ophioglossum vulgatum	H	-0.894	3	1		7	6	7	7	2	0		SR	1	1
Ornithogalum umbellatum	F	0.017	5	24	0	6	6	5	7	7	0		CSR	1	2
Ornithopus perpusillus	H	0.777	5	33	0	7	6	3	2	2	0	2	SR	0	2
Orobanche rapum-genistae	H	-0.135	3	10			6	5	3	2	0			0	2
Osmunda regalis	F	-0.388	3	7		5	6	8	4	5	1		C	0	1
Oxalis acetosella	F	-0.312	4	14	0.27	1		5	4	6	0	1	S	1	2
Pedicularis palustris	H	-1.924	5	1	1	8		9		2	0	2	CS	0	2
Pedicularis sylvatica	H	-1.502	5	6	0	7	5	8	1	2	1	1	SR	0	2
Peucedanum palustre	H	-0.396	4	13	0	7	6	9		4	1	1	CS	1	2
Platanthera bifolia	H	-0.810	3	2		6		5	7		1	1	CSR	0	2
Polygala serpyllifolia	H	0.110	4	19	0.50	8	4	6	2	2	0	1	S	0	2
Polygonatum multiflorum	F	1.629	4	37	0	2		5	6	5	0	1	CS	1	2
Polypodium vulgare	F	-0.996	5	12		5	5	4	2	2			S	1	1
Polystichum aculeatum	F	0.051	1	0		3	6	6	6	7	0		CS	0	1
Populus tremula	F	1.199	5	38	0	6	5	5			1	1	CS	1	4
Potentilla argentea	H	-1.325	4	2	0.67	9	6	2	3	1	0	3	S	0	2
Potentilla erecta	H	0.777	5	33	0.44	6				2	1	2	S	1	2
Primula elatior	F	0.034	3	12	0	6		6	7	7	1	1	CSR	1	2
Pteridium aquilinum	F	1.283	5	39		6	5	5	3	3	0	1	C	1	1
Pyrola minor	F	-1.494	4	0	0	6		5	3	2	0		S	1	2
Quercus petraea	F	-0.810	3	2	0	6	6	5			0	1	CS	0	4
Quercus robur	F	1.882	4	40	0	7	6				1	1	CS	0	4
Ranunculus auricomus	F	-0.557	3	5	0.08	5	6		7		1	1	SR	1	2
Ranunculus ficaria	F	0.768	6	39	0	4	5	6	7	7	1	1	R	1	2
Ranunculus flammula	H	0.430	6	35	0.63	7		9	3	2	1	3	CR	1	2
Rhynchospora alba	H	0.220	1	2	0.67	8	5	9	3	2	0		S	1	3
Rumex acetosella	H	0.852	6	40	0.69	8	5	3	2	2	1	3	SR	1	2
Salix alba	F	1.199	5	38	0.78	5	6	8	8	7	1	3	C	0	4
Salix aurita	F	0.945	5	35	0.25	7		8	4	3	0		C	0	4
Salix caprea	F	0.852	6	40	0	7		6	7	7	0	1	C	0	4

Species	H/F	StRes	HA	PA	SLI	L	T	F	R	N	EcolAmp	SB	Strat	VegSp	GrF
Salix cinerea	F	-1.587	5	5	0	7		9	5	4			C	1	4
Salix repens	H	1.824	1	21	0	8	5	7			1	1	CS	1	4
Sanicula europaea	F	-0.219	3	9		4	5	5	8	6	0	1	S	1	2
Scirpus cespitosus	H	-0.894	3	1	0.14	8	4	9	1	1	0	1	CS	1	3
Scrophularia nodosa	F	0.945	5	35	0.92	4	5	6	6	7	0	3	CR	1	2
Scutellaria minor	H	0.203	3	14	0	7	6	9	2	3	0		S	1	2
Sedum telephium	F	0.878	3	22	0	7	6	4	7		0	1	S	0	2
Selinum carvifolia	H	-0.557	3	5	0	7	5	7	5	3	1	1	CS	0	2
Serratula tinctoria	H	0.296	2	9	0	6	6		7	3	0	1	S	1	2
Solidago virgaurea	F	0.355	5	28	0.06	5		5		4	0	1	S	1	2
Sorbus aucuparia	F	2.397	3	40	0.04	6			4		1	1	CS	0	4
Spergula morisonii	H	0.136	1	1	1	9	5	3		2	0		SR	0	2
Stachys officinalis	F	-0.810	3	2	0.29	7	6			3	0	2	S	1	2
Stachys sylvatica	F	0.684	6	38	0.39	4		7	7	7	0	2	C	1	2
Stellaria alsine	F	0.701	4	26	0.62	5	4	8	4	4	0	3	CR	1	2
Stellaria holostea	F	0.430	6	35	0	5	6	5	6	5	0	1	CSR	1	2
Stellaria palustris	H	-0.219	3	9	0.18	5	5	9	4	2	0	1	CSR	1	2
Succisa pratensis	H	0.616	4	25	0.24	7	5	7		2	0	1	S	1	2
Teesdalia nudicaulis	H	-0.573	5	17		8	6	3	1	1	0	3	SR	0	2
Teucrium scorodonia	F	1.283	5	39	0.60	6	5	4	2	3	0	3	S	1	2
Thymus serpyllum	H	-2.523	6	0		7	6	2	5	1	0		CSR	1	4
Ulmus minor	F	2.406	2	34		5	7		8		1		C	1	4
Urtica dioica	F	0.852	6	40	0.78			6	7	9	1	3	C	1	2
Vaccinium vitis-idaea	H	-0.464	2	0	0.03	5		4	2	1	1	1	S	1	4
Valeriana dioica	H	-1.325	4	2	0	7		8	5	2	0	1	S	1	2
Veronica officinalis	H	0.186	5	26	0.65	6		4	3	4	1	3	S	1	2
Veronica scutellata	H	-0.903	4	7	0.29	8	5	9	3	3	1	3	CR	1	2
Vicia sepium	F	-1.165	5	10	0.04			5	6	5	0	1	C	1	2
Viola canina	H	-0.911	5	13	0.69	7		4	3	2	1	2	S	1	2
Viola palustris	H	-1.502	5	6	0.11	6		9	2	3	0	1	S	1	2
Viscum album	F	-0.979	3	0		7	6						CS	0	4
Vulpia bromoides	H	0.895	1	10	0.33	9	7	3	4	1	0		SR	0	3

H/F: heathland (H) or forest (F) species (Stieperaere and Fransen, 1982); StRes: Standardised residual obtained from the regression between present and historical abundance;

HA: historical abundance category, ranging from 1= very very rare to 6= very common (Crépin, 1860); PA: number of present occupied 4 x 4 km cells (Van Landuyt et al., 2000); SLI: seed longevity index (Thompson et al., 1997); L: Ellenberg indicator value for light; T: Ellenberg indicator value for temperature; F: ellenberg indicator value for soil moisture content; R: Ellenberg indicator value for soil acidity; N: Ellenberg indicator value for soil nutrient content (Ellenberg et al., 1992); EcolAmpl: Ecological Amplitude (0: narrow amplitude; 1: broad amplitude) (Runhaar et al., 1987); SB: seed bank type (1: transient, 2: short term persistent, 3: long term persistent) (Tamis et al., 2004); Strat: plant strategy (Grime et al., 1988); VegSp: ability for vegetative spread (1: present; 2:absent) (Klotz et al., 2002); GrF: growth form (1: fern; 2: herbaceous; 3: gramineous; 4: woody) (Biesbrouck et al., 2001).

CHAPTER 3

PLANT SPECIES RICHNESS AND COMPOSITION OF HEATHLAND RELICS IN NORTH-WESTERN BELGIUM: EVIDENCE FOR A RESCUE EFFECT?

Introduction

Heathlands are one of the principal semi-natural landscapes of the Atlantic parts of Western Europe (Webb, 1998) and they contain a high diversity of specific plant species (de Smidt, 1975; Schaminée et al., 1996; Van Landuyt et al., 1999). Heaths are restricted to nutrient-poor, relatively acid environments and need considerable management to be able to persist, two conditions not achieved easily today (e.g. Aerts and Berendse, 1988; Bullock and Pakeman, 1997; Alonso and Hartley, 1998; Bobbink et al., 1998; Bakker and Berendse, 1999).

Next to the decrease in habitat quality of heathland systems, heathland habitat has also become more and more fragmented. In the past, it extended over several millions of hectares in Europe, but due to the cessation of traditional agricultural practices and changes in land use, total heathland area has decreased strongly (de Smidt, 1975; Gimingham, 1976; Pott, 1996; Webb, 1990; Webb, 1998; Odé et al., 2001). The fragmentation process includes both a reduction of the area and an increase of the isolation of the remaining heathland fragments. Unlike, for example, for forests (e.g., Dzwonko and Loster, 1992; Grashof-Bokdam, 1997; Honnay et al., 1999a) or calcareous grasslands (e.g., Fischer and Stöcklin, 1997; Maurer et al., 2003), we found no studies that have focused on the effects of fragmentation of heathland patches on their plant species richness. The fact that many heathland species, contrary to calcareous grassland species and forest species, form a persistent seed bank (e.g. Bossuyt and Hermy, 2003) may have hampered and complicated fragmentation studies in these habitats, because this dispersal in time can interfere with fragmentation effects.

One of the most commonly found relationships in this context of habitat fragmentation is the decrease in species number with decreasing patch area. Theory predicts that smaller patches contain less species because they are more sensitive to area-dependent extinction processes (Shaffer, 1981; Pimm et al., 1988). Because habitat diversity may also play an important role as determinant for species richness, area-effects on species number can be confounded with habitat diversity-effects. Indeed, larger fragments often contain a wider variety of abiotic conditions (e.g. Honnay et al., 1999b; Brose, 2001). The decrease in species richness due to increased extinction rates can theoretically be counteracted by the colonization of individuals of species, the so-called rescue-effect (Brown and Kodric-Brown, 1977). The rescue effect can be defined as the averting of extinction by the colonization of conspecifics from nearby patches. This, however, is only possible when habitat patches are not too isolated for a species to be able to bridge the distance between the patches. In the other case the process of species relaxation may lead to a new lower equilibrium species number in the relic patches.

Although species number is probably the most studied aspect of plant communities, species number as such does not give a complete view of a plant community (Worthen, 1996). Communities with the same total species number can be composed of a completely different set of species, and hence community composition is another important aspect to be investigated. Communities of fragmented habitats often exhibit non-random patterns of species composition. A frequently observed example of such a non-random pattern of species composition is the nested subset pattern. This can be defined as a system where each species is present in all fragments richer than the most depauperate one in which that species occurs (Patterson and Atmar, 1986). Several mechanisms can cause this pattern. In most cases area-dependent extinction processes seem to be the underlying factors causing nestedness (Patterson and Atmar, 1986; Patterson, 1987; Lomolino, 1996; Kerr et al., 2000; Hecnar et al., 2002; Mac Nally et al., 2002; Bruun and Moen, 2003). Nestedness can also be the result of differential colonization caused by a difference in the degree of isolation of the habitat fragments (Cook and Quinn, 1995; Kadmon, 1995; Lomolino, 1996; Sfenthourakis et al., 1999; Butaye et al., 2001), nested habitats (Honnay et al., 1999c; Sfenthourakis et al., 1999) or passive sampling (Connor and McCoy, 1979).

Heathlands in the north-western part of Belgium have been subjected to a fragmentation process that started some 200 years ago (chapter 2). The once dominating heaths are now restricted to small relics. Since the 18th century, heathland area in the region has continuously decreased, from almost 10000 ha at the end of the

18th century to less than 100 ha of heathland fragments, scattered through the landscape nowadays. They thus seem to form an excellent example to study the effects of fragmentation.

The aims of this part of the study are to investigate whether the effects of the decreased area and increased isolation are reflected in species richness and species composition of the remaining heathland patches. To achieve this, we will

- study the effects of the degree of fragmentation on present species richness
- study the effects of the degree of fragmentation on species composition
- infer the most likely ecological mechanism behind the observed patterns.

Materials and Methods

Study area

The study area is located in the north-western part of Belgium, in the region south of Bruges (Fig. 3.1). Total area of the investigated region comprises about 35 x 20 km², and largely coincides with the area studied in chapter 2. Heathland, for a long time an important part of the landscape in this region, is now limited to very small relics due to a fragmentation process that started some 200 years ago (chapter 2).

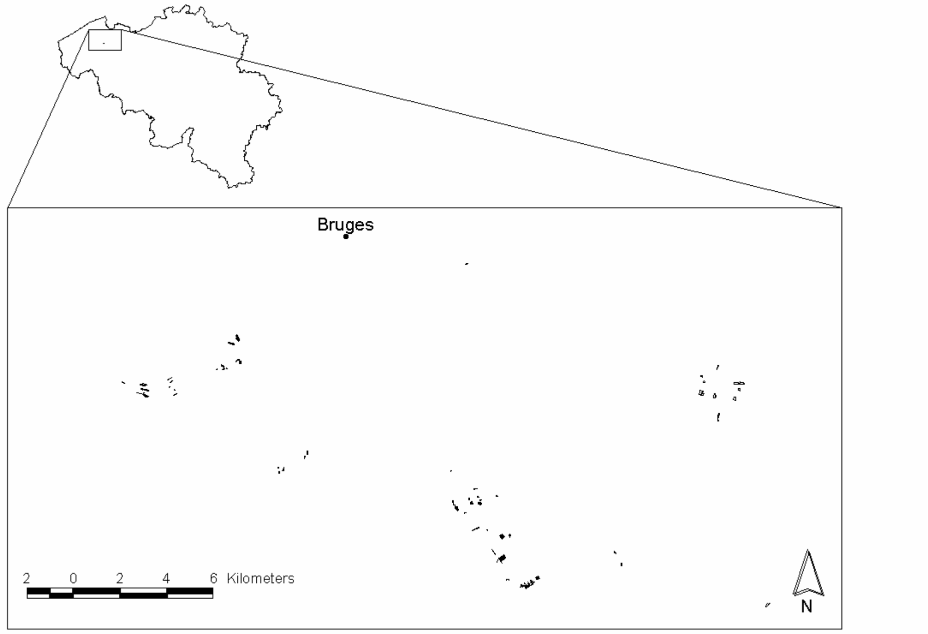


Fig. 3.1 *Location of the study area*

Although the heaths in this area are highly fragmented, the relic patches are unique from a conservation viewpoint because they form a transition between the northern Atlantic heaths of the Campine region and the Atlantic heaths of southern England and northern France (Stieperaere, 1969). Plant species typical for Atlantic regions, like for example *Erica cinerea* and *Carex binervis*, and species with a northern Atlantic or boreal character, such as *Eriophorum polystachion*, *Calluna vulgaris* and *Erica tetralix* (Van Rompaey et al., 1972), occur together here.

The studied area is separated from other heathland areas in the east by the industrial area and build-up area of the surroundings of Ghent and its harbour, and from heathland areas in the south by a large, intensively used agricultural area, so the possible inflow of heathland species from these areas is negligible.

Data collection

During the summer of 2002 the presence or absence of plant species was recorded in 153 fragments of heathland and related vegetation types, such as grassheaths, species-poor and acid grasslands and roadsides. This resulted in an area covering survey of all heathland vegetation in a zone of 35 x 20 km². Patches were all inventoried by two persons simultaneously by walking transects through the patch. The time spent in each patch was proportional to its size and heterogeneity. All patches were situated in areas formerly occupied by one of the large heathland areas of the De Ferraris-map. The species lists were checked and supplemented with data available from recent inventories from local botanists and nature conservation organizations. A total of 248 plant species was found, of which 54 belong to the groups of heathland, grassheaths or acid grasslands, as defined by Stieperaere and Fransen (1982). These species are listed in the appendix. Nomenclature follows Lambinon et al. (1998). Some measures describing the species richness of the patches are listed in Table 3.1.

For each patch also a set of variables describing the abiotic conditions of the patch was recorded: the management types (grazing, mowing, sod cutting), the vertical structure of the vegetation and the occurrence of microhabitats like ditches, roads, pools, microrelief, Molinia-tussocks, … in the patch and bordering the patch were recorded. From this the number of microhabitas and the number of management types per patch was calculated. Afterwards each patch was digitised using ArcView 3.2 (ESRI, 2000) and overlaid with the digital soil map (scale 1/20 000). This made it possible to determine the number of different soil types found in each patch. The soil type is a unique combination of soil substrate, soil texture class, soil moisture level class and soil profile development, as defined in the Belgian soil classification (IWONL, 1950).

Table 3.1 *Minimum, maximum and mean of total species richness (NTOT) and of the number of heathland specific species (NHSP) per patch, and their relation (N=153).*

	Minimum	**Maximum**	**Mean**
NTOT	7	86	28.1
NHSP	2	27	9.5
NHSP/NTOT (%)	12	80	34.62
Spearman Rank Correlation NHSP-NTOT: r = 0.852 (p<0.001)			

Isolation measures

For each patch, several isolation measures were calculated. Three types of isolation measures were used: linear isolation measures, buffer measures and connectivity measures. The first category quantifies isolation of a patch by using distance to other patches in the neighbourhood. In its simplest form, this isolation measure is the distance to the nearest heathland patch (DIST1). We also calculated the mean distance to the five nearest heathland patches (DIST5). Because these measures oversimplify reality, they often fail to describe isolation adequately. Both other categories not only consider distance, but also take into account area, and are in many cases superior to linear isolation measures (Moilanen and Nieminen, 2002). Buffer measures calculate the amount of heathland occurring in a buffer of a certain threshold distance around the focal patch. In this study, area in buffers of 100m (A100) and 500m (A500) around the patches was calculated. These distances were chosen because plant species not often migrate over large distances, and 500m seems to be a good threshold (Grashof-Bokdam, 1997; Butaye et al., 2001). Because patches in the close neighbourhood will probably be more important contributors to species richness of a patch than patches further away, also the distance of 100m was used. Finally, the connectivity measure (Hanski, 1994) takes into account distances to all other heathland patches and combines area and distance by weighing the distance to a patch by its area. This measure is calculated using the equation $IFM_i = \sum A_j \exp(-\alpha d_{ij})$

(Hanski, 1994), where i symbolizes the focal patch, j each of the other patches, d_{ij} is the edge-to-edge distance from patch i to patch j and A_j is the area of patch j. The constant α is a parameter to scale the effects of the dispersal capacities of the species. Because the value of this constant was not known, different values of α (1 to 5) were tried (Bastin and Thomas, 1999; Johansson and Ehrlén, 2003).

Data analysis

First the species richness of the heathland patches was examined. Because matrix species can obscure trends in species richness (Cook et al., 2002) only the 54 species characteristic for the investigated vegetation types were included in further analyses. These include species belonging to the socio-ecologic groups of dry heath, wet heath, grassheath and acid grassland, as defined by Stieperaere and Fransen (1982) (see appendix). To rule out the possibility that these species are only occupying niches left empty by the other 194 species, an extra preliminary analysis was performed. For each patch, a four-dimensional habitat space was calculated (Pärtel et al., 1996). This is a four-dimensional hypervolume determined by the minimum and maximum values for the Ellenberg indicator values (Ellenberg et al., 1992) for the factors light, soil moisture, pH and soil nutrient status of the non-heathland species present in that patch (Butaye et al., 2001). Then it was tested for each of the 54 heathland species occurring in that patch if their Ellenberg indicator values for these factors fall within the range determined by the non-heathland species. This analysis, performed using the program developed by Butaye et al. (2001), yielded a median value of 1.96% of the patches being occupied by a species which could not be present there based on the range determined by the habitat space model, and thus occupying niches left unoccupied by the other species. From this, it can be concluded that most species occur in patches where they experience competition from other species, and that keeping the species not characteristic for heathland out of the following analyses does not mask possible competitive effects of these species. Using exclusively the species characteristic for heathland can only make the analysis more meaningful.

In a first step, the effects of habitat diversity on species richness were investigated. A principal component analysis (PCA) was performed on the habitat variables to obtain an overall measure of habitat diversity. The scores of the 153 patches on the first PCA-axis were then correlated with species richness (NHSP) using Kendall Tau Correlations (Siegel and Castellan, 1988). We used Kendall Tau Correlations instead of the more commonly used Spearman Rank Correlations as this is a non-parametric correlation coefficient enabling the calculation of partial correlations (see below).

The influence of isolation and area on species richness (NHSP) was examined using Kendall Tau Correlations. When both area and isolation had significant effects on species richness, Kendall Tau Partial correlations (Siegel and Castellan, 1988) were used to determine whether isolation-effects also remained after area has been controlled for.

Because some heathland species have a long term persistent seed bank, these species are possibly less sensitive to isolation or area effects. To investigate the possible effects of the seed bank, the seed longevity index (SLI) (Bekker et al., 1998) was calculated for each of the encountered species. This index is calculated based on the number of records for a species in one of the 3 seed bank types (transient (*T*), short-term persistent (*SP*), long-term persistent (*LP*)) in the database of Thompson et al. (1997), using the formula $SLI = (SP + LP)/(T + SP + LP)$ (Bekker et al., 1998). The higher the value of this index, the more persistent the seed bank of the species is. All the species encountered were arbitrarily subdivided in four groups according to the value of this index (*SLI1*: $0 \leq SLI < 0.25$; *SLI2*: $0.25 \leq SLI < 0.5$; *SLI3*: $0.5 \leq SLI < 0.75$; *SLI4*: $0.75 \leq SLI \leq 1$). Number of species in each of the 4 categories was then correlated with the isolation measures and area. For each patch, also the median seed longevity index was calculated and correlated with species richness.

Finally, species composition of the heathland patches, based on the 54 heathland-specific species, was investigated. It was tested whether these patches show the pattern of a nested subset. The most commonly used method to test for nestedness is the Matrix Temperature approach developed by Atmar and Patterson (1993). This procedure arranges the presence-absence matrix in a way the number of deviations from a perfectly nested matrix (unexpectedness) is minimal. This unexpectedness is then standardized to the matrix temperature T to allow comparison between matrices of different sizes. Significance is determined by comparing the observed matrix temperature to the temperatures calculated for 1000 randomly ordered matrices. By correlating the ranks of the sites in the maximally packed matrix with area and isolation, the factor potentially underlying this pattern can be determined.

Because it has been shown that this method sometimes leads to false conclusions (Fischer and Lindenmayer, 2002), the method of Lomolino (1996) was used also. It sorts the matrix by species richness, habitat diversity, area or isolation, and then calculates deviation from perfect nestedness (D) by scanning down the matrix and recording the number of times the absence of a species is followed by its presence on the next (lower) patch. Statistical significance is estimated by comparing the observed number of departures to those obtained for 1000 randomly ordered matrices. By calculating the percent of perfect nestedness (%PN) using the formula %PN=100*(R-D)/R, with R being the mean number of departures for the random simulations, a measure quantifying nestedness is obtained. We wrote a program in C++ to perform these calculations. This program was derived from that originally developed by Lomolino (1996).

Results

One PCA-axis with an eigenvalue greater than 1 could be extracted, explaining 53% of the variance in the habitat variables. The PCA factor loadings of the habitat variables were 0.77 for the number of microhabitats, 0.74 for the number of management types and 0.67 for the number of soil types per patch. Correlating this axis with species richness did not show any significant effects ($\tau=0.08$; $p=0.19$), so habitat diversity does not seem to have a significant influence on the species richness of the investigated heathlands.

Table 3.2 *Kendall Tau correlations between species richness (NHSP) and area and isolation measures (N=153).*

	Area	**DIST1**	**DIST5**	**A100**	**A500**	**IFM**
NHSP	0.147 **	-0.170 **	-0.197 ***	0.223 ***	0.222 ***	0.249 ***

****: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$; (*): $0.05<p\leq0.1$*

DIST1: distance to the nearest heathland patch; DIST5: mean distance to the 5 nearest heathland patches; A100: area of heathland in a buffer of 100m surrounding the focal patch; A500: area of heathland in a buffer of 500m surrounding the focal patch; IFM: Hanski connectivity measure.

However, both isolation and, to a lesser extent, area affect the species richness of the heathland patches (Table 3.2). The fact that isolation seems to be the most important factor is confirmed when correlations between species richness and the different isolation measures are controlled for patch area. The correlation coefficients remain almost unchanged, as well as their significance (Table 3.3).

Table 3.3 *Kendall Tau partial correlations between species richness (NHSP) and isolation measures, controlled for area (N=153) (abbreviations: see table 3.2).*

	DIST1	DIST5	A100	A500	IFM
NHSP	-0.159 **	-0.196 ***	0.209 ***	0.221 ***	0.239 ***

****: p<0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1*

Correlating the median seed longevity index per patch with its species richness does not yield significant correlations (τ=-0.028; p=0.62). However, correlating the number of species in the SLI-groups with the isolation measures does indicate some significant effects. Generally, species belonging to the groups with the lowest seed longevity indices, thus being the species with short living seed banks, seem to be more affected by isolation than species with long term persistent seed banks (Table 3.4). Correlations between number of species in the SLI-groups with area are less straightforward. Particularly the number of species in the lowest and highest SLI-category show significant correlations with area (Table 3.4).

Table 3.4 *Kendall Tau correlations between the number of species in the different categories of the seed longevity index and isolation measures and area (N=153).*

	SLI1	SLI2	SLI3	SLI4
Number of species	74	52	45	49
DIST1	-0.068	-0.248 ***	-0.040	-0.073
DIST5	-0.100	-0.266 ***	-0.047	-0.094
A100	0.145 *	0.254 ***	0.147 *	0.137 *
A500	0.238 ***	0.348 ***	0.152 **	0.061
IFM	0.244 ***	0.328 ***	0.189 **	0.132 *
Area	0.264 ***	0.101 (*)	0.180 **	0.269 ***

***: p<0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1

SLI1: number of species with 0≤SLI<0.25; SLI2: number of species with 0.25≤SLI<0.5; SLI3: number of species with 0.5≤SLI<0.75; SLI4: number of species with 0.75≤SLI≤1; other abbreviations: see table 3.2.

Based on the algorithm of Atmar and Patterson (1993) the species composition of the investigated heaths (T=11.24) shows a significantly nested subset pattern (p<0.001). This pattern seems to be primarily determined by isolation. Area explains only a small part of this ordering (Table 3.5). As was also the case for species richness, habitat diversity does not affect species composition.

Table 3.5 *Spearman rank correlations between the ordering of the patches in the maximally nested matrix (T) and area and isolation measures (N=153).*

	Area	**NHSP**	**DIST1**	**DIST5**	**A100**	**A500**	**IFM**	**Habdiv**
T	-0.167*	-0.986***	0.230**	0.267***	-0.296***	-0.330***	-0.352***	-0.094

****: p<0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1*

Habdiv: habitatdiversity; other abbreviations: see table 3.2.

Following the procedure of Lomolino (1996) the conclusion that species composition of the heathland patches exhibits significant nestedness holds. Roughly the same conclusions can be drawn as obtained with the algoritm of Atmar and Patterson (1993). Isolation is the factor best explaining the nested subset pattern, and area does not seem to show any effect (Table 3.6). Ordering the patches by their sequence in the maximally packed matrix (T) leads to the same number of departures as ordering by species number, and gives the highest value for %PN. With this procedure, it was not possible to determine the influence of habitat diversity on species composition. Because the PCA-analysis only yielded a few different values for habitat diversity, many patches have the same value, and ordering the patches following habitat diversity reflects almost completely the original ordering of the patches.

Table 3.6 *Number of departures from perfect nestedness as calculated by the algorithm of Lomolino (1996) and significance based on 1000 random permutations (N=153) (abbreviations: see table 3.2).*

	Area	**NHSP**	**DIST1**	**DIST5**	**A100**	**A500**	**IFM**	**T**
D	708	590 ***	647 ***	675 ***	702 (*)	677 **	671 ***	590 ***
%PN	2.5	18.73	10.95	6.92	3.39	6.85	7.56	18.82

****: p<0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1*

Discussion

Effects of area and isolation

Fragmentation has important effects on the species richness of heathlands. Like in many other habitat types (e.g. Ouborg, 1993; Quintana-Ascencio and Menges, 1996; Honnay et al., 1999a; Brose, 2001; Jacquemyn et al., 2001a; Pysek et al., 2002), a positive plant species-area relationship also holds for the heathland patches in the studied region. This positive species-area relationship is not caused by higher habitat heterogeneity in larger fragments, probably because the patches are quite monotonic as far as abiotic conditions are concerned. Isolation-effects however seem to be most important. When controlled for fragment area, species richness remains largely affected by the isolation of the heathland fragment.

The community composition of the heathland patches, another important aspect of the plant community, shows a nested subset pattern, as is found in many other ecological communities (e.g. Patterson, 1990; Cook and Quinn, 1995; Wright et al., 1998). Both the matrix temperature method of Atmar and Patterson (1993) and the method developed by Lomolino (1996) lead to this conclusion. Although in some cases the factors determining species richness and those underlying nestedness do not coincide (Cutler, 1994), both measures describing the heathland community seem to be mainly caused by the same factors. As is the case for species richness, habitat diversity does not show a significant effect on species composition. The hypothesis of nested habitats as a factor causing nestedness cannot be confirmed here. Although area appears to be of significant importance in explaining the nestedness pattern in the Atmar and Patterson method, it is clearly much less important than isolation.

Both the species richness and the species composition analysis indicate that smaller patches contain less species, not because small patches show less heterogeneity in abiotic characteristics, but because species in these patches are probably more sensitive to extinction. Our results indicate however that this area effect is overcompensated by a rescue-effect (Brown and Kodric-Brown, 1977). If a patch is close to other patches, species seem to be able to disperse between them and prevent the species from going extinct. This interaction between area-dependent extinction and isolation-dependent recolonization thus leads to the relaxation of the flora in the investigated heathland patches to a certain equilibrium species number.

