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Community ecology of moths in floodplain forests of Eastern Austria

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Frontispiece: Male of the Giant Peacock Moth (*Saturnia pyri*), a regular component of floodplain forest moth communities in Eastern Austria. © C. Truxa.

Table of contents

Chapter Page

1. Abstract

In this thesis I investigated moth communities in relation to flood regime across three riparian regions of lowland Eastern Austria (viz. Danube, Morava and Leitha rivers) using light traps once a month over a period of two consecutive years.

Although light trapping is the most widely used method to survey nocturnal moths, little is still known about the distances at which moths respond to an artificial light source. Two community-wide mark-release-recapture experiments were carried out in order to investigate the attraction radius of a weak artificial light source (2 × 15 W UV-light tubes). Altogether 2,331 moths belonging to 167 species were caught at light traps, individually marked, and released again at distances of 2–100 m. Of these only 313 moths returned to the light trap within 5 min of release. Percentage recapture was generally low (gross rate 13.4%) and strongly decreased with increasing the distance at which they had been released. The data confirm that the attraction radius of low-power light traps for moths is very small, often even below 10 m. Therefore, moth samples assembled with such light traps reflect the communities from which they are drawn at a sufficiently high spatial resolution (in the range of tens of meters) to allow for comparisons in a finely grained forest landscape.

As one major question of this thesis was the impact of flooding on moth species diversity, it was important to select an appropriate measure of local diversity which is sensitive at precisely the ecological scales under study. I used a large data set of 448 moth species and 32,181 individuals, collected in the three floodplain forests mentioned above, to empirically explore the performance of a range of alpha-diversity measures. Earlier comparisons of diversity measures have mostly been made using modelled data sets. The studied forests comprised regularly flooded and non-flooded habitats, thus, I expected that local moth diversity should be shaped by both, regional differences and local flood effects. Surprisingly, observed species numbers as well as eight methods to extrapolate species totals completely failed to reflect differences between the three study regions or between flooded and non-flooded habitats. Rarefied species numbers and Fisher's α of the log-series distribution did capture differences in moth diversity between the regions, but failed to mirror flooding impact. Only Shannon's diversity captured all expected diversity differences, at high significance levels. Whether using Shannon's diversity in its original formulation, or a recently developed bias-correction for small sample sizes, did not affect conclusions about species diversity patterns, but the original formulation tended to underestimate species diversity in smaller samples. I therefore decided to adopt the bias-corrected Shannon diversity as the most meaningful species diversity measure for my subsequent analyses.

I then proceeded to compare moth species diversity and species composition between the three floodplain forest regions and between differentially flood-impacted forest stretches. Today's floodplain forests in Austria consist of small stretches embedded into non-forested cultivated landscape. Accordingly, and in view of the high mobility of these insects, moth samples taken inside forests always contain a fraction of non-breeding individuals that have immigrated from this landscape matrix. To test the impact of these stray species on diversity patterns, moths were segregated into resident and strays according to their larval resource and habitat requirements. Resident moths were further partitioned into arboreal and ground-layer species based on their larval habitat, to find out if flooding affects these groups differently. Stray species were quite numerous, accounting for 17 % of observed species and 6 % of

sampled individuals, but they only marginally influenced diversity and species composition patterns. Contrary to expectation, total moth diversity and ground-layer moth diversity were generally not reduced in flooded habitats relative to non-flooded habitats. In two of three riverine regions species diversity of these terrestrial insects was even higher in flood-impacted habitat fractions. I attribute these patterns to the higher heterogeneity and naturalness of flood-impacted areas plus the strong re-colonisation potential of mobile moths after disturbances through floods. Species diversity of arboreal moths did not show any significant differences between flood regimes at all. With regard to species composition, there was a strong differentiation of moth communities between the three floodplain regions and to a lesser degree between flooded and non-flooded forests. Moth ensembles from flooded habitats in different riverine regions did not group together in ordination diagrams. This contradicts to the hypothesis that flooding would result in a characteristic moth community tolerant to frequent inundation. Differences in species composition were mostly caused by changes in abundance relations of eurytopic moths, and could not be attributed to specialist species bound to wetland habitats.

I further investigated if subsamples of moth assemblages differ in their potential to reveal ecological patterns, i.e. such subsamples can serve as surrogates for overall beta-diversity. Concomitantly, I analysed the extent of structural redundancy in the dataset. Various taxonomically or ecologically defined moth subsamples mirrored total beta-diversity patterns to quite different degrees. For these analyses, I compared the three largest superfamilies (Noctuoidea, Geometroidea, and Pyraloidea) as well as 10 functional groups defined by their larval habitats and resource affiliations. Even tough the Noctuoidea showed the highest concordance with all moths, the Geometroidea provide a better surrogate for beta-diversity, because they scored almost as well as the Noctuoidea, but working effort is much lower since they are not that rich in species and less numerous in individuals (i.e. 31.25% of total species and 21.22% of total individuals).

Regarding to structural redundancy I was able to reduce the dataset down to only 8–15 species (i.e. only 1.5–3.35 % of all recorded moth species) that were fully sufficient to reflect the species composition patterns in the overall moth community. The most abundant species did not necessarily carry the greatest weight in that regard. Rather, the results suggest that representation of all (common) functional types which may be expected within an ecosystem is more important to define surrogate groups to monitor species turnover. These observations also lead to hypothesize that floodplain forest moth assemblages likely show considerable functional redundancy.

Overall, the results assembled in this thesis indicate that for moths, as a representative and species-rich group of terrestrial herbivorous insects, floodplain forests cannot be characterised as ‘hotspots’ of biodiversity. Moth species diversity and species composition were more strongly modulated by regional factors than by local habitat conditions.

2. Zusammenfassung

In der vorliegenden Arbeit habe ich Nachtfaltergemeinschaften aus Wäldern unterschiedlicher Überflutungsregime in drei verschiedenen Auenregionen (Donau, March und Leitha) im Tiefland Ost-Österreichs untersucht. Für die Erfassung der Falter wurden, über einen Zeitraum von 2 Jahren, einmal pro Monat Lichtfallen betrieben.

Obwohl der Lichtfang die am häufigsten verwendete Methode ist, um Nachtfalter zu erfassen, weiß man immer noch erstaunlich wenig über die Entfernungen, aus denen Falter zum Licht fliegen. Um den Attraktionsradius einer schwachen Lichtquelle (2 × 15 W UV-emittierende Leuchtstoffröhren) zu untersuchen, wurden zwei Fang-Wiederfang-Experimente durchgeführt. Insgesamt wurden 2.331 Nachtfalter aus 167 Arten gefangen, individuell markiert und aus Entfernungen von 2–100m zur Lichtquelle erneut freigelassen. Von diesen Nachtfaltern kamen nur 313 Tiere innerhalb von 5 Minuten wieder zum Leuchtturm zurück. Generell war die Wiederfangrate mit 13,4 % gering und nahm mit steigender Entfernung immer mehr ab. Die Ergebnisse bestätigen, dass der Attraktionsradius einer schwachen Lichtquelle für Nachtfalter sehr klein ist und oft sogar unter 10 m liegt. Mit solchen Fallen erhobene Stichproben bilden daher die Artengemeinschaften, aus denen sie gezogen wurden, mit der erforderten hohen räumlichen Auflösung ab, um auch in einer heterogenen Landschaft kleinräumige Unterschiede zwischen Habitaten beurteilen zu können.

Da eine Hauptfrage dieser Untersuchung dem Einfluss von Überflutung auf die Nachtfalter-Diversität gewidmet war, war es zunächst wichtig, ein geeignetes Maß für lokale Arten-Diversität auszuwählen. Dieses Maß sollte auf den betrachteten räumlichen und ökologischen Skalen ausreichend hohe Auflösung erbringen. Ich habe anhand eines großen empirischen Datensatzes (448 Nachtfalter-Arten und 32.181 Individuen) eine Reihe von α-Diversitätsmaßen miteinander verglichen. Für ähnliche Vergleiche wurden bisher überwiegend modellierte Datensätze verwendet. Die betrachteten Auwälder umfassten sowohl regelmäßig überflutete als auch heute nicht mehr (bzw. nur kaum) überflutete Bereiche. Ich erwartete daher, dass regionale wie auch lokale Einflüsse die Artendiversität der Nachtfalter beeinflussen. Überraschenderweise ließen sich weder mittels beobachteter Artenzahlen noch mit acht verschiedenen Extrapolationsmethoden für die Gesamtartenzahlen Unterschiede zwischen den Regionen oder zwischen überfluteten und nicht überfluteten Habitaten abbilden. Rarefaction-Analysen und der Formparameter der logarithmischen Reihe (Fishers α) zeigten Unterschiede zwischen den Regionen auf, nicht aber zwischen den beiden Habitattypen. Nur mittels Shannons Diversität konnten alle erwarteten Differenzierungen auf hohem Signifikanzniveau abgesichert werden. Dabei machte es wenig Unterschied, ob Shannons Diversität in ihrer ursprünglichen Form oder unter Berücksichtigung einer kürzlich entwickelten Bias-Korrektur für kleine Stichproben zum Einsatz kam. Letztere vermied aber die Unterschätzung der lokalen Diversität an Standorten mit kleinen Fangzahlen, weshalb ich die Bias-korrigierte Fassung für alle weiteren Analysen verwendete.

Sodann verglich ich die Artendiversität und -zusammensetzung der Nachtfalter-Faunen zwischen den drei Auenregionen und den beiden Überflutungsregimen. Heutige Auwaldreste in Ost-Österreich sind kleinräumig in eine waldarme Kulturlandschaft eingebettet. Daher – und angesichts der hohen Mobilität vieler Nachtfalter – enthalten auch Stichproben, die im Inneren eines Waldes gezogen werden, stets einen beträchtlichen Anteil von Individuen, die

aus der umgebenden Landschaftsmatrix zugeflogen sind. Um den Einfluss solcher Irrgäste zu testen, wurden die Nachtfalter anhand der spezifischen Ressourcenansprüche ihrer Raupen in „Residente“ und “Irrgäste” eingeteilt. Irrgäste waren zahlreich vertreten (17 % der beobachteten Arten, 6 % der Individuen), beeinflussten aber die Muster der Artendiversität nur marginal. Residente wurden in weiterer Folge unterteilt in Tiere, die ihre Larvalentwicklung in der Baum- und Strauchschicht vollziehen, und jene, die sich bodennah entwickeln. Damit sollte festgestellt werden, ob diese Gruppen unterschiedlich von der Überflutungsdynamik beeinflusst werden. Überraschenderweise war weder die Gesamtdiversität der Nachtfalter noch die Diversität der Arten mit bodennaher Entwicklung in überfluteten Waldanteilen vermindert. In zwei der drei Auenregionen war die Artendiversität dieser terrestrischen Insekten sogar in Waldgebieten mit Überflutungsdynamik höher. Ich erkläre dies mit der größeren Heterogenität und Natürlichkeit überfluteter Waldbereiche wie auch mit dem hohen Wiederbesiedlungspotenzial mobiler Nachtfalter nach Störungen durch Hochwasserereignisse. Die Diversität der arborealen Arten zeigte überhaupt keine Unterschiede zwischen überfluteten und nicht überfluteten Habitaten. Es gab eine starke Differenzierung der Artenzusammensetzung bezüglich der Regionen und schwächer, aber trotzdem signifikant, zwischen überfluteten und nicht überfluteten Waldanteilen. Allerdings war die Artenzusammensetzung der überfluteten Gebiete in den drei Regionen unterschiedlich, so dass man, anders als erwartet, keine Nachtfalterfauna ausmachen kann, die typisch für überflutete Habitate wäre. Die Differenzierung der Artengemeinschaften war im Wesentlichen durch Verschiebungen der Abundanzverhältnisse eurytoper Arten verursacht, Spezialisten für Feuchtgebiete spielten nur eine untergeordnete Rolle.

Weiters wurde untersucht, ob verschiedene Teilgruppen einer Nachtfaltergemeinschaft sich in dem betrachteten Habitatmosaik unterschiedlich verhalten bzw. ob es Teilgruppen gibt, die als Stellvertreter (und damit ggf. als Indikatoren) des Gesamtmusters dienen können. Damit verbunden war die Frage nach dem Ausmaß struktureller Redundanz im Datensatz. Drei taxonomisch definierte (Überfamilien Noctuoidea, Geometroidea und Pyraloidea) und 10 funktionell definierte Teilgruppen spiegelten das Gesamtmuster in unterschiedlichen Graden wider. Zwar reflektierten die Noctuoidea die Beta-Diversität am besten, doch aufgrund ihrer hohen Arten-und Individuenzahl sind sie als Stellvertreter nicht optimal. Die Geometroidea hingegen reduzieren den Arbeitsaufwand (sie machen 31.25% der Arten und 21.22% der Individuen aus) und bilden die Beta-Diversität fast genauso gut ab wie die Noctuoidea.

Der gesamte Datensatz konnte auf 8–15 Arten (das sind 1.5–3,35% aller gefundenen Arten) reduziert werden, die das Gesamtmuster nahezu genauso gut abbildeten wie der vollständige Datensatz. Interessanterweise waren nicht unbedingt die abundantesten Arten als Stellvertreter bedeutsam, sondern es scheint wichtiger zu sein, dass alle (häufigen) funktionellen Typen eines Ökosystems in einer Indikatorgruppe vertreten sind. Diese Beobachtungen führen zu der Hypothese, dass Nachtfaltergemeinschaften in Auwäldern ein hohes Ausmaß auch an funktioneller Redundanz aufweisen könnten.

Insgesamt zeigen die Ergebnisse meiner Studie, dass für Nachtfalter – eine sehr artenreiche und durchaus repräsentative Gruppe terrestrischer herbivorer Insekten – Auwälder nicht unbedingt als ‚*Hotspots*’ der Biodiversität zu betrachten sind. Artendiversität und Artenzusammensetzung dieser Insekten wurden zudem stärker von regionalen Faktoren moduliert als von der lokalen Hochwasserdynamik.

3. List of manuscripts with statement of personal contribution

Chapter 5: Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light? (2012) *European Journal of Entomology* 109 (1): 77−84.
C. Truxa & K. Fiedler

Personal contribution:
- Fieldwork in the Orth experiment
- Data analysis under supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 6: Species richness measures fail in resolving diversity patterns of speciose forest moth assemblages. (2012) *Biodiversity and Conservation*. DOI: 10.1007/s10531-012-0311-5
K. Fiedler & C. Truxa

Personal contribution:
- Co-planning and design of surveys
- Fieldwork
- Species identification and examination of genitalia structures
- Data preparation and analysis under supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 7: Down in the flood? How moth communities are shaped in temperate floodplain forests. (2012) *Insect Conservation and Diversity.* DOI: 10.1111/j.1752-4598.2011.00177.x
C. Truxa & K. Fiedler

Personal contribution:
- Co-planning and design of surveys
- Fieldwork
- Species identification and examination of genitalia structures
- Data preparation and analysis under supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 8: Beta-diversity of floodplain forest moths – within-group concordances and structural redundancies (prepared for submission to *Journal of Animal Ecology*)

C. Truxa & K. Fiedler

Personal contribution:

- Co-planning and design of surveys
- Fieldwork
- Species identification and examination of genitalia structures
- Data preparation and analysis under supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

4. Introduction

Floodplain forests are nowadays among the rarest ecosystems in Europe, and with regard to numerous groups of organisms they are particularly species-rich habitats (Robinson et al., 2002). They are located near streams and rivers and are frequently inundated for varying periods of time each year. Floodplains are extremely sensitive and important environments in natural landscapes: they are moderating the extent of flooding risks and have an impact on the ground water levels, natural purification of rivers and nutrient accumulation (Gren et al., 1995; Krause et al., 2007; Venterink et al., 2003). Besides these ecosystem services floodplains serve as a resort in cultivated landscape for many species once common in wetland deciduous forests and shelter lots of specialised animals and plants. Because of dynamic changes in riparian environment a great number of various microhabitats occur in close proximity to each other, which harbour a wide range of different plant and animal species. Many floodplain species, especially those of the most dynamic non-forested areas, are specifically adapted to this challenging environment and cannot be found in other habitats.

However, most of the natural rivers and accompanying forests have already been manipulated or destroyed all over the world: control structures like dams or weirs inhibit rivers to meander and to form wetlands, thereby draining existing floodplains. In Central Europe, 90% of wetlands have already been destroyed (Colditz, 1994). Currently wetlands in Austria cover about 2040 hectares – this is but a tenth of their original size. Only a third of these remaining floodplains are in near-natural state. This is the reason why floodplain habitats as a whole are scored as “endangered” in the *Red List of Endangered Biotopes of Austria* (Essl et al., 2008).

The main research focus in floodplain biodiversity and community ecology is usually on monitoring of vegetation (van Diggelen et al., 2006), birds (Vaughan et al., 2007), fish (Lasne et al., 2007) and aquatic insects (Bunn & Arthington, 2002). Less attention has been paid to the abundance, diversity and community structure of terrestrial insects and other arthropods in floodplain forests (Ballinger et al., 2005; Dziock, 2006; Rothenbücher & Schaefer; 2005; Zulka, 1991). The rather few published studies of butterflies and moths usually do not go beyond descriptive (often non-quantitative) species surveys and mapping efforts (e.g. in Eastern Austria: Cleve 1974 ; Kasy, 1989; Germany: Köppel, 1997).

However, it has been increasingly recognized that terrestrial insects are sensitive indicators for environmental quality and change. Especially phytophagous insects which often show high degrees of host specialization react fast to shifts in habitat quality and climate (Woiwod & Harrington, 1994; Hodkinson & Bird, 1998; Pimm, 2009). Their close connections to host-plants render herbivorous insects an important target of biodiversity research (Janz et al., 2006; Novotny et al., 2006; Dyer et al., 2007). Phytophagous insects are also good indicators for environmental changes as they react rapidly to shifts in vegetation composition (Lewinsohn et al., 2005). Moreover, since the niches of specialist herbivores are often more narrow than those of their host-plants (Strong, 1979), monitoring of herbivorous insects has the potential to reveal subtle environmental effects earlier than they may become visible at the level of primary producers.

The Lepidoptera, i.e. butterflies and moths, turned out to be one particularly suitable indicator taxon for ecological studies (Roy et al., 2007). Especially nocturnal moths provide appropriate targets for ecological studies as there are cost-effective ways to survey them in quantitative manner. Moths comprise the vast majority of lepidopteran diversity and can be found in nearly every terrestrial habitat in substantial numbers of species and individuals (Summerville et al., 2004). In Central Europe, moths are also quite easy to identify to species level and their life-history traits are usually well known. In Austria, moths also represent the far larger number of Lepidoptera species worth protecting, relative to butterflies (Huemer, 1989).

Against this background, the principal goal of my doctoral thesis was to study, for the first time ever, the species diversity and community ecology of one species-rich group of terrestrial herbivorous insects (namely moths) in the few near-natural floodplain forest ecosystems that still persist in Eastern Austria.

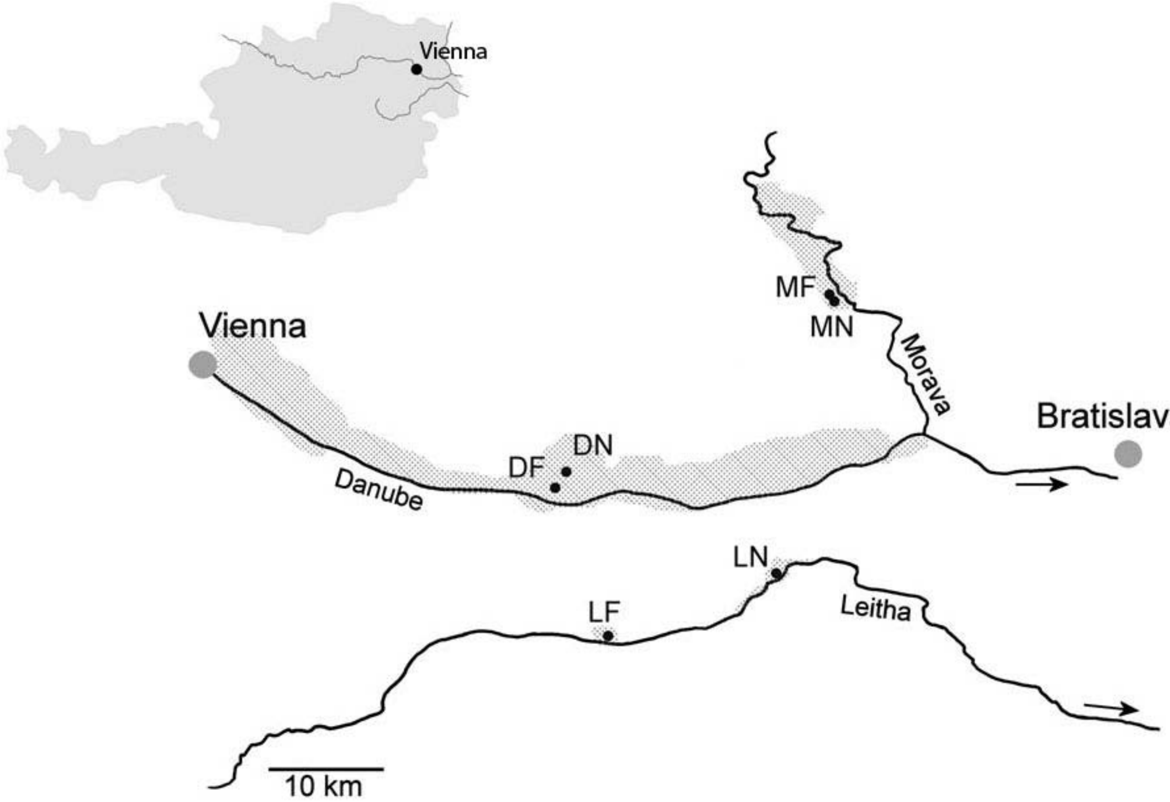

Fig. 4.1: Location of the study regions in Eastern Austria. Shaded in grey are the three floodplain forests. For details see text below. Geographic coordinates are given in Appendix S2.

The study regions were located at the rivers Danube, Morava and Leitha (Fig. 4.1). All three study regions contain regularly flooded and not (regularly) flooded forest habitats (Fig. 4.2). The most significant wetlands in Austria are preserved in the National Park Donau-Auen (Lazowski, 1997). Within that park the Danube still retains the character of an alpine stream (Lazowski, 1997). However, due to a levee ('Marchfeldschutzdamm') built in the late 19th century there is nowadays a clear separation between forest habitats which experience regular flooding (abbreviated as DF in Fig. 1), and others which are not or only occasionally inundated (DN). Spills of high water and flooding of forest areas mostly occur in the summer time and last several days (P. Zulka, pers. comm.). Frequently flooded sites – so called softwood floodplain forests – consist of broad-leaved softwood trees, like white poplar (*Populus alba*), willows (*Salix* sp.) and grey alder (*Alnus incana*). Forest sites which are not frequently flooded – so called hardwood floodplain forests – are composed of trees like oak (*Quercus* sp.), ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), maple (*Acer* sp.), lime (*Tilia* sp.) and elms (*Ulmus* sp.: Klimo & Hager, 2001).

The second study region was the floodplain of the Morava river, and specifically the WWF reserve near Marchegg. The Morava is a tributary stream of 1st order to the Danube. Since there is no levee extending through the forest all areas are flooded regularly, but there are pronounced differences in the duration of flooding. Some areas close to the river are far longer and more frequently inundated (MF) than others (MN). Inundations mostly occur in spring time (Zulka, 1991) and contrary to the Danube-floodplains, floodings usually last 3–4 weeks (P. Zulka, pers. comm.). Most of the forests belong to a unique forest formation termed Fraxino pannonicae-Ulmetum (Lazwoski, 1997).

The third sampling region comprised the alluvial forests at river Leitha, another 1st order tributary stream to the Danube. The river Leitha has been regulated throughout almost its entire length. So flooding events are nowadays rare and only occur after exceptional rain falls or during snow melt. Most of the pronounced and extended inundations in the flooded area that still happen are caused when ground water rises up to the surface (Lazowski, 1989). Periodically flooded forests were located near Königshof (Burgenland; LF) whereas sporadically flooded habitats were situated between Gerhaus and Rohrau (Lower Austria; LN). The near-natural floodplain forests at Königshof are dominated by black alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*). In contrast, the area between Gerhaus and Rohrau comprises managed poplar (*Populus* sp., *Populus canadensis*) forests (Lazowski, 1997). Due to intense river regulation and current land-use floodplain forest relicts are particularly small along the river Leitha and are far more fragmented than along the two other rivers.

A list of woody plant species, vegetation ground cover, tree height and distance of light-trap sites to the edge of the forest and the nearest water is given in Tables 4.1a-c. Woody plant species were recorded in a radius of 10m around each light trap, while average tree height is given as the mean of three measurements (smallest, highest and medium tree within the 10m radius). Some exemplar photographs of light-trap sites are presented in Fig. 4.2. Some common and/or characteristic moths from these sample sites are figured in Fig. 4.3.

Table 4.1a: Details on the vegetation and habitat structure at light trap positions in the Danube floodplain forest.

Plant species	DN1	DN2	DN3	DN4	DN5	DF1	DF2	DF3	DF4	DF5
Acer pseudoplatanus	-	-	-	-	-	-	-	-	-	-
Acer campestre	3	3	6	1	3	12	1	-	1	9
Acer negundo	-	-	-	-	-	-	-	1	-	-
Acer platanoides	-	-	-	1	1	-	-	-	-	-
Aesculus hippocastanum	-	-	1	-	-	-	-	-	-	-
Ailanthus altissima	-	1	-	-	-	-	-	-	-	-
Alnus glutinosa	-	-	-	-	-	-	-	-	-	-
Carpinus betulus	2	-	-	-	-	-	-	-	-	-
Clematis vitalba	-	-	-	-	-	-	-	-	-	-
Cornus mas	1	8	5	3	1	1	-	-	-	-
Cornus sanguinea	-	-	-	-	-	1	15	1	7	1
Corylus avellana	11	6	5	3	14	8	2	-	1	-
Crataegus laevigata	-	-	4	-	-	5	4	-	2	-
Crataegus monogyna	-	-	-	-	-	7	2	3	4	3
Euonymus europaeus	-	-	-	-	-	-	-	-	-	-
Fraxinus excelsior	-	3	1	1	2	9	1	-	-	-
Juglans regia	1	8	4	2	4	-	-	-	-	-
Populus alba	1	-	-	-	-	-	2	4	6	6
Populus nigra	-	-	-	-	-	1	-	-	-	-
Prunus domestica	-	-	-	-	-	-	-	-	-	-
Prunus padus	9	16	4	5	5	-	-	-	-	-
Quercus petraea	-	-	-	-	-	-	-	-	-	-
Quercus robur	1	-	-	-	-	-	-	-	-	-
Robinia pseudoacacia	-	-	-	-	-	-	-	-	-	-
Salix alba	-	-	-	-	-	-	-	-	-	-
Salix sp.	-	-	-	-	-	-	-	-	-	-
Sambucus nigra	1	-	-	-	-	-	-	-	-	1
Tilia platyphyllos	-	1	2	-	-	-	-	-	-	-
Ulmus laevis	-	-	1	-	-	-	-	-	-	-
Ulmus minor	-	-	-	-	-	-	1	2	2	1
Number of stems	30	46	33	34	39	44	28	11	23	21
Ground cover [%]	60	90	100	70	100	40	90	80	80	30
Average tree height [m]	19	18	18	18	25	29	31	19	18	16
Distance to the edge of the forest [m]	120	200	90	220	60	200	190	250	160	120
Distance to the nearest water [m]	210	170	70	200	260	70	80	70	90	90

Table 4.1b: Details on the vegetation and habitat structure at light trap positions in the Morava floodplain forest.

Plant species	MN1	MN2	MN3	MN4	MN5	MF1	MF2	MF3	MF4	MF5
Acer pseudoplatanus	-	-	-	-	-	-	-	-	7	-
Acer campestre	17	-	-	12	-	13	1	2	7	6
Acer negundo	-	-	-	-	-	-	-	-	-	-
Acer platanoides	-	-	-	-	-	-	-	-	-	-
Aesculus hippocastanum	-	-	-	-	-	-	-	-	-	-
Ailanthus altissima	-	-	-	-	-	-	-	-	-	-
Alnus glutinosa	-	-	4	-	-	-	-	-	-	-
Carpinus betulus	-	-	-	-	1	-	-	-	-	-
Clematis vitalba	-	-	-	-	-	-	-	-	-	-
Cornus mas	-	-	-	-	-	-	-	-	2	-
Cornus sanguinea	-	18	23	14	7	5	23	12	-	1
Corylus avellana	-	-	-	-	-	-	-	-	-	-
Crataegus laevigata	-	-	-	-	-	7	1	3	1	-
Crataegus monogyna	1	-	-	-	3	2	-	1	-	-
Euonymus europaeus	-	-	-	-	-	1	-	-	-	-
Fraxinus excelsior	4	56	2	2	5	-	1	36	-	3
Juglans regia	-	-	-	-	-	-	-	-	-	-
Populus alba	-	1	-	-	1	-	-	-	1	5
Populus nigra	-	2	7	-	2	-	-	3	-	-
Prunus domestica	-	1	-	-	-	-	-	-	-	-
Prunus padus	-	4	1	-	-	-	-	1	-	1
Quercus petraea	2	-	-	1	1	-	3	-	-	2
Quercus robur	-	-	-	-	-	-	-	-	-	-
Robinia pseudoacacia	-	-	-	-	-	-	-	-	-	-
Salix alba	-	-	-	-	2	-	-	-	-	-
Salix sp.	-	-	-	-	-	-	-	-	-	-
Sambucus nigra	-	-	-	-	-	-	-	-	-	-
Tilia platyphyllos	-	-	-	-	-	-	-	-	-	-
Ulmus laevis	-	-	-	-	-	-	-	-	-	-
Ulmus minor	-	2	2	6	-	1	1	-	2	-
Number of stems	24	84	39	35	22	29	39	58	20	27
Ground cover [%]	10	70	80	80	90	20	40	70	100	80
Average tree height [m]	19	17	22	18	24	7	18	24	20	25
Distance to the edge of the forest [m]	100	110	160	130	40	80	120	110	160	200
Distance to the nearest water [m]	80	180	140	60	40	30	100	60	80	50

Table 4.1c: Details on the vegetation and habitat structure at light trap positions in the Leitha floodplain forest.

