

Alternative landscape elements in typical polder grasslands increase moth diversity, with woody structures emerging as key drivers

BSc Research Project – 24 EC

Biology, Leiden University

By Louis ten Hacken (s4105664)

Supervisors:

F.C.M. van Duin PhD

Dr. K.B. Trimbos

Dr. M.J.J. Schrama

Internship partner: Tim Arnsdorf (s4057643)

Institute of Environmental Sciences (CML)

Einsteinweg 2, 2333 CC Leiden, The Netherlands

02/03/2026 – 07/07/2026

Contact person for lab journal and raw data

F.C.M. van Duin – f.c.m.van.duin@cml.leidenuniv.nl

1 ABSTRACT

Agricultural intensification is one of the main drivers of the ongoing insect decline. Moths being one of the most affected groups, which also makes them great indicator species for insect decline. This study looked at how landscape heterogeneity influences moth diversity, abundance and community composition within polders and between three polders. With one of these polders having a heterogeneous landscape (Polderlab) and the other two a uniform landscape (Vrouw Vennepolder Zuid and Boterhuispolder). Here during April and May moths were sampled using LED-traps across 68 plots. Additional vegetation surveys were conducted to see if there is a plant species richness and moth richness correlation. Boxplots for species richness and abundance and NMDS plots together with Venn diagrams were made to investigate differences among and within polder community compositions.

During this research a total of 1,104 individuals spread across 86 species and 18 families were caught. The Polderlab had a significantly higher abundance and species richness compared to one of the reference polders, while also harbouring many species that were exclusively found there. Within the Polderlab, woody structures and alternative crop systems yielded significantly higher moth abundance and species richness compared to the grasslands. Additionally, we observed differences in moth community compositions between the woody structures, alternative crops and grasslands. Where the grasslands were dominated by ubiquitous generalist species, the woody structures and alternative crops harboured many species exclusive to these landscape elements.

All these findings show that landscape elements – particularly woody structures – positively impact moth diversity and abundance in archetypical polder landscapes. Integrating these elements into agricultural landscapes may serve as a stepping stone towards moth conservation, and perhaps by extension insect conservation.

2 ACKNOWLEDGEMENTS

I would like to show gratitude to several people regarding this project.

Firstly, I would like to thank my supervisors: Fleur van Duin, Dr. Krijn Trimbos and Dr. Maarten Schrama. Thank you for all the help and guidance throughout the entire project. And thank you for allowing me to work on this amazing project. This project has taught me many things and re-ignited an old passion within me, which will most likely guide me for future choices.

Secondly, I would like to thank my internship partner: Tim Randsdorp. Last couple of months were characterised by a lot of fun moments, even when we had tough times due to weather conditions and very early mornings. I appreciated the balance between good times and hard work ethic. Thank you for all the laughs and the moments of shared mental pain.

Finally, I would like to thank Sander Roeleveld and all the others aiding in the Polderlab project. Not only for making a suitable site for interesting and relevant research but also in working on a project that aims on making the world a better and more sustainable place.

To all these people, my sincere thanks. This project would not have been possible without all your support provided.

3 TABLE OF CONTENTS

CONTENTS

1	Abstract.....	1
2	Acknowledgements.....	2
3	Table of contents.....	3
4	Introduction	4
5	Materials and methods.....	7
5.1	Study sites.....	7
5.2	Vegetation in the polders.....	8
5.3	Landscape elements plots information.....	9
5.4	Moth sampling.....	9
5.5	Statistical analyses.....	10
6	Results	12
6.1	Polder comparison: species richness and abundance.....	12
6.2	Polder comparison: communities.....	12
6.3	Landscape elements comparison with grassland in the Polderlab: species richness and abundance.....	13
6.4	Landscape elements comparison with grasslands in the Polderlab: communities	14
6.5	Explanatory variables: spatial drivers and weather conditions	15
6.6	The effect of plant species richness on micro- and macromoths.....	15
7	Discussion.....	16
8	References	19
9	Appendices.....	25
9.1	Appendix A: Grouping of the plots.....	25
9.2	Appendix B: Sampling rotation.....	25
9.3	Appendix C: Woody structures around landscape elements	26
9.4	Appendix D: Moth species and their corresponding taxonomic families	26
9.5	Appendix E: Plant species richness effects on micro- and macromoth diversity	29
9.6	Appendix F: Model fit, diagnostic plots and AIC values	30

4 INTRODUCTION

Humanity, and the world, is facing the sixth mass extinction in the history of life (Schickhoff et al., 2024). Whereas prior mass extinctions had causes external to life itself, this biodiversity crisis is undeniably man-made (Jarne, 2025). This crisis will take toll on almost all eukaryotic taxa, but some will take heavier hits than others. And because it is estimated that more than half of eukaryotic life are insects (Dunn, 2005), the biodiversity crisis is predominantly an insect biodiversity crisis. Counterintuitively, most conservation studies focus on the conservation of mammals, birds and amphibians (Clausnitzer et al., 2009; Cowie et al., 2022). For pollutants, often named as a main driver for biodiversity loss, many studies have been conducted regarding these extensively studied taxa. However, similar studies are often limited or even absent for insect taxa (Goulson, 2019). This absence of knowledge often results in insects not being part of conservation efforts, even though the highest extinction risk and thus the greatest loss of biodiversity is expected to be suffered by invertebrates (Clausnitzer et al., 2009). The studies that have taken place which are becoming more numerous predict that 100,000 of every 1 million species is expected to go extinct by 2050 (Dunn, 2005). This would imply that more than 50,000 of every 1 million insect species is expected to go extinct by mid-century (Dunn, 2005).

However, this insect biodiversity crisis did not start yesterday. On the contrary, these bitter future estimations are in line with prior study results. In Germany a shocking seasonal decline of 76%, and mid-summer decline of 82% in flying insect biomass was estimated over 27 years (Hallmann et al., 2017). These numbers indicate that insect decline has been happening for a while and is not stopping any time soon (Dunn, 2005). Most of this decline can be credited towards agricultural intensification (Habel et al., 2021; Raven & Wagner, 2021). As this directly results in decreasing farmland quality due to the loss of habitat and functional connectivity, which especially takes a heavy toll on specialist species that require certain niches to exist (Grevé et al., 2024; Habel et al., 2021). Furthermore, the scope of this problem becomes evident when the realisation sets in that around 11% of the Earth's land area is devoted to crops, and 30% more is used for grazing (Raven & Wagner, 2021). An increase in agricultural areas also result in the decrease of semi-natural grasslands regionally, nationally and globally (Bullock et al., 2011). Illustrating this is the decline of 40% to 3% in land cover of semi-natural grasslands over the last century in the Netherlands (Van Strien et al., 2019).

In the context of long-term insect decline, the loss of semi-natural grassland area and the decrease in farmland quality, it is important to research taxa that can signal these ongoing changes. Moths are helpful in this regard: they are an established indicator species for both insect decline (Conrad et al., 2006) and farmland quality (Macdonald & Feber, 2015). This is because they are ecologically diverse and can therefore represent a wide range of insect taxa (Conrad et al., 2006; Macdonald & Feber, 2015).

Besides their role as indicator species, moths are of importance in many different ecosystems, fulfilling different roles. With one of these roles being their place in food webs, accounting for a substantial portion of insect biomass available to insectivores, both as caterpillars and adults (Wagner et al., 2021). This biomass is a valuable food source for many species of birds, bats and even small mammals (Fuentes-Montemayor et al., 2011; Wagner et al., 2021). Besides their role as prey, the importance moths hold in flower pollination appears to be underestimated (Hahn & Brühl, 2016). As a matter of fact, moths are of considerable importance for flowering plants (New, 2004). Some studies suggest moths are second in importance only to bees. Additionally, species of at least 75 plant families are pollinated partially or even exclusively by moths (New, 2023). This is backed up by the findings that moths accumulate electrostatic charges when airborne. The electrostatic charges generate an electric field that is sufficient to attract pollen contactless. Important to note, bees and bumblebees, that are well-known pollinators, share this ability as well (England & Robert, 2024). The plant's reliance on moths works both ways. Moths, especially during the larval stage, are generally confined to feeding on one or a few plant genera or even species (Miller, 1992). This plant-moth relationship means that moth diversity mirrors the broader diversity present in the polder landscapes, which emphasises the need to transform uniform polders into more

complex landscapes, as higher plant diversity also enhances corresponding moth diversity, and vice versa.

However, despite their ecological value and sensitivity to landscape structure, moths themselves are facing challenges. The ramifications of external pressures, and habitat disappearance, are very evident in moths. Even though moth trends differ spatially and temporally, prevalent moth declines are undeniably clear-cut (Bell et al., 2020; Wagner et al., 2021). For example, in Great Britain a 31% decline was modelled over 47 years. However, short-term trends reveal periods of steep decline, but also of recovery (Bell et al., 2020). Within the same country, data was collected for 337 species across 35 years. Results revealed that two-thirds of species showed a declining trend and an additional 21% showed a >30% decline in abundance (Conrad et al., 2006). Furthermore, another study conducted in the Netherlands opportunistically modelled a decline of 87% for 71 moth species that were sampled during 1890 and 2017 (Van Strien et al., 2019). These steep declines highlight the importance of understanding the ecological requirements of moths and the factors – such as plant diversity – that aid in their conservation.

Given that moth and plant diversity are tightly interlinked it becomes evident that moth conservation strategies should in part be aimed towards increasing plant diversity. Currently, existing knowledge regarding this is mainly focussed on economically important and easy-to-observe plant species. And ecologically not enough is known about the habitat (plant) requirements and behaviour of the adult moths (Tyler, 2020). A study in Sweden found that moth abundance and moth species richness were positively correlated with woody plant genera within sight of the trapping site. Additionally, higher plant diversity suggested a positive relationship with higher moth abundance and species richness (Tyler, 2020). With micromoths being less mobile than macromoths, they are influenced more strongly by plant species richness (Kühne et al., 2022). In line with this, woody landscape elements, like hedgerows, have proven to positively impact grassland species richness and abundance on farmland (Coulthard et al., 2016; Merckx et al., 2012). This positive correlation is built upon the idea that hedgerows provide food and shelter for moths, especially macromoths (Coulthard et al., 2016; Kühne et al., 2022). Clearly, woody structures prove useful in moth diversity and abundance for the reasons mentioned above. These woody elements are a powerful addition to landscape heterogeneity. This results in a wider variety of niches and habitats for moths to live in. Adding to this landscape heterogeneity is the presence of semi-natural patches and areas with higher vegetation diversity, like wildflower-rich field margins. This spatial complexity, or heterogeneity, has proven key in obtaining the highest moth diversity and abundance (Botham et al., 2015; Dantas de Miranda et al., 2019). These insights are particularly relevant for traditional polder landscapes, which are dominated by uniform grasslands. Such homogeneity limits the availability of a wide range of niches, making polders ideal systems for implementing these heterogeneity-promoting landscape elements.