Other studies have also pointed at the importance of isolation affecting species number and composition of habitat fragments (Kadmon, 1995; Grashof-Bokdam, 1997; Butaye et al., 2001). These studies differ with this study in the fact that they considered a chronosequence, i.e. they focused on the colonisation of recently established habitats. The patches were initially completely free of plant individuals or diaspores of the plant species, so plant community building in these patches had to start from scratch. The nested subset pattern and species richness patterns resulted from the interaction between the dispersal capacity of the colonising species and the distance from the older source patches or the 'mainland' in the area. In this study, all patches are much older, and initial colonization happened a few centuries ago. The processes of recolonization and extinction can be thought of as the determinants of the plant community here, while in the above mentioned studies the patches are probably too young for extinction to play a significant role.

Colonization is not the only process affected by isolation. Isolation can also have important effects on the persistence of a plant species through its influence on pollen flow. Large distances between populations can seriously reduce pollen flow, leading to a reduced reproductive success (Groom, 1998; Steffan-Dewenter and Tscharntke, 1999), and hence a reduced population persistence. Interpopulation movement of pollen can on the other hand also be an important component in maintaining or restoring genetic diversity in plant populations, and hence in increasing viability and long-term survival of the populations (Richards, 2000; Newman and Tallmon, 2001).

Effect of seed bank type on isolation-sensitivity

Some characteristic heathland species, e.g. *Calluna vulgaris*, *Erica cinerea, Juncus squarrosus, ...* are known for having a long term persistent seed bank (for a review see Thompson et al., 1997; Bossuyt and Hermy, 2003). Although this is often emphasized in heathlands, seed banks, maybe to a lesser extent, also exist in other habitats. The influence of the seed bank on species richness has never been taken into account in studies of area- and isolation effects in other habitat types, like forests or grasslands, although there might also be some effects there.

The role of the seed bank in determining species richness is not easy to determine. When the median seed longevity index per patch was correlated with species richness, there did not seem to be an effect. The correlations of the number of species in the different classes of the seed longevity index with isolation however indicate that there is a significant influence from the seed bank. Species having a short living seed bank seem to be more sensitive for isolation than species with a long living seed bank, indicating that the last category most probably depends on the seed bank to survive periods when environmental conditions are harsh. A seed bank is thus a way of dispersal in time. The existence of a seed bank can in this way act as a buffer against stochastic extinctions. Analogously to the spatial rescue-effect described above, where recolonization from neighbouring patches prevents a species from going extinct, the existence of a persistent seed bank can in this way lead to a sort of temporal rescue-effect, where the extinction of a plant species is prevented through survival in the seed bank of a patch.

The fact however that for many species the database where the seed longevity index is calculated from (Thompson et al., 1997), gives records in all three of the seed bank types indicates that for many species the exact properties of its seed bank are not fully known yet, and this index should therefore be treated with some caution.

Comparison of the different isolation measures

Finally, our results suggest that the connectivity measure is the best measure to quantify isolation, as was suggested by Moilanen and Nieminen (2002). Both for species richness and species composition, this measure seems to be the best predictor. By taking into account each patch in the landscape, and weighing its distance to another patch by its area, this measure best describes the landscape structure. Concentric isolation measures in most cases also describe isolation better than linear measures, as was already pointed out by Vos and Stumpel (1995), and especially the measure A500 closely resembles the connectivity measure in explaining species richness and species composition of the patches.

Conclusion

Our results, both at the species richness and the community composition level, indicate the existence of a rescue-effect. The extinction of a species as a result of area-dependent extinction processes is prevented through isolation-dependent colonization processes, leading to the relaxation of the flora. Next to this spatial rescue-effect, the existence of a persistent seed bank can act as a temporal rescue-effect, preventing the extinction of a species through survival in the seed bank of a patch. Species lacking a persistent seed bank are especially sensitive for isolation. From these results it can be concluded that to preserve a diverse plant community in this heathland relics, it is important to prevent these patches from becoming more isolated. The species lacking a persistent seed bank are most at risk by a further isolation and deterioration of these heathland patches.

CHAPTER 4

THE ROLE OF FRAGMENT AREA AND ISOLATION IN THE CONSERVATION OF HEATHLAND SPECIES

Introduction

In Western Europe, densely populated and large industrial and built up areas threaten non-productive land use types, such as nature conservation, forcing them back into small, isolated reserves. High maintenance vegetation types, such as heathland, are even more at risk. The fact that they are linked with traditional rural practices no longer applied these days, has led to a continuous decline during the past 200 years (e.g. Pott, 1996; Webb, 1998; Odé et al., 2001). Nevertheless, their high specificity in plant and animal species (de Smidt, 1975; Schaminée et al., 1996) and the fact that they are one of the most important semi-natural landscapes in Western Europe (Webb, 1998) confers on them a high conservation value.

An important consequence of the heathland decline is the increasing fragmentation of the remaining heathland (Moore, 1962; chapters 2 and 3). Fragmentation includes both a reduction in the area and an increase in the degree of isolation of the heathland patches (e.g. Meffe and Carroll, 1997). This can affect the distribution patterns of plant species severely. In most cases small patches can support only small populations, which are more sensitive to demographic fluctuations and stochastic perturbations (Pimm et al., 1988). Colonization from other patches however can prevent the extinction of species, simply by the demographic effect of the addition of new individuals, a phenomenon called the rescue-effect (Brown and Kodric-Brown, 1977; chapter 3). Typical for plant populations is that besides seed flow, pollen flow can also act to rescue small populations. The inflow of pollen from plants from other populations can preserve or enhance genetic diversity within the plant population and reduce inbreeding, thereby rescuing it from extinction (Richards, 2000; Ingvarsson, 2001). This rescue, however, is possible only when habitat fragments are not too isolated from each other, disabling seed and/or pollen flow.

The response to habitat fragmentation can differ significantly between species (e.g. Quintana-Ascencio and Menges, 1996; Villard et al., 1999). This difference can be attributed to differences in plant traits linked to dispersal capacity and persistence (Maurer et al., 2003). The most obvious feature influencing dispersal capacity is the dispersal mode. Seeds of species lacking morphological adaptation for dispersal can normally achieve only short-distance dispersal and reach dispersal distances far below those of species that do have dispersal mechanisms favouring long distance dispersal (Willson, 1993; Matlack, 1994b). The latter frequently seem to be less sensitive to isolation (e.g. Dzwonko and Loster, 1992; Grashof-Bokdam, 1997; Honnay et al., 2002b). Other studies however have questioned the importance of these morphologically determinable dispersal mechanisms for long distance dispersal, because the processes that move seeds over longer distances are often complex and involve several different dispersal agents (Higgins et al., 2003).

Persistence of a plant species in a patch on the other hand may be significantly influenced by plant and seed bank longevity. Species with a persistent seed bank or the possibility of extended clonal growth can form remnant populations (Eriksson, 1996, 2000) which enables them to bridge periods of unfavourable environmental conditions. This ‘dispersal in time’ can protect a plant population against extinction (Eriksson, 1996; Husband and Barrett, 1996; Turnbull et al., 2000; chapters 2 and 3). Especially in heathland-ecosystems, where many species form a persistent seed bank (Thompson et al., 1997; Bossuyt and Hermy, 2003), this can have significant effects on the distribution patterns of plant species. Complementary to the rescue effect in space, the functioning of seed bank can be considered as a rescue effect in time, by which extinction of a species is prevented by reestablishment from the seed bank.

In this study, we examined how heathland fragmentation has influenced the patch occupancy patterns of heathland plant species. Heathland area in our study area decreased from almost 10000 ha at the end of the 18th century to less than 100 ha nowadays. We are dealing with pure relaxation of area in this region, i.e. all patches were established centuries ago and have known a more or less continuous land use as heathland ever since. Moreover, we determined how differences in patch occupancy patterns could be explained in terms of plant traits related to dispersal capacity and persistence. From this, we suggest conservation guidelines for these heathland relics.

Material and methods

Study area

The study was conducted in north-western Flanders, in an area south of Bruges (Fig. 3.1). A more detailed description of the study area can be found in chapters 2 and 3.

Floristic data

In this area, all patches of heathland and related vegetation types (e.g. grassheath, acid grassland) that were already classified as heathland on the oldest available map for this region (map of De Ferraris (1775)) were inventoried during the summer of 2002, totalling 153 fragments. Based on consecutive topographic maps, these patches have continuously been heathlands. It may however be that they have known short periods of other land uses in the intervening periods. The survey was done simultaneously by two persons walking transects through the patch. The presence of all higher plant species in these patches was recorded. The species lists collected were checked and supplemented with data from local botanists and nature conservation organizations.

Species data

From the list of plant species recorded, only the 54 species belonging to the groups of heathland, grassheath or acid grassland plants, as defined by Stieperaere and Fransen (1982), were included for further analyses. For the other species, it is not meaningful to calculate isolation measures based on our data set, because they are characteristic for other than the surveyed vegetation types, possibly biasing the results.

For the selected species, information on life history traits was collected from a variety of sources (Table 4.1). The traits were selected on the basis of their possible influence on dispersal (dispersal mode, mean plant height, seed mass, seed number) or persistence (seed longevity, growth form, self compatibility, vegetative spread) of plant species (Table 4.1). Plant longevity, another trait possibly affecting persistence, could not be taken into account because variation in this trait is too limited in our data set. The life history traits of the 54 heathland species are listed in the appendix. Plant species nomenclature follows Lambinon et al. (1998).

Table 4.1 *Overview of the life history traits used in the analyses.*

Life history trait	Symbol	Values
Seed longevity index[a]	SLI	Continuous
Mean plant height[b]	H	Continuous
Seed mass[c]	SM	Continuous
Dispersal mode[d]	DISP	Anemochoreous (1), exozoochoreous (2), myrmecochoreous (3), hydrochoreous (4), barochoreous (5), unspecified (6)
Growth form[e]	GROW	Gramineous (1), herbaceous (2), dwarf shrub (3), shrub (4)
Self compatibility[c]	COMP	Self compatible (1), self incompatible (0)
Vegetative spread[d]	CLON	Present (1), absent (0)
Seed number (per plant)[f]	SN	1 (1-1000); 2 (1000-10000); 3 (>10000)

a: calculated from Thompson et al. (1997) using the formula developed by Bekker et al. (1998); b: Lambinon et al. (1998); c: Klotz et al. (2002); d: Hodgson et al. (1995); e: Biesbrouck et al. (2001); f: Ecological Database of the British Isles and Kleyer (1995)

Patch configuration

All patches were digitised using ArcView 3.2 (ESRI, 2000), enabling the calculation of patch area. Further, for each of the 54 heathland species and for each patch, species-specific isolation was calculated using the connectivity measure defined by Hanski (1994) as $IFM_i = \sum A_j \exp(-\alpha d_{ij})$, where i symbolizes the focal patch, j each of the other patches in which the species is present, d_{ij} is the edge-to-edge distance from patch i to patch j and A_j is the area of patch j. The constant α is a parameter to scale the effects of the dispersal capacity of the species. Because the value of this constant was not known, different values of α (0.5, 1, 2, 3, 5 and 10) were tried for each species (Bastin and Thomas, 1999; Johansson and Ehrlén, 2003).

Patch suitability

Each plant species has its own specific environmental requirements, and consequently can only be present in patches that meet these requirements. Since the inclusion of patches in which a species cannot occur can obscure isolation effects, it is necessary to know for each species which patches are potentially suited and which are not. This was determined using the habitat space model (Pärtel et al., 1996), a four-dimensional hypervolume based on the minimum and maximum values of the Ellenberg indicator values (Ellenberg et al., 1992) for the factors light, soil moisture, pH and soil nutrient status of all species present in that patch (Butaye et al., 2001). A patch is classified as suitable for a certain species when the Ellenberg indicator values of the species for each of these four factors fall within the range defined by the habitat space model.

Data analysis

First the relation between the different life history traits and patch occupancy was examined. Patch occupancy was defined as the percentage of the total number of suitable patches, as determined by the habitat space model, occupied by the plant species. Pearson product-moment correlations (Kent and Coker, 1992) were used to study the effects of the continuous plant traits on patch occupancy, while the effects of the categorical variables were tested using one-way ANOVA (Neter et al., 1996). Patch occupancy, seed mass and plant height were log-transformed to obtain normality and homoscedasticity.

For each of the heathland species the influence of patch area and isolation on their presence/absence data was examined using multiple logistic regression models (Hosmer and Lemeshow, 1989). Only the patches meeting the abiotic requirements of the species, as determined by the habitat space model, were included. Because multiple logistic regressions do not make sense if a species occurs in few or almost all of the patches, these analyses were restricted to the heathland species occurring in 10 to 90% of the patches, resulting in a total of 25 species.

Next, it was examined whether differences between species in isolation- or area-dependence could be attributed to differences in the selected plant traits. One-way ANOVA and chi-square statistics were used to determine whether species showing significant effects of area or isolation differed in these traits from species showing no significant effects. Because the coefficients (β-area, β-isolation) resulting from the logistic regressions can be considered as an indication of the importance of area and isolation (Dupré and Ehrlén, 2002), the relation between these coefficients and the different plant traits was evaluated using one-way ANOVA for the nominal traits and Pearson correlations for the continuous traits. Coefficients for non-significant effects were assigned a value of zero. Seed mass, mean plant height and β-isolation were log-transformed to meet the requirements of the statistical methods.

Results

Patch occupancy is influenced only by seed longevity and, to a smaller extent, by seed mass (Table 4.2). As these variables are themselves significantly intercorrelated (Table 4.3), partial correlations were performed. This led to somewhat lower values of the correlation coefficients, with a partial correlation coefficient of 0.344 ($p=0.03$) between seed longevity index and patch occupancy, when controlled for seed mass, and a value of –0.218 ($p=0.18$) between seed mass and patch occupancy, controlled for seed longevity index. From this it can be concluded that the time seeds can survive in the soil is the only factor determining the number of patches occupied by a species.

Table 4.2 *Relation between patch occupancy and the investigated plant traits (continuous traits: Pearson product moment correlations; nominal plant traits: one-way ANOVA).*

	Patch Occupancy	**p-value**
Seed longevity index	$r=0.47$	0.001
Mean plant height	$r=0.07$	0.594
Seed mass	$r=-0.38$	0.010
Dispersal mode	$F_{5,47}=0.93$	0.470
Growth form	$F_{3,50}=1.47$	0.234
Self compatibility	$F_{1,42}=0.45$	0.508
Clonality	$F_{1,42}=0.05$	0.829
Seed number	$F_{1,14}=1.56$	0.245

Table 4.3 *Intercorrelations of the investigated plant traits as determined by Pearson product moment correlations, one-way ANOVA and χ^2-statistics (N=54). Abbreviations: see Table 4.1.*

	SLI	**H**	**SM**	**DISP**	**GROW**	**COMP**	**CLON**
H	$r=-0.11$						
SM	$r=-0.49$**	$r=0.31$*					
DISP	$F_{5,40}=1.19$	$F_{5,47}=0.29$	$F_{4,38}=4.68$**				
GROW	$F_{3,43}=0.05$	$F_{3,50}=9.27$***	$F_{3,40}=6.55$***	$\chi^2=34.58$**			
COMP	$F_{1,37}=0.02$	$F_{1,42}=1.27$	$F_{1,36}=0.45$	$\chi^2=8.20$	$\chi^2=4.41$		
CLON	$F_{1,37}=0.04$	$F_{1,42}=0.07$	$F_{1,36}=0.16$	$\chi^2=9.38$*	$\chi^2=6.75$(*)	$\chi^2=0.16$	
SN	$F_{2,12}=0.57$	$F_{2,14}=4.63$*	$F_{2,12}=0.81$	$\chi^2=5.96$	$\chi^2=3.32$	$\chi^2=0.58$	$\chi^2=0.53$

***: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$; (*): $0.05<p\leq0.1$

.**Table 4.4** *Multiple logistic regression equations between species presence and patch area and connectivity (IFM) for the 25 species present in 10 to 90% of the surveyed patches.*

Species	Regression equation	
Agrostis spec.	1.916-0.967Area	*
Calluna vulgaris	-	ns
Carex binervis	-	ns
Carex demissa	-2.184+0.641IFM	*
Carex pilulifera	-	ns
Cytisus scoparius	-	ns
Dactylorhiza maculata	-2.900+2.600IFM	***
Danthonia decumbens	-1.150+0.859IFM	***
Erica cinerea	-3.726+1.786IFM	***
Erica tetralix	-0.709+0.504IFM	*
Festuca filiformis	-2.052+0.550IFM	***
Hieracium umbellatum	-1.503+1.735IFM	**
Hydrocotyle vulgaris	-1.149+2.449IFM	*
Hypericum perforatum	-	ns
Juncus acutiflorus	-0.893+11.062IFM	***
Juncus conglomeratus	-2.375+5.064Area+0.488IFM-0.684Area*IFM	**
Juncus squarrosus	-	ns
Luzula campestris	-2.388+1.317IFM	**
Luzula congesta	-0.679+1.316IFM	*
Luzula multiflora	-0.866+1.038IFM	**
Polygala serpyllifolia	-2.292+5.576Area*IFM	***
Potentilla erecta	-1.496+1.589IFM	***
Rumex acetosella	-	ns
Salix repens	-3.690+3.821IFM	***
Veronica officinalis	-2.411+0.786IFM	*

****: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$; ns: not significant*

The logistic regression analysis yielded significant regression equations for 18 of the 25 species (Table 4.4). Isolation is the main factor affecting species presence, showing a significant negative effect for 16 species (64%). Area on the other hand only entered the regression equation for 2 species (8%), whereas the interaction term area-isolation also was significant for only 2 species. *Juncus conglomeratus* was the only species for which all variables were included in the regression equation.

Table 4.5 *One-way ANOVA and chi-square statistics to examine differences in life history traits between species showing significant area or isolation effects, and species showing no significant effects.*

	Area	**Isolation**
Seed longevity index	$F_{1,20}$=0.06	$F_{1,20}$=17.47***
Mean plant height	$F_{1,23}$=1.80	$F_{1,23}$=1.56
Seed mass	$F_{1,18}$=2.02	$F_{1,18}$=0.77
Dispersal mode	χ^2=4.68	χ^2=3.97
Growth form	χ^2=2.61	χ^2=2.27
Self compatibility	χ^2=0.93	χ^2=2.37
Clonality	χ^2=1.22	χ^2=0.62
Seed number	χ^2=2.26	χ^2=1.49

****: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$; (*): $0.05<p\leq0.1$*

The differences between the species in isolation-sensitivity can be mainly attributed to differences in seed bank characteristics (Tables 4.5 and 4.6). Species having long living seeds are less affected by isolation, as can be derived from the negative correlation between β-isolation and the seed longevity index (Table 4.6). Species for which presence is affected by area do not differ in any of the selected traits from species that are not influenced by area. Correlations between β-area and plant traits could not be calculated because of the low number of species affected by area.

Table 4.6 *Relation between the coefficients for isolation in the multiple logistic regression equations and the different life history traits, as determined by Pearson correlations and one-way ANOVA.*

	β-isolation
Seed longevity index	r= -0.437 *
Mean plant height	r= -0.003
Seed mass	r= -0.278
Dispersal mode	$F_{4,20}$= 0.621
Growth form	$F_{3,21}$= 0.481
Self compatibility	$F_{1,20}$= 1.794
Clonality	$F_{1,23}$= 0.003
Seed number	$F_{2,10}$= 0.610

*: $0.01<p\leq0.05$

Discussion

Landscape configuration is an important factor in determining patch occupancy patterns in the investigated heathlands. Almost 2/3 of the species are affected by isolation. Significant effects of isolation were also found by Quintana-Ascencio and Menges (1996) in scrub communities, by Bastin and Thomas (1999) in different habitat fragments in the city of Birmingham and by Jacquemyn et al. (2003) in forests. In a similar study performed in forests by Dupré and Ehrlén (2002), however, isolation only seemed to play a minor role. This difference can be attributed to several factors. First, they did not use species-specific isolation measures, contrary to our study and the studies performed by Bastin and Thomas (1999) and Jacquemyn et al. (2003), who did find significant effects. Another possible explanation is that they included all surveyed patches in their analyses, irrespective of whether the patch is suited for that species or not. This can explain the high importance of soil variables in their study. Thirdly, while in our study analyses were limited to species characteristic for the vegetation type studied, they included both forest and non-forest species. When comparing isolation sensitivity between specialists and generalists however, they concluded that specialist species, with their optimal habitat in forests, were especially influenced by isolation, which is consistent with our result.

The effect of area on the other hand on patch occupancy patterns was significant for only two species, and these effects were ambiguous. For relaxated systems, like these heathlands, it is often argued that area-dependent extinction processes are of major importance, leading to species extinction and hence a lower species richness as time since fragmentation proceeds. The low importance of area and the high importance of isolation, however, indicate that in our system extinction of species seems to be prevented by dispersal from neighbouring patches, a process described as the rescue-effect (Brown and Kodric-Brown, 1977). These results are consistent with our earlier results dealing with species richness and species composition of the same heathland patches (chapter 3), which also suggested the existence of a rescue-effect.

The importance of habitat configuration in determining patch occupancy patterns differs significantly between the studied species. Contrary to some other studies, in which differences in isolation sensitivity between species could be attributed mainly to differences in dispersal mechanisms (Dzwonko and Loster, 1992;

Grashof-Bokdam, 1997 but see Dupré and Ehrlén, 2002), this does not play a significant role in the heathlands under study. Species with morphological adaptations facilitating long distance dispersal are as much influenced by isolation as species lacking these adaptations. This may indicate that for the species under study the morphological classification of dispersal mechanisms may not be the best way to describe how these species disperse. This classification does not take into account that the seeds of a certain plant species can often be dispersed in a variety of ways (Bakker et al., 1996), of which the morphologically determinable is maybe the most used, but certainly not the only one. Moreover, long distance dispersal, i.e. dispersal between patches, is often complex and mostly results from other, non-standard dispersal mechanisms (Bakker et al., 1996; Cain et al., 2000; Higgins et al., 2003) or from rare or exceptional behaviour of the standard dispersal vector (Higgins et al., 2003). As a result, the correlation between the morphologically defined dispersal syndrome and long-distance dispersal may be poor (Higgins et al., 2003).

Unlike the capacity for dispersal in space, the ability for dispersal in time contributes significantly to differences in isolation sensitivity between the heathland species. Species with a long living seed bank (e.g. *Calluna vulgaris*, *Carex pilulifera*) are less affected by isolation than species with seeds with a limited longevity (e.g. *Festuca filiformis*, *Salix repens*). Seed longevity is also the most important factor determining patch occupancy of the heathland patches. Many of the key species of heathland, like for example *Calluna vulgaris* and *Erica cinerea*, are known to have a long-term persistent seed bank (Thompson et al., 1997; Bossuyt and Hermy, 2003). While a long-term persistent seed bank enables species to survive unfavourable environmental conditions through their seed bank and re-establish afterwards, species with seeds that can survive only for a short time lack this buffer against extinction, and hence are much more sensitive to extinction. The latter have to depend on the often accidental events of long distance dispersal to recolonize the patch, which will obviously be easier when that patch is more closely surrounded by other heathland patches. Plant species with a persistent seed bank thus have the ability to form remnant populations (Eriksson, 1996, 2000). This is in accordance with our earlier results indicating the high importance of seed bank characteristics in determining a species' fragmentation sensitivity (chapters 2 and 3). Clonality, another feature enabling species to form remnant populations, does not contribute to differences in patch occupancy or isolation sensitivity between species in the study area.

As many seed bank studies can only give a rough indication of the time seeds can survive in the soil, and different studies give diverse estimates of this longevity (Bakker et al., 1996; Thompson et al., 1997), it is often impossible to classify unambiguously a species as having a transient, short-term or long-term persistent seed bank. The seed longevity index deals with this variability and therefore probably is the most accurate measure to quantify seed longevity (Bekker et al., 1998).

Of the species with a seed longevity index of 0.75 or higher, *Erica cinerea* is the only one influenced by isolation. This species is characteristic of Atlantic heathlands, such as the heathlands of southern England, western France and northern Spain. In our study area, *Erica cinerea* is present only in the heathlands in the western outer parts of the region, which can be considered as an outpost for the species. Because of this highly clumped occurrence, patches where the species is present always have a higher value for the connectivity measure than patches where the species is absent, and that are situated at the other end of the study area. This points to an inadequacy of the habitat space model, namely it does not take into account climatic information. The clumping of *Erica cinerea* in the western part of the region is probably due to small climatic differences between the western and eastern part, with the former more closely resembling atlantic conditions. Because this factor is not treated in the habitat space model, many patches where the species cannot occur are labelled as being suitable. These small differences are difficult to incorporate in the model. An extra dimension, the Ellenberg indicator value for continentality, could have been added to the model. This, however, would not be adequate to account for these climatic differences, because variation in the region is too limited to be detected by this value. Another drawback is that the original scaling of this variable is poor (Hill et al., 2000).

Heathland conservation

Our results indicate that almost three quarters of the investigated heathland species are negatively affected by fragmentation. The high importance of isolation suggests that for conservation of the flora of these relic heathlands, further isolation should be prevented and connectivity between the patches needs to be assured. Since almost none of the species seems to be negatively affected by a reduced patch area, it can be concluded that for most species even small patches are important for their survival.

Management and conservation should therefore focus not only on the larger heaths, but also on these smaller patches. The latter are often situated in, for example, small open patches in forests or along roadsides, places that do not receive proper regular management or are completely neglected. Hence, these small relics are much more endangered.

As particularly species lacking a long-term persistent seed bank are sensitive to isolation, conservation efforts should focus on these species. The relationship between patch occupancy and seed longevity indicated that these are also the rare species in the study area. The presence of other patches in which these species are present in the neighbourhood can be important. Especially when proper management is abandoned for some time, and environmental conditions become unfavourable for these species, a high connectivity of the patch can increase the species' chances of survival.

CHAPTER 5

HOW SHOULD WE DEAL WITH TRANSECT DATA? THE CASE OF MEASURING THE PENETRATION DISTANCE OF EDGE EFFECTS

Measuring edge effects: a special case of transect data

A transect is a line along which samples are taken or sample plots are laid out. Transects are often used in ecological research in situations where there are rapid changes in vegetation and marked environmental gradients in space (Kent and Coker, 1992), like for example in the study of ecotones (e.g. Bossuyt et al., 1999; Walker et al., 2003) or of the effects of walking pressure on vegetation across paths (e.g. Roovers et al., 2004). Another area of ecology in which transect sampling is commonly applied is the study of edge effects.

Fragmented habitats contain much edge habitat. Numerous studies have demonstrated plant species impoverishment and decreased plant population fitness in fragmented habitats compared to more intact ones (e.g. Quinn and Robinson, 1987; Holt et al., 1995; Jules, 1998; Laurance et al., 1998; Bruna, 2003; Ries et al., 2004). These negative effects on the survival of natural populations usually were related to physical edge effects that are locally deteriorating habitat quality (Harrison and Bruna, 1999). Edge effects are caused by the flux of matter, energy and species flowing from the landscape matrix into the habitat fragment (Wiens, 1992; Ryszkowski, 1992). The main concern in a plant conservation context is how these fluxes directed into the habitat fragment may influence plant dynamics such as regeneration and interspecies competition (Murcia, 1995). Many studies have attempted to quantify the penetration distance of biotic and abiotic fluxes, mainly in forest fragments (Matlack, 1993, 1994a; Cadenasso et al., 1997; Esseen and Renhorn, 1998; Honnay et al., 2002a; Devlaeminck et al., 2005a, b and many others). The typical empirical approach is the establishment of a number of plots along a line perpendicular to the edge, into the habitat fragment. Within these plots species number and cover are then surveyed and/or abiotic variables such as air humidity or temperature are measured.

In this contribution we argue that serious methodological problems may arise with processing data of these kinds of surveys. These difficulties are directly related to the intrinsic nature of transect data but are neglected by most authors. Hence this may imply the reporting of incorrect results and conclusions. We are not aiming at presenting an exhaustive list of ‘good’ and ‘bad’ studies, but rather at proposing a sound methodology to collect and to treat edge data, and more in general, transect data. Edge data can indeed be seen as a special case of transect data and the following can easily be generalized to all types of transect data aiming at measuring environmental or species gradients in space. We use the case of measuring penetration distances as a special case of transect data because it is one of the most straightforward examples of the use of transects in ecological research.

Data collection: Establishing proper replicates

A central issue in setting up an ecological experiment is replication (e.g. Scheiner and Gurevitch, 2001). Replication is necessary to distinguish real effects or trends from chance effects or ‘noise’ associated with the inherent natural variability among samples and with measurement error. When performing a study on edge effects one is usually interested in conclusions that can be generalized. Few ecologists will be interested in the width of the edge zone in a certain forest in northern Belgium. The interest will grow when the researcher is able to generalize its conclusions to, for example, edge effects in temperate, deciduous forest fragments on loamy soils.

The basic condition for a generalization of the results is the establishment of a sufficient number of replicates over as much as possible deciduous forest edges on loamy soil. If all transects are located in the same forest edge, or even in the same forest fragment, one practices what is commonly known as pseudoreplication (Hurlbert, 1984; Murcia, 1995). In the case of pseudoreplication transects are established in one edge or in one habitat fragment and inferences are being made for edge effects at the landscape scale. In the case of not properly spaced replicates inferences should be restricted to that particular edge or forest fragment.

The need for the establishment of replicates in edges that are sufficiently separated from each other does not exclude the possibility of establishing more transects in one edge. These transects, however, should not be treated as independent samples.

