
MACROMOTH COMMUNITIES ALONG FOREST EDGES

Effects of forest structure, surrounding landscape, plant diversity and microclimate.

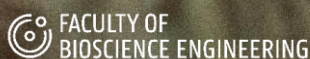
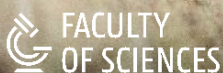
Cyr Mestdagh

Promotor: Prof. Dr. Dries Bonte

Supervisors: Dr. Pieter Vangansbeke, Dr. Pallieter De Smedt

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Introduction

Insect decline

Globally insect populations are declining (Wagner et al., 2021b). In Germany 27 years of study with Malaise traps showed a seasonal decline with 76% and a midsummer decline with 82% of flying insects' biomass. This happens regardless of habitat type (Hallmann et al., 2017)(Figure 1). Formerly common species show a tremendous decline in abundance, in the Netherlands there is a 30% decline in common butterfly species between 1992 and 2007. A similar trend is found for hoverflies in Germany (Hallmann et al., 2021). Strong reductions in both abundance and biomass (80% lower) and species richness (20-40% lower) were found over a period of 25 year. The decline of common species is stronger than for rare species of hoverflies.

In a Puerto Rican rainforest insect abundances already started declining in the 1970s (Lister & Garcia, 2018). Depending on the trapping method they found that Puerto Rican insect biomass had fallen 10 to 60 times, this was linked with the 2°C temperature rise between 1976 and 2012. Some papers dealing with the current decline in insect biomass call it an 'Ecological Armageddon' (Leather, 2017) or 'The insect apocalypse' (Goulson, 2019).

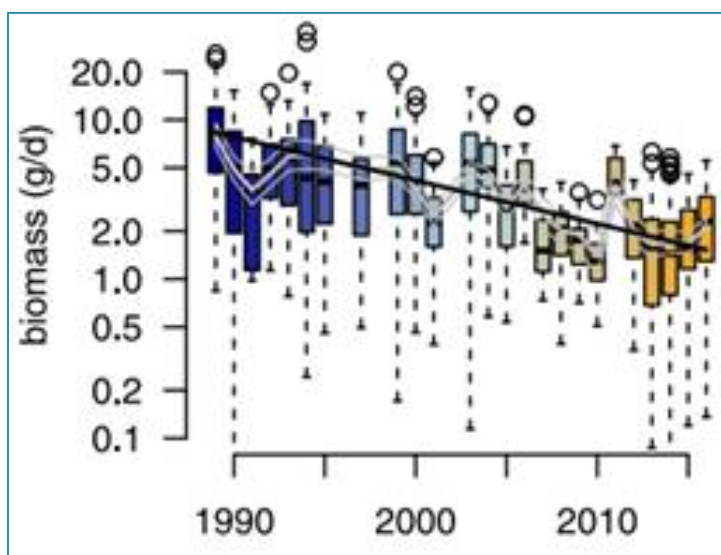


Figure 1: Insect biomass declined during a 27 year study (Hallmann et al., 2017).

The graph depicts the decline in insect biomass of all flying insects over time. A reduction from about 10g/d to 2g/d was found. The g/d or gram per day is the daily amount of flying insect biomass that was caught with Malaise traps.

Endangered species are disappearing (Warren et al., 2021). When their numbers start falling, the species as a whole goes extinct. In Flanders 30% of the butterfly species are already locally extinct and 28% is locally threatened with extinction (Warren et al., 2021). Over the last 600 years, 44.000 insects species have gone extinct (Kellert, 1993). It is estimated that by 2050 10% of all current species will have gone extinct (Pimm & Raven, 2000), insects comprise the majority of these extinctions (57% exactly) (Stork, 1997). Often these rare insect species that go extinct are habitat specialists (Dunn, 2005). Another major part of the insects threatened with extinction are parasitic groups, because these have a 'double' extinction chance: they can go extinct themselves or they can go co-extinct when their host dies out (Dunn, 2005).

Major drivers of biodiversity loss are habitat loss and fragmentation (Secretariat of the Convention on Biological Diversity, 2010). Humans are the main cause of insect declines by driving habitat loss and degradation in general, but also by using polluting and harmful substances and direct overexploitation (Cardoso et al., 2020). Moreover climate change (Cardoso et al., 2020) and artificial lights at night (Stewart, 2021) are important drivers of insect decline. The spread of invasive species poses another threat to native insects.

These invasive species destabilize local communities and impact different trophic levels, this causes factors like hydrology, nutrient cycles, soil chemistry, fire susceptibility, and light availability to change (Wagner & Van Driesche, 2010). Indirect factors also play a role i.e. co-extinction of species dependent on other species (Cardoso et al., 2020).

Moths are one of the largest species groups and are also under threat. About one third of the local species in the Netherlands suffers from climate change (Groenendijk & Ellis, 2011). In Great-Britain a recent report has found a 33% decline in macromoth abundance mostly due to human activity (Fox et al., 2021). These declines were even bigger in the South of Great-Britain, because human influence is higher in that region. Habitat loss (New, 2004) and forest fragmentation (Slade et al., 2013) are other major causes of moth declines, but also artificial light at night (Boyes et al., 2021) and the use of pesticides (Fox, 2013; Fox et al., 2021; Watanabe, 2014), agricultural intensification (Raven & Wagner, 2021), extreme weather events, urbanization and invasive alien species (Wagner et al., 2021a) have a tremendous impact. There are a lot of factors playing a role in moth decline and the current knowledge is not enough to disentangle the strengths of the different drivers (Wagner et al., 2021a).

Without protection, a lot of insects will be lost. It is now that measures should be taken to protect insects and stabilize their populations.

Forest fragmentation

Forests are very important ecosystems, since they harbour almost 70% of the terrestrial biodiversity (Millennium Ecosystem Assessment., 2005). Western European forests are under threat. Humans use a lot of the land for agriculture and building infrastructure. This causes habitat loss of the forests and other natural ecosystems (Jin et al., 2020). In the end only small forest fragments are left, scattered through the landscape. Habitat loss and fragmentation lead to the relative loss of forest cores and an increase of forest edges (Saunders et al., 1991). Forest edges are an important part of the forest ecosystem, since more than 20% of the world's forested areas are closer than 100 meter from the forest edge and 70% lies less than 1km from the edge (Haddad et al., 2015). In Europe 40% of the forest lie within 100 meter from the edge and 60% of those edges occur along intensive land uses (European Commission. Joint Research Centre. Institute for Environment and Sustainability., 2013).

Forest fragmentation can have a huge impact on species occurring in forests. For plants no large-scale extinctions are found because of fragmentation, although the conditions in fragmented forests are often not good enough for the long-term persistence of specialised plant species. This is caused by an extinction debt (Honnay et al., 2005). For instance, because plant populations show clonal growth, the distribution of plants in fragmented forests reflects the historical landscape configuration rather than the present one. For carabid beetles forest fragmentation resulted in a significant decline of forest specialist species (Fujita et al., 2008). For moths forest fragmentation was found to decrease species richness (Schmidt & Roland, 2006). Mostly tree- or shrub-feeding species disappeared. A study on macromoths found that mobile forest specialist were impacted the most by fragmentation (Slade et al., 2013). These species need the forest cores or a high connectivity to be able to persist or spread. Slade et al. suggest that forest fragments need to be larger than five hectares and need to have forest cores further than 100 meter from the edge to protect the populations of forest specialist moth species.

Forest habitat is important for moths and forest species in general. But not all nature can be protected, so among nature conservationists the question has risen whether it is better to protect a single large or several small patches, the so called 'SLOSS-debate' (Baz & Garcia-Boyer, 1996; Diamond, 1975; Lindenmayer et al., 2015; Ovaskainen, 2002) (Figure 2).

To answer this question detailed knowledge is needed about the occurrence of species along the edge-to-interior gradient. If a majority of species would prefer the edges, conservation measurements towards several small patches and connectivity would be most successful. However, if more species prefer core area, large patches should be protected. Research on the edge-to-interior gradient of moths can give insights in the SLOSS debate regarding to moth protection. Little research is done on the edge-to-interior gradient of moth occurrence along forest edges. Although the importance of forest cores for moths should be assessed and used in nature conservation programs.

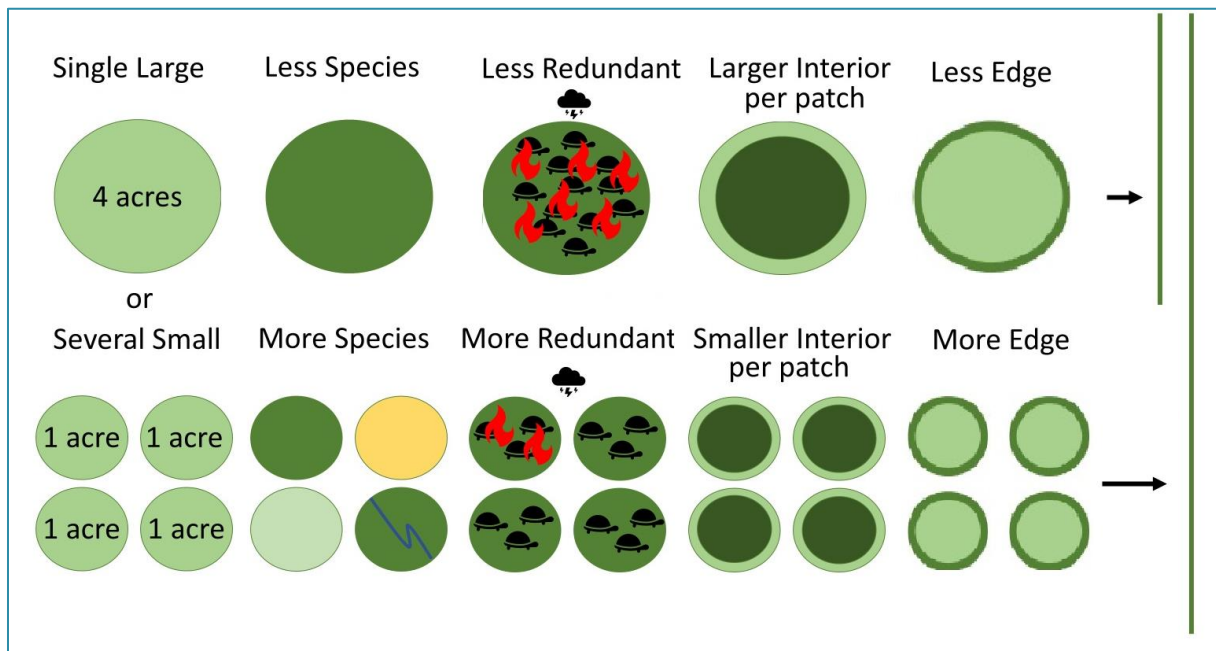


Figure 2: Single large or several small, pro and contra, reworked from (Grade, 2018). A single large patch has more core and so less edge, which results in a larger interior, but it often is less species rich compared to 4 small patches and less redundant against disasters.

Importance of moths in forest ecosystems

Until now about 160.000 species of Lepidoptera have been described globally (Beccaloni et al., 2012; Nieuwerkerken et al., 2011). It is estimated that there are about 16.000 to 34.000 species yet to be described (Costello et al., 2012). Moths comprise all the Lepidoptera that are not Butterflies. About 10% of the Lepidoptera species are Butterflies (17.500 species), so the majority of Lepidoptera species are Moths. Although they are a very large species group, moths are often overlooked and are not well studied in scientific research (Slade et al., 2013). Moths can be divided in two major groups: the micromoths and the macromoths. In this research the focus will be on macromoths. Macromoths comprise the families that contain generally larger species, Figure 3 shows which families are included within the macromoths (Waring & Townsend, 2017). Nevertheless taxonomically macromoths are a paraphyletic clade (Mitter et al., 2017; Qin et al., 2019). Most of the macromoth families are more evolved than micromoths, although there are some exceptions (Figure 3) (Kawahara et al., 2019; Kristensen et al., 2007; Sterling et al., 2018). The most species rich families of macromoths are the Noctuidae and the Geometridae (Salas-Araiza et al., 2015).

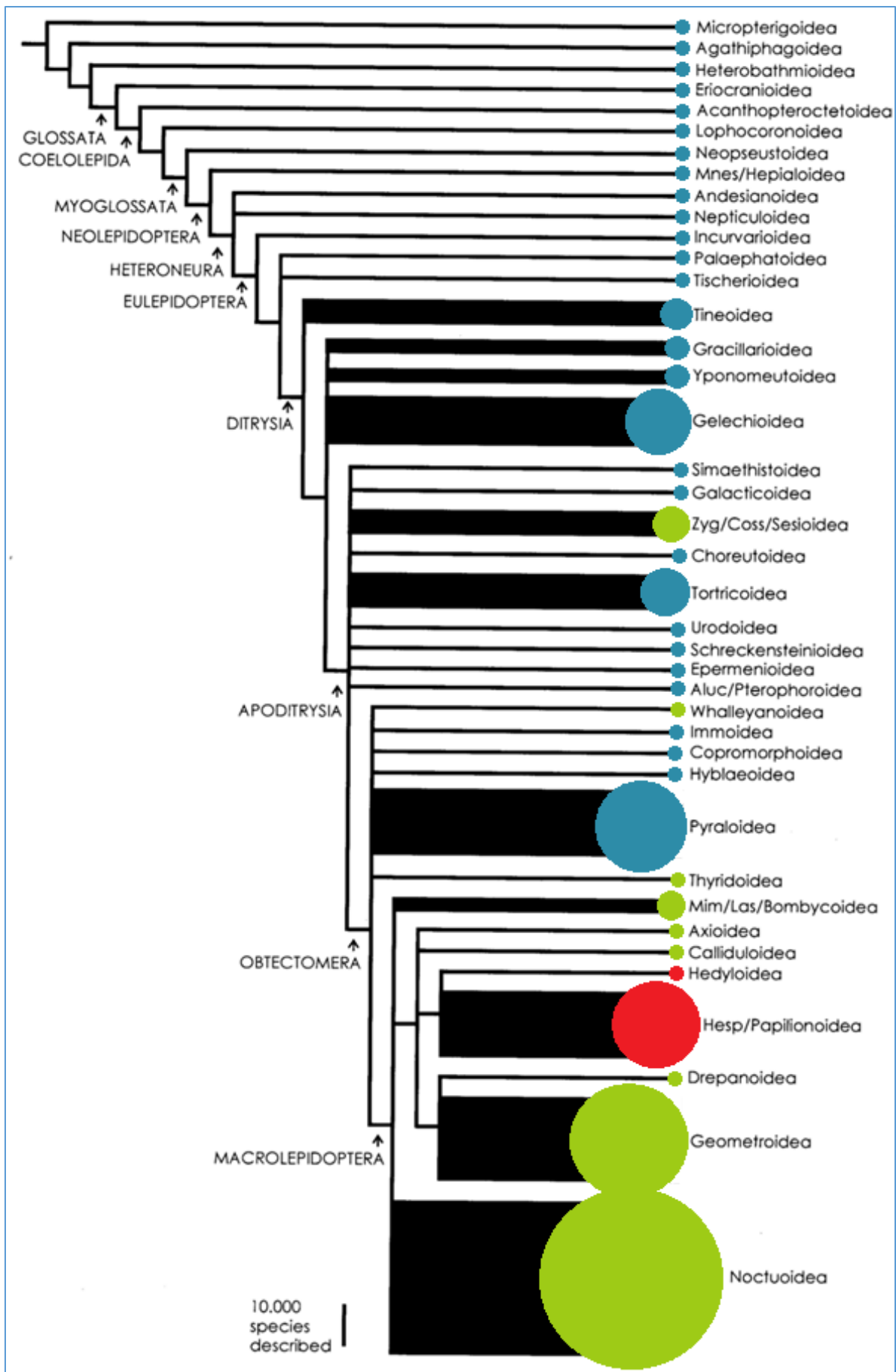


Figure 3: Phylogeny of Lepidoptera (reworked from Kristensen et al., 2007). Macromoths are indicated in green, micromoths in blue and butterflies in red. The number of species described is represented by the height of the black branch. Macromoths thus comprise a polyphyletic clade that is generally 4

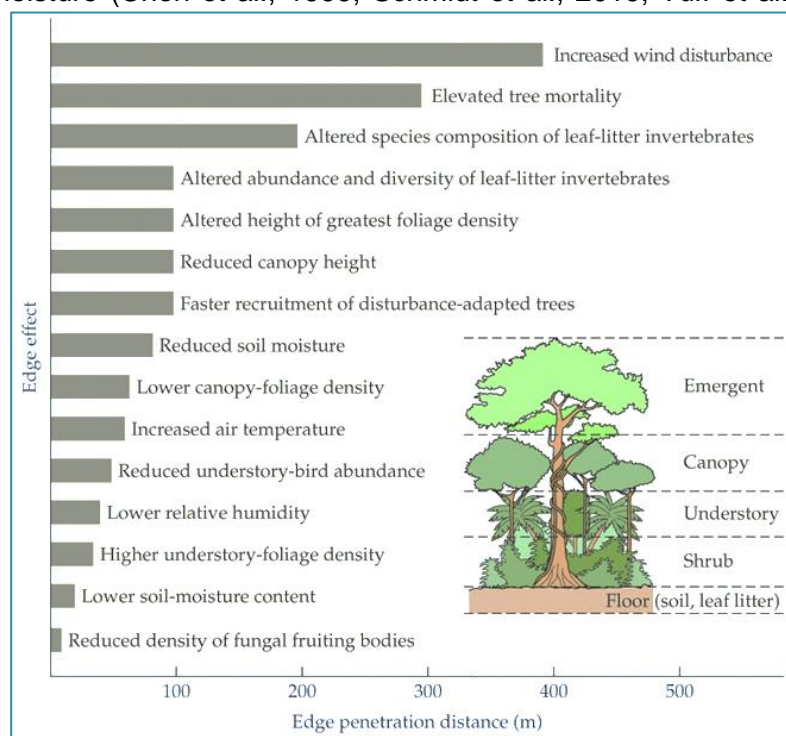
Lepidoptera have important ecological functions like herbivory and play a key role in the food web (Fox, 2013; Hahn & Brühl, 2016). Blue Tits alone need 50 billion caterpillars each year in the UK to raise their young. They highly depend on the amount of moths to sustain their populations (Perrins, 1991). Also the imago's are a main food source for bats (Vestjens & Hall, 1977). Moth pollination is an important service in both nature and agriculture (Hahn & Brühl, 2016). Moth pollinated plants are often characterised by white flowers to increase the low light visibility (Baker, 2015; Macgregor & Scott-Brown, 2020; Young, 2002). In subarctic birch forests it was found that moth herbivory by *Epirrita autumnata* can increase soil nutrients like nitrogen and enhance resource turnover (Kaukonen et al., 2013). This gives decomposers the chance to thrive and increase in biomass because of an early-season peak in resource availability. In semiarid woodlands similar results were found for herbivory of *Dioryctria albovittella* in pine forests (Chapman et al., 2003). They found increased nitrogen concentrations and decomposition rates with more *Dioryctria albovittella* present. Moths are also important as indicator species for habitat disturbance in forests (Summerville et al., 2004; VunKhen, 2006), for environmental quality of forests (Kitching et al., 2000). And also as indicator of restoration of calcareous grassland, although moths are generally better indicator species in forests, whereas butterflies give better responses in open habitats (Rákosy & Schmitt, 2011).

Forest edge effects

Forests have their own microclimate. This means that climatic variables are locally different compared to the larger area around it. Forest microclimates differ in abiotic factors compared to the matrix around it. Some important abiotic differences are reduced wind speeds, reduced light availability and more steady temperatures on a daily and a seasonal timescale. Variation in forest structure, composition and topographic position has big influences on the local microclimate (Zellweger et al., 2019). Which leads to highly heterogeneous forest microclimates across space and time. Also the orientation of the forest edges matter. South facing edges have a stronger edge-to-interior gradient and stronger seasonal variation than north facing edges (Bernaschini et al., 2019; Hofmeister et al., 2019). The canopy cover and composition are very important for keeping the temperature steady, a more open canopy will result in higher maximum temperatures and more variability (Zellweger et al., 2019). Forest cores have also a higher soil moisture (Chen et al., 1999; Schmidt et al., 2019; Tuff et al., 2016).

Figure 4: Forest edge effects (Primack, 2014).

Each edge effect has its own penetration depth. Most effects only influence the first 100 meter of forest that is therefore called the edge and anything deeper is seen as core. Note however that some edge effects such as wind disturbance also penetrate deeper in the forest.



Forest edges are influenced by so called 'edge effects'. These effects are influences of the matrix around the forests on both biotic and abiotic factors of forest ecosystems (Schmidt et al., 2017) (Figure 4). Wind speeds are higher in forest edges, there is more solar radiation, temperature fluctuates more and there is more drought compared to forest cores (Murcia, 1995). Other abiotic effects comprise higher nitrogen and carbon stocks (Meeussen et al., 2021; Remy et al., 2016). Examples of biotic edge effects are changes in distribution of species and changes in species interactions such as predation, competition, pollination, seed dispersal (Murcia, 1995) and herbivory (Sanczuk et al., 2021). But also a higher influx of non-forest species and differences in disturbance (Devlaeminck et al., 2005). Edge effects occur until 50 to 100 meter distance of the forest edge depending on the forest type (Gehlhausen et al., 2000; Matlack, 1993). Thinned (open) forests show a reduced microclimatic buffering capacity and makes the edges more susceptible to atmospheric depositions at low altitudes, in dryer regions thinning can have a positive impact (Meeussen et al., 2020).

Some research is done on the edge-to-interior gradient on species like plants (Erdős et al., 2019; Govaert et al., 2020) and litter-dwelling arthropods (De Smedt et al., 2019a). Research on plants revealed that generalist species richness decreased towards forest cores in south-facing forest edges (Govaert et al., 2020). For specialists no gradient was found. Another study sampling both north- and south-facing edges also found that plant species richness at edge was higher than at the core, with the highest species richness in north facing edges (Erdős et al., 2019). Research on litter-dwelling arthropods showed that there is a strong edge response of these species (De Smedt et al., 2019a). This response depended on the edge distance and forest age, with also higher abundance of arthropods in forest edges and in old forests. For European woodlice it was found that that edge patterns could be linked to drought resistance of the species. (De Smedt et al., 2018). These litter-dwelling arthropods consist of mainly wingless species that thus have a reduced mobility compared to most moth species. Another difference between moths and litter-dwelling arthropods is that moths are. Moths are also adapted to specific plant species (Hahn & Brühl, 2016), so research on plant occurrence along forest gradients can have interesting links with co-occurring moth community gradients. Because of these differences with litter-dwelling arthropods, their patterns in edge-to-interior occurrence cannot be generalised for moths. Some researches were done on moth edge-to-interior gradients in forests. There was a study on moths in the Amazonian rainforest (Jaimes Nino et al., 2019). Here they found that the occurrence of moth families differed along the edge-to-interior gradient and the size of the moths determined the occurrence along this gradient. Larger moths occurred more near edges than smaller moths. This was explained by drought resistance of moths. Larger moths can better withstand droughts that occur more often near forest edges. This is stated in the starvation-resistance hypothesis (Cushman et al., 1993). This hypothesis explains increasing body size with latitude based on the risk of starvation in seasonal/unpredictable environments. Because net energy storage increases with size, species with larger body sizes should be more resistant to starvation. There was a study in Turkey on the caterpillars of one moth species: the Pine processionary (*Thaumetopoea pitycampae*), where a significant edge-to-interior gradient in abundance of this species was found, with more caterpillars occurring near the edge (Parlak et al., 2019). Other species of moths are expected to have an edge-to-interior gradient in occurrence, but to our knowledge this has seldom been investigated in temperate forests.