Putting all these pieces together, it should be clear that landscape-scale conservation efforts should be implemented (Botham et al., 2015; Fuentes-Montemayor et al., 2011; Merckx et al., 2009). A significant share of the studies has investigated the effects of hedgerows and field-margins (Coulthard et al., 2016; Merckx et al., 2009, 2012). Other studies focussed on floral diversity impacts on moth species richness and diversity (Alison et al., 2017; Blumgart et al., 2023; Tyler, 2020). Moths in cranberry and rice fields have been studied, but mainly regarding moths as pest species (Drolet et al., 2019; Kurmi et al., 2021; McMahan et al., 2017; Yaakop et al., 2020). However, no prior research has been done on the effect of a food swamp on moth diversity. But most importantly, no research has been done for a combination of all these landscape elements regarding their individual and combined effects on moth diversity in archetypical polder landscapes. Thereby simultaneously mapping the enhancing effects of landscape heterogeneity on moth diversity. For this, a research site like our own, that contains all these landscape elements, would give opportunity to try to close this knowledge gap, which in turn could bring us a step closer towards grassland moth conservation.

Aiding in these conservation efforts are agri-environment schemes (AES). These schemes are a way to fund farmers for partaking in less intensive management of environmentally sensitive areas (Lécuyer et

al., 2021). Furthermore, these schemes allow for more research being done in these areas regarding biodiversity. Upcoming land-use change problems make this research topic a necessity. Increased food demand in the following decades, together with the predicted 10-25% expansion of cropland areas, due to expected increases in human population, could be troubling for biodiversity (Schickhoff et al., 2024). This gives need for eco-friendly and diversity promoting agricultural practices and policies. To evaluate these eco-friendly and diversity-enhancing practices, we monitored moth diversity, abundance and communities in three Dutch polders sites, using moths as established indicator species for insect decline (Conrad et al., 2006) and for farmland quality (Macdonald & Feber, 2015).

This study aims to investigate landscape elements that influence moth diversity and abundance across multiple spatial scales. For this, we addressed 2 questions:

Question 1: How does landscape heterogeneity within a polder influence moth diversity, abundance and community composition compared to more uniform polders?

Question 2: How do landscape elements influence moth diversity, abundance and community composition in comparison to grasslands within a polder?

Regarding the moth's species richness, we hypothesized that the diversity would be lowest on grasslands, higher in alternative crop systems (e.g. rice fields, food swamp and cranberry fields) and highest around woody structures (e.g. hedgerows, agroforestry and the forest). Furthermore, we expected moth species richness – mainly micromoth richness – to be positively correlated with plant species richness. For the moth's abundance, we hypothesized that the abundance would be highest around woody structures, and not in favour of either grasslands or alternative crop systems. Additionally, we expected that plant species richness would hold little to no explanatory power over the moth's abundance. Finally, community-wise, we hypothesized that communities would significantly differ between the heterogenous polder and the uniform polders. On top of this, we expected that woody structures, alternative crop rotations and grasslands would all yield dissimilar communities.

To answer the research questions, we conducted moth monitoring research in an agricultural area close to Leiden in the Netherlands. Our setup consisted of three polders, one of these had a significantly more heterogeneous landscape than the other two. The other two polders were uniform polders containing relatively homogenous vegetation and thus were used as reference sites. These polders are named the Boterhuispolder (BP) and the Vrouw Vennepolder Zuid (VVZ). The heterogeneous polder, which we call the Polderlab (PL), contains landscape elements and alternative crop systems. Respectively, these are: rice fields, food swamp, agroforestry, cranberry fields with agroforestry, cranberry monoculture fields, a forest island, hedgerows and grasslands (mown and grazed). Using the data gathered we hope to get a general idea of the individual effects of these landscape elements. Furthermore, we will assess how the combined effects of these elements shape polder-level diversity, and how this heterogeneity contrasts to the uniform polders. This knowledge should provide more insight into beneficial landscape elements and approaches that enhance moth, and by extension insect diversity. Eventually, this should lead to policies that can accommodate increasing food demands and worldwide expansion of cropland areas while counteracting the ongoing biodiversity crisis.

5 MATERIALS AND METHODS

5.1 STUDY SITES

During the months April and May of 2026 moths were sampled using light traps in three polders. These typical polders in the Dutch peatland landscape are located in the Western part of The Netherlands. The Polderlab (PL) is a polder that nowadays is being managed extensively and contains multiple landscape elements. Historically the Polderlab was a high productive grassland until late 2020. Regular mowing, fertilisation by injection of liquid slurry, groundwater tables of 40cm during the summer and 60cm during the winter and no grazing characterise this intensively managed polder (Marselis et al., 2024). The Boterhuispolder (BP) was historically a high productive grassland but switched to more extensive management in 2010. The Vrouw Vennepolder Zuid (VVZ) had switched to a more extensive management before this. These polders, used as study sites, are within close proximity of each other (<1km). For this research, 68 sampling sites spread across these polders were used. Of these 68, 40 sampling sites (plots) were in the PL, 10 in the BP and 18 in the VVZ. See figure 1 for the location of the plots and the three polders. It is important to note that only 10 plots were used at the same time in the VVZ. This is due to having to move 8 plots for growing concerns regarding the breeding of meadow birds.

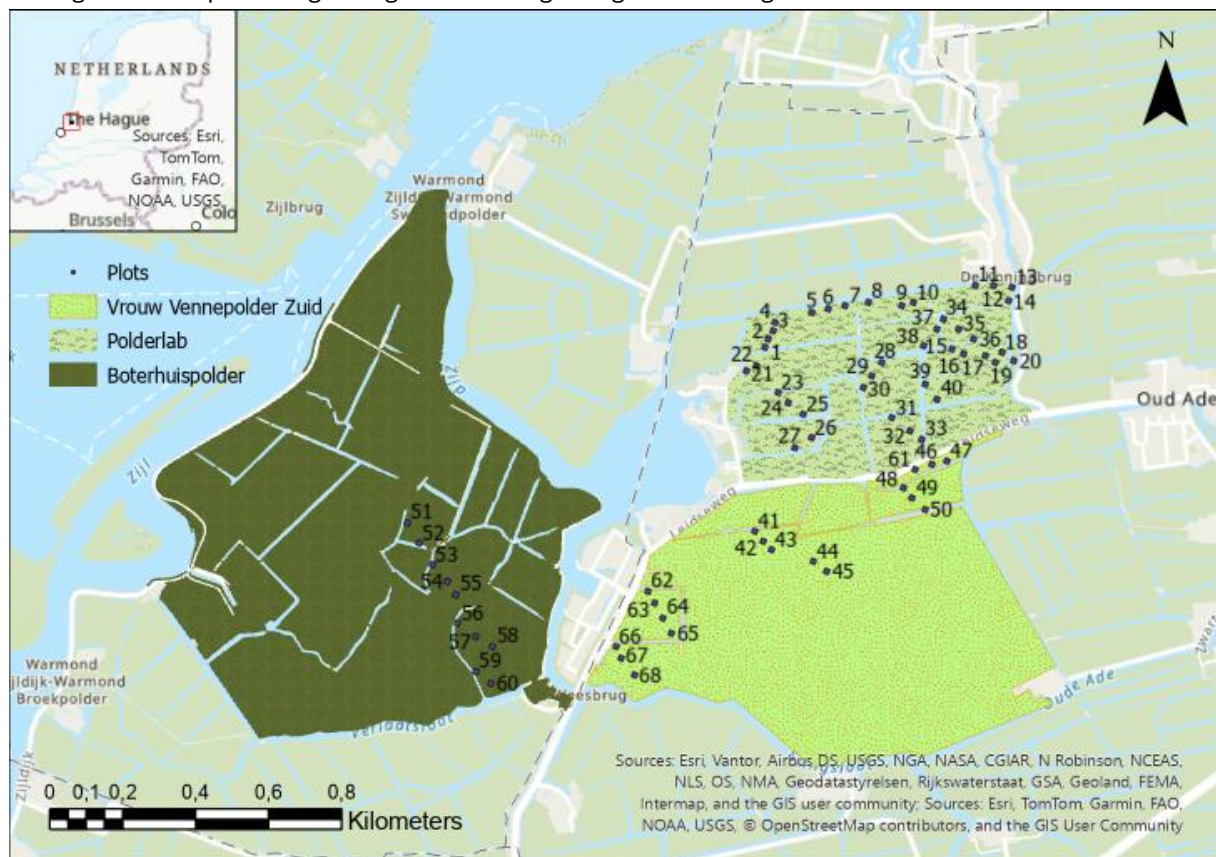


Figure 1. Map showing the three sampled polders: Vrouw Vennepolder Zuid, Boterhuispolder and the Polderlab. Numbered points indicate each sampling plot within the polders.

The landscape-scale heterogeneity differs between these polders. The entirety of the BP and VVZ consists of grassland. However, the PL is a grassland-dominated polder that contains a variety of landscape elements (e.g. rice fields, food swamp, cranberry fields, agroforestry and a small forest island). See figure 2 below for the landscape elements in the Polderlab and their locations.

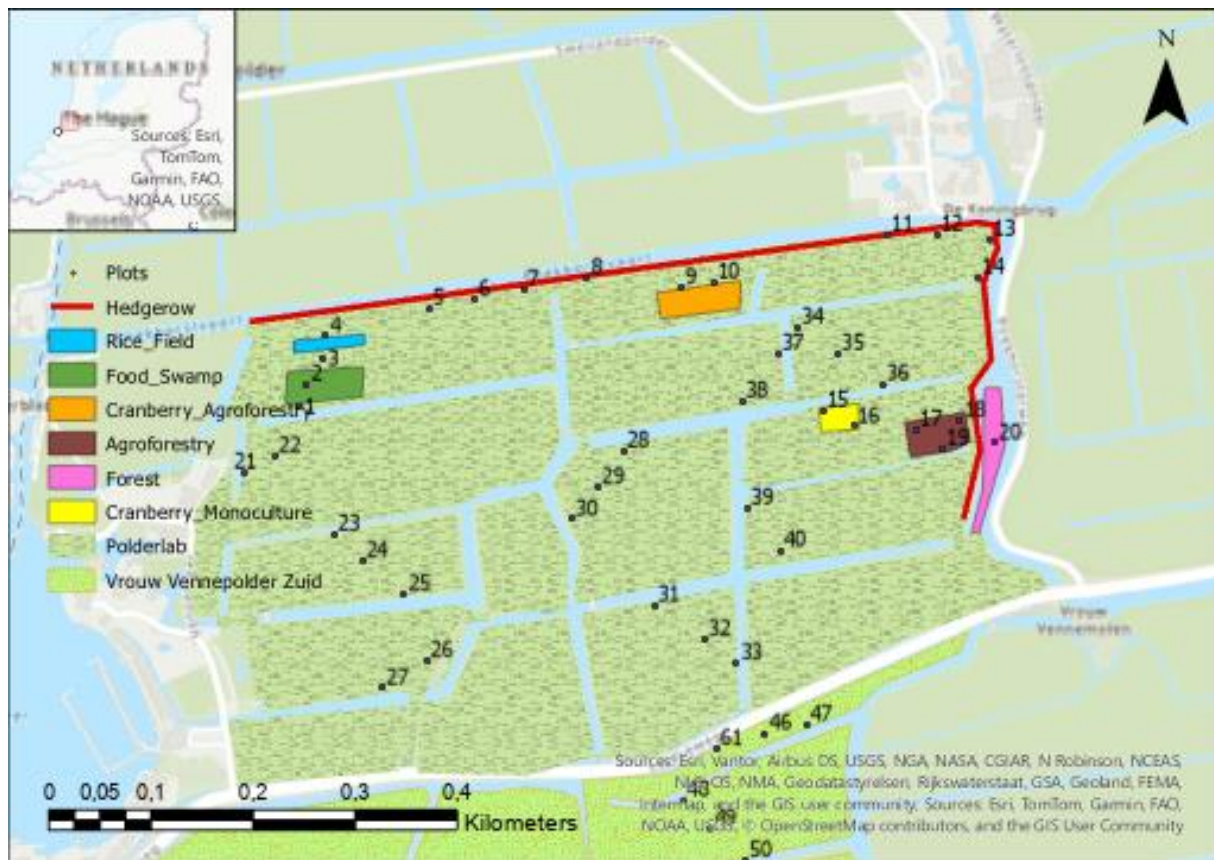


Figure 2. Map zoomed in on the Polderlab, showing all landscape elements in different colours. Numbered points indicate each sampling plot within the polder.