Plant species	LN1	LN2	LN3	LN4	LF1	LF2	LF3	LF4
Acer pseudoplatanus	4	2	-	-	-	-	-	-
Acer campestre	-	-	-	-	-	-	-	1
Acer negundo	1	11	6	-	-	13	-	-
Acer platanoides	-	-	-	-	-	-	-	-
Aesculus hippocastanum	-	-	-	-	-	-	-	-
Ailanthus altissima	-	-	-	-	-	-	-	-
Alnus glutinosa	-	-	-	3	2	1	1	-
Carpinus betulus	-	-	-	-	-	-	-	-
Clematis vitalba	1	-	-	-	1	-	-	-
Cornus mas	1	-	-	-	57	8	38	-
Cornus sanguinea	-	-	-	-	-	-	-	-
Corylus avellana	-	-	-	3	-	-	-	-
Crataegus laevigata	-	-	-	-	-	-	-	-
Crataegus monogyna	-	-	-	-	-	-	-	-
Euonymus europaeus	-	-	-	-	-	-	-	-
Fraxinus excelsior	6	8	7	8	2	29	5	4
Juglans regia	1	-	-	-	-	5	-	-
Populus alba	-	-	-	-	1	-	-	-
Populus nigra	-	3	5	-	-	-	1	3
Prunus domestica	-	-	-	-	-	-	-	-
Prunus padus	5	12	19	-	4	-	4	1
Quercus petraea	-	-	-	-	-	-	-	-
Quercus robur	-	-	-	-	-	-	-	-
Robinia pseudoacacia	-	-	1	-	-	-	-	-
Salix alba	-	-	-	-	-	-	-	-
Salix sp.	-	-	-	2	-	-	-	-
Sambucus nigra	-	-	-	-	-	-	-	-
Tilia platyphyllos	-	-	-	-	-	-	-	-
Ulmus laevis	-	-	-	-	-	-	-	-
Ulmus minor	-	-	-	-	-	-	-	1
Number of stems	19	36	38	16	85	56	49	10
Ground cover [%]	40	10	20	60	10	85	10	70
Average tree height [m]	26	19	16	16	16	20	22	16
Distance to the edge of the forest [m]	170	160	200	250	180	130	90	110
Distance to the nearest water [m]	40	60	50	50	100	90	20	30

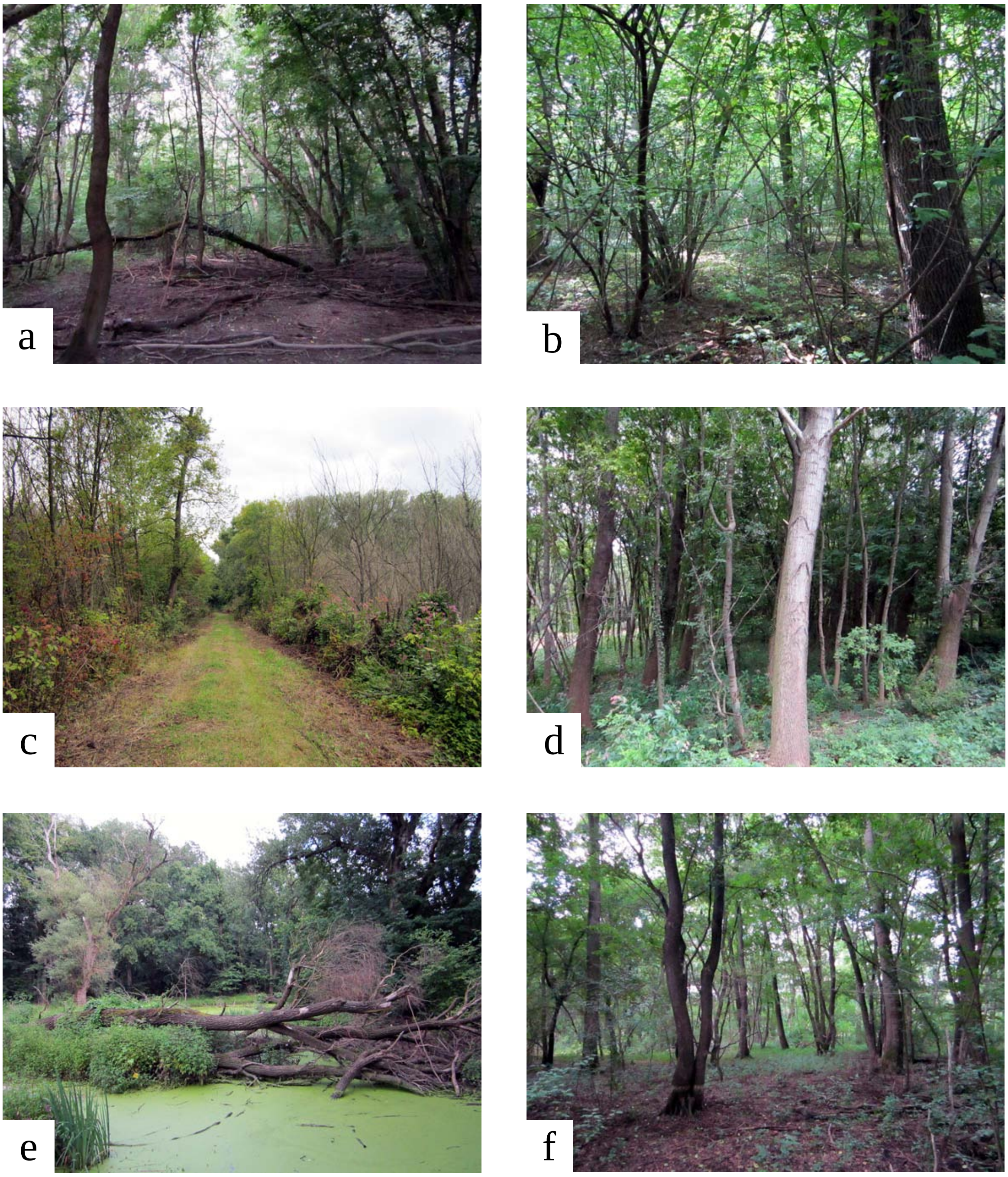

Fig. 4.2: Study habitats. **a**: river Danube, flooded forest, **b**: river Danube, non-flooded forest, **c**: river Leitha, flooded forest, **d**: river Leitha, non-flooded forest, **e**: river Morava, extensively flooded forest, **f**: river Morava, forest flooded only for shorter periods.

Since inundation is a major mortality factor for terrestrial organisms, it is to be expected that flooding will negatively affect the diversity of nocturnal moths (Köppel, 1997; Konvicka et al., 2002). Rather few studies thus far exist which investigated the impact of flooding on the diversity of terrestrial arthropods (for example: Ballinger et al., 2005; Rothenbücher & Schaefer, 2005; Lambeets et al., 2009) with quite divergent results. However, it is to be expected that especially the less mobile early stages of Lepidoptera will suffer from inundations (Köppel, 1997; Konvicka et al., 2002) and therefore overall moth abundance and diversity should be lower in flooded habitats than in non-flooded ones.

Periodical indundations demand specific adaptations of terrestrial invertebrates to survive such tough conditions. These adaptions can range from morphological and physiological adaptions to phenological and behavioural adaptations (Adis & Junk, 2002). In this context flooded habitats should harbour a unique moth community containing many specialised species.

As mentioned above, floodplains are highly threatend ecosystems with a high conservation value. Monitoring species in such habitats is important to reveal changes in species diversity and communities and to take the actions needed to prevent diversity loss. Monitoring species-rich communities, like insects, requires considerable sampling effort. Therefore working with “indicator” taxa – taxa that can serve as surrogates for overall diversity – provides a good way of keeping sampling effort and costs for monitoring low. Structural redundancy – meaning not all species are equally important for characterizing a community (Mistri et al. 2001) – is a related topic, and structural redundancy could be particularly high in species rich communities like moths.

The aim of this thesis is to get new insights into patterns of moth diversity and community structures in species-rich floodplain forests in Central Europe and concomitantly to clarify questions on sampling methodology and biodiversity analysis related to light-trap data.

Specifically, the aims of my study were:

(a) to assess the distance from which moths are attracted to weak artificial light sources – Chapter 5

(b) to empirically explore the performance of a range of alpha-diversity measures to arrive at a selection of a measure that shows sensitivity at the required ecological scale – Chapter 6

(b) to examine local species diversity and community composition of moths in floodplain forests – Chapter 7

(c) to reveal within-group concordances and structural redundancies of moth faunas regarding to their turnover in species composition (i.e. beta-diversity) – Chapter 8

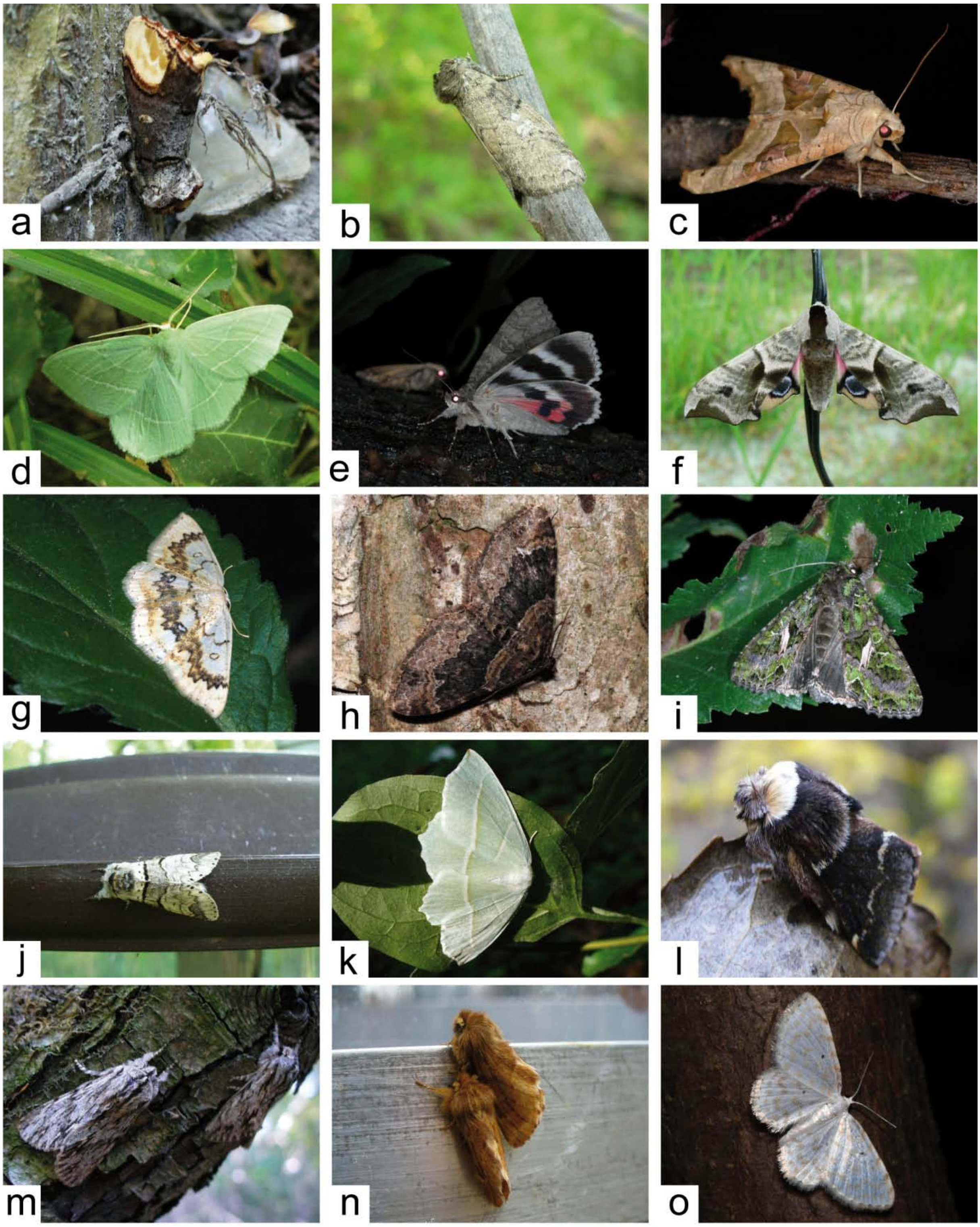

Fig. 4.3: Selected nocturnal Lepidoptera from this study. **a**: *Phalera bucephala*, **b**: *Tethea or*, **c**: *Phlogophora meticulosa* (© F. Bodner), **d**: *Hemistola chrysoprasaria*, **e**: *Catocala nupta* (© F. Bodner), **f**: *Smerinthus ocellata*, **g**: *Cyclophora annularia*, **h**: *Xanthorhoe ferrugata*, **i**: *Trachea atriplicis*, **j**: *Furcula bifida*, **k**: *Campaea margaritata*, **l**: *Poecilocampa populi*, **m**: *Asteroscopus sphinx*, **n**: *Ptilophora plumigera*, **o**: *Asthena anseraria*.
(underlined are those species typical for wet/floodplain forests)

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5. Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light?

Abstract. Moths are frequently used as indicators of biodiversity or habitat quality. Light traps are the most effective and widely used method for gathering data on moth communities. Knowing the distance from which moths are drawn to a light trap is therefore essential for the ecological interpretation of such data. Two community-wide mark-release-recapture experiments were carried out in forest habitats in central Europe in order to investigate whether the percentage of marked moths recaptured at weak artificial light sources (2 × 15 W UV-light tubes) is dependent on the distance they were released from the light source. Altogether 2,331 moths belonging to 167 species were caught at light traps and released at distances of 2–100 m. Of these moths 313 returned to the light trap within 5 min of release. Percentage recapture was generally low (gross rate 13.4%) and strongly decreased with increase in the distance at which they were released. Percentage recapture was not significantly affected by ambient temperature or the sex of the moths. Only for the Geometroidea was the percentage recaptured slightly greater for the larger species. We found no significant differences between moth super-families with regard to the distance dependence of their attraction to light. Our data confirm that the radius of attraction of low powered light traps for moths is very small often even below 10 m. Thus, moths are good indicators of habitat quality and fragmentation as they are rarely attracted from distant habitats to such light traps.

Keywords. Lepidoptera – low power light traps – mark-release-recapture – attraction range

Introduction

Light traps are the most widely used and most efficient method used to survey nocturnal insects – especially moths – at population and community levels (Young, 2005). Although light traps provide an excellent method of gathering standardized and comparable data, there are many factors that influence the abundance and composition of light trap catches. It is known that moth catches are significantly influenced by the type of trap, sampling mode (manual vs. automatic), time of day, season and duration of sampling (Thomas & Thomas, 1994; Axmacher & Fiedler, 2004; Summerville & Crist 2005; Beck & Chey, 2007). Catch size and composition are also determined by the light source employed and its spectral composition (Leinonen et al., 1998; Fayle et al., 2007). In addition to the type of trap and equipment a range of abiotic factors affect the efficiency of light traps, such as temperature, rainfall, moonlight and cloud cover (Holyoak et al., 1997; Yela & Holyoak, 1997; Beck et al., 2011a).

In contrast to the well established effects of environmental conditions and trap characteristics on the size and species composition of catches of nocturnal insects, surprisingly little is known about the distances at which moths respond to an artificial light source. However, this type of knowledge is essential for the correct interpretation of light-trap catches, for example in terms of the spatial scale and resolution of community-wide moth samples in biodiversity studies, or estimating the abundance of insects at a landscape scale from the numbers caught by light traps. There are only a few experimental studies on this topic specifically on moths. Bowden (1982) supposes that the attraction radius of a 15 W mercury vapour lamp ranges from 50-250 m depending on the species. To evaluate the distance at which two temperate-zone noctuid moth species, *Noctua pronuba* and *Agrotis exclamationis*, respond to a light trap Baker & Sadovy (1978) performed pioneering mark-release-recapture (MRR) experiments and concluded the attraction range of a far stronger 125 W mercury vapour lamp is only about 3 m. More recently, Beck & Linsenmair (2006) used a similar approach to estimate the attraction radius of 125 W mercury vapour light sources for 18 species of hawk moth (Sphingidae) in tropical rainforest in Borneo. The distance from which these hawk moths returned to the light was usually below 30 m. However, all these studies are based on a few selected species or one not very diverse family and are not on entire moth assemblages. In contrast, ecological research employing light-traps usually aims at analyses at the community level. As a result of the lack of community-wide experiments there is still uncertainty about the effective radius of attraction of light traps when used to study natural moth communities (Ricketts et al., 2001; Hawes et al., 2009) and usually the few results for single-species are generalized to the community level without supporting experimental evidence (Schmidt & Roland, 2006). In the present study we report on two community-wide MRR experiments used to estimate the dependence on distance of the percentage of marked individuals of temperate-zone moths recaptured at weak light sources.

The hypotheses tested are:

(1) The effective radius of attraction of a light trap is small.

Previous studies (Baker & Sadovy, 1978; Beck & Linsenmair, 2006) indicate that the range of attraction of light traps using 125 W mercury vapour bulbs is small. As we used a much weaker light source (15 W) the radius of attraction should be even smaller.

(2) Higher taxonomic groups (such as moth super-families) differ in their distance-dependent recapture rates.

Sensory and flight physiology are expected to show phylogenetic inertia, which should translate into taxon-specific responses. In particular, more robust flyers (such as many noctuids and arctiids) are expected to return from greater distances than smaller delicate moths (such as many geometrids or pyraloids).

(3) Moths with bigger wing spans return from greater distances than small moths.

Within moth families it is supposed that the larger moths return from greater distances as they are stronger fliers than the more delicate moths.

(4) Temperature affects recapture rates.

As ambient temperature affects moth catches positively, recapture rates should increase with increasing temperature.

Methods

Moth sampling and handling

The first experiment in 2003 was carried out in the Botanical Garden of the University of Bayreuth (Germany). The study area (49°55’ N, 11°35’E, 355 m a.s.l.) was located in a small, dense deciduous secondary forest with trees (mainly *Betula pendula*, *Quercus robur*, *Acer pseudoplatanus*, *Fagus sylvatica* and an admixture of a few *Picea abies*) ranging from 5 to 8 m in height. The light trap used for the experiments was placed on a small gravel road within this area, which provided a near-linear pathway for moths. Such corridors may facilitate moth flight (Mönkkönen & Mutanen, 2003) and therefore increase the likelihood of recaptures. Moths were sampled for a total of 19 nights between 30 April and 30 May. Moth sampling started after dusk (~21:00 CEST). The light source was two battery-driven 15 W UV-light tubes (Sylvania, Blacklight-Blue, F15W/ BLB-T8; and Phillips, TLD, 15W/ 05) inside a white gauze”tower“ (height 170 cm, diameter 70 cm). For practical reasons only moths with a wing span larger than 1.5 cm were used in the experiments. Moths that settled on the gauze were immediately placed individually in small plastic cups and transported to the laboratory. They were kept in the dark and cool (5 °C) over night to avoid damage. On the next day they were identified to species, anesthetized with CO_2 and marked individually by drawing a number on the dorsal forewing (Edding, Paint marker 780, silver) and then kept again at 5 °C until released.

The marked moths were released during the next night at different distances from the light source at which they were caught. MRR experiments started at the beginning of dusk (~21:00 h CEST) and ended three hours later or if the ambient temperature dropped below 10 °C. Release distances were 2, 3, 5, 7, 10, 12, 15, 18, 20, 25, 30, 35 and 40 m in both directions along the small road on which the light trap was situated. For analyses of contingency tables releases at distances up to 20 m were later summed over 5 m intervals. Every specimen was first released 5 m from the light trap. Only individuals of species that were recaptured after being released 5 m from the light trap were subsequently tested at greater distances. Nightly ambient temperatures were recorded from the beginning until the end of each experiment using a minimum-maximum thermometer.

The second experiment was carried out in a floodplain forest in the Donau-Auen Nationalpark (48°08’ N, 16°41 E, 156 m a.s.l.) near Orth (Austria) in 2007. The light trap was placed on a straight, narrow, east-west oriented forest road mainly surrounded by closed-canopy forest made up of *Populus nigra*, *P. alba*, *Fraxinus excelsior, Acer campestre, Carpinus betulus* and *Q. robur*. Again the light source consisted of two battery-driven 15 W UV-light tubes (Sylvania, Blacklight-Blue, F15W/ BLB-T8; Sylvania Blacklight F15W/ 350 BL-T8). Experiments took place on 4 to 5 June 2007 and 12 to 14 June 2007. All moths with a wing span >1.5 cm were used in the MRR study. Unlike in the Bayreuth experiment moths were collected from the light trap, immediately anesthetized (CO2 gas), marked (Edding, Paint marker 780) and then released at various distances from the light source. The moths were released over a greater range of distances than at Bayreuth (5, 10, 15, 20, 30, 40, 50, 60, 70, 80, 90 and 100 m) again in both linear directions along the road on which the light trap was placed. Ambient temperature was recorded during the experiments (~22.00–1.30 h) with a HOBO U12 data logger every 10 min. In this experiment, the record for each moth released was temporally associated with the closest temperature record.

Statistical analyses

The times required by the moths to return to the light sources ranged from a few seconds up to three hours. We analyzed the data using three recapture intervals, i.e. 5, 10 and 20 min after release. There were no significant differences, with regard to the influence of distance, wing span and temperature on the percentage recaptured in these different time intervals. Therefore, we subsequently only counted those moths that returned within 5 min as “recaptures”. The marked moths that arrived after 5 min were treated as “non-recaptures”. We decided to use the 5 min time interval because (1) we considered this time span as sufficient for moths to warm up and fly up to 100 m, but too short to avoid released moths coming across the light trap by chance after a random flight through the habitat and (2) Beck & Linsenmair (2006) use this time interval in their MRR studies on Sphingidae, which means the results of these two studies can be compared.

Wing span data for every species was taken from literature (Palm, 1986; Skou, 1991; Hausmann, 2001, 2004; Mironov, 2003) and the geometric mean of minimum and maximum wing span was used as a proxy for body size in the subsequent analyses. Data from both experiments were analyzed separately as the details differed. Differences between taxa, release distances, wing span classes, sex (Bayreuth experiment) and release direction (Orth experiment) in terms of the probability of being recaptured were evaluated using Chi² tests. The effects of release distance, ambient temperature and body size on the probability of recapture were assessed using multiple logistic regression. All analyses were calculated in Statistica 7.1 (StatSoft Inc.).

Results

In the Bayreuth experiment 217 moths returned within 5 min and a further 108 moths returned within 6–80 min. In the Orth experiment 96 moths returned to the light source within 5 min and a further 264 returned within 6–212 min. If only those moths released at distances up to 40 m from the Orth light trap are considered then 89 moths returned within 5 min.

Bayreuth experiment

A total of 851 individuals belonging to 96 species of moth were caught and released in this experiment (Appendix S1). The number and percentage of moths recaptured was 217 and 25.5%, respectively. The probability of recapture strongly decreased as the distance at which they were released increased. While there were 200 recaptures of 713 releases at distances up to 15 m (percentage recapture: 28.1%) there were only 17 recaptures of the 138 moths released at distances from 16 to 40 m (percentage recapture: 12.3%). This difference is highly significant ($\text{Chi}^2_{1\text{df}} = 15.06$, $p < 0.001$). The moths caught in this MRR experiment belonged to the superfamilies Noctuoidea, Geometroidea and Drepanoidea (Table 5.1). There was only a weak difference in the percentages of moths of the different superfamilies recaptured (Pearson’s $\text{Chi}^2_{2\text{df}} = 7.06$, $p = 0.030$).

Table 5.1: Numbers of released and recaptured individuals of three moth superfamilies and for the entire sample at various release distances to the light trap (Bayreuth experiment).

Distance [m]	Noctuoidea		Geometroidea		Drepanoidea		All moths	
	Released	Recaptured	Released	Recaptured	Released	Recaptured	Released	Recaptured
0-5	76	33	168	47	10	5	254	85
6-10	87	30	140	38	16	7	243	75
11-15	82	18	121	18	13	4	216	79
16-20	33	5	50	8	7	0	90	13
25	7	1	14	1	1	0	22	2
30	6	1	6	0	1	0	13	1
35	5	1	4	0	0	0	9	1
40	4	0	0	0	0	0	4	0
total	300	89	503	112	48	16	851	256

Noctuoidea and Drepanoidea were recaptured more often than expected from marginal totals, while Geometroidea were recaptured less frequently than expected (Fig. 5.1).

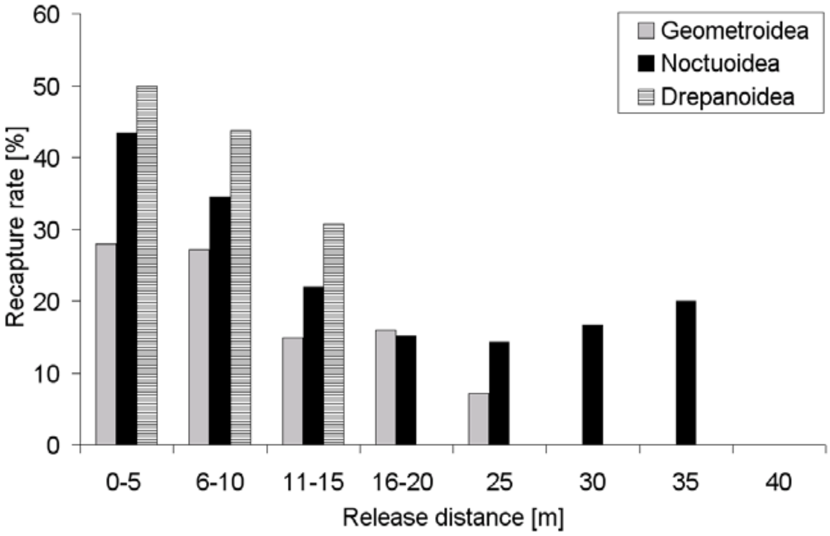

Fig. 5.1: Percentage of recaptures of moths in the Bayreuth experiment, segregated according to the three main superfamilies.

For all moth superfamilies the probability of recapture strongly decreased with increase in the distance at which they were released from the light source (Table 5.2). This distance dependence was more marked for the Geometroidea than the Noctuoidea. The percentage recaptured significantly increased with increase in wing span in the Geometroidea (smallest species: *Eupithecia tantillaria*, 17.9 mm; largest species: *Hypomecis punctinalis*, 44.3 mm), but not in the Noctuoidea (smallest species: *Clostera pigra*, 23.8 mm; largest species: *Pheosia tremula*, 53.4 mm). Ambient mean temperature during each night of the experiment ranged from 10–20 °C and did not significantly affect the percentage recaptured in any of the three moth taxa studied.

We caught fewer female than male moths (deviation from an equal sex ratio: $\text{Chi}^2_{1\text{df}} = 14.745$, $p < 0.0002$). However, the percentages recaptured did not differ between the sexes ($\text{Chi}^2_{1\text{df}} = 0.04$, $p = 0.838$; 434 males released, 113 recaptured; 327 females released, 83 recaptured; for 90 individuals the sex was not recorded).

Table 5.2: Results of multiple logistic regressions for modelling recapture probability as a function of release distance and body size. Release distances ranged from 2–40 m (Bayreuth experiment) and 5–100m (Orth experiment). Release distances up to 40 m in the Orth experiment were used to facilitate comparisons with the Bayreuth experiment. Significant results are highlighted in bold.

		Distance		Wing span		Temperature	
	n	*t*	*p*	*t*	*p*	*t*	*p*
Bayreuth							
total	847	**5.675**	**0.001**	**3.975**	**0.001**	0.203	0.839
Noctuoidea	296	**3.478**	**0.001**	0.517	0.606	1,084	0.279
Geometroidea	499	**4.531**	**0.001**	**3.928**	**0.001**	1,157	0.248
Drepanoidea	44	**2.133**	**0.039**	1.116	0.271	0.540	0.592
Orth 5-100m							
total	1475	**6.421**	**0.001**	**2.348**	**0.019**	0.130	0.897
Noctuoidea	247	**3.138**	**0.002**	1.670	0.091	0.711	0.478
Geometroidea	771	**4.399**	**0.001**	**2.339**	**0.020**	0.623	0.534
Pyraloidea	423	**3.653**	**0.001**	0.187	0.852	0.256	0.798
Orth 5-40m							
total	1028	**5.959**	**0.001**	**2.649**	**0.008**	0.724	0.469
Noctuoidea	174	**3.280**	**0.001**	1.436	0.153	0.697	0.487
Geometroidea	555	**3.967**	**0.001**	**2.970**	**0.003**	1,075	0.283
Pyraloidea	272	**3.278**	**0.001**	0.201	0.841	0.272	0.786

Orth experiment

We captured, marked and released 1,480 moths belonging to 104 species (Appendix S1). In this experiment 96 of the 1,480 moths released were recaptured within 5 min, which is equivalent to a percentage recaptured of only 6.5%. Most of the moths belonged to the superfamily Geometroidea (776 individuals, 43 species), followed by Pyraloidea (427 individuals, 7 species) and Noctuoidea (251 individuals, 51 species) (Table 5.3). Most of the catch of Pyraloidea was made up of individuals of *Pleuroptya ruralis* (412 individuals).

Table 5.3: Numbers of released and recaptured individuals of three moth superfamilies and for the entire sample at various release distances to the light trap (Orth experiment).

	Noctuoidea		Geometroidea		Pyraloidea		All moths	
Distance [m]	Released	Recaptured	Released	Recaptured	Released	Recaptured	Released	Recaptured
5	11	5	40	12	21	6	72	23
10	31	3	74	7	34	3	139	13
15	28	5	116	15	56	6	200	26
20	42	1	119	9	50	4	211	14
30	37	1	123	7	73	1	233	9
40	29	0	87	3	42	1	158	4
50	23	1	57	1	54	0	134	2
60	12	0	57	2	28	0	97	2
70	15	0	37	0	24	1	76	1
80	5	0	28	2	14	0	47	2
90	4	0	19	0	19	0	42	0
100	14	0	18	0	12	0	44	0
total	251	16	775	58	427	22	1453	96

In order to compare these results with those recorded in the Bayreuth experiment we also analyzed the data just for the release distances up to 40 m. Of the 1,032 moths released up to 40 m from the light source only 89 or 8.6% were recaptured. The percentages recaptured were significantly lower than at Bayreuth (Geometroidea: Chi^2_{1df} = 32.98, Noctuoidea: Chi^2_{1df} = 29.60, both $p < 0.0001$; Table 2).