Forest management

Forest management comprises all measures and plans taken by humans that alter forest structure in order to meet specific environmental, economic, social and cultural objectives (*Natural Forest Management*, 2020). Here the focus is only on the effects of forest thinning. This management type is based on removing certain trees to promote tree growth of the remaining trees (*Thinning | OregonForests*, 2021). Forest management has a direct impact on forest structure in general and on the edge-to-interior pattern of forest structure specifically (Meeussen et al., 2020). In the same way forest management has an impact on forest microclimate. Thinned (open) forests have a reduced canopy cover, reduced stem density and a lower amount of plant material (Meeussen et al., 2020),. This results in a higher light availability, temperature and wind speed (Ash & Barkham, 1976; Grayson et al., 2012) (Figure 5). Forest thinning also changes soil conditions, resulting in a reduced soil respiration and root activity, but an increase in soil organic matter (Tang et al., 2005).

Forest management has also an impact on biota. For plants was found that the species richness was highest in open forests (Govaert et al., 2020). This pattern was mainly driven by generalist species, forest specialist's species richness did not show any differences between management types. For other species groups like moths little is known about the effects of thinning. For Gypsy moth (*Lymantria dispar*) no effect of thinning was found on predation. This however does not say anything about the occurrence of the Gypsy moth in open forests (Grushecky et al., 1998). A more general research of ground dwelling arthropods found that ants highly prefer open forests, but other species like spiders, carabids and millipedes depend more on soil moisture than management type per se (Yi & Moldenke, 2005).



Figure 5: open vs dense forest, reworked from (Tague et al., 2019).

Objectives

This research investigates the activity-density (abundance of active macromoths) and composition of moth communities along the edge-to-interior gradient in dense and open deciduous forests in Western Europe. The main hypotheses below are based on literature on the gradient of plants (Erdős et al., 2019; Govaert et al., 2020), litter-dwelling arthropods (De Smedt et al., 2019a) and on the vertical stratification of moths (De Smedt et al., 2019b).

The main hypotheses of this research are:

- **Moth community structure varies along the edge-to-interior gradient in forests, with a higher moth species richness and activity-density at the forest edge.**
 - There are differences between families in community structure along this edge-to-interior gradient, with a stronger gradient for species from less mobile families.
 - Moths with a higher forest affinity have a higher preference for forest cores and they show a stronger response to the forest edge-to-interior gradient.

- **Management type has an impact on moth community structure, with more moths in open forests and a stronger edge-to-interior gradient in dense forests.**

- **Moth community structure depends on forest structure, temperature, floristic diversity and the surrounding landscape.**

Material and methods

Data collection

Sample locations

Macromoths were sampled in four regions: the Haute Fagnes (Belgium), the Flemish Ardennes (Belgium), Marche-en-Famenne (Belgium) and Compiègne (France). Each region comprised two sampling sites with a different management type: a thinned (open) and an unthinned (dense) forest (Figure 6). The open forests were recently thinned (Govaert et al., 2020). At each sampling location, four traps were placed along the edge-to-interior gradient at following distances from the forest edge: 1.5 m, 12.5 m, 35.5 m and 99.5 m. The trap at 99.5 m distance from the edge is considered to be the forest core. All sample sites were south-facing edges of oak or mixed oak forests that were selected for other scientific research within the FORMICA project (<https://formica.ugent.be>). The forests patches are all ancient forests where the inner plot is at least 100 m from all forest edges. The forest edges are characterised by a sharp transition to grassland, meadow or arable field. Each forest has a comparable understorey. Some other characteristics of the sample sites are listed in Table 1. The elevation level is a category assigned to a site based on the elevation (meters above sea level).

Table 1: Overview of the sample locations.

	Management type	GPS location	Nearest village	Elevation (MASL)
Flemish Ardennes	Thinned	N 50.9731169 E 3.8035539	Gontrode	29.800489
	Un-thinned	N 50.7696403 E 3.7534763	Flobecq	114.20464
Marche-en-Famenne	Thinned	N 50.2306984 E 5.2879426	Aye	247.77803
	Un-thinned	N 50.2283808 E 5.2833031	Aye	242.28137
Haute Fagnes	Thinned	N 50.5189109 E 5.8927511	Tiège	340.44647
	Un-thinned	N 50.5767564 E 5.9394485	Hèvrement	344.56649
Compiègne	Thinned	N 49.3210825 E 2.9281248	Morienval	156.56340
	Un-thinned	N 49.3407423 E 2.8177097	Lacroix-Saint-Ouen	60.094371

All values in the table (GPS location and Elevation) belong to the first plot, this is the plot at 1.5 meter of the forest edge.



Figure 6: Sampling locations.

The thinned/open forests are indicated by light green tags, the dark green tags are the dense forests. The 2 transects in Marche-en-Famenne lie very close to each other, so only the dark green tag is visible on this figure.

Moth sampling campaign

On each location four replications took place. Trapping at different forest types within each region was done within maximum 2 days, mostly on consecutive nights. The replications were spread throughout the moth season starting in the end of June with the first replication. The second one was in the beginning of August, the third one was in the beginning of September and the last one was mid-October. The samplings were spread as much as possible over summer in order to get a complete idea for all the moth species occurring in the forests.

Trapping set-up

Light traps are commonly used to catch moths in monitoring programmes, in scientific research and for determining moth distribution. A lot of studies are published about moth behaviour towards light (Baker & Sadovy, 1978; Hsiao, 1973; Taher et al., 2019) and the efficiency of different types of lights and different light traps (van Langevelde et al., 2011). There are differences in light attraction between moth families and species (Merckx & Slade, 2014). Most species are well attracted to light, a minor part of the species are less attracted to light. Merckx & Slade also found that low intensity light traps give better results for sampling the local moth communities. Using low intensity lamps one can catch almost the whole local community, while using high intensity lamps traps most of the species in a 500 meter range, but not all species.

We used these low intensity lamps for our sampling. There are only few downsides to this trapping method, one of those few is that males are better attracted to light traps than females (Altermatt et al., 2009). For this research this does not matter a lot, since only differences in occurrence are modelled and no differences between males and females were studied. With the vast amount of knowledge about light traps and the high efficiency of light traps in catching moths, light traps are the ideal equipment to study moth occurrence along an edge-to-interior gradient.

We used light traps of the Skinner model (Fry & Waring, 1996) with two low intensity Kendo light 8 Watt TL-lamps. The radius of these low intensity lamps in attracting moths is less than 10 meter (Truxa & Fiedler, 2012). Low intensity lamps were chosen in order to be able to sample moth communities as local as possible and to avoid interference between different traps. The light traps were powered by a lead battery. The trapping system uses 2 Plexiglas plates placed in a V-shape under the lamps, in the middle between these plates there is an opening of 2 centimetre. The traps use a funnel principle where moths can easily get in the trap, but cannot find the way out. We chose to use only light traps and no bait traps consisting of a wine/beer-sugar mixture (Pettersson & Franzén, 2008; Süssenbach & Fiedler, 1999). Bait traps would result in only a subsample of the species caught with light traps (Merckx et al., 2018). Catches with bait traps also have a strong daily variability (De Smedt et al., 2019b).

The traps were placed on a white wooden plate of 1 m² and only the individuals in the trap, on the trap, on the wooden plate and on the pole with temperature sensor next to the trap were counted. The lamps of the trap were facing upwards and placed perpendicular to the forest edge (Figure 7).

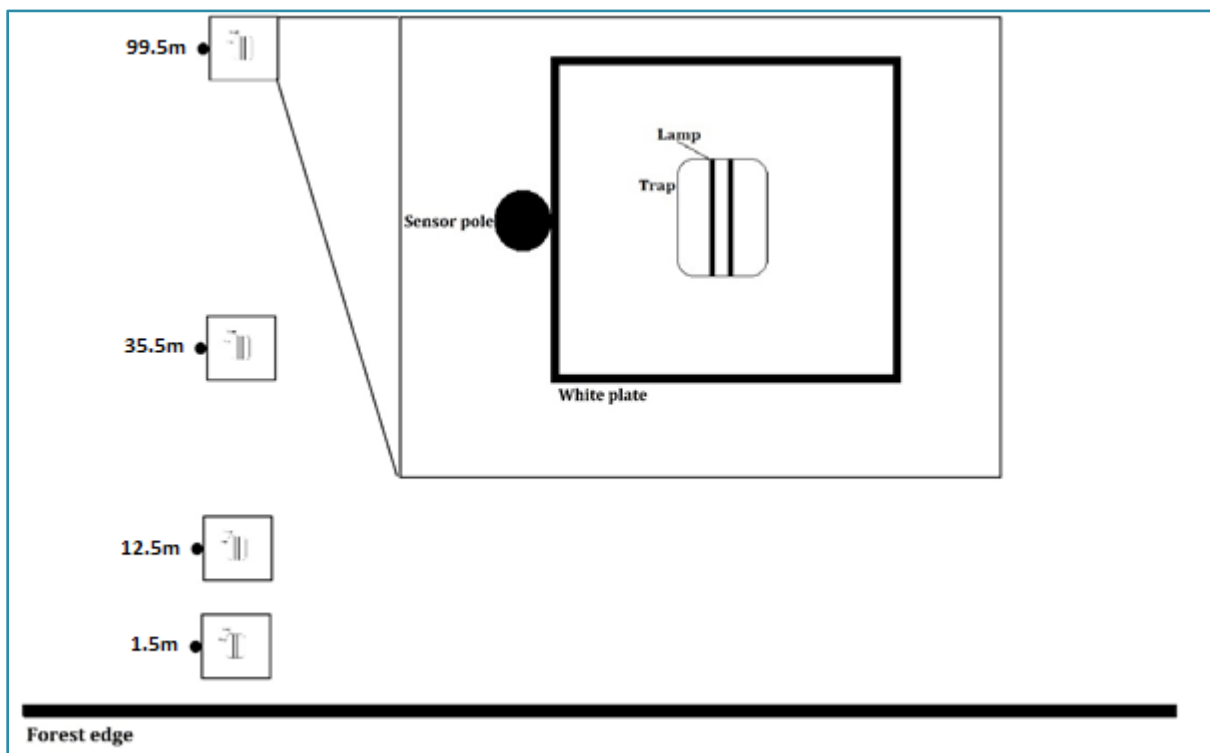


Figure 7: Trapping set-up. The traps were placed in a standardised way in order to avoid any confounding factors. The transect follows a logarithmic gradient.

In the trap and around the trap egg cartons were placed (Figure 8). On these egg cartons moths can rest and do not disturb each other. This leads to less moths escaping during the night (Brehm & Axmacher, 2006). The lights were illuminated one hour before sunset, they were on during the whole night. The traps were checked half an hour before sunrise with the lamps still on starting from the forest edge, because the forest cores stayed dark for a little longer in the morning. Only macromoths were identified and counted. See appendix I for the trapping protocol.



Figure 8: Light trap.

Environmental parameters

On each sampling location a set of environmental parameters was determined in May 2018 in the framework of the Formica project (www.formica.ugent.be). In each plot a sensor pole with a temperature sensor at one meter height was placed to investigate the microclimate. (Figure 9). The sensor was protected by a radiation shield. Temperature was measured every hour. On these exact locations also other environmental data were collected in 2018: all vascular plants in the herb layer and their cover were recorded in a plot of 3 * 3 m² and the species richness, the forest specialist species richness (Govaert et al., 2020) and phylogenetic species richness were calculated. Also forest cover in the 250 meter and 500 meter area around each plot was determined. LIDAR data of the forest structure, among others canopy openness, canopy height, plant area index and foliage height diversity were obtained with a RIEGL VZ400 LIDAR (RIEGL Laser Measurement Systems GmbH, Horn, Austria) (Meeussen et al., 2020).



Figure 9: Example of a transect.

These are the first three traps of the thinned forest in Marche-en-Famenne. This is the most open forest of all the sampling locations. Next to each trap there is a pole with a white radiation shield containing the temperature sensor.

Identification

Every macromoth in the trap was identified to species level and the number of individuals per species was counted (Figure 10). For the identification *Nachtvinders: De nieuwe veldgids voor Nederland en België* by Paul Waring was used (Waring & Townsend, 2018). In case of doubt experts have confirmed the identification (www.waarnemingen.be).

Certain species can only be identified based on the structure of their genital organs. On beforehand, a list was made with all species complexes. These comprise the genera *Acronicta*, *Aplocera*, *Epirrita*, *Horisme*, *Mesapamea*, *Noctua*, *Oligia*, *Scotopterix* and *Thera*. Species complexes that were expected to occur at low abundance (if any at all) were collected for preparation and microscopic identification (see Appendix II for the methods). Also complexes where the different species have a different forest affinity were collected. In the end it turned out, that only one species complex remained in the data. This complex, *Noctua janthe/janthina*, was not caught in large numbers as expected, so these should have been prepared for further identification.

Forest affinity of a variety of invertebrates in Germany, including moths, is described recently by (Dorow et al., 2020). Forest affinity of moths was assessed based on expert knowledge on the host plants of the caterpillars.



Figure 10: Scorched Wing – *Plagodis dolabraria*.
Caught on the 5th of August during the second replication in the dense forest in Compiègne at trap 3.

Data analysis

The data was analysed in R (R Core Team, 2021) using generalised linear mixed effect models with the lme4 package (Bates et al., 2015). There were two dependent variables: moth activity-density and moth species richness. Moth activity-density is the amount of caught moth individuals. This is no absolute measure of abundance, since light traps only attract active moths. For each analysis a mixed model was built for each dependent variable. For all models the most complex model, including all independent variables and their interactions, were used as basis. Each time, the non-significant term was left out until each term was significant or no significance was found at all. On each final model the assumptions of linearity and normality of the residuals was tested and if not specifically indicated, this was not violated.

Moth communities along edge-to-interior gradients and management type

Data exploration

To explore the main effects, more simple mixed models were run, with distance from the edge, management type and the interaction as fixed effects and region and transect as random effects. At first, models were built by lumping the data over the first three periods only, to have a dataset without NA-values, but covering as much of the total biodiversity as possible. The NA-values are light traps that did not burn the whole long enough, because of the cold, long nights during the last sampling period. Secondly each period was analysed separately to check whether the effects of edge-to-interior gradient and management type stays the same during all periods. Every time the activity-density, species richness and the Shannon-diversity were analysed. Shannon diversity showed no significances in any of the exploratory models, so this was not analysed further.

Moth species richness and activity-density in general

After the exploration a general, Poisson distributed model was fit on all the data, including the four periods. Period, region and transect were included in these models as a random effect term to account for the hierarchical data structure. The region was nested within period and transect was nested within region within period. The fixed variables included two main effects: $\ln(\text{edge-distance})$ (continuous variable) and management type (discrete variable) and the interaction effect between edge-distance and management type. The edge-distance was log transformed, since sampling of the edge-to-interior gradient occurred on a logarithmic gradient. A log transformation on edge-distance makes the response linear and strengthens the model. During the last sampling period some traps fell out resulting in some data gaps. Accounting for period as random effect and excluding NA-values from the final model overcomes this problem. This results in model code like this:

```
glmer(Species richness~ln(Edgedistance)+Foresttype+ln(Edgedistance) :  
Foresttype+ (1|Period)+(1|Period:Region)+(1|Period:Region:Transect) ,  
family= poisson, data=Allperiods, na.action=na.exclude)
```

This was also done for moth activity-density, Shannon-diversity was not further analysed since there were no significances in any of the exploratory models.

Moth families

The general model was also run for each moth family separately as dependent variable, since moth families differ a lot in mobility. Only the families with more than 100 individuals in the dataset were used. These families were (in order of decreasing amounts of captured individuals): Geometridae, Noctuidae, Erebidae, Drepanidae and Notodontidae.

Forest specialists & generalists

Four last models were built regarding the forest affinity of moths. The first two containing forest specialist moth species richness and activity-density and the last two containing generalist moth species richness and activity-density as dependent variables. For the forest affinity (Dorow et al., 2020), moths that were classified in the groups **w** (“Wald”, strong affinity to forest habitats, without known preference for light or dense forests), **wg** (“Geschlossenen wald”, mainly found in forests, with strong affinity to dense forest habitats) and **wl** (“Lichten wald”, mainly found in forests, with strong affinity to open forests, forest edges, or glades) were assigned to the group of **forest specialists**. Moths included in the other groups being **mm** (“Mittelmäßig”, occurring equally in open landscapes and forest habitats), **mo** (“Mittelmäßig offenland”, strong affinity to open landscapes, but also regularly occurring in forests, at forest edges, or in glades) and **o** (“Offenland”, only occurring in open landscapes or other habitats without forest cover like caves or buildings) were included in the group of **generalists**.

Moth communities and their environment

The most relevant available environmental parameters were used to analyse their effect on moth occurrence. These parameters also differ along the edge-to-interior gradient and between forest management types (Appendix III). Each parameter was analysed in a model with the parameter as independent variable and species richness or activity-density as dependent variable. In total thirteen environmental parameters were analysed (Table 2).

Table 2: Overview of the dependent and independent variables used in the model linking environment with moth occurrence.

Dependent variables	Moth species richness
	Moth activity-density
Independent variables	Openness of the canopy measured with the LIDAR (proportion)
	Canopy height (m)
	Forest cover in the 500 meter area around the plot (%)
	Plant area index (m ³ leaf area/ m ³)
	Foliage height diversity
	Plant species richness
	Forest specialist plant species richness
	Phylogenetic plant species richness
	Average temperature during the trapping nights (°C)
	Minimum temperature during the trapping night (°C)
	Maximum temperature during the trapping nights (°C)
Growing season temperature, being an average temperature of a plot over the whole sampling campaign. (°C)	

Simple models

First, each environmental effect was analysed separately, to avoid confounding. The general model correcting for error variation between periods, between regions and between transects was also used to analyse the environmental data that were available. Models looked like this:

```
glmer(Species richness~Environment+(1|Period.f)+(1|Period.f:Region)+(1|Period.f:Region:Transect_All.f), family=poisson, data=Environment_All)
```


Model selection

In a second step all environmental parameters were included, after testing for multicollinearity, and used in a model selection procedure to determine the environmental parameter that explains moth communities best. Only parameters without NA-values were included in a first step, since the dredge function does not allow NA-values. After the selection of the best models based on AIC, the parameters with NA-values were included (phylogenetic species richness, average temperature and growing season temperature) and this model was manually selected until only significant results were left. Minimum and maximum temperature were not included because there was multicollinearity with average temperature (VIF of 37).

Multivariate analysis

A multivariate Principal component analysis (PCA) was used to visualise the moth communities per period, region, plot and forest management and type to visualise the environmental effects. The log transformed number of moths caught per species were used to calculate the PC-axes, a log transformation results in a smaller effect of locally abundant species. The most important environmental parameters were included in the PCA plot as arrows indicating in which direction their values get higher. Phylogenetic plant species richness and temperature were not included in the PCA, because these parameters have missing data points and this would result in a reduced dataset that could be plotted. Temperature was fitted on a separate PCA, since this is the only parameter measured during each sampling period. As summary a PCA was done on a lumped dataset over all periods.

Results

All data and r-scripts can be found here: <https://github.ugent.be/cbmestda/Moth-occurrence-along-forest-transects.git>. In total 4743 individuals of 264 species were caught. The species that were caught the most are: *Cymatophorina diluta* (446 individuals), *Idaea aversata* (297 individuals), *Eilema lurideola* (233 individuals), *Thaumetopoea processionea* (174 individuals), *Hypomecis roboraria* (148 individuals), *Epirrita dilutata* (146 individuals), *Lymantria monacha* (125 individuals), *Campaea margaritaria* (117 individuals), *Zanclognatha lunalis* (113 individuals) and *Hypomecis punctinalis* (102 individuals). Together these represent 40% of the caught moths. Four of these are forest specialist species, the others are generalists. As for most other species, these were caught more near forest cores with the exception of *Thaumetopoea processionea*. Seven of these were caught more in dense forests.

For more total amounts of caught moths see Appendix V: Totals.

Moth communities along edge-to-interior gradients and management type

An overview of the final models can be found in Table 3.

Table 3: Overview of all the final models on moth communities along edge-to-interior gradients and management type that are further discussed in the results.

	Group	Dependent variable	Independent variables		Interaction effect	R ² m	R ² c
			Ln(edge-distance)	Management type			
Moth species richness and activity-density in general	All moths	Species richness	+ 0.065	X	X	0.015	0.885
		Activity-density	+ 0.087	- 0.392	+ 0.074	0.043	0.977
Moth families	Geometridae	Species richness	+ 0.076	- 0.228	X	0.028	0.840
		Activity-density	+ 0.057	- 0.885	+ 0.168	0.064	0.960
	Noctuidae	Species richness	X	X	X	/	/
		Activity-density	- 0.115	- 0.505	- 0.188	0.017	0.915
	Erebidae	Species richness	+ 0.089	X	X	0.003	0.981
		Activity-density	+ 0.232	X	X	0.012	0.999
	Drepanidae	Species richness	+ 0.206	X	X	0.032	0.738
		Activity-density	+ 0.365	- 0.106	+ 0.110	0.031	0.988
Notodontidae	Species richness	+ 0.266	X	X	0.047	0.803	
	Activity-density	+ 0.337	- 0.039	+ 0.333	0.049	0.985	
Forest specialists & generalists	Forest Specialists	Species richness	+ 0.125	X	X	0.045	0.819
		Activity-density	+ 0.150	- 0.601	+ 0.086	0.064	0.971
	Generalists	Species richness	X	X	X	/	/
		Activity-density	+ 0.040	- 0.210	+ 0.084	0.018	0.962

In columns 4-6 is indicated with a '+' or '-' if this parameter was included in the final model, followed by the model estimate. '+' indicates a positive correlation, '-' indicates a negative correlation, for management type, '+' indicates that open forests were preferred, '-' indicates that dense forests contained more moths. A positive interaction indicates that both open and dense forests increased or decreased in moth occurrence along the gradient, with one forest type having a significantly stronger gradient. A negative interaction means that there is an opposite gradient for open and dense forests. If the parameter was not significant (indicated with a cross), it was left out of the final model. A green symbol indicates a significant parameter. In case the assumptions were not met, black symbols were used, significances of these models cannot be interpreted.