5.2 VEGETATION IN THE POLDERS

Naturally, the vegetation differs between the polders due to differences in landscape elements. Typical grassland and ditch bank vegetation dominated in the BP and VVZ. The PL, besides grassland, contained a very diverse hawthorn-dominated (*Crataegus monogyna*) hedgerow, a willow-dominated agroforestry containing a variety of trees like wild cherry (*Prunus avium*), common hazel (*Corylus avellana*) and the European crab apple (*Malus sylvestris*), a willow-dominated forest island containing trees like the rowan (*Sorbus aucuparia*) and the red currant (*Ribes rubrum*). The remaining alternative crop systems were characterised with a high floral diversity and mainly juvenile trees and shrubs.

The BP contained fields of grass with high density and overall length (up to one meter). The VVZ had fields of grass with plots that were mown and grazed during and before the research. The grazing took place in the second week of May. And the mowing took place on the 7th of May. Both of which resulted in an overall lower floral diversity and vegetation coverage. The PL had areas that were mown and areas that were grazed before the research. This management choice resulted in dissimilar floral diversity and communities. Additionally, ditch banks in the PL were mown once during the research in May, which resulted in reduced ditch bank vegetation coverage and diversity. This floral diversity, and the changes over time have been mapped by the conducting of vegetation surveys.

These vegetation surveys were conducted throughout both months as a way of getting an idea of plant species present around plots. Plant species richness contributes to landscape heterogeneity by creating gradients ranging from areas of high to low plant diversity, thereby supporting a wide array of ecological niches suitable for corresponding diverse moth communities. And changing plant compositions, especially during spring, give need to frequently conducted vegetation surveys.

The surveys were conducted using a standardised protocol. After placing the LED-trap, a vegetation survey was conducted of 1m² around the trap. Then, two extra vegetation surveys were conducted 15m from the LED-trap. This is because the attraction radius of LED-traps is less than 30 meters (Truxa & Fiedler, 2012). Besides, there are different attraction radii for different families of moths (Merckx & Slade, 2014). It is noteworthy that this experiment was done with 15W LED-traps. The LED-traps we used contained a LED strip with the following specifications: 12-volt SMD 2835 UV LED Strip light of 395-405nm ("LedEmmers", z.d.). Together with the electric current output of the powerbank this results in a 18W LED-trap. This together with the vegetation blocking some of the light, we estimated an average attraction radius of 15m. Hence, doing the 1m² vegetation survey 15m from the trap gives somewhat of an idea of the vegetation from which the moths can be attracted from.

When conducting the vegetation survey, solely the plant species present were written down. No information regarding density or coverage was gathered. Where possible, the plant species were identified at species level by using the app ObsIdentify and our own knowledge. In other cases, the plants were identified at genus level. Furthermore, trees and shrubs were present in the landscape elements. These did not always end up in the vegetation surveys conducted and therefore, these were added in a different dataset. This data was used for knowledge on the woody structures present and the ecology of the moths.

5.3 LANDSCAPE ELEMENTS PLOTS INFORMATION

Every plot is associated with a type of landscape element or a type of grassland (Appendix A). For the statistical analyses these plots were grouped for comparison. Each of these groups had unique vegetation structures and types, of which most contained some type of shrubs or woody structures (Appendix C). The hedgerow ran across the North and East side of the Polderlab, and its plots were characterised by the most diverse array of woody plant species and the highest overall plant species richness. The agroforestry was a willow-surrounded area that contained numerous other trees and many herbaceous species. The forest island was located near the hedgerow and the agroforestry and had a unique but homogenous vegetation, containing a small number of tree species that formed a dense, homogenous canopy. The rice fields and the food swamp were located next to each other and were alternated by ridges containing a diverse mix of small trees and shrubs. The cranberry agroforestry plots were located on the edge of cranberry fields next to a ridge containing small trees and herbaceous species. The cranberry monoculture plots were located within a square area characterised by very low vegetation diversity, containing only a few tree species and barely any ground-layer plants due to wood-shavings covering the ground around.

5.4 MOTH SAMPLING

In 2026, moths were sampled during the months of April and May. Across these 8 weeks there were 24 sampling days. Every sampling night, 20 traps were placed across the plots following a fixed rotation (Appendix B) designed to equalize sampling efforts across the polders. Because the VVZ and the BP contained four times fewer plots than the PL, they were sampled four times more frequently. Additionally, the 40 plots in the PL were split into two groups of 20, both containing 10 plots associated with landscape elements and 10 with grasslands. Within these grassland plots, half were historically mown and half historically grazed.

On the sampling days we distributed light-traps across the 20 alternating plots, according to the rotation. These light-traps (LED-traps) were put down at the plots during the late afternoon, and always before sunset. We sampled on days if the mean nightly temperature was above 5 degrees Celsius. And no traps would be set for nights with temperatures reaching below this value. For rain and wind there were no sampling requirements set, as these factors were deemed to not influence moth catching significantly (Jonason et al., 2014). Every sampling day, the assembling of the LED-traps happened accordingly to the manual provided by the Vlinderstichting, except for the addition of a light sensor. The next morning, starting from 07:00 we began checking the traps. For every trap the present species and their abundance were written down. Where possible, identification was done to species level using the phone app ObsIdentify. For species that were difficult to identify we looked at literature to try to determine the species. When not being able to identify the exact species, we identified to genus or, in some cases, family level.

5.5 STATISTICAL ANALYSES

All analyses were run in RStudio (2026.05.0+218) and for all analyses a significance threshold of $p < 0.05$ was applied. Firstly, a linear model (LM) was fitted for both richness and abundance, wherein plant species richness nested in the type of management (Type:Plant_Spec) and the distance from the hedgerow (Near_Dist) were explanatory factors. Model selection was based on AIC, a likelihood-based criterion that evaluates model fit. The linear model had lower AIC values for both richness (AIC = 397.2) and abundance (AIC = 544.9) compared to the Poisson GLM (richness AIC = 412.7; abundance AIC = 699.6). Despite richness and abundance being count data, which normally requires a Poisson GLM, a linear model fitted better. Additionally, diagnostic checks revealed that the Poisson GLM contained several influential observations (Appendix F). Herein the residuals-vs-leverage plots showed observations with relatively high leverage and exceeded Cook's distance thresholds, indicating greater sensitivity of the model to individual data points. Diagnostic checks on the linear model revealed no aberrations (Appendix F). Because plant species richness was closely correlated with the type of management it was modelled as a factor nested within management type. In line with this was a lower AIC for the nested model (richness AIC = 397.2; abundance AIC = 544.9) compared to the unnested model (richness AIC = 410.6; abundance AIC = 549.8). Therefore, the model with the best fit was richness/abundance ~ Type/Plant_Spec + Near_Dist. To analyse individual explanatory power of each predictor an ANOVA was conducted to determine the proportion of variance (PropVar) explained by each model factor.

For weather conditions, a linear model was fitted that included the average nightly wind speed (MeanWind), the rain as binary factor, moon brightness (MoonIllum), moon visibility (MoonVis) and the average temperature (MeanTemp), with average temperature added as a second-degree polynomial term. For all weather effects the data was extracted for the period of 22:00 to 06:00 of the sampling night. The windspeeds and information on the rain was extracted from the KNMI website (*Uurgegevens van het weer in Nederland*, z.d.). Information regarding the temperature was extracted using a measuring device on site. The moon brightness (MoonIllum) was extracted in RStudio using the lunar package. The proportion of the night the moon was above the horizon (MoonVis) was calculated using <http://www.mooncalc.org>. The temperature being included as a second-degree polynomial term was done because when the temperature reached above a certain point the richness and abundance increased exponentially. Therefore, this second-degree polynomial term was fitted for temperature to capture this non-linear relationship with species richness and abundance. In line with this was the lower AIC this polynomial model had (richness AIC = 167.5; abundance AIC = 242.7) compared to the regular linear model (richness AIC = 168.6; abundance AIC = 272.9).

Using the package ggplot2, boxplots were created to visualise the differences in richness and abundance across polders. Due to unequal sample sizes and number of plots, the abundance was expressed in abundance per unit effort (sampling night) per plot. A selection of PL plots was made for richness to even out the sampling effort. For this, 10 random plots from the first PL and 10 random plots from the second PL sampling day were chosen and these were put against all the plots from the BP and the VVZ. After

visualisation of each boxplot a Kruskal-Wallis test was run to see whether there were differences between the polders for richness and abundance. Subsequently, the package FSA was used to conduct Dunn's tests with a Bonferroni correction to analyse pairwise differences between the polders.

Before the analysis of the grouped management types, all PL plots were assigned to one of three management categories (Woody, AltCrops, Grass). The hedgerow, agroforestry and forest island plots were grouped together for the woody structures (Woody). And the rice field, food swamp, cranberry agroforestry and cranberry monoculture plots were grouped together for the alternative crops (AltCrops). All grassland plots were grouped together (Grass). Using the package ggplot2, boxplots were created to visualise the differences in richness and abundance across these management types. The species richness and abundance were expressed in richness/abundance per plot. Despite the unequal sample sizes (Woody = 12; AltCrops = 8; Grass = 20), no random selection of 10 plots from the grassland was made. This was because of the small sample sizes and to avoid the unnecessary loss of information. After visualisation Kruskal-Wallis tests were run to see whether there were differences between the management types for richness and abundance. Subsequently, the package FSA was used to conduct Dunn's test with a Bonferroni correction to analyse pairwise differences between the management types.

For all Non-metric Multidimensional Scaling plots (NMDS) the packages vegan and dplyr were used. NMDS plots were made to visualise community composition for both the polders and the grouped management types. For the polder NMDS all sampling sites (points) were used except for the ones with no observations, which were filtered out of the dataset. Community dissimilarities across the polders and grouped management types were analysed using Sørensen distance (presence/absence). A subsequent PERMANOVA tested for differences between community compositions, whereas the beta-dispersion analysis assessed differences in within-group variability (polders or management types). Pairwise differences among polders were looked at using Tukey post-hoc tests.