Gross percentages recaptured did not significantly differ between the super-families Geometroidea, Noctuoidea and Pyraloidea (Chi^2_{2df} = 2.43, $p = 0.296$; Fig. 5.2). Logistic regression analyses confirmed the highly significant negative effect of release distance on percentages recaptured for each of the major superfamilies (Table 5.2). Ambient temperature ranged from 16–22 °C and did not affect the percentages recaptured (Orth [all data up to 100 m]: t_{1475} = 0.13, $p = 0.870$) and neither did the release direction relative to the light source (Chi^2_{1df} = 0.91, $p = 0.341$). Like at Bayreuth wing span had a positive influence on the percentages of Geometroidea recaptured, which translated into a weak positive effect at the community level.

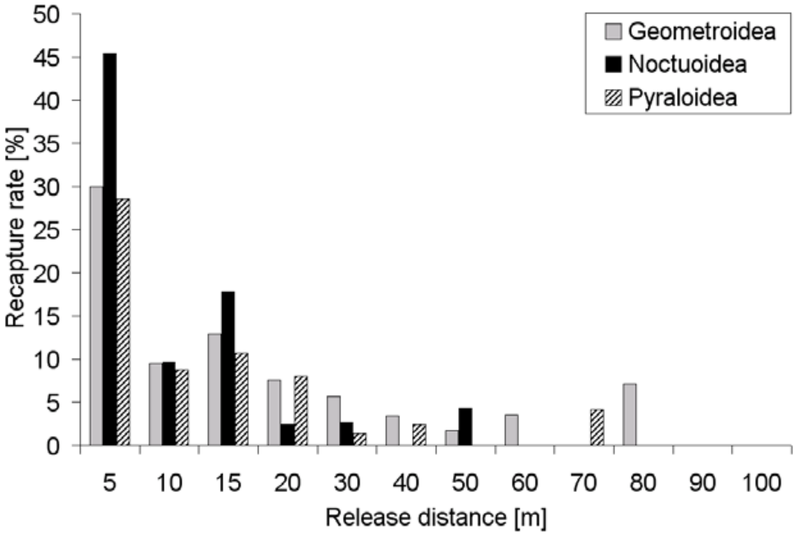

Fig. 5.2: Percentage of recaptures of moths in the Orth experiment, segregated according to the three main superfamilies.

Discussion

Percentage recapture of moths

In order to estimate the attraction radius of a weak artificial light source for moths we carried out two mark-release-recapture experiments. Overall the percentage recaptured was low ranging from 6.5% (Orth, release distances 5-100 m) to 25.5% (Bayreuth, 5-40 m). This difference was likely due to differences in the experimental design. At Bayreuth the moths were first released at a distance of 5 m from the light trap. Subsequently, only individuals of each species that were recaptured after first releasing them at a distance of 5 m were released at greater distances. This design was chosen to obtain at least some recaptures since it was anticipated that the probability of recapture would be very low. At Orth the range of release distances was increased and individual moths were assigned to be released at great distances irrespective of earlier success in recapturing representatives of the same species. This procedure resulted in low percentages of recapture.

MRR studies on moths tend to yield low percentages of recapture (Nieminen, 1996; Keil et al., 2001; Merckx et al., 2009; Merckx et al., 2010), which are in accordance with our results. The reasons for low percentages of recapture are poorly known. Low percentages of recapture recorded in studies of the dispersal by moths may result from transporting them from the field to the laboratory and back again. These sudden changes in environmental conditions might trigger unnatural dispersal behaviour (Qureshi et al., 2005). However, in our study the percentages recaptured were higher in the Bayreuth experiment, which included transportation of the moths to the laboratory and back, than in the Orth experiment in which moths were not brought back to the laboratory. All MRR experiments suffer from behavioural biases as the catchability of the moths may be influenced by the behavioural context of movements (Van Dyck & Baguette, 2005), landscape patterns (Merckx et al., 2010), handling effects (Mallet et al., 1987) and other potential sources of error. The important point relevant to our study is that even when we increased the percentage recaptured by increasing the time intervals within which returning moths were counted as “recaptures” (we also analysed return time thresholds of 10 and 20 min; data not shown) this did not lead to any statistically significant changes in the results. We therefore accepted the shortest time threshold as the most representative one for measuring the spontaneous movement patterns of moths immediately after release.

Factors influencing percentage recaptured

For all super-families of moths in both experiments the percentage recaptured strongly decreased with increase in the distance at which they were released. This was expected since the visual stimulus provided by an artificial light source decreases exponentially with distance. Contrary to our expectation that the higher taxonomic groups would differ in their distance-dependent percentages recaptured there were no obvious differences in the shape of this distance dependency among the major super-families included in our study, viz. Noctuoidea, Geometroidea, Drepanoidea and Pyraloidea. If responsive to a light trap, then representatives of all these super-families of moths were similarly attracted to the light as there were no significant biases in their distance dependent responses to the light traps. Percentage of Geometroidea recaptured increased with body size in both experiments, but the strength of this effect was much weaker than that of the distance at which they were released. We expected a body size effect as there are positive relationships between body size and dispersal range for various moth species (Nieminen, 1996; Dulieu et al., 2007). Our results might indicate that body size is more important in moth families with a more delicate morphology such as geometrids. To further explore the importance of moth body size in determining the composition of light trap catches one should systematically check a wider range of species of noctuid or pyraloid moths of different sizes.

Although temperature affects the size of light trap catches of moths (Butler et al., 1999; Beck et al., 2011a) and we expected such an effect on the percentages recaptured, ambient temperature did not affect the percentages recaptured in our experiments. The reason for this might be that both experiments took place under rather favourable environmental conditions. No experiments were carried out when temperature dropped below 10 °C. Therefore, the species pool for this study was limited to those moths that fly spontaneously under these conditions, which also includes abiotic factors like cloud cover and phase of the moon that might also influence moth catches.

Light traps usually catch fewer females than males as occurred in our study. Beck & Linsenmair (2006) propose that this could be due to differences in the activity of the sexes as well as differences in their attraction to light. Such a behavioural bias was recently confirmed experimentally by Altermatt et al. (2009). In our study there were no discrepancies in the percentages of males and females recaptured suggesting that once individuals of a moth species react to a light source their attraction radius is similar irrespective of their sex. However, our results do not rule out that in certain species such sex-related differences might occur.

Attraction radius of light traps

Our community-wide experiments show that percentage of moths recaptured decreases with increase in the distance at which they are released. Very few recaptures occurred at release distances beyond 40 m. We anticipated the attraction radius of a light trap would be short, because previous studies report attraction only over short distances and we used an even weaker light source. The predicted percentage recapture based on logistic regression of the results for the moths included in our experiments that were released at a distance of 3 m (the attraction range claimed by Baker & Sadovy (1978) for Noctua pronuba and Agrotis exclamationis) only ranged from 19% to 39%. Hence, even at this short distance the majority of the moths that were released did not fly to the light trap. The findings of this multi-species comparison accord with those of other studies based on fewer species. Beck & Linsenmair (2006) report a mean attraction radius for Sphingidae in Borneo to a more intense 125 W MV-lamp in their MRR experiments of below 30 m. So even for large, robust moths that are known to be excellent and very fast flyers like hawk moths the attraction radius of a light source much brighter than the one we used in our experiments, is surprisingly low. Qureshi et al. (2005) found no difference in the numbers of male European corn borers caught by 15 W black light traps and pheromone traps, which were placed only 2 m apart from each other, suggesting that there was no interference between these traps even at this small spatial scale. Various studies (Beck et al., 2002; Schulze & Fiedler, 2003) indicate clear differences in the samples of insects caught by light traps located in different forest strata (20-40 m height). All the more recent data support the earlier results of Baker & Sadovy (1978) but not the estimates of Bowden (1982).

A reason for these different views could be that there is a conceptual misunderstanding of the sampling range and the distance from which insects respond to light traps. Shelly & Edu (2010) define sampling range as the maximum distance from which an insect can physically reach a trap in a given time interval, whereas attraction range is the maximum distance from which an insect shows directed movement towards the attractant. Accordingly, the (potential) sampling range is always larger than the (real) attraction range, since the sampling range encompasses any area that the insect has crossed by spontaneous movements before entering the attraction radius. The low percentage of moths recaptured and the short distances from which moths returned to a weak light source in our experiments support the notion that the attraction radius of weak light traps for moths is much lower than their sampling range.

As mentioned above all the results from well-controlled studies concur that the effective attraction radius of an artificial light source for moths is rather low, mostly < 30 m and often < 10 m. In addition, as the earlier studies were only on single species or small taxon assemblages novel empirical data was needed in order to assess if the generalizations based on these results can be applied to larger communities. Our experiments using a broad range of central European moth species confirm that short attraction distances are not only a trait of single species, but can safely be extrapolated to larger assemblages.

What do these findings imply for moth biodiversity studies?

Moths are increasingly being used as indicators of habitat quality or biodiversity (Beck et al., 2011b; Kitching et al., 2000; Summerville et al., 2004). Species richness and assemblage composition are surveyed in a standardized manner in order to compare different sites or monitor changes over time. Serving as surrogates for more inclusive fractions of biodiversity, moth inventory data can be related to various environmental parameters. For example, moth community studies have addressed aspects such as effects of logging, habitat conversion and the effects of succession or fragmentation on insect biodiversity (Intachat et al., 1999; Fiedler & Schulze, 2004; New, 2004; Schmidt & Roland, 2006; Fiedler et al., 2007; Maleque et al., 2009). All these inventories rely exclusively on samples collected by light traps. Therefore spatial resolution of such samples is critical in interpreting the data and providing insights into ecological patterns and processes.

In many of the aforementioned studies light trap samples of moths revealed a high spatial resolution at the range of some dozens of meters and below, despite the potentially large mobility of flying moths. Our data from two community-wide MRR experiments together with that from other recent studies (Wirooks, 2005; Beck & Linsenmair, 2006) now confirm that the attraction of moths to light traps largely occurs at very small spatial scales, often even below 10 m. In the Bayreuth experiment only 32% and in the Orth experiment just 17% of the moths released at distances up to 10 m were recaptured. Therefore, our results corroborate the perception that weak artificial light sources are an excellent way to accurately characterize and monitor moth communities in a selected habitat, since the low attraction radius means that few species from adjacent habitats are likely to be caught by such traps.

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6. Species richness measures fail in resolving diversity patterns of speciose forest moth assemblages

Abstract: We used data from a light-trapping study at 28 sites on floodplain forest moths in eastern Austria to assess the performance of a variety of species richness and species diversity measures. At each site the data (32,181 individuals from 448 species) contain a large fraction of species represented only as singletons. Sampling effort was evenly spread across sites, but sampling success varied greatly. Influx of moths from the landscape matrix surrounding floodplain forest patches lead to substantial proportions of stray individuals from the regional species pool. Under these conditions, observed species numbers as well as eight extrapolation estimators of species totals failed to reflect differences between three study regions or between flooded and non-flooded forest habitats. Rarefied species numbers and Fisher's α of the log-series distribution captured differences in moth diversity between regions, but failed to mirror flooding impact. Only Shannon's diversity captured all expected diversity differences, at high significance levels. Application of Chao & Shen's bias correction increased figures of Shannon's diversity, but did not affect the outcome of statistical comparisons. We conclude that for species-rich incompletely sampled communities of highly mobile insects the evaluation of the complete species-abundance information using Shannon's diversity is the most promising mode to compare local species diversity with a high degree of ecological resolution. Species richness measures apart from those obtained through rarefaction cannot be recommended, as they are sensitive to sources of bias that pertain to many empirical sets of field data.

Keywords. diversity indexes – Shannon's diversity – Fisher's alpha – species richness estimators – sampling effects – ecological resolution

Introduction

Following Whittaker's seminal idea (Whittaker 1972) biodiversity can be conceptually partitioned into two components: alpha-diversity (i.e. the variety and abundance distribution of species at a site) and beta-diversity (i.e. the between-site variation). Irrespective of whether one connects alpha- and beta-diversity in an additive (Crist et al. 2003) or multiplicative (Whittaker 1972) manner (see Jost 2007), the challenge remains to find the appropriate measures for both these dimensions of biodiversity. There exists a large literature on measuring biodiversity (Magurran 2004; Reiss et al. 2009; Rosenzweig 1999) and ecologists as well as mathematicians have developed a striking range of quantitative diversity measures. There has been much debate, based on theoretical arguments, numerical simulations and results of empirical surveys, as to what measure of diversity should be preferably adopted (e.g. Buckland et al. 2005).

Still, there is controversy amongst scientists and practitioners in that regard. In recent years the classical Shannon entropy has re-gained strong support as a unifying mode to quantify species diversity (Jost 2006). Specifically, the exponential form of Shannon's entropy (subsequently termed Shannon's diversity, to distinguish it from the non-exponentiated Shannony entropy) has manifold qualities that let this approach perform superior to many other diversity measures, and simulation studies (Beck & Schwanghart 2010) have confirmed its versatility. Like all diversity measures, Shannon's diversity may be affected by stochastic sampling effects: especially in small empirical samples, the relative frequencies of species may not match their 'real' (and unknown) proportions in the community from which the samples have been drawn. The magnitude of such sampling bias decreases with increasing sample size, but also depends on the number of observed species. Chao & Shen (2003) developed a method by which this sampling bias can be corrected for in estimates of Shannon's diversity derived from real samples, and later (Chao & Shen 2009) provided a software tool to perform this bias correction.

In the study of Beck & Schwanghart (2010), however, an alternative diversity measure, derived from the geometry of log-series type species-abundance distributions (termed Fisher's α: Fisher et al. 1943), gained largely the same level of support as a useful diversity measure. Moreover, theoretical work on species-abundance distributions (Magurran 2007; Wilson & Lundberg 2004; Zillio & He 2010) has pointed out the generality of log-series type or related geometries in nature, lending support to the usefulness of parameters derived from such distributions as diversity measures. In addition, Fisher's α has proven to be both sensitive and robust in a huge number of empirical field studies that aimed at discriminating between communities (Beck et al. 2002; Fiedler & Schulze 2004; Vormisto et al. 2004). From a practical point of view, Fisher's α has the advantage that it can be estimated if only aggregate statistics of samples (such as total numbers of species and individuals) have been reported. Shannon's diversity, in contrast, can only be calculated if abundances of all species in all samples are known – which quite frequently does not apply in published studies.

When no abundance information is available, species numbers are the only way to quantify local diversity. Even though raw species numbers are particularly prone to sampling effects, they are still frequently used in current biodiversity studies (Pöyry et al. 2009; Sattler et al. 2010). However, in the last two decades an alternative mode of using species count information has gained popularity, i.e. the extrapolation of expected species totals from survey counts. The underlying concept of species accumulation curves implies that with ever more spatially or temporally replicated samples being drawn, the observed species number should asymptotically converge to the true species number in a community (Colwell et al. 2004). Various extrapolation tools have been suggested to arrive at estimates of total species richness, and their performance has been tested both in simulation studies (Brose and Martinez 2004) and empirical surveys (Longino et al. 2002). Since many such algorithms have been implemented in a widely used and freely accessible software package (Colwell 2009), these extrapolation methods are now routinely implemented in biodiversity studies (e.g. Coscaron et al. 2009; Danielsen et al. 2009). In analogy to extrapolation, also rarefaction methods are frequently used to overcome influences of uneven sampling effort or sampling success on species counts (Irmler et al. 2010).

We here use a large data set, collected with light traps, on species rich and abundant arthropods to empirically explore the performance of a range of alpha-diversity measures. Our data set is typical in many respects for invertebrate studies: (1) the number of species is in the range of hundreds, those of individuals in the range of thousands; (2) individual counts are available from trap data; (3) numerous species are only recorded in one individual (singletons) or from one trap site (uniques); (4) while many species are 'rare', only a small number of species is abundant, and one was even hyper-abundant (i.e. accounted for more individuals than expected by classical log-series or related models); (5) accordingly, species-abundance distributions share the geometry of rather steep hollow curves (Colwell et al. 2004), even though not all of them well fit to a log-series distribution.

To determine the performance of each diversity measure we explore how well it is able to reflect ecological patterns that are expected to exist in the data set. Specifically, from our field survey design (see below) we expected that the insect communities under study should differ in regard to region as well as habitat (i.e. flooded vs. non-flooded). Differences in the tree and understory vegetation of the three studied floodplain forest regions (Lazowski 1997) should translate into effects on communities of moths whose larvae are trophically bound to the vegetation. Likewise, flood events are expected to impact communities of terrestrial arthropods (Ballinger et al. 2007). Indeed, moth communities differ in species diversity and species composition between riverine regions as well as in relation to flood regimes (Chapter 7). But it remains to be assessed which of the many measures of species richness or diversity would most sensitively reflect such patterns. We therefore established observed, extrapolated and rarefied species numbers, Fisher's α, and Shannon's exponential diversity (with and without bias-correction) for each local moth sample and examined if these measures were revealing faunal differences between riverine regions as well as with regard to flood regimes.

Methods

Survey data

Three lowland floodplain forests in eastern Austria (along the rivers Danube, Morava and Leitha) were chosen for gathering data on moth diversity. Each floodplain forest comprised regularly flooded and not (regularly) flooded fractions of habitat, resulting in six sites to be compared. At each site, 4-5 low-power (2 x 15 W) light traps (depending on the size of the forest fragments, minimum distance between traps within a site was 100 m) were operated simultaneously once a month during the vegetation period over two complete annual cycles. For further details on moth sampling and site conditions see Chapter 7. All 'macro-moths' and the Pyraloidea (together forming a monophyletic group: Mutanen et al. 2010) were collected and identified to species level. Overall 32,181 individuals out of 448 species entered into the analyses.

Statistical methods

For the analyses presented here, all 14-17 nightly moth samples from each trap site were aggregated to yield one representative estimate of the local moth assemblage, resulting in quantitative species lists for 28 trap sites distributed across three regions and two flood regimes. We calculated eight estimators of species richness (ACE, ICE, Chao1, Chao2, Jacknife1, Jacknife2, Bootstrap, MMMeans) using EstimateS (Colwell 2009). Individual-based rarefaction was calculated with the programme Primer (Clarke & Gorley 2006), by estimating the expected species richness at the largest common sample size of 371 moth individuals per trap. We computed Shannon's diversity exp(H_S) and its bias-corrected version as well as Fisher's α with the software SPADE (Chao & Shen 2009). Differences in mean species richness or diversity between flood regimes and forest regions were then assessed with two-way PERMANOVAs (Anderson et al. 2006).

Results

Mean observed species richness per trap site did not reveal any significant differences between flood regimes and regions, neither did any of the extrapolated richness estimators

(Table 1, Fig. 1). In contrast, rarefied species richness did disclose significant differences between the three forest regions. Flooding, however, did not score as a statistically significant main effect with rarefied species numbers. There was a weak, but non-significant interaction effect of flooding and region. At the river Leitha, but not in the two other forest regions, rarefied species richness tended to be higher in flooded habitats. In contrast, all of the diversity measures that utilize the geometry of the species-abundance distribution, i.e. both versions of Shannon's diversity and Fisher's α captured strong differences in species diversity between the three regions. Analyses based on Shannon's exp(H_S) generally yielded higher F-values than those based on Fisher's α. Notably, only Shannon's diversities revealed significant differences between flood regimes and also a significant flood × region interaction term, whereas Fisher's α showed no sensitivity with regard to flooding effects on moth assemblages. The bias-corrected version of Shannon's diversity did not score any better than the classic exp(H_S) with regard to the strength of statistical outcomes.

Table 6.1: Results of two-way PERMANOVAs (with flood regime and region as factors) for observed species number (Sobs), eight different extrapolation estimators of total species richness, rarefied species richness (at N = 371 moths per site), and three diversity measures that use information on the geometry of species-abundance distributions.

Measure	Factor	df	Pseudo-F	P	Measure	Factor	df	Pseudo-F	P
S_{obs}	flood	1	0.839	0.372	ACE	flood	1	0.460	0.507
	region	2	3.053	0.071		region	2	1.082	0.352
	flood × reg.	2	2.601	0.099		flood × reg.	2	0.244	0.792
ICE	flood	1	0.369	0.548	Bootstrap	flood	1	0.640	0.435
	region	2	0.331	0.724		region	2	2.606	0.095
	flood × reg.	2	0.490	0.62		flood × reg.	2	2.394	0.118
Chao1	flood	1	0.134	0.717	Chao2	flood	1	0.191	0.669
	region	2	1.739	0.199		region	2	1.112	0.351
	flood × reg.	2	1.009	0.386		flood × reg.	2	0.640	0.543
Jacknife1	flood	1	0.465	0.496	Jacknife2	flood	1	0.329	0.566
	region	2	2.122	0.143		region	2	1.656	0.214
	flood × reg.	2	2.029	0.154		flood × reg.	2	1.526	0.233
MMMeans	flood	1	0.239	0.636	Rarefaction	flood	1	2.615	0.125
	region	2	0.643	0.533		**region**	2	**33.628**	**0.0001**
	flood × reg.	2	2.196	0.136		flood × reg.	2	4.021	0.020
exp(H_S)	**flood**	1	**11.366**	**0.0031**	bc-exp(H_S)	**flood**	1	**11.812**	**0.0033**
	region	2	**126.72**	**0.0001**		**region**	2	**122.02**	**0.0001**
	flood × reg.	2	**6.602**	**0.0041**		**flood × reg.**	2	**6.797**	**0.004**
Fisher's α	flood	1	2.290	0.143					
	region	2	**11.443**	**0.0005**					
	flood × reg.	2	0.570	0.595					

Given are Pseudo-F statistics (from 9999 permutations) and their associated P values. Significant results after correction for a table-wide false discovery rate at $P<0.05$ (Waite & Campbell 2006) are highlighted in bold.

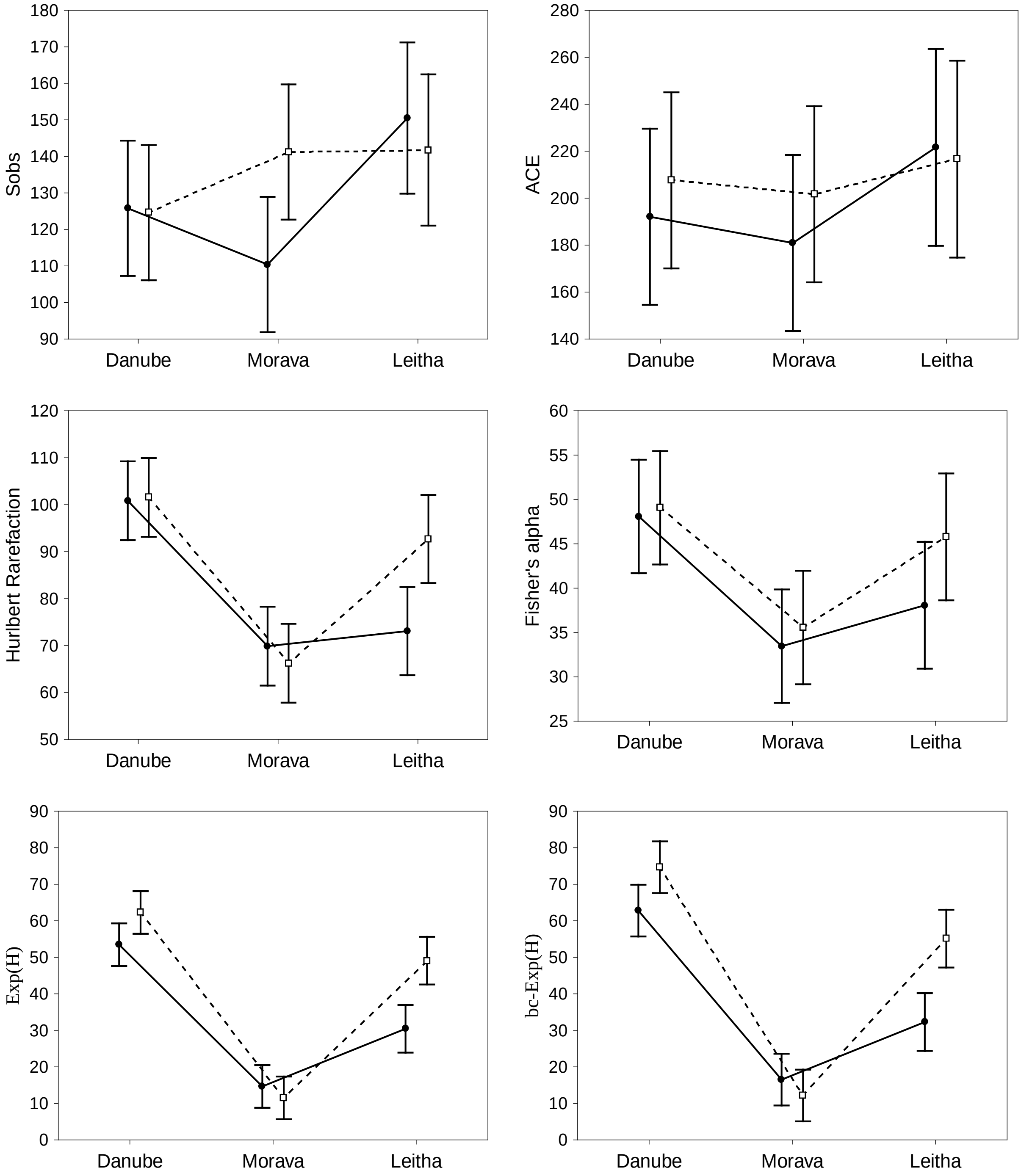

Fig. 6.1: Observed moth species richness (S_{obs}), estimated species richness (ACE), rarefied species richness and three diversity measures (all other panels) per trap site across the three study regions (floodplain forests along three rivers in Eastern Austria) and two flood regimes. Given are means ± 95 % confidence intervals. Filled dots – non-flooded areas. Open squares – regularly flood-impacted areas. For statistics see Table 6.1.

Discussion

Even though observed species counts are still frequently used in studies of species-rich insect communities (Pöyry et al. 2009; Sattler et al. 2010), they turned out to be completely inappropriate for detecting diversity patterns in floodplain forest moth ensembles. Observed species richness of moths does not only depend on the time of sampling in temperate-zone ecosystems with their distinct phenological species turnover (Summerville & Crist 2005), but is particularly biased by undersampling. The latter occurs if many rare species occur in an ecosystem, which is a typical feature of almost all ecological communities (Magurran & Henderson 2003). Phenological biases can be excluded in our analyses since light-trapping effort was spread evenly across seasons in all habitats. Yet, our samples give evidence for severe undersampling. Between 29-37% of all species within a habitat occurred as singletons, suggesting that many more 'rare' species could have been added with more intense sampling. Complete sampling, however, is almost impossible for most organisms (Colwell & Coddington 1994). Even if the sampling effort is the same in every habitat, strong differences in the numbers of collected individuals may occur, which then may translate into differences in species numbers. In our study, despite identical sampling effort we observed fewer species in the Danube region (311 species), where samples were much smaller in terms of trapped individuals (5865 moths), than in the Morava region (317 species; 14,114 moths). Although sampling effort was slightly lower in the Leitha region (only 4 light traps per habitat due to the small size of floodplain forest patches persisting along this river), more species (329 spp.) were caught here than elsewhere, and catch size was similarly high as in the Morava floodplain forest (12,202 moths).

To avoid bias induced through incomplete sampling extrapolation estimators of total species richness have been developed (Colwell & Coddington 1994). We calculated various estimators for species richness, but none of them captured any significant differences between flood regimes or forest regions. A number of studies have tried to elaborate which extrapolation method to employ depending on the types of organisms under study and data structures available (Brose and Martinez 2004; Brose et al. 2003; Wei et al. 2010), but with our moth data all these estimators failed to the same degree. Completeness of sampling relative to extrapolated species totals, averaged across all 28 sites (mean ± 1 SD), ranged from 51.8±4.0% (Michaelis-Menten estimator) to 81.3±0.8% (bootstrap estimator). For the remaining six estimators mean observed species richness amounted to 53-68% of estimated species richness. Under these circumstances Brose and Martinez (2004) recommended the use of Jacknife-type estimators for organisms with variable mobility (as is the case with moths). Notably, there were no significant differences between regions or flood regimes with regard to sample completeness for these Jackknife estimators (K. Fiedler and C. Truxa, data not shown). This indicates that the degree of faunal coverage achieved through our sampling scheme did not systematically vary between the sites and also was not responsible for the failure of extrapolation estimators to depict regional and habitat differences.

We attribute this complete failure of all species richness measures to reflect differences between floodplain forest moth communities to two properties of the sampled habitats and organisms, viz. the fragmented nature of floodplain forests and the high mobility of moths. Firstly, floodplain forests in landscapes under strong anthropogenic influence nowadays comprise narrow stripes of habitats embedded in a large matrix of completely different ecosystems (Tockner et al. 1998). Hence, mobile organisms like moths will constantly disperse into floodplain forests from surrounding habitats. Much of this species introduction will occur at low abundances, thereby increasing the long tail of rare species in the respective species-abundance distributions (Zillio & Condit 2007). These strays (as identified by comparing the life-histories of all moth species with larval resources available in the sampled habitats: see Chapter 7) made up a substantial fraction of all our samples (10-15% of observed species, up to 16% of sampled individuals), especially so in not regularly flood-impacted habitats close to agricultural habitats. At the same time, these strays pose severe challenges to species accumulation, since over time large proportions of mobile moth species from the entire regional species pool are expected to show up at almost every sampling site. These strays may eventually level out any site-specific community patterns if only species numbers are considered. With regard to Shannon's diversity, however, comparisons of moth communities across riverine regions and flood regimes were not altered substantially if strays had been included, or excluded, respectively (see Chapter 7). Secondly, as typical for arthropod communities (see Summerville & Crist (2005) for moth communities in temperate deciduous forests) our dataset contains many rare species, also amongst those moth species that form a functional part of floodplain communities. In our investigations, singletons and doubletons ranged from 43–53% of all species in a habitat, whereas common species that occurred with 20 individuals or more only covered 12–18% of all species in a habitat. With such a high fraction of rare species, extrapolation estimates attain a substantial degree of statistical uncertainty. Due to these factors, observed as well as extrapolated species numbers did not vary much between the habitats.