Moth species richness and activity-density in general

Moth species richness

In the model for general species richness, only the edge distance had a significant effect on moth occurrence ($\text{Chi}^2 = 15$, $P < 0.001$), with an increase of 2.9 species from the edge to the core (Figure 11). Although on the figure there seems to be a lot of variation, the difference is significant with the correct error structure. There were more species caught deeper in the forest.

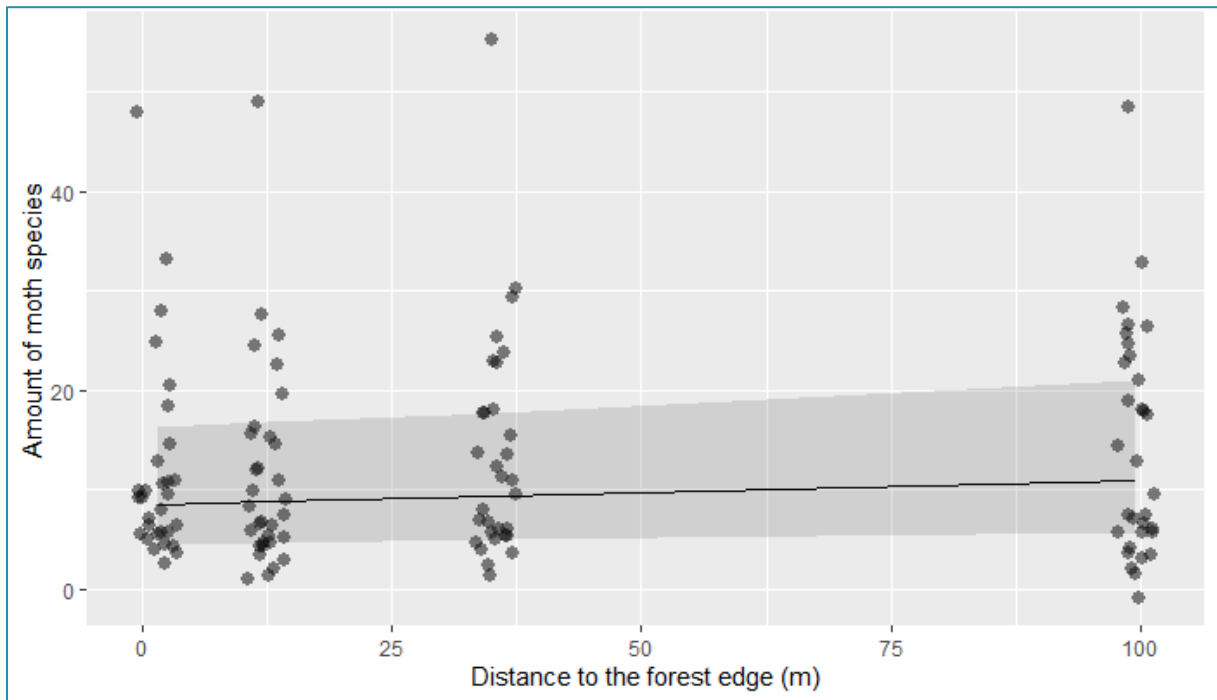


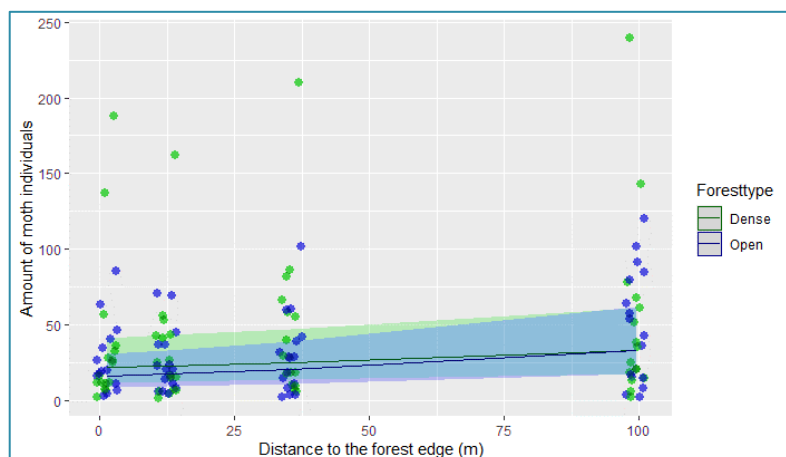
Figure 11: The edge-to-interior gradient found for moth species richness. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter.

Moth activity-density

Moth activity-density was significantly correlated with both management type and edge distance, moreover there was a significant interaction effect (Figure 12). A higher moth activity-density was found further away from the edge and in dense forests. The edge-to-interior gradient is stronger for open forests ($\text{Chi}^2 = 13$, $P < 0.001$).

Figure 12: The edge-to-interior gradient found when modelling moth activity-density.

The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter. There was a lot of variation, but when correcting for the correct error structure, this trend was significant. The variation is caused by the large difference between periods.



Moth families

A stronger gradient was expected for less mobile species, so the effect of edge distance, forest management and the interaction was tested for each family with more than 100 observations, these families from most caught to least caught are Geometridae with 1902 individuals consisting of 115 species, followed by Noctuidae with 1005 individuals consisting of 79 species, Erebidae with 909 individuals consisting of 34 species, Drepanidae with 504 individuals consisting of 12 species and Notodontidae with 248 individuals consisting of 11 species. Species from the families Hepialidae, Lasiocampidae, Limacodidae, Nolidae and Sphingidae were also caught, but only in very small amounts, so these families were not analysed separately.

Geometridae

When analysing moth species richness from the family Geometridae over all periods, effects of edge distance and forest management were found. The interaction was nonsignificant so left out of the model. More Geometridae species can be found in dense forests and more in the core (edge distance: $\text{Chi}^2 = 10$, $P < 0.01$; forest management: $\text{Chi}^2 = 4.7$, $P = 0.03$) (Figure 13: Left). For Geometridae activity-density there was an interaction effect between management type and edge distance. The same response is found as for the species richness, but here the gradient is stronger in open forests ($\text{Chi}^2 = 26$, $P < 0.001$). There is almost no difference between open and dense forest cores (Figure 13: Right).

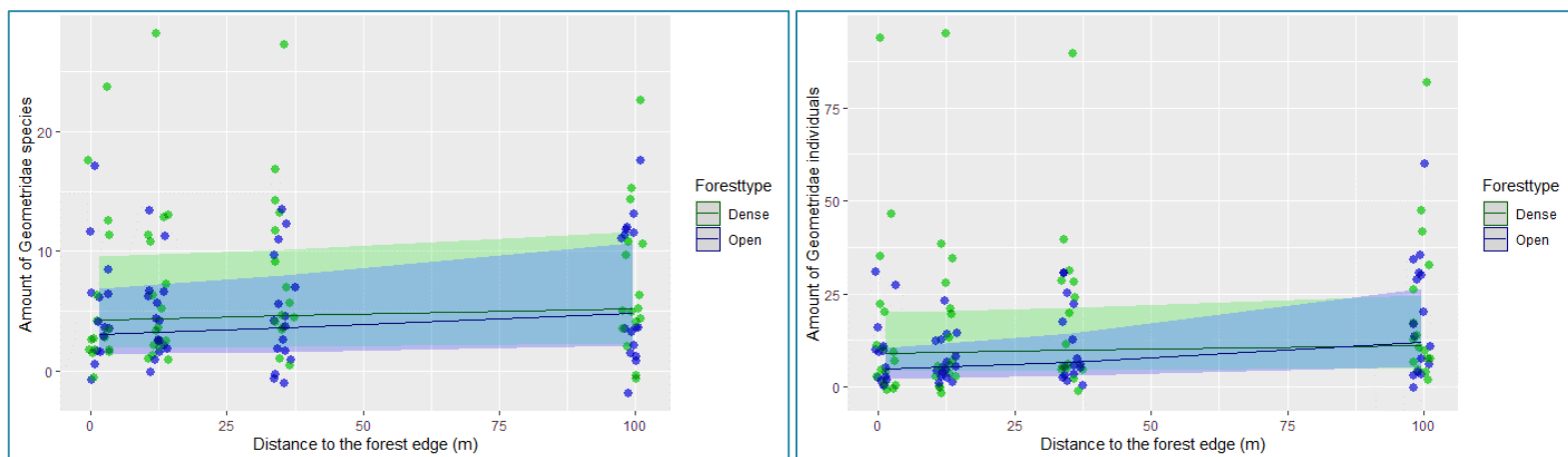
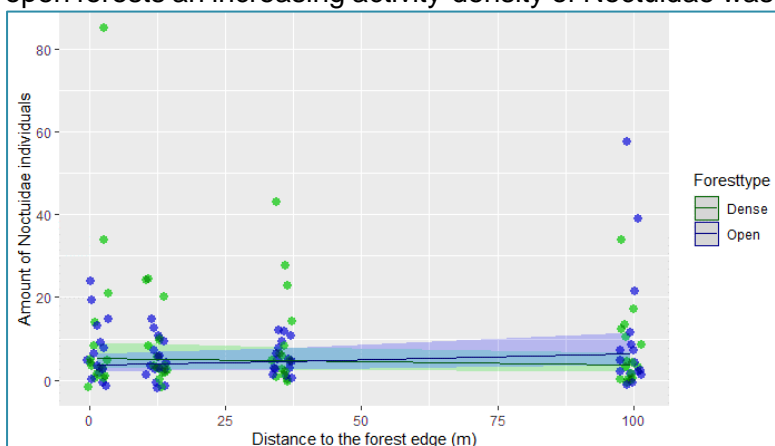


Figure 13: Responses to the edge-to-interior gradient and forest management of species richness and activity-density of Geometridae. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter. Left: Geometridae species richness. Right: Geometridae activity-density.

Noctuidae

For Noctuidae species richness no significant effects of edge-to-interior gradient or forest management type were found. When looking at the occurrence of Noctuidae activity-density over all periods, a significant interaction between forest management and edge distance was found ($\text{Chi}^2 = 21$, $P < 0.001$) (Figure 14). The gradient differed for open and dense forests. In open forests an increasing activity-density of Noctuidae was found towards the forest core. For



dense forests this gradient was reversed, with a higher activity-density at the forest edge.

Figure 14: The edge-to-interior gradient found when modelling Noctuidae activity-density. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter.

Erebidae

Forest management has no impact on the occurrence of Erebidae species richness, but a slight edge-to-interior gradient is found ($\text{Chi}^2 = 4.5$, $P = 0.03$). There were more Erebidae species near forest cores (Appendix IV: Erebidae gradient). When analysing Erebidae activity-density, only a significant effect of edge distance was found. Erebidae were found more in forest cores. The difference between edge and core was very small, and the assumptions were not completely met. For mixed models a more conservative cut-off value of 0.001 for a Shapiro test of normality is often used. The P-value is 0.0001704, this means that even with this more conservative P-value there was a violation of the assumption of normality.

Drepanidae

The assumption of normality of the residuals in the models on Drepanidae (for both species richness and activity-density) was not met, although there were quite some observations of Drepanidae. The found effect of edge distance and management cannot be confirmed.

Notodontidae

An edge-to-interior gradient was found on the occurrence of Notodontidae species, with a higher species richness near forest cores ($\text{Chi}^2 = 9.9$, $P < 0.01$). Here as well, the difference in moth occurrence between edge and interior was small. When modelling the activity-density of Notodontidae, the assumption of normality of the error structure was violated. The results of the model are not interpreted.

Forest specialists & generalists

It was expected that forest specialists occur more in forest cores. When analysing richness of moth species that have a high forest affinity based on caterpillar preference, no significant differences between open and dense forest were found, but there was a significant edge-to-interior gradient ($\text{Chi}^2 = 20$, $P < 0.001$). At the forest core an extra 3.1 species were present compared to the edge. When looking at the activity-density of forest specialist species, a significant interaction between edge distance and management type was found ($\text{Chi}^2 = 6.3$, $P < 0.05$) (Figure 15: Left). More specialist moths were caught in dense forest cores, with a slightly stronger gradient in open forests. When analysing the more generalist species richness (species with affinity for more open habitat, but caught in forests) no significant differences were found. However, when modelling the generalist moth activity-density, there was a significant interaction effect ($\text{Chi}^2 = 11$, $P < 0.001$) (Figure 15: Right). Also in this case, more moths were found at the cores with a stronger gradient in open forests. In the end most generalist moths were found in open forest cores, whereas most specialist moths were found in dense forest cores.

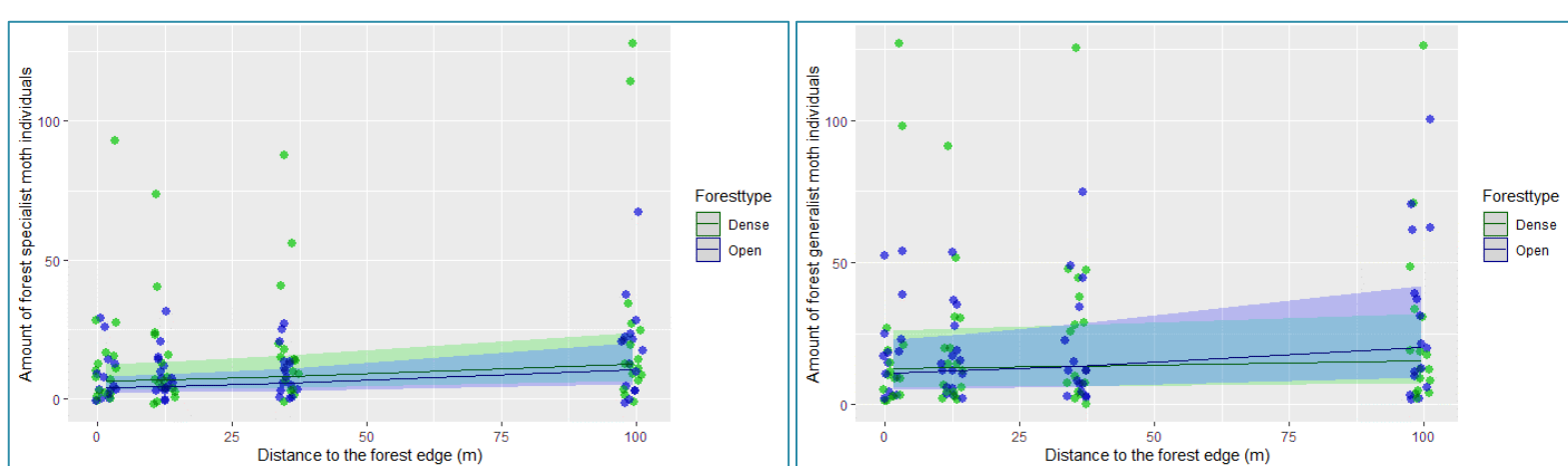


Figure 15: The edge-to-interior gradient found when modelling forest specialists and generalists. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter. Left: Forest specialist moth activity-density. Right: Forest generalist moth activity-density.

Moth communities and their environment

An overview of all the parameters included in the final models can be found in Table 4.

Table 4: Overview of all the final models on the moth communities and their environment that are further discussed in the results.

	Dependent variable	Independent variable	Significant	R ² m	R ² c
Forest structure	Species richness	Openness of the canopy (LIDAR)	− 0.657	0.007	0.881
	Activity-density		− 1.229	0.015	0.977
	Species richness	Canopy height	+ 0.040	0.040	0.891
	Activity-density		+ 0.092	0.109	0.981
	Species richness	Plant area index	+ 0.069	0.021	0.887
	Activity-density		+ 0.115	0.035	0.978
	Species richness	Foliage height diversity	+ 0.892	0.044	0.893
	Activity-density		+ 1.613	0.082	0.980
Forest cover	Species richness	500 meter scale	+ 0.010	0.039	0.883
	Activity-density		+ 0.055	0.330	0.989
Plant diversity	Species richness	Overall plant species richness	X	/	/
	Activity-density		− 0.027	0.021	0.976
	Species richness	Forest specialist plant species richness	X	/	/
	Activity-density		− 0.018	0.003	0.975
	Species richness	Phylogenetic species richness	X	/	/
	Activity-density		X	/	/
Temperature	Species richness	Average temperature (microclimate)	+ 0.101	0.299	0.865
	Activity-density		+ 0.230	0.577	0.983
	Species richness	Minimum temperature (microclimate)	+ 0.092	0.217	0.862
	Activity-density		+ 0.236	0.524	0.983
	Species richness	Maximum temperature (microclimate)	+ 0.094	0.227	0.873
	Activity-density		+ 0.071	0.270	0.971
	Species richness	Growing season temperature	− 0.316	0.033	0.893
	Activity-density		− 0.187	0.057	0.979

In the right column is indicated if the model was significant or not. A red cross indicates the model was not significant, followed by the model estimate. A green '+' or '-' indicates significant results. '+' means a positive correlation, '-' indicates a negative correlation.

Simple models

Each parameter is measured along the same environmental gradient. The analyses of the edge-to-interior gradient and the effect of management type on the environmental parameters can be found in Appendix III. Since all these parameters were correlated with management type and edge distance, it is hard to disentangle the effect of the parameter and the effect of management and edge-to-interior gradient. None of the following environmental parameters can be confirmed as the cause of moth occurrence, but either way it gives an indication of the preference of moths for a particular forest environment.

Forest structure

Openness of the canopy

The canopy openness did not show significant results in the analysis on both species richness and activity-density (Figure 16). More moths (both species richness and activity-density) could be found in places with a denser canopy (Species richness: $\text{Chi}^2 = 5.2$, $P < 0.05$; activity-density: $\text{Chi}^2 = 56$, $P < 0.001$).

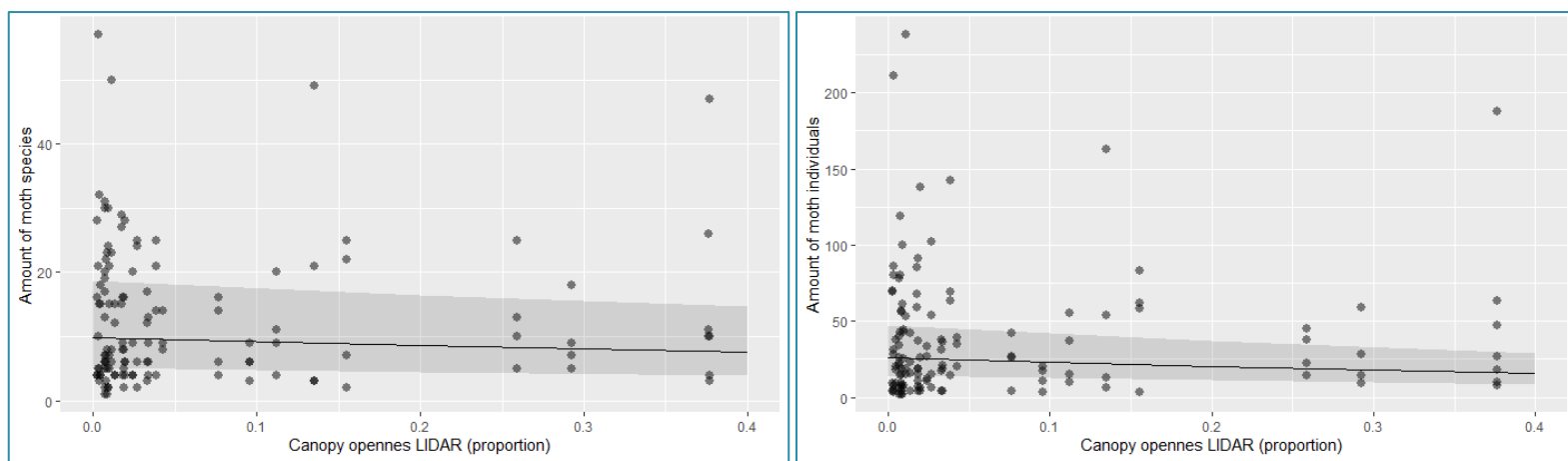


Figure 16: Moth communities in function of Canopy openness. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Moth species richness. Right: Moth activity-density.

Canopy height

Moth occurrence in forests differed between different canopy heights, more moths (both species richness and activity-density) are found in forests with a higher canopy (Species richness: $\text{Chi}^2 = 5.4$, $P < 0.05$; activity-density: $\text{Chi}^2 = 55$, $P < 0.001$). The gradient appears to be quite strong for moth activity-density, with on average in every trap ~1 extra individual caught per meter extra canopy height (Figure 17).

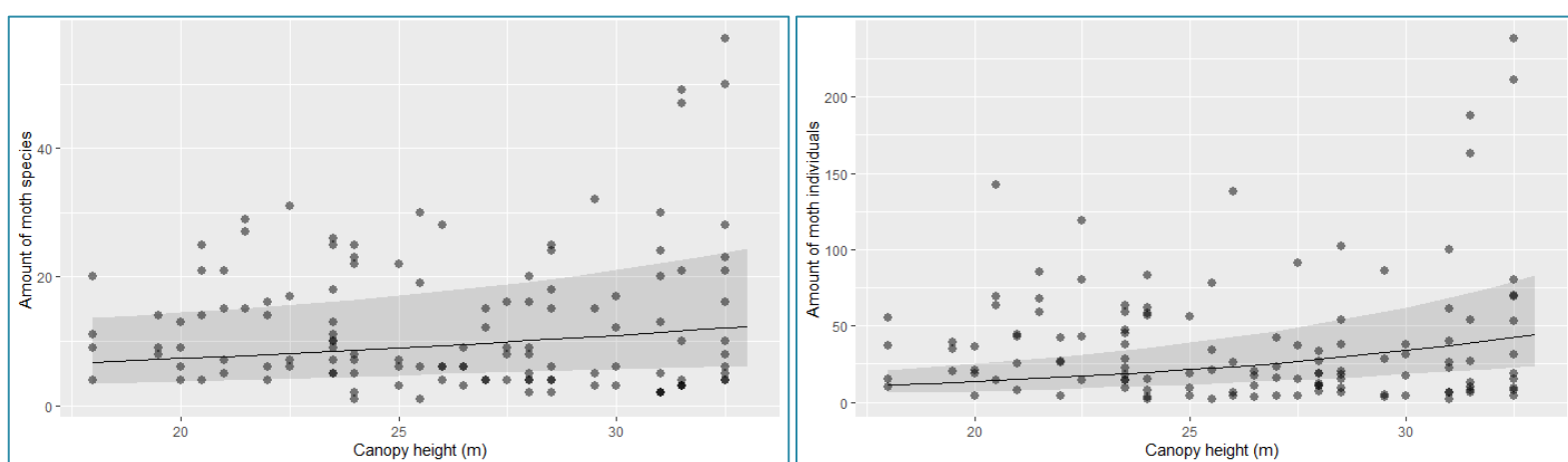


Figure 17: Moth communities in function of Canopy height. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Moth species richness. Right: Moth activity-density.