To investigate the effects of plant species richness on micro- and macro moths, the moths had to be divided into these groups. This division was based on published literature and the taxonomic families the moths belonged to as shown in the appendix (Appendix D). For each group, a scatterplot was made for both species richness and abundance. Subsequent Pearson correlation tests were run to investigate the relationships between plant species richness and micro- and macromoth abundance and species richness. Differences between micro- and macromoths were looked at using interaction models, wherein the interaction term tested whether the slopes of micro- and macromoths differed significantly. All this was done using the packages ggplot2 and dplyr.

6 RESULTS

A total of 1104 individuals were captured throughout the 2-month trapping period. These individuals were spread out across 86 species from 18 different families of moths. Most of the moths came from the families Noctuidae and Tortricidae which both had 20 representatives (each 22% of the total). Other families included the Crambidae and the Geometridae which both had 13 representatives (each 14.3% of the total). All other families contained 5 or less representatives.

6.1 POLDER COMPARISON: SPECIES RICHNESS AND ABUNDANCE

Overall, a Kruskal-Wallis test showed significant differences in species richness per plot between the polders ($\chi^2 = 11.69$, $df = 2$, $p = 0.002895$). Post-hoc pairwise comparisons (Dunn's test) between polders revealed a significant difference between the PL and VVZ ($z = 3.25$, $p = 0.0072$); see the right boxplot of Figure 3. However, no difference was found between the BP and the PL ($z = -0.32$, $p = 0.5503$) and the BP and the VVZ ($z = 2.36$, $p = 0.05426$).

The abundance (individuals caught per unit effort per plot) also differed significantly between polders (Kruskal-Wallis: $\chi^2 = 12.695$, $df = 2$, $p = 0.001751$). Pairwise comparisons (Dunn's test) revealed that there was a significant difference in abundance between the PL and the VVZ ($z = 3.70$, $p = 0.00124$); see the left boxplot of Figure 3. However, there was no significant difference between the BP and the PL ($z = -1.67$, $p = 1.00$) and the BP and VVZ ($z = 1.17$, $p = 0.0924$).

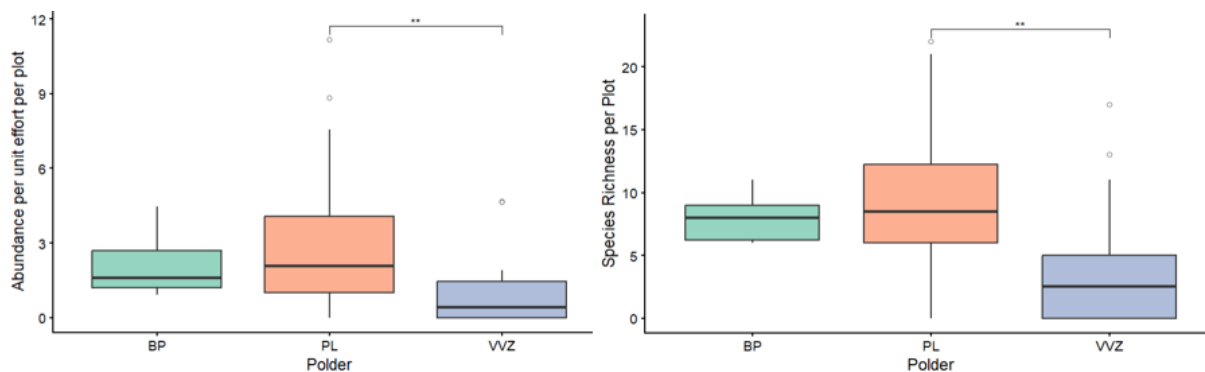


Figure 3. Boxplots showing abundance (left) and species richness (right) for the three sampled polders: the Boterhuispolder (green), the Polderlab (orange) and the Vrouw Vennepolder Zuid (blue). Both show the distribution of values, with the abundance calculated per unit effort per plot and the total species richness value per plot. The two asterisks indicate a significant difference ($p < 0.01$).

6.2 POLDER COMPARISON: COMMUNITIES

Seeing that there are differences in species richness across the polders, the next step is to look at the communities. The moth communities can illustrate the impact of spatial heterogeneity in polders. Additionally, unique and shared species between polders give an idea of the number of ubiquitous species and species typical for the polders. The NMDS plot on the left in figure 4 shows that the PL hosts a community (ellipse) that almost encompasses both the BP and VVZ communities. Meaning that the communities of the BP and VVZ are less species rich and barely contain species unique to their grassland. The many orange points (PL) that fall outside the blue (VVZ) and green (BP) ellipses show that the PL plots host many communities that are different from the communities on the grasslands of the BP and the VVZ. The PERMANOVA revealed that there were significant differences in community composition

between polders ($F(2, 55) = 2.62, p = 0.001, R^2 = 0.087$). A subsequent test of multivariate dispersion (betadisper) revealed a significant difference in within-community variance ($F(2, 55) = 7.67, p = 0.005$). Post-hoc pairwise comparisons (Tukey test) showed that the BP differed significantly with the PL ($p = 0.00072$) and the VVZ ($p = 0.03526$). No significant differences were present between the within-community variance (heterogeneity) of the PL and the VVZ ($p = 0.76401$).

These differences are backed up by the Venn diagram on the right in figure 4. Here 52 species are unique to the PL. While the BP and VVZ respectively have 3 and 6 unique species. And in the middle are the 14 ubiquitous species that are shared across all 3 polders, most of which are generalists. Which include species like the shuttle-shaped dart (*Agrotis puta*) and the small square-spot (*Diarsia rubi*) that feed on a wide variety of grassland herbs and common species including dandelions and sorrel. Despite having a lower species richness per plot, the VVZ yields a higher total species richness (31). Additionally, more species are solely shared between the PL and the VVZ (9) than the PL and the BP (6). And only 2 species are shared by the VVZ and the BP that do not occur in the PL.

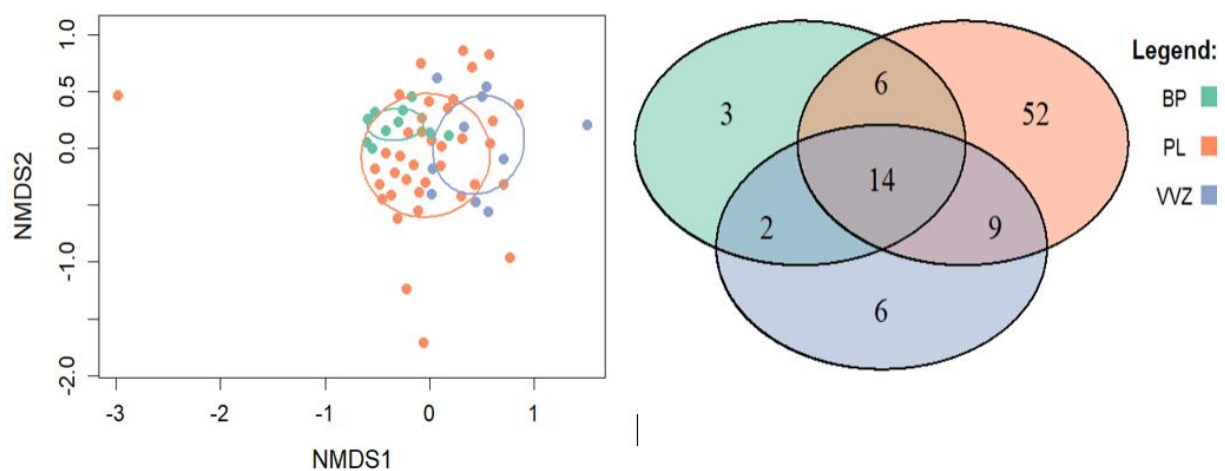


Figure 4. A NMDS plot (left) and a Venn diagram (right) of the three sampled polders: the Boterhuispolder (green), the Polderlab (orange) and the Vrouw Vennepolder Zuid (blue). On the left ellipses are fitted around the individual communities of each plot (dots) within the polder, thereby showing similarities and dissimilarities in moth community composition between the polders. On the right is a Venn diagram that illustrates the number of unique and shared species between these polders, highlighting overlap and uniqueness in species composition.

6.3 LANDSCAPE ELEMENTS COMPARISON WITH GRASSLAND IN THE POLDERLAB: SPECIES RICHNESS AND ABUNDANCE

Overall, a Kruskal-Wallis test showed significant differences between the landscape elements and grasslands in species richness ($\chi^2 = 16.33, df = 2, p = 0.0002849$). Post-hoc pairwise comparisons (Dunn's test) revealed that the species richness in the grasslands differed from the woody structures ($z = -3.77, p = 0.00051$). The alternative crop groups also differed significantly from the grasslands ($z = 2.64, p = 0.02502$), see the right plot in Figure 5. No significant difference was found between the alternative crop group and the woody group ($z = -0.59, p = 1.0000$).

When looking at the number of individuals caught there was again a significant difference found (Kruskal-Wallis: $\chi^2 = 12.19$, $df = 2$, $p = 0.002252$). Post-hoc pairwise comparisons (Dunn's test) revealed that only the grassland differed significantly with the woody structures ($z = -3.37$, $p = 0.00221$), see the left plot in Figure 5. No significant differences were found for the alternative crop systems in comparison to the woody structures ($z = -0.91$, $p = 1.0000$) and grasslands ($z = 1.95$, $p = 0.1528$).

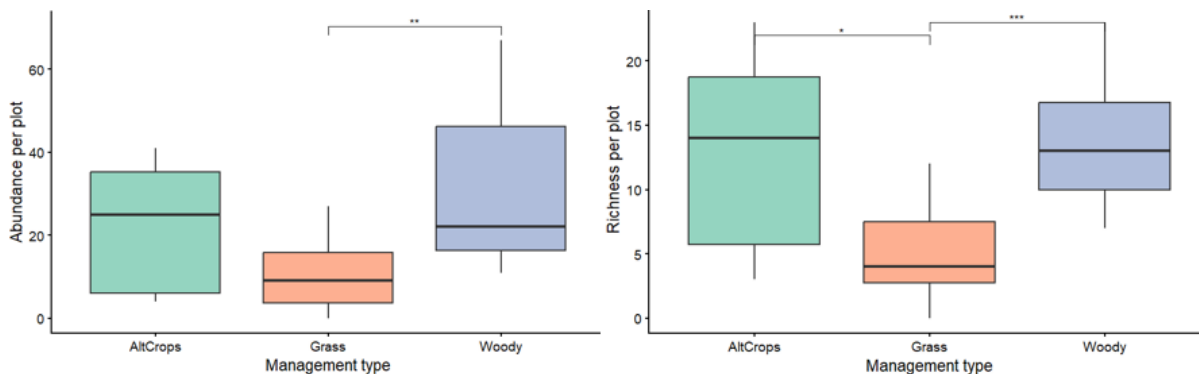


Figure 5. Boxplots showing abundance (left) and species richness (right) for the three grouped management types: the alternative crops (green), the grasslands (orange) and the woody structures (blue). Both show the distribution of values per plot, with asterisks representing a p -value for significance: * = 0.05, ** = 0.01, *** = 0.001.