The obtained measurements at each distance along the transects in one edge should be averaged into one value per distance from the edge and further analyses should be based on these average values. This approach will increase the precision with which the edge characteristics are estimated (Hurlbert, 1984).

The vision of Hurlbert (1984) on proper replications in ecological experiments has recently been the subject of vivid debate (Oksanen, 2001; Cottenie and De Meester, 2003). The controversy was mainly based on the question whether a scientist may make compromises on experimental design in order to get an answer to the scientific question behind the experiment. In many landscape ecological studies it is not feasible to establish proper replicates and therefore, landscape scale studies will be rejected during the peer review process, resulting in a report bias favouring small scaled, well designed studies. For the specific case of edge effects there seems to be no problem to establish properly spaced transects and the guidelines of Hurlbert on replication should be followed.

Data analysis

Suppose that proper replicates were established in different habitat fragments and that variables like species richness and air humidity within the plots along the transects were measured. The aim now is to relate these dependent variables with the distance to the edge. The collected data, and transect data more in general, contain three components of random variability (Diggle et al., 1994; Verbeke and Molenberghs, 2000):

1) Measurement error and error due to natural variation. These errors result from assessing species cover or measuring environmental variables in the plots and from natural variability in the edge. These errors are the well known residuals in a regression analysis or an ANOVA.
2) Distance varying stochastic variation within a transect, resulting in a correlation between measurements within the plots at short distance. Residuals closer together are more similar than residuals further apart. The measurements in the plots within the transect are also said to be spatially correlated.
3) The ‘random’ effects, resulting from inter-transect variability and originating from the fact that the established transects are just a random sample from all possible transects (cf. random effects in an ANOVA).

Almost all studies on edge effects that we found through the Web of Science dealt only with random variation of type (1). They applied a least square regression technique or a one way ANOVA to relate species richness or cover with distance to the edge (e.g. Williams-Linera, 1990; Chen et al., 1992; Matlack, 1994a; Cadenasso et al., 1997). Honnay et al. (2002a) used a somewhat intermediate technique by first controlling for spatial autocorrelation between quadrats (random error type (2)), and subsequently applying an ANOVA. We found only one study that included random effects (error type (3)) using a General Linear Model (GLM) approach (Esseen and Renhorn, 1998). As will be discussed below, this approach is not ideal because in a GLM, random effects are not really treated as random but as fixed effects.

It is difficult to generalize the precise consequences of not appropriately dealing with all three types of random variation in the data. Generally it can be expected that neglecting the variance structure of the data, and especially the dependence of the data, results in incorrect inferences and hence false conclusions about the presence and the extant of edge effects. The approach proposed by Harper and MacDonald (2002) for determining edge width overcomes these inference problems by using randomization tests. Yet it allows no curve fitting across the transect and hence no precise quantification of the edge gradient at each distance.

An appropriate method to analyse transect data should be able to account for all three sources of variability. Therefore, Linear Mixed Modelling is introduced as a very flexible technique able to account for all three sources of random variability. This technique has its origin in social sciences where it is known as multilevel modeling (e.g. Singer, 1998; Goldstein, 1999). Although its widely accepted use in social science and medicine, it is still not commonly used in ecology (but see e.g. Buckley et al., 2003). We found one edge transect study that applied a Mixed Model. However, it was not clear from the publication how the model was structured and whether and how the three sources of variation where accounted for (Williams-Linera et al., 1998).

We will stepwise build a model that copes with all sources of variability by making it gradually more complex and realistic. For the sake of simplicity the edge effect is supposed to be linear. This means that the response variable, for example, the species richness in a sample plot, is linearly related to the distance of the edge. Below it is shown that it is easy to adapt the model to a more realistic situation where there is a quadratic or even higher order response to the distance from the edge.

A regression approach to the pooled data

The most straightforward analysis is to pool all plot data, ignore the transect structure of the data, and fit a regression line through all plots. This is what is called establishing the marginal relationship between the response variable and the distance variable (Verbeke and Molenberghs, 2000).

The following relation can be written for each single observation or plot i:

$$Y_i = \beta_0 + X_i\beta_1 + \varepsilon_i$$

With Y the normally distributed response variable and X the distance to the fragment edge, β_0 is the intercept of the regression line and β_1 is the slope. ε is the random error term representing the residual of each observation in each plot and has a mean of zero. ε results from natural variability in the dataset and from measurement error (the type (1) error from above).

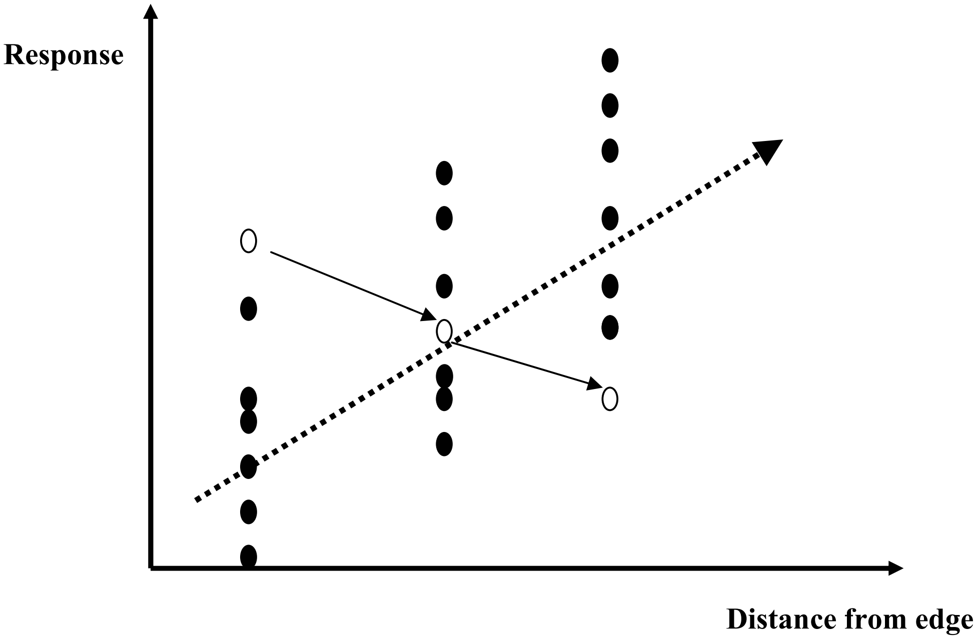


Fig. 5.1 *Marginal relation between a response variable and distance to the edge for seven transects each consisting of three plots. The overall relationship is positive although one transect (open dots) exhibits a negative relationship between the response variable and distance.*

This approach obviously suffers from a major drawback. The general trend in the pooled data may be the opposite from the trend in an individual transect. This is illustrated in figure 5.1, representing data from 7 transects, each consisting of three sample plots at three different distances from the edge. The general average trend indicates a positive relation between distance from the edge and the response variable. The trend within the transect presented by the open dots, however, shows a completely opposite pattern. For a more appropriate analysis the transect identity of all plots should be taken into account.

A multivariate approach

The model can be refined by introducing the transect identity of each plot. A regression line is fitted for each transect separately. This yields a multivariate response model that allows separating differences between transects from differences within transects.
Suppose that n_j transects were established, each consisting of m_i plots, then the model becomes:

$$Y_{ij} = \beta_{0j} + X_{ij}\beta_{1j} + \varepsilon_{ij}$$

with β_{0j} the intercept of transect j, and β_{1j} its slope. ε_{ij} is the random error associated with plot i in transect j. This equation relates every plot i to the regression line fitted through the transect j where it belongs.

Adding serial correlation

Besides the measurement error a component of spatial correlation should be also added to this multivariate model. This spatial correlation term reflects that part of the trend observed for each transect resulting from spatially-varying stochastic processes operating within that transect. This random variation causes a correlation between quadrat measurements which is typically a decreasing function of the distance between the plots. This error term for plot i belonging to transect j is represented by ε'_{ij} (type (2) error).

$$Y_{ij} = \beta_{0j} + X_{ij}\beta_{1j} + \varepsilon_{ij} + \varepsilon'_{ij} \qquad (1)$$

The model now contains two error terms, both representing the within transect residuals of each plot. One residual is associated with measurement error and natural edge variation, the other with the spatial autocorrelation of the plots.

Mixed or multilevel model approach

If the only interest is to make inferences about those transects sampled, the above described multivariate approach would be appropriate. If, however, the established transects are considered as a random sample of a population of all possible transects, a multilevel approach is necessary. Moreover, because there are usually relatively few plots per transect, fitting a separate model for each transect would not yield very reliable estimates; it would be more appropriate to use the information of all plots by regarding the transects as a sample from a population of transects. In the next step the second level of the model is modelled (the transect level) by allowing the slope and the intercept of each transect profile to vary. This is done by introducing b_j, the random, transect specific, error term (error type (3)).

$$\begin{cases} \beta_{0j} = \beta_{00} + b_{0j} \\ \beta_{1j} = \beta_{10} + b_{1j} \end{cases} \qquad (2)$$

These two relations express that the intercept of transect j is equal to the average intercept of all transects β_{00} and a random deviation b_{0j}. Equally, the slope of transect j is equal to the average slope of all transects β_{10} and a random deviation b_{1j}. The meaning of all coefficients is graphically presented in figure 5.2.

Through substitution of (2) in (1) we obtain:

$$Y_{ij} = (\beta_{00} + b_{0j}) + X_{ij}\,(\beta_{10} + b_{1j}) + \varepsilon_{ij} + \varepsilon'_{ij}$$

or after rearranging:

$$Y_{ij} = \underbrace{\beta_0 + X_{ij}\,\beta_1}_{\text{Fixed part}} + \underbrace{b_{0j} + X_{ij}\,b_{1j} + \varepsilon_{ij} + \varepsilon'_{ij}}_{\text{Random part}} \qquad (3)$$

The obtained multilevel model (3) is expressed as the sum of two parts: a fixed part, containing two fixed effects (one for the intercept β_0, and one for the distance effect β_1) and three random effects (the variation in intercepts among transects b_{0j}, the variation in slopes among transects b_{1j} and the quadrat specific errors $\varepsilon_{ij} + \varepsilon'_{ij}$).

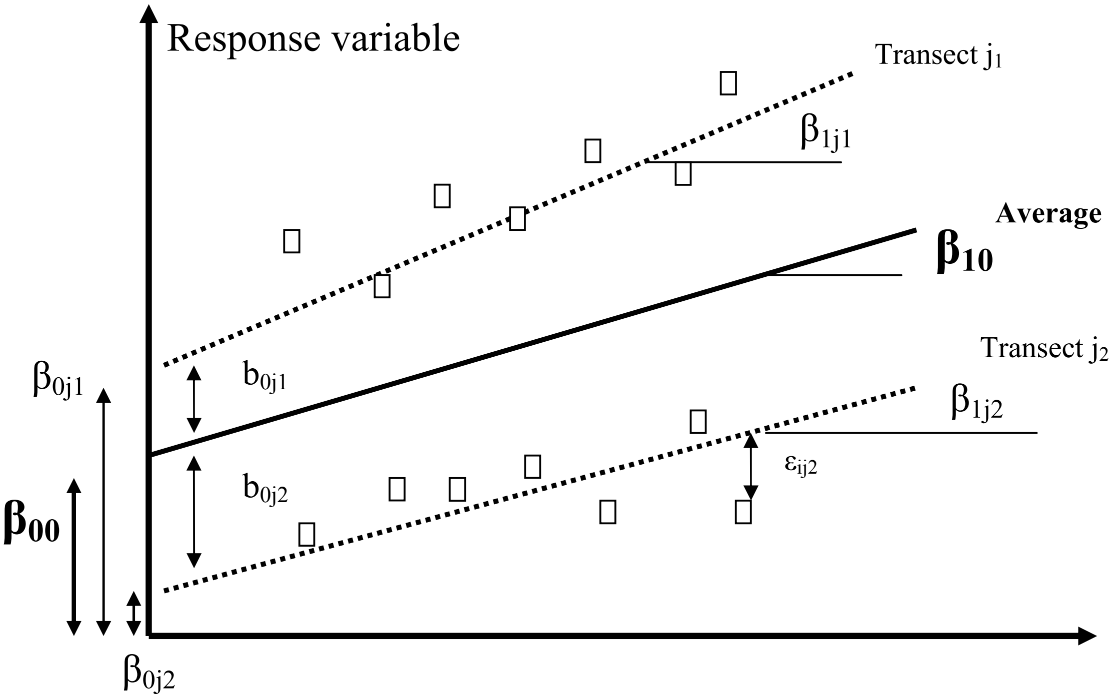


Fig. 5.2 *Graphical presentation of the random effects (b) in the mixed model. For clearness only the intercepts and not the slopes are allowed to vary randomly. Two transects each consisting of 7 plots and the average evolution of the response variable over the two transects are represented. For explanation of the different coefficients see text.*

Adding covariates and treatment effects

Usually one is not only interested in the variation of species richness along a transect but one wants to test more specific hypotheses. A common hypothesis is whether edge effects differ according to the orientation of the transects. It is known, for example, that in Western Europe edge effects may penetrate deeper into the forest edge at south facing edges (e.g. Honnay et al., 2002a). Such a 'treatment' variable is now introduced at level 2 of the model: the categorical variable 'aspect' of the transect. Other possibilities for treatment variables may be e.g. the categorical variable ‘adjacent land use type’ for each transect or the covariate ‘average soil phosphate content’ of the transect.

Suppose that Aspect = 1 for north facing transects and Aspect = 0 for south facing transects, then the variation in slope and intercept between transects can be written as follows:

$$\begin{cases}\beta_{0j} = \beta_{00} + \beta_{01}\mathrm{ASPECT}_j + b_{0j} & (4)\\ \beta_{1j} = \beta_{10} + \beta_{11}\mathrm{ASPECT}_j + b_{1j} & \end{cases}$$

with β_{00} the mean intercept for S facing transects
β_{01} the mean difference in intercept between N and S facing transects
β_{10} the mean slope for S facing transects
β_{11} the mean difference in slope between N and S facing transects

The full model, substituting (4) into (1), becomes:

$$Y_{ij} = \underbrace{\beta_{00} + \beta_{01}\mathrm{ASPECT}_j + X_{ij}\beta_{10} + X_{ij}\beta_{11}\mathrm{ASPECT}_j}_{\text{Fixed part}} + \underbrace{b_{0j} + X_{ij}b_{1j} + + \varepsilon_{ij} + \varepsilon'_{ij}}_{\text{Random part}} \quad (5)$$

Practically fitting the model and the difference with GLM

It would be possible to fit the obtained models (3) and (5) using a traditional GLM approach. In GLM procedures, however, random effects are not treated as random but as fixed (Littell et al., 1996; Saavedra and Douglass, 2002). This may result in incorrect estimates for the model variables. To fit the random part of models (3) and (5) correctly, *i.e.* including the three sources of random variation and not only type 1 variation, a maximum likelihood algorithm is required. This maximum likelihood approach is provided in a Mixed Model. When dealing with balanced data, the result is usually similar to that obtained from a GLM. When performing plot surveys at in advance determined locations, it is however very likely that some plots cannot be sampled due to e.g. the vicinity of a ride or a fallen tree. This often leads to highly unbalanced data sets due to missing values and results in considerable differences in parameter estimates between the Mixed Model and GLM approach. A Mixed Model will provide much better estimates in this case (Saavedra and Douglass, 2002). For an extensive treatment of the differences between a Mixed Model approach and a GLM approach we refer to Littell et al. (1996).

Although many statistical packages are currently offering a routine to solve Mixed Models based on a maximum likelihood algorithm the use of SAS code (PROC MIXED) is demonstrated here.

The basic SAS code for fitting model (5) is the following:

```
proc mixed dataset;
class transectID aspect distanceclass;
model Y = aspect distance aspect*distance/ solution ddfm=kr;
random intercept distance/ subject=transectID;
repeated distanceclass/type=sp(exp)(distance) subject=transectID;
```

The ‘model’ statement contains the response variable and the fixed effects of the model (aspect, distance and their interaction), completely in accordance with (5). An intercept is included by default in the model statement. In the ‘model’ statement the option ‘ddfm=’ can be used to specify the method to be used to estimate the denominator degrees of freedom. Because of the often small sample size in transect studies, the method of Kenward and Roger (‘ddfm=kr’; Kenward and Roger, 1997) is best suited. The ‘random’ statement contains the random effects (see again (5)). If an intercept is required it should be stated explicitly, this in contrast with the ‘model’ statement. The ‘repeated’ statement allows to model the spatial correlation (resulting in ε'_{ij}) between plots belonging to the same transect. Here an exponentially decaying correlation function with distance between plots is specified. Another possibility is a Gaussian autocorrelation function (see e.g. Verbeke and Molenberghs, 2000). The variable ‘distance’ is declared a class variable (distanceclass) because it is used both as a covariate in the ‘random’ and ‘model’ statement and as a grouping variable in the ‘repeated’ statement. Subjects in the ‘random’ and ‘repeated’ statement are the different transects (transectID). For a more extensive overview of the SAS code and for information on the interpretation of the output we refer to Singer (1998), Littell et al. (1996) and, especially for spatially correlated data, to Verbeke and Molenberghs (2000). Also for more specific guidelines regarding model selection, using likelihood ratios and an information criterion, can be referred to the mentioned specialized literature.

A quadratic response model

A linear response of edge effects across the complete transect is not very realistic (Murcia, 1995). Some studies tried to cope with this by using piecewise linear regression techniques (e.g. Williams-Linera, 1990), although this approach also deals with only one source of random variability. It is very easy to fit a Linear Mixed Model with a quadratic (or even higher order) term through the data. The level one model is the following:

$$Y_{ij} = \beta_{0j} + X_{ij}\beta_{1j} + X_{ij}^2\beta_{2j} + \varepsilon ij + \varepsilon'_{ij}$$

And after allowing the intercept, the linear distance effect and the quadratic distance effect to vary randomly we obtain:

$$Y_{ij} = \beta_0 + X_{ij}\,\beta_1 + X_{ij}^2\,\beta_2 + b_{0j} + X_{ij}\,b_{1j} + X_{ij}^2\,b_{2j} + \varepsilon_{ij} + \varepsilon'_{ij}$$

The according SAS code is:

```
proc mixed dataset;
class transectID distanceclass;
model Y = distance distance2;
random intercept distance distance2/ subject=transectID;
repeated distanceclass/type=sp(exp)(distance) subject=transectID;
```

Determining edge penetration distance

In many edge studies, the aim is not only to model the gradient of a certain variable along the edge, but also to determine up to how far into the fragment edge effects can be observed, i.e. the edge penetration distance. Because in edge studies measurements are taken at predefined distances along the transect, a simple adjustment of the Mixed Model outlined above makes this possible. By defining the distance-variable as a class variable, it is possible to calculate the least square means for each value of the variable studied, i.e. at each distance sampled. This is achieved by adding the ‘lsmeans’ statement. Differences between the least square means can then be calculated. The option ‘pdiff=all’ requests all pairwise differences, which makes it feasible to detect significant differences between the distances sampled, and hence, to delimit the edge penetration distance. The SAS code for achieving this is:

```
proc mixed dataset;
class transectID aspect distanceclass;
model Y = aspect distanceclass aspect*distanceclass/ solution
ddfm=kr;
random intercept/ type = un solution subject=subject;
repeated distanceclass/type=sp(exp)(distance) subject=transectID;
lsmeans distanceclass/pdiff=all;
```

Example

To illustrate the use of Mixed Modeling in edge studies, we applied the model described above to an edge dataset. The dataset involves 15 edges of dry heathland adjacent to forest situated in Flanders. Vegetation was sampled in the heathland at 5 distances from the heathland-forest edge. More detailed information about these edges, data sampling and experimental set up, can be found in the next chapter. The dataset is unbalanced, with 11 edges for which data is present for all distances and four edges in which one distance could not be sampled due to e.g. the presence of a small path. This dataset was studied by applying i) a one-way ANOVA, ii) a repeated measures GLM and iii) a Mixed Model analysis to compare the performance and restrictions of these different methods in analyzing transect data. As already mentioned, the repeated measures GLM is not able to model unbalanced datasets. Using this method, subjects with missing data are not included, and analyses are performed using only the complete subjects, hence using a balanced dataset. For simplicity, only the effect of distance from the edge was studied, and a linear response model was used. As dependent variables the relative cover of forest species, the relative cover of heathland species, the Shannon diversity index and the characteristic indicator values (Persson, 1981) for soil acidity and relative light intensity, calculated from the respective Ellenberg indicator values (Ellenberg et al., 1992), were studied. Also the plot scores on the first axis obtained from a Detrended Correspondence Analysis (DCA) were included as a measure of species composition.

One-way ANOVA

Data were first analyzed using a one-way ANOVA, the most commonly used approach in analyzing edge data. Therefore, the following SAS-statements were run:

```
proc anova dataset;
class distance;
model Y=distance;
means distance/tukey;
```

This analysis yields significant effects of distance on all variables studied, except for the scores of the plots on the first DCA axis (Table 5.1). Using this approach, edge effects seem to be limited to the first distance sampled, with the 5-m plots acting as transition plots between the heathland edge and interior.

Table 5.1 *F-values and significance for variables describing the plant community along the heathland edge, and differences between the different distances from the edge (indicated by letters), as obtained from the one-way ANOVA-analysis.*

	F	p	0m	5m	10m	20m	40m
Cover of forest species	4.68	0.002	a	ab	ab	b	b
Cover of heathland species	5.76	<0.001	a	ab	bc	bc	c
Ellenberg reaction figure	6.07	<0.001	a	ab	b	b	b
Ellenberg light	7.73	<0.001	a	ab	b	b	b
DCA1	0.53	0.713					
Shannon index	4.79	0.002	a	ab	b	b	b

DCA1: scores of the plots on the first axis obtained from the Detrended Correspondence Analysis

Repeated measures GLM

The spatial correlation between plots within the same transect can be dealt with by applying a repeated measures GLM. This method incorporates the non independency of the quadrats within a transect. A repeated measures GLM was applied to the dataset in SAS by running the program:

```
proc glm dataset;
model y1-y5 = / nouni;
repeated distance 5 (0 5 10 20 40) profile / summary printe;
```

In contrast to the ANOVA approach applied in the previous paragraph and the Mixed Model, the repeated measures GLM requires the dataset to be arranged in a multivariate way, with each row representing a transect and with the values for the response variable in the columns for each distance sampled (here labelled y1 to y5). The 'repeated' statement indicates that response variables, hence the values for y1 through y5, are repeated measures within each transect, and hence are not independent. The word 'distance' is not a response variable in the dataset, but is only a name to refer to these variables. The number '5' indicates that there are five distances sampled within each transect, and the numbers between brackets are the different distances at which observations were made. Trends over distance are analyzed through a set of contrast variables, which can be used to make comparisons between the different distances along the transect. Hence, the original data for the correlated distances are transformed into a new set of variables given by a set of contrast variables (Littell et al., 2002). There are different functions available to define these contrasts, but it is not possible to define a contrast yourself. For the transect data under study, the most suited options are 'profile', which generates contrast variables based on differences of adjacent distances, or 'helmert', in which a certain distance is compared to the mean of the subsequent distances. The type of contrast used should be added in the 'repeated' statement.

Results from this analysis are presented in Table 5.2. Largely the same conclusions can be drawn as with the one-way ANOVA analysis, with all variables showing a significant effect of distance except for the first DCA-axis scores. There are however small differences in the p-values. Furthermore, also the penetration distance of edge effects, as obtained from the analysis of contrasts, does not yield completely the same results, although overall, both methods indicate the presence of edge effects up to the second distance sampled, and hence a depth of edge zone of 8m.

Table 5.2 *F-values and significance for variables describing the plant community along the heathland edge, and differences between the different distances from the edge (indicated by letters), as obtained from the repeated measures GLM-analysis.*

	F	**p**	**0m**	**5m**	**10m**	**20m**	**40m**
Cover of forest species	4.71	0.037	a	a	b	b	b
Cover of heathland species	4.74	0.036	a	a	b	b	b
Ellenberg reaction figure	4.99	0.032	a	b	c	c	c
Ellenberg light	21.36	<0.001	a	b	c	c	c
DCA1	1.03	0.454					
Shannon index	10.68	<0.001	a	b	c	c	c

DCA1: scores of the plots on the first axis obtained from the Detrended Correspondence Analysis

As pointed out above, the repeated measures GLM incorporates the relatedness of the plot measures belonging to the same transect, and hence is better suited to deal with transect data than a one-way ANOVA, in which this is completely neglected. It does however not allow to directly accommodate the covariance structure. With transect data, observations closer together are often more alike than observations further apart. Hence, observations show declining correlations with increasing distance between them. This is also observed for the data studied. As an example, the correlation structure for the cover of heathland species is shown in Table 5.3. As can be observed, the value of the correlation coefficient between the cover of heathland species at 0m and the other distances sampled declines from 0.87 to 0.24 with increasing distance between the measurements. Similar patterns were observed for the other variables. The GLM procedure assumes a very general correlation pattern, with a unique value for the correlation between every pair of observations. Because a simpler model is often adequate to model this correlation, this procedure wastes a great deal of information, which consequently adversely affects efficiency and power of the test (Littell et al., 2002). The power is also negatively affected by the fact that transects with a missing observation are not included in the analysis, and hence a lot of data remains unused. Furthermore, only specific comparisons are available in the ‘repeated’-statement, and it is not possible to define any other contrasts that could be better suited to study the research question. In the case of edge studies for example, it would be interesting not only to know the contrasts between measurements at adjacent distances, but also between measurements at all distances sampled, which would lead to a better view of the gradient of a certain variable along the edge. Therefore, Mixed Modelling can be a better option.

Table 5.3 *Correlation matrix between the cover of heathland species at the different distances along the transect.*

	0m	**5m**	**10m**	**20m**	**40m**
0m	1	0.798**	0.581(*)	0.406	0.233
5m	0.798**	1	0.791**	0.757**	0.583(*)
10m	0.581(*)	0.791**	1	0.934***	0.787**
20m	0.406	0.757**	0.934***	1	0.865***
40m	0.233	0.583(*)	0.787**	0.865***	1

***: $p<0.001$; **: $0.001\leq p<0.01$; *: $0.01\leq p<0.05$; (*): $0.05\leq p<0.1$

Linear Mixed Model analysis

In Mixed Modelling, the covariance structure of the data can be modelled using different functions. For spatially correlated data, the exponential and gaussian functions are best suited (Verbeke and Molenberghs, 2000). The choice of the most appropriate covariance model is very important, since by using a model that is too simple and hence ignores the real structure, there is a risk for an increased type I error rate and an underestimation of standard errors. A model that is too complex will on the other hand decrease the power and efficiency of the procedure (Littell et al., 2002). With an approximately correct covariance model, the Mixed Model analysis is a very robust method (Littell et al., 2002). For our data set, comparison of the log-likelihood values pointed out that the exponential function best fitted our data for all variables studied. Hence, distance related patterns were studied using the SAS program

```
proc mixed dataset;
class subjec distance;
model Y = distance / solution ddfm=kr;
random intercept/ type = un solution subject=subject;
repeated distance/ type = sp(exp)(distance) subject=subject;
lsmeans distance/pdiff=all;
```

In this program, only the intercept of the different transects is included as a random effect due to the relatively limited dataset. Including also the slope of the different transects as a random variable leads to an overspecification of the model and did not result in convergence of the restricted maximum likelihood algorithm.

Table 5.4 *F-values and significance for variables describing the plant community along the heathland edge, and differences between the different distances from the edge (indicated by letters), as obtained from the Mixed model analysis.*

	F	p	0m	5m	10m	20m	40m
Cover of forest species	9.23	<0.001	a	a	b	b	b
Cover of heathland species	9.49	<0.001	a	a	b	b	b
Ellenberg reaction figure	9.39	<0.001	a	b	c	bc	c
Ellenberg light	15.22	<0.001	a	b	c	c	c
DCA1	1.21	0.324					
Shannon index	8.07	<0.001	a	a	b	b	b

DCA1: scores of the plots on the first axis obtained from the Detrended Correspondence Analysis

Results of this analysis can be seen in Table 5.4. Again, all variables except for DCA1 show a significant effect of distance along the transect. However, compared to the GLM repeated measures, p-values are much lower (e.g. cover of forest species: p= 0.037 in repeated measures GLM (Table 5.2) while p<0.001 in Mixed Model (Table 5.4)). This can be explained by the fact that the covariance structure is adequately modelled, and no information, and hence power and efficiency, is wasted on calculating each correlation separately. With a correctly modelled covariance structure, the Mixed Model approach is much more powerful and hence will result in lower p-values. Although in this case this does not result in different conclusions, the difference in p-value is large (e.g. 0.037 ↔ <0.001), and can possibly give rise to different results between both procedures in other cases. Furthermore, all transects sampled are included in the analysis, whether they are complete or not. This again raises the power of the analysis. Also the small differences in the depth of edge zone when calculated from the repeated measures GLM or from the Mixed Model analysis (e.g. for the Shannon index (Tables 5.2 and 5.4)) can probably be attributed to the incapability of the GLM to deal with unbalanced datasets. In the Mixed Model procedure, the differences between the distances along the transect are calculated based on the least square means, which are adjusted means corrected for the missing data. In the GLM however, contrasts are based exclusively on the complete transects, and on the arithmetic means of the variables along these transects only.

Conclusions

Although largely neglected in most studies dealing with transect data, a correct modelling of the correlation between the data collected at the different distances along the transect can significantly improve the efficiency and performance of the analysis. While traditional methods overlook this correlation (e.g. one way ANOVA) or do not fully accommodate its specific characteristics (e.g. repeated measures GLM), Mixed Modelling is capable of accounting for the distinct characteristics of transect data. When the covariance structure is adequately modelled, the Mixed Model can be a very flexible and powerful tool in analyzing transect data.