Plant area index & foliage height diversity

Moths occurred more at places in forests where there was a higher plant area index. The results were significant for both species richness and activity-density (Species richness: $\text{Chi}^2 = 14$, $P < 0.001$; activity-density: $\text{Chi}^2 = 113$, $P < 0.001$) (Figure 18: Upper). When looking at the foliage height diversity, a significant link was found with both moth species richness and moth activity-density (Species richness: $\text{Chi}^2 = 13$, $P < 0.001$; activity-density: $\text{Chi}^2 = 115$, $P < 0.001$). More moths can be found when there was a higher foliage height diversity (Figure 18: Lower).

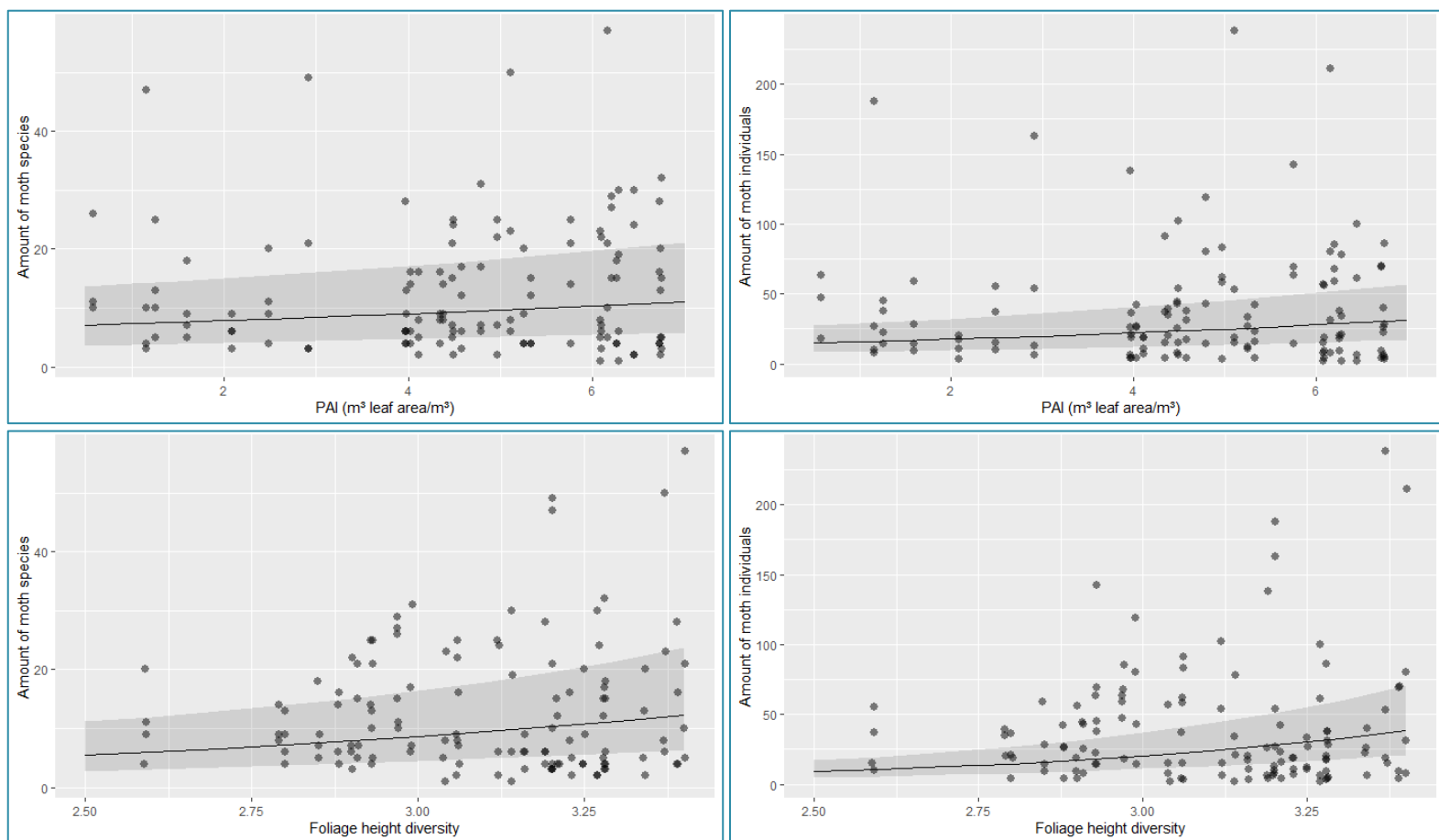


Figure 18: Effects of forest structure on moth communities. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Upper: Moth occurrence in function of plant area index. Lower: Moth occurrence in function of foliage height diversity. Left: Moth species richness. Right: Moth activity-density.

Forest cover

The amount of forest in the area did have a significant effect on moth occurrence. Both species richness and activity-density were higher when there was more forest cover in the 500 meter surroundings (Species richness: $\text{Chi}^2 = 5.6$, $P < 0.05$; activity-density: $\text{Chi}^2 = 125$, $P < 0.001$). The effect was strongest for moth activity-density. At the 500 meter scale a doubling in forest cover (from 40% to 80%) results in a sevenfold increase in moth the amount of individuals (Figure 19).

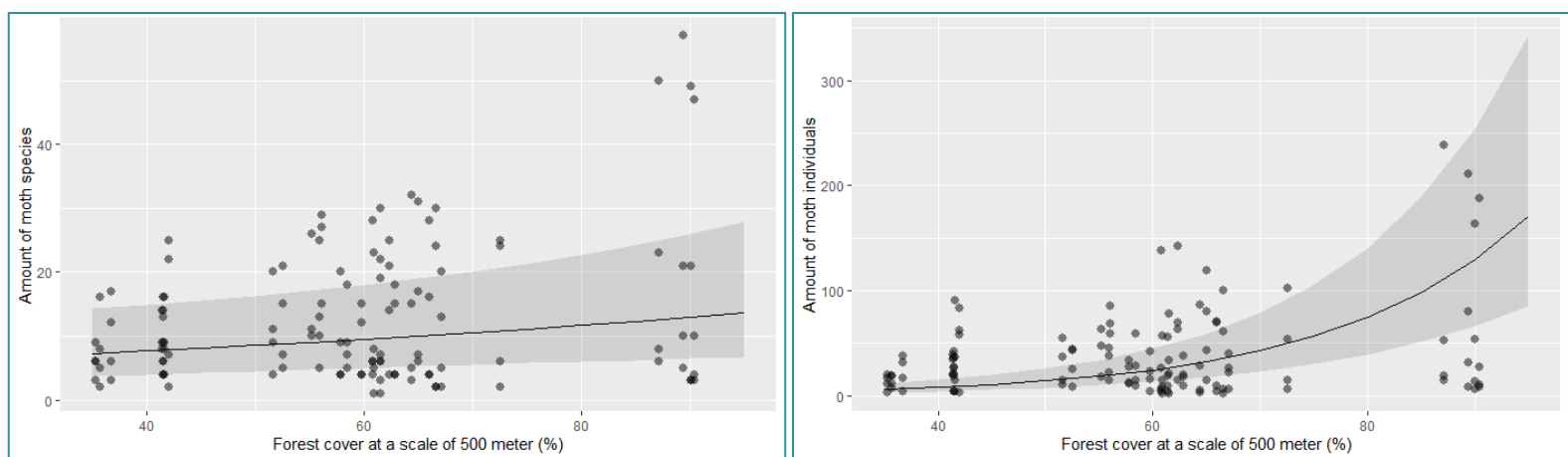


Figure 19: Moth occurrence in function of forest cover in the 500 meter area around the plot. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Moth species richness. Right: Moth activity-density.

Plant diversity

A lot of measures of plant diversity were analysed: plant species richness, forest specialist species richness, phylogenetic and plant species richness.

For the phylogenetic plant species richness, no link was found with moth occurrence, neither for the species richness and activity-density. For plant species richness, only significant effects were found when looking at moth activity-density ($\text{Chi}^2 = 59$, $P < 0.001$) (Figure 20: Left). Here, a higher moth activity-density was found with less plant species richness. The same result is obtained when analysing the forest specialist plant species richness ($\text{Chi}^2 = 4.0$, $P < 0.05$) (Figure 20: Right). The trend was smaller in comparison in the model looking at general plant species richness.

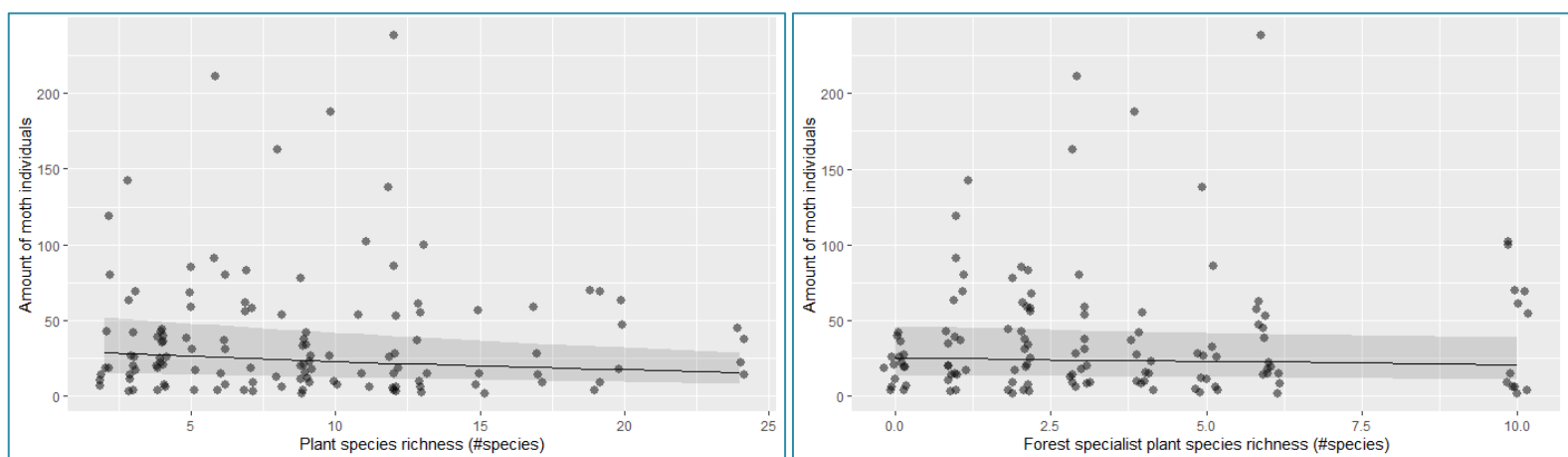


Figure 20: Effects of plant diversity on moth communities. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Moth activity-density in function of plant species richness. Right: Moth activity-density in function of the forest specialist plant species richness.

Temperature

When comparing microclimatic data with moth species richness and activity-density we found significances with average temperature, minimum temperature and maximum temperature. All models showed a similar pattern. The model with average temperature gave the best fit with R^2 -values of 0.86 for the species richness model and 0.98 for the activity-density model and the highest slope. More species richness ($\text{Chi}^2 = 19$, $P < 0.001$) and activity-density ($\text{Chi}^2 = 56$, $P < 0.001$) were found with higher temperatures (Figure 21).

Also growing season temperature had a significant effect on both moth activity-density ($\text{Chi}^2 = 46$, $P < 0.001$) and species richness ($\text{Chi}^2 = 6.6$, $P < 0.05$). Here more moths were found on places where the temperature was on average lower during the whole sampling season.

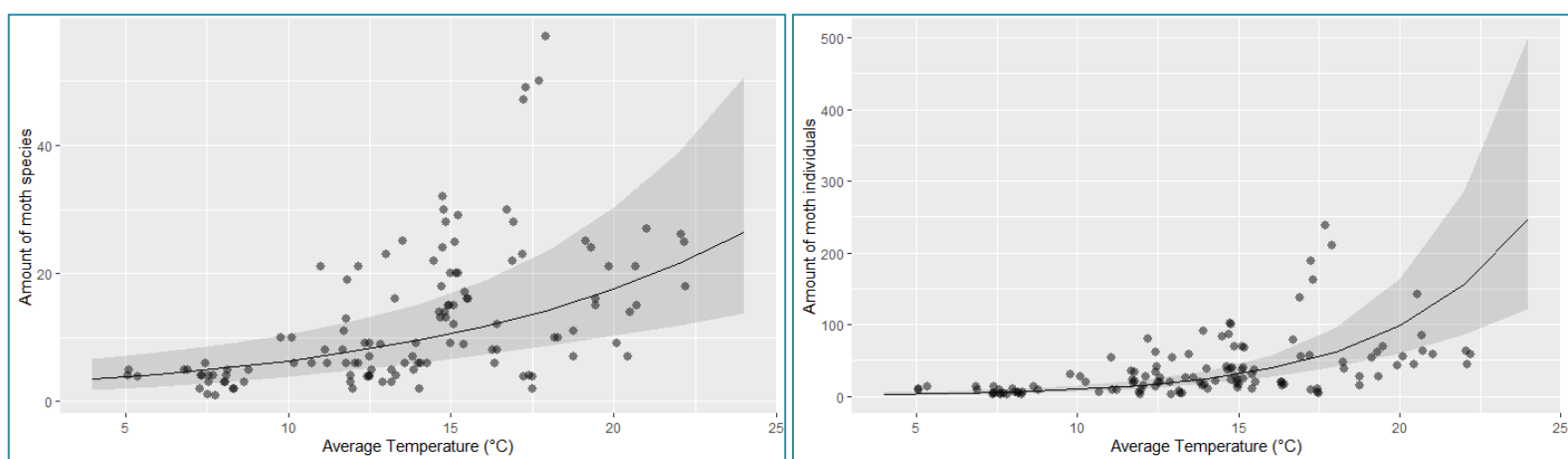


Figure 21: Effects of average temperature on moth activity-density. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Moth species richness. Right: Moth activity-density.

Model selection

A model selection was done on all the environmental parameters using the dredge function. No interaction effects were included, since there are more than ten parameters to be tested. The species richness model looks like this:

```
glmer(Species~CanOpen+Forcov_500+CanHei+PAI+PlantSR+FHD+
Plant_specialistSR+Mean_Temp + (1|Period)+(1|Period:Region)+
(1|Period:Region:Transect), na.action="na.fail", family=poisson,
data=Environment_All.no_NA)
```

Here the best model included forest cover, average temperature and plant area index with an AIC of 669.9. The second best model did not include plant area index, but foliage height diversity, with an AIC of 670.2. These 4 parameters were selected and in a second step the parameters with a lot of NA-values were included, these are phylogenetic species richness and growing season temperature. The dredge-function cannot handle NA-value, so the second model was selected manually and looked like this:

```
glmer(Species~Forcov_500+PAI+FHD+Plant_phylogeneticSR+Mean_Temp+
Grow_season_Temp +(1|Period)+(1|Period:Region)+(1|Period:Region:
Transect), na.action=na.exclude, family=poisson, data=Environment_All)
```

In the end it turned out that these two added parameters and foliage height diversity were not significant. Average temperature, plant area index and forest cover had the most important effect on moth species richness (Table 5). A higher moth species richness was found in forests with a higher average temperature, plant area index and more forest cover in the 500 meter area around the exact location. The average temperature had the highest slope in the final model after the model selection procedure, so this parameter is linked with the biggest increase in moth species richness.

Also moth activity-density was analysed with a model selection function. The same model as for the moth species richness was used to start. The first automatic selection returned a final best model with an AIC of 1126.3 including forest cover, average temperature, foliage height diversity and forest specialist plant species richness as independent variables. In a second step the two parameters with a lot of NA-values were added to this model and manually selected. In the end a model with significances for forest cover, foliage height diversity, forest specialist plant species richness and average temperature was obtained (Table 5). More moth individuals were caught with higher values of these parameters. Average temperature and forest cover showed the biggest slope. Foliage height diversity and forest specialist plant species richness had a rather small impact, with effect sizes that were three and five times lower respectively compared to the other parameters (Table5: effect size).

Table 5: Significant parameters and effect sizes after the model selection procedure.

	Independent variables in final model	Effect size (standardised)	95% CI	Chi ² -value	P-value	R ² m	R ² c
Species richness	Forest cover at 500 meter scale	0.17	[0.06, 0.29]	8.3	< 0.01	0.321	0.860
	Average temperature	0.39	[0.24, 0.55]	26	< 0.001		
	Plant area index	0.07	[0.00, 0.14]	4.2	< 0.05		
Activity-density	Forest cover at 500 meter scale	0.84	[0.66, 1.03]	78	< 0.001	0.527	0.990
	Average temperature	0.68	[0.40, 0.97]	22	< 0.001		
	Foliage height diversity	0.24	[0.17, 0.30]	52	< 0.001		
	Forest specialist plant species richness	0.14	[0.08, 0.20]	19	< 0.001		

In the table all significant parameters after the model selection procedure are presented with their effect sizes and 95% confidence interval of the effect sizes. The Chi²-values and P-values were calculated by an ANOVA on the final model.

Multivariate analysis

A principal component analysis was used to visualise the data. In Figure 24 an overview, using data lumped over all periods, is shown. Figure 25 gives the more detailed differences in moth communities between different periods, regions, forest management types and distances from the edge.

PCA with data lumped over periods

When lumping the data over all periods, the difference between regions was very large (Figure 22). Within transects, the plots towards the forest core tended to be different from those at the edge. The environmental parameters revealed that the forest cover was much bigger in Compiègne (dense forest), also canopy height, foliage height diversity and plant area index was higher in this region. Other environmental parameters had a smaller potential impact on moth communities. The variation in moth communities seemed to increase towards the forest core. There was also a higher variation in moth communities in dense forests.

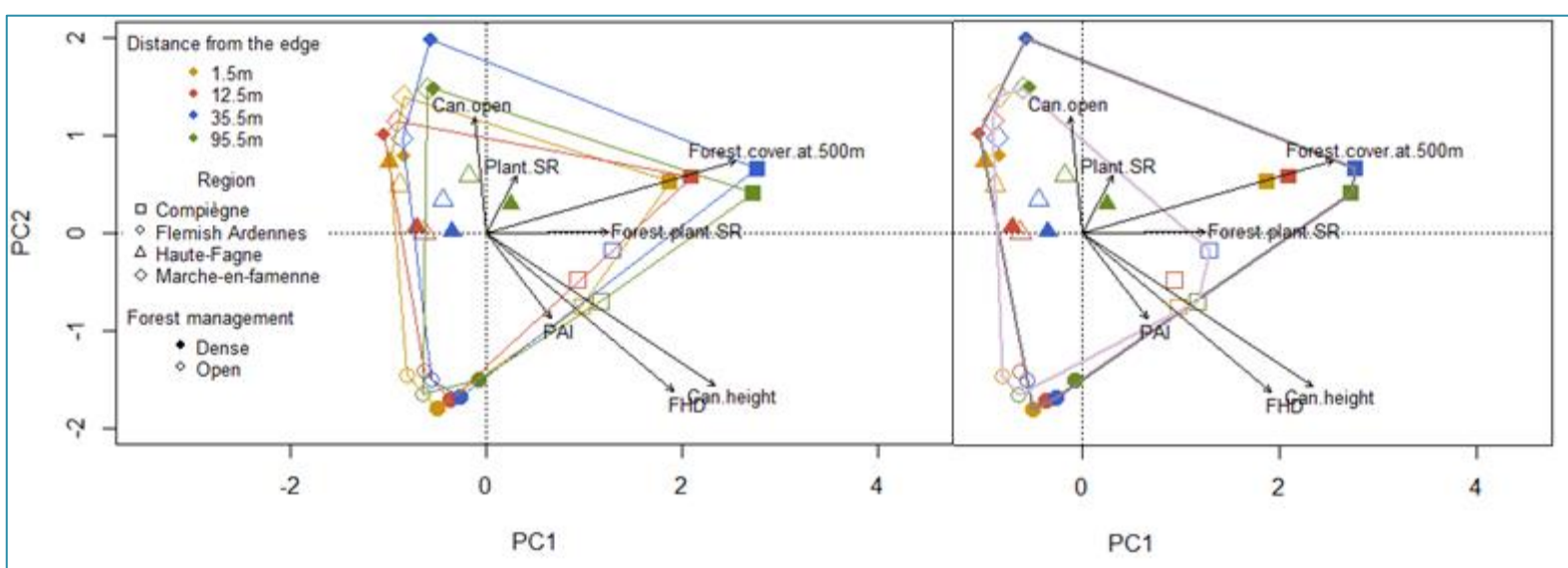


Figure 22: PCA of the moth communities when the data is lumped over all periods. Each point represents a plot in a particular transect. Left: The coloured envelopes include all the data points at that specific distance from the edge. Right: the pinkish envelopes include all points from that particular forest type, with the darker pink for the dense forests. Differences between regions were very large. Other differences were more subtle: forest cores and dense forests showed a little more variation in moth communities. Forest cover, foliage height diversity and canopy height were larger in Compiègne, other environmental parameters had a lower potential impact on moth communities, since the arrows are shorter.

PCA with data per sampling point

When the data are not lumped per period, the differences were less clear. There was a huge variation between periods (Figure 23: Upper left), since different moth species occurred at different moments during the year. The environmental parameters fitted on these graphs did not explain the variation in moth communities very well. Only during the first and second sampling period these environmental parameters could potentially explain part of the variation in moth communities. The sampling period in June was strongly correlated to the first PC axis, the sampling period in September had a strong correlation with the second PC axis (Figure 23: Upper left). But the axes did not explain much of the variation. The first axis explained 23.27% of the variation and the second axis 14.55%. The explanation for this is that in June most moths were caught, while in September and October a completely different set of moth species were trapped, resulting in very different moth communities, however with smaller numbers of species and individuals. Secondly, the variation between regions was still visible (Figure 23: Upper right). All this variation, that is not the main goal of this study, masked the real forest

management effect and edge-to-interior gradient. Although our models confirm these parameters did have a difference in moth activity-density and species richness. The variation in moth communities was larger in dense forests (Figure 23 Lower left). There was also a lot of variation in moth communities at all edge distances (Figure 23: Lower right), but in general there was a trend towards more variation in moth communities towards the forest core.