6.4 LANDSCAPE ELEMENTS COMPARISON WITH GRASSLANDS IN THE POLDERLAB: COMMUNITIES

Next to species richness and abundance, communities are a great way of showing differences between land-use types, as mentioned above. In figure 6 the NMDS plot on the left reveals that all three groups are closely clustered and overlap with each other, suggesting that their communities share a fair amount of species. At the same time, several points fall outside of the ellipses, suggesting that the community structures are not homogenous and some sites may contain different species compositions. The PERMANOVA revealed that there is a significant difference in community structures between the woody, alternative crops and the grassland groups ($F(2, 35) = 2.51$, $p = 0.001$, $R^2 = 0.125$). A subsequent test of multivariate dispersion (betadisper) revealed no significant difference in within-community variance between the landscape elements ($F(2, 35) = 0.5001$, $p = 0.602$).

The Venn diagram on the right in Figure 6 shows a great number of shared species in the middle (23). These species are ubiquitous in the PL with most of them being generalists, like the small square-spot (*Diarsia rubi*) and the white ermine (*Spilosoma lubricipeda*). These generalist species feed on a wide variety of grassland herb species like plantain and sorrel. It is noteworthy that the grasslands only contain 3 unique species, showing that the grasslands mainly contain generalists and only few specialist species. Differently, the woody structures contain 27 species that do not occur in the other land-use types. Showing that these woody structures are not only good for generalists but especially for specialists. Additionally, the alternative crop systems contain 16 species not found in the other land-use types. Which again shows that these alternative crop systems are good for both generalists and specialists. Together with the 11 shared species the woody structures and the alternative crop systems host 54 unique species which are not present in the grasslands. A shared community of the woody structures and the alternative crops systems yields 76 species out of the 80 species present. Whereas the grassland community yields only 26 species.

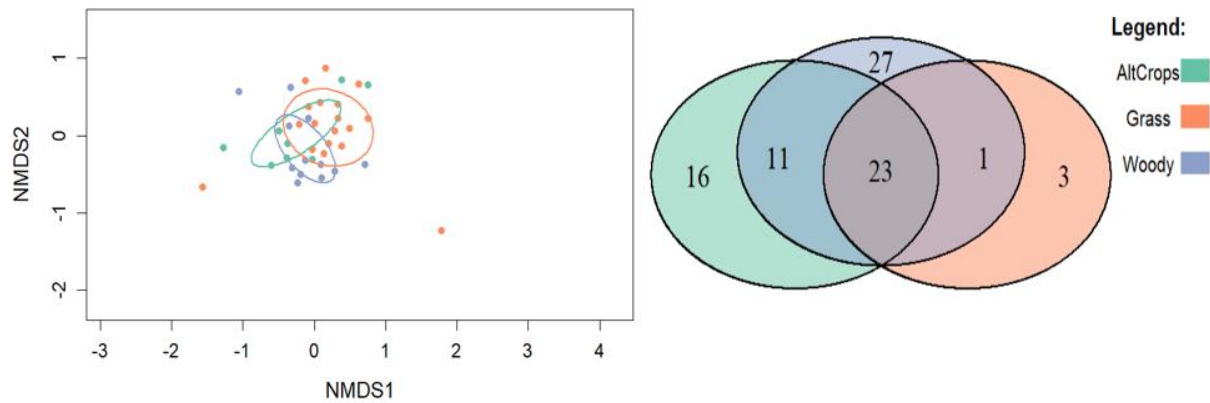


Figure 6. A NMDS plot (left) and a Venn diagram (right) of the three grouped management types: the alternative crops (green), the grasslands (orange) and the woody structures (blue). On the left ellipses are fitted around the individual communities of each plot (dots) within the management types, thereby showing similarities and dissimilarities in moth community composition between these types. On the right is a Venn diagram that illustrates the number of unique and shared species between these management types, highlighting overlap and uniqueness in species composition.

6.5 EXPLANATORY VARIABLES: SPATIAL DRIVERS AND WEATHER CONDITIONS

Spatial drivers (management type, plant species richness and distance from hedgerow) and weather conditions (temperature, rain, windspeed, brightness and phase of the moon) are drivers for the abundance and the species richness displayed by the boxplots in figures 3 and 5.

The model with plant species nested in the type explained 42.7% (Adjusted R-squared = 0.427) of the variance for abundance and 59.8% (Adjusted R-squared 0.598) for species richness. Leaving 57.2% of the abundance variance and 40.2% of species richness variance unexplained by the model. The species richness ANOVA results showed that management type explained the largest proportion of variance (PropVar = 0.552), followed by the nested Type:Plant_Spec term (PropVar = 0.169). Whereas the near distance from hedgerow contributed negligibly (PropVar = 0.002). For abundance, management type similarly explained the largest proportion of variance (PropVar = 0.448), with the nested Type:Plant_Spec term contributing some additional explanatory power (PropVar = 0.162). Near distance from the hedgerow again showed a negligible effect (PropVar = 0.0003).

The polynomial model with the weather conditions explained 88.6% (Adjusted R-squared = 0.886) of the variance for species richness and 71.8% (Adjusted R-squared = 0.717) of the variance for abundance. Leaving 11.4% of the species richness variance and 28.3% of the abundance variance unexplained by the model. For both abundance (PropVar = 0.872) and species richness (PropVar = 0.738) the polynomial temperature term explained the greatest proportion of variance. Whereas all other factors contributed negligibly (PropVar < 0.05).

6.6 THE EFFECT OF PLANT SPECIES RICHNESS ON MICRO- AND MACROMOTHS

For both micro- and macromoths scatterplots were made to see the relationship between plant species richness and moth richness and abundance (Appendix E). The Pearson correlation test for micromoths revealed a significant inclining trend is visible for both species richness ($r = 0.52$; $p = 5.007e-06$) and abundance ($r = 0.55$; $p = 1.027e-06$). The same inclining trend is visible for macromoths for both species richness ($r = 0.57$; $p = 3.961e-07$) and abundance ($r = 0.38$; $p = 0.001548$). The interaction model revealed no differences between micro- and macromoths for both species richness ($t = 0.17$, $p = 0.87$) and abundance ($t = 1.04$, $p = 0.30$).

7 DISCUSSION

In this study we aimed to investigate the impact of landscape elements on the diversity of moths in archetypical polder landscapes. Two interlinked research questions were formed that investigated this at different spatial scales. The first looked at the impact of landscape-scale heterogeneity on moth diversity in polders. Here we found that this landscape heterogeneity enhanced the moth diversity and supported numerous species that were not found in the reference polders. Whereas the second question zoomed in on the heterogeneous polder and examined the effects of grouped landscape elements in comparison to the polder grasslands. Here we found that mainly woody structures, but also alternative crop systems yielded a significantly higher moth diversity and contained numerous species that were not found in the grasslands. In contrast to other studies that focus on the effects of single landscape elements, our results show that combinations of these landscape elements not only enhance moth diversity within polders but also at a broader scale – between polders.

Landscape complexity allows for a wide variety of niches, and therefore also potential moth habitats, which in turn enhances overall moth species richness (Botham et al., 2015). The significantly higher species richness and abundance in the PL compared to the VVZ is consistent with this assumption. Despite the difference in heterogeneity, no difference was found between the PL and the BP. This most likely being the result of unequal sample sizes for the polders. For future research, it should be aimed for to use equal sample sizes for more reliable and stronger statistical analyses. Besides species richness and abundance, we used an NMDS plot to look at the community compositions across the polders. In contrast to patterns observed for species richness and abundance, the BP differed significantly in community composition with both the PL and the VVZ, which did not show dissimilar communities. A possible explanation being that the BP is spatially isolated from the other polders, whereas only a single road separates the PL and the VVZ. More interestingly are the shared and unique species across the polders. Wherein more than half of the total species found were unique to the PL, and only few were unique to only the VVZ or the BP. The majority of the species found in the VVZ and the BP were ubiquitous and found across all three polders. Showing that archetypical polder landscapes mainly host generalists or grassland species and give little way to specialist species. Whereas the heterogeneous landscape of the PL is favoured by specialist species that require certain niches or host plants to exist, which is in line with a prior study (Botham et al., 2015).

Zooming in on the elements that contribute to this heterogeneous landscape provides an insight into effects of landscape elements on moth diversity. Woody structures, like hedgerows enhance moth diversity by providing shelter and passageways for moths (Kühne et al., 2022; Merckx et al., 2012). Our results are consistent with this as the woody structures have a significantly higher abundance and species richness compared to the grassland. Furthermore, the alternative crops also have a significantly higher species richness compared to the grassland, due to the wide variety of niches. Abundance-wise there was no difference, which is most likely due to the alternative crops providing shelter to a lesser extent than the woody structures. However, analysis revealed no differences between communities, which is probably because of the spatial overlap due to them being in the same polder. The Venn-diagram showed that the grasslands almost only comprised of species that were ubiquitous throughout the Polderlab. In contrast, more than two-thirds of species in the PL were found exclusively in the woody structures or the alternative crops, highlighting the strong enhancing effect of these landscape elements on moth diversity within the polder. These enhancing effects are in line with the results of prior research (Coulthard et al., 2016; Merckx et al., 2012).

The landscape elements enhance moth diversity within the polder but also at a broader scale and thereby outperforming the other polders. Interestingly, there are also species present in the BP and the VVZ that are not present in the PL. These species are the water veneer (*Acentria ephemerella*) and the small china-mark (*Cataglyphis lemnata*), both of which are aquatic moths from the family Crambidae. Aquatic moths are one of the least studied groups within the order of Lepidoptera (Mariani et al., 2021). The presence of

these species is an indication for a healthy aquatic ecosystem, as they feed on numerous aquatic plants. The small china-mark is even researched as biological control for aquatic plant invaders (Mariani et al., 2020). Both aquatic moths feed on numerous aquatic plants as larvae. The small china-mark preferably feeds on duckweed, whereas the water veneer can feed on many plants including watercress, American waterweed and knotweed. The absence of this plant in the PL could be an indication for bad water quality or low aquatic plant species richness. To further increase the diversity in the PL, the next step should be to enhance water quality and increase aquatic plant diversity.

The same way aquatic plant diversity contributes to a higher moth diversity, overall terrestrial plant species richness also plays a major role, wherein a higher floral diversity consistently corresponds with higher moth diversity (Blumgart et al., 2023; Tyler, 2020). Micromoths, that are often predominantly plant host specific species (Uhl et al., 2016) showed a clear increase in species richness and abundance with increasing plant species richness. Macromoths, that show plant host specificity to a lesser degree, also followed this same trend. However, there was no significant difference between the relationships of micro- and macromoths with plant species richness. So, moth diversity overall is clearly promoted by a higher plant diversity. It is noteworthy that woody structures often were affiliated with a high plant diversity, thus making it hard to capture individual effect of plant species richness on moth diversity. Future research should also include notes on vegetation density and vegetation type, as this gives a more complete understanding of how vegetation influences moth diversity. Additionally, this can also give insights on why seemingly similar grasslands can yield different species richness and abundance.