CHAPTER 6

BIOTIC AND ABIOTIC EDGE EFFECTS IN HIGHLY FRAGMENTED HEATHLANDS ADJACENT TO CROPLAND AND FOREST

Introduction

Continuing heathland fragmentation has resulted in an increased relative amount of edge of the remaining heathland patches (Saunders et al., 1991) and hence an increasing influence from the surrounding land use types on the heathland vegetation. Edge effects result from a flux of energy, nutrients and species across the boundary of two adjacent land use types, which can lead to an alteration in species composition, structure and ecological processes in the vicinity of this edge (Wiens, 1992; Murcia, 1995; Cadenasso et al., 2003). Especially in small patches edge effects can be expected to play an important role (Kiviniemi & Eriksson, 2002).

Until now edge effects have mainly been examined in forests (e.g. Murcia, 1995; Honnay et al., 2002a; Devlaeminck et al., 2005a), and have hardly been studied in heathlands (but see Angold (1997)). Heathland plant communities are adapted to nutrient-poor, acid soils (Gimingham, 1976) and an increase in soil nutrient status may bring on changes in competitive interactions between the plant species present. Studies dealing with effects of atmospheric deposition and fertilisation on heathland plant community composition have shown that increased nutrient input can lead to a shift from a dwarfshrub community dominated by *Calluna vulgaris* to a grass-dominated vegetation with *Deschampsia flexuosa* and *Molinia caerulea* (e.g. Bakker and Berendse, 1999; Bobbink and Lamers, 2002).

Nutrient enrichment can result from atmospheric deposition, fertilizer addition or over land flow and erosion of nutrients (Dumortier et al., 2001). Although forests in former heathland areas generally originate from afforestation of heathland or as a consequence of succession on unmanaged heathland, these forest soils differ from heathland soils (Nielsen et al., 1999; Sorensen and Tybirk, 2000). Soils underneath *Betula* or *Pinus* successional stages of heathland have increased soil nutrient concentrations compared with heathlands (Mitchell et al., 1997). Hence leaching of these nutrients can lead to increased nutrient levels in the adjacent heathland soil. Furthermore, the high rates of atmospheric deposition in forest edges (Draaijers et al., 1988; Weathers et al., 2001) can also affect the adjacent heathland. Since these deposition rates appear to be higher for coniferous than for deciduous forests (De Schrijver et al., 2000; Rothe et al., 2002), and because changes in soil properties differ according to tree species (Nielsen et al., 1999), even differences between heathland adjacent to either forest type can be expected.

In Flanders, heathland area was reduced to some 15 000 ha (0.27% of the total land area) (De Bruyn, 2003), scattered throughout the landscape. Hence edge effects are expected to affect a considerable area of the remaining fragments. Since little is known about edge effects on plant species composition in heathlands, the aim of this research was (1) to examine whether adjacent land use has eutrophying effects on heathland vegetation, (2) to study whether these effects differ between different land use types, being forest and cropland, and (3) to test for differences following edge orientation. Because of the typical variance structure of transect data, which is not accounted for in most edge studies, a mixed model approach for analysing the data is presented here (chapter 5).

Material and methods

Study sites

To investigate possible effects of the adjacent land use on heathland vegetation, 20 heathland edges were selected, of which five were adjacent to cropland and 15 to forest (seven coniferous - eight deciduous forest). All cropland and coniferous forest edges were situated in the Campine region, whereas most of the deciduous forest edges were situated on the dry sandy hills around the city of Leuven (Table 6.1).

All heathlands were dry heathland dominated by *C. vulgaris*. Although different management types were applied in the various heathlands, preliminary analyses showed that this did not result in differences in vegetation composition. The deciduous forest stands were classified as *Querco roboris-Betuletum* communities (Hermy, 1992), with *Quercus robur*, *Q. rubra* and *Betula pendula* as characteristic tree species. The coniferous forests were mostly uniform planted *Pinus sylvestris* stands, with a poorly developed herbaceous layer often consisting almost exclusively of *M. caerulea*. The croplands were all maize fields. Semi-liquid manure was used as fertilizer on all fields, and was applied at a rate of 45 to 70 m^3 ha^{-1} yr^{-1}. On two of these croplands the maize was grown in a crop rotation with winter cereals. For the latter, the after-effects of the maize crop gave enough nutrients and only a restricted amount of semi-liquid manure was applied in early spring.

Table 6.1 *Characteristics of the surveyed heathland transects*

Transect	Study area	Location	Adjacent land use	Orientation
1	Mechelse heide	Maasmechelen	Cropland	NE
2	Mechelse heide	Maasmechelen	Cropland	SW
3	Mechelse heide	Maasmechelen	Cropland	NW
4	Hageven	Neerpelt	Cropland	NW
5	Hageven	Neerpelt	Cropland	NE
6	Beninksberg	Rotselaar	Deciduous forest	N
7	Beninksberg	Rotselaar	Deciduous forest	N
8	Rodebos	Huldenberg	Deciduous forest	NE
9	Rodebos	Huldenberg	Deciduous forest	SE
10	Rodebos	Huldenberg	Deciduous forest	SW
11	Eikelberg	Aarschot	Deciduous forest	N
12	’s Hertogenheide	Aarschot	Deciduous forest	SW
13	De Teut	Zonhoven	Deciduous forest	N
14	De Teut	Zonhoven	Coniferous forest	N
15	De Teut	Zonhoven	Coniferous forest	S
16	Mechelse heide	Maasmechelen	Coniferous forest	SW
17	Mechelse heide	Maasmechelen	Coniferous forest	N
18	Mechelse heide	Maasmechelen	Coniferous forest	NE
19	Mechelse heide	Maasmechelen	Coniferous forest	SE
20	Kalmthoutse heide	Kalmthout	Coniferous forest	NW

Data collection

Within each edge a transect was set up perpendicular to the edge, extending from the heathland-forest or heathland-cropland border to 40m into the heathland. The location of the 0m point was based on the position of the first trees (heathland-forest) (Fraver, 1994; Oosterhoorn and Kappelle, 2000) or on the end of plowing activity (heathland-cropland) (Honnay et al., 2002a; Devlaeminck et al., 2005a). All edges were sharply delineated. At five distances along these transects (0-5-10-20-40m), strips of 3 x 40m parallel to the edge were established. In each of these strips five randomly selected 3 x 3m plots were located, in which vegetation was recorded in the summer of 2003 (Fig. 6.1). Cover of all vascular plant species in the herbaceous and the shrub layer was estimated using the decimal cover scale of Londo (Londo, 1976). This resulted in 25 plots per edge and an overall total of 480 plots. 20 plots had to be omitted because they were located in the vicinity of e.g. a small road.

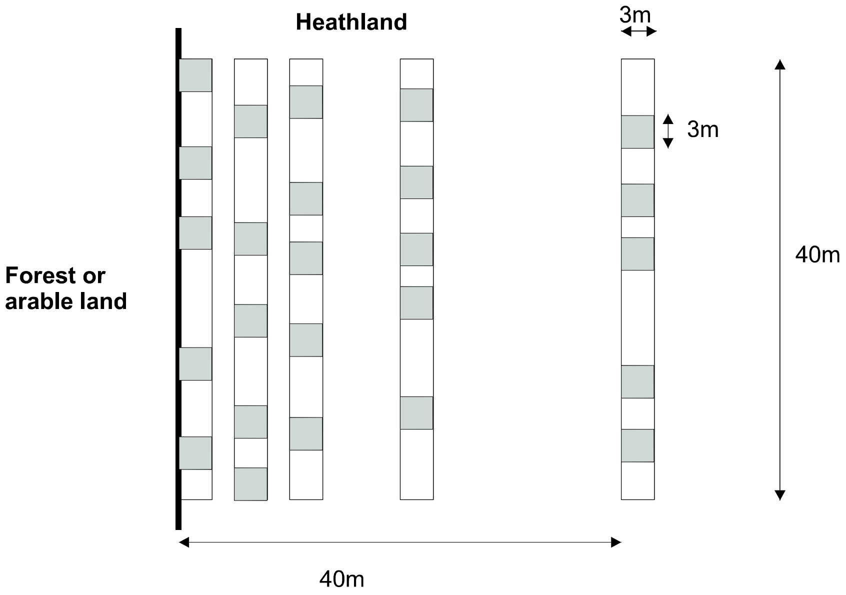


Fig. 6.1 *Experimental set-up. Each transect extended from the border (0m) to 40m into the heathland. At distances of 0, 5, 10, 20 and 40m strips of 3 x 40m were laid out, parallel to the border, in which five 3 x 3m plots were located.*

In 14 edges (four heathland-cropland, five heathland-deciduous forest, five heathland-coniferous forest) soil samples were collected for soil analysis. For each of the five distances along the transect several samples were taken at random and bulked together resulting in one sample per distance (five per transect). pH was measured in a KCl-solution. Phosphate and available Ca, K, Na and Mg contents were assessed using atomic absorption spectrophotometry (cations) or colorimetry (P), after extraction in an ammonium lactate solution. Carbon content was determined using the modified Walkley and Black method. Finally, nitrate (colorimetrically after KCl-extraction) and total N content (Kjeldahl-Lauro method) were measured.

Data analysis

To avoid pseudo-replication (Hurlbert, 1984), vegetation cover data in the five plots at each distance along the different transects were averaged, resulting in one average cover value per species per distance for each edge (Honnay et al., 2002a). A detrended correspondence analysis (DCA) was performed on the vegetation data to obtain a measure of plant community composition. Next, total species richness and the Shannon diversity index (Kent and Coker, 1992) were determined per strip for each transect. Furthermore, the cover of species belonging to the different categories defined by Grime et al. (1988) (competitive (C), stress-tolerant (S), ruderal (R), and intermediate categories (CS, CR, SR, CSR)) and the characteristic indicator values for light, nutrient content and reaction figure (Persson, 1981), based on the Ellenberg indicator values (Ellenberg et al., 1992), were calculated for each distance along all transects. Finally, the cover of heathland species, forest species and species of tall herb vegetation and nutrient rich habitats (sensu Stieperaere and Fransen, 1982) and the cover of the different growth forms (dwarf shrub, grass, herbaceous) was calculated per distance for each transect.

The relation between the different variables calculated and distance was analysed by applying a mixed model (Verbeke and Molenberghs, 2000), using PROC MIXED in SAS 8.02 (SAS Institute Inc., 1999-2001). This technique takes into account the three components of random variability inherent to the data collected (Diggle et al., 1994; Verbeke and Molenberghs, 2000), being (a) measurement error and error due to natural variation; (b) spatial correlation, i.e. correlation between measurements at short distance, in this case between distances along the transect; (c) random effects resulting from heterogeneity between the different transects. Traditional edge studies often include only the first type, but neglecting these other sources of variability can possibly bias results and hence lead to false conclusions about the presence and extent of edge effects (chapter 5).

Analyses were first performed to test for differences in the extent of the edge effects between the adjacent land use types cropland and forest. Therefore, mixed models were tested containing adjacent land use, distance, and the interaction term between adjacent land use and distance as fixed effects and intercept as a random effect. Due to the relatively limited data set, allowing the slope of the different transects to vary randomly did mostly not result in convergence of the restricted maximum likelihood algorithm. Dependent variables were species richness, Shannon diversity index, the scores of the plots on the first two DCA-axes, Ellenberg indicator values and cover of species of the different socio-ecological groups, growth forms and Grime C, S and CS strategies. Species having one of the other Grime strategies (R, CR, SR or CSR) turned out to be too rare in our dataset to include these strategies in the analyses. Differences between the distances from the heathland edge were determined by calculating the differences of the least-square means, using the LSMEANS statement. Because for forests also orientation effects were expected, the analysis was rerun for the same dependent variables, but now also including aspect and the interaction term of aspect and distance as fixed effects, next to those already present in the previous model. When necessary, dependent variables were transformed prior to analysis to obtain normality (Sokal and Rohlf, 1995).

The parameters of the mixed models were estimated using restricted maximum likelihood estimation, the default method in SAS. Due to the restricted dataset, including only five distances per transect, no polynomials were fitted, and distance was treated as a class variable, which also allowed us to determine significant differences between the distances, as described above. Significance of the fixed effects was tested using the F-test. Because of the small sample size, denominator degrees of freedom were estimated by the Kenward-Roger method (Kenward and Roger, 1997). By adding the REPEATED statement spatial correlation between the distances along the transect was taken into account. Both models with an exponential and a Gaussian spatial correlation function, the two most frequently used functions (Verbeke and Molenberghs, 2000), were run, and the model with the best fit, as could be derived from comparison of the model log-likelihood values, was retained.

Results

All dependent variables describing the plant community composition across the heathland edge showed a significant effect of distance from the edge (Table 6.2). In most cases this relation with distance differed between heathlands adjacent to forest and heathlands adjacent to cropland. Only three variables (species richness and cover of both heathland species and stress-tolerant species) showed no difference between adjacent land use types (Table 6.2).

Table 6.2 *F-values and significance for the effects of adjacent land use type (LUT), distance from the edge (DIST) and their interaction (LUT*DIST) on the different variables describing vegetation composition along the heathland-cropland and heathland-forest edges, and differences in their mean values between the distances from the edge (indicated by letters), as obtained from the mixed model analysis.*

	LUT		DIST		LUT*DIST		LUT$^{\$}$	0m		5m		10m		20m		40m	
Shannon index	7.12	*	12.96	***	3.24	*	C	1.78	a	1.18	b	1.02	b	0.66	c	1.01	bc
							F	1.03	a	0.98	a	0.57	b	0.56	b	0.51	b
Number of species	2.11		6.14	***	0.97			11.95	a	10.00	b	8.75	c	8.30	c	8.41	bc
DCA axis1	12.90	**	12.95	***	1.61		C	2.21	a	1.02	b	0.97	c	0.78	c	0.77	c
							F	0.70	a	0.42	b	0.16	c	0.14	c	0.15	c
DCA axis2	1.19		4.72	**	5.08	**	C	2.02	a	1.24	b	0.98	b	1.25	b	1.53	ab
							F	1.55		1.51		1.60		1.61		1.59	
CIV-L	8.02	*	8.83	***	2.65	*	C	7.14		7.43		7.41		7.58		7.59	
							F	7.44	a	7.62	b	7.86	c	7.83	c	7.86	c
CIV-N	6.33	*	13.60	***	2.52		C	3.65	a	1.63	b	1.56	c	1.46	c	1.63	c
							F	1.68	a	1.43	b	1.17	c	1.20	c	1.18	c
CIV-R	6.64	*	14.48	***	1.21		C	4.10	a	1.57	b	1.24	c	1.52	c	1.71	bc
							F	1.73	a	1.26	b	1.13	c	1.15	c	1.11	bc
GF grass	14.01	**	6.45	***	1.38		C	0.61	a	0.51	b	0.48	c	0.42	c	0.40	c
							F	0.39	a	0.25	b	0.09	c	0.09	c	0.09	c
GF dwarf shrub	14.58	**	10.46	***	1.72		C	0.06	a	0.41	b	0.43	c	0.57	c	0.56	c
							F	0.54	a	0.68	b	0.87	c	0.87	c	0.88	c
GF herbaceous	11.97	**	24.37	***	14.52	***	C	0.20	a	0.01	b	0.00	b	0.01	b	0.02	b
							F	0.01	a	0.00	b	0.00	c	0.00	c	0.00	bc

Table 6.2 *continued*

	LUT		DIST		LUT*DIST		LUT[$]	0m		5m		10m		20m		40m	
Heathland species	3.45		13.55	***	2.41			0.74	a	0.82	b	0.91	c	0.95	c	0.94	c
Forest species	0.75		4.36	**	3.53	*	C	0.12		0.18		0.17		0.05		0.08	
							F	0.18	a	0.15	a	0.06	b	0.05	b	0.05	b
TH-NR species	2.75		25.11	***	20.01	***	C	0.30	a	0.01	b	0.00	b	0.00	b	0.00	b
							F	0.02		0.02		0.01		0.00		0.00	
Grime C	0.03		10.08	***	4.07	**	C	0.22	a	0.05	b	0.06	b	0.05	b	0.05	b
							F	0.04	a	0.04	a	0.03	ab	0.02	b	0.02	b
Grime S	1.46		2.68	*	0.49			0.10	a	0.06	ab	0.03	c	0.03	bc	0.03	bc
Grime CS	5.66	*	15.54	***	4.07	**	C	0.44	a	0.83	b	0.92	b	0.93	b	0.85	b
							F	0.80	a	0.88	b	0.94	c	0.93	bc	0.95	c

****: $p<0.001$; **: $0.001<p\leq 0.01$; *: $0.01<p\leq 0.05$*

CIV-L: Ellenberg indicator value for light; CIV-N: Ellenberg indicator value for soil nutrient content; CIV-R: Ellenberg indicator value for soil acidity; GF: growth form; TH-NR species: species characteristic for tall herb vegetations and nutrient rich situations.

[$]: For variables showing a significant effect of adjacent land use type, differences between the distances from the edge are analyzed for heathland-cropland (C) and heathland-forest (F) edges separately.

Figure 6.2 *Gradients of the Ellenberg indicator values for light (CIV-L), soil acidity (CIV-R) and soil nutrient content (CIV-N) and of the cover of species of tall herb vegetation and nutrient rich habitats, dwarf shrubs and grasses along the heathland-cropland (dotted line) and the heathland-forest (full line) edges. Error bars show 1 S.E.*

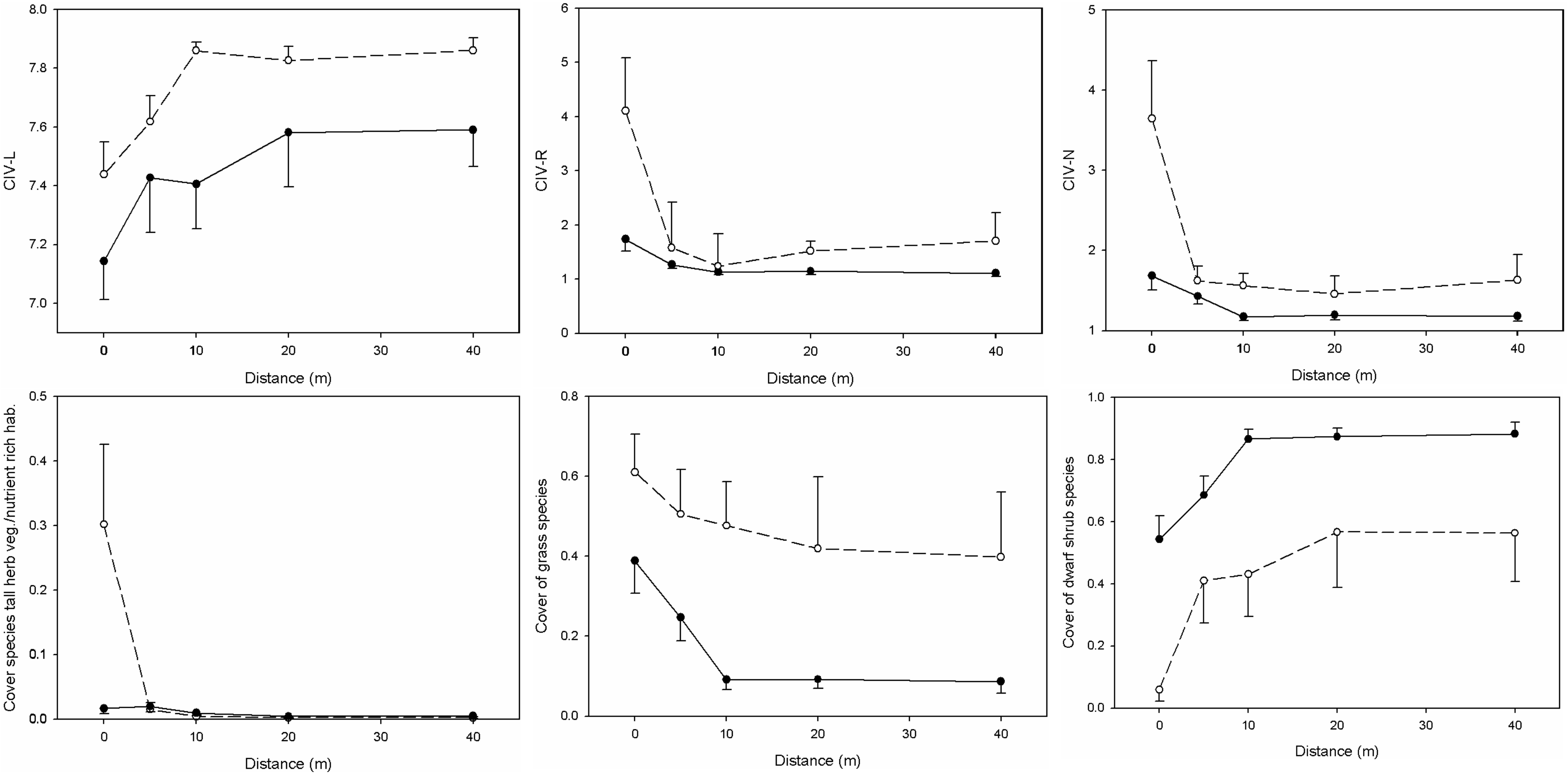


Table 6.3 *F-values and significance for the effects of adjacent land use type (LUT), distance from the edge (DIST) and their interaction (LUT*DIST) on the different soil variables along the heathland-cropland and heathland-forest edges, and differences in their mean values between the distances from the edge (indicated by letters), as obtained from the mixed model analysis.*

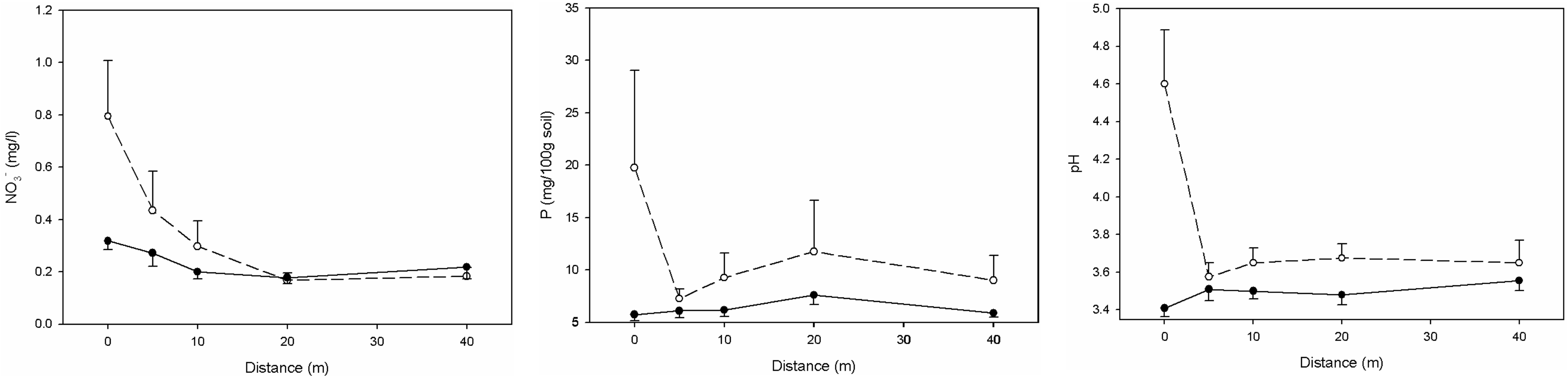
	LUT		**DIST**		**LUT*DIST**		**LUT$^{\$}$**	**0m**		**5m**		**10m**		**20m**		**40m**	
K	0.01		1.11		0.32												
Kjeldahl N	1.51		1.62		1.07												
$NO_3^{-\circ}$	0.92		15.47	***	2.33			0.45	a	0.32	b	0.23	c	0.18	c	0.21	c
Ca	0.16		7.29	***	4.25	**	C	36.25	a	5.50	b	3.50	b	3.25	b	3.25	b
							F	10.91		12.60		8.36		5.80		7.56	
C$^{\$}$	0.22		1.89		2.12												
Na	1.44		0.49		2.53												
Mg	0.27		1.95		0.58												
P	2.69		3.07	*	3.99	**	C	19.75	a	7.25	b	9.25	ab	11.75	ab	9.00	b
							F	5.73		6.10		6.18		7.60		5.89	
pH$_{(KCl)}$	8.92	*	4.08	**	10.67	***	C	4.60	a	3.58	b	3.65	b	3.68	b	3.65	b
							F	3.41		3.51		3.50		3.48		3.56	

***: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$

Soil characteristics given in mg/100g soil, except for $^{\circ}$ in mg/l and $^{\$}$ in %

$^{\$}$: For variables showing a significant effect of adjacent land use type, differences between the distances from the edge are analyzed for heathland-cropland (C) and heathland-forest (F) edges separately.

Fig. 6.4 *Nitrate, available phosphor and pH gradients along the heathland-cropland (dotted line) and heathland-forest (full line) edges. Error bars show 1 S.E.*



For about half of the soil variables (K, Kjeldahl N, C, Na and Mg) a relation with distance along the transect was lacking. For the soil variables that did exhibit a significant effect of distance, this relation differed according to adjacent land use type (Table 6.3).

The zone over which edge effects occurred was limited. Both for heathlands adjacent to forest and heathlands adjacent to cropland, edge effects were prominent only in the 0-3m plots. In most cases, the 5-8m plots formed the transition between the edge plots and the heathland interior (Tables 6.2 and 6.3). From this an extent of the edge zone of c. 8m could be derived. Although this zone coincided for both types of adjacent land use, the differences between the edge and the heathland interior were more pronounced for heathlands adjacent to cropland. Croplands had more eutrophying effects on the heathland than forests. The Ellenberg values for soil nutrient status, and soil phosphate and nitrate concentration showed a larger gradient and were higher in the edge zone of heathlands adjacent to cropland than in that of heathlands adjacent to forest (Tables 6.2 and 6.3; Fig. 6.2 and 6.4). Furthermore, the fact that species characteristic of tall herb vegetations and nutrient rich habitats occurred almost exclusively at the heathland-cropland edge seemed to confirm this (Fig 6.3).

When the mixed models were rerun for forests only, including orientation as a class variable, orientation effects turned out to be rare. Only the cover of species with Grime's C-strategy showed an effect of orientation (Tables 6.4 and 6.5). Differences in distance-related patterns between deciduous and coniferous forests as adjacent land use were much less pronounced than between forests and croplands, both when considering the biotic (Table 6.4) and the abiotic variables (Table 6.5). Hence no significant distinction in the eutrophying effects of both forest types could be found, nor differences in the penetration distances of edge effects (Tables 6.4 and 6.5). The most striking dissimilarity was that the edge zone of heathlands bordering coniferous forests seemed to be much more grass-dominated than that of heathlands bordering deciduous forest (Table 6.4).

Table 6.4 *F-values and significance for the effects of orientation (ASP), adjacent land use type (LUT), distance from the edge (DIST) and their interactions (DIST*LUT and DIST*ASP) on the different variables describing vegetation composition along the heathland-deciduous and heathland-coniferous forest edges, and differences in their mean values between the distances from the edge (indicated by letters), as obtained from the mixed model analysis.*

	ASP	LUT		DIST		DIST*ASP		DIST*LUT		LUT$^{\$}$	0m		5m		10m		20m		40m	
Shannon index	0.54	1.87		6.89	***	0.67		0.45			1.03	a	0.98	a	0.57	b	0.56	b	0.51	b
Number of species	1.67	6.03	*	6.12	***	2.28		2.50		D	12.13	a	11.13	ab	10.75	b	11.25	b	8.40	b
										C	9.57	a	7.83	ab	6	b	5.14	b	6.57	b
DCA axis 1	1.48	0.88		0.64		0.58		0.47												
DCA axis 2	1.46	0.01		11.15	***	0.48		1.17			1.36	a	1.54	a	1.85	b	1.88	b	1.87	b
CIV-L	0.23	0.85		13.48	***	0.76		1.05			7.44	a	7.62	b	7.86	c	7.83	c	7.86	c
CIV-N	0.54	0.40		7.82	***	0.99		0.31			1.68	a	1.43	b	1.17	c	1.20	c	1.18	c
CIV-R	1.26	0.31		11.42	***	0.85		4.84	**	D	1.36		1.32		1.19		1.19		1.20	
										C	2.16	a	1.18	b	1.05	b	1.10	b	1.04	b
GF grass	1.47	0.06		20.24	***	0.46		3.06	*	D	0.24	a	0.18	ab	0.11	c	0.10	bc	0.10	bc
										C	0.56	a	0.33	b	0.07	c	0.08	c	0.07	c
GF dwarf shrub	0.98	0.02		20.34	***	0.61		3.19	*	D	0.70		0.73		0.83		0.84		0.85	
										C	0.37	a	0.62	a	0.91	b	0.91	b	0.90	b
GF herbaceous	0.63	1.09		4.47	**	2.24		0.11			0.01	a	0.00	b	0.00	c	0.00	c	0.00	bc
Heathland species	0.11	5.13	*	9.36	***	1.52		0.82		D	0.78	a	0.79	a	0.89	b	0.91	b	0.89	b
										C	0.82	a	0.89	a	0.98	b	0.99	b	0.98	b
Forest species	0.39	5.65	*	10.88	***	0.83		2.90	*	D	0.19		0.18		0.09		0.08		0.10	
										C	0.17	a	0.10	a	0.02	b	0.01	b	0.02	b
TH-NR species	0.06	3.30		2.89	*	1.99		0.25												
Grime C	3.36	3.92		4.54	**	2.78	*	2.80	*	D-N	0.01		0.05		0.03		0.04		0.03	
										D-S	0.10	a	0.04	b	0.05	b	0.04	b	0.01	b

Table 6.4 *continued*

	ASP	LUT	DIST		DIST*ASP	DIST*LUT	LUT[$]	0m		5m		10m		20m		40m	
Grime C							C-N	0.02	a	0.03	a	0.01	ab	0.00	b	0.00	b
							C-S	0.06	a	0.04	a	0.02	b	0.01	b	0.02	b
Grime S	0.70	0.16	2.21		0.38	1.19		0.07		0.05		0.03		0.03		0.03	
Grime CS	0.55	0.16	4.57	**	0.49	2.10		0.80		0.88		0.94		0.93		0.95	

***: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$

Abbreviations: see table 1

[$]: *For variables showing a significant effect of adjacent land use type, differences between the distances from the edge are analyzed for heathland-deciduous forest (D) and heathland-coniferous forest (C) edges separately.*

Table 6.5 *F-values and significance for the effects of orientation (ASP), adjacent land use type (LUT), distance from the edge (DIST) and their interactions (DIST*ASP and DIST*LUT) on the different soil variables along the heathland-deciduous and heathland-coniferous forest edges, and differences in their mean values between the distances from the edge (indicated by letters), as obtained from the mixed model analysis.*

	ASP	**LUT**		**DIST**		**DIST*ASP**	**DIST*LUT**		**LUT$^{\$}$**	**0m**		**5m**		**10m**		**20m**		**40m**	
K	0.23	1.79		0.28		1.73	5.97	**	D	8.3		7.3		6.5		6		8	
									C	4	a	5.25	bc	4.6	ac	6.2	b	5.2	ab
Kjeldahl N	2.60	1.49		2.52		1.20	3.66	*	D	160.8	a	136.8	ab	88.6	c	79.6	c	99	bc
									C	111.4		133.25		105.8		135		116.8	
$NO_3^{-\circ}$	1.32	0.03		7.25	***	0.33	0.30			0.32	a	0.27	b	0.20	c	0.18	c	0.22	c
Ca	1.89	0.77		1.14		0.75	2.51												
C§	2.32	4.72		0.53		0.25	3.56	*	D	4.03	a	3.27	ab	2.60	b	2.30	b	2.73	b
									C	3.12		3.48		3.54		4.40		3.86	
Na	1.30	9.17	*	1.51		0.47	1.10												
Mg	1.33	4.01		0.41		0.07	0.38												
P	0.02	0.08		0.65		0.13	1.77												
pH(KCl)	0.54	0.42		0.95		0.22	0.58												

****: $p<0.001$; **: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$*

Soil characteristics given in mg/100g soil, except for $^{\circ}$ in mg/l and § in %.