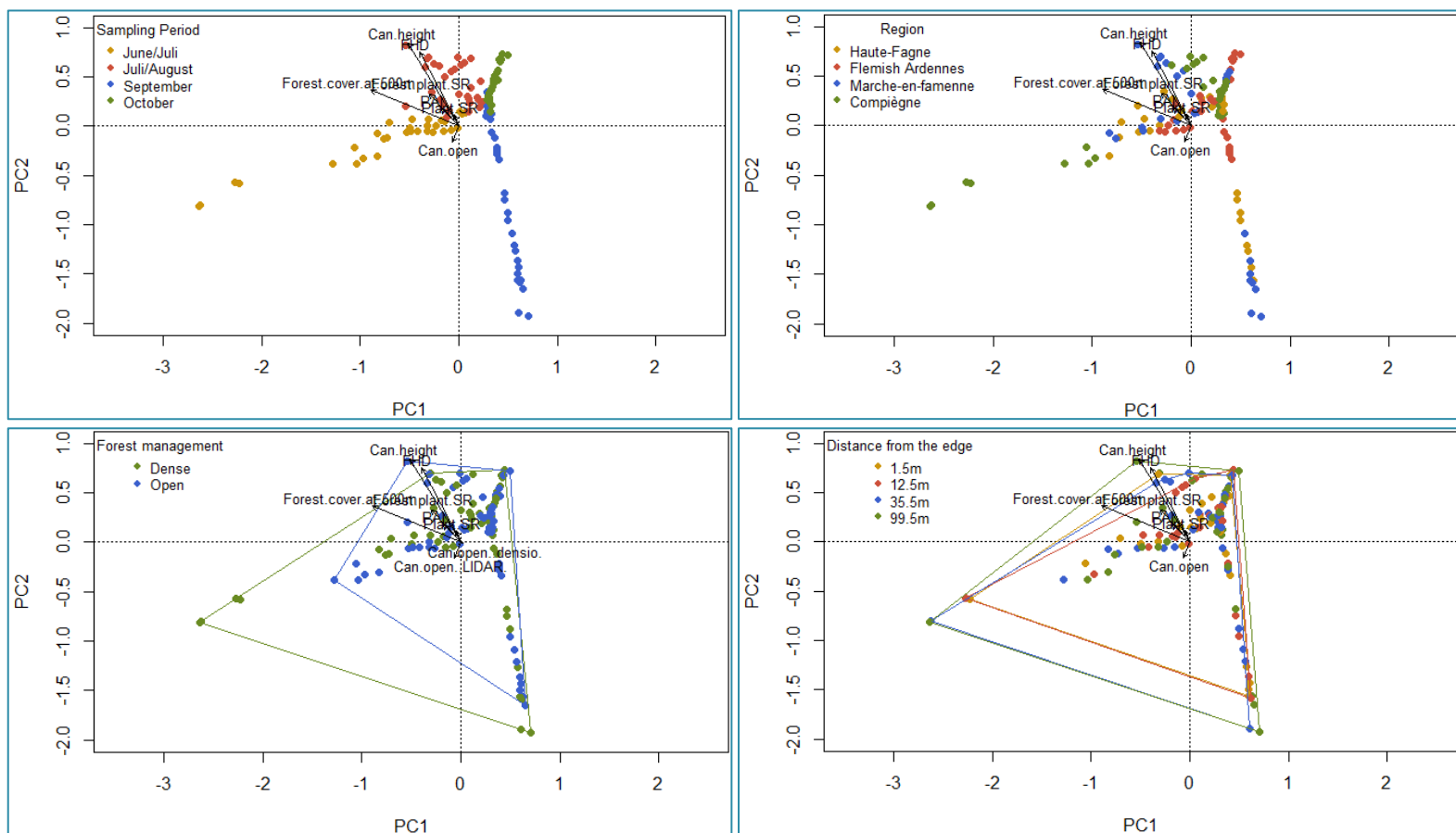


Figure 23: PCA of moth communities.

Each point represents a sampling point, being a plot in a particular transect during a particular period. Upper left: Each colour represents a different sampling period. These periods are clustered together, thus differed a lot in moth community. Upper right: Each colour represents another region. Regions clearly differed from each other. Lower left: The different colours represent different forest management types. The envelopes include all the data points for that particular forest management type. There was more variation in moth communities in dense forests. Lower right: The different colours represent different edge distances. The envelopes include all the data points at that particular distance from the edge. There tended to be a little bit more variation in moth communities that occurred further away from the forest edge.

Temperature PCA with data per sampling point

Since the temperature had some missing data points, because some temperature sensors got lost or stolen during the sampling season, these parameters were plotted in a separate PCA (Figure 24). The points on the PCA biplot are the same points as plotted in Figure 23, but here some points are lacking. According to this PCA plot, higher temperatures were correlated with the forest core. There was a clear distinction between open and dense forests, with in particular a different moth community during one sampling event in the dense forest in Compiègne. This was a warm night, with huge amounts of trapped moths, which influenced the temperature PCA results. Maximum temperature seemed to be less correlated with this one sampling night. Average temperature gave as expected an average response between maximum and minimum temperature. The effect of growing season temperature was lower, but it explained other variation than microclimate. The sampling points that showed a strong correlation with the second PC-axis had a colder growing season temperature, but a higher maximum microclimatic temperature during the samplings.

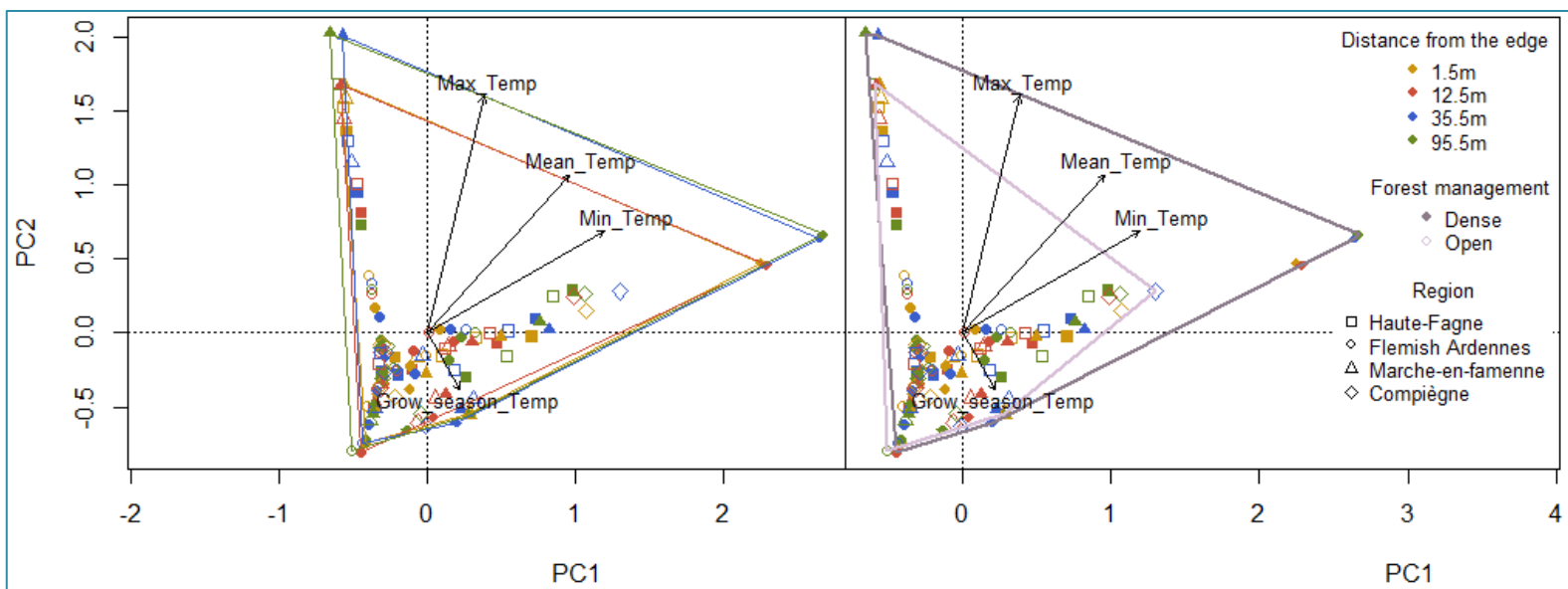


Figure 24: PCA of moth communities fitted with temperature measures. Each point represents a sampling point, being a plot in a particular transect during a particular period. Each colour represents a different distance from the edge, open forests have open symbols and dense forest are depicted with closed symbols. Left: The coloured envelopes include all the data points at that specific distance from the edge. Right: the pinkish envelopes include all points from that particular forest type, with the darker pink for the dense forests. There was more variation deeper into the forest and in dense forests. Microclimate had a stronger effect on moth communities compared to growing season temperature.

Discussion

Moth communities along edge-to-interior gradients and management type

Moth species richness and activity-density

There was an effect of edge distance and forest management type on moth species richness and activity-density, with more moths near the forest cores and in dense forests. This contrasts with our main hypothesis, where we expected more moths in open forest edges and a stronger gradient in dense forests. Our hypothesis was based on studies of other taxa like plants (Govaert et al., 2020; Łuczaj & Sadowska, 1997) and fungi (Łuczaj & Sadowska, 1997) where more species occurred in open forest edges. Also for arthropods, a lot of studies found that there is a higher species richness or abundance at the forest edge (Barbosa et al., 2005; Didham et al., 1996; Erdős et al., 2019; Fowler et al., 1993; Magura, 2002) or in open forests (Grushecky et al., 1998). However, for moths little is known about their exact occurrence along forest edges. It is known that a lot of moth species prefer forest habitat (Potocký et al., 2018) and opposed to most studies on arthropods, some studies suggested that the highest moth diversity and abundance would be found in large, unfragmented, compact woodlands with little edge effects (Fuentes-Montemayor et al., 2012; Lintott et al., 2014). Our forests were also mainly located next to intensive agricultural fields and meadows (except Marche-en-Famenne). These agricultural fields are generally species poor (Ekroos et al., 2010; Fox, 2013; Mangels et al., 2017), thus in our study, less inflow of matrix species could be possible. We found that some forest species did occur at the edge, but species from the matrix were mostly lacking. Only 15 species (83 individuals in total) with an affinity for open landscapes were caught during the whole sampling campaign. There was almost no species loss towards the forest edge when looking at moth species that were caught more than 20 times. Only *Phalera bucephala* (24 observations) did not occur at the edge plot.

Whereas moth species richness only showed an edge-to interior gradient, moth activity-density also differed significantly between open and dense forests. This was not significant for species richness since both forest types shared the same species pool. Species that were caught in smaller numbers were mostly caught at one particular transect and thus did not necessarily indicate species loss due to management type. The fact that only differences were found between open and dense forests for activity-density and not for species richness could also be caused by one species that occurred near the forest core and was caught in large amounts (i.e. *Cymatophorina diluta*). This forest species is linked with oak trees and it is a rare species in Belgium that can be locally very abundant (Waring & Townsend, 2018, p. 53). This species was only caught during the third sampling period in Marche-en-Famenne and the Haute Fagnes. 800 individuals of this species were caught, whereas in total 4743 individuals were caught during the complete sampling campaign, consisting of 264 different species (Appendix V). As a result, *Cymatophorina diluta* had a large impact on the analyses, but with the correction for period and location, this species cannot be the only reason for the difference between open and dense forests, since it was not caught at all locations, nor periods. Another species that can give a skewed representation of overall moth activity-density is *Zanclognatha lunalis*. This rare moth was within the 10 most abundant species. It was caught in three of the four regions. Only in Flanders none were caught. Although abundant in our research, this species is declining and in the Netherlands it is indicted as severely threatened on the red list (*De Vlinderstichting | Zanclognatha lunalis*, 2020; Waring & Townsend, 2018, p. 204). On the other hand, the larger amount of data on activity-density resulted in more significances compared to species richness. With a more extensive sampling, it could be expected that

differences in species richness will also be found between open and dense forests. This difference is already slightly indicated in the total amount of species we caught in each forest type. We trapped 217 species in dense forest compared to 199 species in open forests.

Moth activity-density patterns per management type and along edge-to-interior gradients are linked together. Dense forests edges were more resembling to open forest cores, when looking at the environmental parameters (Appendix III). So if more moths occur in forest cores, they should prefer dense forests, instead of open forests as was hypothesized. Dense forests have (like forest cores) less canopy openness, a higher plant area index, more forest cover around them (in our trapping set-up) and a lower plant diversity (Govaert et al., 2020). The significant interaction effect between management type and edge distance on the activity-density of moths shows that the gradient is stronger in open forests. In dense forests, the forest edge has lower influence of environmental effects of the matrix around it (Meeussen et al., 2020), so the difference between edge and core is smaller. In open forests, there is a larger difference between edge and core, which results in a stronger edge-to-core gradient for moth species that prefer core habitat.

Another factor influencing the results could be related with the trapping set-up. We sampled on a logarithmic edge-to-interior gradient, because the biggest environmental differences were expected closer to the edge. Along this exact gradient, all the environmental parameters were available. The poles with sensors were fixed, thus guaranteed that we sampled the exact same plot during each period. The drawback of this design is that the first two plots at the forest edge were only 11 meter away from each other, while our low intensity lamps had a moth attraction radius of less than 10 m (Truxa & Fiedler, 2012). This means that there was a possible overlap between these two traps. This could result in a dilution of the amount of moths found at the forest edge, only because the traps were standing close to each other. This should be kept in mind when interpreting the results. After comparing the plots as discrete variable, a significant difference for moth activity-density was found between plot three and four, indicating that the detected gradient is not only caused by this trapping artefact, but that there is an actual moth gradient with more moths near the core. For moth species richness, plot three and four were not significantly different.

Moth families

The families with the clearest gradient and difference in management type were the Geometridae and Noctuidae. For these families we had enough data available and a lot is known about their mobility. Noctuidae are far more mobile compared to Geometridae (Berwaerts et al., 2002; Betzholtz & Franzén, 2011, 2013; Rydell & Lancaster, 2000). The hypothesis stating that there is a stronger gradient for species from less mobile families like Geometridae was confirmed. More Geometridae were found at forest cores and in dense forests. For Noctuidae this pattern was less clear and seemed to differ between differently managed forests, with an increase in Noctuidae activity-density towards the core in open forests, but a decrease in dense forests. It is known that Noctuidae have a lower attraction rate to light traps compared to Geometridae and Erebidae (Merckx & Slade, 2014), so these could be underrepresented. The high mobility of Noctuidae is a possible explanation for the inverse gradient in open and dense forests. A study in northern Belgium found a vertical moth stratification with more mobile species like Noctuidae occurring more at the canopy level and less mobile species like Geometridae being more restricted to the herb layer (De Smedt et al., 2019b). Although the vertical stratification should be different from the horizontal one, some patterns were expected to be similar. For instance, in open forests, these Noctuidae could easily fly from further away towards the traps, since less plant material blocks the light. At dense forests edges, light was less blocked by plant material compared to the dense forest cores, potentially resulting in more Noctuidae trapped at the forest edge. Also, inflow of

non-forest moths from the matrix, like *Agrotis* species, could be larger for Noctuidae because of their higher mobility.

Forest specialists & generalists

Forest specialist species were caught more in dense forests and forest cores as could be expected. Generalist moths also occurred in larger numbers at forest cores, however these preferred open forests. Either way, forest cores were beneficial for both forest specialist and generalist moths. Specialist insect species need core habitat (Botham et al., 2015; Mangels et al., 2017), and are more affected by habitat fragmentation and degradation (Devictor et al., 2008), this also holds for moths (Slade et al., 2013). For generalist species this should be less important, although we found most generalists in the forest cores. Forest patches need to be larger than 5ha and have forest cores further than 100 meter from the edge to sustain populations of forest specialists (Slade et al., 2013), but based on our study, this can also be beneficial for generalists.

The differences in moth occurrence between management types showed that open forests had a lower activity-density of forest specialist moth species, while the number of generalist moths increased. Thus, management has an impact on moth communities. Where forest specialists cannot thrive, generalists replace them (Mangels et al., 2017). In this research, dense forests had more forest in the surroundings compared to open forests (Appendix III: Forest cover). So the impact of forest cover can be partly reflected in the differences between management types. We can conclude that there is a difference in moth specialist and generalist communities in differently managed forest edges. More research needs to be done to know whether this difference is caused by forest management, forest cover or another (environmental) parameter.

In general, species with a high affinity for forests were caught more in dense forests, but all species with a particular affinity for dense forests, indicated with “wg” (Dorow et al., 2020), did occur more in open forests. From these species with an affinity for dense forests, 17 individuals were caught in open forests and only 6 in dense forests. These comprised four species: *Ecliptopera silaceata*, *Euphyia biangulata*, *Parascotia fuliginari* and *Pungeleria capreolaria*. Only the first one was also caught in dense forests (6 individuals), but still in lower amounts compared to open forests (12 individuals). In our study these species, that would prefer dense forests according to Dorow et al. (2020), seemed to prefer open forest cores. This remarkable pattern can be explained: Dorow et al. based their affinities on caterpillar host plants, which do not need to occur in the exact same habitat as the moths themselves. For instance, *Ecliptopera silaceata* caterpillars are found on *Impatiens noli-tangere* (Wagner, 2021). This is a plant species that can be found in humid, dense forests (Hatcher, 2003). However according to literature *E. silaceata* moths occur near forest edges or at open patches within forests or even in dunes and heather (Wagner, 2021; Waring & Townsend, 2018, p. 87). Thus, it is not surprising that we found them more in open forests. *Euphyia biangulata* caterpillars occur on *Stellaria sp.* in open, moist woods (Wagner, 2021; Waring & Townsend, 2018, p. 98). So in Belgium and northern France, this species should get classified within the group with an affinity for open forests instead of dense forests. *Parascotia fuliginari* is also a species that can occur in moist forests and heather (Waring & Townsend, 2018, p. 200), this is not necessarily a species for dense forests. Also in this case the classification within the group with an affinity for dense forests should be adapted to an affinity for open forests or forests in general in Belgium and northern France. *Pungeleria capreolaria* is a southern species that is seen as a climate species in Belgium (*De Vlinderstichting | Pungeleria capreolaria*, 2020). Populations of these species are occurring more and more northwards and only recently appeared in Belgium (Hackray, 1979). This species is dependent on *Abies sp.* (Waring & Townsend, 2018, p. 154),

which mostly form dense forests, but dense forests are not needed for this species to occur (Wagner, 2021).

Moth communities and their environment

Forest structure

We found more moths in forests with a denser canopy. A link can be expected between canopy openness and management type. It turned out that all dense plots in this study had more or less the same canopy openness, but within open forests there were a lot of differences in openness. The four plots with a very high canopy openness were all located in one transect, being the open forest in Marche-en-Famenne. As a matter of fact the LIDAR measures only gave a significant effect of edge-to-interior differences in canopy openness instead of a difference between differently managed forests (Appendix III: Openness of the canopy).

More moths were found in forests with a higher canopy. The canopy height increased from the edge towards the core (Appendix III: Canopy height), this holds for forests in general and not only for the ones that were sampled (Meeussen et al., 2020; Simard et al., 2011). As a consequence, this result cannot be separated from the edge-distance effect. Either moths prefer forests with a higher canopy openness, either they prefer forest cores or either they prefer both.

Plant area index and foliage height diversity were two other important forest structure measures that were positively correlated with moth occurrence. More moths were found with a higher plant area index (i.e. a higher amount of tree and shrub biomass per cubic meter) and with a more diverse vertical distribution of the canopy cover. The plant area index was higher in dense forests and at forest cores (Appendix III: Plant area index & Foliage height diversity). In the same way as for canopy height, this relationship between plant area index and moth occurrence cannot be uncoupled from the edge-to-interior gradient and the effect of management type. The foliage height diversity on the other hand did show a significant relationship with moth activity-density, but did not show any edge-to-interior pattern, nor a difference between forest management types. This environmental parameter was not correlated with other measures that were obtained. Since forest moths mostly prefer trees and shrubs over herbaceous plants (Robinson et al., 2010; Waring & Townsend, 2018), the foliage height diversity could play an important role in determining forest moth occurrence. Also the principal component analysis suggested that foliage height diversity, plant area index and canopy height had a strong effect on moth communities. Canopy height had a similar effect on moth communities as foliage height diversity, so this is probably the reason canopy height was not selected after the model selection procedure. The model selection indicated that foliage height diversity should be a better predictor for macromoth occurrence than canopy height.

Forest structure was an important parameter influencing moth communities, although the effect sizes were much smaller compared to the effect of forest cover and temperature on moth communities. In general, more structural variation, either because of variety in the canopy height or because of more plant area per cubic meter, results in more diverse moth communities.

Forest cover

The effect of forest cover on moth occurrence seemed to be very large. With a doubling of forest cover in the surroundings on a 500 meter scale, a sevenfold of the amount of moth individuals was trapped. The forest cover did get larger when going towards the core, so the edge-to-interior gradient could explain some of these results. Also, after the model selection procedure that included all environmental parameters, forest cover was retained and had a

very strong correlation with moth species richness and activity-density. These results are in line with findings of other studies. New (2004) already stated that habitat loss is a major cause of moth decline. Furthermore, fragmentation has a similar effect on moth occurrence (Slade et al., 2013). Both habitat loss and fragmentation are correlated with forest cover in the surroundings.

The strong increase in moth species richness and moth activity-density with more forest cover is correlated with our results that moths would prefer forest cores. The dense forests that were sampled had a significantly higher forest cover in the surrounding at a 500 meter scale compared to open forests (Appendix III: Forest cover). It is possible that the forest cover in the surroundings explains part of the difference in moths between edge and core and the difference in moths between management types. Also one extreme trapping night during the first sampling period in the dense forest of Compiègne showed us the huge diversity present in large, old forests. The dense forest in Compiègne was located at an internal forest edge, which resulted in a larger forest cover for this transect. This extremely rich sampling can be seen in most graphs as four data points with extremely high values for moth species and individuals. During that sampling night, we caught 800 individuals of 92 different species. In each trap about 200 individuals of 50 species were present. Nowhere else a comparable amount of moths was caught. Moths were dependent on enough forest in the surroundings, no matter when looking at a 500 meter scale, a 250 meter scale (Appendix IV) or the edge-to-interior gradient. The larger the scale, the more the increase in moth species richness and activity-density. All our traps were placed at maximum 100 meter from the edge and 500 meter was our largest scale for forest cover, but it is possible that when looking at even larger scales, this effect increases even more. More research should be done with traps deeper into the forest to see if the amount of moths keeps increasing, or stops further away than 100m from the edge. This way the optimal forest size for moths can be determined. It is expected that the ideal scale lies higher. In Costa Rica moths showed the strongest correlation with forest cover at a scale between 1000 and 1400 meter around the plot (Ricketts et al., 2001). Although the tropical rainforests in Costa Rica are completely different from our Western-European deciduous forests, it would be interesting to look at the effect of forest cover on these scales.

The forest of Compiègne (including both the open and the dense edge) was by far the largest forest we sampled. Here 53 species were caught that were not caught in any other region during our samplings. These comprised eighteen rare and eleven very rare species, which include two species that do not even occur anywhere in Belgium (*Athetis hospes* and *Polyphaenis sericata*). This again indicates that a larger forested area results in a tremendous increase of macromoth species richness.