Beyond the effects of plant species richness, the type of landscape element accounts for the most explained variance in the linear models. In these models, it was revealed that models with plant species nested in the type provided a better fit. Therefore, showing that plant richness explains additional variation only after accounting for the differences among landscape elements. Meaning that the landscape elements all have their own habitats with distinct vegetation compositions that hold more effect than plant species richness alone. Besides these aforementioned factors, there are others that influence moth diversity. Weather conditions have proven to have of significant impact on the species and individuals caught on trapping nights, with temperature having the most impact (Jonason et al., 2014), whereas windspeeds and rain had no effect on moth diversity. The moon as external factor is often named to influence moth diversity by the light reflected by the moon (Mangels et al., 2017). However, no significant effects were found for this model. It even seemed that species richness and abundance increased with a higher moon brightness and a longer period of the moon being visible, whilst this ought to be the other way around (Jonason et al., 2014). This is mainly because during the last sampling week – in which we caught the most moths – it was nearly full moon.

Looking at the broader scale, it is evident that a more heterogeneous landscape enhances moth species richness and abundance. With the main effects becoming clear at a community level, where the PL has significantly more species unique to its polder than the uniform polders. Showing that the availability of many different niches promotes many specialist species that contribute to overall community composition, wherein plant species richness also plays a significant role. This landscape heterogeneity is created by numerous landscape elements present in the polder. All of which hold their own effects on moth diversity by having unique niches. Together, their cumulative effects become evident and surpass the moth diversity in the archetypical polder grasslands. With woody structures giving rise to largest number of unique species, followed by alternative crops that also adds significantly to the community composition. Ideally, you would want to combine both types of landscape elements to yield the highest diversity and most diverse community composition, supporting both generalists and specialists. However, there is not always the possibility to include both in polders due to it costing grassland area and extra time to manage. From an ecologist's perspective, it would be logical to include the landscape element that yields the highest diversity. Although, the woody structures do not necessarily aid in the rising problem of increasing food demands worldwide, unless fruit trees are implemented. The alternative crops enhance moth diversity significantly whilst simultaneously playing a part in resolving the impending

food shortages. Depending on the goal, different approaches could be chosen to design polder landscapes.

Using this research, information was gathered on the effects of landscape elements on moth species richness, abundance and communities. Elements enhancing moth diversity have been shown. This knowledge hopefully functions as a stepping stone for the conservation of moths in agricultural landscapes. In addition, it could help designing polders in nature-friendly way, while still aiding in decreasing worldwide food shortages. These designs could act as a base for policy making regarding agricultural landscapes. These policies could be a great start in slowing down or even halting the current insect crisis, and by extension the biodiversity crisis.

8 REFERENCES

- Alison, J., Duffield, S. J., Morecroft, M. D., Marrs, R. H., & Hodgson, J. A. (2017). Successful restoration of moth abundance and species-richness in grassland created under agri-environment schemes. *Biological Conservation*, 213, 51-58.
<https://doi.org/10.1016/j.biocon.2017.07.003>
- Bell, J. R., Blumgart, D., & Shortall, C. R. (2020). Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. *Insect Conservation and Diversity*, 13(2), 115-126.
<https://doi.org/10.1111/icad.12412>
- Blumgart, D., Botham, M. S., Menéndez, R., & Bell, J. R. (2023). Floral enhancement of arable field margins increases moth abundance and diversity. *Journal of Insect Conservation*, 27(3), 455-465. <https://doi.org/10.1007/s10841-023-00469-9>
- Botham, M. S., Fernandez-Ploquin, E. C., Brereton, T., Harrower, C. A., Roy, D. B., & Heard, M. S. (2015). Lepidoptera communities across an agricultural gradient: How important are habitat area and habitat diversity in supporting high diversity? *Journal of Insect Conservation*, 19(2), 403-420. <https://doi.org/10.1007/s10841-015-9760-y>
- Bullock, J. M., Jefferson, R. G., Blackstock, T. H., Pakeman, R. J., Emmet, B. A., Pywell, R. J., Grime, J. P., & Silvertown, J. (2011). Semi-natural Grasslands. In *UK National Ecosystem Assessment: Technical Report* (1st ed., Vol. 6, pp. 161-195). UNEP-WCMC.
- Clausnitzer, V., Kalkman, V. J., Ram, M., Collen, B., Baillie, J. E. M., Bedjanič, M., Darwall, W. R. T., Dijkstra, K.-D. B., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, D., Schütte, K., Suhling, F., Villanueva, R. J., von Ellenrieder, N., & Wilson, K. (2009). Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation*, 142(8), 1864-1869. <https://doi.org/10.1016/j.biocon.2009.03.028>

- Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132(3), 279-291. <https://doi.org/10.1016/j.biocon.2006.04.020>
- Coulthard, E., McCollin, D., & Littlemore, J. (2016). The use of hedgerows as flight paths by moths in intensive farmland landscapes. *Journal of Insect Conservation*, 20(2), 345-350. <https://doi.org/10.1007/s10841-016-9864-z>
- Cowie, R. H., Bouchet, P., & Fontaine, B. (2022). The Sixth Mass Extinction: Fact, fiction or speculation? *Biological Reviews*, 97(2), 640-663. <https://doi.org/10.1111/brv.12816>
- Dantas de Miranda, M., Pereira, H. M., Corley, M. F. V., & Merckx, T. (2019). Beta diversity patterns reveal positive effects of farmland abandonment on moth communities. *Scientific Reports*, 9(1), 1549. <https://doi.org/10.1038/s41598-018-38200-3>
- Drolet, I., Guay, J.-F., Fournier, V., & Cloutier, C. (2019). Biodiversity of lepidopteran pests and their parasitoids in organic and conventional cranberry crop. *Biological Control*, 129, 24-36. <https://doi.org/10.1016/j.biocontrol.2018.11.003>
- Dunn, R. R. (2005). *Modern Insect Extinctions, the Neglected Majority*. <https://doi.org/https://doi.org/10.1111%2Fj.1523-1739.2005.00078.x>
- England, S. J., & Robert, D. (2024). Electrostatic pollination by butterflies and moths. *Journal of The Royal Society Interface*, 21(216), 20240156. <https://doi.org/10.1098/rsif.2024.0156>
- Fuentes-Montemayor, E., Goulson, D., & Park, K. J. (2011). The effectiveness of agri-environment schemes for the conservation of farmland moths: Assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology*, 48(3), 532-542. <https://doi.org/10.1111/j.1365-2664.2010.01927.x>
- Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, 29(19), R967-R971. <https://doi.org/10.1016/j.cub.2019.06.069>

- Grevé, M. E., Marx, M. T., Eilmus, S., Ernst, M., Herrmann, J. D., Baden, C. U., & Maus, C. (2024). Insect Decline—Evaluation of Potential Drivers of a Complex Phenomenon. *Insects*, 15(12), 1021. <https://doi.org/10.3390/insects15121021>
- Habel, J. C., Samways, M. J., & Schmitt, T. (2019). Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodiversity and Conservation*, 28(6), 1343-1360. <https://doi.org/10.1007/s10531-019-01741-8>
- Hahn, M., & Brühl, C. A. (2016). The secret pollinators: An overview of moth pollination with a focus on Europe and North America. *Arthropod-Plant Interactions*, 10(1), 21-28. <https://doi.org/10.1007/s11829-016-9414-3>
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, 12(10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Jarne, P. (2025). The Anthropocene and the biodiversity crisis: An eco-evolutionary perspective. *Comptes Rendus. Biologies*, 348(G1), 1-20. <https://doi.org/10.5802/crbiol.172>
- Jonason, D., Franzén, M., & Ranius, T. (2014). Surveying Moths Using Light Traps: Effects of Weather and Time of Year. *PloS one*, 9, e92453. <https://doi.org/10.1371/journal.pone.0092453>
- Kühne, I., Arlettaz, R., & Humbert, J.-Y. (2022). Landscape woody features, local management and vegetation composition shape moth communities in extensively managed grasslands. *Insect Conservation and Diversity*, 15(6), 739-751. <https://doi.org/10.1111/icad.12600>
- Kurmi, A., Pachori, R., Bhowmick, A. K., Sharma, A., Sharma, H., Thomas, M., & Namdev, B. (2021). Diversity analysis of nocturnal lepidopteran insect fauna in rice eco-systems of district Jabalpur, Madhya Pradesh, India. *JOURNAL OF ENTOMOLOGY AND ZOOLOGY STUDIES*, 9, 645-650.

LedEmmers. (z.d.). *Vlinderstichting*. Geraadpleegd 26 maart 2026, van

<https://vlinderstichting.nl/wat-kan-jij-doen/tellen/meetnetten/meetnet-nachtvlinders/ledemmers/>

Macdonald, D. W., & Feber, R. (2015). *Wildlife Conservation on Farmland: Managing for nature on lowland farms*. Oxford University Press.

Mangels, J., Fiedler, K., Schneider, F. D., & Blüthgen, N. (2017). Diversity and trait composition of moths respond to land-use intensification in grasslands: Generalists replace specialists. *Biodiversity and Conservation*, 26(14), 3385-3405.
<https://doi.org/10.1007/s10531-017-1411-z>

Mariani, F., Ellwood, N., Zuccarello, V., & Ceschin, S. (2020). Compatibility of the Invasive Alien *Lemna minuta* and Its Potential Biocontrol Agent *Cataclysta lemnata*. *Water*, 12, 2719.
<https://doi.org/10.3390/w12102719>

Mariani, F., Fattorini, S., Di Giulio, A., & Ceschin, S. (2021). Development and reproduction of *Cataclysta lemnata*, a potential natural enemy of the invasive alien duckweed *Lemna minuta* in Italy. *The European Zoological Journal*, 88(1), 216-225.
<https://doi.org/10.1080/24750263.2021.1872721>

Marselis, S. M., Hannula, S. E., Trimbos, K. B., Berg, M. P., Bodelier, P. L. E., Declerck, S. A. J., Erisman, J. W., Kuramae, E. E., Nanu, A., Veen, G. F. (Ciska), van 't Zelfde, M., & Schrama, M. (2024a). The use of living labs to advance agro-ecological theory in the transition towards sustainable land use: A tale of two polders. *Environmental Impact Assessment Review*, 108, 107588. <https://doi.org/10.1016/j.eiar.2024.107588>

McMahan, E. E., Steffan, S. A., & Guédot, C. (2017). Population Densities of Lepidopteran Pests in Selected Cranberry Cultivars in Wisconsin. *Journal of Economic Entomology*, 110(3), 1113-1119. <https://doi.org/10.1093/jee/tow274>

Merckx, T., Feber, R. E., Dulieu, R. L., Townsend, M. C., Parsons, M. S., Bourn, N. A. D., Riordan, P., & Macdonald, D. W. (2009). Effect of field margins on moths depends on species