On the other hand, using rarefaction, a method destined to compare samples of very different sizes, revealed significant differences between regions, but was not sensitive enough to disclose differentiation across flood regimes. The reason for the superiority of rarefaction is that it is less prone to inaccuracies of statistical estimates that accrue to extrapolation approaches from the enormous variation in the number of sampled moth individuals between our samples. The lowest number of individuals (371) at one single light-trapping site was caught in the Danube region (DN2), whereas the highest number of individuals (2,657) was found in the Leitha region (LN2), i.e. the range spanned between local sample sizes attained almost an order of magnitude. More generally, local samples were always the smallest in the forests of the Danube floodplain, ranging from 371 to 813, whereas local samples in the Leitha region ranged from 463 to 2,657 individuals, and in the Morava region 814 to 2,398 moth individuals were caught per trap site. The disadvantage of rarefaction is, however, that a lot of information is lost when reducing the dataset to the maximum number of individuals that has been caught in every sample.

Under these conditions, diversity measures like Fisher's α and Shannon's diversity, which consider both, species numbers and the distribution of individuals across species, turned out to be superior to species richness estimators. Fisher's α is known to be a robust measure of diversity and is mainly influenced by species with medium abundances. Its application assumes that the abundance of species follows a log-series distribution. This assumption, however, was violated at 18 of 28 light-trapping sites in our study (χ^2 tests: $\chi^2_4 > 11.75$, $P < 0.05$), and this mismatch may have contributed to the inferior performance of Fisher's α relative to Shannon diversities. Mismatches to log-series distributions in our data set originated from two peculiarities. Firstly, some few species were more abundant than expected from a log-series model, notably the hyper-abundant lichen moth *Pelosia muscerda* in the Morava floodplain forests (Chapter 7). Secondly, the high prevalence of singletons and doubletons (see above) indicates an excess of 'too rare' species relative to a log-series distribution model. It is therefore not surprising that a diversity index fails to elucidate ecological patterns if its mathematical preconditions are not met.

In contrast to observed species numbers, extrapolated species numbers and Fisher's α, the exponential version of Shannon's diversity very clearly displayed differences with regard to forest region, flood regime, and the interaction thereof. Summerville & Crist (2005) also showed in their study of temporal patterns in Nearctic forest moths that species richness and Shannon diversity responded in different ways. While species richness was most affected by increasing sampling effort or by covering a wider range of seasons within a year, Shannon diversity was less influenced by seasonal differences, but was rather determined already at the scale of individual sampling units. We did not observe any superiority of the bias-corrected version of Shannon's diversity over its classic version with regard to its statistical sensitivity. We suggest that this is mainly due to the fact that at all 28 sites our samples were sufficiently large to allow for meaningful estimates of $\exp(H_S)$. Still, application of the bias correction resulted in substantially higher estimated diversity values in contrast to the classic version. This was particularly obvious for the numerically smallest samples from the Danube floodplain forest, for which values of bc-$\exp(H_S)$ were about 16 % higher than without bias correction.

Beck & Schwanghart (2010) compared measures of species diversity with modelled data sets and concluded that the bias-corrected version of Shannon's diversity is the most suitable measure if undersampling is suspected and especially if at least half of the expected species were sampled. Our empirical results based on extensive field data confirm the superiority of Shannon's diversity, also relative to Fisher's α. Shannon diversities were the only measures that revealed statistically significant diversity patterns along all three possible dimensions to be seen in our study design (i.e. regional, habitat, and interaction effects). It should be noted, however, that with any empirical data set (in contrast to modelled data) this superiority of Shannon diversities rests on the assumption that differences in diversity do exist across the ecological dimensions under study. Moreover, our results provide a striking example that differences between assemblages in species numbers are not necessarily coupled with differences in species-abundance relationships. Differences in richness or diversity, and also their non-existence, may both be equally relevant, but for different ecological questions.

Conclusions

Observed species richness is not a good choice to determine arthropod species diversity in rich and undersampled communities. Using only raw species counts cannot reveal differences in species abundances and results may be severely biased by sampling effects. Our data provide a striking example that also extrapolated species richness measures, which have been recommended and widely used during the past 15 years, may completely fail in capturing differences between samples drawn from real-world communities. Rarefaction more effectively controlled sampling bias than extrapolation and therefore scored better than all other richness measures. The underlying problems with species richness measures pertinent to our moth light-trap data most likely affect many other data sets: incomplete sampling of species-rich communities; large differences in sampling success across sites, even if sampling effort is rather even; high mobility of study organisms in fragmented landscapes, and accordingly a substantial continuous influx of transient stray species into each community, which alters the long tail of local species-abundance distributions. Under these conditions, measures like Shannon's diversity and Fisher's α were highly superior in reflecting local species diversity patterns.

The use of Shannon's diversity for analysing species diversity has re-gained prominence only in recent years (following Jost 2007), whereas Fisher's α has been commonly used in many studies across different taxa and ecosystems for a long time (Cayuela et al. 2006; Fiedler & Schulze 2004; Thomas & Thomas 1994). To render empirical biodiversity studies comparable we therefore suggest analysing both, Shannon's bias-corrected diversity and Fisher's α. Moreover, publication strategies are encouraged for valuable inventory data which make complete information accessible for subsequent evaluation (Moritz et al. 2011).

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7. Down in the flood? How moth communities are shaped in temperate floodplain forests

Abstract. We investigated moth communities in relation to flood regime across three riparian regions in lowland eastern Austria. Moths sampled with light traps were segregated into resident and stray species. Resident moths were further partitioned into arboreal and ground-layer species based on their larval habitat. Regional differences in species diversity and species composition were far stronger than local differences related to flood regime. Stray species (17% of all species and 6% of all individuals sampled) as well as uniques had only negligible influence on diversity and species composition patterns. The single most abundant species turned out to be more problematic for diversity comparisons across regions and habitats than the many rare species and strays. Overall moth diversity and ground-layer moth diversity were generally not reduced in flooded habitats relative to non-flooded habitats, and diversity of arboreal moths did not show significant differences between flood regimes. Differences between habitats in their ground-layer vegetation appear to be more important for floodplain forest moth diversity than variation in woody vegetation with its associated arboreal moth fauna. Patterns in species composition were largely governed by ubiquitous forest species and not by floodplain or wetland habitat specialists. Eighteen of the 44 commonest species were more abundant in flooded habitats, only 10 of them were more frequent in non-flooded habitats. Our results revealed no general negative impact of flooding on the diversity and species composition of one rich group of terrestrial herbivorous insects.

Keywords. Lepidoptera – floodplain forests – stray species – Austria – flooding – herbivorous insects – species diversity – species composition

Introduction

Floodplain forests are rare and highly threatened ecosystems all over the world (van Diggelen et al., 2006). Because of dynamic changes in riparian environments a great number of microhabitats are continuously generated which harbour a wide range of plant and animal species. The main research focus in floodplains is usually on monitoring of vegetation (van Diggelen et al., 2006), birds (Vaughan et al., 2007), fish (Lasne et al., 2007) and aquatic invertebrates (Bunn & Arthington, 2002). Less attention has been paid to the abundance, diversity and community structure of terrestrial invertebrates in floodplain forests (Ballinger et al., 2005, Rothenbücher & Schaefer, 2005).

Insects are the most diverse group of terrestrial Metazoa in the world and a large number of them feed on plants (Foottit & Adler, 2009). Most herbivorous insects are specialised to feed on a small subset of available plant taxa (Funk et al., 2002). Their close connections to host-plants render herbivorous insects an important target of biodiversity research (Novotny et al., 2006; Dyer et al., 2007). Phytophagous insects are also good indicators for environmental change as they react fast to shifts in vegetation composition (Lewinsohn et al., 2005). The Lepidoptera, i.e. butterflies and moths, are a particularly suitable indicator taxon for ecological studies (Roy et al., 2007). Nocturnal moths provide especially useful targets for ecological studies as there are cost-effective ways to survey them in a quantitative manner.

Moths comprise the vast majority of lepidopteran diversity and can be found in nearly every terrestrial habitat in substantial numbers of species and individuals (Summerville et al., 2004). In Central Europe, moths are also quite easy to identify to species level and their life-history traits are well known. Such traits are important for understanding drivers of diversity patterns (Summerville & Crist, 2004; Summerville, 2008; Ober & Hayes, 2010; Öckinger et al., 2010).

Here we investigate how floodplain forests of varying flooding regimes in three regions in lowland eastern Austria differ with regard to moth diversity and species composition. We also studied these impacts of flooding and region on different subsets of moths, i.e. moths whose caterpillars feed on shrubs, trees or lianas, and moths that have their larval stages near the ground.

Our hypotheses are as follows:

(1) Within each floodplain region moth-diversity is lower in regularly flooded than in non-flooded habitats, since flooding is a major mortality factor for terrestrial phytophagous organisms, especially for their less mobile immature stages (Köppel, 1997; Konvicka et al., 2002).

(2) Diversity patterns in small floodplain forest fragments embedded in a matrix of cultivated landscape are substantially influenced by stray individuals, i.e. dispersing moths from adjacent or even distant habitats that show up in light trap samples (Ricketts et al., 2002). Such stray individuals, especially if they account for a substantial fraction of the samples, might obscure diversity patterns.

(3) Flooding has a stronger impact on moths whose larval stages live near the ground than on species with arboreal early stages.

(4) Species composition differs strongly between flooded and non-flooded habitats and less so between regions with broadly similar forest vegetation. Moreover, flooding should act as a filter such that wetland species become more prevalent in flooded habitats. As a result, the moth faunas of different floodplain regions are expected to converge under the common influence of regular floods.

Methods

Study areas and sites

Three floodplain forest regions in eastern Austria which differ in flood regimes and forest vegetation were chosen for this study (Fig. 7.1; Appendix S2).

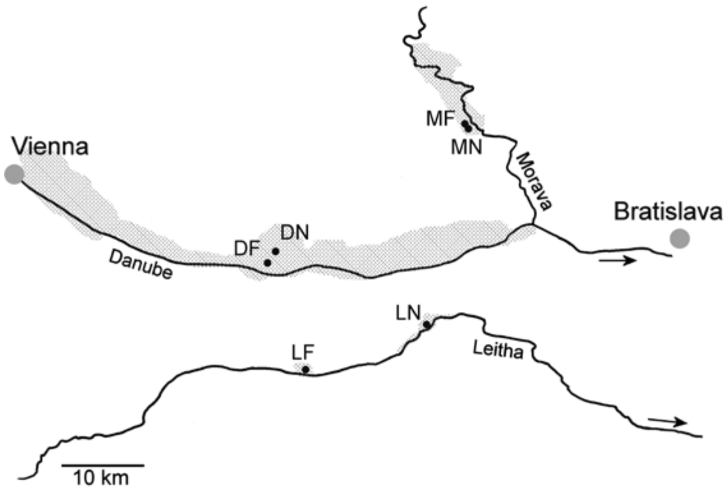

Fig. 7.1: Location of study sites in eastern Austria. Shaded: floodplain forest areas. See text and Appendix S2 for site codes and coordinates.

All three regions contain regularly flooded and non- (regularly) flooded habitats, and they all have attained conservation status. The Danube floodplain forests are protected as a national park, major parts of the Morava floodplain are managed as a WWF nature reserve, and the floodplain forests of the Leitha are part of the Natura 2000 network according to the EU habitats directive. (1) In the Danube floodplain inundation of forest areas mostly occurs in summer after alpine snowmelt (Lazowski, 1997; P. Zulka, in lit.). Due to a levee built in the 19th century there is currently a clear separation between habitats which experience regular flooding (DF), and others which are not or only occasionally flooded (DN). Frequently flooded habitats are dominated by poplars, willows and grey alder, whereas forest habitats which are not frequently flooded are composed of oak, ash, hornbeam, maple, linden trees and elms (Willner & Grabherr, 2007). In the study years 2006 to 2008 water levels causing inundations occurred on approximately 40 days altogether (P. Zulka, pers. communication). (2) The Morava river is a 1st order tributary stream to the Danube. Inundations mostly occur in spring and contrary to the Danube-floodplains, floods may last three to four weeks (P. Zulka, pers. communication). Since there is no levee extending through the forest all areas are flooded regularly, but there are pronounced differences in the duration of flooding. Habitats coded as MF were longer and more frequently flooded than habitats coded MN. During 2006 to 2008 high water levels causing inundations occurred on approximately 110 days altogether (P. Zulka, pers. communication). Most of the sampled forest habitats belong to a peculiar wood formation, namely the Fraxino pannonicae-Ulmetum (Willner & Grabherr, 2007). (3) Alluvial forests at river Leitha comprised the third sampling region. The river Leitha has been regulated throughout almost its entire length, so flooding events in the land-side habitats currently only occur after exceptional summer rainfalls or during snowmelt. Extended periods of inundations in areas near the river still occur, mostly in spring time, when ground water rises up to the surface (Lazowski, 1989). The near-natural periodically flooded forests (LF) are dominated by black alder and ash, whereas the non-flooded habitat (LN) comprises managed poplar stands (Lazowski, 1997). Inundations during 2006 to 2008 at Deutsch Haslau, an area comparable to LF, occurred on about 192 days altogether (P. Zulka, pers. communication). Floodplain forests along river Leitha are the most isolated and fragmented of the three study regions and experienced the most extended flood impact during the study period.

Moth sampling

In each of the habitats DN, DF, MN, and MF five light trap sites were located in closed-canopy riparian forest at a distance of about 100m to each other. In the Leitha region (LN, LF) only four light traps were used because of the small size of the forest fragments. Automatic light traps were run once a month at each site from August 2006 to August 2008, situated one meter above ground (for detailed information on moth sampling see Appendix S3). All 'macro-moths' including the Pyraloidea were collected and identified to species level using faunal treatments (Appendix S3). For the analyses presented here, all moth samples from each trap site were aggregated to yield one representative estimate of the local moth assemblage, resulting in quantitative species lists for 28 sites distributed across three regions and two flood regimes.

Data analysis

We chose the bias-corrected version of the exponential Shannon diversity (Chao & Shen, 2003; Jost, 2006; hereafter termed Shannon's diversity) as measure of local species diversity (calculated with the software SPADE: Chao & Shen, 2009). As recently shown, this measure is broadly insensitive to sampling effects as they could arise from different numbers of trap sites or different catch sizes (Beck & Schwanghart, 2010; see Chapter 6). Stray individuals – i.e. individuals that can not complete their life cycle in floodplain forests, because their larval host plants or microhabitats were absent – may pose a serious problem for analyses of local diversity of highly mobile animals (Magurran & Henderson, 2003; Schulze & Fiedler, 2003). We therefore re-calculated diversity measures after excluding the strays to examine their impact on diversity patterns. As strays we defined (a) all long-distance migratory species; (b) all species that are strictly bound to xerothermic habitats; and (c) all species whose larval host plants do certainly not occur anywhere in the study habitats (see Appendix S2 for sources of scoring and S3 for status of each species). A conservative approach was adopted, i.e. in cases of doubt species were retained in the data set. Moths remaining after the exclusion of these strays are subsequently termed 'residents'. One resident species, the lichen moth *Pelosia muscerda*, was hyper-abundant in the Morava floodplains (especially in the year 2007). Therefore, we re-calculated all analyses again, excluding this species from every habitat and region, to assess its impact on diversity measures.

Furthermore we analysed species diversity separately for resident moths that have their larval stages near ground as opposed to those which develop in the shrub or canopy layer of the forest. For this purpose we collated information on larval food plants and habitats from published literature (Appendix S3). A species was scored as belonging to the ground layer fauna if the larvae feed on grasses, herbs, mosses, fallen leaves, or below ground on roots. If larval food plants are shrubs, trees or lianas, the species were scored as belonging to the arboreal fauna. Three pyraloids for which literature data are inconclusive were excluded. Nine species, whose larvae feed on trees as well as ground-layer plants, were included in both categories. Diversity scores per site were compared across regions and flood regimes using ANOVAs with the two habitat types nested within the three regions. We considered light-trap sites within habitats as sufficiently independent replicates since the attraction ranges of the weak light-traps did hardly overlap (see Chapter 5). Moreover, even though some degree of spatial dependence does certainly apply to our data, it is still debated controversially as to whether and how this could be optimally accounted for (Bini et al., 2009).

To display beta-diversity patterns of moth assemblages in relation to flooding and regional differences we applied non-metric multidimensional scaling (NMDS). This was based on the Bray-Curtis similarity measure, using log-transformed moth counts to account for great differences of species abundances. The significance of flood and region effects was assessed by ANOSIM. As the abundant species are expected to carry most of the information with regard to community patterns, we used two-way ANOVAs to test if mean counts of these species differed significantly according to flood regime and region. For these analyses we considered relative abundances of those 44 species that were represented by at least 100 individuals. We used literature from south-west-Germany for grouping these most abundant species into ubiquists or wetland species. Analyses were performed using Primer 5.0 (Clark and Gorley, 2001) and Statistica 7.1 (StatSoft Inc.).

Results

A total of 32.181 moth individuals belonging to 448 species were recorded and identified. The highest proportions of species were represented by Noctuoidea (211 species, 47% of all species; 22.383 individuals), Geometroidea (150 species, 33% of all species; 6.829 individuals), and Pyraloidea (77 species, 17% of all species; 2.603 individuals). In flooded habitats a total of 16.233 moth individuals belonging to 375 species were identified. Very similar numbers were obtained in the non-flooded habitats with a total of 15.948 individuals, also belonging to 375 species. Further details are presented in Table 7.1, full species lists are included in Appendix S4, and rank-abundance plots for the six habitats in Appendix S6.

Table 7.1: Summary statistics of moth light trap catches in three floodplain forest regions in lowland eastern Austria, segregated according to the status and larval microhabitat affiliation of moth species.

Habitat/ Region	All moths		Resident moths		Ground-layer moths		Arboreal moths	
	species	individuals	species	individuals	species	individuals	species	individuals
DN	247	3.083	220	2.608	122	1.219	105	1.457
DF	241	2.782	213	2.717	110	1.318	108	1.487
Danube	311	5.865	269	5.325	144	2.537	132	2.944
MN	238	4.728	203	4.608	113	3.605	97	1.076
MF	257	9.386	222	9.250	123	7.270	105	2.069
Morava	317	14.114	264	13.858	152	10.875	120	3.145
LN	257	8.137	227	7.267	139	6.151	93	1.223
LF	246	4.065	214	3.866	129	3,001	91	1.055
Leitha	329	12.202	285	11.133	169	9.151	123	2.278
total	448	32.181	373	30.316	209	22.564	173	8.367

The overall proportion of stray species neither differed between flooded and non-flooded habitats ($\chi^2_1 = 0.01$, $P = 0.919$), nor between the three regions ($\chi^2_2 = 1.841$, $P = 0.399$; Fig. 7.2).

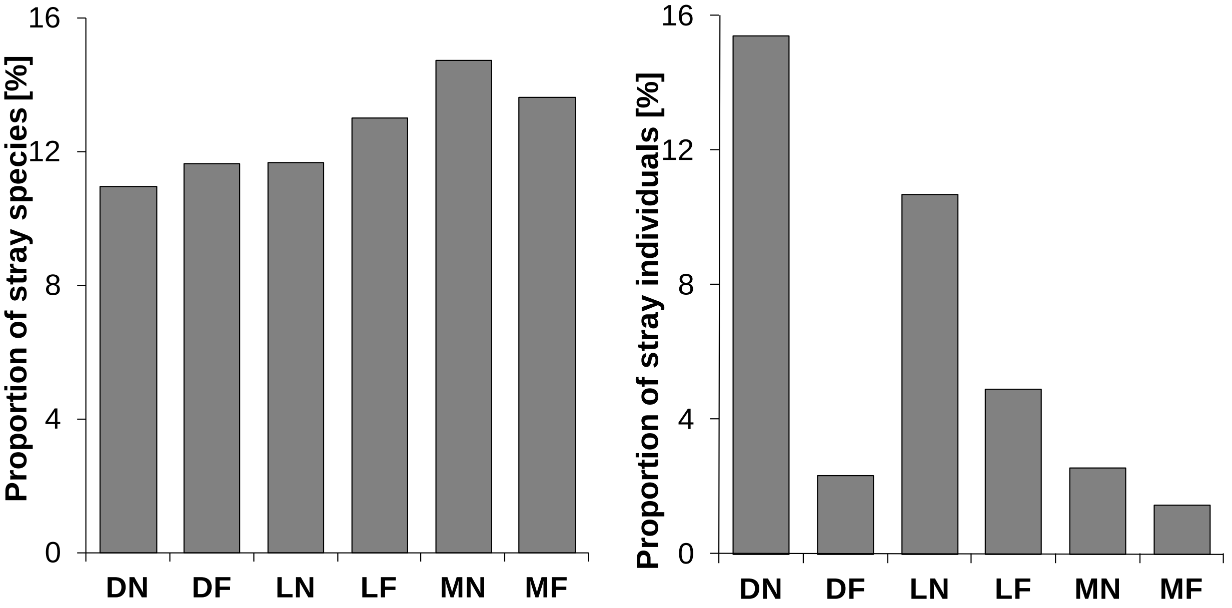

Fig. 7.2: Distribution of the percentage of stray moths across the six study habitats. Left panel: species; right panel: individuals. D: Danube, L: Leitha, M: Morava river; N: non-flooded, F: flooded forest.

In contrast, the proportion of stray individuals differed strongly between regions ($\chi^2_2 = 731.43$, $P < 0.0001$) as well as between habitats ($\chi^2_1 = 665.81$, $P < 0.0001$). Far fewer strays occurred in flooded habitats than in non-flooded habitats, and in the Morava floodplain forest as compared to the Danube and Leitha region. The major portion of all stray individuals was represented by the grassland noctuid moth *Agrotis segetum*, which commonly attains pest status in grain fields. In the habitats DN and LN this species alone accounted for 411 (43%) and 719 (83%) of the stray individuals, respectively.

Shannon’s diversity captured strong differences in species diversity between the three regions and also between flood regimes nested within regions (Table 7.2). Confining the analysis to resident moth species hardly changed these results. Amongst the resident moth fauna, diversity patterns strongly differed between arboreal and ground-layer assemblages. Arboreal moth species revealed no significant differentiation relative flood regime (Table 7.2, Fig. 7.3). In contrast, assemblages of moths with ground-developing early stages showed highly significant differences between the three regions and within two of three regions diversity differed relative to flood regime. Ground-layer moth diversity was significantly lower in the flooded habitat along the Danube, whereas it was significantly higher in the flooded habitat along the Leitha.

Diversity patterns again radically changed after the hyper-dominant *P. muscerda* had been excluded. Now the Morava region scored higher than the Leitha floodplain and very similar to the Danube region. When considering only the ground-layer moths, exclusion of *P. muscerda* hardly changed diversity patterns across and within regions.

Table 7.2: Results of ANOVAs (with the factor flood nested within regions) for Shannon's diversity H_s as measure of moth diversity. *F*-statistics and associated *P*-values are reported for all moths, for residents only (i.e. excluding strays), separately for resident ground-layer and arboreal moth species, and after exclusion of the hyper-dominant lichen moth *Pelosia muscerda*. Significant results (after controlling for a table-wide false discovery rate at $P < 0.05$: Waite & Campbell, 2006) are highlighted in bold.

All moths		df	*F*	*P*	Residents		df	*F*	*P*
Shannon's H_S	**flood (region)**	**1**	7.85	**0.001**	Shannon's H_S	**flood (region)**	**1**	5.54	**0.005**
	region	**2**	348.38	**<0.001**		**region**	**2**	454.22	**<0.001**
Arboreal					Ground				
Shannon's H_S	flood (region)	1	1.31	0.30	Shannon's H_S	**flood (region)**	**1**	11.02	**<0.001**
	region	**2**	192.78	**<0.001**		**region**	**2**	424.24	**<0.001**
Excluding *Pelosia muscerda*									
All moths					Ground				
Shannon's H_S	flood (region)	1	2.84	0.06	Shannon's H_S	**flood (region)**	**1**	5.95	**0.004**
	region	**2**	175.54	**<0.001**		**region**	**2**	358.61	**<0.001**

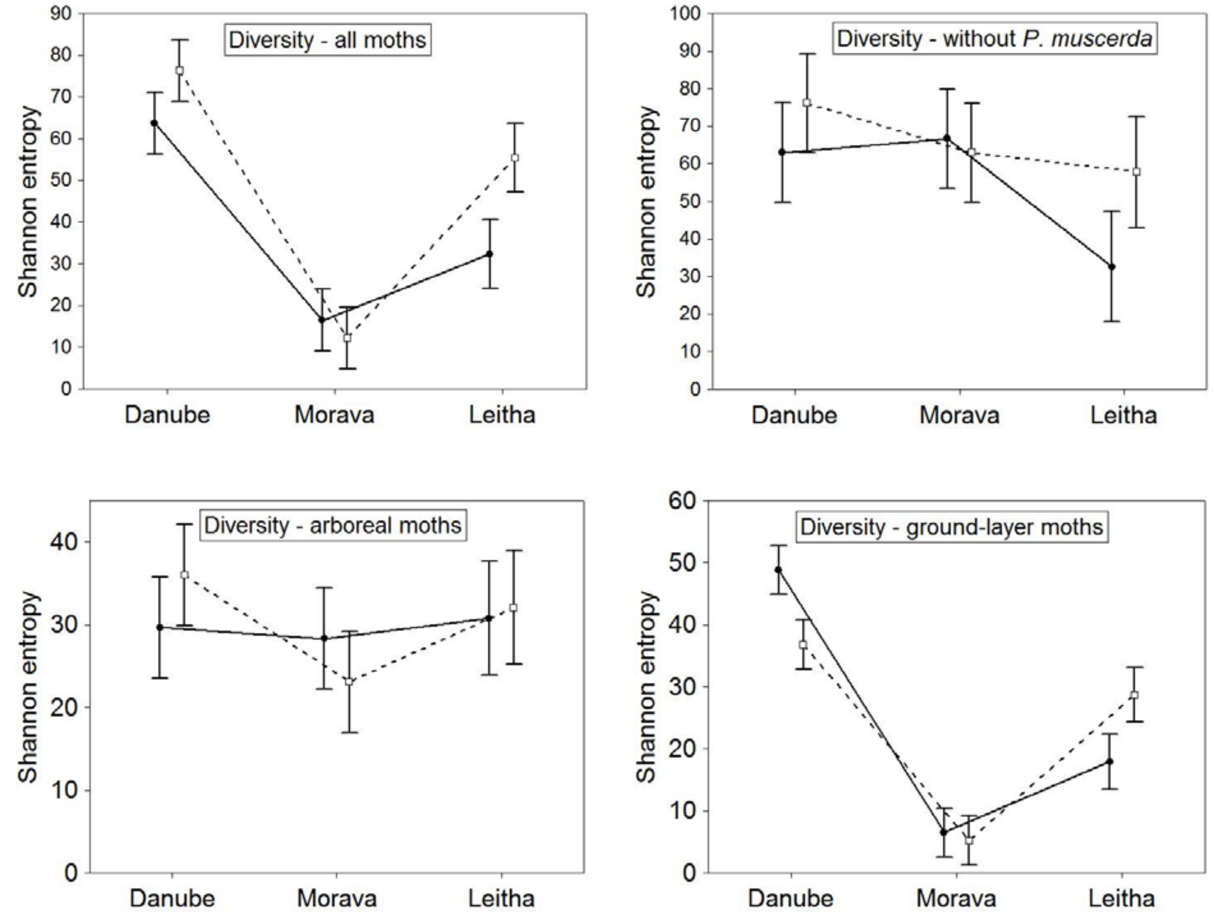

Fig. 7.3: Moth diversity across the three study regions and two flood regimes. Given are means per trap site ± 95 % confidence intervals. Filled dots – non-flooded areas. Open squares – regularly flooded areas. For statistics see Table 2.

An ordination revealed a clear differentiation of the moth communities among the three regions (Fig. 7.4). In the Danube floodplain forests, and less strongly so along the Leitha, moth assemblages differed between regularly flooded and rarely flooded habitats. At the Morava, in contrast, no such grouping was apparent. ANOSIM results confirmed the significance of faunal differences related to flood regime (R = 0.724, P < 0.001) and region (R = 0.999, P < 0.001).

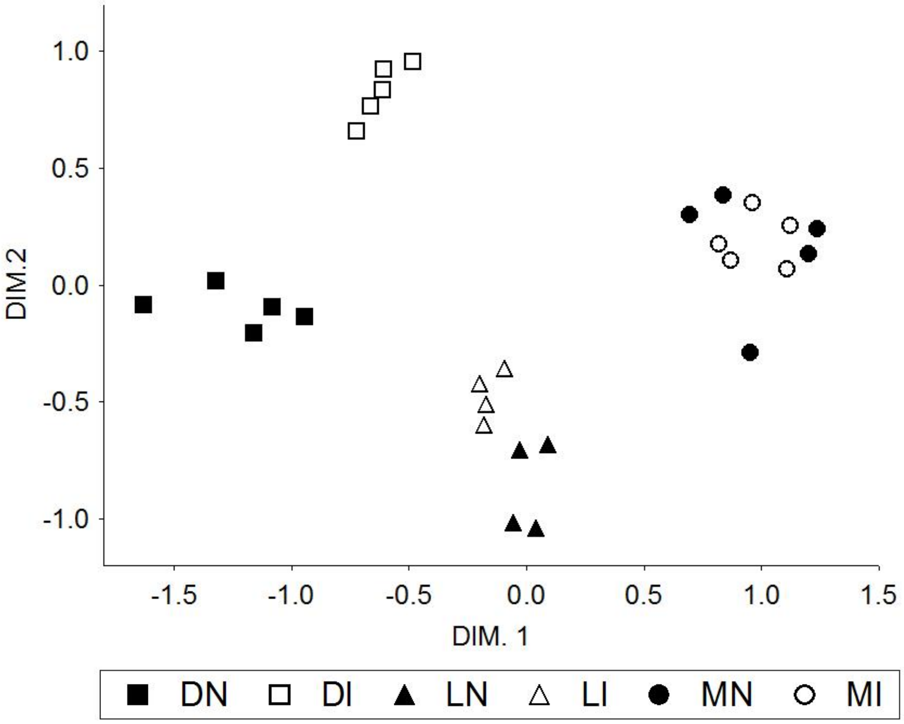

Fig. 7.4: The NMDS ordination diagram displays a clear segregation between regions, while effects of flooding on moth community composition are only visible for the Danube and the Leitha river. D: Danube, L: Leitha, M: Morava river. Filled symbols – non-flooded habitats; open symbols – flooded habitats.