Plant diversity

The negative relationship between moth occurrence and plant diversity could be explained by the fact that plant species richness was higher at the forest edge (Appendix III: Plant diversity) and moths occurred more in forest cores, independent of each other. This result was probably rather driven by the edge-to-interior gradient, than it was representing an actual negative correlation between plant species richness and moth activity-density. Here we found that plant structure and cover of the canopy layer, rather than plant diversity, played a more important role for moth communities. Although, studies have found tight links between plant species richness and arthropod species richness, especially with herbivores (Welti et al., 2017) and most moth species have a specific tree or shrub species as a host plant (Robinson et al., 2010; Waring & Townsend, 2018), all species that were caught frequently in this research were generalists regarding host plants. Caterpillars of the frequently caught species were found on lichens, leaf litter, various herbs, shrubs, trees, grasses, oak and birch (Waring & Townsend, 2018). As a result, it could be expected that plant species richness of the herb layer did not

have a big influence on moth occurrence. It was striking that forest specialist plant species richness seemed to have a high correlation with moth activity-density after a model selection procedure with all environmental parameters included, although the increase in moths with more forest specialist herbs was small. Possibly, this parameter was selected because the little unexplained variation, showed a slight correlation with this parameter.

Temperature

Microclimate did not show a clear edge-to-interior gradient nor differences between management types (Appendix III: Temperature). Although, there was a large correlation between the amount of caught moth species and individuals and microclimatic temperature, with a strong increase in moths when it was warmer. On nights with an average temperature of 20°C, more than double the amount of moths were caught compared to nights with a temperature of 15°C. However, this result only gave an indication of differences in moth activity between colder and warmer nights, since only active moths are trapped with light traps. The fact that moth activity is higher on warmer nights has been studied extensively (Bartholomew & Casey, 1973; Hanegan et al., 1970; Holyoak et al., 1997; Jonason et al., 2014; Truxa & Fiedler, 2012).

The model on growing season temperature showed a negative relationship with moth occurrence. Even though Compiègne, which had by far the largest amount of moths, had a rather high average growing season temperature. This result can be explained by the fact that growing season temperature was significantly warmer at the forest edges and in open forests, due to their higher diurnal temperatures. Whereas moths were mostly caught in forest cores and in dense forests. This means that the correlation between edge distance or management type and moth occurrence is stronger than the correlation of growing season temperature with moth occurrence.

Implications for macromoth conservation

We researched the occurrence of macromoths in south-facing edges of old oak- and mixed oak forests, with a sharp transition to grassland at the edge. Our findings suggest that macromoths living in old oak- or mixed oak forests, have a significant preference for dense forest cores. In thinned forests moth species richness and activity-density was lower compared to dense, un-thinned forests. On the other hand, forests need to be large enough. Forest cores were richer in moths compared to edges. Some microclimatic edge effects occur until 100 meter from the edge (Gehlhausen et al., 2000; Matlack, 1993), so forests smaller than 3.14 hectare cannot have forest core. But 3.14 hectare is not enough. The significant links between moth occurrence and edge distance and between moth occurrence and forest cover suggests that the further from the edge and the more forest in the surroundings, the more moths are present. Other studies also suggested that large forests are needed since habitat loss and fragmentation threatens moths (New, 2004; Slade et al., 2013). Likewise, some studies indicated that the highest moth diversity and activity-density is found in large, unfragmented, compact woodlands with little edge effects. (Fuentes-Montemayor et al., 2012; Lintott et al., 2014). Moreover, according to Fuentes-Montemayor et al. (2012) forest extent influenced moths the most. They found that most moths (including micromoths) were influenced by forest extent at a scale of less than 500 meter. Forest specialist macromoths were affected by forest extent on a 1500 meter scale. They suggest a landscape-management approach for moth conservation.

Apart from forest cover and forest management type, also forest structure seemed to be important for moth occurrence. All forest structure parameters had a significant relationship with moth communities. In order to conserve moths, conservationists should be aiming on protecting forests with a low canopy openness, high trees, a high plant area index and a high

foliage height diversity. The last two parameters had the strongest correlation with moth occurrence. This means that management should be focused on maintaining a dense vegetation and a lot of variation in the vertical distribution of the canopy cover.

Conclusion

Macromoths occur along an edge-to-interior gradient, a higher species richness and activity-density was found at a larger distance from the edge. There are differences in occurrence between moth families. Less mobile families like Geometridae showed a stronger edge-to-interior gradient compared to more mobile families like Noctuidae. Forest affinity of macromoths did not determine their exact occurrence along the edge-to-interior gradient. Forest specialist macromoth species richness and activity-density was higher near forest cores, but also generalist activity-density increased when going further away from the edge. Both forest specialist and generalist species that occur in forests prefer the forest core.

In general, macromoth activity-density was greatest in dense forest cores. Open forests have a lower activity-density of macromoths.

This edge-to-interior gradient and effect of forest management, might be driven by different environmental parameters. Plant diversity of the herb layer turned out to be independent of macromoth occurrence. Forest structure on the other hand had a clear link with macromoth occurrence. Especially forests with a higher foliage height diversity and plant area index harboured more macromoth species and a higher activity-density. Also temperature during the trapping nights had a clear link with the amount of macromoth species and individuals caught, although this is a representation of moth activity rather than moth occurrence. Furthermore, forest cover in the surroundings was tightly linked with macromoth occurrence.

Our results emphasise the need for very large, dense, unfragmented forests, with a lot of core area, to maximize macromoths conservation.

Summary

English

Insects are declining rapidly. Major drivers of insect declines are habitat loss, forest fragmentation and climate change. Moths are a very important and species-rich group that serve as pollinators, herbivores, but also as an important food source for other taxa. They are also used as indicator species for forest habitat quality and diversity. However, the effect of forest fragmentation and forest management on moth communities is not exactly known. With this research we wanted to determine macromoth species richness and activity-density (abundance of active macromoths) along forest edge-to-interior transects. On the other hand, forest management like thinning alters forest structure, which in turn can impact moth occurrence. We assessed the difference between macromoth communities along forest-edge-to-interior gradients in open and dense forests. Finally, we linked macromoth species richness and activity-density to environmental parameters such as: forest structure, forest cover, plant diversity and temperature.

We sampled moths locally (radius <10 m) with low intensity lamps. Samplings took place in four regions and within each region a dense and an open forest was sampled. Four traps were placed along each forest edge-to-interior transect, starting at 1.5 meter from the edge, a second trap at 12.5 meter, the third at 35.5 meter and ending at the forest core at 99.5 meter from the edge. All this was replicated four times, during different months. The data were analysed using mixed models accounting for period, region and transect as random effects. A model selection was used to identify the most important environmental parameters.

We found that macromoths had a higher activity-density and a higher species richness at dense forest cores. Forest specialists and generalists showed a similar response. Less mobile families like Geometridae showed a stronger edge-to-interior gradient compared to more mobile families like Noctuidae. Moth occurrence had links with the environment. Moth species richness and activity-density increased with more forest cover at a 500 meter scale, but also with a higher plant area index and foliage height diversity. Another important parameter was the local temperature, but this gave a reflection of moth activity rather than actual moth occurrence. These results have implications for moth conservation. Protecting large, unfragmented, dense forests, will increase moth occurrence. Together with moths, other species might benefit as well, since moths are important indicator species for forest habitat.

Nederlands

Insecten gaan sterk achteruit. De belangrijkste oorzaken hiervoor zijn habitatverlies, bosfragmentatie en klimaatverandering. Nachtvinders zijn een zeer belangrijke en soortenrijke groep, die een belangrijke rol vervullen als bestuivers, herbivoren, maar ook als voedselbron voor andere organismen. Ze worden ook gebruikt als indicatorsoorten voor habitatkwaliteit en soortenrijkdom in bossen. Het exact effect van bosfragmentatie en bosbeheer op nachtvindergemeenschappen is echter niet gekend. In dit onderzoek hebben we de soortenrijkdom en activiteit-densiteit (abundantie van actieve nachtvinders) van macronachtvlinders langsheen rand-kern gradiënten in bossen bepaald. Anderzijds zorgt ook bosbeheer zoals dunnen voor een aangepaste bosstructuur, wat op zijn beurt een impact kan hebben op het voorkomen van macronachtvlinders. Dit verschil in voorkomen van macronachtvlinders langs bos rand-kern gradiënten in open en gesloten bossen hebben we onderzocht. Finaal hebben we soortenrijkdom en activiteit-densiteit van macronachtvlinders gelinkt aan omgevingsparameters zoals bosstructuur, bosbedekking, planten diversiteit en temperatuur.

We hebben nachtvinders lokaal (straal <10 m) bemonsterd met behulp van lichtvallen met een lage lichtintensiteit. De staalnames vonden plaats in vier regio's en in elke regio werden telkens een open en een gesloten bos bemonsterd. Per rand-kern transect werden vier vallen geplaatst, startend op 1.5 meter van de rand, de volgende op 12.5 meter van de rand, de derde op 35.5 meter en de laatste in de boskern op 99.5 meter van de bosrand. Er waren vier replicaties, telkens tijdens een andere maand. Alle data werden geanalyseerd met mixed models, die de random effecten van periode, regio en transect in rekening brengen. Om de belangrijkste omgevingsparameters te identificeren werd een modelselectie gebruikt.

We vonden een hogere activiteit-densiteit en soortenrijkdom van macronachtvlinders in gesloten boskernen. Bosspecialisten vertoonden een respons die gelijkaardig was aan die van generalisten. Voor minder mobiele families, zoals Geometridae, werd een sterkere rand-kern gradiënt gevonden dan voor de meer mobiele families zoals Noctuidae. Het voorkomen van nachtvinders was gebonden aan de omgeving. Soortenrijkdom en activiteit-densiteit waren beduidend hoger in bossen met een grotere bosbedekking op een schaal van 500 meter. Ook een verhoogde bladoppervlakte-index en grotere verticale variatie in bladbiomassa hadden een sterk positief effect op macronachtvindergemeenschappen. Een andere belangrijke omgevingsparameter was de lokale temperatuur, maar deze geeft eerder een reflectie weer van nachtvinderactiviteit in plaats van het eigenlijke voorkomen van nachtvinders. Deze resultaten kunnen bijdragen tot behoud en bescherming van nachtvinders. Het beschermen van grote, ongefragmenteerde, gesloten bossen zal resulteren in meer nachtvinders. Samen met nachtvinders kunnen ook andere soorten meegenieten, aangezien nachtvinders indicatorsoorten zijn voor boshabitat.

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Appendix I – Trapping protocol

- Place wooden plates next to pole 1 (1.5 m), pole 3 (12.5 m), pole 4 (35.5 m) and pole 5 (99.5 m).
- Place the traps with the lamps perpendicular to the forest edge.
- Turn the lamps so they face upwards.
- Fill traps with two egg cartons inside and one at each side outside the trap.
- Place the Plexiglas with a two-centimetre opening in the middle.
- Illuminate one hour before sunset.
- Check the traps in the morning half an hour before sunrise, starting from the forest edge.
- Identify and count all individuals in the trap, on the trap and on the wooden plate.
- Collect all complex species and label them.
- Turn off the lamps only when every individual is counted.

Appendix II – Genital preparation

Collected moths were killed and preserved in the freezer. This way the scales on the wings were not damaged and could still be helping further identification. For the identification of the genitalia the characteristics as described by Townsend et al. (Townsend et al., 2011) were used. Pictures of moth genitalia are available on “British Lepidoptera” (*British Lepidoptera*, 2020) and “Moth dissection” (*Moth dissection: Macro moths*, 2020) to compare with.

In order to clarify the chitin structures that have the distinguishing characteristics, Potassium hydroxide was used. This liquid solves the organic structures inside the abdomen and leaves the genitalia of both males and females intact. After the reaction with KOH, the structures can easily be extracted, photographed and identified (Figure 25). A more precise protocol for this is found in the next paragraph.

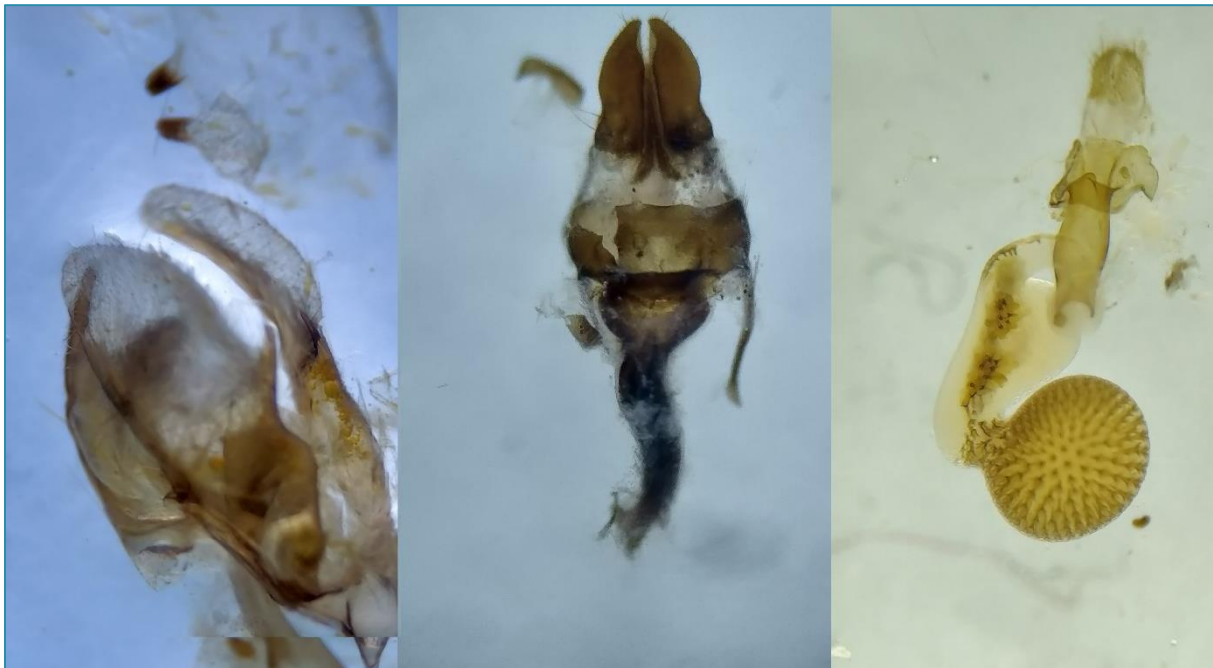


Figure 25: Genitalia after preparation.
From left to right: *Epirrita christyi* ♂, *Oligia strigilis* ♂, *Horisme tersata* ♀.

Protocol

- Remove the abdomen and place in 10% KOH.
- Put the Eppendorf tubes in hot water.
- Wait 20 minutes.
- Remove the abdomen from the KOH and place in water.
- Gently remove scales with tweezers or paint brush.
- If a male:
 - Tease out the genital capsule by stroking over the abdomen.
 - Place genitalia in 30% ETOH, and clean them.
 - Place genitalia in 100% ETOH to dehydrate for 30 seconds, open the valves.
- If a female
 - Clean thoroughly with a brush in 30% ETOH.
 - Open the abdomen by separating the sternites and tergites starting at the basal end, stop at the last segment.
 - Remove first the ventral and then the dorsal scales from the tip, be careful not to damage the corpus bursae.
 - Leave the last segment on the genitalia.
 - Place genitalia in 100% ETOH to dehydrate for 30 seconds.
- Place the genitalia in 70% ETOH.
- Take pictures of the characteristics.
- Preserve the genitalia in an Eppendorf tube with 70% ETOH.



Figure 26: preparing moth genitalia.

Appendix III – Environment along edge-to-interior gradients and management type

The edge-to-interior gradient and effect of management was analysed for all eleven environmental parameters. These models were built in the same way as all the previously described models. Here a normal distribution was used, since this are measurements and no count data. An overview of different models and the parameters that were included in the final model are given in Table 6. The coding of the models looked like this:

```
lmer(Environment ~ ln(Edgedistance) + Foresttype + ln(Edgedistance) :
Foresttype + (1|Region) + (1|Region:Transect.f), data=Environment)
```

Table 6: Overview of all the final models the environment along edge-to-interior gradients and management type.

	Dependent variable	Independent variables		Interaction effect	R ² m	R ² c
		Ln(edge-distance)	Management type			
Forest structure	Openness of the canopy (LIDAR)	–	X	X	0.107	0.477
	Canopy height	–	X	X	0.011	0.922
	Plant area index			+	0.271	0.703
	Foliage height diversity	X	X	X	/	/
Forest cover	500 meter scale	+	–	X	0.235	0.977
Plant diversity	General plant species richness	X	X	X	/	/
	Forest specialist plant species richness	X	X	X	/	/
	Phylogenetic plant species richness	X	X	X	/	/
Temperature	Average temperature (microclimate)			✓	0.002	0.994
	Minimum temperature (microclimate)	+	X	X	0.003	0.990
	Maximum temperature (microclimate)	X	X	X	/	/
	Growing season temperature	–	+	X	0.230	0.935

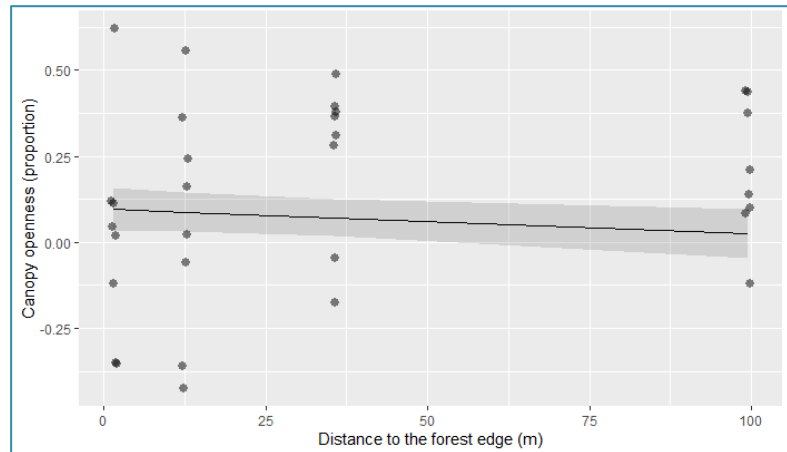
In the cells is indicated with a '+' or '-' if this parameter was included in the final model, followed by the model estimation. '+' indicates a positive correlation, '-' indicates a negative correlation, for management type, '+' indicates that open forests had higher values of the parameter, '-' indicates that dense forests had higher values of the parameter. A positive interaction indicates that both open and dense forests increased or decreased together in parameter value along the gradient, a negative interaction means that there is an opposite gradient for open and dense forests. If the parameter was not significant (indicated with a cross), it was left out of the final model. A green symbol indicates a significant parameter. In case the assumptions were not met, black symbols were used, significances of these models cannot be interpreted.

Forest structure

Openness of the canopy

Canopy openness did not differ significantly between the differently managed forests, but the differences in canopy openness from edge to core were significant ($\text{Chi}^2 = 6.4$, $P < 0.05$) (Figure 27). Forest edges had a more open canopy than forest cores.

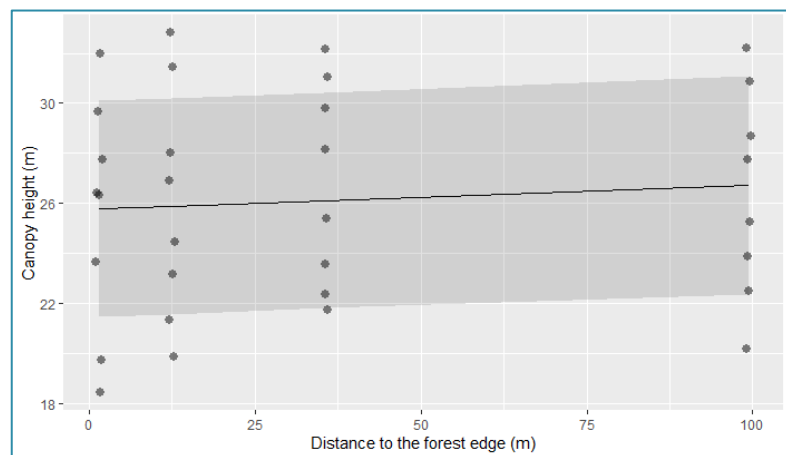
Figure 27: Difference in canopy openness measured with the LIDAR. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter.



Canopy height

No significant differences were found in canopy height regarding the forest management. When looking at the edge-to-interior gradient in Canopy height, a significant increase in canopy height was found towards the forest core ($\text{Chi}^2 = 4.5$, $P < 0.05$) (Figure 28). The difference in height between edge and core was about 1 meter.

Figure 28: Edge-to-interior gradient of canopy height. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter.



Plant area index & Foliage height diversity

There was a significant interaction from plant area index with forest management type and edge distance ($\text{Chi}^2 = 3.9$, $P < 0.05$). There was a higher plant area index further away from the edge. This gradient was stronger in dense forests (Figure 29). The edges of open and dense forests had a similar plant area index. When analysing the relationship between foliage height diversity and distance from the edge and management type, no significances were found.

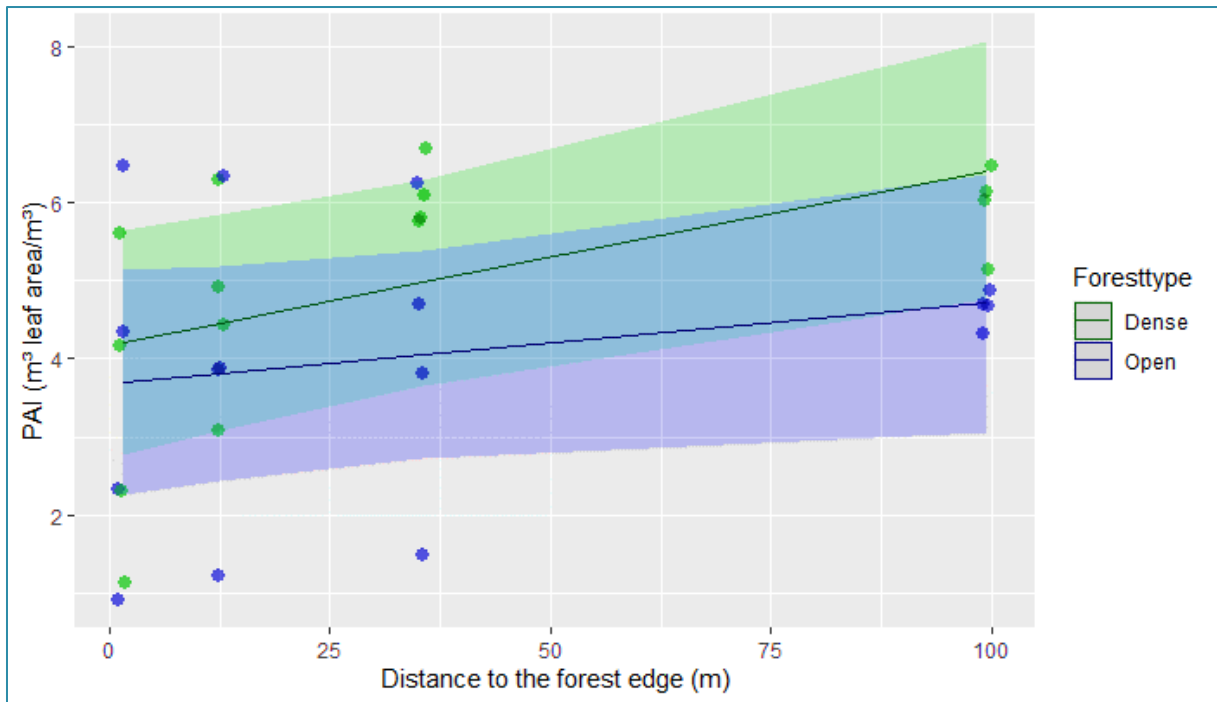


Figure 29: Plant area index in function of edge distance. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter.