- mobility: Field-based evidence for landscape-scale conservation. *Agriculture, Ecosystems & Environment*, 129(1), 302-309.
<https://doi.org/10.1016/j.agee.2008.10.004>
- Merckx, T., Marini, L., Feber, R. E., & Macdonald, D. W. (2012). Hedgerow trees and extended-width field margins enhance macro-moth diversity: Implications for management. *Journal of Applied Ecology*, 49(6), 1396-1404. <https://doi.org/10.1111/j.1365-2664.2012.02211.x>
- Merckx, T., & Slade, E. M. (2014). Macro-moth families differ in their attraction to light: Implications for light-trap monitoring programmes. *Insect Conservation and Diversity*, 7(5), 453-461. <https://doi.org/10.1111/icad.12068>
- Miller, J. S. (1992). Host-Plant Associations among Prominent Moths. *BioScience*, 42(1), 50-57.
<https://doi.org/10.2307/1311628>
- MoonCalc moon position- and moon phases calculator*. (z.d.). Geraadpleegd 24 juni 2026, van <https://www.mooncalc.org>
- New, T. R. (2004). Moths (Insecta: Lepidoptera) and conservation: background and perspective. *Journal of Insect Conservation*, 8(2), 79-94.
<https://doi.org/10.1023/B:JICO.0000045807.04047.bd>
- New, T. R. (2023). Moth Ecology and Conservation Importance. In T. R. New (Red.), *The Other Lepidoptera: Moth Conservation in Australia* (pp. 21-37). Springer International Publishing. https://doi.org/10.1007/978-3-031-32103-0_2
- Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2002548117.
<https://doi.org/10.1073/pnas.2002548117>
- Schickhoff, U., Bobrowski, M., Oates, I., & Mal, S. (2024). *The Biodiversity Crisis in the Anthropocene* (pp. 79-111). <https://doi.org/10.26650/B/SS19.2023.020.05>

Truxa, C., & Fiedler, K. (2012). Attraction to light—From how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology*, 109, 77-84.
<https://doi.org/10.14411/eje.2012.010>

Tyler, T. (2020). Relationship between moth (night active Lepidoptera) diversity and vegetation characteristics in southern Sweden. *Journal of Insect Conservation*, 24(6), 1005-1015.
<https://doi.org/10.1007/s10841-020-00270-y>

Uhl, B., Wölfling, M., Fiala, B., & Fiedler, K. (2016). Micro-moth communities mirror environmental stress gradients within a Mediterranean nature reserve. *Basic and Applied Ecology*, 17(3), 273-281. <https://doi.org/10.1016/j.baae.2015.10.002>

Uurgegevens van het weer in Nederland. (z.d.). knmi.nl. Geraadpleegd 21 juni 2026, van <https://www.knmi.nl/nederland-nu/klimatologie/uurgegevens>

Van Strien, A. J., Van Swaay, C. A. M., Van Strien-van Liempt, W. T. F. H., Poot, M. J. M., & WallisDeVries, M. F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation*, 234, 116-122.
<https://doi.org/10.1016/j.biocon.2019.03.023>

Wagner, D. L., Fox, R., Salcido, D. M., & Dyer, L. A. (2021). A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proceedings of the National Academy of Sciences*, 118(2), e2002549117.
<https://doi.org/10.1073/pnas.2002549117>

Yaakop, S., David-Dass, A., Shaharuddin, U. S., Sabri, S., Badrulisham, A. S., & Che-Radziah, C. M. Z. (2020). Species Richness of Leaf Roller and Stem Borers (Lepidoptera) Associated with Different Paddy Growth and First Documentation of Its DNA Barcode. *Pertanika Journal of Tropical Agricultural Science*, 43(4). <https://doi.org/10.47836/pjtas.43.4.08>

9 APPENDICES

9.1 APPENDIX A: GROUPING OF THE PLOTS

Table 1. The landscape elements with their corresponding plots and the sampling rotation identifiers.

Landscape element	Day sampled	Plot numbers
Rice field	PL1	3, 4
Food swamp	PL1	1, 2
Cranberry agroforestry	PL1	9, 10
Hedgerow	PL1 & PL2	5-8 & 11-14
Agroforestry	PL2	17-19
Forest	PL2	20
Cranberry monoculture	PL2	15, 16
Mown grassland	PL1 & PL2	23-27, 34-36, 39, 40
Grazed grassland	PL1 & PL2	21, 22, 28-33, 37, 38
Grassland BP	VVZ & BP	51-60
Grassland VVZ	VVZ & BP	41-50, 61-68

9.2 APPENDIX B: SAMPLING ROTATION

Table 2. Sampling rotation schedule showing sampling days and the corresponding plots sampled. The middle column lists the rotation identifier (PL1 = Polderlab 1; PL2 = Polderlab 2; VVZ & BP = Vrouw Vennepolder Zuid & Boterhuispolder).

Sampling day	Sampling day rotation	Plots
1	PL1	1-10, 21-27, 31-33
2	VVZ & BP	41-50 & 51-60
3	PL2	11-20, 28-30, 34-40
4	VVZ & BP	41-50 & 51-60
5	PL1	1-10, 21-27, 31-33
6	VVZ & BP	41-50 & 51-60
7	PL2	11-20, 28-30, 34-40
8	VVZ & BP	46-47, 61-68 & 51-60
9	PL1	1-10, 21-27, 31-33
10	VVZ & BP	46-47, 61-68 & 51-60
11	PL2	11-20, 28-30, 34-40
12	VVZ & BP	46-47, 61-68 & 51-60
13	PL1	1-10, 21-27, 31-33
14	VVZ & BP	46-47, 61-68 & 51-60
15	PL2	11-20, 28-30, 34-40
16	VVZ & BP	46-47, 61-68 & 51-60
17	PL1	1-10, 21-27, 31-33
18	VVZ & BP	46-47, 61-64, 66-68 & 51-60
19	PL2	11-20, 28,29, 34-40
20	VVZ & BP	46-47, 61-64, 66-68 & 51-60
21	PL1	1-10, 22-27, 31-33
22	VVZ & BP	46-47, 61-64, 66-68 & 51-60
23	PL2	11-20, 28,29, 34-40
24	PL1	1-10, 22-27, 31-33

9.3 APPENDIX C: WOODY STRUCTURES AROUND LANDSCAPE ELEMENTS

Table 1. Woody plant species recorded around the landscape elements.

Landscape element	Rice & foodswamp	Cranberry agroforestry	Hedgerow	Agroforestry	Forest island	Monoculture cranberry
	Wild cherry	Cranberry	Medlar	Wild cherry	Rowan	Highbush blueberry
	Sea buckthorn	Hazel	Hawthorn	Willow	Willow	Wild cherry
	Almond	Japanese silverberry	Wild cherry	Red currant	June berry	Hazel
	Firethorn	Pear tree	Rowan	Hazel	Red currant	Bog-myrtle
	Pear tree		Wild privet	Apple tree		Blackthorn
	Red currant		Oak	Russian olive		Pear tree
	Hazel		Black elderberry	Cherry laurel		Red currant
	Grey willow		Bird cherry	Linden		Cranberry
	Highbush blueberry		Birch	Black alder		
	Japanese silverberry		Hornbeam			
	Grapevine		Linden			
	Gooseberry		Blackthorn			
			Holly			
			Elm			

9.4 APPENDIX D: MOTH SPECIES AND THEIR CORRESPONDING TAXONOMIC FAMILIES

Table 2. Latin names of moth species, their corresponding taxonomic families, and classification as micro- or macromoths.

Latin Name	Family	Type
Orthosia incerta	Noctuidae	Macro
Orthosia gothica	Noctuidae	Macro
Mompha epilobiella	Momphidae	Micro
Elachista canapennella	Elachistidae	Micro
Gymnoscelis rufifasciata	Geometridae	Macro
Ochropleura plecta	Noctuidae	Macro
Agrotis puta	Noctuidae	Macro
Autographa gamma	Noctuidae	Macro

<i>Xanthorhoe ferrugata/spadecearia</i>	Geometridae	Macro
<i>Elachista maculicerusella</i>	Elachistidae	Micro
<i>Plutella xylostella</i>	Plutellidae	Micro
<i>Celypha lacunana</i>	Tortricidae	Micro
<i>Bactra lancealana</i>	Tortricidae	Micro
<i>Pharmacia lupulina</i>	Hepialidae	Macro
<i>Cydia nigricana</i>	Tortricidae	Micro
<i>Mythimna pallens</i>	Noctuidae	Macro
<i>Laothoe populi</i>	Sphingidae	Macro
<i>Agriphila straminella</i>	Crambidae	Micro
<i>Lacanobia oleracea</i>	Noctuidae	Macro
<i>Triodia sylvina</i>	Hepialidae	Macro
<i>Charanyca trigrammica</i>	Noctuidae	Macro
<i>Spilosoma lubricipeda</i>	Erebidae	Macro
<i>Clepsia spectrana</i>	Tortricidae	Micro
<i>Glyphipterix simplicella</i>	Geometridae	Macro
<i>Schrankia costaeistrigalis</i>	Erebidae	Macro
<i>Chiasmia clathrata</i>	Geometridae	Macro
<i>Smerinthus ocellatus</i>	Sphingidae	Macro
<i>Apamea unanimitis</i>	Noctuidae	Macro
<i>Dichrorampha acuminatana</i>	Tortricidae	Micro
<i>Epinotia immunadana</i>	Tortricidae	Micro
<i>Agonopterix yeatiana</i>	Depressariinae	Micro
<i>Scrobipalpa costella</i>	Gelechiidae	Micro
<i>Evergestis forficalis</i>	Crambidae	Micro
<i>Xestia c-nigrum</i>	Noctuidae	Macro
<i>Orthonama vittata</i>	Geometridae	Macro
<i>Diarsia rubi</i>	Noctuidae	Macro
<i>Clostera curtula</i>	Notodontidae	Macro
<i>Apamea crenata</i>	Noctuidae	Macro
<i>Earias clorana</i>	Nolidae	Macro
<i>Eupaithecia centaureata</i>	Geometridae	Macro
<i>Donacaula forficella</i>	Crambidae	Micro
<i>Xanthorhoe designata</i>	Geometridae	Macro
<i>Trachea atriplicis</i>	Noctuidae	Macro
<i>Rivula sericealis</i>	Erebidae	Macro
<i>Oligia fasciuncula</i>	Noctuidae	Macro
<i>Scopula floslactata</i>	Geometridae	Macro
<i>Eupoecilia angustana</i>	Tortricidae	Micro
<i>Bactra furfurana</i>	Tortricidae	Micro
<i>Caradrina morpheus</i>	Noctuidae	Macro
<i>Phycitodes maritima</i>	Crambidae	Micro
<i>Aethes smeathmanniana</i>	Tortricidae	Micro
<i>Hedya nubiferana</i>	Tortricidae	Micro
<i>Cochylimorpha straminea</i>	Tortricidae	Micro
<i>Acentria ephemerella</i>	Crambidae	Micro