$^{\$}$: For variables showing a significant effect of adjacent land use type, differences between the distances from the edge are analyzed for heathland-deciduous forest (D) and heathland-coniferous forest (C) edges separately.

Discussion

Effects of adjacent land use

Adjacent land use had significant effects on the heathland plant community. Towards the edge, community composition changed because biotic and abiotic conditions become marginal for some species (Walker et al. 2003). Both in heathlands adjacent to cropland and heathlands adjacent to forest, the characteristic dwarf shrubs (in this case almost exclusively *C. vulgaris*) were much less prominent at the edge, and were replaced by grass species, and by dicotyleous herbaceous species in heathlands bordering cropland. At the heathland-cropland border dwarf shrub species were in fact almost completely absent. This high abundance of gramineous species suggests eutrophication near the edge, as in heathlands an increase in soil nutrient status has often resulted in the outcompeting of the characteristic dwarf shrub dominated community by grass species (e.g. Bakker and Berendse, 1999; Bobbink and Lamers, 2002). The graphs depicting the gradients in the Ellenberg values for nitrogen and reaction figure illustrate this process. These effects differed according to adjacent land use, however, with the effects of cropland being more prominent. Deeper into the heathland, both values approached each other and differences between both land use types became less pronounced.

The hypothesis of eutrophication was confirmed when the soil variables were considered. At the edge, soil nitrate concentration was higher both for heathland adjacent to cropland and heathland adjacent to forest, with the values being somewhat lower for forest. Since the leaf area index of forests is much larger than that of the dwarfshrub dominated heathlands, forests capture large amounts of nitrogen, especially at forest edges (e.g. De Schrijver et al., 1998; Devlaeminck et al., 2005b). This explains the increased concentrations for this element at the edge, both with cropland (through fertilizer application) and forest (through deposition) as adjacent land use. Soil phosphate, another important plant nutrient, also showed a gradient along the transect, with higher values at the heathland-cropland edges compared with the heathland-forest edges. In the latter case, soil phosphate concentration remained more or less constant along the transect. In areas where very high rates of fertilizer are applied, phosphate may leach into the ground water, and can consequently be transported to neighbouring areas (Overloop et al., 2003). Potassium, another key element in plant nutrition, did not show any gradients along the edge-interior gradient, nor did it differ between forest and cropland as adjacent land use.

An additional explanation for the higher abundance of grasses at the heathland-forest edge could be that these grasses, although they also prefer full light, are more shade-tolerant than *C. vulgaris* (Weeda et al., 1988, 1994), and hence replace heather at the edge, where less light penetrates because of shading from the adjacent forest canopy. For both types of adjacent land use, a clear gradient could be seen from a higher abundance of more shadow tolerant species to light demanding species further into the heathland. The fact that this gradient was also present in the heathland-cropland border can be explained by the often occurring isolated shrubs or single small trees at this boundary.

Differences between the effects of coniferous and deciduous forests were limited. No differences between both forest types could be found in the gradient of the Ellenberg figure for light, although effects of coniferous forests were expected to be more pronounced because their canopy is present throughout the year. While various studies have indicated dissimilarities between the deposition rates and related effects on soil variables in coniferous and deciduous forests (e.g. Rothe et al., 2002; De Schrijver et al., 2004), this did not result in different effects on the neighbouring heathlands.

Orientation effects

Orientation, a factor often mentioned as being an important determinant of edge effects in studies concerning forest edges (e.g. Matlack, 1993; Murcia, 1995; Honnay et al., 2002a), did not seem to affect edge effects in the studied heathland edges. Differences in orientation of the forest relative to the heathland lead to differences in shading, which influences the microclimate in the vicinity of the edge, leading to lower irradiance with forest to the north of the heathland compared with forest to the south. Hence, one would expect especially gradients in Ellenberg light figures to be more prominent in the latter case. However, although a gradient in light intensity existed with the transition from forest to heathland, no differences following forest orientation were present.

Edge zone

Changes along the edge-interior transect occurred gradually, and hence point at the existence of a gradual transition zone, incorporating characteristics of both land use types, rather than a distinct edge zone. Edge effects were present in a zone of c. 8 m, and values for most variables examined remained quite constant afterwards. Despite the fact that for most variables edge effects were more severe in heathlands adjacent to cropland, the width of this edge zone did not differ between the studied adjacent land use types. To our knowledge, no other estimates of the depth of edge effects in heathlands exist. For forests, the ecosystem on which most edge research has focused in the past, values for depth of edge influences on vegetation in the temperate region vary widely, ranging from 3m to 60m, with values of up to 20m being predominant (e.g. Murcia, 1995, Euskirchen et al., 2001).

In earlier studies on the effects of extreme heathland fragmentation in Belgium, we found isolation to be the most important factor determining heathland species diversity and single species distribution patterns, while area-effects were limited (chapters 3 and 4). The results of the present study however seem to suggest that area does have an effect on the heathland vegetation. Because an edge zone of approximately 8m exists, this would lead to the conclusion that a minimum area is required to exclude these edge effects and retain a characteristic heathland vegetation. Nonetheless, even in this edge zone the species typical of heathland were present, though at lower abundance, except maybe in the 0m plots in the heathlands adjacent to cropland. As pointed out by Ries and Sisk (2004), edge responses are strongly dependent on the characteristics of the surrounding habitat. Since patches may be surrounded by a variety of different habitat types, this can result in a lack of congruence between edge responses and area sensitivity (Ries and Sisk 2004).

CHAPTER 7

EFFECTS OF GRAZING AND ADJACENT FOREST LAND USE ON THE BRYOPHYTE COMMUNITY OF DRY HEATHLANDS

Introduction

Heathland is an important semi-natural vegetation type in Northwestern Europe. It is, however, strongly threatened by decreasing habitat quality and quantity. Due to changes in agricultural practices, heathland lost its economical importance and often was converted to other land use types (Gimingham, 1994). Additionally, afforestation, industrialisation and urbanisation further threatened the remaining heathlands (Moore, 1962; Webb, 1990; Gimingham, 1994), leading to a reduction of more than 95% of the total heathland area in The Netherlands and Flanders since 1850 (Odé et al., 2001). Furthermore, the remaining heathlands often suffer from grass, shrub and tree encroachment as a result of inadequate or insufficient management (Mitchell, et al., 1997; De Bruyn, 2003) and increased atmospheric deposition (e.g. Bobbink et al., 1998; Lee, 1998). Most studies until now focussed on the higher plant species richness of these systems (e.g. Alonso and Hartley, 1998; Roem and Berendse, 2000; Bokdam and Gleichman, 2000). The bryophyte community received much less attention. Yet in dry heathland this is much more diverse than the vascular plant community (Rodwell, 1991; Schaminée et al., 1996), and therefore constitutes an important component of heathland plant diversity.

The bryophyte community composition is strongly influenced by management type (e.g. van Tooren et al., 1990; Bergamini et al., 2001a; Vanderpoorten et al., 2004). Management type and intensity profoundly affect vegetation structure, especially of the dwarf shrub *Calluna vulgaris*, the dominant plant species in dry heathlands (Schaminée et al., 1996). This also has an effect on the microclimate underneath the plant canopy, an important ecological determinant for the bryophyte vegetation (During and Van Tooren, 1990). The growth phase of *Calluna*, which affects bryophyte cover and composition as well (Barclay-Estrup and Gimingham, 1969), can also be controlled by management. Especially the older phases of *Calluna* may bare an abundant bryophyte flora (Barclay-Estrup and Gimingham, 1969). Furthermore, management influences the amount of litter and the presence of gaps in the vegetation canopy and of bare ground, other factors determining bryophyte community composition. Overall, grazing causes higher environmental heterogeneity due to trampling, dung deposition and selective defoliation (Bergamini et al., 2001a; Cosyns and Hoffmann, 2004). Mowing, on the other hand, creates a more uniform vegetation structure (Cosyns and Hoffmann, 2004; De Blust, 2004). As a consequence, grazed sites often contain a more diverse and species rich bryophyte flora than mown sites (cf. Bergamini et al., 2001a; Aude and Ejrnaes, 2005).

Continuing heathland fragmentation has resulted in the subdivision of formerly large heathland areas into small, isolated patches. This process can be seen throughout Western Europe (Gimingham, 1976; Pott, 1996; Webb, 1990; Odé et al., 2001) and also in Belgium (chapter 2). An important consequence of fragmentation is the increase in the relative amount of edge habitat. Especially in small patches of heathland, it can be expected that the bryophyte composition is influenced by fluxes of light, heat, moisture and wind from neighbouring patches (Matlack, 1993; Chen et al., 1995). Especially heathlands adjacent to forests are susceptible to increased shading, and subsequently, to lower temperatures and higher humidities, which are positive factors for hepatics and mosses. Since bryophytes are poikilohydric, meaning that they do not show specialized mechanisms for regulating uptake and loss of water, they are especially sensitive to changes in microclimate (Esseen and Renhorn, 1998; Moen and Jonsson, 2003; Hylander, 2005). The effects of adjacent land use on bryophytes have hardly been studied. Moreover, the few previous studies focused on epiphytic species (Moen and Jonsson, 2003) and forests (Moen and Jonsson, 2003; Hylander, 2005). As heathlands in Flanders are highly fragmented and form a threatened habitat in which bryophytes make up an essential part of the diversity, it is also important to study edge effects in this habitat.

Besides their direct effects on the bryophyte community composition, management and adjacent land use may also influence species composition through promoting or restricting the abundance of invasive species. In Europe, four bryophyte species can be considered invasive, being *Orthodontium lineare*, *Campylopus introflexus*, *Riccia rhenana* and *Lophocolea semiteres* (Hassel and Söderström, 2005). Of these, both *Campylopus introflexus* and *Lophocolea semiteres* occur in dry heathlands in Belgium. Especially the former forms a major problem in many nutrient-poor acid grasslands and heathlands, because it forms dense carpets that inhibit regeneration of the original vegetation (Equihua and Usher, 1993). *Lophocolea semiteres* has only been found relatively recently in Belgium, and has not yet become as abundant as *Campylopus introflexus* (Stieperaere, 1994). However, since it seems to displace the native *Lophocolea*-species (Stieperaere et al., 1997), this species may also become an important problem. Both species benefit from bare ground and low, open vegetation (Stieperaere et al., 1998), which is often created by disturbance like high recreational pressure or management.

The aims of this part of the study are to investigate (i) whether adjacent land use, in this case forest, affects the bryophyte community in the heathland patch; (ii) up to how far into the heathland possible edge effects extend; (iii) if and how the type of management applied interacts with the effects of adjacent land use and, finally, (iv) if and how invasive bryophyte species are affected by these factors.

Material and methods

Study sites

To study the effects of management type and adjacent forest land use on the bryophyte layer of heathlands, 11 heathland edges adjacent to forest were selected (Table 7.1; Fig. 7.1). All heathland patches are dry heathlands dominated by *Calluna vulgaris*. Although these heathlands are distributed over two different phytogeographic regions (Brabant and Campine), this does not give rise to differences in vegetation composition. Half of these forests are deciduous *Querco roboris-Betuletum* forests (Hermy, 1992), with *Quercus robur*, *Q. rubra* and *Betula pendula* as characteristic tree species. The other forests are coniferous *Pinus sylvestris* forest stands with a species-poor herbaceous layer dominated by *Molinia caerulea*. Five of these heathlands are managed by extensive grazing while the other six are managed by mowing (Table 7.1).

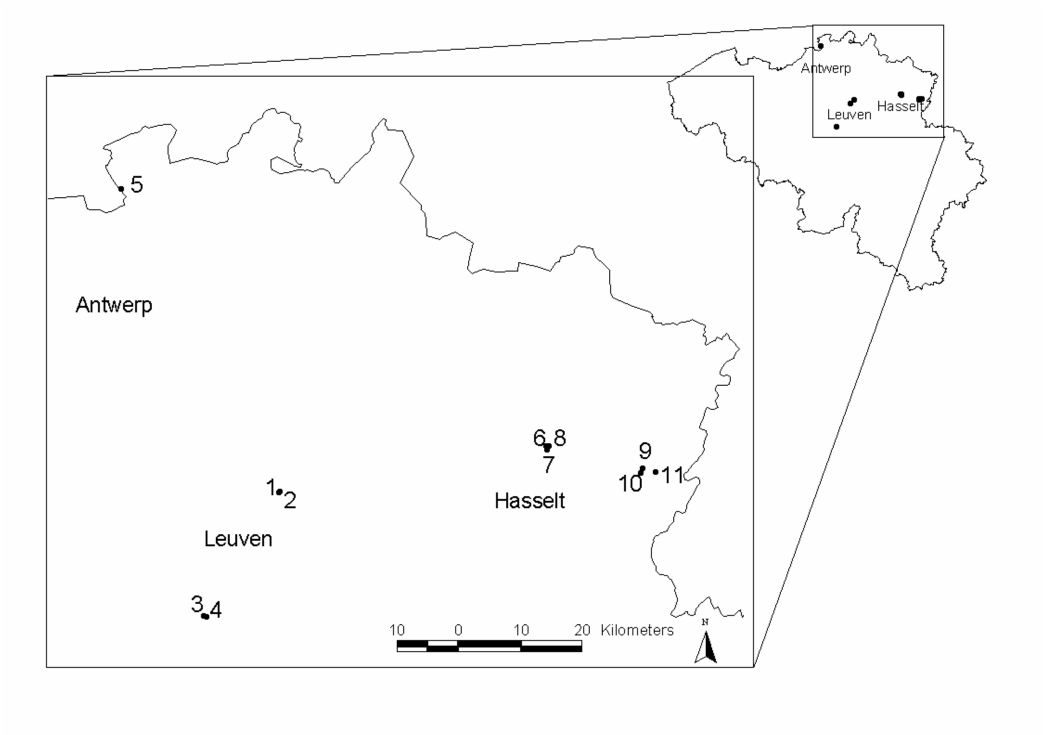


Fig. 7.1 *Location of the heathland edges studied (numbers refer to table 7.1).*

Table 7.1 *Characteristics of the 11 heathland edges studied.*

	Site	Location	Management	Adjacent landuse
1	Beninksberg	Rotselaar	Grazing	Deciduous forest
2	Beninksberg	Rotselaar	Grazing	Deciduous forest
3	Rodebos	Huldenberg	Grazing	Deciduous forest
4	Rodebos	Huldenberg	Grazing	Deciduous forest
5	Kalmthoutse heide	Kalmthout	Grazing	Coniferous forest
6	De Teut	Zonhoven	Mowing	Deciduous forest
7	De Teut	Zonhoven	Mowing	Coniferous forest
8	De Teut	Zonhoven	Mowing	Coniferous forest
9	Mechelse heide	Maasmechelen	Mowing	Coniferous forest
10	Mechelse heide	Maasmechelen	Mowing	Coniferous forest
11	Mechelse heide	Maasmechelen	Mowing	Coniferous forest

Data collection

Within each edge a transect was set up perpendicular to the edge, extending from the heathland-forest border to 40m into the heathland. The location of the 0m point was based on the position of the first trees (Fraver, 1994; Oosterhoorn and Kappelle, 2000). All edges were sharply delineated. At 5 distances along these transects (0-5-10-20-40m), strips of 2 x 40m parallel to the edge were established. In each of these strips five randomly selected 2 x 2m plots were located, in which the bryophyte vegetation was recorded in the summer of 2004 (Fig. 6.1). Bryophytes on tree bases were not surveyed, i.e. only the bryophyte species occurring terrestrial on the soil or plant litter, were recorded. Cover of all bryophyte species was estimated using the decimal cover scale of Londo (1976). This resulted in 25 plots per edge and an overall total of 260 plots. 15 plots had to be omitted because they were located in the vicinity of e.g. a small road, or because the distance to the opposite border was less than 80 m. Samples of all bryophyte species encountered were collected and microscopically checked in the laboratory afterwards.

Data analysis

To avoid pseudo-replication (Hurlbert, 1984), bryophyte cover data in the five plots at each distance along the different transects was averaged, resulting in one average cover value per species per distance for each edge (Honnay et al., 2002a). First an ordination was performed on these mean cover data using non metric multidimensional scaling (NMDS) in PC-ORD 4 (McCune and Mefford, 1999). This method is particularly well suited to analyze ecological data since it is both a sensitive and robust method to depict changes in community composition (Clarke, 1993). A preliminary analysis was run to determine the number of dimensions to be used in the final run. The maximum number of iterations in this analysis was set to 400. The Sörensen (Bray-Curtis) index was used as a distance measure.

Next, bryophyte species richness, bryophyte cover and the Shannon diversity index (Kent and Coker, 1992) were calculated per strip per transect, based on the mean cover data of the five plots in each strip. Furthermore, the indicator values of light, temperature, humidity and acidity (Düll, 1992) were collected for all species. These are comparable to the Ellenberg indicator values for higher plant species (Ellenberg, 1992), and give an indication for the optimal abiotic conditions for a species. For each distance along all transects, the characteristic indicator value for these factors was calculated as an average of the indicator values of the species present, weighted by their mean cover at that distance.

The relationship between the variables described above and distance was studied using linear mixed models (Verbeke and Molenberghs, 2000; chapter 5). Furthermore, the changes in the cover values of the 20% most frequent species with distance along the transect were studied. Because management can significantly affect the bryophyte layer in heathlands, management was added as an independent variable in the mixed model analysis, together with the distance x management interaction term. These variables were included as fixed effects, while intercept was specified as a random effect. Due to the relatively limited data set, allowing also the slope of the different transects to vary randomly did mostly not result in convergence of the restricted maximum likelihood algorithm. Analyses were performed using PROC MIXED in SAS 8.02 (SAS Institute Inc., 1999-2001). Management in this context is a dichotomous variable, dividing the sites into grazed and mown sites. This dichotomy also partly covers the difference between the different stages of heather development. Grazing prevents the heather from fully maturing, as the animals keep the dwarf shrubs in a younger stage (building phase) and consequently prevent them from attaining the mature and degenerate phase (Gimingham, 1976). At the mown sites, however, management intervention occurs at longer intervals, and heathlands can grow into the mature phase. As time since last management intervention is over 10 years for the majority of the mown sites, these sites are mostly at the transition between building or mature phase or in the mature phase. As this growth phase of *Calluna* also has important effects on the bryophyte layer (Barclay-Estrup and Gimingham, 1969), the variable management covers important influencing variables. In other edge studies, orientation has often been mentioned as affecting edge effects. However, since preliminary analyses showed the effects of orientation to be limited here, only distance and management were included in the mixed models. Including also orientation would lead to an overspecification of the model and hence to meaningless results. Differences between the values of the dependent variables at the five distances from the heathland edge were determined by calculating the differences of the least square means (estimated marginal means), using the LSMEANS statement. When necessary, dependent variables were transformed prior to analysis to obtain normality (Sokal and Rohlf, 1995).

Parameters of the mixed model were estimated using restricted maximum likelihood, the default method in SAS. Due to the restricted dataset, including only five distances per transect, no polynomials were fitted, and distance was treated as a class variable. This also allowed us to determine significant differences between the distances, as described above. Spatial correlation between the distances along the transect was accounted for by adding the REPEATED statement. Significance of the fixed effects was tested using the F-test with type III sums of squares, the default method in PROC MIXED. The denominator degrees of freedom were estimated using the Kenward-Roger method (Kenward and Roger, 1997). This method was chosen because of the relatively small sample size. Both models with an exponential and a Gaussian spatial correlation function, the two most frequently used spatial correlation functions (Verbeke and Molenberghs, 2000), were run, and the model with the best fit, as could be derived from comparison of the model log-likelihood values, was retained.

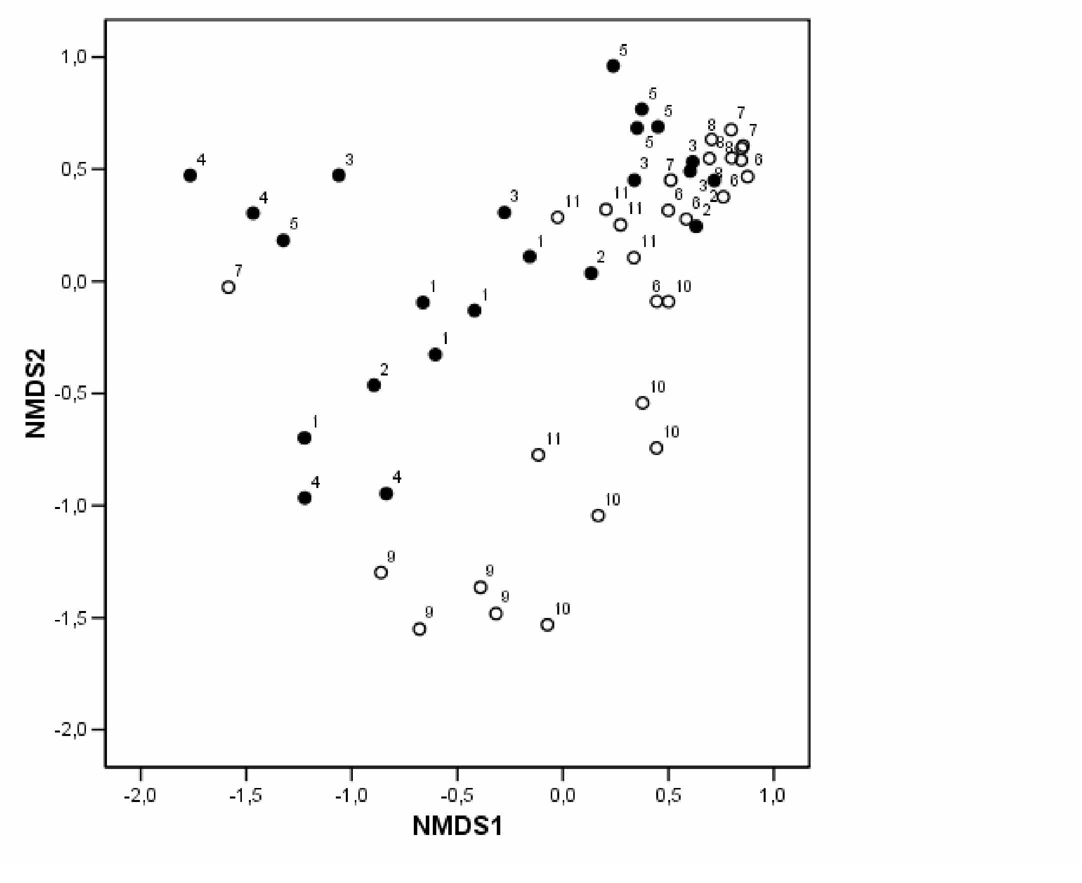


Fig. 7.2 *NMDS-ordination plot of the mean cover of the bryophyte species (n=56) in the 56 strips surveyed (open circles: grazed strips; closed circles: ungrazed strips). The numbers refer to the site numbers in table 7.1.*

Results

A total of 52 bryophyte species was observed in the surveyed heathland edges, of which 27 are present at more than 10% of the distances sampled. In the preliminary NMDS analysis, the two-dimensional solution turned out to be the best option for our dataset. The final stress for this two-dimensional solution was 11.65. The ordination plot (Fig. 7.2) shows the clear division between the samples from grazed and ungrazed plots, and hence points at the importance of management in shaping the heathland bryophyte community.

Adjacent forest has significant effects on heathland bryophyte species diversity, as can be concluded from the significant effect of distance in the mixed model analysis on the number of bryophyte species (Table 7.2). This distance related pattern differs according to the type of management applied. The number of bryophytes is quite constant along the transect at the grazed sites, but decreases significantly at the edge plots for the mown sites. Furthermore, bryophyte cover significantly increases with distance from the edge. For this variable no differences between grazed and mown sites are observed (Table 7.2; Fig. 7.3).

Also heathland bryophyte community composition, described by the scores on the axes obtained in the non metric multidimensional scaling analysis, varies significantly with distance from the edge (Table 7.2). Although the ordination plot showed large effects of management on the bryophyte community composition, edge effects turn out to be more important since the mixed model studying both the effects of management and distance only revealed significant effects of distance. Differences along the heathland edge, however, are limited to the first plot, i.e. until 2 m into the heathland (Table 7.2).

Of the characteristic indicator values, only the temperature and humidity figure show an effect of distance from the forest edge (Table 7.2). For the latter, the distance related pattern differs according to the management applied, with the mown sites showing no effect of distance. For the grazed sites, edge effects extent up to 12 m into the heathland (Table 7.2; Fig. 7.3). The temperature figure only differs significantly at the 0 m-plots (Table 7.2; Fig. 7.3). Contrary to expectations, the characteristic indicator value for light is not significantly related with distance to the forest edge (Table 7.2).