Forest cover

At a scale of 500 meter, a significant difference in forest cover along the edge-to-interior gradient ($\text{Chi}^2 = 15$, $P < 0.001$) and a significant difference between different management types ($\text{Chi}^2 = 6.2$, $P < 0.05$) was found (Figure 30). It turns out that at this scale the open forests were situated within less forested areas and more forest cover is found near the core.

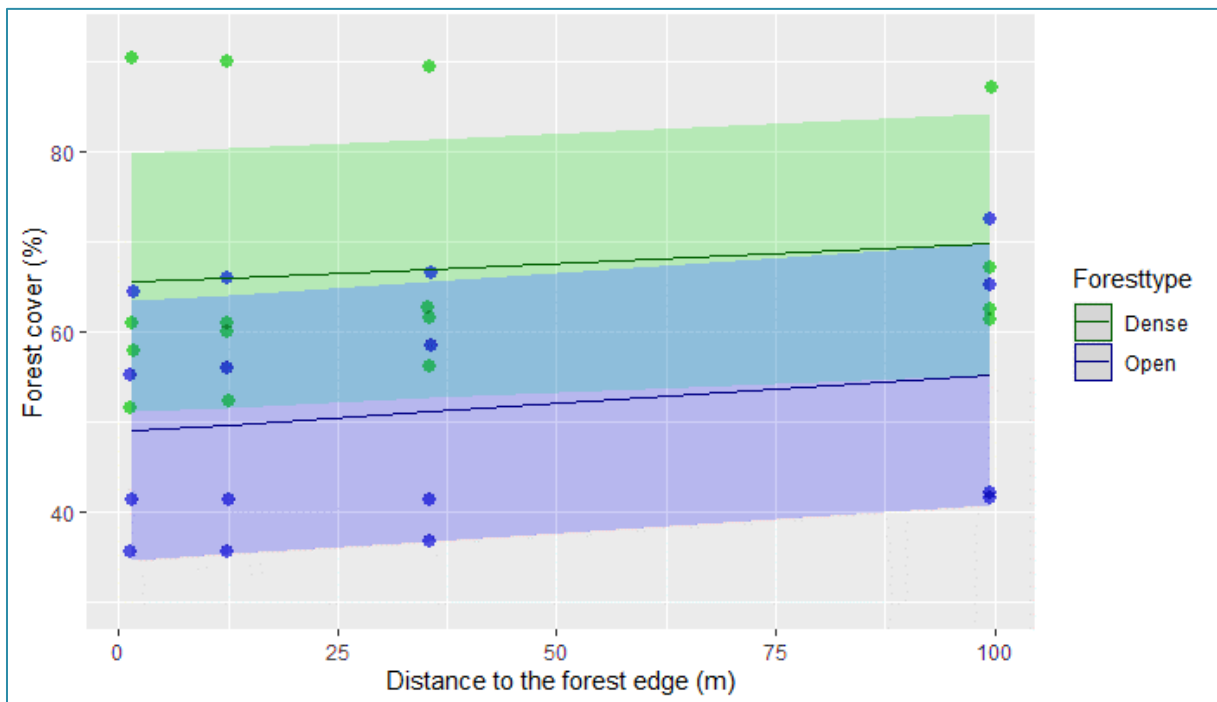


Figure 30: Forest cover at a 500 meter scale in function of edge distance. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter.

Plant diversity

When looking at the different plant diversity measures. No significant gradient, nor differences between management types were found, both for general plant species richness, for forest specialist plant species and for phylogenetic plant species richness.

Temperature

When analysing the gradient and forest management effect of average temperature, a significant interaction was found. The data are however not normally distributed and no transformation could solve this. When looking at maximum temperature, no significances were found and the assumptions are not met either. A square root transformation gave a better distribution but still not good enough to reach normality of the residuals. Minimum temperature however was normally distributed. No differences in minimum temperature were found in differently managed forest, but there was a significant edge distance effect ($\text{Chi}^2 = 43$, $P < 0.001$). The forest core had a higher minimum temperature compared to the edge (Figure 31: Left). So forest cores did not cool that much, however the difference in minimum temperature between edge and core was minimal ($0.714\text{ }^\circ\text{C}$). The temperature sensors had an accuracy of $0.5\text{ }^\circ\text{C}$. This means that there was a quite large error on these temperatures. This error was not accounted for in the models, so finding a difference of $0.714\text{ }^\circ\text{C}$ over four plots can be purely by chance.

When looking at growing season temperature a significant forest management effect ($\text{Chi}^2 = 23$, $P < 0.001$) and edge distance effect ($\text{Chi}^2 = 26$, $P < 0.001$) were found. Open forests had a warmer growing season temperature compared to dense forests and forest edges were warmer than forest cores (Figure 31: Right).

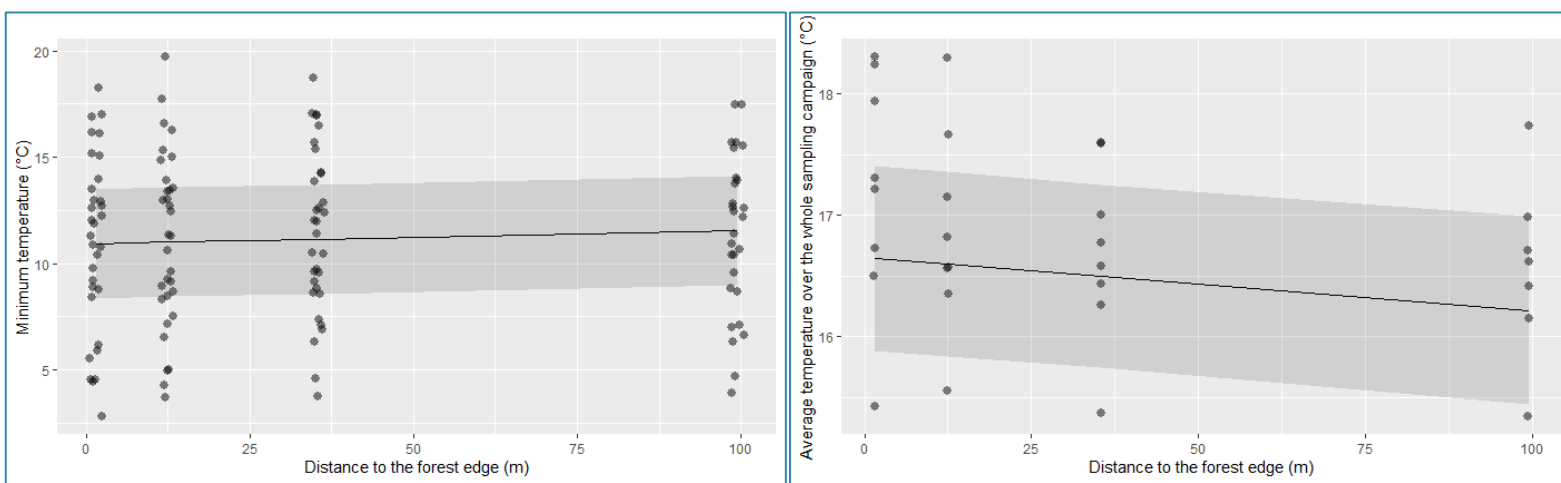


Figure 31: Climatic gradient along forest edges. The line indicates the modelled relationship, the shaded area represents the confidence interval. The dots are the raw data points, with some jitter. Left: Microclimatic minimum temperature in function of the edge-to-interior gradient. Right: Average growing season temperature.

Appendix IV – Extra graphs

Forest cover on a 250 meter scale

When running the simple model that links forest cover at a scale of 250 meter with moth occurrence, a significant difference along the edge-to-interior gradient was found for both species richness and activity-density (species richness: $\text{Chi}^2 = 13$, $P < 0.001$; activity-density: $\text{Chi}^2 = 216$, $P < 0.001$). At a 250m scale the moth activity-density triples if the forest cover goes from 40% to 90% (Figure 32: Left).

Forest cover increases towards the forest core (Chi² = 30, P < 0.001), but does not differ between differently managed forests at this scale (Figure 32: Right).

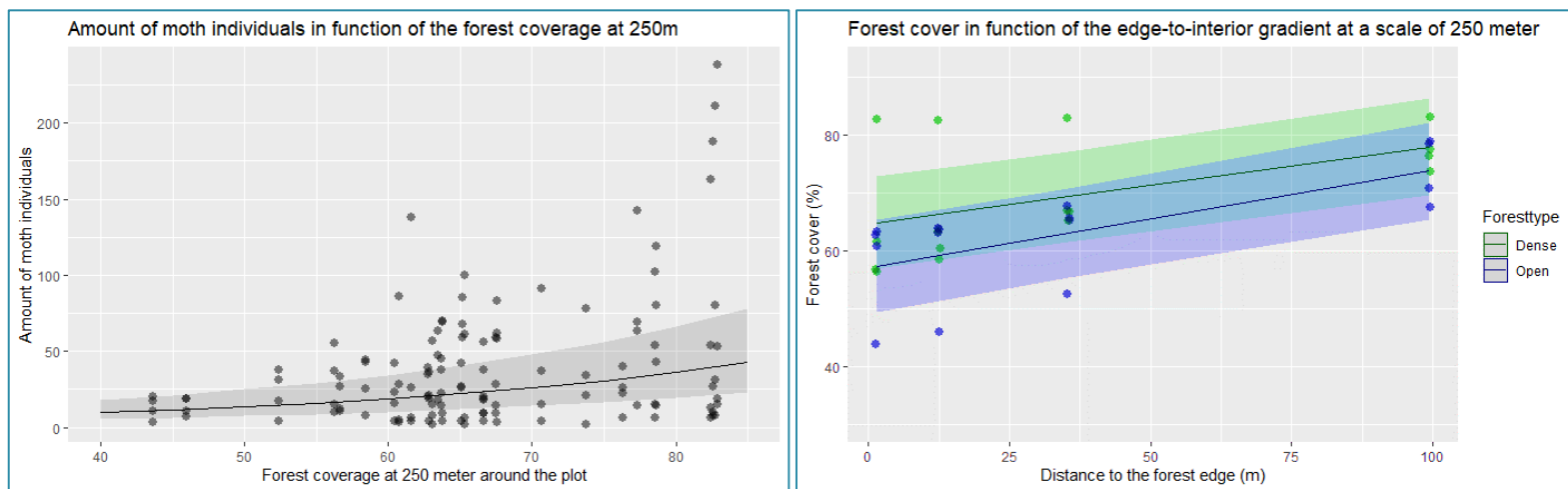
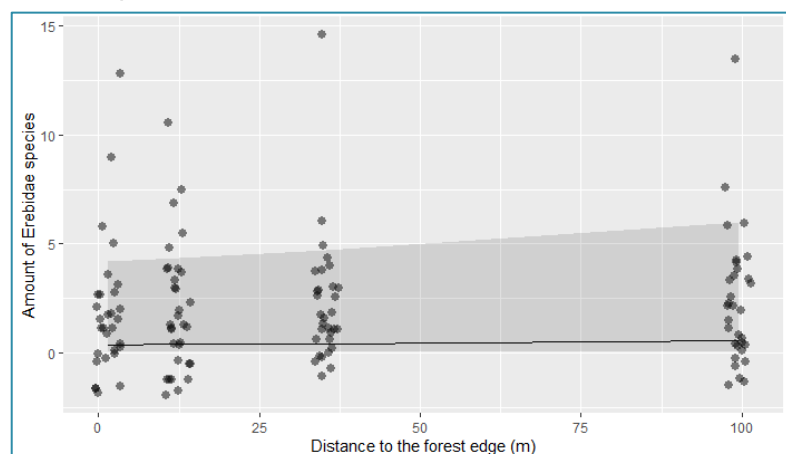


Figure 32: Forest cover at a 250 m scale. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter. Left: Forest cover in function of moth activity-density. Right: Forest cover in function of edge.

Erebidae gradient

For Erebidae species richness a slight edge-to-interior gradient is found ($\text{Chi}^2 = 4.5$, $P = 0.03$) (Figure 33). There were more Erebidae species near forest cores.

Figure 33: Edge-to-interior gradient on Erebidae species richness. The lines indicate the modelled relationship, the shaded areas represent the confidence intervals. The dots are the raw data points, with some jitter.



Appendix V – Species list

Table 7: List of all caught species.

Scientific name	English name	Dutch name	Rarity	Forest affinity	Family	Total amount trapped
<i>Abraxas grossulariata</i>	Magpie	bonte bessenvlinder	fairly common	mm	Geometridae	1
<i>Acronicta auricoma</i>	Scarce Dagger	goudhaaruil	fairly common	mm	Noctuidae	1
<i>Acronicta psi</i>	Grey Dagger	psi-uil	common	mm	Noctuidae	1
<i>Acronicta rumicis</i>	Knot Grass	zuringuil	fairly common	mo	Noctuidae	1
<i>Acronicta strigosa</i>	Marsh Dagger	moerasbos-uil	rare	wl	Noctuidae	1
<i>Actinotia polyodon</i>	Purple Cloud	gevlamde uil	fairly common	mo	Noctuidae	1
<i>Agrochola circellaris</i>	The Brick	bruine herfstuil	fairly common	mm	Noctuidae	7
<i>Agrochola helvola</i>	Flounced Chestnut	roodachtige herfstuil	rare	mm	Noctuidae	1
<i>Agrochola litura</i>	Brown spot Pinion	zwartgeklede herfstuil	rare	mm	Noctuidae	1
<i>Agrochola lota</i>	Red line Quaker	zwartstipvlinder	fairly common	mm	Noctuidae	1
<i>Agrochola lunosa</i>	Lunar Underwing	maansikkeluil	fairly common	mo	Noctuidae	81
<i>Agrochola lychnidis</i>	Beaded Chestnut	variabele herfstuil	rare	mm	Noctuidae	2
<i>Agrotis exclamationis</i>	Heart and Dart	gewone worteluil	common	mo	Noctuidae	73
<i>Agrotis segetum</i>	Turnip Moth	gewone velduil	fairly common	o	Noctuidae	6
<i>Alcis repandata</i>	Mottled Beauty	variabele spikkelspanner	common	mm	Geometridae	75
<i>Allophyes oxyacanthae</i>	Green brindled Crescent	meidoornuil	fairly common	mm	Noctuidae	21
<i>Amphipyra berbera</i>	Svensson's Copper Underwing	schijnpiramidevlinder	fairly common	w	Noctuidae	3
<i>Angerona prunaria</i>	Orange Moth	oranje iepentakvlinder	common	mm	Geometridae	14
<i>Apamea epomidion</i>	Clouded Brindle	zwartrandgrasuil	very rare	wl	Noctuidae	1
<i>Apamea monoglypha</i>	Dark Arches	graswortelvlinder	common	mo	Noctuidae	4
<i>Apeira syringaria</i>	Lilac Beauty	seringenvlinder	fairly common	wl	Geometridae	1
<i>Aplocera efformata</i>	Lesser Treble bar	sint-janskruidblokspanner	fairly common	o	Geometridae	1
<i>Apoda limacodes</i>	Festoon	slakrups	common	w	Limacodidae	14
<i>Aporophyla lutulenta</i>	Deep-brown Dart	bruine witvleugeluil	very rare	mo	Noctuidae	8
<i>Arctia caja</i>	Garden Tiger	grote beer	fairly common	mm	Erebidae	6
<i>Arctornis l-nigrum</i>	Black V Moth	zwarte-l-vlinder	rare	w	Erebidae	11
<i>Asthena albulata</i>	Small White Wave	wit spannertje	fairly common	wl	Geometridae	8
<i>Atethmia centrigo</i>	Centre barred Sallow	essengouduil	fairly common	mm	Noctuidae	1
<i>Athetis hospes</i>	Porter's Rustic	vale stofuil	very rare		Noctuidae	1
<i>Axylia putris</i>	Flame	houtspaander	common	mm	Noctuidae	2
<i>Bena bicolorana</i>	Scarce Silver-lines	grote groenuil	fairly common	wl	Nolidae	1
<i>Biston betularia</i>	Peppered Moth	peper-en-zoutvlinder	common	mm	Geometridae	10
<i>Brachylochia viminalis</i>	Minor Shoulder-knot	katwilgultje	rare	mm	Noctuidae	14
<i>Cabera exanthemata</i>	Common Wave	bruine grijsbandspanner	common	wl	Geometridae	18
<i>Cabera pusaria</i>	Common White Wave	witte grijsbandspanner	common	mm	Geometridae	12
<i>Callopietria juvenina</i>	The Latin	varenuil	very rare	wl	Noctuidae	1

<i>Campaea margaritaria</i>	Light Emerald	appeltak	common	mm	Geometridae	117
<i>Camptogramma bilineata</i>	Yellow Shell	gestreepte goudspanner	common	mm	Geometridae	5
<i>Caradrina morpheus</i>	Mottled Rustic	morpheusstofuil	fairly common	mo	Noctuidae	1
<i>Catarhoe cuculata</i>	Royal Mantle	bonte walstrospanner	rare	mm	Geometridae	1
<i>Catarhoe rubidata</i>	Ruddy Carpet	roodbruine walstrospanner	rare	w	Geometridae	1
<i>Catocala promissa</i>	Light Crimson Underwing	eikenweeskind	rare	wl	Erebidae	1
<i>Cepphis advenaria</i>	Little Thorn	kleine herculesspanner	fairly common	wl	Geometridae	1
<i>Charanyca ferruginea</i>	Brown Rustic	randvlekuil	fairly common	mm	Noctuidae	95
<i>Charanyca trigrammica</i>	Treble Lines	drielijnuil	fairly common	mo	Noctuidae	1
<i>Chesias legatella</i>	Streak	herfstbremspanner	fairly common	mo	Geometridae	4
<i>Chiasmia clathrata</i>	Latticed Heath	klaverspanner	common	o	Geometridae	2
<i>Chloroclysta siterata</i>	Red green Carpet	papegaaaitje	fairly common	wl	Geometridae	5
<i>Chloroclystis v-ata</i>	V-Pug	v-dwergspanner	fairly common	mm	Geometridae	4
<i>Cidaria fulvata</i>	Barred Yellow	oranje bruinbandspanner	rare	mm	Geometridae	4
<i>Cilix glaucata</i>	Chinese Character	witte eenstaart	fairly common	wl	Drepanidae	2
<i>Clostera pigra</i>	Small Chocolate-tip	donkere wapendrager	rare	mm	Notodontidae	3
<i>Colocasia coryli</i>	Nut-tree Tussock	hazelaaruil	fairly common	wl	Noctuidae	42
<i>Colotois pennaria</i>	Feathered Thorn	gepluimde spanner	common	mm	Geometridae	34
<i>Comibaena bajularia</i>	Blotched Emerald	gevlekte zomervlinder	fairly common	wl	Geometridae	2
<i>Conistra erythrocephala</i>	Red headed Chestnut	roodkopwinteruil	fairly common	wl	Noctuidae	1
<i>Conistra rubiginea</i>	Dotted Chestnut	gevlekte winteruil	fairly common	mm	Noctuidae	1
<i>Conistra vaccinii</i>	Chestnut	bosbesuil	common	mm	Noctuidae	95
<i>Cosmia trapezina</i>	Dun bar	hyena	common	mm	Noctuidae	58
<i>Cosmorhoe ocellata</i>	Purple Bar	blauwbandspanner	fairly common	wl	Geometridae	3
<i>Craniophora ligustri</i>	The Coronet	schedeldrager	fairly common	wl	Noctuidae	2
<i>Crocallis elinguaris</i>	Scalloped Oak	kortzuiger	common	mm	Geometridae	14
<i>Cryphia algae</i>	Tree lichen Beauty	donkergroene korstmosuil	fairly common	mm	Noctuidae	8
<i>Cybosia mesomella</i>	Four-dotted Footman	vierstipbeertje	fairly common	wl	Erebidae	40
<i>Cyclophora albipunctata</i>	Birch Mocha	berkenoogspanner	common	wl	Geometridae	3
<i>Cyclophora annularia</i>	Mocha	nekspindertje	rare	w	Geometridae	4
<i>Cyclophora linearis</i>	Clay Triple-lines	gele oogspanner	common	w	Geometridae	12
<i>Cyclophora punctaria</i>	Maiden's Blush	gestippelde oogspanner	common	wl	Geometridae	7
<i>Cyclophora ruficiliaria</i>	Jersey Mocha	geelbruine oogspanner	very rare	wl	Geometridae	5
<i>Cymatophorina diluta</i>	Oak Lutestring	eiken-orvlinder	rare	w	Drepanidae	446
<i>Deltote bankiana</i>	Silver Barred	zilverstreep	fairly common	o	Noctuidae	2
<i>Deltote pygarga</i>	Marbled White Spot	donkere marmereuil	fairly common	wl	Noctuidae	16
<i>Denticucullus pygmina</i>	Small Wainscot	zeggeboorder	fairly common	mo	Noctuidae	2
<i>Diarsia brunnea</i>	Purple Clay	bruine breedvleugeluil	fairly common	mm	Noctuidae	7
<i>Diarsia mendica</i>	Ingrailed Clay	variabele breedvleugeluil	fairly common	mm	Noctuidae	4
<i>Dicycla oo</i>	Heart Moth	nullenuil	rare	wl	Noctuidae	1
<i>Diloba caeruleocephala</i>	Figure of Eight	krakeling	fairly common	mm	Noctuidae	5
<i>Drepana curvatula</i>	Dusky Hook tip	bruine eenstaart	common	wl	Drepanidae	6
<i>Drepana falcataria</i>	Pebble Hook-tip	berkeneenstaart	common	wl	Drepanidae	2