The ordination plot does not reveal a grouping of all flooded or non-flooded habitats. Nor is there a concordant directional shift in assemblage composition associated with flooding. Species composition showed similar patterns as did species diversity: regional differences were more prominent than flooding effects. This was particularly evident for the 44 commonest species (together accounting for 25,193 individuals, i.e. 78% of the total catch). Only three of these (*Caradrina morpheus*, *Spilosoma lutea*, *Cabera exanthemata*) did not show any significant response either to region or flooding. ANOVA results for these commonest species hardly changed, after controlling the table-wise False Discovery Rate (FDR) according to Benjamini-Hochberg's procedure (Waite & Campbell, 2006). Relative abundances of 37 species (36 after FDR correction) differed significantly with regard to region, 28 species (FDR: 25) to flooding, and for 21 species (FDR: 17) the interaction term was significant (Fig. 7.5). Mean effect sizes E (plus 95% confidence intervals CI, calculated from Fisher's z, based on the P-values: Rosenberg et al., 2000) revealed the same ranking (region: E = 0.655; CI: 0.549–0.745; flooding: E = 0.430; CI: 0.316–0.529; interaction: E = 0.374; CI: 0.286–0.486).

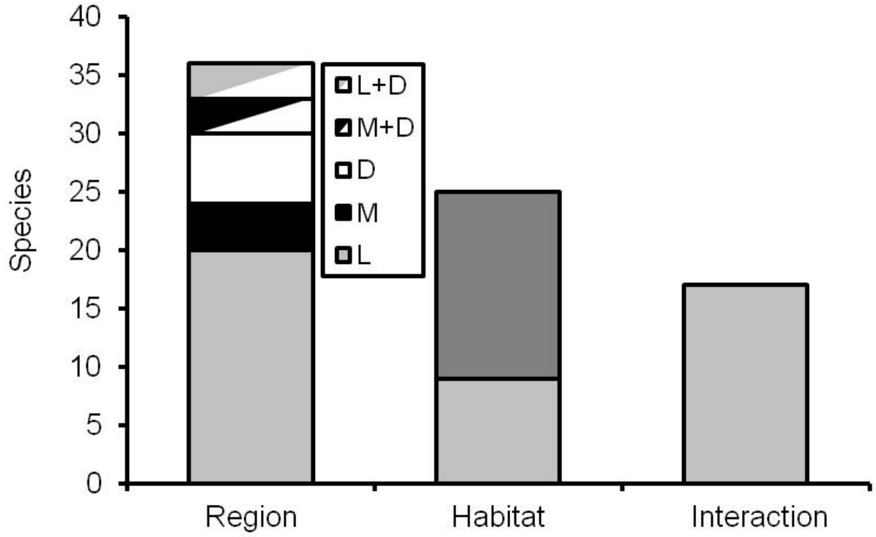

Fig. 7.5: Partitioning of abundance differences of the 44 most common moth species with regard to region, habitat, or the interaction thereof. Considered are only species with significant ANOVA results for at least one factor. First bar: number of species with preference for one or two specific regions; second bar: species with preference for one habitat type, dark shaded: flooded habitats, light shaded: non-flooded habitats; third bar: species with significant region × habitat interaction. D: Danube, L: Leitha, M: Morava.

No abundant species only occurred in either flooded or non-flooded habitats. Similarly none of these 44 species was entirely lacking in any of the three regions, i.e. faunal differences were largely due to variation in relative abundances. Of the 25 moth species with significant habitat responses (Appendix S5), 17 were more common in flooded habitats. Among these possible beneficiaries of flooding, however, there was no obvious pattern with regard to habitat preferences. Only seven of them have arboreal larvae and five species are characteristic of floodplains or other wetland habitats.

Discussion

Environmental determinants of moth diversity: region, flood regime, and larval microhabitat

Floodplain forest moth diversity varied more strongly, and more consistently, between the three regions than according to flood regime. After exclusion of the hyper-dominant *P. muscerda*, moth diversity was greatest in the Danube and Morava region, and lowest in the Leitha floodplain forests. This higher moth diversity of the Danube and Morava floodplain compared to those of the Leitha matches well to the larger size and the more natural state of their riparian forests. Moth diversity in the Leitha floodplain forests, however, was still rather high, considering their small size, fragmented nature and long duration of flooding.

Contrary to our expectations, total moth diversity was even higher in flood-affected forest habitats along the Danube and the Leitha rivers, and only marginally lower in the Morava floodplain. In the latter region, MF and MN habitats were located close to each other and all were flooded in spring, although inundations lasted only about one week longer per year on MF sites. This environmental similarity is reflected in the high similarity between moth assemblages of both habitats in the Morava region. The lower moth diversity in the non-flooded habitat of the Leitha floodplain can probably be attributed to the type of forest, which predominantly consists of managed plantations of Canadian poplar. Flooded forest along the Leitha is in a more natural state with a more strongly developed herb layer (ground cover 44%, vs. 33% in the non-flooded habitat).

When considering only ground layer moths, flooding had a negative impact on moth diversity in the Danube floodplain, but not along the Leitha, even though yearly duration of floods was about six times longer in the Leitha floodplain. Regional differences in moth diversity occurred within all examined groups of moths, whereas flood-related effects only emerged if species whose larval stages live near ground were included. Hence, differences between habitats in their ground-layer vegetation appear to be more important for floodplain forest moth diversity than variation in woody vegetation with its associated arboreal moth fauna.

Rather few studies have so far addressed species diversity of terrestrial arthropods in floodplain landscapes of temperate zones. Ballinger et al. (2007) found a negative effect of flooding on species richness of ants. Non-flooded habitats had the highest species richness, whereas species richness was intermediate in moderately flooded habitats and lowest on sites subject to extended inundation. Rothenbücher & Schaefer (2005) observed most leafhopper species in sites that were not flooded; sites with medium flood intensities had the lowest species richness. Carabid beetles and spiders responded differently to flooding events in regard to their life history traits (Lambeets et al., 2009). In the Rhine floodplain in Germany, Köppel (1997) found more moth species and individuals in hardwood forests (H_S: 75.1) than in frequently flooded softwood forests (H_S: 51.5). In our study total moth diversity patterns suggest that flooded habitats (like LF or DF) may support even a slightly richer moth fauna, but this is locally counteracted by negative impacts of inundations that act more severely on ground-layer species (especially visible in DF) than on arboreal moths. Moreover, the type and heterogeneity of local vegetation appeared to be more relevant for the diversity of plant-feeding moths, since regional patterns were far more consistent than flooding effects. Collectively, these results indicate that river dynamics can neither be viewed as generally constraining, nor fostering, the diversity of terrestrial arthropods in riparian habitats. Rather, local habitat conditions and life-history traits of the species under study are responsible for the observed patterns.

Moth community composition

We found a strong differentiation of moth communities between the three floodplain regions and – unlike species diversity – a lesser, yet still significant distinction of moth communities in regard to flooding. Differences in moth communities between flooded and non-flooded habitats were greatest in the Danube floodplain forests, intermediate at the Leitha, and smallest in the Morava floodplain. We suggest this is due to a clearer spatial as well as ecological segregation between flooded and non-flooded habitats in the Danube and Leitha floodplains, whereas the habitats in the Morava forests were located close to each other. Flooded habitats from different regions did not group together in the NMDS, in contrast to our hypothesis that flooding would result in a characteristic moth community tolerant to inundation. In line with this, only seven moths out of those most abundant species that revealed abundance differences according to flood regime were characteristic moths of wetland habitats. Rather, community differentiation was largely due to abundance variation of ubiquitous forest species. Bonn et al. (2002) found that invertebrates responded differently to flood regimes and habitat in Germany. Ground beetle assemblages were differentiated between flood regimes, whereas spider communities were mainly shaped by habitat structure. Van Helsdingen (1997) even suggested that there is no typical floodplain spider community. Considering our data, we could not identify a typical floodplain moth community for eastern Austria either.

Flooding did not have a general negative effect on occurrences of the most abundant species. Some species preferred the flooded habitats, whereas others occurred more often in the non-flooded habitats. We could not identify any clear pattern in these abundance profiles between ground-layer and arboreal moths. As expected, most of the common wetland moth species were more abundant in flooded habitats (5 vs. 2 species).

Hyper-dominant and stray species

Very common as well as very rare or allochthonous species may obscure the deduction of community patterns from ecological field samples. Indeed, Shannon’s diversity turned out to be severely affected by one hyper-dominant species. For example, diversity of riparian moth faunas at river Morava was distinctly underestimated. Only after exclusion of the most abundant species (*P. muscerda*, accounting for 37–64% of the catch at the six Morava sites) it became apparent that local moth diversity in that floodplain region was not much lower than in the Danube area.

Since most relevant life-history traits of Central European moth species are known, incorporating this information allowed us to confidently eliminate stray species from our analyses and explicitly check for their impact on statistical analyses. Contrary to our expectation, these strays did not affect the diversity comparisons. Even though absolute diversity values were, of course, considerably smaller after exclusion of the strays, regional as well as flood effects remained largely unchanged. Since the fraction of stray species was similar in all habitats, ranging from 11% (DN) to 14% (MN) of all species, their negligible influence on species diversity patterns was not too surprising. The fraction of stray individuals, however, varied strongly across regions and habitats. In two non-flooded habitats (DN and LN) more strays showed up in our samples than elsewhere. Nevertheless, ordination analyses yielded very clear results despite the inclusion of these strays, and their exclusion did not alter these results (C. Truxa and K. Fiedler, unpublished results). Overall, our explorations indicate that the inclusion of stray individuals is not problematic for ecological interpretation of light trap samples in temperate forests, even if a rather substantial fraction of specimens (up to 15% per habitat in our case) must be considered as stray or dispersing individuals. Hence, in order to reliably deduce community patterns it appears not to be important to partition samples into ‘core’ (or ‘frequent’) and ‘occasional’ species (Ulrich & Ollik, 2004) on the grounds of their statistical occurrence properties. Also the exclusion of species only found at one trap site (‘uniques’) to reduce their effect on statistical analyses does not seem to be necessary (Ricketts et al., 2001; Choi, 2008). Rather, in our data set the single most abundant species turned out to be more problematic for diversity comparisons across regions and habitats than the many rare species and strays. While the difficulties to account for hyper-abundant species in diversity analyses are commonly seen with invertebrate samples, it remains to be tested whether the unexpectedly low impact of strays may rather be a peculiarity of moths, associated with their high mobility and dispersal potential.

Conservation aspects

Our surveys revealed that forest moth communities in all three floodplain regions are moderately diverse, when compared to other Central European lowland forests. With regional values of Shannon's diversity of 13.7 (Morava river), 44.5 (Leitha river) and 93.3 (Danube river), two out of three eastern Austrian lowland floodplains scored higher than beech forests (H_S = 25.2: Lemke, 2002), but far lower than oak-hornbeam forest (H_S = 127.1: Hacker & Müller, 2008; in all cases excluding the Pyraloidea to render studies comparable). In the only other quantitative study on riparian forest moths in central Europe (at river Rhine, SW Germany) rather similar diversities were observed, with H_S ranging between 51.5 (softwood) and 75.1 (hardwood forest; calculated from data in Köppel, 1997). Also with regard to the representation of species of conservation concern, eastern Austrian floodplain forests did not rank very highly. Only 25 of the moth species recorded by us are scored as near threatened, one as vulnerable, two as endangered, and two more as critically endangered according to the Austrian Red List (Huemer, 2007). Seven of these Red List species occurred only as strays. Relative to the taxa covered, the fraction of Red List species amongst residents was only 5%. Therefore, the moth communities of the studied floodplain forests do not qualify as priority targets for conservation measures, in contrast to the high conservation value of the same habitats for organisms such as birds or aquatic vertebrates and invertebrates (Tockner et al., 1998; Dvorak, 2009).

Conclusions

Despite their high mobility, moth samples turned out to be mostly unbiased by strays. Using bionomic traits of species to identify resident species, and to allocate these into groups with differential microhabitat affiliation during early stages, allowed an even better understanding of diversity patterns. Arboreal moths were hardly sensitive to inundation, whereas species that have their larval stages near the ground showed more differentiation in relation to flood regimes and regions. Contrary to moth diversity, moth communities differed strongly, but idiosyncratically between flooded and non-flooded habitats. We could not identify a characteristic moth community of severely flood-impacted in our data set, as distribution patterns were mainly governed by widely distributed moth species rather than wetland habitat specialists.

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8. Beta-diversity of floodplain forest moths – within-group concordances and structural redundancies

Abstract. Gathering data on insect biodiversity requires considerable sampling, processing and identification effort. We investigated if various subsets of species-rich moth communities, surveyed in three Austrian floodplain forest areas, can serve as surrogates for their overall beta-diversity patterns. We examined three large monophyletic superfamilies (Noctuoidea, Geometroidea and Pyraloidea), and two ecologically defined groups (larval stages live near ground, or develop in the shrub or tree layer). Noctuoidea showed highest concordance with all moths, whereas Pyraloidea ranked lowest. Geometroidea were slightly less correlated with the full moth ensemble, but qualified as optimal compromise as surrogate group, since working effort for processing amounted to less than 22% of the total sample. Flooding affected subsets differentially. Geometroidea showed stronger sensitivity to flooding in their arboreal fraction, whereas among Noctuoidea ground-layer species responded more clearly. We observed massive structural redundancy in the moth community using the BVSTEP algorithm. 373 subsets of 8–15 species (1.5–3.35% of all recorded species) displayed overall moth beta-diversity with high precision and better than equally small subsets, defined by species abundances or functional group affiliations. High abundance only loosely corresponded with the frequency a species was included in BVSTEP subsets. Thus, also rare species contribute importantly to species composition patterns. An exploration of moth functional type affiliations based on larval host plant use revealed that effective 'surrogate' subsets usually contained 6–9 of the 12 recognized functional types.

Keywords. functional types – Lepidoptera – species composition – BVSTEP algorithm – community patterns – diversity indicators

Introduction

Beta-diversity – i.e. changes in species composition between sites – is a key concept in community ecology (Legendre et al., 2005). Community turnover reflects variation in abiotic (such as climate or soil substrate) and biotic site conditions. The extent of this turnover is also important for conservation biology: it connects species diversity from local to larger scales (Condit et al., 2002). However, gathering data to analyse turnover amongst species-rich communities requires considerable sampling effort. This has stimulated to search for 'indicator' taxa that may serve as surrogates for total biodiversity patterns. Numerous studies have addressed possible surrogate taxa or landscape metrics for local species richness (Báldi, 2003; Rodrigues & Brooks, 2007; Sauberer et al., 2004; Schindler et al., 2012; Schulze et al., 2004). Almost two decades of research revealed that at local spatial scales covariance of species diversity across taxa is often erratic due to idiosyncratic responses of organisms along environmental gradients. Only few studies, however, have addressed in a similar manner the concordance of beta-diversity across target groups (Buckley & Jetz, 2008; Kessler et al., 2009; Terlizzi et al., 2009).

Structural redundancies in community composition are a related topic and have attracted considerable attention in ecological research (Bennet et al., 2008; Clarke & Warwick, 1998; Magierowski & Johnson, 2006; Mistri et al. 2001). Structural redundancy implies that not all species are equally informative in characterizing assemblages or their turnover (Mistri et al., 2001). Ignoring 'uninformative' species would thus still yield roughly the same general pattern. Structural redundancy is not necessarily equivalent to functional redundancy (which means that ecological processes may work equally well with fewer species: Lawton & Brown, 1994; Purvis & Hector, 2000; Reiss et al., 2009). Yet, high structural redundancy indicates a strong potential for functional redundancy to exist in a given system. Studies in aquatic ecosystems (Mistri et al. 2001, Magierowski & Johnson, 2006; Nohrén et al., 2009) have shown that as little as 10% of all taxa initially surveyed were sufficient to describe the overall multivariate ordination pattern. We could, however, not find analogous investigations of structural redundancies in terrestrial animal assemblages, although functional redundancy, on the other hand, is a major scientific issue in the field of biodiversity and ecosystem-research (Hooper et al., 2005; Lyons et al., 2005; Reich et al., 2012; Rosenfeld, 2002).

The search for structural redundancies offers promising ways to contribute to the debate about biodiversity and ecosystem function, because structural redundancies can be analytically recognized from comparing natural communities along environmental gradients. In contrast, functional redundancies require resource-demanding experimental approaches to be confirmed.

Here we investigate if (1) different subsets of one species-rich arthropod order (the Lepidoptera) display beta-diversity patterns in a congruent manner and can therefore be used as surrogates for one another, and (2) quantify the extent of structural redundancy in this community. We have chosen moths as object of study, because they bear various functional roles in many terrestrial ecosystems (Summerville & Crist, 2004), are sensitive indicators for shifts in environmental conditions (Lewinsohn et al., 2005; New, 1997), and can easily be surveyed in a standardized quantitative manner. Therefore, moths are often used in biodiversity studies (Brehm, 2007; Fiedler et al., 2008; Müller et al., 2011).

Our hypotheses are:
(1) Subsets of moth assemblages differ in their potential to reveal ecological patterns.
(1a) Phylogenetically delimited groups (in our case superfamilies) of herbivorous insects should respond in a largely concordant manner, as long as data sets are sufficiently large and functional affiliations of their component species with the vegetation are similar across taxa.
(1b) In contrast, ecologically defined groups should reveal more discordant spatial patterns.
(2) Data sets can be drastically minimized and still represent species turnover patterns properly. Very abundant species carry most information, so we expect them – as well as species characteristic for the studied habitats – to prevail in optimally reduced subsets.

Material and methods

Field survey data

Three floodplain forest regions in eastern Austria which differ in flood regimes and forest vegetation were chosen for this study (for detailed information on study sites see Chapter 7 and Appendix S2). Each region contained two classes of forest habitats: ones that are regularly inundated, whereas others are not or only rarely flooded. In each forest habitat five light trap sites were selected at a distance of about 100m from each other to avoid interference between the traps. In the Leitha floodplain only four light traps were used because of the small size of forest fragments. Automatic light traps, each equipped with two 15W lamps, were run once a month at each of the 28 sites. All light traps within a habitat were operated simultaneously (for detailed information on moth sampling see Appendix S3/ Chapter 7). Altogether, sampling went over two complete annual cycles. In total, data from 442 nightly trap samples were analysed, considering all Macrolepidoptera plus Pyraloidea species (a monophyletic unit according to Mutanen et al., 2010). A total of 32,181 moth individuals belonging to 448 species were recorded and identified (Appendix S4 shows how these catches segregated according to region, habitat type and larval stratum).

Statistical methods

We created species-abundance matrices, with all sampling nights per each site aggregated into one species list. To display beta-diversity patterns of moth assemblages in relation to flooding and regional differences, we used the Bray-Curtis similarity measure, calculated from log-transformed individual counts to account for large differences of species abundances. Analogous matrices were constructed for moths of the three largest monophyletic superfamilies Noctuoidea, Geometroidea, and Pyraloidea. We further analysed beta-diversity separately for moths that have their larval stages near ground as opposed to those which develop in the shrub or canopy layer of the forest. For this purpose we collated information on larval food plants and habitats from published literature (see Appendix S3). A species was scored as ‘ground layer’ moth if the larvae feed on grasses, herbs, mosses, fallen leaves, or below ground on roots. If larval food plants are shrubs, trees or lianas, the species were scored as ‘arboreal’. Nine species whose larvae feed on trees as well as ground-layer plants were included in both categories. Within ground-layer and arboreal moths, similarity matrices were also constructed separately for the three largest superfamilies Geometroidea, Noctuoidea, and Pyraloidea.

All Bray-Curtis matrices were subjected to non-metric multidimensional scaling (NMDS) for visualization of faunal relationships using Statistica 7.1 (StatSoft Inc.). To test for significant differences in assemblage composition between regions and habitat types, we applied two-way Analyses of Similarities (ANOSIM; 9999 randomisations) to all aforementioned moth sets. The test statistic R served as a measure of effect size in these comparisons. Concordance between faunal matrices was assessed by Spearman matrix rank correlation coefficients (9999 randomisations, routine RELATE in Primer 6.0: Clarke & Gorley, 2006).

To determine the minimum number of species that is sufficient to reveal the overall species turnover pattern, we reduced our dataset using the BVSTEP algorithm in Primer 6.0 (Clarke & Gorley, 2006). An exhaustive examination of all possible species subsets is computationally not feasible with more than ca. 16 species. To facilitate convergence of the search algorithm, we therefore performed two searches (with 3000 restarts each) on reduced datasets. In one run, we included only those 78 moth species that accounted for at least 0.9% of all individuals at any of the 28 light-trapping sites. In the second run, we included all 117 moth species that occurred in overall at least 28 individuals (i.e. the number of light-trap sites). For details on the BVSTEP algorithm see Clarke & Warwick (1998) and Clarke & Gorley (2006). We then examined the subsets retrieved by the BVSTEP algorithm that showed a matrix rank correlation with the total data set of $r_S \geq 0.900$ and comprised only 8–15 species. We constructed various equally small subsets, defined by species abundances and functional type affiliation, and tested whether these subsets would yield comparably good surrogates for overall beta-diversity patterns. Moth species were allocated into 12 functional types regarding to their larval host plant affiliations: species that feed on lichens/mosses, herb generalists, herb specialists, woody plant generalists, woody plant specialists, softwood (*Alnus*, *Salix* or *Populus*) tree specialists, liana specialists (on *Clematis*), conifer feeders, detritivores, feeders of (semi-)aquatic plants, grass feeders, or root feeders, respectively (see Appendix S3 for literature sources evaluated for this functional classification; cf. Müller et al., 2011, for a similar approach). Moths whose larvae feed on hosts in only one plant family were scored as specialists. We compared distributions of functional types between the entire fauna and the species represented in the smallest BVSTEP subsets.

Results

An NMDS ordination of the full data set revealed a clear differentiation of moth assemblages among the three regions (Fig. 8.1a). In the Danube floodplain, and less strongly so along the Leitha river, moth assemblages also differed between regularly inundated and rarely flooded habitats. At the Morava river, in contrast, no such grouping was apparent (see Chapter 7). Inspection of the NMDS ordinations for the subsets (Table 8.1) revealed basically two types of patterns. (1) Most subsamples (all Noctuoidea [Fig. 8.1b] and Geometroidea [Fig. 8.1c], arboreal Noctuoidea and Geometroidea, and ground-layer Noctuoidea and Geometroidea) showed similar patterns of faunal differentiation according to region and flooding regime as the entire data set. Two-dimensional ordinations had stress values between 0.09 and 0.18, indicating acceptable representation of the raw similarity matrix in reduced ordination space. (2) Ordinations of Pyraloidea samples were far less clear, with stress values of 0.21. Especially for sites in the Danube floodplain forest pyraloid samples did not cluster together (Fig. 8.1d). All ground-layer moths and all arboreal moths (i.e. disregarding systematic groupings) showed similar patterns as the entire data set (Figs. 8.1 e–f).

ANOSIM results confirmed that faunal differences related to flood regime and region were highly significant (Table 8.1). Regional differences were invariably far stronger than the influence of flooding, as revealed by the much higher R values for all kinds of subsets (Table 8.1), whether based on ecological criteria (arboreal vs. ground-layer species) or on systematic units (superfamilies). Regional differentiation of Pyraloidea assemblages ($R<0.70$) was much less pronounced than for all other subsets tested ($R>0.83$). The influence of flood regime did vary more widely among subsets. Again, Pyraloidea showed the weakest segregation ($R<0.275$). Assemblages of Geometroidea with larval stages in the herb layer were also less distinct between flooded and non-flooded habitats. Species turnover among total Geometroidea and Noctuoidea assemblages did not differ much from another, but these two clades scored differently when analysing only arboreal or ground-layer species, respectively. Arboreal Geometroidea had a slightly higher global R than arboreal Noctuoidea, but the pattern became reversed for the ground-layer moth species of these two superfamilies. Spearman rank correlations showed that all Noctuoidea correlated highest with the complete dataset, followed by the ground-layer subsample (Table 8.1). Ground-layer as well as arboreal Geometroidea showed almost identical correlations to the complete dataset, whereas ground-layer Noctuoidea performed considerably better than their arboreal relatives. Once more, all subsets of the Pyraloidea showed the weakest correlations.

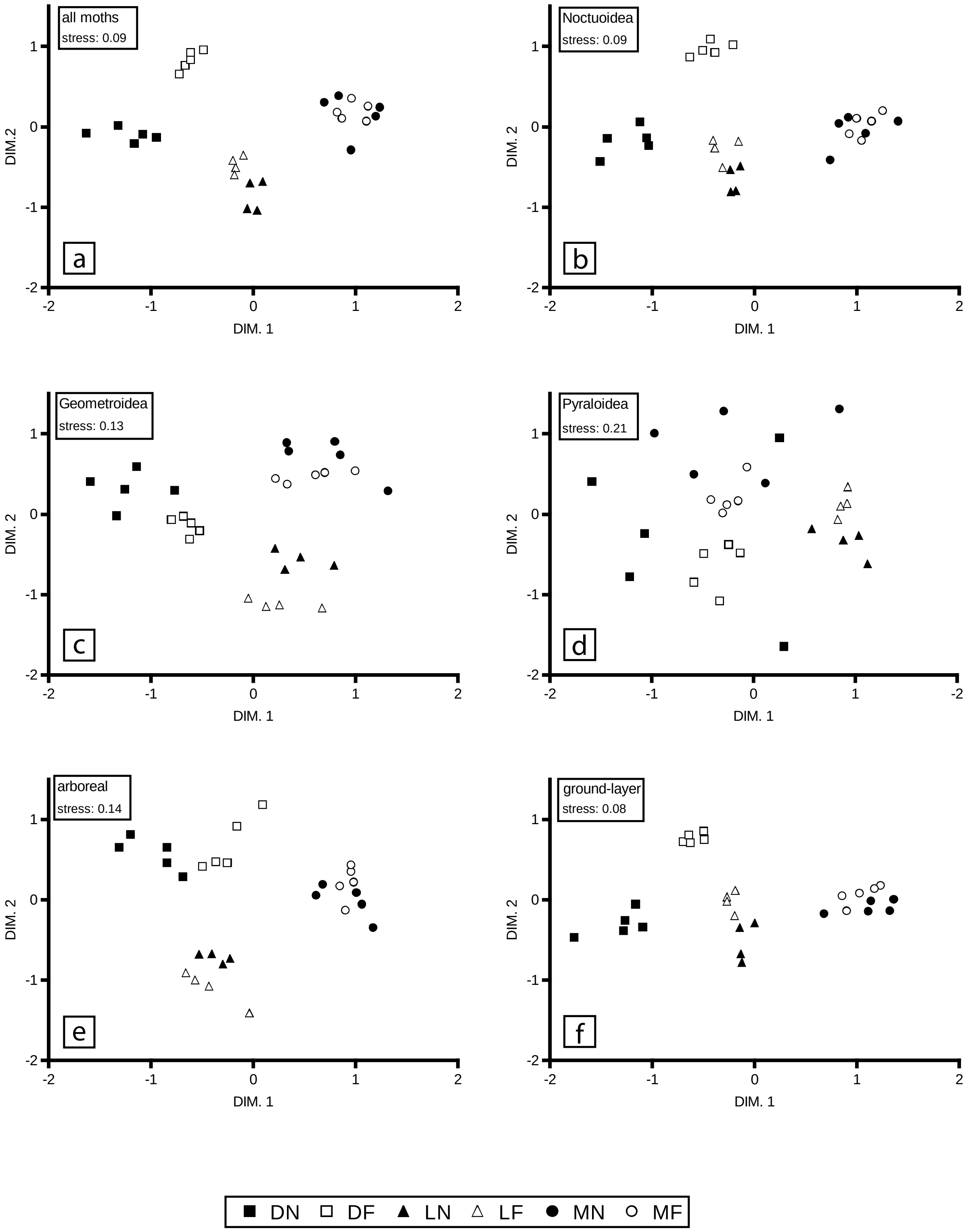

Fig. 8.1: Selected NMDS ordination diagrams of floodplain forest moth assemblages, based on Bray-Curtis faunal similarity matrices. Each symbol represents one light trap location. D: Danube (squares); L: Leitha (triangles); M: Morava (circles); F: flooded forest (filled symbols); NF: non-flooded forest (open symbols).

Table 8.1: Matrix rank correlations (r_S) of various floodplain moth subsamples with the entire dataset, and results of two-way ANOSIMs of moth species composition (*R* statistics), according to forest region and flood regime. ***: *p*<0.001, **: *p*<0.01, n.s.: *p*>0.05.

Data selection	Species	Individuals	r_S to full data set	ANOSIM *R* region	ANOSIM *R* flooding
all moths	448	32,181	1.000	0.999 ***	0.724 ***
all Geometroidea	140	6,829	0.743 ***	0.999 ***	0.647 ***
all Noctuoidea	211	22,383	0.937 ***	0.985 ***	0.680 ***
all Pyraloidea	77	2,603	0.339 ***	0.681 ***	0.238 ***
all arboreal moths	178	8,391	0.698 ***	0.999 ***	0.627 ***
arboreal Geometroidea	77	4,490	0.669 ***	0.983 ***	0.644 ***
arboreal Noctuoidea	75	3,439	0.600 ***	0.912 ***	0.470 ***
arboreal Pyraloidea	12	179	0.155 **	0.242 *	0.031 n.s.
all ground-layer moths	279	24,405	0.933 ***	0.982 ***	0.738 ***
ground-layer Geometroidea	70	2,920	0.674 ***	0.837 ***	0.376 **
ground-layer Noctuoidea	138	18,978	0.913 ***	0.948 ***	0.715 ***
ground-layer Pyraloidea	65	2,424	0.327 ***	0.640 ***	0.272 ***
BVSTEP best subset #1	15	10,911	0.946 ***	0.998 ***	0.772 ***
BVSTEP best subset #2	14	10,911	0.946 ***	0.983 ***	0.684 ***
BVSTEP best subset #3	13	12,119	0.937 ***	0.993 ***	0.665 ***
BVSTEP best subset #4	12	11,568	0.936 ***	0.999 ***	0.727 ***
BVSTEP best subset #5	11	12,093	0.937 ***	0.999 ***	0.712 ***
BVSTEP best subset #6	10	12,079	0.926 ***	0.996 ***	0.700 ***
BVSTEP best subset #7	9	10,816	0.916 ***	0.999 ***	0.773 ***
BVSTEP best subset #8	8	10,175	0.902 ***	0.999 ***	0.751 ***

Data selection	Species	Individuals	rs to full data set	ANOSIM R region	ANOSIM R flooding
most abundant species (N≥358)	15	20,822	0.722 ***	0.996 ***	0.752 ***
most abundant resident species (N≥353) [1]	15	19,854	0.733 ***	0.998 ***	0.749 ***
most prominent abundance variation (ANOVAs) [2]	15	18,017	0.801 ***	0.999 ***	0.661 ***
most abundant species (N≥670)	8	17,560	0.694 ***	0.999 ***	0.717 ***
most abundant resident species (N≥595) [1]	8	16,834	0.732 ***	0.999 ***	0.759 ***
most prominent abundance variation (ANOVAs) [2]	8	6,844	0.550 ***	0.974 ***	0.700 ***
most abundant species of each FT, residents only [3]	11	15,250	0.760 ***	0.999 ***	0.755 ***

[1] most abundant species, excluding one stray species whose larvae cannot complete their life-cycle in floodplain forest; [2] species with highest F-values from ANOVAs of relative abundances (Chapter 7); [3] most abundant species representing each moth functional type (FT), excluding stray species (such as conifer feeders).