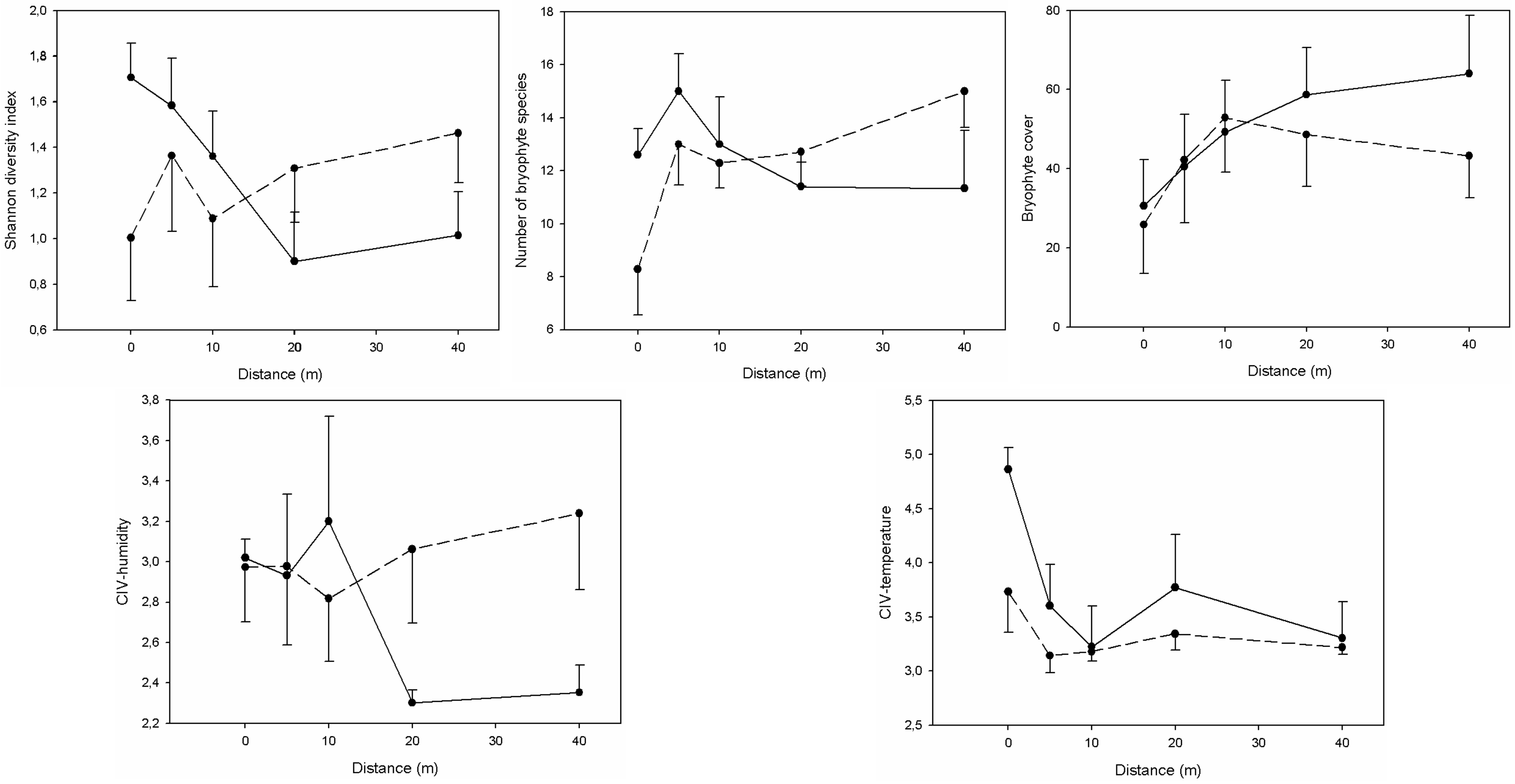
Table 7.2 *F-values and significance of the variables describing bryophyte diversity and community composition along the heathland edge and of the characteristic indicator values for light, humidity, soil acidity and temperature, as obtained from the mixed model analysis. Differences in their mean values between the distances along the transect (p=0.1) are indicated by letters.*

	Management		**Distance**		**Man*Dist**		**type**	**0m**		**5m**		**10m**		**20m**		**40m**	
Shannon index	$F_{1;9.10}=0.49$		$F_{4;24}=0.74$		$F_{4;24}=2.10$												
Nr of species	$F_{1;9.10}=0.07$		$F_{4;33.2}=3.60$	*	$F_{4;33.2}=3.60$	*	G	12.6	a	15	b	13	a	11.4	a	11.33	a
							M	8	a	13.8	b	12.67	b	13.17	b	14.67	b
Bryoph.cover	$F_{1;9.13}=0.00$		$F_{4;22.4}=3.85$	*	$F_{4;22.4}=0.59$			29.70	a	44.84	b	54.20	b	56.96	b	53.84	b
NMDS1	$F_{1;9.21}=2.31$		$F_{4;20.3}=8.16$	***	$F_{4;20.3}=0.68$			-0.675	a	0.064	b	0.197	b	0.161	b	0.242	b
NMDS2	$F_{1;8.98}=0.46$		$F_{4;24.2}=2.05$		$F_{4;24.2}=0.28$												
CIV-L	$F_{1;8.93}=0.73$		$F_{4;28.1}=0.39$		$F_{4;28.1}=0.81$												
CIV-F	$F_{1;9.03}=0.00$		$F_{4;23.6}=3.50$	*	$F_{4;23.6}=3.98$	*	G	3.02	a	2.93	a	3.20	a	2.30	b	2.35	ab
							M	2.97		2.74		2.78		2.83		3.12	
CIV-R	$F_{1;17.60}=3.19$	(*)	$F_{4;31.4}=0.59$		$F_{4;31.4}=1.52$												
CIV-T	$F_{1;9.75}=1.20$		$F_{4;27}=6.41$	***	$F_{4;27}=1.44$			4.29	a	3.33	b	3.19	b	3.51	b	3.22	b

***: $p<0.001$; **: $0.001\leq p<0.01$; *: $0.01\leq p<0.05$; (*): $0.05\leq p<0.1$

G= grazed sites; M= mown sites

Fig. 7.3 *Changes in bryophyte species number, Shannon diversity index and bryophyte cover and in the characteristic indicator values for humidity and temperature along the heathland edge (solid line: grazed sites; dashed line: mown sites).*



At the individual species level, effects of distance from the edge could be found on the relative cover values of *Hypnum jutlandicum*, *Lophocolea heterophylla, Pohlia nutans* and *Campylopus introflexus*. For *Pohlia nutans* these edge responses differ between grazed and mown sites (Table 7.3). Edge effects are present up to 2 m into the heathland patch (Table 7.3). The proportion of the exotic species *Campylopus introflexus* declines with distance from the edge (Fig. 7.4). However, in absolute cover values, it is present throughout the transect (distance: $F_{4;20.3}=1.79$; $p=0.17$). Also for *Pohlia nutans* effects are no longer significant (interaction term: $F_{4;24.9}=2.02$; $p=0.12$). For *Hypnum jutlandicum* ($F_{4;20.8}=12.40$: $p<0.001$) and *Lophocolea heterophylla* ($F_{4;24.9}=5.71$; $p=0.002$) on the other hand, distance effects become even more significant when absolute cover values are considered.

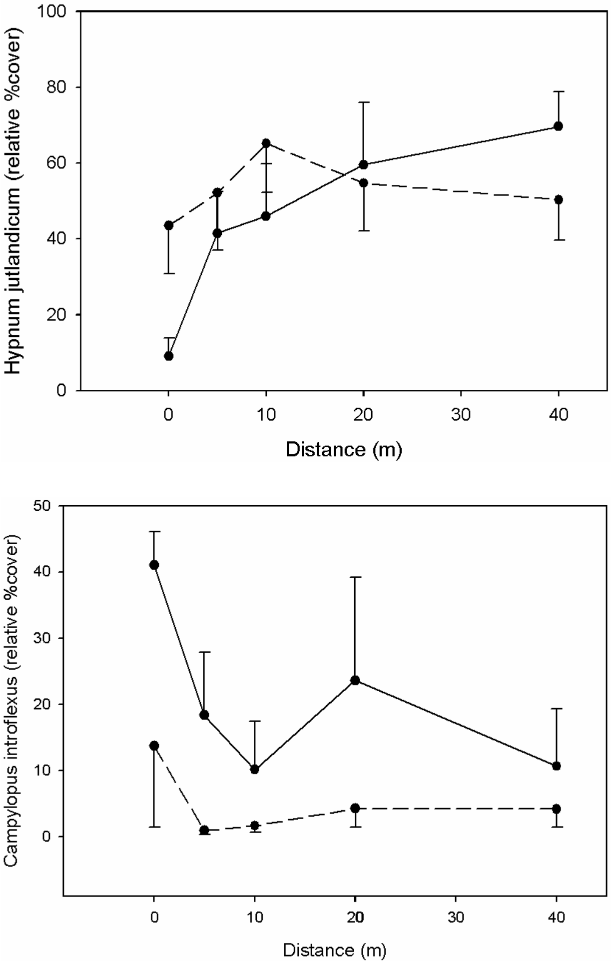


Fig. 7.3 *Changes in the relative cover of Hypnum jutlandicum and Campylopus introflexus with distance from the heathland edge (solid line: grazed sites; dashed line: mown sites).*

Table 7.3 *F-values and significance of the relative cover values of the 20% most frequent bryophyte species, as obtained from the mixed model analysis. Differences in their mean values between the distances along the transect (p=0.1) are indicated by letters.*

	Management		**Distance**		**Man*Dist**		**type**	**0m**		**5m**		**10m**		**20m**		**40m**	
Hypnum jutlandicum	$F_{1;9.08}=0.77$		$F_{4;18.7}=6.11$	**	$F_{4;18.7}=1.23$			26.08	a	49.92	b	56.44	b	60.74	b	59.55	b
Dicranum scoparium	$F_{1;8.74}=0.17$		$F_{4;19.2}=0.51$		$F_{4;19.2}=1.49$												
Pohlia nutans	$F_{1;9.27}=0.02$		$F_{4;33.6}=0.56$		$F_{4;33.6}=2.29$	(*)	G	4.02	a	1.31	b	1.16	b	0.46	b	0.84	b
							M	1.00	a	2.27	b	2.29	b	1.85	b	2.46	b
Lophocolea heterophylla	$F_{1;9.06}=0.35$		$F_{4;26.9}=2.32$	(*)	$F_{4;26.9}=1.04$			1.00	a	2.70	b	2.05	bc	1.21	ac	1.19	abc
Brachythecium rutabulum	$F_{1;9.16}=1.29$		$F_{4;33.4}=0.15$		$F_{4;33.4}=0.54$												
Campylopus introflexus	$F_{1;10.5}=6.12$	*	$F_{4;30.7}=3.52$	*	$F_{4;30.7}=0.78$		G	41.02	a	18.34	b	10.13	b	23.61	b	10.63	b
							M	15.90	a	1.10	b	1.75	b	4.91	b	4.84	b
Eurynchium praelongum	$F_{1;9.58}=0.46$		$F_{4;22.8}=1.30$		$F_{4;22.8}=0.54$												
Campylopus pyriformis	$F_{1;9.16}=2.49$		$F_{4;25}=0.72$		$F_{4;25}=0.20$												
Pleurozium schreberi	$F_{1;9.08}=0.79$		$F_{4;26.3}=0.19$		$F_{4;26.3}=0.61$												
Cephaloziella divaricata	$F_{1;9.42}=0.38$		$F_{4;27}=0.69$		$F_{4;27}=0.95$												
Pseudoscleropodium purum	$F_{1;8.68}=4.92$		$F_{4;32.9}=0.71$		$F_{4;32.9}=1.15$												

***: $p<0.001$; **: $0.001 \le p<0.01$; *: $0.01 \le p<0.05$; (*): $0.05 \le p<0.1$

G= grazed sites; M= mown sites

Discussion

Management effects

Management is an important determinant for bryophyte community composition, as is indicated by the non metric multidimensional scaling analysis. The bryophyte species composition of grazed sites differs significantly from that of sites managed by mowing. Effects of management type are mainly indirect, as it primarily affects the structure and biomass of the overgrowing herb and shrub layer. Studies have indicated that the key factor controlling the cryptogam flora is competition from higher plants (Gilbert, 1993; Virtanen et al., 2000; Bergamini et al., 2001b). Especially the structure of the canopy and the presence of favourable microsites are important (Gilbert, 1993; Økland and Eilertsen, 1994), which are both mainly determined by management. Hence, the microclimate experienced by the bryophyte layer is largely shaped by management in the studied heaths. Grazing causes a more continuous opening of the dwarfshrub canopy compared to mowing or burning, where the canopy is more severely affected, but only at certain periods in time, with intervals of 10 to 15 years in which the canopy can regrow vigorously. During the second half of this interval, the stage in which the surveyed heathlands are, a closed *Calluna*-canopy covers the underlying bryophytes. Consequently, microclimate underneath the dwarfshrubs is much more tempered here than at grazed sites.

Furthermore, grazing causes high environmental heterogeneity compared to other management practices, due to trampling, dung deposition and selective defoliation by the grazing animals (Bergamini et al., 2001a; Cosyns and Hoffmann, 2004). Bryophyte species react strongly on this microscale heterogeneity. Hence, these fine-scale disturbances are important structuring factors for the bryophyte species composition (Økland and Eilertsen, 1994). The spots of bare ground created by trampling of the grazing animals provide the optimal environment for many pioneer or short lived species (van Tooren et al., 1990). However, none of the species characteristic of these disturbed sites (e.g. *Bryum subapiculatum*) were frequent in our study sites.

Effects of adjacent land use

Adjacent forest influences the bryophyte layer of dry heathlands. The most remarkable effect is the increased dominance of the exotic species *Campylopus introflexus* at the edge. This species is a serious problem in oligotrophic ecosystems like heathlands in Flanders and most other parts of north-western Europe (Biermann and Daniels, 1997; Stieperaere et al., 1998), and poses a threat on the native bryophytes. Effects differ however when relative or absolute cover values are considered. The lack of effect on absolute cover indicates that *Campylopus* is present throughout the edge. On the other hand, its relative cover, and hence its importance within the bryophyte community, is significantly higher at the edge. Since bryophyte cover is significantly lower at the edge, the relative cover value probably gives a better picture of reality. Moreover, the fact that *Campylopus*, especially at the grazed sites, is the dominant bryophyte at the edge indicates that it represses the native species there. Its higher abundance at grazed sites is probably due to the fact that grazing causes disturbance, and creates gaps in the vegetation cover and spots of open soil, circumstances ideal for *Campylopus* to colonize. Furthermore, *Campylopus* can spread quickly vegetatively through leaf or stalk fragments (Biermann and Daniels, 1997; Stieperaere et al., 1998; Hassel and Söderström, 2005). Trampling by the grazing animals significantly contributes to this fragmentation, and hence promotes further dispersal and expansion of the species. The animals often rest or search for shelter underneath the trees adjacent to the heathland, hence in the edge zone, which explains the higher presence of this invasive species at the edge. An increased cover of *Campylopus introflexus* in moorland plots with higher levels of grazing was also found by Pakeman et al. (1997). *Lophocolea semiteres* is not yet as abundant as *Campylopus introflexus*, and was only present at more than one distance from the edge at one study site, a grazed heathland in the Campine region (site 5 in table 1). Consequently, no conclusions can be drawn for this invasive species. However, like for *Campylopus*, relative cover of *Lophocolea* is higher at the edge at this site, while the absolute cover values show no clear pattern.

Also other aspects of the bryophyte community are significantly influenced by the neighbouring forest in the vicinity of the edge although the extent of the effect is rather low. Community composition, as indicated by the scores on the axes of the non metric multidimensional scaling, is significantly different in the edge plots (0-2m), compared to plots more distant from the edge. Species richness also changes at the heathland-forest ecotone. Although in most cases, species richness increases at the ecotone because species of both adjacent land use types co-occur there or due to an increase in species using novel edge habitat (Ries et al., 2004), this pattern is not universal and species richness can also be lower at the edge (Walker et al., 2003; Ries et al., 2004). In the latter case, microclimatic fluctuations at the ecotone make this environment unfavorable for plant growth (Walker et al., 2003). In the edges studied, bryophyte species richness is lower at the edge at mown sites, while no clear edge effects on species richness could be found at grazed sites. The lower species richness at the ecotone for the mown sites can be due to the fact that at the edge only more generally occurring bryophyte species typical for both forest and heathland (e.g. *Dicranum scoparium*, *Hypnum jutlandicum*) are present. Further into the heathland on the other hand, these species are supplemented by species typical for old, mature heaths (e.g. *Ptilidium ciliare*) and by species growing on heather-litter (e.g. *Pohlia nutans*, *Cephaloziella spec.*).

Contrary to expectations, effects on the bryophyte layer seem to be much more limited than those on vascular plant species. We studied effects of adjacent forest on vascular plants in the same edges as those used in this study (chapter 6). More significant differences between the heathland edge and interior were found there. Furthermore, while edge effects stretched out until about 8 m into the heathland patches, effects are mostly limited to only the first meters when the bryophyte layer is considered. A possible explanation is that the bryophyte layer of heathlands and dry, acid forests is rather similar, and hence differences between both are limited.

Additionally, as the dwarf shrub layer is relatively dense in heathlands, bryophytes live in the shelter of the *Calluna*-canopy. Only in the first distance sampled, the canopy of the vascular plants is less dense, and consequently the bryophytes are less covered there. This can also account for the higher Ellenberg temperature figure at the edge, while one would expect it to be lowest there due to increased shadowing of the trees in the forest (Cadenasso et al., 1997). As the dwarf shrub canopy is nearly absent or very open at that distance, bryophytes are more exposed, and hence experience more sunlight, at the edge. Since preliminary tests showed no effects of orientation here, although one would expect these to be present especially in the case of light and temperature figures, this indicates that the impact of the forest is tempered by the herb and dwarf shrub layer, and edge effects occur indirect by differences in the vascular plant layer. This predominant effect of the vascular plant layer on the cryptogam community has also been found in other studies (Gilbert, 1993). Furthermore, air temperature, like humidity, often shows extreme values at the edge compared to either the adjacent forest zone or the open area, probably due to stable air masses created at the edges (Chen et al., 1995; Saunders et al., 1999), which is in accordance with the higher temperature figure there.

Since bryophyte species in the ecosystems studied mainly respond to microclimatic variations, microclimatic gradients over the ecotone, although tempered and severely influenced by the vascular plant layer, seem to be the underlying variable causing differences in bryophyte community composition across the edge, as is also indicated by the Ellenberg figures. However, since no microclimatic measurements were taken, this cannot be confirmed empirically. On the other hand, this is not really a shortcoming since microclimatic variables show large diurnal and seasonal variations (Chen et al., 1995; Saunders et al., 1999), which makes it difficult to obtain a reliable measure for these variables. Hence, delineations of depth of edge influences based on these measurements can vary considerably (Chen et al., 1995; Saunders et al., 1999).

Relative importance of management and adjacent land use

Although both management and adjacent land use affect the heathland bryophyte community, the mixed model analysis showed effects of adjacent land use to dominate and overrule management effects. Consequently, neither grazing nor mowing, the two most frequently applied management types in dry heathlands, succeed in preventing or mitigating the presence of edge effects. Since most heathland areas in western Europe are severely fragmented, and hence show a relatively high amount of edge, these edge effects, even though they are limited mostly to the first few meters of the heathland patch, can form a problem for the conservation of the typical heathland bryophyte species, especially in very small heathland patches.

CHAPTER 8

LONG-TERM (1978-2003) EFFECTS OF EXTENSIVE GRAZING REGIME ON PLANT SPECIES COMPOSITION OF A HEATHLAND RESERVE

Introduction

Throughout Western Europe heathland area is continuously decreasing since at least the beginning of the 19th century. Particularly during the last 100 years a huge decline occurred mainly due to agricultural intensification, urbanization and afforestation (Gimingham, 1976; Webb, 1998; Odé et al., 2001; De Blust, 2004). Hence the conservation and restoration of the remaining heathlands is an important topic nowadays, not only for their specific biodiversity, but also as an example of a once widespread cultural landscape (Gimingham, 1976; Webb, 1998). Although most heathlands are protected by national or European nature legislation, this does not guarantee their preservation as a high quality habitat rich in characteristic plant and animal species (De Bruyn, 2003).

Heathlands typically occur on acid, nutrient-poor soils (Gimingham, 1976; De Blust, 2004), which renders them very sensitive to all kinds of nutrient enrichment. Increased atmospheric deposition and the consequential increase in nutrient availability has led to a shift from the typical dwarf shrub vegetation to more grass-dominated communities where *Molinia caerulea* or *Deschampsia flexuosa* prevail (Bobbink et al., 1998; Bakker and Berendse, 1999; Bobbink and Lamers, 2002). In Flanders, atmospheric N-deposition adds up to an average of about 45 kg N ha^{-1} yr^{-1} (Overloop et al., 2004), which is far in excess of the median critical load of 11 kg N ha^{-1} yr^{-1} suggested for heathlands (Dumortier et al., 2003). Furthermore, atmospheric deposition of nitrogenous and sulphuric compounds has caused significant soil acidification (Bobbink et al., 1998; Lee, 1998; Bakker and Berendse, 1999). Although heathlands characteristically grow on acid soils, deposition has lowered the pH of many heathland soils to extreme values far below those optimal for many endangered species (Bakker and Berendse, 1999). Especially herbaceous heathland species and species of the related acid grasslands and grassheaths seem to be sensitive to acidification (Houdijk et al., 1993; Roelofs et al., 1996; Roem and Berendse, 2000), resulting in a decline in species richness (Roem et al., 2002).

All of this urges for an appropriate external and internal management, which aims at counteracting these negative effects of deposition. Furthermore, because of the anthropogenic origin of heathlands in Western Europe, adequate management is also crucial for the preservation of this ecosystem (Gimingham, 1976; De Blust, 2004). In many of the remaining heathlands, a lack of proper management has resulted in succession to shrub, grass or forest communities (Marrs et al., 1986; Webb, 1990; Diemont, 1996). In the past, traditional agricultural practices assured the removal of excessive nutrients and prevented shrub and tree encroachment. Nowadays, nature management has to fulfil this role. A major problem with this is that nature management is most often applied on an intuitive base (Pullin et al., 2004). Conservation practitioners seem to primarily base their management plans on personal experience and opinions, and hardly ever rely on scientific research to support these decisions (Pullin et al., 2004; Sutherland et al., 2004). One of the main reasons seems to be the fact that there often is a gap between scientific research and conservation practice. Another may be decreasing financial possibilities for this kind of applied, basic research. Hence, in the absence of evidence to the contrary, managers inevitably fall back on traditional methods and personal experience (Pullin and Knight, 2001). Furthermore, although each management intervention could give information to base future decisions on, the management implemented is hardly ever systematically documented and monitored (Vanreusel, 2004).

Long-term vegetation studies can be important tools in bridging this gap between research and practice. By studying the vegetation over a certain time period under specific management practices in real life systems, (semi-) permanent plots can provide valuable insights into vegetation succession and vegetation change, and hence into the effects of the applied management (Bakker et al., 1996b; Bakker et al., 2002; Smits et al., 2002). Therefore, they can provide the nature manager with the necessary information for choosing the most suited management practices and for redirecting current management (Bakker et al., 2002). Also in heathland ecosystems the importance of long term vegetation studies has been acknowledged (Bokdam and Gleichman 2000; Mitchell et al., 2000).

In 1978 a vegetation survey was carried out in one of the key heathland habitats in Flanders, being the nature reserve ‘De Maten’ (Kenis, 1979). This reserve is characterized by a diverse vegetation. Almost all types of heathland vegetation occur here, next to some smaller patches of forest or tall herb habitats (Aerts, 2004). As a consequence of the first study, the reserve has been managed by extensive grazing for almost 20 years.

The aims of this study are to examine whether vegetation composition and diversity have changed over a 25-year period in the nature reserve ‘De Maten’, and hence to study and evaluate the long term effects of extensive grazing on vegetation composition and diversity under the prevailing conditions of increased nitrogen deposition and acidification. Finally, our results will aid in determining if and how management practices need to be adjusted to preserve or restore the typical, often rare, vegetation types present in the reserve.

Material and methods

Study area

The study area ‘De Maten’ (50°57’ N, 5°27’ E) is a nature reserve situated in Genk and, for a small part, Diepenbeek, in the eastern part of Flanders (Fig. 8.1). In this area, atmospheric N-deposition adds up to about 35 kg N ha^{-1} yr^{-1} (Overloop et al., 2004). The reserve is about 220 ha large, and has been managed as a nature reserve since 1956 by Natuurpunt vzw, the largest private nature organization in Flanders, which makes it one of the oldest nature reserves in Belgium.

The reserve is situated along the rivulet Stiemerbeek, in the transition zone between the Campine plateau (NE) and the Campine lowland plain (SW), leading to a variation in height from about 60m in the northeast to some 40m above sea level in the southwest. Most soils in the reserve are sandy or loamy-sandy, ranging from undifferentiated sandy soils on the land dunes to dry to very wet podzols and peaty soils in the wettest parts (OC GIS-Vlaanderen, 2001).

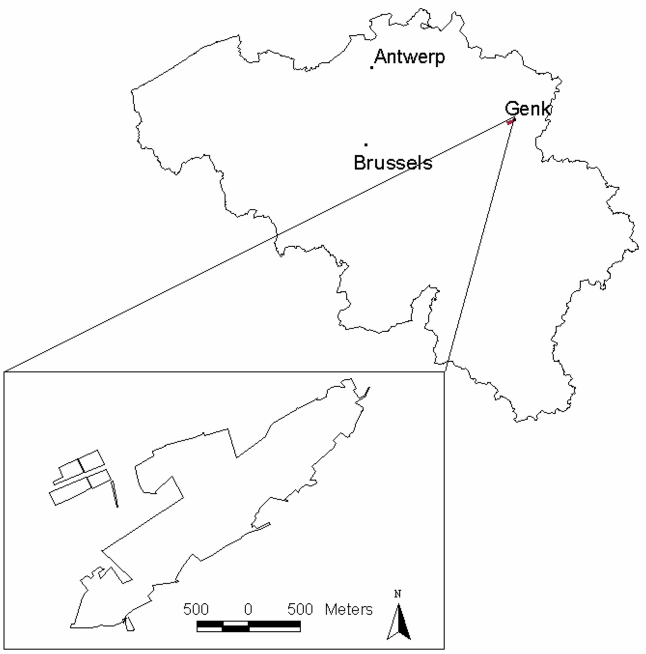


Fig. 8.1 *Location of reserve 'De Maten' in Belgium. All surveyed plots are situated in the large central part of the reserve.*

The area is characterized by a highly diverse vegetation, consisting for a large part of dry to wet heathland, together with land dunes and forests (mostly moist to wet forests dominated by *Alnus glutinosa*) (Aerts, 2004). Along the rivulet different ponds are situated, surrounded by moist to wet tall herb vegetation and reed beds. Although these ponds make up the largest part of the area of the reserve, this study exclusively focuses on the terrestrial parts of the reserve. Management in 'De Maten' was rather anecdotal until 1978, when a better insight into the area was gained by an extensive phytosociological study of the area (Kenis, 1979). This led to a more systematic and extended management, especially aimed at counteracting grass- and bush encroachment, preserving and improving floral and faunal diversity and ensuring a structurally diverse area. For the last 20 years management consisted of extensive grazing by Galloways from May to September at a density of about 0.1 cow ha^{-1}. When necessary, this was supplemented locally with mechanical management practices, like tree-cutting or mowing (Dewyspelaere, 1999).

Data collection

In 1978 a vegetation survey was carried out (Kenis, 1979). In order to obtain a representative overview of the vegetation in the reserve, a total of 179 plots, scattered throughout the area, were surveyed using the Braun-Blanquet scale (Kent and Coker, 1996). A quarter of a century later, in 2003, a new survey of the vascular plant vegetation was conducted. Cryptogams were not recorded. We tried to retrace the plots of the 1978 survey based on their position indicated on a map and descriptions made during the original survey. Because of doubts about their exact location, only 97 of the 179 plots could be relocated exactly. Hence, 97 relevés, distributed over the whole area and over all vegetation types, are available to analyse vegetation changes.

To allow an ecological interpretation of the observed vegetation changes, information about environmental conditions is needed. However, as in many other studies dealing with long-term vegetation changes (e.g. ter Braak and Wiertz, 1994; Diekmann and Dupré, 1997; Lameire et al., 2000), measurements of environmental variables in the past are lacking. In these studies this problem was overcome by taking advantage of the fact that plant species themselves indicate environmental conditions, as quantified by the Ellenberg indicator values (Ellenberg et al., 1992). Therefore, the characteristic Ellenberg indicator values for light intensity, soil moisture, pH and soil nutrient status (Persson, 1981) were calculated for each plot. These values have proven to be reliable estimates for environmental variables and have often been used to analyse floristic changes (Thompson et al., 1993; Diekmann, 2003).

Another way of interpreting the observed vegetation changes is by means of plant strategies (Grime et al., 1988; Lameire et al., 2000; Hunt et al., 2004). Therefore, the C-S-R-signature of each plot was calculated using the methodology of Hunt et al. (2004). Finally, total species richness and the Shannon diversity index (Kent and Coker, 1996) were calculated to examine changes in plant diversity.

Data analysis

Changes in vegetation composition during the past quarter of a century were studied at different hierarchical levels (community level, plot level, species level) to gain a comprehensive insight into the changes in the plant communities. To reduce the prevalence of dominant species, % vegetation cover data were arcsine transformed.

To study changes at the community level, a multivariate analysis was performed. A Detrended Correspondence Analysis (DCA) was run on the transformed cover values of all 189 higher plant species in the 2 × 97 sample plots, combining the data of the two survey periods. To interpret the variation along the DCA-axes, plot ordination scores were correlated with the Ellenberg indicator values using Spearman rank correlations. Vegetation in the nature reserve can roughly be subdivided into six groups, being inland dunes (13 plots), dry heathlands (28 plots), moist heathlands (15 plots), wet heathlands (19 plots), tall herb vegetation (12 plots) and forests (10 plots), based on a TWINSPAN analysis of the 2003 data. Because these six types are characterised by widely divergent species compositions and abiotic conditions, these groups were treated separately in further analyses. Shifts in vegetation composition between the two periods were visualized on the ordination plot by means of arrows connecting the corresponding plots. Significance of these plot displacements was tested statistically using Wilcoxon signed ranks tests.

Secondly, temporal variation in the vegetation was studied at the plot level. Significant differences in species richness, Shannon diversity index, the characteristic indicator values and the plot CSR-signatures between both periods were examined through Wilcoxon signed ranks tests.

Finally, the Wilcoxon signed ranks test was applied to test for differences in species cover values between both time periods. The frequency of occurrence of species in the two sample periods was compared using the χ^2-test. The Fisher exact test was used for species for which the expected frequency in the contingency tables was less than 5 (Siegel and Castellan, 1988).

Statististical analyses were performed using SPSS 11.0 (SPSS 2001). Canoco 4.5 and Canodraw 4.5 (ter Braak and Šmilauer, 2002) were used for the DCA.

Results

Community level

The first joint 1978-2003 DCA axis (eigenvalue 0.76) clearly showed the major variation in vegetation composition from inland dunes and heathlands over tall herb vegetation to forests (Fig. 8.2). This was further reflected in the negative correlation of this axis with the Ellenberg value for light, and the positive correlations with the

Ellenberg values for soil moisture status, soil nutrient content and pH (Table 8.1). The clear seperation of the six vegetation types justifies the subdivision of the data.

Next to this variation in vegetation types, the DCA-axes also represented a temporal gradient. Changes in vegetation composition between both periods were directional, and patterns of change differed between the six groups (Fig. 8.2, Table 8.2). Whereas for forests and inland dunes a clear, though opposite temporal gradient in vegetation composition was present along DCA axis 1, changes in the wet and dry heathland plots and the tall herb vegetation predominantly occurred along DCA axis 2. For the moist heathlands changes in vegetation composition took place along both axes. The second DCA-axis (eigenvalue 0.423) showed a strong negative correlation with the Ellenberg value for light and a positive correlation with soil nutrient content (Table 8.1). These correlations can be largely explained by the position of the forests and most of the tall herb vegetation plots in the upper parts of figure 8.2.