<i>Drymonia obliterata</i>	Indistinct Marbled Brown	beukentandvlinder	rare	w	Notodontidae	9
<i>Dysstroma truncata</i>	Common Marbled Carpet	schimmelspanner	fairly common	wl	Geometridae	12
<i>Ecliptopera silaceata</i>	Small Phoenix	marmerspanner	fairly common	wg	Geometridae	18
<i>Ectropis crepuscularia</i>	Small Engrailed	gewone spikkelspanner	common	mm	Geometridae	44
<i>Eilema caniola</i>	Hoary Footman	vaal kokerbeertje	fairly common	o	Erebidae	37
<i>Eilema complana</i>	Scarce Footman	streepkokerbeertje	fairly common	mm	Erebidae	30
<i>Eilema depressa</i>	Buff Footman	naaldboombeertje	fairly common	mm	Erebidae	6
<i>Eilema griseola</i>	Dingy Footman	glad beertje	common	w	Erebidae	68
<i>Eilema lurideola</i>	Common Footman	plat beertje	fairly common	mm	Erebidae	233
<i>Elaphria venustula</i>	Rosy Marbled	gemarmerd heide-uiltje	fairly common	mm	Noctuidae	16
<i>Ennomos alniaria</i>	Canary shouldered Thorn	geelschouderspanner	fairly common	w	Geometridae	4
<i>Ennomos erosaria</i>	September Thorn	gehakkelde spanner	rare	w	Geometridae	4
<i>Ennomos fuscantaria</i>	Dusky Thorn	essenspanner	fairly common	w	Geometridae	1
<i>Ennomos quercinaria</i>	August Thorn	geelblad	fairly common	w	Geometridae	39
<i>Epione repandaria</i>	Bordered Beauty	puntige zoomspanner	fairly common	wl	Geometridae	7
<i>Epirrhoe alternata</i>	Common Carpet	gewone bandspanner	common	mm	Geometridae	9
<i>Epirrita christyi</i>	Pale November Moth	bleke novemberspanner	rare	w	Geometridae	78
<i>Epirrita dilutata</i>	November Moth	herfstspanner	common	w	Geometridae	146
<i>Erannis defoliaria</i>	Mottled Umber	grote wintervlinder	common	mm	Geometridae	11
<i>Eublemma purpurina</i>	Beautiful Marbled	prachtpurperuiltje	very rare	o	Erebidae	1
<i>Eulithis populata</i>	Northern Spinach	gewone agaatspanner	fairly common	mm	Geometridae	4
<i>Eulithis prunata</i>	Phoenix	wortelhoutspanner	fairly common	mm	Geometridae	1
<i>Eulithis testata</i>	Chevron	oranje agaatspanner	fairly common	mm	Geometridae	10
<i>Euphyia biangulata</i>	Cloaked Carpet	dubbelhoekbandspanner	very rare	wg	Geometridae	2
<i>Euphyia unangulata</i>	Sharp-angled Carpet	scherphoekbandspanner	fairly common	wl	Geometridae	9
<i>Eupithecia centaureata</i>	Lime speck Pug	zwartvlekdwergspanner	fairly common	mo	Geometridae	1
<i>Eupithecia haworthiata</i>	Haworth's Pug	bosrankdwergspanner	rare	wl	Geometridae	3
<i>Eupithecia inturbata</i>	Maple Pug	esdoorndwergspanner	rare	mm	Geometridae	1
<i>Eupithecia linariata</i>	Toadflax Pug	vlasbekdwergspanner	fairly common	mo	Geometridae	5
<i>Eupithecia plumbeolata</i>	Lead-coloured Pug	hengeldwergspanner	very rare	wl	Geometridae	5
<i>Eupithecia valerianata</i>	Valerian Pug	valeriaandwergspanner	rare	mm	Geometridae	1
<i>Eupithecia virgaureata</i>	Golden rod Pug	guldenroededwergspanner	fairly common	mm	Geometridae	5
<i>Eupithecia vulgata</i>	Common Pug	gewone dwergspanner	common	mm	Geometridae	3
<i>Euplagia quadripunctaria</i>	Jersey Tiger	spaanse vlag	fairly common	wl	Erebidae	1
<i>Euplexia lucipara</i>	Small Angle Shades	levervlek	fairly common	mm	Noctuidae	2
<i>Euproctis chrysorrhoea</i>	Brown-tail	bastaardsatijnvlinder	fairly common	mo	Erebidae	1
<i>Euproctis similis</i>	Yellow-tail	donsvlinder	common	wl	Erebidae	31
<i>Eupsilia transversa</i>	Satellite	wachtervlinder	common	mm	Noctuidae	5
<i>Euthrix potatoria</i>	Drinker	rietvink	fairly common	wl	Lasiocampidae	27
<i>Falcaria lacertinaria</i>	Scalloped Hook tip	bleke eenstaart	fairly common	wl	Drepanidae	2
<i>Gandaritis pyraliata</i>	Barred Straw	gele agaatspanner	common	mm	Geometridae	25
<i>Geometra papilionaria</i>	Large Emerald	zomervlinder	common	wl	Geometridae	4
<i>Gluphisia crenata</i>	Dusky Marbled Brown	populierentandvlinder	fairly common	w	Notodontidae	4

<i>Gymnoscelis rufifasciata</i>	Double-striped Pug	zwartkamdwergspanner	common	mm	Geometridae	9
<i>Habrosyne pyritoides</i>	Buff Arches	vuursteenvlinder	fairly common	wl	Drepanidae	15
<i>Hada plebeja</i>	The Shears	schaaruil	rare	mm	Noctuidae	2
<i>Hemitheia aestivaria</i>	Common Emerald	kleine zomervlinder	common	mm	Geometridae	30
<i>Herminia grisealis</i>	Small Fan-foot	boogsnuituil	fairly common	mm	Erebidae	1
<i>Herminia tarsicrinalis</i>	Shaded Fan-foot	schaduwsnuituil	fairly common	wl	Erebidae	11
<i>Herminia tarsipennalis</i>	Fan-foot	lijnsnuituil	fairly common	wl	Erebidae	2
<i>Heterogenea asella</i>	Triangle	kleine slakrups	rare	w	Limacodidae	3
<i>Hoplodrina ambigua</i>	Vine's Rustic	zuidelijke stofuil	fairly common	mo	Noctuidae	1
<i>Hoplodrina blanda</i>	The Rustic	egale stofuil	fairly common	mo	Noctuidae	2
<i>Hoplodrina octogenaria</i>	The Uncertain	gewone stofuil	common	mo	Noctuidae	77
<i>Horisme tersata</i>	Fern	egale bosrankspanner	rare	wl	Geometridae	6
<i>Hydrelia flammeolaria</i>	Small Yellow Wave	geel spannertje	fairly common	w	Geometridae	1
<i>Hydrelia sylvata</i>	Waved Carpet	elzenspannertje	rare	w	Geometridae	1
<i>Hydria undulata</i>	Scallop shell moth	gegolfde spanner	fairly common	wl	Geometridae	2
<i>Hylaea fasciaria</i>	Barred Red	rode dennenspanner	fairly common	w	Geometridae	9
<i>Hypena proboscidalis</i>	Snout	bruine snuituil	common	mm	Erebidae	17
<i>Hypomecis punctinalis</i>	Pale Oak Beauty	ringspikkelspanner	common	mm	Geometridae	102
<i>Hypomecis roboraria</i>	Great Oak Beauty	grote spikkelspanner	fairly common	w	Geometridae	148
<i>Idaea aversata</i>	Riband Wave	grijze stipspanner	fairly common	mm	Geometridae	297
<i>Idaea biselata</i>	Small Fan-footed Wave	schildstipspanner	common	mm	Geometridae	28
<i>Idaea dimidiata</i>	Single-dotted Wave	vlekstipspanner	common	mm	Geometridae	24
<i>Idaea fuscovenosa</i>	Dwarf Cream Wave	dwergstipspanner	fairly common	mm	Geometridae	17
<i>Idaea ochrata</i>	Bright Wave	okergele spanner	very rare	o	Geometridae	6
<i>Idaea rusticata</i>	Least Carpet	schaduwstipspanner	fairly common	o	Geometridae	2
<i>Idaea straminata</i>	Plain Wave	egale stipspanner	rare	mm	Geometridae	1
<i>Idaea trigeminata</i>	Treble Brown Spot	zuidelijke stipspanner	very rare	wl	Geometridae	8
<i>Ipimorpha retusa</i>	Double Kidney	heremietuil	rare	mm	Noctuidae	1
<i>Jodis lactearia</i>	Little Emerald	melkwitte zomervlinder	fairly common	wl	Geometridae	1
<i>Lacanobia oleracea</i>	Bright-line Brown-eye	groente-uil	common	mm	Noctuidae	3
<i>Laothoe populi</i>	Poplar Hawk-moth	populierenpijlstaart	common	mm	Sphingidae	2
<i>Lasiocampa quercus</i>	Oak Eggar	hageheld	common	wl	Lasiocampidae	4
<i>Laspeyria flexula</i>	Beautiful Hook-tip	bruine sikkelluil	fairly common	w	Erebidae	2
<i>Ligdia adustata</i>	Scorched Carpet	aangebrande spanner	fairly common	mm	Geometridae	3
<i>Lithophane ornitopus</i>	Grey Shoulder knot	lichtgrijze uil	rare	wl	Noctuidae	1
<i>Lithosia quadra</i>	Four-spotted Footman	viervlakvlinder	rare	w	Erebidae	5
<i>Lomaspilis marginata</i>	Clouded Border	gerande spanner	common	mm	Geometridae	31
<i>Lomographa bimaculata</i>	White-pinion Spotted	tweevlekspanner	common	wl	Geometridae	1
<i>Lomographa temerata</i>	Clouded Silver	witte schaduwspanner	fairly common	wl	Geometridae	2
<i>Luperina testacea</i>	Flounced Rustic	gewone grasuil	common	o	Noctuidae	18
<i>Lymantria dispar</i>	Gypsy Moth	plakker	common	wl	Erebidae	2
<i>Lymantria monacha</i>	Black Arches	nonvlinder	fairly common	w	Erebidae	125
<i>Macaria alternata</i>	Sharp-angled Peacock	donker klaverblaadje	common	wl	Geometridae	29
<i>Macaria liturata</i>	Tawny barred Angle	gerimpelde spanner	common	mm	Geometridae	3
<i>Macaria notata</i>	Peacock Moth	klaverblaadje	common	wl	Geometridae	8
<i>Macaria wauaria</i>	V-Moth	zwarte-w-vlinder	fairly common	mm	Geometridae	4

<i>Macrochilo cribrumalis</i>	Dotted Fan-foot	stippelsnuituil	fairly common	mm	Erebidae	1
<i>Malacosoma neustria</i>	Lackey Moth	ringelrups	fairly common	wl	Lasiocampidae	29
<i>Mamestra brassicae</i>	Cabbage Moth	kooluil	common	mm	Noctuidae	1
<i>Meganola albula</i>	Kent Black Arches	groot visstaartje	fairly common	wl	Nolidae	2
<i>Meganola strigula</i>	Small Black Arches	donker visstaartje	very rare	wl	Nolidae	1
<i>Melanchra persicariae</i>	Dot Moth	perzikkruiduil	common	mm	Noctuidae	1
<i>Mesapamea secalella</i>	Lesser Common Rustic	weidehalmuiltje	fairly common	mm	Noctuidae	3
<i>Mesapamea secalis</i>	Common Rustic	halmrupsvlinder	fairly common	mm	Noctuidae	1
<i>Mesoligia furuncula</i>	Cloaked Minor	zandhalmuiltje	fairly common	mm	Noctuidae	3
<i>Mesotype didymata</i>	Twin-spot Carpet	pijlkruidspanner	rare	wl	Geometridae	1
<i>Miltochrista miniata</i>	Rosy Footman	rozenblaadje	common	wl	Erebidae	68
<i>Minoa murinata</i>	Drab Looper	bruin spannertje	rare	o	Geometridae	1
<i>Mythimna albipuncta</i>	White point	witstipgrasuil	fairly common	o	Noctuidae	3
<i>Mythimna ferrago</i>	The Clay	gekraagde grasuil	common	mm	Noctuidae	7
<i>Mythimna impura</i>	Smoky Wainscot	stompvleugelgrasuil	common	mm	Noctuidae	27
<i>Mythimna pallens</i>	Common Wainscot	bleke grasuil	common	mo	Noctuidae	3
<i>Noctua comes</i>	Lesser Yellow Underwing	volgeling	common	mm	Noctuidae	9
<i>Noctua janthe/janthina</i>	Lesser Broad bordered/Langmaid's Yellow Underwing	open/kleine breedbandhuismoeder	common	mm	Noctuidae	11
<i>Noctua pronuba</i>	Large Yellow Underwing	huismoeder	common	mm	Noctuidae	84
<i>Nycteola revayana</i>	Oak Nycteoline	variabele eikenuil	common	mm	Nolidae	1
<i>Ochropacha duplaris</i>	Common Lutestring	tweistip-orvlinder	common	w	Drepanidae	1
<i>Ochroleura plecta</i>	Flame Shoulder	haarbos	common	mo	Noctuidae	3
<i>Odonestis pruni</i>	Plum Lappet	kersenspinner	very rare	wl	Lasiocampidae	2
<i>Oligia latruncula</i>	Tawny Marbled Minor	donker halmuiltje	fairly common	mo	Noctuidae	3
<i>Oligia strigilis</i>	Marbled Minor	gelobd halmuiltje	common	mo	Noctuidae	4
<i>Oligia versicolor</i>	Rufous Minor	bont halmuiltje	very rare	mm	Noctuidae	1
<i>Opisthograptis luteolata</i>	Brimstone Moth	hagedoornvlinder	common	mm	Geometridae	18
<i>Orgyia antiqua</i>	Vapourer	witvlakvlinder	fairly common	mm	Erebidae	3
<i>Ourapteryx sambucaria</i>	Swallow-tailed Moth	vliervlinder	fairly common	mm	Geometridae	3
<i>Paracolax tristalis</i>	Clay Fan-foot	gele snuituil	rare	wl	Erebidae	60
<i>Parascotia fuliginaria</i>	Waved Black	paddenstoeluil	fairly common	wg	Erebidae	1
<i>Parastichtis suspecta</i>	Suspected	populierenuil	fairly common	mm	Noctuidae	1
<i>Parectropis similaria</i>	Brindled White-spot	witvlekspikkelspanner	fairly common	mm	Geometridae	2
<i>Pasiphila debiliata</i>	Bilberry Pug	bosbesdwergspanner	rare	wl	Geometridae	2
<i>Pechipogo strigilata</i>	Common Fan-foot	baardsnuituil	rare	w	Erebidae	1
<i>Peribatodes rhomboidaria</i>	Willow Beauty	taxusspikkelspanner	common	mm	Geometridae	63
<i>Peribatodes secundaria</i>	Feathered Beauty	geveerde spikkelspanner	fairly common	mm	Geometridae	2
<i>Perizoma alchemillata</i>	Small Rivulet	hennepnetelspanner	common	mm	Geometridae	28
<i>Perizoma bifaciata</i>	Barred Rivulet	donkere ogentroostspanner	very rare	o	Geometridae	1
<i>Perizoma flavofasciata</i>	Sandy Carpet	silenspanner	fairly common	wl	Geometridae	2
<i>Petrophora chlorosata</i>	Brown Silver-line	varensparner	fairly common	wl	Geometridae	41
<i>Phalera bucephala</i>	Buff-tip	wapendrager	common	wl	Notodontidae	24

<i>Pharmacis lupulina</i>	Common Swift	slawortelboorder	fairly common	mo	Hepialidae	76
<i>Pheosia gnoma</i>	Lesser Swallow Prominent	berkenbrandvlerkvinder	common	mm	Notodontidae	3
<i>Pheosia tremula</i>	Swallow Prominent	brandvlerkvinder	common	wl	Notodontidae	4
<i>Philereme transversata</i>	Dark Umber	wegedoornspanner	rare	mm	Geometridae	2
<i>Philereme vetulata</i>	Brown Scallop	sporkehoutspanner	rare	mm	Geometridae	1
<i>Photedes extrema</i>	Concolorous	vale duinrietboorder	rare	mo	Noctuidae	5
<i>Photedes fluxa</i>	Mere Wainscot	gele duinrietboorder	rare	wl	Noctuidae	4
<i>Photedes minima</i>	Small Dotted Buff	bochtige smele-uil	rare	mm	Noctuidae	2
<i>Phragmatobia fuliginosa</i>	Ruby Tiger	kleine beer	common	mm	Erebidae	2
<i>Plagodis dolabraria</i>	Scorched Wing	lindeknotsvlinder	fairly common	wl	Geometridae	1
<i>Plagodis pulveraria</i>	Barred Umber	geelbruine bandspanner	fairly common	wl	Geometridae	3
<i>Plemyria rubiginata</i>	Blue-bordered Carpet	blauwrandspanner	fairly common	mm	Geometridae	2
<i>Polia nebulosa</i>	Grey Arches	marmereuil	rare	wl	Noctuidae	1
<i>Polyphaenis sericata</i>	Guernsey Underwing	groene geelvleugeluil	very rare	mm	Noctuidae	10
<i>Pseudoips prasinana</i>	Green Silver lines	zilveren groenuil	fairly common	w	Nolidae	2
<i>Pseudoterpna pruinata</i>	Grass Emerald	grijsgroene zomervlinder	rare	mo	Geometridae	7
<i>Pterostoma palpina</i>	Pale Prominent	snuitvlinder	common	mm	Notodontidae	1
<i>Ptilodon capucina</i>	Coxcomb Prominent	kroonvogeltje	fairly common	mm	Notodontidae	15
<i>Ptilodon cucullina</i>	Maple Prominent	esdoorntandvlinder	fairly common	wl	Notodontidae	2
<i>Pungeleria capreolaria</i>	Banded Pine Carpet	dennenbandspanner	fairly common	wg	Geometridae	2
<i>Schranksia taenialis</i>	White line Snout	gelijnde micro-uil	very rare	wl	Erebidae	1
<i>Scopula imitaria</i>	Small Blood-vein	ligusterstipspanner	fairly common	o	Geometridae	1
<i>Scopula nigropunctata</i>	Sub-angled Wave	zwartstipspanner	fairly common	wl	Geometridae	29
<i>Scopula ornata</i>	Lace Border	kantstipspanner	rare	o	Geometridae	1
<i>Scotopteryx chenopodiata</i>	Shaded Broad bar	bruinbandspanner	fairly common	mo	Geometridae	3
<i>Scotopteryx luridata</i>	July Belle	late bremspanner	rare	mo	Geometridae	1
<i>Selenia dentaria</i>	Early Thorn	herculesje	common	mm	Geometridae	22
<i>Selenia lunularia</i>	Lunar Thorn	lindeherculesje	fairly common	w	Geometridae	3
<i>Selenia tetralunaria</i>	Purple Thorn	halvemaanvlinder	common	mm	Geometridae	38
<i>Spilosoma lutea</i>	Buff Ermine	gele tijger	fairly common	mm	Erebidae	21
<i>Stauropus fagi</i>	Lobster Moth	eekhoorn	fairly common	w	Notodontidae	9
<i>Tethea ocularis</i>	Figure of Eighty	peppel-orvlinder	fairly common	wl	Drepanidae	3
<i>Tethea or</i>	Poplar Lutestring	orvlinder	fairly common	wl	Drepanidae	1
<i>Tetheella fluctuosa</i>	Satin Lutestring	berken-orvlinder	fairly common	wl	Drepanidae	4
<i>Thalera fimbrialis</i>	Sussex Emerald	geblokte zomervlinder	rare	o	Geometridae	1
<i>Thaumetopoea processionea</i>	Oak Processionary	eikenprocessierups	common	mm	Notodontidae	174
<i>Thera britannica</i>	Spruce Carpet	schijn-sparspanner	common	mm	Geometridae	4
<i>Thumatha senex</i>	Round-winged Muslin	rondvleugelbeertje	fairly common	mo	Erebidae	2
<i>Thyatira batis</i>	Peach Blossom	braamvlinder	fairly common	wl	Drepanidae	8
<i>Timandra comae</i>	Blood vein	lieveling	common	mo	Geometridae	5
<i>Trachea atriplicis</i>	Orache Moth	meldevlinder	fairly common	mm	Noctuidae	1
<i>Triodia sylvina</i>	Orange Swift	oranje wortelboorder	common	mo	Hepialidae	11
<i>Trisateles emortualis</i>	Olive Crescent	geellijnsnuituil	common	w	Erebidae	5
<i>Watsonalla binaria</i>	Oak Hook-tip	gele eenstaart	common	wl	Drepanidae	14

<i>Xanthia icteritia</i>	The Sallow	gewone gouduil	fairly common	mm	Noctuidae	1
<i>Xanthorhoe designata</i>	Flame Carpet	koolbandspanner	common	w	Geometridae	2
<i>Xanthorhoe ferrugata</i>	Dark barred Twin spot Carpet	vierbandspanner	fairly common	mm	Geometridae	9
<i>Xanthorhoe fluctuata</i>	Garden Carpet	zwartbandspanner	fairly common	mo	Geometridae	5
<i>Xanthorhoe spadicearia</i>	Red Twin spot Carpet	bruine vierbandspanner	fairly common	mm	Geometridae	3
<i>Xestia c-nigrum</i>	Setaceous Hebrew Character	zwarte-c-uil	common	mo	Noctuidae	7
<i>Xestia ditrapezium</i>	Triple-spotted Clay	trapeziumuil	rare	mm	Noctuidae	6
<i>Xestia triangulum</i>	Double Square-spot	driehoekuil	common	mm	Noctuidae	5
<i>Xestia xanthographa</i>	Square-spot Rustic	vierkantvlekkuil	common	mm	Noctuidae	96
<i>Zanclognatha lunalis</i>	Jubilee Fan-foot	maansnuituil	rare	mm	Erebidae	113

The forest affinity is noted down with the abbreviations used in the original paper (Dorow et al., 2020): **w** = "Wald", strong affinity to forest habitats, without known preference for light or dense forests; **wg** = "Geschlossenen wald", mainly found in forests, with strong affinity to dense forest habitats; **wl** = "Lichten wald", mainly found in forests, with strong affinity to open forests, forest edges, or glades; **mm** = "Mittelmäßig", occurring equally in open landscapes and forest habitats; **mo** = "Mittelmäßig offenland", strong affinity to open landscapes, but also regularly occurring in forests, at forest edges, or in glades; **o** = "Offenland", only occurring in open landscapes or other habitats without forest cover like caves or buildings.

Totals

Table 8: Summary of the total amounts of trapped moth species and individuals per rarity, forest affinity, family and the overall total.

	Rarity		Forest affinity		Family	Total	
Individuals	Common	2061	o	83	Drepanidae	504	4743
	Fairly common	1815	mo	398	Erebidae	909	
	Rare	813	mm	240	Geometridae	1902	
	Very rare	54	w	7	Hepialidae	87	
			wl	116	Lasiocampidae	62	
			wg	1	Limacodidae	17	
			670	Noctuidae	1005		
			23	Nolidae	7		
				Notodontidae	248		
				Sphingidae	2		
Species	Common	83	o	15	Drepanidae	12	264
	Fairly common	121	mo	30	Erebidae	33	
	Rare	45	mm	111	Geometridae	115	
	Very rare	16	w	31	Hepialidae	2	
			wl	72	Lasiocampidae	4	
			wg	4	Limacodidae	2	
				Noctuidae	79		
				Nolidae	5		
				Notodontidae	11		
				Sphingidae	1		