The BVSTEP procedure revealed 373 subsets comprising 8–15 species each (1.8–3.3% of all recorded moth species and about one third of all individuals). These subsets represented overall beta-diversity equally well as, or better than, any subset defined by superfamilies or larval stratum (Table 8.1). These subsets scored also better than selections of the 8 or 15 most common species, or the most abundant resident representative species of each functional type (Table 8.1). The subset defined by those 15 species which showed strongest abundance differentiation between regions and flood regimes (see Chapter 7) came closest to the minimal BVSTEP subsets.

In total, 84 moth species were represented in the 373 reduced subsets, but at very different frequencies. One species, the hyper-dominant lichen moth *Pelosia muscerda*, was almost always included. Other species that recurred over 150 times in reduced subsets were *Ecliptopera silaceata*, *Hemistola chrysoprasaria*, *Lomaspilis marginata*, *Lomographa bimaculata*, *Macaria alternata* (Geometridae), *Herminia tarsicrinalis* (Erebidae), *Leucania obsoleta*, and *Ochropleura plecta* (Noctuidae; Fig. 8.2). Abundant species tended to show up more frequently in subsets extracted by BVSTEP (r_S=0.4285, p<0.0001). However, some of the most abundant moth species (e.g. *Pleuroptya ruralis*, *Cyclophora annularia*, *Rivula sericealis*, *Spilosoma lubricipeda*, *Epirrhoe alternata*) were never included in reduced subsets and hence did not carry much information that is important for beta-diversity. Moth species which occurred very frequently in the subsets covered all functional types except grass or root feeders and host-plant specialists of woody plants.

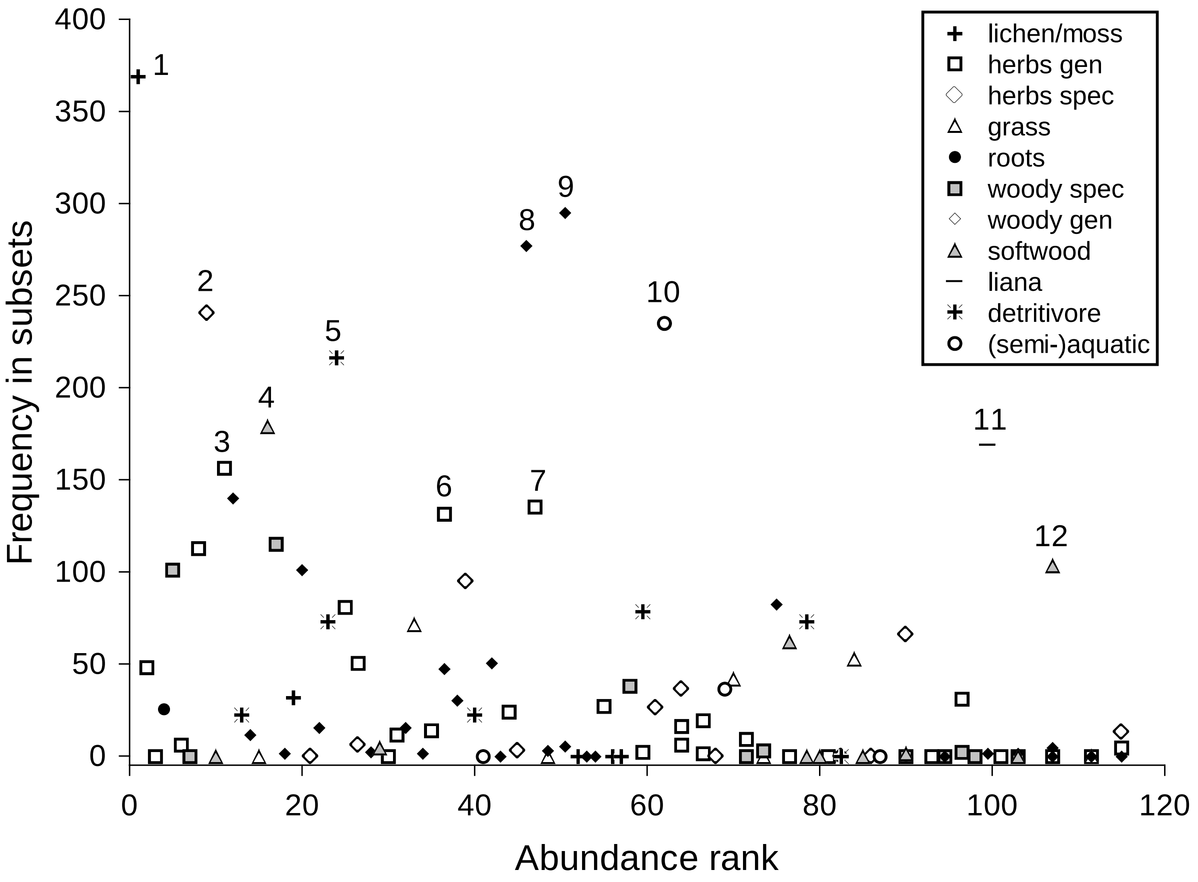

Fig. 8.2: Frequency of the representation of 117 abundant moth species (*N*≥28) in 373 reduced subsets retrieved by the BVSTEP algorithm, relative to their abundance rank.

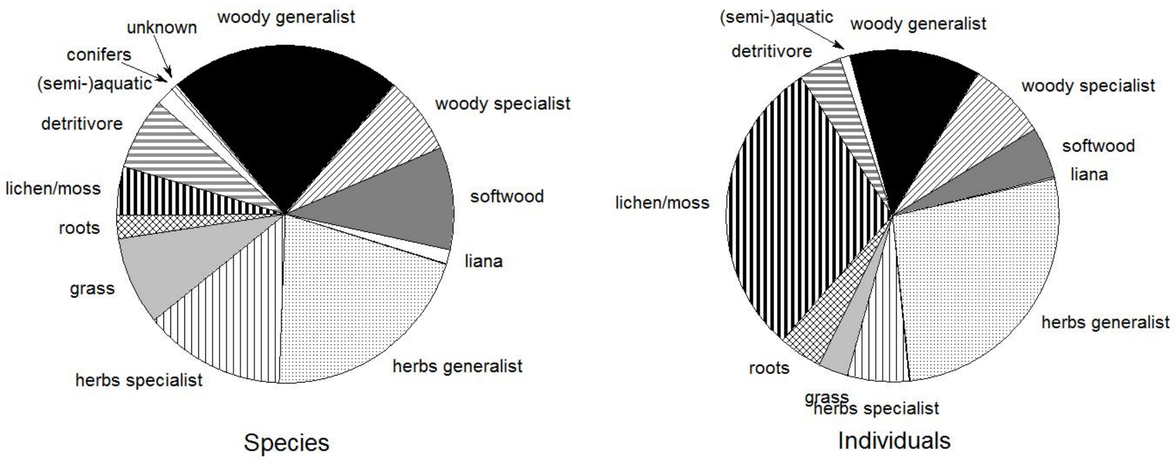

Fig. 8.3: Functional composition of the entire floodplain forest moth assemblages according to species (left, 448 species in total) and individuals (right, total: 32,181 moths).

Moth assemblages in the studied floodplain forests were dominated by species whose larvae feed on woody plants or understorey herbs (Fig. 8.3a). Detritivores, lichen/moss feeders, grass feeders and softwood specialists play minor roles, whereas other functional types were rare. This patterns changes slightly if viewing at abundance rather than species richness (Fig. 8.3b). Then, lichen feeders (due to the dominance of *Pelosia muscerda*) and polyphagous herb feeders gain stronger prominence. Frequency distributions look quite different amongst those 84 moth species that showed up in reduced subsets (Fig. 8.4). Softwood or liana feeders and species that feed on (semi-)aquatic plants (i.e. species characteristic for riverine forests) now gain relatively more weight. In contrast, root feeders are very weakly represented. Overall, these subsets are dominated by generalist feeders of either herbs or woody plants.

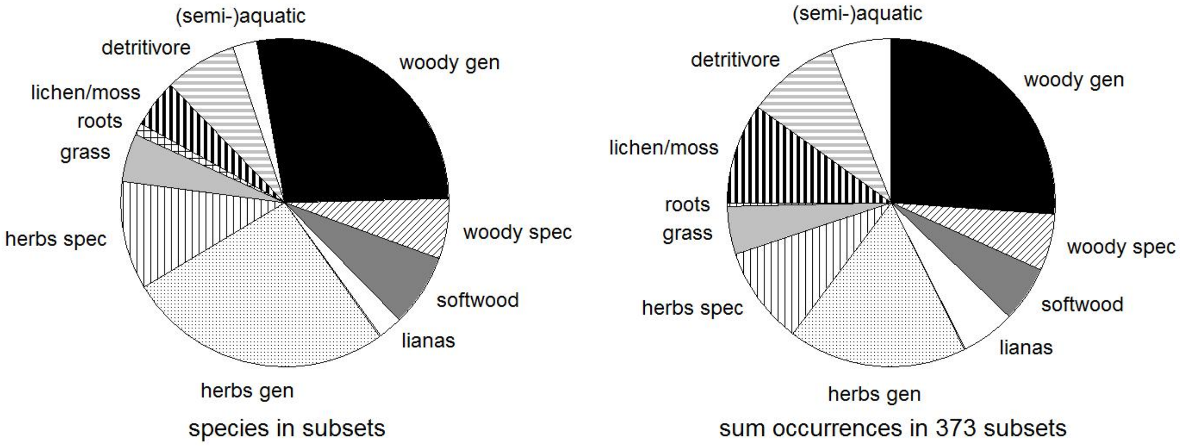

Fig. 8.4: Composition of 373 reduced floodplain forest moth subsets (comprising 8–15 species, retrieved by the BVSTEP algorithm) according to the functional type allocation of represented species (left, 84 species in total), and the frequency of these species in the subsets (right).

Three functional types, viz. generalist feeders of woody as well as herbaceous plants and lichen/moss feeders, were almost always included in reduced subsets (Fig. 8.5). Detritivores and specialist feeders of herbs were also very regularly included, whereas root herbivores played almost no role. Species with (semi-)aquatic larval stages or feeding on *Clematis* lianas were not numerous in the total data set, but appeared quite frequently in reduced subsets.

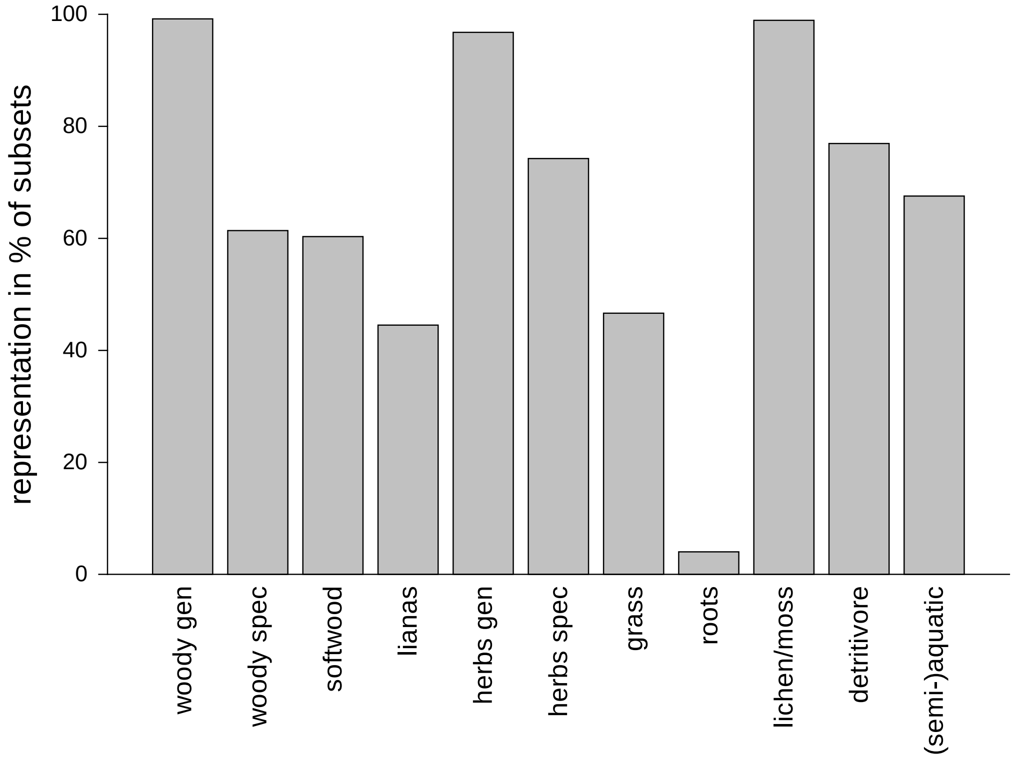

Fig. 8.5: Representation of 11 moth functional types in the 373 subsets of 8–15 species, extracted by the BVSTEP algorithm (gen: generalist, larvae feed on plants in several families; spec: specialist, larval food plants in only one family).

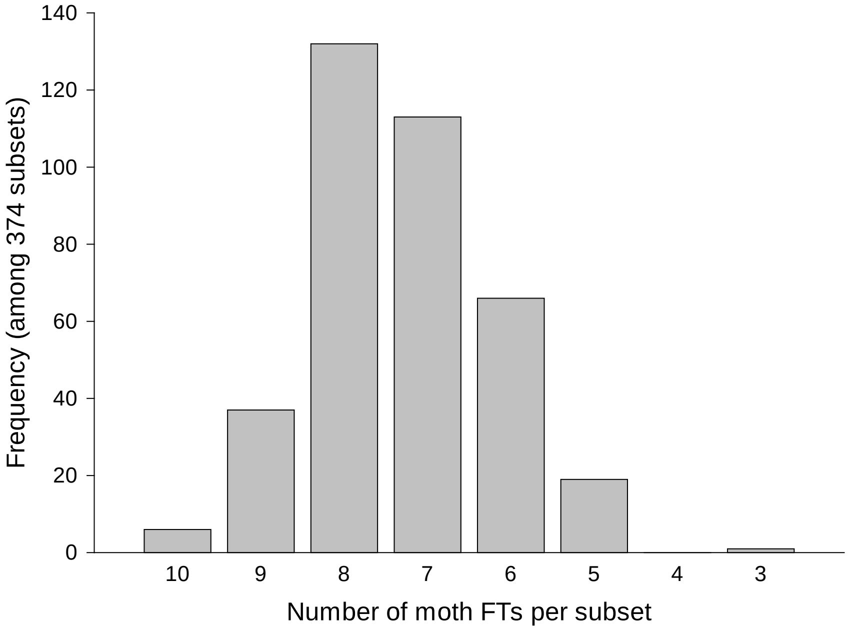

Fig. 8.6: Frequency distribution of the number of moth functional types represented in the 373 reduced subsets (8–15 species, extracted by the BVSTEP algorithm).

The majority of reduced subsets comprised representatives of 6–9 functional types (Fig. 8.6). Inclusion of fewer functional types made it less likely that a species subset would still accurately reflect overall moth beta-diversity. On the other hand, a nearly full coverage of all regionally available functional types was also not required.

Discussion

Species turnover among taxonomically and ecologically defined moth subsamples

Given that species diversity cannot be monitored exhaustively for diverse groups of organisms like arthropods, much effort has been devoted to explore the effectiveness and usefulness of surrogates or ‘biodiversity indicators’, to extrapolate from small handy sampling targets to community levels (Rodrigues & Brooks, 2007). With regard to local species diversity, these studies have revealed variable, and frequently low, concordances among plant or animal taxa (Kati et al., 2004; Santi et al., 2010; Virtanen et al., 2009). Patterns of beta-diversity can be more congruent between unrelated taxa than alpha-diversity patterns, at small (Kessler et al., 2009) to large spatial scales (Buckley & Jetz, 2008). However, most of these studies deal with surrogates between phylogenetically or ecologically very distinct taxa (such as plants, vertebrates, and arthropods) across extensive ecological gradients. In contrast, our present study explores possible surrogates within one species-rich taxon across more restricted habitat gradients. In far more species rich tropical assemblages, beta-diversity patterns were indeed highly concordant ($r_S \geq 0.800$) between geometrid, arctiid and pyraloid moths along elevational (Fiedler et al., 2008) as well as disturbance gradients (Fiedler et al., 2007).

For Austrian floodplain forest moths, variance in species turnover was surprisingly more pronounced across taxonomic and ecological groups (Fig. 8.1, Table 8.1). Especially the Pyraloidea sent a different signal than the other two superfamilies (Pyraloidea vs. Noctuoidea: $r_S=0.243$, $p=0.008$; Pyraloidea vs. Geometroidea: $r_S=0.415$, $p<0.001$, Geometroidea vs. Noctuoidea: $r_S=0.597$, $p<0.001$). This can be explained by the strong differences in life-histories and larval resource use. Larvae of many Pyraloidea (66 out of 77 observed species) are concealed feeders which develop within roots, flowers or stems, or they feed in silken shelters. Many also occupy unusual food niches relative to other Lepidoptera (feeding on mosses, detritus or aquatic plants: Munroe & Solis, 1999; Powell et al., 1999). Moreover, the great majority of recorded pyraloids belonged to the ground-layer fauna. Hence, differences in habitat and resource requirements are likely responsible for the deviant pattern in pyraloid species turnover across forest regions and flooding regimes.

Hirao et al. (2009) found that in temperate deciduous forests lepidopteran species richness, abundance and family richness was significantly greater in the understory than in the canopy. This underpins the importance of the understory vegetation for forest Lepidoptera. In our study, species turnover among ground-layer moths revealed almost exactly the same pattern as the entire moth assemblage. The assemblage of moths with arboreal larvae had only a slightly weaker, though still highly significant correlation with the entire species set. Regional and habitat differences among the arboreal fauna attained almost identical strength as within ground-layer moths, except for the Pyraloidea where the arboreal component of the fauna was very poorly represented. This concordance was unexpected. Rather, we had anticipated ground-layer moths to be more consistently affected by flood impacts. We attribute this concordance to the high mobility of many moth species allowing for rapid recolonization after flood events. Hence, there was no distinct moth community characteristic for only the dynamic, regularly inundated forest parts (see Chapter 7).

With regard to phylogenetically defined subsets, the Noctuoidea served best as surrogate for overall beta-diversity patterns, followed by the Geometroidea. Ecological resolution among pyraloid moths was much weaker, though still significant. One reason for the prominence of Noctuoidea as excellent surrogates for overall beta-diversity might be that, besides their large number of species and individuals, 11 of the 12 functional types defined by larval host-plant affiliations were represented within this superfamily. But Noctuoidea are so rich in species and so numerous that focussing surveys on them would hardly spare resources. The recorded Geometroidea species lack some functional types, such as lichen, moss, root, or (semi-)aquatic feeders, which were otherwise prominent in the floodplain forest moth fauna. Nevertheless, this more manageable data subset (31.25% of species, 21.22% of individuals) was almost as efficient as the far larger Noctuoidea assemblage in depicting regional and flood-related differentiations of the moth fauna. These observations confirm that geometrid moths are a particularly suitable group to monitor environmental change (Choi & Chun, 2009; Beck et al., 2011; Fiedler et al., 2007; Intachat et al., 1997).

Our results show that species composition of floodplain forest moths sensitively reflects environmental differences between habitats even at small spatial scales. Regional differences were, however, always far stronger than local flooding effects. Similar patterns were observed for alpha-diversity (see Chapter 7). These findings indicate that regional differences (e.g. in the species composition of forest vegetation) are more important in shaping the assembly of moth communities from the regional species pool, relative to local habitat conditions caused by river dynamics.

Overall, we did not find support for our hypothesis that resolution of ecological patterns would differ more consistently between ecologically, as opposed to phylogenetically, defined groups. Our explorations indicated that a suitable surrogate for beta-diversity should comprise many (though not necessarily all) functional moth types that may occur in a specific habitat, but should be more convenient than the speciose Noctuoidea at large.

Structural redundancy – the role of abundant species and functional types

Using the BVSTEP algorithm to extract small subsets of key taxa that reflect overall community turnover is a common approach in aquatic ecology (Mistri et al., 2001; Magierowski & Johnson, 2006), but has so far rarely been applied to terrestrial communities (Adams et al., 2010; Aragón et al., 2010). We were able to reduce our dataset down to 8 species (i.e. only 1.5 % of all recorded moth species) that were largely sufficient to reflect the patterns in the overall moth community. We could not find any other study that retrieved a similarly massive structural redundancy. Alvarez-Filip & Reyes-Bonilla (2006), who investigated coral reef fish communities, were able to reduce their datasets only down to 22% and 32%, respectively. The smallest subset of macrozoobenthos assemblages from lagoonal habitats that matched to the wider community patterns in the study of Mistri et al. (2001) still contained seven species (15%). Nohrén et al. (2009) were able to condense 110 motile epibenthic taxa in coastal habitats along a salinity gradient down to 10% of the original species list.

These studies investigated structural redundancies in aquatic ecosystems with far fewer species (totals ranging from 46 to 110) than we had to consider in our analyses (448 species). To our knowledge, similar studies have not yet been conducted with other large terrestrial arthropod samples. We hypothesize that massive structural redundancy will show up in many more cases. Such explorations would be most rewarding, for example to compare the extent of structural redundancy between long and short environmental gradients, or between very rich (e.g. tropical) and less speciose (e.g. temperate-zone) insect communities.

Contrary to our expectation, high abundance did not necessarily mean that these species are important for the overall beta-diversity pattern (Fig. 8.2). The smallest subsets extracted through the BVSTEP algorithm contained 8–15 species, yet matched the total community pattern better than a selection of the 8 or 15 most abundant species (Table 8.1). Therefore we suggest to routinely applying the BVSTEP algorithm for uncovering those fractions of species-rich terrestrial arthropod assemblages that are shaping their species turnover patterns. Just focusing on the most abundant species might be misleading, since rare species can have important roles in ecosystems (Lyons et al., 2005). For example, they can act as keystone species, be important in nutrient cycles and retention, or may improve the resistance of a community against species invasions. In line with these functional considerations, our structural explorations likewise revealed that moth species with a low abundance were contained in all reduced subsets and obviously, therefore, comprise important information on species turnover. Two functional types, viz. moths whose larvae feed on *Clematis* lianas or on (semi-)aquatic plants, were quite important for depicting species turnover, but were overall not very common. Both these functional types are characteristic for riverine forests of Central Europe.

To get an idea of what functional affiliations might be reflected through the observed structural redundancies in beta-diversity, we assigned moth species to 12 functional types. In most reduced subsets at least six functional types were included. Besides lichen and moss feeders, which were mainly represented by one hyper-dominant species (*Pelosia muscerda*), tree and herb generalists were almost always included. Also detritivorous moths whose larvae feed on withered or fallen leaves and herb specialists were included in the majority of reduced subsets. Root feeders scored low. In riverine forests subject to frequent flooding and high groundwater levels, moth species with rhizophagous caterpillars are likely to experience strong constraints (Köppel, 1997). Moth species whose larvae thrive on classical floodplain forest softwood trees (*Populus, Salix*) or feed on (semi-)aquatic plants were relatively more prominent in these subsets than in the entire moth assemblage. From this we conclude that the overall species turnover pattern in floodplain forest moths is dominated by abundance shifts of widely distributed deciduous forest species, but habitat specialists do play an important role in shaping these gradients (see also Chapter 7).

Clarke & Warwick (1998) found in their study on structural redundancy in marine macrozoobenthos that subsets identified with BVSTEP encompass a wide taxonomic and functional range. Their subsets contained representatives of all functional groups that might occur in such habitat. Our study does not fully confirm this suggestion for moth communities in temperate forests. Though the majority of functional types was usually represented in reduced subsets, some were rarely covered. In particular, grass and root feeders played but a minor role in moth assemblages of riverine forests. Many of these moths, however, have to be rated as strays from the surrounding landscape matrix (Chapter 7). Hence, the high mobility of moths leads to a less clear pattern than observed amongst benthic aquatic animals whose mobility is more restricted to larval (planktonic) stages. It would be most rewarding to investigate how structural redundancy is related to functional type composition in other terrestrial arthropod communities.

Conclusions

Functional redundancy has become a main topic of biodiversity research in recent years, especially in the context of biodiversity loss and its impact on ecological processes (Laliberte´ et al., 2010; Schmera et al., 2012; Schwartz, et al., 2000) The major question in this context is how many, and which, species are needed to maintain ecosystem functionality. To answer these questions, it is mostly necessary to perform experiments where species richness and species composition are manipulated (Joner et al., 2011; Mermillod-Blondin et al., 2001). Surprisingly few studies have thus far investigated the extent of structural redundancy in species turnover, even though this aspect would be far more accessible with data derived from surveys of naturally existing, species-rich communities as presented here.

We found strong structural redundancies in moth communities in floodplain forests – only a very small subset of less than 2% of all species was sufficient to represent overall beta-diversity. The most abundant species do not necessarily carry the greatest weight in that regard. Rather, representation of all the more common functional types within an ecosystem is crucial. Our data indicate that the unexpectedly extensive structural redundancies might also reflect functional redundancies, but further investigations will be needed to test this hypothesis.

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9. Synopsis

The results of this thesis provide new findings not only on the diversity and community structure of moths in floodplain forests, but also on more general aspects like from how far do moths return to weak artificial sources of light, which diversity-measure should be applied to analyse light-trap data, how strong is the impact of stray species on diversity patterns revealed by trap samples from mobile insect faunas, or how much redundancy can be found in species-rich terrestrial insect communities.

Light traps are very commonly used to survey nocturnal insects. Although there are many studies that investigated factors influencing light trap catches (Axmacher & Fiedler, 2004; Beck et al., 2011; Fayle et al., 2007), little is still known about the effective attraction radius of such traps (Beck & Linsenmair, 2006 and references therein). In order to estimate the attraction radius of a weak artificial light source for moths, two community-wide mark-release-recapture experiments were carried out (Chapter 5). Overall the recapture rate was low (13.4%) and strongly decreased with increasing release-distance. The results emphasize that the effective attraction radius of an artificial light source for moths is rather low, mostly <30°m and often <10°m. Contrary to the expectation that higher taxonomic groups among the Lepidoptera would differ in their distance-dependence of recapture rates, there were no obvious differences in the shape of this distance dependency among the major super-families included in our study. Light traps usually catch fewer females than males (Altermatt et al., 2009; Beck & Linsenmair, 2006), and this was also true for my data. There were, however, no discrepancies in the percentages of males and females recaptured after marking. Most of the few experimental studies that deal with the attraction radius of light traps for moths are based on single species (Baker & Sadovy, 1978) or one family (Beck & Linsenmair, 2006). In the present thesis a broad range of central European moth species was investigated to assess the attraction range of light traps. This finding is very important as it corroborates the view that weak artificial light sources are an excellent way to gather data on moth communities in a specific habitat. Moths from adjacent habitats are not likely to be attracted actively by such traps over distances of hundreds of meters or beyond.

Measuring biodiversity of species-rich and incompletely known assemblages remains a controversial topic in ecological research. There exists a wide range of diversity measures, and many ecologists as well as mathemathicians have dealt with the question which diversity measure to adopt in a specific context (e.g. Buckland et al., 2005; Hayek & Buzas, 1997; Legendre & Legendre, 1998). Still, no agreement has been reached on this point. Recent advances on the selection of diversity measures have been obtained using modelled data sets (Beck & Schwanghart, 2010). In the present thesis a large empirical data set of species rich and abundant arthropods was used to explore the performance of a range of alpha-diversity measures (Chapter 6). It was expected that the insect communities under study should differ in regard to region (i.e. three riverine forest areas) as well as habitat (i.e. flooded vs. non-flooded). Observed, extrapolated and rarefied species numbers, as well as Fisher's α, and Shannon's exponential diversity (with and without bias-correction) were compared in their potential to reveal ecological differences in species diversity. Interestingly, mean observed species richness per trap site did not reveal any significant differences between flood regimes and regions, nor did any of the extrapolated richness estimators. In contrast, rarefied species richness did show significant differences between the three forest regions, but not between the flooding regimes. All diversity measures derived from species-abundance relationships, i.e. both versions of Shannon's diversity and Fisher's α, captured strong differences in species diversity between the three regions. Notably, only Shannon's diversities revealed significant differences between flood regimes and also a significant flood × region interaction term. Applying the bias-correction to estimating Shannon's diversity (Chao & Shen, 2003) did not affect the strength of statistical analyses, but scores were distinctly elevated relative to the classic exp(H_S). The failure of all species richness measures to reflect differences between floodplain forest moth communities can be explained by undersampling. Even after two full annual cycles of surveys the moth fauna was certainly not covered exhaustively at any of the 28 sites. Moreover, all moth assemblages contained many rare species which is typical for almost all ecological communities (Magurran & Henderson, 2003). Hence, sampling effects are still too large to allow for meaningful analyses based on mere species counts. Rarefaction, a method specifically developed to compare samples of very different sizes, overcomes these defects of simple richness estimates. But one disadvantage of this method is that a lot of information is lost when reducing the dataset to the maximum common number of individuals that has been caught in every sample. Therefore, measures like Fisher's α and Shannon's diversity, which consider both, species numbers and abundances, are superior to species richness estimators at the local ecological scales of my study. In line with Beck & Schwanghart (2010), Chao & Shen (2003) and Jost (2006) I therefore suggest to apply Shannon's diversity, in its bias-corrected version, as the most appropriate measure of alpha-diversity when analysing species-rich, incompletely sampled arthropod communities at local ecological scales.