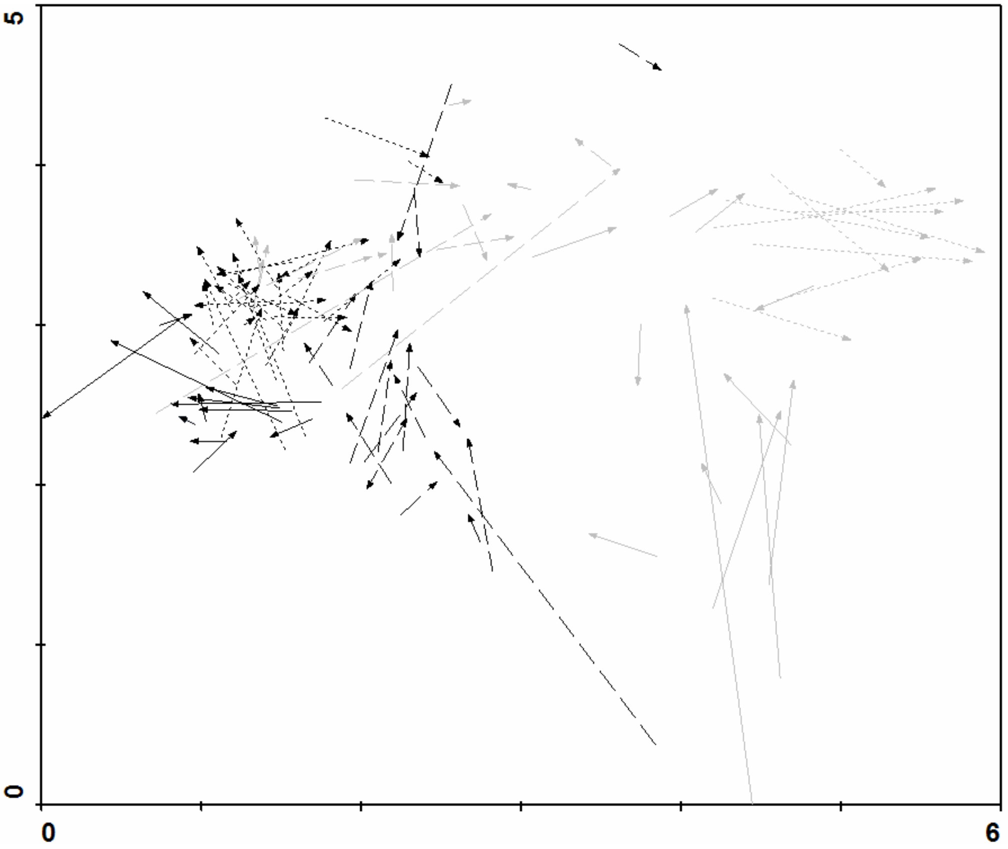


Fig. 8.2 *Ordination diagram showing the first two axes of the joint 1978-2003 DCA-analysis, and the plot displacements (arrows) during this period for the six vegetation types (inland dunes: black; dry heath: black dotted; moist heath: grey dashed; wet heath: black dashed; tall herb vegetation: grey; forest: grey dotted arrows).*

Table 8.1 *Spearman rank correlations between the Ellenberg values for soil moisture (CIV-M), soil nutrient status (CIV-N), soil pH (CIV-R) and light intensity (CIV-L) and the DCA plot ordination scores (n=194).*

	DCA axis 1		DCA axis 2	
CIV-M	0.811	***	-0.012	
CIV-N	0.794	***	0.215	***
CIV-R	0.589	***	0.127	(*)
CIV-L	-0.604	***	-0.641	***

***: p≤0.001; (*): 0.05<p≤0.1

Table 8.2 *Plot displacements between 1978 and 2003 on the first two axes obtained by the DCA- analysis. Significance was tested using Wilcoxon signed ranks tests*

	Median 78	Median 03	Median displacement	z-value
All plots (n=97)				
DCA axis 1	1.881	2.163	0.070	1.704 (*)
DCA axis 2	3.006	3.256	0.179	4.867 ***
Inland dunes (n=13)				
DCA axis 1	1.163	0.934	-0.447	2.621 **
DCA axis 2	2.464	2.512	0.060	1.503
Dry heathland (n=28)				
DCA axis 1	1.465	1.369	0.099	0.478
DCA axis2	3.043	3.294	0.241	3.302 **
Moist heathland (n=15)				
DCA axis 1	1.961	2.610	0.137	2.329 *
DCA axis 2	3.299	3.559	0.168	2.556 *
Wet heathland (n=19)				
DCA axis 1	2.246	2.285	0.046	0.443
DCA axis 2	2.204	2.689	0.383	2.294 *
Tall herb vegetation (n=12)				
DCA axis 1	4.224	4.249	-0.074	0.157
DCA axis 2	2.075	2.681	0.247	2.353 ***
Forest (n=10)				
DCA axis 1	4.583	5.569	0.909	2.803 **
DCA axis 2	3.699	3.506	-0.169	1.376

***: p≤0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1

Plot level

During the 25 year period between the two surveys, no significant changes in species richness were observed in the study area (Table 8.3). On the other hand, a significant decline in the Shannon diversity index was noticed. This is mainly attributable to the dry and moist heathland plots, since for the other types no significant differences were found (Table 8.3).

Table 8.3 *Changes in species richness and the Shannon diversity index between 1978 and 2003. Significance of differences was tested using Wilcoxon signed ranks tests.*

	Median 78	**Median 03**	**Median displacement**	**z-value**
All plots (n=97)				
Species richness	7	7	0	1.027
Shannon diversity index	1.295	1.257	-0.088	2.024 *
Inland dunes (n=13)				
Species richness	5	4	-1	0.941
Shannon diversity index	0.780	1.202	0.159	1.852(*)
Dry heathland (n=28)				
Species richness	5	5.5	0	0.739
Shannon diversity index	1.055	0.922	-0.132	2.209 *
Moist heathland (n=15)				
Species richness	8	9	0	0.252
Shannon diversity index	1.448	1.147	-0.504	2.556 *
Wet heathland (n=19)				
Species richness	6	7	0	0.726
Shannon diversity index	1.397	1.526	0.016	0.443
Tall herb vegetation (n=12)				
Species richness	16	17	2	1.069
Shannon diversity index	2.172	1.811	-0.125	0.078
Forest (n=10)				
Species richness	14.5	14	2	0.360
Shannon diversity index	1.789	1.703	-0.132	0.866

*: $0.01<p\leq0.05$; (*): $0.05<p\leq0.1$

Considering all plots, only a significant decline in the characteristic indicator value for soil pH could be observed (Table 8.4). However, when the six vegetation types were studied separately, apparent differences were found (Table 8.4). The indicator values for soil nutrient status and soil pH showed a significant decline for the inland dune and dry heathland plots. Furthermore, an increase in the Ellenberg indicator value for light was found for the inland dune plots. The forest plots on the other hand displayed an opposite trend, as was already seen on the ordination plot, indicating a shift to a higher dominance of species characteristic for more nutrient rich conditions and of shade tolerant species. The dry and moist heathland plots have become slightly wetter, as pointed out by the increase in the indicator value for soil moisture. For the plots of tall herb vegetation no significant differences in the studied indicator values were present.

Table 8.4 *Changes in the Ellenberg indicator values for moisture (CIV-M), soil nutrient status (CIV-N), soil pH (CIV-R) and light intensity (CIV-L) for the surveyed plots between 1978 and 2003. Significance was tested using Wilcoxon signed ranks tests.*

	Median 78	**Median 03**	**Median difference**	**z-value**
All plots (n=97)				
CIV-M	6.314	6.676	0.005	0.713
CIV-N	1.931	1.806	-0.100	0.772
CIV-R	2.467	2.193	-0.129	2.272 *
CIV-L	7.644	7.609	0	0.624
Inland dunes (n=13)				
CIV-M	2.859	2.362	-0.162	1.883 (*)
CIV-N	1.877	1.586	-0.332	3.059 **
CIV-R	2.687	2.456	-0.215	2.981 **
CIV-L	7.725	8.119	0.338	3.059 **
Dry heathland (n=28)				
CIV-M	3.667	4.196	0.500	3.086 **
CIV-N	1.792	1.522	-0.190	2.186 *
CIV-R	2.103	1.674	-0.318	2.667 **
CIV-L	7.630	7.762	0.080	1.898 (*)
Moist heathland (n=15)				
CIV-M	6.311	6.720	0.747	2.040 *
CIV-N	1.943	1.936	-0.101	0.852
CIV-R	2.078	2.128	-0.096	0.682
CIV-L	7.424	7.324	0.017	0.341

Table 8.4 *continued*

	Median 78	**Median 03**	**Median difference**	**z-value**
Wet heathland (n=19)				
CIV-M	8.125	8.105	-0.177	1.368
CIV-N	1.828	1.864	0.054	0.443
CIV-R	1.650	1.845	-0.032	0.762
CIV-L	7.792	7.695	-0.070	1.569
Tall herb vegetation (n=12)				
CIV-M	8.272	8.063	-0.372	1.255
CIV-N	3.694	3.950	0.427	1.334
CIV-R	4.222	4.837	0.482	0.784
CIV-L	7.572	7.229	-0.191	1.647 (*)
Forests (n=10)				
CIV-M	7.912	7.538	-0.314	1.376
CIV-N	4.981	5.778	0.769	2.090 *
CIV-R	5.278	5.363	-0.036	0.051
CIV-L	6.190	5.532	-0.753	2.803 **

**: $0.001<p\leq0.01$; *: $0.01<p\leq0.05$; (*): $0.05<p\leq0.1$

In terms of plant strategies, the community as a whole showed an increase in competitive strategy and a decline in stress-tolerant species (Table 8.5), although once again the different vegetation types showed different trends. For the forest plots a significant decrease in the C-component and an increase in the R-component was noticed. To the contrary, the plots situated in dry and moist heathland showed a higher C-component and a lower R-component compared to 25 years ago. The moist heathland plots further showed a small decrease in the S-component. Plots of tall herb vegetation did not display significant shifts in plant strategies.

Species level

At the individual species level, differences in species cover between both sample periods were observed. Changes in species frequencies appeared to be rare. Overall, only 25 of the encountered species (12.7%) showed a significant change in frequency, while for about a quarter or 43 of the surveyed species significant shifts in species cover were found.

Table 8.5 *Changes in the CSR-signature of the surveyed plots between 1978 and 2003. Significance was tested using Wilcoxon signed ranks tests.*

	Median 78	**Median 03**	**Median difference**	**z-value**
All plots (n=95)				
C	0.360	0.388	0.040	2.955 ***
S	0.556	0.537	-0.021	2.101 *
R	0.084	0.075	-0.003	1.257
Inland dunes (n=13)				
C	0.273	0.367	0.003	1.334
S	0.547	0.484	-0.063	1.647 (*)
R	0.122	0.147	0.008	0.863
Dry heathland (n=28)				
C	0.262	0.297	0.035	2.330 *
S	0.651	0.672	0.006	0.192
R	0.074	0.032	-0.010	2.234 *
Moist heathland (n=15)				
C	0.316	0.415	0.046	2.556 *
S	0.614	0.576	-0.032	2.158 *
R	0.043	0.007	-0.011	1.961 *
Wet heathland (n=19)				
C	0.288	0.351	0.037	1.569
S	0.649	0.618	-0.014	1.529
R	0.022	0.008	-0.007	1.726 (*)
Tall herb vegetation (n=12)				
C	0.564	0.632	0.094	1.883 (*)
S	0.327	0.271	-0.035	1.490
R	0.109	0.097	-0.002	0.471
Forests (n=10)				
C	0.572	0.471	-0.110	2.497 *
S	0.340	0.355	0.003	0.459
R	0.089	0.174	0.117	2.395 *

***: $p \leq 0.001$; *: $0.01 < p \leq 0.05$; (*): $0.05 < p \leq 0.1$

Fig. 8.3 *Plots depicting the changes in CSR-functional types for the inland dune plots (a), the dry (b), moist (c) and wet heathland plots (d), the forests (e) and the tall herb vegetation (f) between 1978 and 2003.*

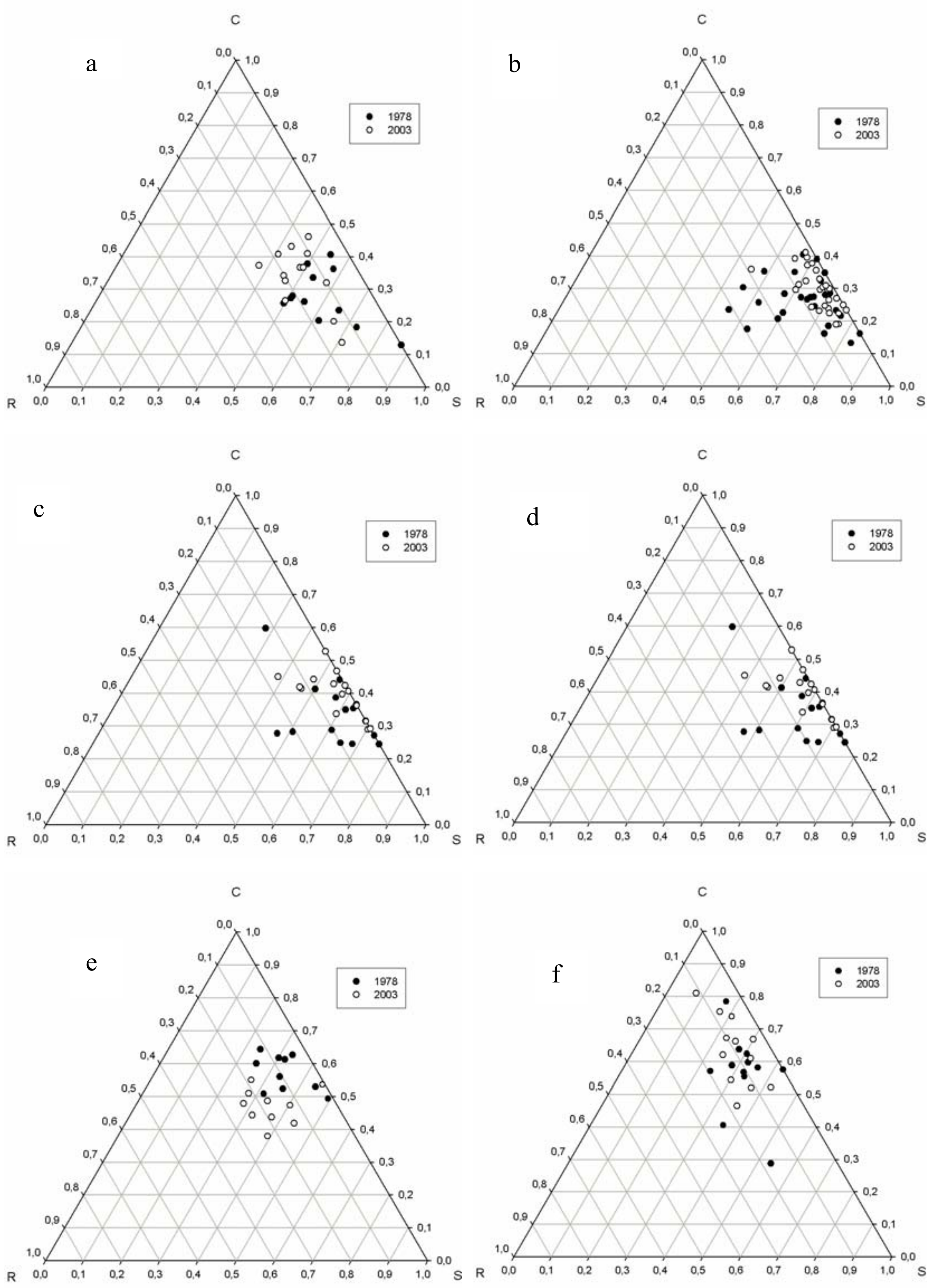


Table 8.6 *Overview of species for which a change in frequency (freq) and/or abundance (transformed cover values, cov) between 1978 and 2003 was observed, listed per vegetation type. Significance of changes in abundance was tested using Wilcoxon signed ranks tests, while* χ^2*-test or Fisher exact tests were applied to test for significant shifts in species' frequencies*

	freq78	**freq03**	**χ^2-value**	**cov78**	**cov03**	**z**	
Inland dunes (n=13)							
Agrostis vinealis	10	13	3.391 n.s.	0.101	0.368	3.065	**
Aira praecox	0	4	4.727 (*)	0	0.051	1.841	(*)
Jasione montana	4	1	2.229 n.s.	0.053	0.008	1.841	(*)
Rumex acetosella	5	3	0.722 n.s.	0.101	0.025	1.706	(*)
Spergula morisonii	6	1	4.887 (*)	0.071	0.008	2.156	*
Dry heathland (n=28)							
Agrostis vinealis	13	21	4.791 *	0.071	0.115	1.474	n.s.
Aira praecox	0	3	3.170 n.s.	0	0.011	1.732	(*)
Calluna vulgaris	25	28	3.170 n.s.	0.520	1.118	3.834	***
Corynephorus canescens	9	2	5.543 *	0.083	0.022	1.691	(*)
Festuca filiformis	23	19	1.524 n.s.	0.271	0.134	2.787	**
Frangula alnus (h)	1	4	1.976 n.s.	0.004	0.015	1.732	(*)
Luzula campestris	0	4	4.308 n.s.	0	0.015	2.000	*
Molinia caerulea	6	9	0.820 n.s.	0.058	0.125	1.823	(*)
Pinus sylvestris (h)	0	3	3.170 n.s.	0	0.011	1.732	(*)
Prunus serotina	0	5	5.490 (*)	0	0.019	2.236	*

Rubus fruticosus coll.	3	13	8.750 **	0.024	0.087	3.003	**
Rumex acetosella	15	6	6.171 *	0.124	0.024	2.838	**
Spergula morisonii	4	0	4.308 n.s.	0.030	0	1.841	(*)
Moist heathland (n=15)							
Calluna vulgaris	14	15	1.034 n.s.	0.432	0.674	2.168	*
Festuca filiformis	10	4	4.821 *	0.165	0.028	2.805	**
Genista pilosa	8	2	5.400 *	0.100	0.014	2.388	*
Juncus acutiflorus	0	4	4.615 (*)	0	0.031	1.890	(*)
Molinia caerulea	10	15	6.000 *	0.284	0.799	3.097	**
Nardus stricta	6	2	2.727 n.s.	0.096	0.041	1.826	(*)
Prunus serotina	1	6	4.658 (*)	0.007	0.043	1.890	(*)
Wet heathland (n=19)							
Betula alba (h)	3	8	3.199 (*)	0.014	0.049	1.901	(*)
Betula pendula (h)	0	4	4.471 n.s.	0	0.022	1.841	(*)
Calluna vulgaris	11	16	3.199 (*)	0.228	0.435	2.552	*
Drosera intermedia	2	6	2.533 n.s.	0.019	0.049	2.060	*
Drosera rotundifolia	4	1	2.073 n.s.	0.022	0.004	1.841	(*)
Eriophorum polystachion	10	9	0.105 n.s.	0.110	0.066	1.869	(*)
Molinia caerulea	18	19	1.027 n.s.	0.296	0.566	3.221	**
Myrica gale (h)	2	7	3.640 n.s.	0.024	0.074	2.201	*
Myrica gale (s)	3	8	3.199 (*)	0.087	0.212	1.895	(*)

Table 8.6 *continued*

	freq78	freq03	χ^2-value	cov78	cov03	z	
Tall herb vegetation (n=12)							
Agrostis canina	9	2	8.224 **	0.137	0.062	1.482	ns
Calamagrostis canescens	2	5	1.815 ns	0.040	0.186	2.023	*
Calluna vulgaris	1	4	2.274 ns	0.013	0.035	1.826	(*)
Carex nigra	4	1	2.274 ns	0.037	0.004	1.826	(*)
Carex rostrata	4	1	2.274 ns	0.105	0.008	1.826	(*)
Cirsium palustre	3	7	2.743 (*)	0.028	0.116	2.371	*
Comarum palustre	4	0	4.800 (*)	0.037	0.000	1.826	(*)
Juncus effusus	10	12	2.182 ns	0.275	0.472	1.735	(*)
Lysimachia vulgaris	6	12	8.000 *	0.061	0.185	2.314	*
Phragmites australis	5	10	4.444 (*)	0.064	0.213	1.788	(*)
Forests (n=10)							
Alnus glutinosa (t)	10	10	/ ns	0.721	1.332	2.532	*
Athyrium filix-femina	4	6	0.800 ns	0.059	0.198	1.859	(*)
Carex paniculata	4	1	2.400 ns	0.000	0.081	1.826	(*)
Dryopteris carthusiana	8	3	5.051 (*)	0.114	0.098	1.263	ns
Dryopteris dilatata	4	5	0.202 ns	0.071	0.276	2.060	*
Holcus lanatus	2	5	1.978 ns	0.049	0.180	2.032	*
Lonicera periclymenum	7	2	5.051 (*)	0.095	0.026	2.226	*

Lysimachia vulgaris	8	4	3.333 ns	0.094	0.043	2.271	*
Myosoton aquaticum	0	3	3.529 ns	0.000	0.032	1.732	(*)
Oxalis acetosella	0	6	8.571 *	0.000	0.350	2.226	*
Poa trivialis	0	9	16.364 ***	0.000	0.425	2.673	**
Polygonum hydropiper	0	5	6.667 *	0.000	0.191	2.032	*
Scutellaria galericulata	0	5	6.667 *	0.000	0.053	2.236	*

***: p≤0.001; **: 0.001<p≤0.01; *: 0.01<p≤0.05; (*): 0.05<p≤0.1; n.s.: not significant

h: herb layer; s: shrub layer; t: tree layer; underlined significances: significances tested using Fisher exact tests.

When looking at the six vegetation types separately, a significant increase in cover of both *Calluna vulgaris* and *Molinia caerulea* in the different heathland types was observed (Table 8.6). Furthermore, a trend towards increased tree and shrub encroachment in the heathland plots was noticed, as indicated by the increased presence of seedlings of species like *Prunus serotina* (dry and moist heaths), *Pinus sylvestris*, *Rubus fruticosus* (dry heaths), *Betula alba*, *B. pendula* and *Myrica gale* (wet heaths). Additionally, some shifts in the cover and/or frequency of some species characteristic for one of the three heathland types were observed. *Rumex acetosella* (dry heaths) and *Genista pilosa* (moist heaths) have significantly declined both in frequency and cover in the 25 years between both surveys. The wet heathland species *Drosera intermedia* has significantly increased in cover, while the cover of *D. rotundifolia* has significantly decreased during the study period.

In the species poor inland dunes, *Agrostis vinealis* has significantly increased in cover, while *Spergula morisonii* showed a significant decrease both in frequency and cover, and almost disappeared in this vegetation type. Plots of tall herb vegetation were mostly characterized by an increase of *Lysimachia vulgaris, Phragmites australis* and *Cirsium palustre,* tall growing species characteristic for nutrient-rich conditions. Only *Agrostis canina* showed a significant decline in frequency. In the forest plots, cover of *Alnus glutinosa* has significantly increased in the tree layer. *Oxalis acetosella* and *Poa trivialis* were the most important species showing both an increase in frequency and cover. Both species, as also *Polygonum hydropiper, Scutellaria galericulata* and *Myosoton aquaticum*, were not recorded in the forest plots during the 1978 survey.

Discussion

Vegetation changes

The different vegetation types present in ‘De Maten’ have evolved in different ways over the 25 year period, and hence react differently on the management applied. In the heathland plots and the inland dunes, extensive grazing has been able to retain the nutrient-poor and acid character of the vegetation, as indicated by the Ellenberg indicator values. However, the increased cover of *Molinia caerulea* and of some shrub species or seedlings of tree species, suggest that it has not succeeded in fully preventing grass invasion and shrub or tree encroachment.

A shift to grass prevalence currently is one of the major threats to heathland quality and persistence (Bakker and Berendse, 1999). High levels of atmospheric deposition often have resulted in the dominance of grass species like *Molinia caerulea* and *Deschampsia flexuosa* in heathlands (e.g. Bobbink et al., 1998; Bakker and Berendse, 1999; Bobbink and Lamers, 2002). Grazing is an effective tool in preventing and decreasing this grass dominance when the appropriate grazing pressure is applied at the right time (e.g. Alonso and Hartley, 1998; Hester and Baillie, 1998; Bokdam and Gleichman, 2000; Hulme et al., 2002; Pakeman et al., 2003). In the dry heaths, the unchanged cover of *Deschampsia flexuosa* and the only slight increase in cover of *Molinia caerulea* between 1978 and 2003 indicate that grazing has managed to keep these grasses under control here. In the moist and wet heaths, however, the significant increase in both frequency and cover of *Molinia caerulea* suggests that for this species the applied grazing management is not sufficient to prevent further invasion, and additional mechanical management is necessary. This inconsistency may be explained by the fact that the cattle more frequently graze *Deschampsia flexuosa* compared to *Molinia caerulea* (Bokdam and Gleichman, 2000). *D. flexuosa,* the characteristic grass species in dry heaths, retains green leaves throughout the year, and hence can be grazed year round (Weeda et al., 1994), while the nutrient value of *Molinia* can only meet the animals' needs during summer and early autumn, periods when there are many food resources available for the grazing cattle. In the reserve, the Galloway cows are present during spring and summer, and hence can graze *Deschampsia* for a much larger period than *Molinia*.

Grazing of the heathlands has positively affected the cover of *Calluna vulgaris*, the dominant heathland species. A similar increase in *Calluna* cover after the introduction of grazing in dry heathlands was found by Bokdam and Gleichman (2000). However, the response of *C. vulgaris* to grazing is strongly dependent on grazing intensity. Low-intensity grazing may stimulate *Calluna* cover, height, and biomass, while overgrazing can damage the heather plants by repeated grazing of new shoots, uprooting of shoots and trampling (Lake et al., 2001; Pakeman et al., 2003). In the reserve 'De Maten' the grazing regime of about 0.1 cow per ha from May to September seems to be beneficial for the *Calluna* plants. Furthermore, *C. vulgaris* can respond to grazing by assuming a prostrate growth form (Gimingham, 1976; MacDonald et al., 1995), hence increasing cover.

This increased cover of *Calluna vulgaris* can also explain the decrease in the Shannon diversity index between both surveys. Species richness of the heathland and inland dune plots remained quite constant, although grazing often is a factor leading to increased species richness (Olff and Ritchie, 1998; Lake et al., 2001). However, since heathlands are intrinsically species poor (Rodwell, 1991), this unchanged species richness does not necessarily point at a negative evolution. An increase in species richness in these communities often indicates the introduction of species characteristic of more nutrient-rich conditions, hence being species not considered desirable by heathland conservation managers (Webb and Vermaat, 1990; Lake et al., 2001).

Contrary to the heathland and inland dune plots, management has not been able to prevent nutrient enrichment and succession in the tall herb vegetations and forests. For the former, this succession is probably just in a starting phase, as almost no significant changes in CSR-strategies or Ellenberg indicator values could be observed. Although both vegetation types are not separated from the heathland and hence are accessible for the cattle, they are hardly grazed. In the tall herb vegetation, the often very wet soils probably hinder access for the cows. The forests, on the other hand, are almost exclusively used for shelter during the night because Galloway cows prefer open areas for grazing (Bokdam and Gleichman, 2000). Furthermore, since management of the area is almost entirely focused on the conservation of the heathland vegetation, additional mechanical management is not applied at a regular base in the tall herb vegetations.

Management implications

The study of long term vegetation changes can provide the necessary insights into and consequences of the management applied, and can therefore aid at evaluating and eventually redirecting management (e.g. Bakker et al., 2002; Smits et al., 2002). Currently, management in ‘De Maten’ is chiefly focused at the conservation of the heathlands and heathland related vegetation, because these vegetations are most endangered and make out the largest part of the exceptional value of the reserve.

Overall, management has succeeded in preserving the characteristic heathland vegetation and in retaining or even enhancing its typical nutrient poor, acid character. In the dry heaths, the current grazing management seems to be successful at retaining the dominance of *Calluna vulgaris* and preventing the expansion of *Deschampsia flexuosa*. However, the increased frequency and cover of some shrub and tree species, which can also be observed in the moist and wet heathlands, indicates the need for the occasional application of additional management practices aimed at removing tree and shrub encroachment. This corresponds to the findings of Bokdam and Gleichman (2000), who found free-ranging grazing combined with tree cutting to be a suitable management regime to maintain a species-rich open heathland. For the moist and wet heathlands grazing does not seem to be sufficient to prevent a growing dominance of *Molinia caerulea*. Hence, in these parts grazing should best be supplied with some form of mechanical management, especially mowing and sod-cutting, which provide a greater removal of biomass and nutrients (De Blust, 2004).

Species characteristic of grassheaths perform well under the current management. Since these species thrive under conditions somewhat less acid than those typical for heathlands, the recent deposition related acidification of many areas has made these species very vulnerable and has led to their decline (Roem and Berendse, 2000; De Blust, 2004). In our study area, frequency and cover of species like *Pedicularis sylvatica, Polygala serpyillifolia* and *Succisa pratensis*, did not change significantly during the past 25 years. The combined application of grazing and occasional mowing seems to be successful in preserving this vegetation type. Therefore, these management practices should certainly be continued, as a less intensive management would most probably cause their local extinction and replacement by typical heathland species like for example *Calluna vulgaris*.