<i>Chrysoteuchia culmella</i>	Crambidae	Micro
<i>Cataglyphis lemnae</i>	Crambidae	Micro
<i>Borkhausenia nefrax</i>	Oecophoridae	Micro
<i>Agapeta hamana</i>	Tortricidae	Micro
<i>Clepsia senecionana</i>	Tortricidae	Micro
<i>Gynnidomorpha alismana</i>	Tortricidae	Micro
<i>Elophila nymphaeata</i>	Crambidae	Micro
<i>Crambus perlella</i>	Crambidae	Micro
<i>Schoenobius gigantella</i>	Crambidae	Micro
<i>Coleophora spec.</i>	Coleophoridae	Micro
<i>Hoplodrina ambigua</i>	Noctuidae	Macro
<i>Nascia ciliaris</i>	Crambidae	Micro
<i>Furcula furcula</i>	Notodontidae	Macro
<i>Noctua pronuba</i>	Noctuidae	Macro
<i>Eucosma cana</i>	Tortricidae	Micro
<i>Idaea dimidiata</i>	Geometridae	Macro
<i>Lomaspilis marginata</i>	Geometridae	Macro
<i>Oligia strigilis</i>	Noctuidae	Macro
<i>Nematopogon swammerdemella</i>	Yponomeutidae	Micro
<i>Eilema caniola</i>	Erebidae	Macro
<i>Celypha striana</i>	Tortricidae	Micro
<i>Deltote bankiana</i>	Erebidae	Macro
<i>Jodis lactearia</i>	Geometridae	Macro
<i>Pandemis heparana</i>	Tortricidae	Micro
<i>Deilephila elpenor</i>	Sphingidae	Macro
<i>Cerura vinula</i>	Notodontidae	Macro
<i>Idaea subsericeata</i>	Geometridae	Macro
<i>Mythimna impura</i>	Noctuidae	Macro
<i>Peribatodes rhomboidaria</i>	Geometridae	Macro
<i>Phycitodes binaevella</i>	Crambidae	Micro
<i>Cnephasia spec.</i>	Tortricidae	Micro
<i>Anania perlucidalis</i>	Crambidae	Micro
<i>Cochylidia implicitana</i>	Tortricidae	Micro
<i>Apamea monoglypha</i>	Noctuidae	Macro
<i>Bactra spec.</i>	Tortricidae	Micro
<i>Gelechiidae indet.</i>	Gelechiidae	Micro
<i>Bucculatrix ulmella</i>	Bucculatricidae	Micro
<i>Microlepidoptera indet.</i>	N.A.	Micro

9.5 APPENDIX E: PLANT SPECIES RICHNESS EFFECTS ON MICRO- AND MACROMOTH DIVERSITY

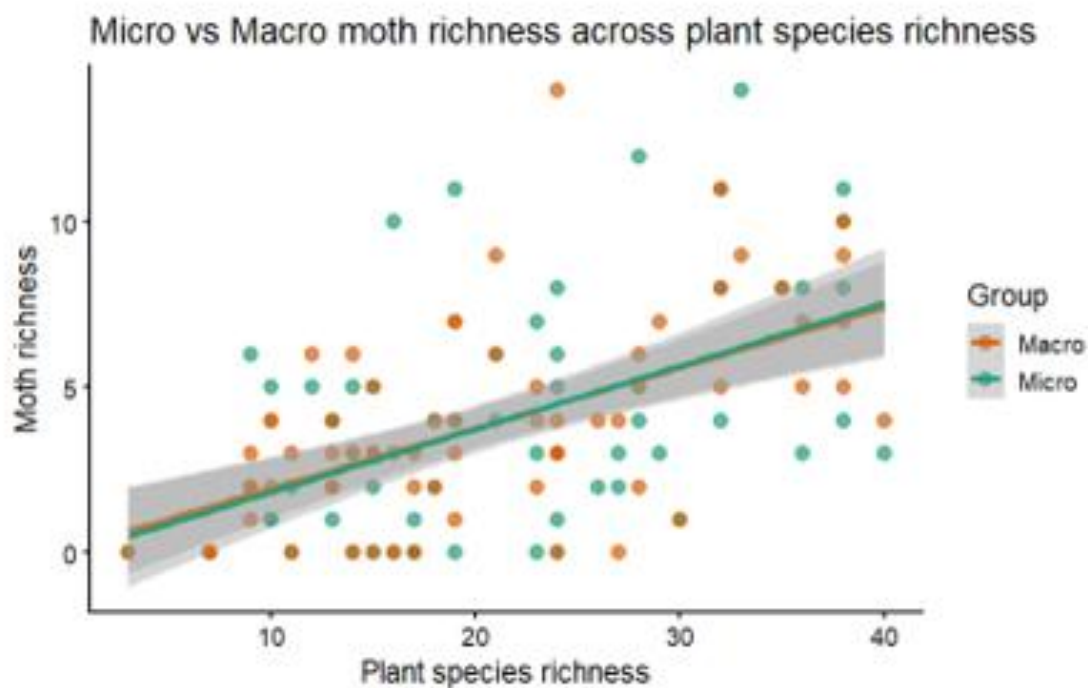


Figure 8. The relationship between plant species richness and micromoth (green) and macromoth (orange) species richness. The shaded area represents the 95% confidence interval around the fitted relationship.

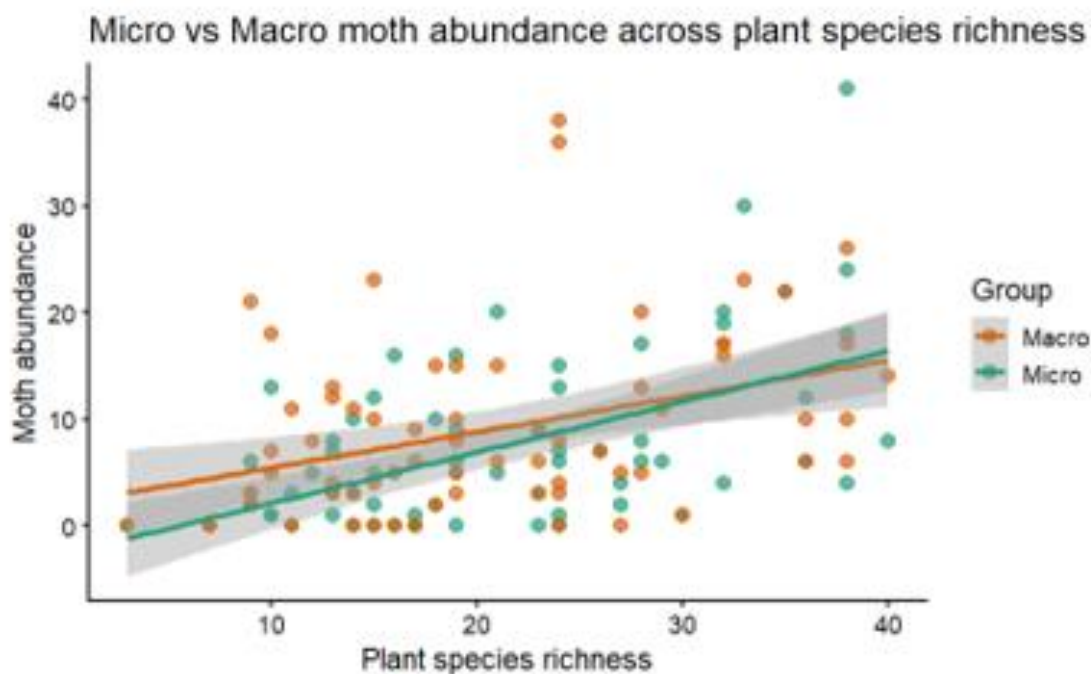


Figure 7. The relationship between plant species richness and micromoth (green) and macromoth (orange) abundance. The shaded area represents the 95% confidence interval around the fitted relationship.

9.6 APPENDIX F: MODEL FIT, DIAGNOSTIC PLOTS AND AIC VALUES

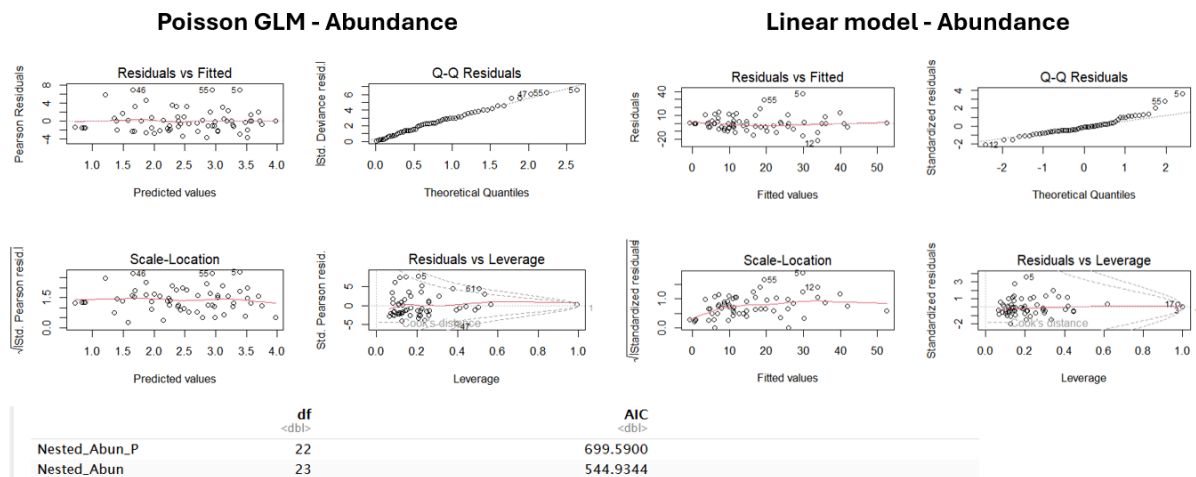


Figure 9. Diagnostic plots and corresponding AIC values for the Poisson GLM and the Linear Model regarding the moth abundance. The Nested_Abun_P corresponds to the Poisson GLM and the Nested_Abun to the Linear Model.

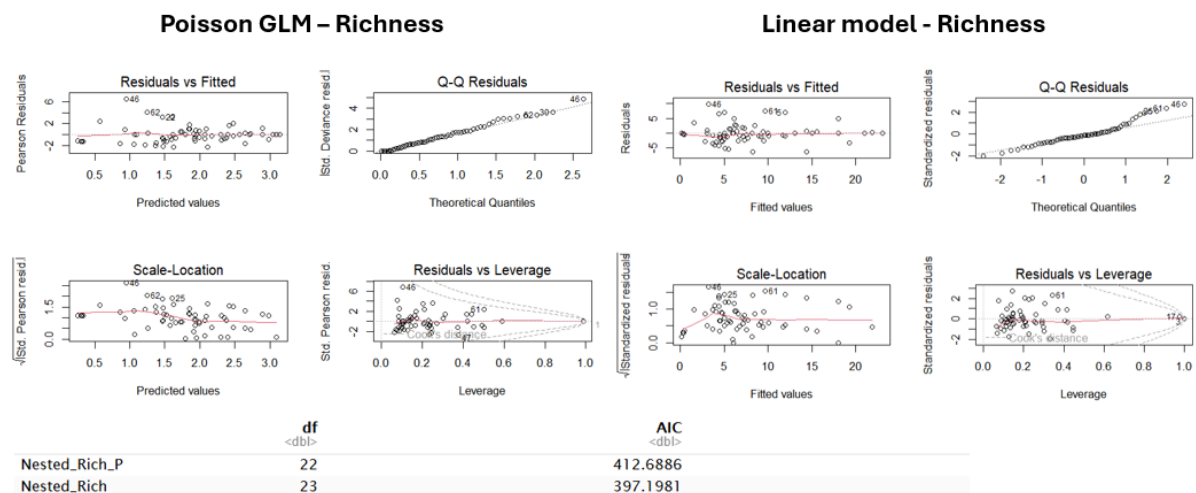


Figure 10. Diagnostic plots and corresponding AIC values for the Poisson GLM and the Linear Model regarding the moth species richness. The Nested_Rich_P corresponds to the Poisson GLM and the Nested_Rich to the Linear Model.