Moth diversity and species composition was investigated in three floodplain forests with varying flooding regimes (Chapter 7). A total of 32,181 moth individuals belonging to 448 species were recorded and identified. Species numbers and individuals were very similar in flooded and non-flooded habitats. Shannon's diversity captured strong differences in species diversity between the three regions and less pronounced between flood regimes nested within regions. The Danube region showed the highest overall diversity, followed by the Leitha floodplain forests, whereas the Morava region scored lowest. The low diversity in the Morava region was surprising, because of their large size it was expected that the overall diversity would be similar to that in the Danube floodplain. It turned out that one hyper-dominant species in the Morava floodplain forest, *Pelosia muscerda*, influenced diversity patterns radically. Excluding this species produced higher overall diversity values in the Morava region. Now the Morava region scored higher than the Leitha floodplain and very similar to the Danube region. This higher moth diversity of the Danube and Morava floodplain compared to those of the Leitha matches well to the larger size and the more natural state of their riparian forests.

Interestingly, flooding did not have a general negativ effect on moth diversity: the flooded forest habitats at the rivers Danube and Leitha showed higher diversity values than the non-flooded habitats. The small number of floodplain specialists and the lack of a specific floodplain community lead to the assumption that flooded habitats offer many niches for new colonization or recolonization. There are only few studies that have dealt with the impact of flooding on arthropod diversity so far and their conclusion are to some degree inconsistent: Ballinger et al. (2007) found that ants are negatively impacted by flooding, Rothenbücher & Schaefer (2005) observed most leafhoppers in non-flooded sites, and Lambeets et al. (2009) found that carbid beetles and spiders responded diferrently to flooding regarding to their life history traits. It seems that flooding does not have a general negative effect on various terrestrial arthropds – further investigations on other terrestrial arthropods would be interesting to confirm these suggestions.

Another remarkable result was that strays species – i.e. dispersing moths that originated from other habitats – hardly influenced the diversity patterns, although their contribution was substantial and their proportion differed strongly between regions as well as between habitats. Overall, our analyses indicate that the inclusion of stray individuals is not problematic for ecological interpretation of light trap samples in temperate forests, even if a rather sizeable fraction of specimens (up to 15% per habitat in our case) must be considered as strays or dispersing individuals. These findings are not only relevant for temperate regions, but might also be an indication for tropical arthropod communities, where for example many species observed in disturbed areas around nature reserves are suspected to be represented only by strays from adjacent near-natural forest (Hilt et al., 2006).

Resident moth species – i.e. all species excluding the strays – were further divided into “arboreal” and “ground-layer” species regarding to the habitat of their larval stages to identify the impact of flooding and region. Again, regional differences were highly significant for all the different groupings of moths. As expected, flooding affected resident ground-layer moth species more strongly than arboreal species, for which no differences in local diversity between flooded and non-flooded forest habitats could be found.

Beta-diversity was examined to find out if flooding affects moth assemblages to form a unique species set. There was a clear differentiation of moth communities among the three regions. In the Danube region and less pronounced in the Leitha region, species composition of moth assemblages differed between regularly flooded and non-flooded habitats. At the Morava region no different moth assemblages could be found between flooded and non-flooded habitats. This latter observation was not too surprising as these habitats were located closely together and only differed by the length of the annual innundation period.

However, contrary to the hypothesis that flooding would shape a characteristic (specifically adapted) moth community, no such assemblage could be identified. Taking a closer look at the 44 most abundant species (together accounting for 25,193 individuals, i.e. 78% of the total catch) none of these species only occurred in either flooded or non-flooded habitats. Similarly none of these 44 species was entirely lacking in any of the three regions, i.e. faunal differences were largely due to variation in relative abundances of rather widespread eurytopic forest moth species.

Compared to other Central European lowland forests the moth communities in all three floodplain regions were moderately diverse (see Table 9.1). Relative to the taxa covered, the fraction of Red List species amongst residents was only 5%. Therefore, the moth communities of the studied floodplain forests in Eastern Austria do not qualify as priority targets for conservation measures, in contrast to the high conservation value of the same habitats for organisms such as birds or aquatic vertebrates and invertebrates (Dvorak, 2009; Tockner et al., 1998).

Table 9.1: Moth diversity (Shannon's exp(H_S) and Fisher's α) of various lowland forest types in Europe, assessed from quantitative light-trap samples and ordered from high to low species diversity. To render studies comparable all Pyraloidea were omitted from Habeler (2005), Hacker & Müller (2009) and own samples (see Chapter 7, data from the present thesis are highlighted in bold). Light-trap locality names are taken from original sources.

Author & study region	Habitat description	Shannon	Fisher's α
Habeler_2005_Wildon-Auen	Deciduous forest	236.5	114.3
Habeler_2005_Mellach	Deciduous forest, reed	197.0	100.7
Habeler_2005_Diepersdorf	Harwdood floodplain	194.7	93.9
Kristal_1995_Lorscher Wald	Mixed forest with oak	144.6	81.7
Habeler_2005_Kalsdorf	Mixed forest with poplar und spruce	132.7	82.0
Habeler_2005_Gralla	Harwdood floodplain	131.8	86.5
Hacker&Müller_2008_Nedensdorf	Coppice with oak and hornbeam	127.1	70.1
Mörtter_1987_Schlaggesellschaft	Succession habitat after clear-cut	111.0	62.6
Hausmann_1990_Wald	Deciduous forest	110.7	66.3
Hacker&Müller_2008_Moritzanger	Mixed forest with oak, beech	108.3	62.1
Mörtter_1987_Kiefern-Buchenwald	Mixed forest with pine, beech	107.7	57.3
Hausmann_1990_Au	Floodplain	103.7	67.0
Hacker&Müller_2008_Kosterlangheim	Lime forest	98.2	48.4
Habeler_2005_Unterschwarza	Mixed forest with spruce afforestations	97.7	51.7
Kristal_1995_Lampertheimer Wald	Mixed forest with oak, pine	94.7	55.3
Kristal_1995_Viernheimer Wald	Mixed forest with oak	87.0	55.1
Hacker&Müller_2009_Gleisenau Fi	Spruce forest	86.6	63.9
Mörtter_1987_Eichen-Hainbuchenwald	Mixed forest with oak and hornbeam	85.0	51.2
Hacker&Müller_2008_Aspenwald	Oak forest	80.3	50.0
Hacker&Müller_2009_Banz Fi	Spruce forest	77.5	57.3
Mörtter_1987_Fichtenhochwald	Spruce forest	76.1	53.6
Köppel_1997_Hartholzau	Hardwood floodplain	75.1	56.4
Chapter 7_DF	Softwood floodplain	**73.7**	**51.8**
Hacker&Müller_2009_Banz Dgl	Douglas fir forest	69.6	52.8
Köppel_1997_HoHa_Krone	Hardwood floodplain – canopy	65.1	46.3
Chapter 7_DN	Harwdood floodplain	**63.9**	**52.7**
Lemke_2002_A2_Buche+Fichte	Mixed forest with beech, spruce	58.8	39.0
Kofler_1989_Lendorfer_Au	Floodplain	57.9	44.5
Chapter 7_LF	Softwood floodplain	**56.9**	**48.4**
Lemke_2002_A2_Fichte	Spruce forest	53.1	39.9
Köppel_1997_Weichholzau	Softwood floodplain	51.5	47.2
Hausmann_1990_Moorbirkenwald	Moor birch forest	49.3	44.1
Lemke_2002_A1_Fichte	Spruce forest	45.0	27.9
Hacker&Müller_2008_Klein_Engelein	Oak forest	40.7	35.1
Lemke_2002_A3_Fichte	Spruce forest	39.2	22.9
Lemke_2002_A3_Buche+Fichte	Mixed forest with beech and spruce	37.3	26.8
Lemke_2002_A1_Buche	Beech forest	33.9	33.4
Lemke_2002_A1_Buche+Fichte	Mixed forest with beech and spruce	32.5	26.8
Hausmann_1990_Weiher	Floodplain	31.5	48.4
Chapter 7_LN	Harwdood floodplain	**28.7**	**41.6**
Mörtter_1987_Fichtendickung	Spruce forest	22.8	30.4
Lemke_2002_A3_Buche	Beech forest	20.2	21.1
Hacker&Müller_2008_Eichhall	Oak forest	19.5	31.2
Lemke_2002_A2_Buche	Beech forest	19.0	22.0
Chapter 7_MN	Harwdood floodplain	**12.7**	**42.2**
Chapter 7_MF	Softwood floodplain	**10.0**	**38.3**

Different subsets of the moth community (based on phylogenetically and ecologically defined groups) were examined to determine potential surrogates for overall beta-diversity patterns. Further the amount of structural redundancy was examined to reveal how few species are sufficient to reveal species turnover patterns (Chapter 8). BVSTEP was used to reduce the dataset to the minimum number of species that were sufficient to show the overall diversity-pattern. The smallest subsets were analysed by allocating moth species into 10 functional types based on their larval life-histories and resource requirements: species that feed on lichens or mosses, herb generalists, herb specialists, tree generalists, tree specialists, softwood (*Salix* or *Populus*) tree specialists, detritivores, and feeders of (semi-)aquatic plants, grasses, and roots.

Subsets of moths mirrored the overall beta-diversity patterns to quite different degrees. As expected, flooding affected ground-layer subsets more strongly than arboreal moths. But within moth superfamilies, flooding differentially affected ecologically defined groups. Geometroidea showed the strongest effect of flooding in the arboreal moths, whereas among the Noctuoidea and the Pyraloidea the ground-layer fauna responded more clearly. These results are in contrast to the hypothesis that ecologically defined groups would be impacted by flooding more consistently.

Overall the Noctuoidea mirrored the beta-diversity patterns best, followed by the Geometroidea. The Pyraloidea (and their subsamples) always scored lowest. These findings were attributed to the fact that the Pyraloidea were low in species numbers and individuals and that pyralids have quite contrasting larval life-histories as opposed to the other surveyed moth groups. The Noctuoidea were the most species-rich superfamily with individuals occurring in high numbers and – perhaps more important – included all functional types (contrary to the Geometroidea). However, a suitable surrogate should contain (nearly) all functional types that are to be expected within a habitat, but should also be more convenient to handle than the speciose Noctuoidea. Under this perspective, the Geometroidea would serve as the most promising surrogate taxon for moth beta-diversity in floodplain forests, because they revealed diversity-patterns almost as good as the Noctuoidea, but only amounted to 31.25% of total species and 21.22% of total individuals. This suggestion is also in line with other studies that have shown that geometrid moths are a particularly suitable group to monitor environmental change (Axmacher et al., 2004; Beck et al., 2002; Fiedler et al., 2007; Intachat et al., 1997).

The extent of structural redundancy in the dataset was surprisingly large. The dataset could be reduced down to 15 species that were sufficient to display the overall beta-diversity patterns. No other study that retrieved a similarly massive structural redundancy could be found. Structural redundancies in aquatic ecosystems ranged from 68–90% (Alvarez-Filip & Reyes-Bonilla, 2006; Mistri et al., 2001; Nohrén et al., 2009). However, these studies investigated structural redundancies in aquatic ecosystems with far fewer species (ranging from 46 to 110 species, in contrast to 448 species that were considered in this thesis). To my knowledge, similar studies have not yet been conducted with other large terrestrial arthropod samples, but I hypothesize that massive structural redundancy will show up in many more cases.

Against expectations, highly abundant species did not necessarily carry the most information for overall beta-diversity patterns. Rather, my results suggest that the representation of all (or at least of all common) functional types within an assemblage of organisms is more important. It would be most rewarding to investigate if these findings also apply to other terrestrial arthropod communities, including trophic levels beyond herbivores and detritivores (as represented by the Lepidoptera).

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10. Curriculum vitae

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11. Appendix

The following tables, texts and figures contain raw data and supplementary information. These appendices have either been included in the electronic supplementary materials of the published versions of the respective chapters, or have directly been appended at the end of these papers.

Appendix S1: Moth species (in alphabetical order, presence only indicated by x) encountered in the two MRR experiments (Chapter 5) to test responses to low-power light traps. Nomenclature follows Fauna Europaea (URL: http://www.faunaeur.org/)

Species	**Superfamily**	**Orth**	**Bayreuth**	**Recaptured**
Abraxas sylvata	Geometroidea	x	x	
Abrostola triplasia	Noctuoidea	x	x	
Acasis viretata	Geometroidea		x	
Acronicta rumicis	Noctuoidea		x	x
Actinotia polyodon	Noctuoidea		x	
Aethalura punctulata	Geometroidea		x	x
Agrotis exclamationis	Noctuoidea	x	x	x
Alcis repandata	Geometroidea	x	x	x
Anania hortulata	Pyraloidea	x		x
Anaplectoides prasina	Noctuoidea		x	
Angerona prunaria	Geometroidea	x		x
Anticlea derivata	Geometroidea		x	x
Apamea crenata	Noctuoidea	x		
Apamea monoglypha	Noctuoidea	x		
Aphomia sociella	Pyraloidea	x		
Aplocera plagiata	Geometroidea		x	
Arctornis l-nigrum	Noctuoidea	x		
Ascotis selenaria	Geometroidea	x		
Atypha pulmonaris	Noctuoidea	x		
Axylia putris	Noctuoidea	x	x	x
Biston betularius	Geometroidea	x		x
Cabera exanthemata	Geometroidea	x	x	x
Cabera pusaria	Geometroidea	x	x	x
Callimorpha dominula	Noctuoidea	x		x
Calliteara pudibunda	Noctuoidea		x	x
Campaea margaritata	Geometroidea	x		
Cepphis advenaria	Geometroidea		x	
Cerastis rubricosa	Noctuoidea		x	x
Cerura erminea	Noctuoidea	x		
Charanyca trigrammica	Noctuoidea		x	x
Chiasmia clathrata	Geometroidea	x	x	x
Chloroclysta siterata	Geometroidea		x	
Cleora cinctaria	Geometroidea	x		x
Clostera curtula	Noctuoidea	x	x	x
Clostera pigra	Noctuoidea		x	x
Colocasia coryli	Noctuoidea		x	
Conistra vaccinii	Noctuoidea		x	x
Cosmorhoe ocellata	Geometroidea		x	x
Cucullia umbratica	Noctuoidea	x		
Cyclophora albipunctata	Geometroidea		x	x
Cyclophora annularia	Geometroidea	x	x	
Cyclophora punctaria	Geometroidea	x	x	
Deltote pygarga	Noctuoidea		x	x
Diachrysia chrysitis	Noctuoidea	x	x	x
Diarsia florida	Noctuoidea		x	
Drepana falcataria	Drepanoidea		x	x
Drymonia dodonaea	Noctuoidea	x		

Drymonia ruficornis	Noctuoidea		x	x
Dysstroma truncata	Geometroidea		x	
Earophila badiata	Geometroidea		x	x
Ecliptopera silaceata	Geometroidea	x	x	x
Ectropis crepuscularia	Geometroidea	x		x
Epione repandaria	Geometroidea	x		
Epirrhoe alternata	Geometroidea	x	x	x
Euchoeca nebulata	Geometroidea	x		
Eulithis mellinata	Geometroidea	x		
Euphyia unangulata	Geometroidea		x	
Eupithecia subfuscata	Geometroidea		x	x
Eupithecia tantillaria	Geometroidea		x	
Euplexia lucipara	Noctuoidea	x	x	x
Euproctis similis	Noctuoidea	x		
Euxoa obelisca	Noctuoidea	x		
Furcula furcula	Noctuoidea		x	
Gandaritis pyraliata	Geometroidea	x		
Gluphisia crenata	Noctuoidea	x		
Harpyia milhauseri	Noctuoidea		x	
Hemistola chrysoprasaria	Geometroidea	x		
Hemithea aestivaria	Geometroidea	x		x
Herminia grisealis	Noctuoidea	x		
Herminia tarsicrinalis	Noctuoidea	x		x
Hoplodrina ambigua	Noctuoidea	x		x
Hoplodrina blanda	Noctuoidea	x		
Horisme corticata	Geometroidea	x		
Horisme tersata	Geometroidea	x		
Horisme vitalbata	Geometroidea	x		
Hydria cervinalis	Geometroidea		x	x
Hydria undulata	Geometroidea		x	x
Hydriomena impluviata	Geometroidea		x	x
Hylaea fasciaria	Geometroidea		x	x
Hypena proboscidalis	Noctuoidea	x	x	
Hypomecis punctinalis	Geometroidea	x	x	x
Hypomecis roboraria	Geometroidea	x		x
Hypsopygia glaucinalis	Pyraloidea	x		
Idaea aversata	Geometroidea	x	x	x
Lacanobia contigua	Noctuoidea	x		
Lacanobia oleracea	Noctuoidea	x		
Lacanobia thalassina	Noctuoidea	x		
Lampropteryx suffumata	Geometroidea		x	x
Laothoe populi	Sphingoidea	x		
Leucania obsoleta	Noctuoidea	x		
Ligdia adustata	Geometroidea	x	x	x
Lithophane socia	Noctuoidea		x	
Lithosia quadra	Geometroidea	x		x
Lobophora halterata	Geometroidea		x	x
Lomaspilis marginata	Geometroidea	x	x	x
Lomographa bimaculata	Geometroidea		x	x
Lomographa temerata	Geometroidea	x	x	x
Lycia hirtaria	Geometroidea		x	x
Macaria alternaria	Geometroidea		x	
Macaria liturata	Geometroidea	x	x	x
Macaria notata	Geometroidea		x	

Mamestra brassicae	Noctuoidea		x	x
Melanthia procellata	Geometroidea	x		x
Mesapamea secalis	Noctuoidea	x		
Mimas tiliae	Sphingoidea	x		
Mythimna albipuncta	Noctuoidea		x	x
Mythimna comma	Noctuoidea		x	
Mythimna l-album	Noctuoidea	x		
Mythimna turca	Noctuoidea	x		
Noctua pronuba	Noctuoidea	x		x
Notodonta ziczac	Noctuoidea		x	
Ochropacha duplaris	Drepanoidea		x	x
Ochropleura plecta	Noctuoidea	x	x	x
Odontopera bidentata	Geometroidea		x	x
Odontosia carmelita	Noctuoidea		x	x
Oligia strigilis	Noctuoidea	x		
Opisthograptis luteolata	Geometroidea		x	x
Orthosia cerasi	Noctuoidea		x	x
Orthosia gothica	Noctuoidea		x	x
Orthosia gracilis	Noctuoidea		x	
Orthosia incerta	Noctuoidea		x	
Orthosia opima	Noctuoidea		x	
Ostrinia nubilalis	Pyraloidea	x		
Ourapteryx sambucaria	Geometroidea	x		x
Panolis flammea	Noctuoidea		x	x
Paracolax tristalis	Noctuoidea	x		
Paradarisa consonaria	Geometroidea	x		
Parectropis similaria	Geometroidea	x		x
Pasiphila rectangulata	Geometroidea	x		
Pelosia muscerda	Noctuoidea	x		
Peribatodes rhomboidarius	Geometroidea	x		x
Phalera bucephala	Noctuoidea	x		
Pheosia tremula	Noctuoidea	x	x	x
Philereme transversata	Geometroidea	x		
Phragmatobia fuliginosa	Noctuoidea	x		
Plagodis dolabraria	Geometroidea		x	x
Plemyria rubiginata	Geometroidea	x		
Pleuroptya ruralis	Pyraloidea	x		x
Polypogon tentacularia	Noctuoidea	x		
Pterostoma palpina	Noctuoidea	x	x	x
Ptilodon capucina	Noctuoidea		x	x
Ptilodon cucullina	Noctuoidea	x	x	x
Sclerocona acutella	Pyraloidea	x		
Scoliopteryx libatrix	Noctuoidea	x		
Scopula immorata	Geometroidea	x		
Selenia dentaria	Geometroidea		x	
Selenia tetralunaria	Geometroidea	x	x	x
Spargania luctuata	Geometroidea		x	x
Spatalia argentina	Noctuoidea	x		
Spilosoma lubricipeda	Noctuoidea	x	x	x
Spilosoma lutea	Noctuoidea	x		
Stauropus fagi	Noctuoidea	x		x
Subacronicta megacephala	Noctuoidea		x	
Tethea or	Drepanoidea	x	x	x
Thera obeliscata	Geometroidea		x	

Thyatira batis	Drepanoidea	x	x	x
Timandra comae	Geometroidea	x		
Trichopteryx carpinata	Geometroidea		x	x
Tyta luctuosa	Noctuoidea	x		
Watsonalla binaria	Drepanoidea		x	x
Xanthorhoe designata	Geometroidea	x	x	
Xanthorhoe ferrugata	Geometroidea		x	x
Xanthorhoe fluctuata	Geometroidea		x	x
Xanthorhoe spadicearia	Geometroidea	x	x	x
Xestia c-nigrum	Noctuoidea	x	x	x
Xestia ditrapezium	Noctuoidea	x		
Xestia stigmatica	Noctuoidea	x		

Appendix S2: Location of the six study sites across the three floodplain regions in lowland Eastern Austria

Region	Location	Forest type	Site code	Latitude N	Longitude E	Elevation m a.s.l.
Danube	near Orth an der Donau	non-flooded	DN	16°41’24”	48°08’41”	154
Danube	near Orth an der Donau	flooded	DF	16°41’02”	48°07’53”	154
Morava	near Marchegg	non-flooded	MN	16°53’26”	48°17’00	145
Morava	near Marchegg	flooded	MF	16°53’22”	48°17’06”	145
Leitha	between Gerhaus and Rohrau	non-flooded	LN	16°51’32”	48°03’28”	146
Leitha	near Königshof, Wilfleinsdorf	flooded	LF	16°42’20”	48°00’19”	164

Appendix S3: Detailed information on moth sampling and identification for this study

Traps were of a type similar to that used by Wirooks (2005; source: www.fiebig-lehrmittel.de; see Fig. S1), equipped with two 15W tubes (Sylvania Blacklight-Blue, F15W/BLB-T8; and Philips TLD, 15W/05) and powered by a 12V car battery. At dusk the light was automatically switched on and run for about 6 hours. All light traps within a habitat were operated simultaneously. All habitats were sampled on consecutive days, or as soon as possible if spells of unfavourable weather had to be avoided. Traps were never run during the 5 days before and after full moon to avoid negative impact of moonlight on trap catches (Yela & Holyoak, 1997). Sampling did not take place during rainy weather, in which cases sampling was postponed until conditions improved.

Altogether, sampling went over two complete annual cycles on 103 nights between 20.VIII.2006 and 24.VIII.2008. The sampling season ended with the first incidence of frost in autumn (last sampling dates: 26.XI.2006 and 08.XI.2007) and started again at spring time (first sampling dates: 26.III.2007 and 07.IV.2008). Overall, data from 442 nightly trap samples were analysed. The number of moths caught during a single trap night ranged from 0 to 1092 (MI 5, 08.VIII.2007) individuals. Eighteen trap samples did not contain any moths, likely due to cold temperatures and generally low moth abundance in March, April, October and November. Three further samples did not contain moths due to equipment failure.

Moths were killed with chloroform, returned to the laboratory in the morning after sampling, and stored in a freezer (–20°C) until further evaluation.

All ‘macro-moths’ including the Pyraloidea were identified to species level using faunal treatments (see references below). If required, identification was confirmed through microscopic examination of genital structures.


Fig. S1: Light trap used in the study

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Appendix S4: Species-site matrix of moths including classification according to residency status or larval stratum use.

Nomenclature follows Karsholt, O., & Nieukerken, E.J. van (eds.) (2010) *Lepidoptera, Moths*. Fauna Europaea version 2.4, http://www.faunaeur.org

					Site code					
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Deilephila porcellus	Bombycoidea		x		0	0	0	0	1	0
Laothoe populi	Bombycoidea			x	0	2	1	0	0	1
Mimas tiliae	Bombycoidea			x	0	0	0	0	0	2
Smerinthus ocellata	Bombycoidea			x	0	1	0	0	0	1
Phragmataecia castaneae	Cossoidea		x		0	0	0	1	4	15
Cilix glaucata	Drepanoidea			x	0	1	0	0	0	0
Drepana falcataria	Drepanoidea			x	0	1	1	8	2	0
Habrosyne pyritoides	Drepanoidea		x		2	1	6	4	3	6
Ochropacha duplaris	Drepanoidea			x	1	5	0	0	0	0
Sabra harpagula	Drepanoidea			x	1	0	0	0	0	0
Tethea ocularis	Drepanoidea			x	1	2	3	0	2	5
Tethea or	Drepanoidea			x	30	111	23	6	4	9
Thyatira batis	Drepanoidea		x		4	6	9	9	2	4
Watsonalla binaria	Drepanoidea			x	0	1	0	1	4	9
Abraxas grossulariata	Geometroidea			x	0	0	5	6	0	0
Abraxas sylvata	Geometroidea			x	0	0	27	6	0	0
Acasis viretata	Geometroidea			x	0	0	0	1	0	0
Aethalura punctulata	Geometroidea			x	0	0	0	3	0	0
Agriopis aurantiaria	Geometroidea			x	6	10	4	0	1	8
Agriopis bajaria	Geometroidea			x	1	2	0	0	0	0
Agriopis marginaria	Geometroidea			x	0	0	0	0	1	0
Alcis repandata	Geometroidea		x	x	1	1	1	0	1	0
Alsophila aescularia	Geometroidea			x	9	0	1	0	0	0
Angerona prunaria	Geometroidea			x	16	4	0	1	0	1
Anticollix sparsata	Geometroidea		x		1	0	0	0	0	0
Apeira syringaria	Geometroidea			x	1	1	0	1	1	2
Aplocera plagiata	Geometroidea	x			0	1	0	1	0	2
Artiora evonymaria	Geometroidea			x	1	0	0	0	2	1
Ascotis selenaria	Geometroidea		x		1	2	6	0	14	18
Asthena anseraria	Geometroidea			x	0	0	0	3	1	1
Biston betularia	Geometroidea			x	3	0	5	0	1	1
Cabera exanthemata	Geometroidea			x	17	7	22	46	22	32
Cabera pusaria	Geometroidea			x	3	4	2	20	0	1
Campaea margaritata	Geometroidea			x	96	50	86	166	20	38
Camptogramma bilineata	Geometroidea		x		0	0	1	3	0	0
Catarhoe cuculata	Geometroidea		x		0	0	0	0	1	0
Cepphis advenaria	Geometroidea		x		10	3	0	0	0	0
Chiasmia clatratha	Geometroidea	x			3	9	1	2	0	2
Chlorissa cloraria	Geometroidea		x	x	0	0	0	0	1	2
Chloroclysta siterata	Geometroidea			x	2	0	1	1	1	3
Chloroclystis v-ata	Geometroidea		x	x	1	0	0	2	0	0
Colostygia pectinataria	Geometroidea		x		1	7	6	4	5	9
Colotois pennaria	Geometroidea			x	6	5	0	0	2	4
Comibaena bajularia	Geometroidea			x	1	0	0	0	0	5
Cosmorhoe ocellata	Geometroidea		x		1	1	4	5	2	1
Costaconvexa polygrammata	Geometroidea		x		0	0	2	0	0	0

							Site code			
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Crocallis elinguaria	Geometroidea			x	1	1	1	0	0	0
Cyclophora annularia	Geometroidea			x	357	91	52	18	77	114
Cyclophora linearia	Geometroidea			x	0	1	0	0	0	0
Cyclophora punctaria	Geometroidea			x	4	0	5	1	7	21
Dysstroma truncata	Geometroidea		x		1	0	1	1	1	0
Ecliptopera silaceata	Geometroidea		x		48	68	226	220	9	24
Ectropis crepuscularia	Geometroidea		x	x	23	42	49	73	23	39
Electrophaes corylata	Geometroidea			x	3	0	0	0	0	0
Ennomos autumnaria	Geometroidea			x	0	5	2	5	4	14
Ennomos fuscantaria	Geometroidea			x	0	0	0	0	0	5
Epione repandaria	Geometroidea			x	0	0	0	1	1	1
Epirrhoe alternata	Geometroidea		x		15	74	69	34	30	43
Epirrita dilutata	Geometroidea			x	5	0	0	1	0	1
Erannis defoliaria	Geometroidea			x	7	41	9	17	10	67
Euchoeca nebulata	Geometroidea			x	1	11	3	23	0	0
Eulithis mellinata	Geometroidea		x		0	0	1	0	0	0
Eupithecia absinthiata	Geometroidea		x		1	1	0	0	0	0
Eupithecia assimilata	Geometroidea		x		1	1	0	0	0	2
Eupithecia centaureata	Geometroidea		x		2	2	7	2	3	13
Eupithecia haworthiata	Geometroidea		x		1	0	0	0	0	0
Eupithecia inturbata	Geometroidea			x	6	3	1	0	0	0
Eupithecia satyrata	Geometroidea		x		1	0	1	0	0	0
Eupithecia selinata	Geometroidea		x		0	0	1	1	1	7
Eupithecia tenuiata	Geometroidea			x	0	0	0	0	0	1
Eupithecia virgaureata	Geometroidea		x		2	4	20	20	10	9
Gandaritis pyraliata	Geometroidea		x		12	52	21	11	0	5
Gymnoscelis rufifasciata	Geometroidea		x	x	0	0	2	2	1	0
Heliomata glarearia	Geometroidea	x			1	0	0	0	2	0
Hemistola chrysoprasaria	Geometroidea		x		10	12	1	10	0	0
Hemithea aestivaria	Geometroidea			x	32	10	7	16	11	16
Horisme corticata	Geometroidea			x	1	1	0	1	0	0
Horisme tersata	Geometroidea			x	2	0	0	0	0	0
Horisme vitalbata	Geometroidea			x	0	1	0	0	0	0
Hydrelia flammeolaria	Geometroidea			x	0	0	1	0	0	0
Hydriomena furcata	Geometroidea			x	0	0	0	2	0	0
Hydriomena impluviata	Geometroidea			x	0	2	0	0	0	0
Hydriomena ruberata	Geometroidea			x	1	4	0	8	0	0
Hypomecis punctinalis	Geometroidea			x	18	20	7	10	40	17
Hypomecis roboraria	Geometroidea			x	27	12	12	8	13	14
Idaea aversata	Geometroidea		x		26	1	37	14	17	25
Idaea biselata	Geometroidea		x		40	13	4	8	1	8
Idaea degeneraria	Geometroidea	x			4	0	24	4	2	11
Idaea dimidiata	Geometroidea		x		13	62	72	60	105	137
Idaea fuscovenosa	Geometroidea	x			0	0	0	1	0	0
Idaea humiliata	Geometroidea	x			0	0	0	1	1	0
Idaea muricata	Geometroidea		x		0	0	1	0	0	0
Idaea pallidata	Geometroidea	x			0	0	0	1	0	0
Idaea rubraria	Geometroidea		x		2	0	2	0	0	1
Idaea rusticata	Geometroidea	x			2	1	0	0	1	2
Idaea subsericeata	Geometroidea		x		1	0	0	0	0	1
Idaea trigeminata	Geometroidea		x		2	0	2	3	2	0