In the tall herb vegetation, grazing and the only sporadically applied mowing cannot prevent *Alnus glutinosa* and some tall growing species like *Phragmites australis* from becoming dominant. A more intensified mowing regime is necessary here to avoid further succession. For the forests, the option of no management was chosen. This seems to be the best option since only very generally occurring species are present there. Nonetheless, because of their high diversity value (Aerts, 2004), the current management focus on heathland vegetation seems to be justified.

Methodological remarks

Even though only one site was studied, our results support the findings of other studies (e.g. Hester and Baillie, 1998; Bokdam and Gleichman, 2000; Hulme et al., 2002: Pakeman et al., 2003), and give a clear indication of the efficacy of grazing in maintaining a diverse and vital heathland vegetation. Additionally, while other, mostly experimental studies are in fact only a small-scale imitation of reality (e.g. Hester and Baillie, 1998; Hulme et al., 2002; Pakeman et al., 2003), our study allows to investigate the effects of grazing in a real life situation. Hence, it may give a more realistic picture of how heathland vegetation reacts to grazing.

However, long-term vegetation studies, especially when semi-permanent plots are used, are subjected to several methodological inconveniences, which can often be sources of extra variation not related to changes in vegetation composition (Lameire et al., 2000). The fact that the surveys in both periods were conducted by different researchers, can lead to some extra variation. Furthermore, no measured environmental variables were present for the original dataset, and hence Ellenberg indicator values were used to study changes in environmental conditions instead. Although the former are most reliable, Ellenberg values have been used for this purpose in many studies in the past (e.g. ter Braak and Wiertz, 1994; Diekmann and Dupré, 1997; Lameire et al., 2000). Generally, these indicator values have a high reliability and can be used to monitor the change in environmental variables instead of direct measurements (Thompson et al., 1993; Diekmann, 2003). Overall, although these factors have their effect on the results obtained, their influence is probably negligible and does not radically alter the obtained results. As we studied vegetation changes at three different levels (community, plot and species level), and the results of the different levels are quite consistent, this further illustrates their reliability.

Further, this type of study forms a promising approach to bridge the gap between scientific research and management practice. (Semi)-permanent plots form an affordable, feasible instrument to monitor changes in vegetation composition and diversity in nature reserves. This method of studying vegetation changes provides objective indications of the effects of management, and hence forms a scientific base for the nature manager to base his future management decisions on, and to evaluate and if necessary redirect current management. This instrument is however not able to find the underlying causes of change. For that purpose, experimental research is needed.

CHAPTER 9

CONCLUSIONS

Heathland fragmentation and its effects on the heathland plant community

Heathlands have suffered severe area losses and have become severely fragmented throughout the whole of western Europe (chapter 1). In the northwestern part of Flanders, for example, heathland area was drastically reduced to less than 1% of the area present in 1775 (chapter 2). Older maps indicate that habitat loss is probably even much larger. Nevertheless, the consequences of heathland fragmentation on the heathland plant community have been hardly explicitly addressed before. Therefore, we tried to provide some insights into these fragmentation effects. First, direct effects of reduced area and increased isolation of heathland patches were studied both at the level of the whole heathland plant community and at the individual species level. Next, the influences of adjacent land use (i.e. edge effects), which have become more and more important due to fragmentation were explored. Finally, the interaction of fragmentation effects with management was investigated by studying the effects of long term extensive grazing in one of the larger heathland areas in Flanders. Results of this research provided useful guidelines for the conservation of this rapidly disappearing habitat.

Direct fragmentation effects

Despite the serious area losses, historical records showed the loss of heathland species in the study area over a 200 year period to be relatively limited (chapter 2). 10 of the 91 heathland species present in the oldest records (1792-1939) have no longer been observed in the recent period (1972-2003). Since the first record showing a species that has gone extinct dates from 1874 (Vander Meersch, 1874), this adds up to an extinction rate of 0.15 species or 0.09% per year (1874-2003). Probably most heathland species were able to survive in gaps and glades in the forests that replaced the heathlands in the study area. On the other hand, this relatively low extinction rate may be an indication that the heathland flora has not yet reached an equilibrium with the present landscape configuration, and future species losses are to be expected, hence pointing to the existence of an extinction debt (Tilman et al., 1994).

Nevertheless, the study of the vascular plant community of the individual heathland patches revealed a relaxation of their flora as a consequence of fragmentation (chapters 3 and 4). We showed that species richness was reduced by fragmentation. Both the reduced area of the remaining heathland patches and their increased isolation contributed to this relation. However, isolation effects overruled the often observed species-area relation. Also plant community composition was largely affected by the isolation between the different patches. Differences in the degree of isolation between the heathland patches caused their plant community to show a nested subset pattern. Area differences did not explain this pattern. The overriding importance of isolation effects relative to area effects, pointed at the existence of a rescue effect (Brown and Kodric-Brown, 1977), through which area-dependent extinction of species in a patch is prevented by species dispersal from neighboring patches. However, if the distances between the patches become too large, the species are no longer able to cross this distance, and the species will become extinct.

The sensitivity of heathland species to fragmentation was mainly determined by their seed bank characteristics. Species lacking a persistent seed bank showed higher rates of decline (chapter 2) and turned out to be more sensitive to fragmentation related changes in area and especially isolation (chapters 3 and 4). The ability to build up a persistent seed bank buffers the species against extinction (chapters 2, 3 and 4) and consequently acts as a temporal rescue effect, complementary to the spatial rescue effect described above. Other plant traits, like for example dispersal mechanism, did not affect the species' reaction to increased fragmentation. The latter however is very likely an indication that the morphologically determined dispersal mechanisms do not adequately fit the way the seeds are actually being dispersed (Higgins et al., 2003).

Edge effects

In the highly fragmented present-day landscape, edges form an increasingly important part. Understanding the ecologically distinct character of edges compared to patch interiors is one of the key elements in assessing fragmentation impacts. Edges have been studied extensively, but mainly in forest ecosystems (e.g. Murcia 1995; Honnay et al., 2002a; Devlaeminck et al., 2004). Yet there still is a large lack of congruency between the results of these studies. One of the reasons may be the fact that previous edge studies failed to take the intrinsic characteristic of transect data into account, and data were consequently not analyzed optimally. Therefore, we introduced linear mixed modelling as a novel approach to analyze typical edge data more correctly (chapter 5). An extended example further illustrated the suitability of this technique in edge studies.

Like in other ecosystems, for example forests (e.g. Honnay et al., 2002a; Devlaeminck et al., 2004), fluxes of species, materials and energy over the common boundary between heathland and adjacent land resulted in changed abiotic conditions and an altered plant community composition, both of vascular plants and bryophytes, in the vicinity of the edge (chapters 6 and 7). For vascular plants, eutrophication near the edge caused a shift from the typical heathland vegetation to a dominance of grasses and species representative for nutrient-rich conditions, yielding an edge zone of about 8m wide (chapter 6). These effects were more pronounced in heathlands adjacent to cropland compared to heathlands adjacent to forest. The latter indicates the importance of the landscape matrix in shaping fragmentation effects.

On the other hand, edge effects on bryophyte species were much more limited, and only extended up to about 2m into the heathland (chapter 7). For this group of plant species management significantly affected community composition. A remarkable edge effect in this vegetation layer was the higher dominance of the exotic invasive species *Campylopus introflexus* near the edge, especially at grazed sites. This species currently is one of the major threats to native bryophyte species in oligotrophic systems like heathlands (Biermann and Daniels, 1997; Stieperaere et al., 1998). Edge effects turned out to prevail over management effects. Consequently, management cannot be used as a tool to mitigate edge effects.

The presence of edge effects, especially on the vascular plant layer, at first sight seems to contrast with the fact that area effects turned out to be relatively unimportant in the heathland patches. However, in this edge zone typical heathland species are still present albeit at a lower abundance and not as the dominant vegetation component. Hence this edge zone does not mean that these species are not present, but only that conditions there are probably not optimal. The lack of congruence between edge responses and area sensitivity can be caused by the fact that edge responses are strongly dependent on the characteristics of the surrounding habitat, and patches are typically surrounded by a variety of different habitat types (Ries and Sisk, 2004).

Management effects

Even in relatively large heathland nature reserves conservation of a diverse heathland flora cannot be assured unless it is properly managed. In the reserve De Maten, heathland vegetation has changed little over the 25 year study period. Overall, extensive grazing has succeeded in preserving a species rich and diverse heathland flora. However, in the moist and wet heathland parts *Molinia caerulea* increased significantly both in cover and frequency, indicating that grazing cannot sufficiently prevent further grass invasion and additional mechanical management is necessary there. Also the increased frequency of some shrub and tree species in all heathland types suggest that the occasional application of additional mechanical management practices might be necessary, which is in accordance with earlier findings in Dutch heathlands (Bokdam and Gleichmann, 2000). This combination of grazing combined with mechanical management is in accordance with the so-called ‘communal model’ of grazing management described by Van Vessem and Stieperaere (1989).

Implications for heathland conservation and management

Their intrinsically nutrient-poor character, together with their high management need, causes heathlands, like many other (semi-)natural land use types, to be severely threatened in the present day landscape. Heathlands, as a land use, are not that evident to re-create. Both the changed soil conditions and the biotic constraints of limited dispersal and impoverished seed banks seriously hamper the restoration of heathland on former heathland sites (Bakker and Berendse, 1999; Walker et al., 2004), and especially on sites where heathland was converted to agricultural land (Pywell et al., 1994; Marrs et al., 1998; Walker et al., 2004). Consequently, the conservation of present heathland patches and the restoration of degraded heathlands are the most important ways to assure the persistence and survival of this habitat. Results of this study have highlighted the importance of regional processes in the conservation of a species rich, diverse heathland vegetation. As described above, especially a reduced connectivity of the heathland patches has significant negative consequences on the persistence of many characteristic heathland plant species, and subsequently also on the heathland plant community as a whole. Consequently, further destruction of heathland patches should certainly be prevented as this would result in a further decrease in connectivity of the remaining patches. Through continuing heathland destruction, the maximum distance that seed and pollen can bridge will be exceeded for more and more species, leading to further extinction and species loss.

The limited effects of patch area on the heathland plant community indicate that even small patches can contain a diverse and species rich heathland plant community. Consequently, these small patches can contribute significantly to the survival of many heathland plant species. Therefore management should not only focus on the large heathland patches. Also small heathland relics, like heathland on road verges or along small forest paths, should be preserved. These patches can be important refuges for the heathland plant species. However, it should also be highlighted that even the best connected heathland patches can only survive when management is applied at a regular base, to preserve the characteristic environmental conditions needed for heathland survival and to prevent succession to forest. Especially for the relics in forested areas, management should be aimed at assuring the appropriate light conditions necessary for these species to survive. These are probably better maintained through traditional forms of forest management (e.g. coppice/coppice-with-standards) as these result in regular light phases. It should be pointed out however, that these guidelines are only valid for plant species. For many characteristic heathland animal species, like for example butterflies (Maes and Van Dyck, 1999), chances for persistence are better on large heathland patches.

The presence of edge effects further indicates the importance of a proper management of even the smallest heathland patches, as in these patches the chances that characteristic heathland species are impeded by competitive species indicative for more nutrient rich conditions are higher. The differences in edge effects between heathlands adjacent to forest and heathland adjacent to cropland points at the importance of neighbouring land use, and hence of the characteristics of the landscape matrix. The more pronounced aspect of the edge effects when heathlands are adjacent to cropland urges for measures preventing further eutrophication. When heathlands are situated in agricultural areas, special care should be taken by the farmers on how fertilizer is applied, to prevent as much as possible direct nutrient inflow into the heathland. The creation of buffer zones might help to achieve this (e.g. De Snoo and De Haes, 1994; Hermy and Honnay, 1997).

Another important aspect of edge effects in heathlands is the increased dominance of the invasive bryophyte species *Campylopus introflexus*, indicating that invasion primarily occurs from the heathland-forest edge. This can be an important point to take into consideration when taking measures to prevent the further spread of this species. Grazing management seems to promote *Campylopus introflexus* invasion (e.g. Pakeman et al., 1997). In contrast with this, extensive grazing was shown to be an effective management method in preserving a diverse heathland vascular plant flora. The grazers succeeded quite well in maintaining the nutrient-poor character of the heathlands, together with keeping the dominating heathland species in a vital condition. Grazing has been shown to promote a diverse bryophyte community in other habitats also (e.g. Bergamini et al., 2001a; Aude and Ejrnaes, 2005). In general, extensive grazing can be an effective and cost-efficient tool in the management of large heathland reserves. An additional advantage is that grazers can also promote seed dispersal between different parts of the grazed area (e.g. Couvreur, 2005). However, grazing, nor other management types, succeed in reducing the presence of edge effects.

Although nature management should preferably be aimed at protecting the whole ecosystem, the differences in fragmentation sensitivity between the different heathland species indicate that species-specific measures might be necessary to assure survival of the whole community. Overall, species lacking the ability to build up a persistent seed bank turned out to be most sensitive to fragmentation (e.g. *Festuca filiformis, Salix repens*). Hence conservation efforts should especially focus on these species. Many of these species already are rare, such as for example many species characteristic for grassheaths (e.g. *Danthonia decumbens*), a part of the heathland vegetation that at present only covers a limited area in Belgium.

Recently, heathland conservation and restoration has been receiving more attention (e.g. European Heathland Network, EU Habitat directive), and maybe the continuous decline of heathland area can finally be stopped. Due to the relative long life span of the dominating heathland species, restoration of heathland vegetation through the removal of trees on former heathlands has been taking place. Although this type of heathland re-creation has the highest chance of succeeding (e.g. Walker et al., 2004; Pywell et al., 2002), it mostly relies on the seed bank composition to restore the heathland vegetation. Consequently, in these restoration projects, again, those heathland species having a long term persistent seed bank have the largest chances to reappear. The importance of a high connectivity between the heathland patches to assure dispersal between the patches, thereby preventing species extinction, can also provide essential clues in this context. For species lacking a persistent seed bank, colonization from nearby heathland patches is required. The same is true when the time period since heathland afforestation is long, and the seed bank has been depleted. The latter is likely to happen more and more with current forestry practices promoting the replacement of coniferous plantation with indigenous broadleaved species with a much longer rotation period. In these cases it can therefore be important to recreate these heathlands at locations well connected with existing heathlands to make recolonization of heathland species possible.

Suggestions fur future research

This study aimed at providing insights into the effects of heathland fragmentation on the heathland plant community. However, since traditional heathland studies have been mainly focused on local processes, like for example management and nutrient addition effects (e.g. Aerts et al., 1990; Alonso et al., 2001; Britton et al., 2001; Pakeman et al., 2003; Marrs et al., 2004), fragmentation research has been a largely neglected element in heathland research. Consequently, this study has only been able to provide some general clues on how fragmentation can affect the characteristic heathland plant community, and further research is urgently needed. This study focused mainly on fragmentation effects by studying patch occupancy patterns. However, the mere fact that a species is present in a habitat patch does not provide any information on the viability of the constituent plant populations. Furthermore, to obtain a more comprehensive insight into the effects of heathland fragmentation on the regional persistence of plant populations, a shift from the study of patterns of plant distribution to the underlying ecological processes is necessary (Debinski and Holt, 2000; Eriksson and Ehrlén, 2001; Ehrlén and Eriksson, 2003; Jacquemyn, 2004). Therefore, research on the effects of fragmentation on the regional dynamics of plant populations is needed. Genetic research can provide valuable insights in this context

(Honnay et al., 2005; Flinn and Vellend, 2005). A final largely neglected area in (heathland) fragmentation research deals with the consequences of fragmentation on the bryophyte community.

Regional persistence of vascular plant populations

Ongoing habitat fragmentation can have severe consequences on the reproductive success, the population structure and the genetic structure, and hence on the viability of the plant population living in the habitat remnant. Despite the high degree of fragmentation, the characteristic species can still be present in the remaining patches in a fragmented landscape. However plant populations in small and isolated patches frequently show a reduced fitness (e.g. Aizen and Feinsinger, 1994; Heschel and Paige, 1995; Agren, 1996; Fischer and Matthies, 1998; Oostermeijer et al., 1998; Kéry et al., 2000; Luijten et al., 2000; Vergeer et al., 2003a,b; Kolb, 2005). Yet, results from different studies are not conclusive (Aizen and Feinsinger, 1994; Ouborg and Van Treuren, 1995; Leimu and Syrjänen, 2002). For most of the threatened heathland plant species, the way fragmentation affects the persistence and viability of the population is unknown, exceptions being *Gentiana pneumonanthe* (Oostermeijer, 1996), *Arnica montana* (Luijten et al., 2002), a species extinct in Flanders, and *Succisa pratensis* (Vergeer et al., 2003a, b; Herben et al., 2006), the latter being more characteristic of acid grassland.

Different processes can be responsible for a reduced fitness and viability in fragmented populations. These processes were described in more detail in chapter 1, and include processes such as increased inbreeding, loss of genetic variation due to genetic drift and reduced gene flow (Ellstrand and Elam, 1993; Young et al., 1996; Keller and Waller, 2002), and interrupted plant-pollinator interactions which result in lower pollen quality and quantity in fragmented populations (e.g. Jennersten, 1988; Agren, 1996; Groom, 1998; Brys et al., 2004; Kolb, 2005).

As a consequence of this reduced reproductive success, the demographic structure of fragmented populations is often seriously disrupted (e.g. Endels, 2004). Assessing the demographic structure of these populations will provide valuable insights in the viability of these populations. Relic populations often show a dominance of adult stages and a reduced proportion of seedlings and juveniles. This senescent population structure can be detrimental to the long term survival of these populations. The reduced presence of younger life stages can also be due to dispersal limitation or recruitment limitation. The assessment of the relative importance of both processes can provide important clues on the conservation of these populations (Turnbull et al., 2000). Furthermore, the long term monitoring of the demographic structure, combined with the use of matrix population models (Caswell, 2001), helps to understand the viability and survival of these populations.

Ultimately, the outcomes of these population level processes are patch occupancy patterns in species presence and consequently community composition and diversity of the heathland community. By having a sound grasp of these population level processes, more accurate conservation and management measures can be taken to prevent, reduce or reverse the deleterious effects of heathland fragmentation.

Regional dynamics of fragmented plant populations

Many attempts have been made to classify the spatial dynamics of plants at a regional scale (e.g. Freckleton and Watkinson, 2002; Bullock et al., 2002). Metapopulation theory has become one of the key concepts in understanding species dynamics in fragmented landscapes (Hanski, 1999). Although it has been widely used in animal population studies, its applicability to plant populations is still under debate (e.g. Freckleton and Watkinson, 2002, but see Ehrlén and Eriksson, 2003; Verheyen et al., 2004; Ouborg and Eriksson, 2004). Because different types of regional dynamics have very different properties, are dominated by processes working at different spatial scales and consequently need different conservation focuses, it is important to determine whether certain species or systems can be considered as metapopulations or should be assigned to another regional dynamics type (Bullock et al., 2002; Freckleton and Watkinson, 2002). Key measures in determining the best fitted regional population structure are the estimation of dispersal and the assessment of extinction and colonization dynamics (Ouborg and Eriksson, 2004).

Extinction rates are difficult to quantify, especially for heathland species, because many characteristic heathland species have the ability to build up a persistent seed bank (e.g. Bullock et al., 2002; Ouborg and Eriksson, 2004). Consequently, the fact that a species is no longer visually present in a patch, does not necessary mean that it has gone extinct. A possible method to estimate the probability of extinction or to include seed bank studies in the study of extinction and colonization rates is the use of matrix population models combined with stochastic simulations (Caswell, 2001). To be able to apply such models, data on population structure for three or more consecutive years are necessary.

An important feature in regional population persistence is long distance dispersal. However, in our study we did not find a significant relation between patch occupancy patterns and the morphologically determined seed dispersal type. This is in accordance with many other studies relating plant distribution patterns or patch colonization with dispersal mechanism (e.g. Butaye et al., 2001; Flinn and Vellend, 2005). The most plausible explanation is that seeds are dispersed in other ways than suggested by the morphological characteristics of the seed. This is in accordance with the findings of Higgins et al. (2003), who stated that long distance dispersal is a complicated process in which several ways and vectors of dispersal are involved, and is not exclusively the result of the morphological adaptation of the seed to dispersal. Empirical measurements on how far seeds of a certain species can disperse are currently very scarce (but see Bullock and Clarke, 2000; Couvreur et al., in press).

Other approaches that can be used to directly measure actual dispersal distances are stable isotope analysis and molecular genetic techniques (Ouborg et al., 1999; Cain et al., 2000; Wang and Smith, 2002; Nathan et al., 2003). By studying molecular markers that are inherited through seeds (e.g. mitochondrial and chloroplast DNA) estimates of dispersal distances can be obtained. They can also be important in revealing the importance of seed flow in determining the genetic relationship between populations. Furthermore, genetic approaches can further be used to uncover the relative importance of seed and pollen flow on gene flow in plant populations by comparing patterns of differentiation in both chloroplast and nuclear markers (Ouborg et al., 1999; Wang and Smith, 2002).

Bryophytes and fragmentation

Bryophytes have been a neglected part of the plant community in most ecological research. In most studies, the focus is on the vasular plant species, probably because they make up the most visible component of most vegetation types. Furthermore, bryophytes are more difficult to identify than vascular plant species. Finally, because bryophytes are taxonomically much less straightforward, bryological studies are still largely focused on taxonomy and systematics. However, although they often are less visible because they are almost completely covered by the vascular plant layer, bryophytes do form an important component of plant diversity in many vegetation types, like for example heathlands (Rodwell, 1991; Schaminée et al., 1996).

Studies on the effects of habitat fragmentation on bryophytes, and also on the even more difficult to study lichens, are very scarce (Pharo et al., 2004). Furthermore, the few available studies are limited to forests, and mostly focus on epiphytic species (Berglund and Jonsson, 2001; Zartman, 2003; Moen and Jonsson, 2003; Pharo et al., 2004; Zartman and Nascimento, 2006; but see Wilson and Provan, 2003). However, because different taxonomical groups are expected to react in a different way to increased habitat fragmentation, and because of their high diversity, compared to the relatively species poor vascular plant layer in heathlands, the study of effects of heathland fragmentation on bryophytes should certainly receive more attention in the future.

Our results on the effects of adjacent land use on the heathland bryophyte layer have indicated that this part of the plant community is strongly affected by the type of management applied, much more than the vascular plant species. Therefore, future research should also explicitly incorporate studies on the effects of different types of management on the bryophyte layer. Although this aspect of bryophyte ecology has received more attention than fragmentation studies (e.g. Bergamini et al., 2001a; Vanderpoorten et al., 2004), little research on this topic has been performed in heathlands.

Concluding remarks

Although this study has indicated the important consequences of increased heathland fragmentation on the heathland plant community, many aspects and underlying processes remain unexplored. Therefore, continuing research on heathland fragmentation, combining research on different hierarchical levels (community-population) and on different categories of plant species (bryophytes, lichens and vascular plants) and their interactions, using an integrated approach of plant ecological, genetic and demographic research, is certainly needed. Only a thorough understanding of these various aspects and processes can result in better insights in fragmentation-caused changes in heathland vegetation, and consequently adequate conservation of this important semi-natural habitat.

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1. Honnay, O., Piessens, K., Van Landuyt, W., Hermy, M., & Gulinck, H. (2003) Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. *Landscape and Urban Planning* **63**, 241-250.
2. Piessens, K., Honnay, O., Nackaerts, K., & Hermy, M. (2004) Plant species richness and composition of heathland relics in north-western Belgium: evidence for a rescue-effect? *Journal of Biogeography* **31**, 1683-1692.
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Appendix

List of the 54 species characteristic for heathland, their plant traits, the number of patches they occupy (NP) (N=153) and the number of patches suited for that species (NSP), as determined by the habitat space model.

Species	**SLI**	**H**	**SM**	**DISP**	**GROW**	**COMP**	**CLON**	**SN**	**NP**	**NSP**	**Socio-ecological group**
Agrostis spec.	0.66	45	0.06	6	1	0	1		126	151	Acid grassland
Aira caryophyllea		22	0.17	2	1	1	0		1	10	Acid grassland
Aira praecox	1.00	11.5	0.18	2	1		0		9	10	Acid grassland
Botrychium lunaria		14.5		1	2				1	126	Grassheath
Calluna vulgaris	0.88	47.5	0.03	1	3	0	0	3	128	131	Dry heath
Carex binervis	0.60	65	1.50	6	1	1	1		20	131	Grassheath
Carex demissa		30		4	1	1	1		24		Peat moor
Carex echinata	0.17	40	0.90	4	1	1	1		10	142	Peat moor
Carex lasiocarpa	0.50	55	0.60		1	1			2	37	Peat moor
Carex nigra	0.19	37.5	0.81	6	1	0	1		1	142	Peat moor
Carex panicea	0.35	30	1.88	4	1	1	1		14	141	Acid grassland
Carex pilulifera	0.93	20	1.17	3	1	1	1		92	132	Dry heath
Cytisus scoparius	0.67	145	7.60	3	4	0	0		36	126	Dry heath
Dactylorhiza maculata		35	0.10	1	2	1	0	3	19	143	Acid grassland
Danthonia decumbens	0.29	37.5	0.87	3	1	1	0		51	152	Grassheath
Drosera intermedia	1.00	9	0.03	1	2	1		1	6	31	Wet heath
Drosera rotundifolia	1.00	15	0.01	1	2	1		1	10	62	Wet heath
Erica cinerea	0.75	32.5	0.04	1	3	1	0	2	42	135	Dry heath
Erica tetralix	0.41	32.5	0.02	1	3	1	0		54	126	Wet heath
Eriophorum polystachion	0.15	40	0.44	1	1	1	1		1	78	Wet heath
Festuca filiformis	0.00	12.5		2	1	0	0	1	29	126	Acid grassland
Galium palustre	0.26	57.5	0.91	4	2	1	1		14	75	Peat moor
Galium saxatile	0.50	18	0.56	2	2	0	1		9	142	Grassheath
Genista anglica	0.00	45		5	3	0			2	143	Dry heath
Hieracium umbellatum	0.56	65		1	2		0	2	32	125	Grassheath
Hydrocotyle vulgaris	0.27	13	0.31	4	2	1	1		25	77	Peat moor
Hypericum dubium	0.50	40	0.08	1	2	1			5	147	Acid grassland

Species	**SLI**	**H**	**SM**	**DISP**	**GROW**	**COMP**	**CLON**	**SN**	**NP**	**NSP**	**Socio-ecological group**
Hypericum perforatum	0.90	42.5	0.10	1	2	1	1	3	32	89	Acid grassland
Juncus acutiflorus	0.64	65	0.01	2	1	1	1		35	43	Acid grassland
Juncus conglomeratus	0.51	75	0.02	2	1	1	1	3	79	152	Acid grassland
Juncus squarrosus	0.86	22.5	0.03	2	1	1	1	2	30	131	Wet heath
Luzula campestris	0.37	12.5	0.64	3	1	1	1	1	20	126	Acid grassland
Luzula congesta		37.5	0.42	3	1	1	1	2	64		Grassheath
Luzula multiflora	0.36	37.5	0.42	3	1	1	1	2	54	147	Grassheath
Lycopodiella inundata		9		1	2		1		3	65	Wet heath
Molinia caerulea	0.35	55	0.53	1	1	0	1		143	153	Wet heath
Myrica gale	0.00	120	1.60	4	4				12	77	Wet heath
Nardus stricta	0.20	20	0.38	2	1		1		8	145	Grassheath
Narthecium ossifragum	0.50	17.5	0.10	4	2	1	1	1	1	64	Wet heath
Ornithopus perpusillus	0.00	17.5	1.00	1	2	1	0		4	45	Acid grassland
Pedicularis sylvatica	0.00	16.5	1.10	3	2	1	0		4	126	Wet heath
Platanthera bifolia		32.5		1	2	1			1	83	Acid grassland
Polygala serpyllifolia	0.50	15		3	2	1	0		21	143	Grassheath
Potentilla erecta	0.44	27.5	0.58	6	2	0	1		75	150	Grassheath
Ranunculus flammula	0.63	29	0.37	4	2	0	1		12	77	Peat moor
Rumex acetosella	0.69	35	0.40	6	2		1	1	36	45	Acid grassland
Salix repens	0.00	75		1	3		1		18	153	Acid grassland
Scutellaria minor	0.00	17.5		4	2	1			6	70	Acid grassland
Serratula tinctoria	0.00	55	2.80	1	2				1	83	Acid grassland
Succisa pratensis	0.24	65	1.54	2	2	1	0	1	7	153	Acid grassland
Ulex europaeus	0.75	130	6.59	3	4		0		4	147	Dry heath
Veronica officinalis	0.65	27.5	0.11	1	2	0	1	2	17	125	Grassheath
Viola canina	0.69	22.5	0.70	3	2	1	1		3	126	Grassheath
Vulpia bromoides	0.33	27.5	0.50	2	1	1	0		2	19	Acid grassland

SLI: seed longevity index (Thompson et al., 1997; Bekker et al., 1998); H: mean plant height (Lambinon et al., 1998); SM: seed mass (Klotz et al., 2002); DISP: dispersal mode (Hodgson et al., 1995) (1=anemochoreous; 2=exozoochoreous; 3=myrmecochoreous; 4=hydrochoreous; 5=barochoreous; 6=unspecified); GROW: growth form (Biesbrouck et al., 2001) (1=gramineous; 2=herbaceous; 3=dwarf shrub; 4=shrub); COMP: self compatibility (Klotz et al., 2002); CLON: vegetative spread (Hodgson et al., 1995); SN: seed number (Ecological Database of the British Isles; Kleyer, 1995) (1=1-1000; 2=1000-10000; 3=>10000).