					Site code					
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Jodis lactearia	Geometroidea			x	1	0	1	3	0	0
Lampropteryx suffumata	Geometroidea		x		0	0	0	1	0	0
Ligdia adustata	Geometroidea			x	56	89	24	30	52	93
Lomaspilis marginata	Geometroidea			x	58	89	26	33	54	93
Lomographa bimaculata	Geometroidea			x	39	40	12	1	0	0
Lomographa temerata	Geometroidea			x	3	5	3	0	0	3
Lycia hirtaria	Geometroidea			x	3	6	6	0	4	6
Lythria purpuraria	Geometroidea	x			0	0	0	1	0	0
Macaria alternata	Geometroidea			x	10	2	19	7	40	19
Macaria liturata	Geometroidea	x			0	0	0	0	1	1
Macaria notata	Geometroidea			x	0	0	0	1	0	0
Melanthia procellata	Geometroidea			x	5	7	0	1	0	0
Mesoleuca albicillata	Geometroidea			x	2	1	1	1	1	0
Nycterosea obstipata	Geometroidea	x			0	1	0	0	1	1
Operophtera brumata	Geometroidea			x	8	15	29	7	42	103
Orthonama vittata	Geometroidea		x		0	0	0	0	0	2
Ourapteryx sambucaria	Geometroidea			x	4	6	0	2	0	0
Paradarisa consonaria	Geometroidea			x	0	0	0	1	0	0
Parectropis similaria	Geometroidea			x	1	0	0	0	0	0
Pasiphila rectangulata	Geometroidea			x	5	5	35	24	3	3
Peribatodes rhomboidaria	Geometroidea		x	x	36	38	53	107	37	37
Peribatodes secundaria	Geometroidea	x			0	3	2	2	8	3
Perizoma affinitata	Geometroidea		x		0	0	0	0	1	0
Perizoma alchemillata	Geometroidea		x		0	1	3	32	4	5
Perizoma hydrata	Geometroidea	x			0	0	1	0	0	0
Perizoma lugdunaria	Geometroidea		x		0	0	0	1	0	0
Philereme vetulata	Geometroidea			x	3	1	0	0	4	23
Plagodis dolabraria	Geometroidea			x	1	0	0	0	0	0
Plagodis pulveraria	Geometroidea			x	61	43	4	3	16	7
Plemyria rubiginata	Geometroidea			x	4	6	14	7	0	0
Pterapherapteryx sexalata	Geometroidea			x	0	0	0	3	0	0
Rhodostrophia vibicaria	Geometroidea	x			0	0	0	0	1	0
Scopula flaccidaria	Geometroidea	x			0	0	1	0	1	0
Scopula floslactata	Geometroidea		x		2	0	0	0	0	0
Scopula immorata	Geometroidea	x			1	4	0	5	6	2
Scopula immutata	Geometroidea		x		5	6	4	11	10	15
Scopula marginepunctata	Geometroidea	x			0	1	0	0	1	0
Scopula nigropunctata	Geometroidea		x	x	1	1	0	2	2	3
Scopula ornata	Geometroidea	x			0	0	0	0	1	0
Scopula rubiginata	Geometroidea	x			0	0	0	0	0	1
Scopula virgulata	Geometroidea	x			5	6	1	2	5	2
Selenia dentaria	Geometroidea			x	9	3	0	0	0	1
Selenia lunularia	Geometroidea			x	1	0	0	1	1	1
Selenia tetralunaria	Geometroidea			x	30	109	25	54	22	30
Siona lineata	Geometroidea	x			0	1	0	0	0	0
Stegania cararia	Geometroidea			x	0	0	9	1	8	3
Stegania dilectaria	Geometroidea			x	1	1	3	0	4	14
Thera juniperata	Geometroidea	x			1	0	0	0	0	0
Therapis flavicaria	Geometroidea		x		0	1	1	0	0	0
Thetidia smaragdaria	Geometroidea	x			0	0	1	0	0	0
Timandra comae	Geometroidea		x		8	9	5	20	33	51

							Site code			
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Xanthorhoe biriviata	Geometroidea		x		0	1	1	0	0	0
Xanthorhoe designata	Geometroidea		x		1	1	0	1	1	6
Xanthorhoe ferrugata	Geometroidea		x		8	11	5	22	12	16
Xanthorhoe fluctuata	Geometroidea		x		1	0	0	0	0	2
Xanthorhoe quadrifasiata	Geometroidea		x		0	0	0	1	0	0
Xanthorhoe spadicearia	Geometroidea		x		0	0	0	2	4	0
Triodia sylvina	Hepialoidea		x		1	2	0	1	0	0
Euthrix potatoria	Lasiocampoidea		x		1	1	0	0	0	0
Malacosoma neustria	Lasiocampoidea			x	0	3	0	0	1	5
Poecilocampa populi	Lasiocampoidea			x	2	2	2	3	3	3
Trichiura crataegi	Lasiocampoidea			x	3	3	0	1	1	0
Abrostola tripartita	Noctuoidea		x		0	2	2	2	0	0
Abrostola triplasia	Noctuoidea		x		7	4	10	9	1	5
Acontia trabealis	Noctuoidea	x			0	2	1	0	2	0
Acosmetia caliginosa	Noctuoidea		x		0	0	0	0	0	2
Acronicta alni	Noctuoidea			x	2	1	0	0	0	0
Acronicta auricoma	Noctuoidea		x		1	0	0	2	0	0
Acronicta cuspis	Noctuoidea			x	0	3	0	0	0	0
Acronicta psi	Noctuoidea			x	0	0	0	1	0	0
Acronicta rumicis	Noctuoidea		x		5	4	5	2	2	2
Acronicta strigosa	Noctuoidea			x	0	2	2	0	0	0
Actinotia polyodon	Noctuoidea		x		0	0	1	0	0	0
Aegle semicana	Noctuoidea		x		0	1	0	0	0	0
Agrochola circellaris	Noctuoidea			x	0	13	1	3	7	6
Agrochola litura	Noctuoidea		x		0	0	0	1	0	0
Agrochola lychnidis	Noctuoidea		x		1	0	0	2	0	0
Agrochola nitida	Noctuoidea		x		8	0	1	1	0	1
Agrotis bigramma	Noctuoidea	x			2	1	1	0	0	0
Agrotis cinerea	Noctuoidea	x			0	0	0	1	0	0
Agrotis exclamationis	Noctuoidea		x		19	0	64	5	2	6
Agrotis ipsilon	Noctuoidea	x			6	0	8	3	2	2
Agrotis segetum	Noctuoidea	x			411	6	719	90	41	54
Agrotis trux	Noctuoidea	x			1	0	0	0	0	0
Allophyes oxyacanthae	Noctuoidea			x	2	3	0	1	0	1
Ammoconia caecimacula	Noctuoidea		x		0	1	0	0	1	0
Amphipyra livida	Noctuoidea		x		0	0	0	0	0	4
Amphipyra pyramidea	Noctuoidea			x	8	3	1	0	4	0
Amphipyra tragopoginis	Noctuoidea		x		1	0	1	0	1	0
Anaplectoides prasinus	Noctuoidea		x		0	0	1	0	0	0
Anarta trifolii	Noctuoidea		x		3	0	6	0	0	0
Anortha munda	Noctuoidea			x	0	0	0	0	1	1
Apamea crenata	Noctuoidea		x		0	0	1	0	0	0
Apamea epomidion	Noctuoidea		x		0	0	0	2	0	0
Apamea monoglypha	Noctuoidea		x		5	0	0	0	0	1
Apamea scolopacina	Noctuoidea		x		0	0	0	0	0	1
Apamea unanimis	Noctuoidea		x		0	1	0	0	0	0
Apterogenum ypsillon	Noctuoidea			x	0	3	0	0	0	0
Arctia villica	Noctuoidea	x			0	0	0	0	0	1
Asteroscopus sphinx	Noctuoidea			x	4	8	8	0	6	10
Atethmia centrago	Noctuoidea			x	5	0	5	2	1	0
Athetis gluteosa	Noctuoidea	x			0	0	0	0	0	2

					Site code					
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Athetis lepigone	Noctuoidea		x		0	0	0	0	1	0
Atypha pulmonaris	Noctuoidea		x		17	10	1	0	0	0
Autographa gamma	Noctuoidea	x			0	2	0	0	1	2
Axylia putris	Noctuoidea		x		48	19	610	33	13	32
Calliteara pudibunda	Noctuoidea			x	16	13	12	9	1	1
Caradrina clavipalpis	Noctuoidea	x			2	0	4	0	0	2
Caradrina kadenii	Noctuoidea	x			3	0	11	15	3	3
Caradrina morpheus	Noctuoidea		x		20	5	34	20	35	52
Catephia alchymista	Noctuoidea	x			0	1	0	0	0	0
Catocala electa	Noctuoidea			x	0	1	0	0	0	0
Catocala nupta	Noctuoidea			x	1	0	0	0	1	0
Cerura erminea	Noctuoidea			x	0	2	0	0	0	0
Charanyca ferruginea	Noctuoidea		x		0	0	1	0	1	0
Charanyca trigrammica	Noctuoidea	x			7	4	8	11	3	4
Cleoceris scoriacea	Noctuoidea	x			0	0	0	0	2	1
Clostera anastomosis	Noctuoidea			x	0	0	3	0	0	0
Clostera curtula	Noctuoidea			x	2	8	5	3	3	10
Colobochyla salicalis	Noctuoidea			x	0	0	1	4	4	4
Colocasia coryli	Noctuoidea			x	67	32	22	9	5	4
Conisania luteago	Noctuoidea	x			0	0	1	1	0	0
Conistra eurythrocephala	Noctuoidea			x	0	3	0	0	1	1
Conistra vaccinii	Noctuoidea			x	4	1	0	0	1	2
Cosmia affinis	Noctuoidea			x	0	2	0	0	0	1
Cosmia diffinis	Noctuoidea			x	0	0	0	0	1	0
Cosmia pyralina	Noctuoidea			x	0	0	2	0	2	2
Cosmia trapezina	Noctuoidea			x	50	8	3	5	2	19
Craniophora ligustri	Noctuoidea			x	25	5	169	63	44	77
Cryphia algae	Noctuoidea		x		0	2	4	5	1	6
Cybosia mesomella	Noctuoidea		x		1	0	0	1	0	0
Deltote bankiana	Noctuoidea		x		0	1	0	2	3	0
Deltote pygarga	Noctuoidea		x		15	23	6	5	2	7
Diachrysia chrysitis	Noctuoidea		x		3	4	2	1	1	2
Diacrisia sannio	Noctuoidea		x		0	0	0	0	1	0
Diaphora mendica	Noctuoidea		x		0	1	0	0	4	0
Diarsia brunnea	Noctuoidea		x		0	0	1	0	0	0
Diarsia rubi	Noctuoidea		x		0	0	3	1	0	1
Diloba caeruleocephala	Noctuoidea			x	3	3	0	1	0	5
Drymonia dodonaea	Noctuoidea			x	19	8	0	0	2	7
Drymonia querna	Noctuoidea			x	0	0	0	0	2	0
Dypterygia scabriuscula	Noctuoidea		x		1	0	2	3	13	19
Dysauxes ancilla	Noctuoidea		x		0	0	2	2	4	1
Egira conspicillaris	Noctuoidea		x		0	1	0	0	0	0
Eilema complana	Noctuoidea		x		1	0	10	2	0	1
Eilema griseola	Noctuoidea		x		59	45	37	86	17	29
Eilema sororcula	Noctuoidea		x		6	2	2	0	0	3
Elaphria venustula	Noctuoidea			x	1	0	2	1	7	9
Enargia paleacea	Noctuoidea			x	0	0	1	0	0	0
Episema tersa	Noctuoidea	x			0	0	0	0	1	0
Eucarta virgo	Noctuoidea		x		0	0	1	0	0	0
Eugnorisma depuncta	Noctuoidea		x		38	5	18	18	3	3
Euplagia quadripunctaria	Noctuoidea		x		6	0	1	0	1	0

					Site code					
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Euplexia lucipara	Noctuoidea		x		7	6	17	15	5	6
Euproctis similis	Noctuoidea			x	24	32	4	2	22	27
Eupsilia transversa	Noctuoidea			x	3	1	2	0	4	8
Euxoa distinguenda	Noctuoidea	x			2	0	0	0	0	0
Euxoa vitta	Noctuoidea	x			0	0	9	2	0	0
Furcula bifida	Noctuoidea			x	1	1	1	0	1	2
Furcula furcula	Noctuoidea			x	0	0	1	0	0	0
Gluphisia crenata	Noctuoidea			x	3	2	1	0	4	0
Gortyna flavago	Noctuoidea		x		0	0	1	1	2	1
Hadena bicruris	Noctuoidea	x			0	0	0	0	0	1
Hadena perplexa	Noctuoidea	x			0	1	0	0	0	0
Helicoverpa armigera	Noctuoidea	x			1	1	2	1	2	1
Herminia grisealis	Noctuoidea			x	42	26	88	39	22	21
Herminia tarsicrinalis	Noctuoidea		x		33	84	35	43	14	19
Herminia tarsipennalis	Noctuoidea		x		0	3	1	5	1	0
Hoplodrina ambigua	Noctuoidea		x		36	5	418	105	42	64
Hoplodrina blanda	Noctuoidea		x		17	1	108	8	3	2
Hoplodrina octogenaria	Noctuoidea		x		52	1	7	2	1	1
Hydraecia micacea	Noctuoidea		x		0	3	0	0	0	2
Hypena proboscidalis	Noctuoidea		x		12	46	75	40	11	32
Ipimorpha retusa	Noctuoidea			x	1	6	1	8	0	2
Ipimorpha subtusa	Noctuoidea			x	3	1	39	4	2	1
Lacanobia oleracea	Noctuoidea		x		23	2	101	38	25	27
Lacanobia suasa	Noctuoidea		x		1	0	1	3	0	1
Lacanobia thalassina	Noctuoidea		x		8	4	26	12	3	12
Lacanobia w-latinum	Noctuoidea		x		0	0	0	1	0	0
Laspeyria flexula	Noctuoidea		x		2	4	1	3	9	1
Leucania obsoleta	Noctuoidea		x		7	1	3	0	14	41
Leucoma salicis	Noctuoidea			x	4	5	1	0	16	25
Lithophane ornitopus	Noctuoidea			x	0	0	0	0	4	10
Lithophane socia	Noctuoidea			x	0	0	2	3	1	2
Lithosia quadra	Noctuoidea		x		26	5	4	18	2	21
Litoligia literosa	Noctuoidea	x			1	0	1	0	0	0
Luperina testacea	Noctuoidea	x			0	0	0	0	4	0
Lygephila pastinum	Noctuoidea		x		3	1	1	1	0	0
Lymantria dispar	Noctuoidea			x	0	6	0	1	1	2
Macdunnoughia confusa	Noctuoidea	x			0	1	1	0	2	0
Macrochilo cribrumalis	Noctuoidea		x		0	0	0	1	0	2
Mamestra brassicae	Noctuoidea		x		28	3	87	5	4	13
Meganola albula	Noctuoidea		x		0	0	0	1	0	1
Melanchra persicariae	Noctuoidea		x		0	0	0	1	0	0
Mesapamea secalella	Noctuoidea		x		0	0	5	4	1	0
Mesapamea secalis	Noctuoidea		x		1	0	2	6	0	2
Mesoligia furuncula	Noctuoidea	x			1	0	0	0	1	0
Miltochrista miniata	Noctuoidea		x		0	0	1	0	0	0
Mniotype satura	Noctuoidea		x		2	0	0	1	1	1
Moma alpium	Noctuoidea			x	0	0	2	0	0	1
Mormo maura	Noctuoidea			x	0	0	0	1	0	0
Mythimna albipuncta	Noctuoidea		x		9	5	74	34	14	11
Mythimna conigera	Noctuoidea		x		0	0	1	0	0	0
Mythimna impura	Noctuoidea		x		0	0	0	0	3	0

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Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Mythimna l-album	Noctuoidea	x			4	1	7	2	1	0
Mythimna pallens	Noctuoidea		x		2	3	33	3	4	8
Mythimna straminea	Noctuoidea		x		0	0	0	0	0	2
Mythimna turca	Noctuoidea		x		2	11	7	63	3	7
Mythimna vitellina	Noctuoidea	x			1	0	29	12	0	1
Noctua comes	Noctuoidea		x		4	0	4	2	1	2
Noctua fimbriata	Noctuoidea		x		1	3	11	0	0	1
Noctua interposita	Noctuoidea	x			1	1	9	2	0	1
Noctua janthe	Noctuoidea		x		1	1	5	19	0	2
Noctua janthina	Noctuoidea		x		0	1	7	8	0	8
Noctua orbona	Noctuoidea	x			0	1	3	0	0	0
Noctua pronuba	Noctuoidea		x		23	8	106	58	13	11
Nola confusalis	Noctuoidea			x	0	0	0	0	0	2
Nola cucullatella	Noctuoidea			x	5	3	6	17	1	3
Notodonta dromedarius	Noctuoidea			x	0	1	0	1	0	0
Notodonta tritophus	Noctuoidea			x	0	2	1	0	1	1
Notodonta ziczac	Noctuoidea			x	0	0	1	0	2	0
Nycteola asiatica	Noctuoidea			x	2	8	1	7	1	3
Ochropleura plecta	Noctuoidea		x		31	17	197	56	52	118
Oligia latruncula	Noctuoidea		x		0	0	2	0	0	0
Oligia strigilis	Noctuoidea		x		7	0	14	0	0	0
Oligia versicolor	Noctuoidea		x		0	0	1	1	0	0
Orgyia antiqua	Noctuoidea			x	0	1	0	4	0	0
Orthosia cerasi	Noctuoidea			x	0	1	0	0	3	3
Orthosia cruda	Noctuoidea			x	0	0	0	0	0	1
Orthosia gothica	Noctuoidea		x	x	5	6	0	4	8	7
Orthosia incerta	Noctuoidea			x	1	2	1	0	0	1
Paracolax tristalis	Noctuoidea		x		1	0	0	1	0	1
Parastichtis suspecta	Noctuoidea		x	x	1	0	2	0	0	1
Pechipogo strigilata	Noctuoidea			x	35	0	7	8	0	0
Pelosia muscerda	Noctuoidea		x		16	95	617	240	2541	5234
Phalera bucephala	Noctuoidea			x	1	4	2	3	1	2
Pheosia tremula	Noctuoidea			x	16	182	165	48	45	94
Phlogophora meticulosa	Noctuoidea		x		0	0	2	2	0	1
Phragmatobia fuliginosa	Noctuoidea		x		1	1	1	6	0	7
Polia nebulosa	Noctuoidea			x	1	0	1	1	0	0
Polyphaenis sericata	Noctuoidea			x	0	0	0	0	1	0
Polypogon tentacularia	Noctuoidea		x		1	0	0	2	0	1
Pseudeustrotia candidula	Noctuoidea		x		0	0	3	3	1	0
Pterostoma palpina	Noctuoidea			x	2	12	8	4	9	7
Ptilodon capucina	Noctuoidea			x	2	11	3	5	1	7
Ptilodon cucullina	Noctuoidea			x	16	12	3	3	7	15
Ptilophora plumigera	Noctuoidea			x	3	36	1	2	256	706
Pyrrhia umbra	Noctuoidea	x			0	0	1	0	0	1
Rivula sericealis	Noctuoidea		x		27	51	54	123	26	77
Schrankia costaestrigalis	Noctuoidea		x		0	0	1	0	2	1
Scoliopteryx libatrix	Noctuoidea			x	0	0	1	1	0	1
Sideridis rivularis	Noctuoidea		x		1	2	4	3	1	5
Spatalia argentina	Noctuoidea			x	1	1	4	0	1	1
Spilosoma lubricipeda	Noctuoidea		x		12	24	18	38	28	55
Spilosoma lutea	Noctuoidea		x		23	13	16	21	14	16

							Site code			
Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Stauropus fagi	Noctuoidea			x	12	5	8	10	1	2
Subacronicta megacephala	Noctuoidea			x	0	23	14	3	1	7
Thalpophila matura	Noctuoidea	x			2	0	0	1	0	0
Thaumetopoea processionea	Noctuoidea			x	2	0	0	0	1	1
Thumatha senex	Noctuoidea		x		0	0	1	0	0	0
Tiliacea aurago	Noctuoidea			x	0	1	0	0	0	0
Trachea atriplicis	Noctuoidea		x		8	2	34	12	3	5
Trisateles emortualis	Noctuoidea		x		9	2	12	4	0	0
Tyta luctuosa	Noctuoidea	x			0	1	0	0	2	0
Xanthia gilvago	Noctuoidea			x	0	0	0	0	0	2
Xanthia ocellaris	Noctuoidea			x	0	0	0	0	1	0
Xestia baja	Noctuoidea		x		0	1	6	13	0	3
Xestia c-nigrum	Noctuoidea		x		113	37	1753	504	172	362
Xestia ditrapezium	Noctuoidea		x		0	0	0	5	1	1
Xestia sexstrigata	Noctuoidea		x		1	0	0	1	1	0
Xestia stigmatica	Noctuoidea		x		1	0	1	2	0	0
Xestia triangulum	Noctuoidea		x		13	4	7	3	1	0
Xestia xanthographa	Noctuoidea		x		1	0	2	6	4	3
Acrobasis advenella	Pyraloidea			x	5	27	0	1	2	18
Acrobasis legatea	Pyraloidea			x	0	1	0	0	0	0
Acrobasis sodalella	Pyraloidea			x	0	0	0	0	1	1
Acrobasis suavella	Pyraloidea			x	1	0	0	0	2	4
Acrobasis tumidana	Pyraloidea			x	0	0	1	0	1	4
Agriphila inquinatella	Pyraloidea	x			3	5	3	8	3	7
Agriphila straminella	Pyraloidea	x			2	0	3	3	0	2
Agriphila tolli	Pyraloidea	x			1	2	0	1	0	1
Agriphila tristella	Pyraloidea	x			0	0	0	0	0	1
Agrotera nemoralis	Pyraloidea			x	4	1	0	0	0	0
Anania coronata	Pyraloidea			x	11	14	11	21	8	28
Anania crocealis	Pyraloidea		x		0	0	0	0	2	0
Anania hortulata	Pyraloidea		x		2	2	20	14	2	6
Anania lancealis	Pyraloidea		x		0	2	5	7	0	0
Anania stachydalis	Pyraloidea		x		0	4	4	0	2	3
Anania terrealis	Pyraloidea	x			0	0	0	0	0	1
Anania verbascalis	Pyraloidea		x		0	7	3	1	2	8
Aphomia sociella	Pyraloidea		x		2	1	1	0	2	0
Cadra furcatella	Pyraloidea		x		0	0	2	0	2	1
Cataclysta lemnata	Pyraloidea		x		3	5	24	40	21	23
Catoptria falsella	Pyraloidea		x		6	14	3	2	9	56
Catoptria permutatellus	Pyraloidea		x		0	0	2	0	0	0
Catoptria verellus	Pyraloidea		x		11	27	1	1	5	32
Chilo phragmitella	Pyraloidea		x		3	3	2	0	0	2
Chrysoteuchia culmella	Pyraloidea	x			0	1	0	2	0	0
Crambus pratella	Pyraloidea	x			0	0	0	0	1	0
Delplanqueia dilutella	Pyraloidea		x		2	4	1	0	0	0
Donacaula forficella	Pyraloidea		x		0	0	1	0	0	0
Ecpyrrhorrhoe rubiginalis	Pyraloidea		x		1	1	24	25	5	11
Elophila nymphaeata	Pyraloidea		x		5	3	1	0	4	26
Elophila rivularis	Pyraloidea		x		0	0	0	0	1	0
Ematheudes punctella	Pyraloidea	x			0	0	0	0	0	1
Endotricha flammealis	Pyraloidea		x		0	0	3	9	3	2

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Species	**Superfamily**	**stray**	**ground**	**arboreal**	**DN**	**DF**	**LN**	**LF**	**MN**	**MF**
Ephestia parasitella	Pyraloidea		x		1	1	1	0	0	0
Etiella zinckenella	Pyraloidea	x			0	0	1	0	0	7
Eudonia lacustrata	Pyraloidea		x		1	3	0	0	0	3
Eudonia laetella	Pyraloidea		x		0	4	0	2	0	3
Eudonia mercurella	Pyraloidea		x		1	1	0	0	0	0
Eudonia pallida	Pyraloidea		x		0	6	5	3	2	5
Eudonia truncicolella	Pyraloidea		x		3	0	0	1	0	1
Evergestis aenealis	Pyraloidea		x		0	0	0	0	1	0
Evergestis extimalis	Pyraloidea		x		2	1	2	6	1	7
Evergestis forficalis	Pyraloidea		x		0	0	4	4	3	4
Evergestis limbata	Pyraloidea		x		1	1	0	0	0	0
Evergestis pallidata	Pyraloidea		x		2	3	6	9	15	28
Galleria mellonella	Pyraloidea		x		1	1	2	0	0	7
Gymnancyla hornigii	Pyraloidea	x			0	0	0	0	1	0
Hypsopygia costalis	Pyraloidea		x		0	0	1	3	0	0
Hypsopygia glaucinalis	Pyraloidea		x		0	1	0	1	0	1
Laodamia faecella	Pyraloidea	x			0	1	0	0	0	0
Loxostege sticticalis	Pyraloidea	x			0	0	1	0	1	0
Nephopterix angustella	Pyraloidea			x	1	0	2	0	0	0
Oncocera semirubella	Pyraloidea	x			6	5	15	18	11	10
Ostrinia nubilalis	Pyraloidea		x		3	2	19	1	1	4
Parapoynx stratiotata	Pyraloidea		x		3	4	6	0	4	44
Paratalanta hyalinalis	Pyraloidea		x		0	0	0	0	2	0
Paratalanta pandalis	Pyraloidea		x		1	0	0	0	0	0
Pediasia contaminella	Pyraloidea	x			0	0	0	1	3	1
Phycita roborella	Pyraloidea	x			0	0	0	1	0	1
Phycitodes binaevella	Pyraloidea		x		0	0	0	1	0	0
Pleuroptya ruralis	Pyraloidea		x		36	199	645	409	32	96
Pyralis farinalis	Pyraloidea	x			0	0	0	1	0	0
Pyralis regalis	Pyraloidea		x		0	0	0	0	0	1
Pyrausta aurata	Pyraloidea	x			0	1	1	2	0	1
Pyrausta purpuralis	Pyraloidea	x			0	0	0	0	1	0
Sciota adelphella	Pyraloidea			x	0	0	1	0	0	0
Sciota fumella	Pyraloidea		x		0	0	0	1	0	0
Sciota rhenella	Pyraloidea			x	1	1	1	1	0	1
Sclerocona acutella	Pyraloidea		x		0	0	0	1	0	1
Scoparia basistrigalis	Pyraloidea		x		5	3	8	4	1	1
Scoparia subfusca	Pyraloidea		x		0	0	0	0	1	0
Stemmatophora brunnealis	Pyraloidea	x			0	0	0	1	1	0
Synaphe punctalis	Pyraloidea	x			1	0	0	0	0	0
Trachonitis cristella	Pyraloidea			x	0	1	0	0	0	0
Udea elutalis	Pyraloidea		x		0	0	0	0	0	1
Udea ferrugalis	Pyraloidea		x		0	3	13	12	0	10
Udea fulvalis	Pyraloidea		x		0	0	1	0	3	0
Apoda limacodes	Zygaenoidea			x	7	1	0	1	1	2

Appendix S5: Moth species whose mean relative abundances per site differed significantly (in one-way ANOVAs) between flooded and non-flooded habitats.
* - not significant after controlling for table-wide false discovery rate.
Habitat affiliations (from literature listed in S3): fp = main areas of distribution in floodplains or otherwise humid habitats; ubi = widely distributed

			More abundant in	
Species	Stratum	Habitat	flooded	non-flooded
Axylia putris	ground	fp		x
Colocasia coryli *	arboreal	ubi		x
Craniophora ligustri *	arboreal	fp		x
Cyclophora annularia	arboreal	fp		x
Ecliptopera silaceata	ground	fp	x	
Ectropis crepuscularia	arboreal+ground	ubi	x	
Epirrhoe alternata	ground	ubi	x	
Erannis defoliaria	arboreal	ubi	x	
Eulithis pyraliata	ground	ubi	x	
Herminia tarsicrinalis	ground	ubi	x	
Hoplodrina ambigua	ground	ubi		x
Hoplodrina blanda	ground	ubi		x
Hypena proboscidalis	ground	ubi	x	
Idaea aversata	ground	ubi		x
Idaea dimidiata	ground	fp	x	
Lacanobia oleracea	ground	ubi		x
Ligdia adustata	arboreal	ubi	x	
Lomaspilis marginata	arboreal	fp	x	
Mamestra brassicae	ground	ubi		x
Pheosia tremula	arboreal	fp	x	
Pleuroptya ruralis	ground	ubi	x	
Ptilophora plumigera *	arboreal	fp	x	
Rivula sericealis	ground	ubi	x	
Selenia tetralunaria	arboreal	ubi	x	
Spilosoma lubricipeda	ground	ubi	x	
Tethea or	arboreal	fp	x	
Timandra comae	ground	ubi	x	
Xestia c-nigrum	ground	ubi		x

Appendix S6: Rank-abundance curves of moth assemblages in the six study habitats.

D: Danube, L: Leitha, M: Morava river, N: non-flooded, F: flooded forest.
Note log-scale (natural logarithms) of Y-axis.